Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 124(3): 509-534. **November 2018**

TAXONOMY AND PALAEOECOLOGY OF CONTINENTAL GASTROPODA (MOLLUSCA) FROM THE LATE PLEISTOCENE MAMMOTH-BEARING SITE OF BULLENDORF IN NE AUSTRIA

DARIA CAROBENE[1*], MATHIAS HARZHAUSER[2], OLEG MANDIC[2] & ROBERTO GATTO[3]

[1*]Corresponding author: Castello 6367, 30122 Venezia, Italy. E-mail: carobenedaria@gmail.com
[2]Department of Geology and Palaeontology, Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria. Email: mathias.harzhauser@nhm-wien.ac.at; oleg.mandic@nhm-wien.ac.at
[3]Department of Geosciences, University of Padova, Via G. Gradenigo 6, 35131 Padova, Italy. E-mail: roberto.gatto@unipd.it

To cite this article: Carobene D., Harzhauser M., Mandic O. & Gatto R. (2018) - Taxonomy and palaeoecology of continental Gastropoda (Mollusca) from the Late Pleistocene mammoth-bearing site of Bullendorf in NE Austria. *Riv. It. Paleontol. Strat.*, 124(3): 509-534.

Keywords: *Pupilla*-fauna; loess; palaeoenvironment; Pleistocene; biodiversity.

*Abstract***.** We present a taxonomic and palaeoecological analysis of a continental mollusc fauna from a mammoth-bearing succession near Bullendorf in Lower Austria. The taxonomic analysis comprises morphological descriptions and SEM documentation of 15 Pleistocene gastropod species. A Principal Component Analysis of the quantitative and qualitative composition of the investigated samples reveals a stratigraphic succession of four mollusc assemblages defined herein as *Galba truncatula* assemblage, *Succinella oblonga* assemblage, *Pupilla muscorum/loessica* and *Pupilla alpicola/sterrii* assemblages. The autecological requirements of the species of each assemblage allow a reconstruction of the palaeoenvironmental history of the section with alternating dry and humid conditions within a general cooling trend. Despite generally low mollusc density and species richness, the Bullendorf site allows important insight into latest Quaternary regional environmental conditions and climate. Based on the comparison with similar mollusc sites across Europe, a biostratigraphic correlation with the Late Pleistocene (~110–12 ka) is proposed.

Introduction

The modern continental mollusc fauna of Europe resembles the Pleistocene fauna, except for some extinct or regionally extirpated species and minor changes in taxonomic composition (Ložek 1964). Assemblages heralding the Pleistocene fauna appear at the end of the Pliocene (Ložek 1964), although some species can be traced back to the Miocene and early Pliocene (Esu & Girotti 1991; Georgopoulou et al. 2016a, b). Since then, the fauna has been shaped by climatic fluctuations of the Ice Age, resulting in peculiar assemblages specific for certain glacial and interglacial time-intervals (Ložek 1964, 1990, 2001; Rousseau 1987, 2001; Frank 2006). This development provides a reliable frame for the biostratigraphic dating of continental Quaternary sediments. Moreover, the ecological requirements of the largely still existing taxa provide constrains for palaeoenviromental interpretations (Ložek 1964, 1965, 1990, 2001; Puisségur 1976; Rousseau 1987, 2001; Alexandrowicz et al. 1989; Krolopp & Sümegi 1995; Sümegi & Krolopp 2002; Moine et al. 2005, 2008; Moine 2008; Banak et al. 2012; Antoine et al. 2013; Alexandrowicz et al. 2013, 2014; Alexandrowicz 2014).

This paper focuses on the systematic analysis and palaeoenvironmental interpretation of a continental gastropod fauna from a mammoth-bearing succession near Bullendorf, in Lower Austria. The taxonomic part is based on a morphological analysis of shells, supported by macro- and SEM-photographs. Identifications are based on the rich literature on the Quaternary European malacofauna; systematics and taxonomy follow Welter-Schultes (2012), MolluscaBase (2016) and Bouchet et al. (2017). Based on quantitative and qualitative analyses of several stratigraphically successive samples, shifts in palaeoenvironmental conditions can be deduced for the interval represented by the sec-

Received: April 25, 2018; accepted: July 20, 2018

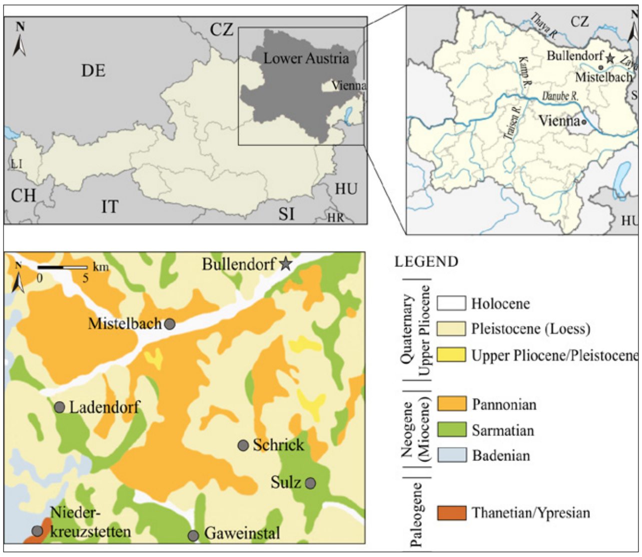


Fig. 1 - Map showing the geographic position of Bullendorf in Lower Austria and the main outcrops in the area. Geology simplified from Schnabel (2002).

tion. Finally, a comparison with similar faunal types across Europe allows a biostratigraphic correlation of the section and a discussion of the palaeogeographic distribution of the fauna.

Geographic and geological setting

The studied section is located 1.6 km NNE of Bullendorf (Mistelbach District, Lower Austria) on the northern slope of a cut of the newly constructed highway A5 (WGS 84: 48° 36' 31.5" N, 16° 40' 11.9" E) (Fig. 1). The succession is 13.6-m-thick and comprises three lithological units (Fig. 2). The basal part of the section is an about 2.6-m-thick unit of bedded clay/silt with fossil leaves and scattered fossil mammal remains. It is overlain by an 8-m-thick sandy and silty unit; the lower boundary of this unit represents an erosional surface with mollusc shell lags. Proboscidean remains occur about 70 cm above this surface, in a sandy silt bed showing ripple bedding, root traces and *Pupilla* gastropod-rich lenses. The rest of the unit is represented by an alternation at ~1 m scale of well-bedded sandy and massive silty packages. The top of the section is represented by an about 3-m-thick unit of loess. All the mollusc-bearing samples derive from the upper two units (see Fig. 2 for sample coding and position). Granulometric data prove very bad sorting for all these samples. Sedimentological features suggest that the middle unit was deposited in a floodplain setting, probably already influenced by aeolian deposition (pers. comm. R. Roetzel). Aeolian deposition becomes predominant in the uppermost loess unit.

Preliminary results from luminescence dating (OSL) of sediments point to an age slightly younger than the LGM (Carobene et al., in prep.).

Methods and materials

Sampling was carried out in July and August 2016. Twelve bulk samples of about 3 kg each were collected every 1–1.5 m of section units 2 and 3. These samples were used for quantitative analyses of mollusc assemblages. Samples were dried at 60°C for 24 h, washed and sieved over a 0.5 mm mesh sieve. Additionally, shells were picked by hand from the surface (samples B_{2hp} and B_{6hp} in Fig. 2) to obtain well-preserved materials supporting the systematic identification. Macro-photographs were taken with a ZEISS Discovery.V20 stereomicroscope connected to an AxioCam MRc5. For SEM investigation, specimens were washed in an ultrasonic cleaner and subsequently coated with platinum. SEM images were made using a JEOL JSM-6610LV operated at 10 kV.

Two statistical analysis (computed in PAST v.3.15, Hammer et al. 2001) were carried out on the Bullendorf molluscan fauna. A biodiversity index (Simpson dominance index as defined in PAST, Hammer et al. 2001) was calculated in order to measure both species richness and evenness of samples, and a multivariate statistical technique (Principal Component Analysis) was performed to detect recurring assemblages.

A total of 548 gastropod specimens were identified, representing 19 species-level taxa, two of which are left in open nomenclature. The material is stored in the Department of Geology and Palaeontology at the Natural History Museum Vienna (NHMW) under the inventory numbers NHMW 2017/0039/0000 – 2017/0049/0000 and NHMW 2017/0063/0000 – 2017/0069/0000.

Abbreviations

Spec. = specimen/specimens; juv. = juvenile specimen; fragm. = fragment/fragments; H = height; W = width; Lw = height of the last whorl.

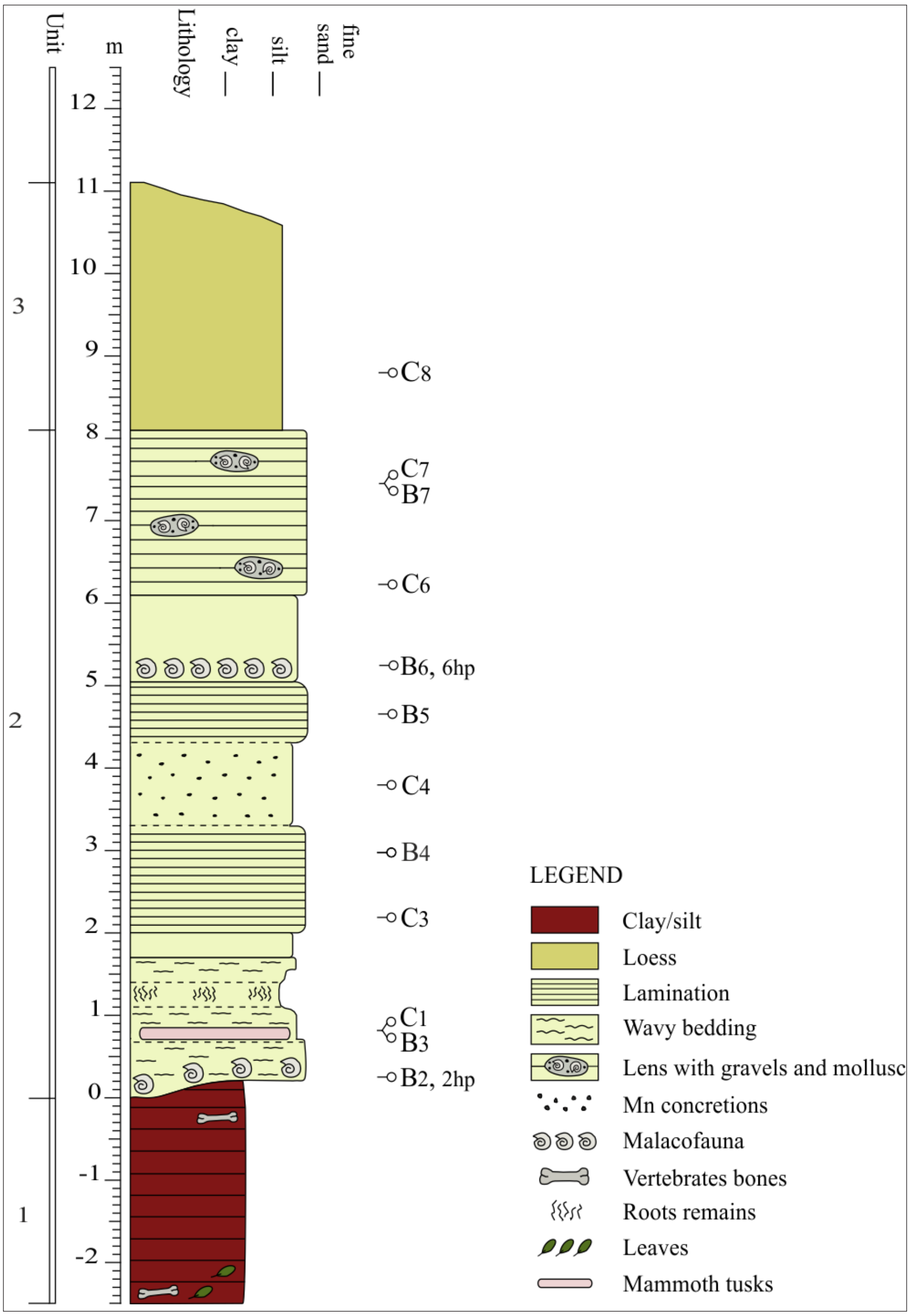
Results

Class **Gastropoda** Cuvier, 1795
Subclass **Heterobanchia** Burmeister, 1837
Superorder **Hygrophila** Férussac, 1822
Superfamily Lymnaeoidea Rafinesque, 1815
Family Lymnaeidae Rafinesque, 1815
Subfamily Lymnaeinae Rafinesque, 1815
Genus *Galba* Schrank, 1803

Type species: *Buccinum truncatulum* Müller, 1774. Recent; Africa, Europe, N- and W-Asia, Alaska. Type fixed by the ICZN under the plenary powers (opinion 1896).

Galba truncatula (Müller, 1774)
Pl. 1, fig. A–C

Fig. 2 - Log of the Bullendorf succession.



1774 *Buccinum truncatulum* Müller, 131.
1964 *Lymnaea* (*G.*) *truncatula* (Müller, 1774) – Ložek, p. 176, pl. 3, fig. 7.
1998 *Galba truncatula* (Müller 1774) – Turner et al., p. 99, unnumbered text-fig. 99.
2006 *Galba truncatula* (Müller 1774) – Frank, p. 73, pl. 5, figs. 9-13.
2012 *Galba truncatula* (Müller 1774) – Welter-Schultes, p. 49, unnumbered text-fig. 49.

Material: 2 spec., 1 juv. fragm. (NHMW 2017/0042/0002), 1 spec. (NHMW 2017/0047/0002), 7 spec. (NHMW 2017/0048/0001) and 35 spec., 18 fragm. (NHMW 2017/0065/0001).

Dimensions: NHMW 2017/0039/0001 (Pl. 1 fig. A–C): H 4.7 mm, W 2.7 mm, Lw 3.4 mm; NHMW 2017/0065/0001: H 4.0 mm, W 1.8 mm, Lw 2.8 mm; NHMW 2017/0065/0001: H 4.3 mm, W 2.2, Lw 2.9 mm; NHMW 2017/0065/0001: H 4.5 mm, W 2.3 mm, Lw 3.1 mm; NHMW 2017/0065/0001: H 4.6 mm, W 2.5 mm, Lw 3.2 mm; NHMW 2017/0065/0001: H 3.8 mm, W 2.2 mm, Lw 2.9 mm.

Description. Ovate-conic, light rose-coloured to whitish shell of 4 to 5 whorls with densely spaced, delicate growth lines. Growth lines strengthening towards aperture. Protoconch comprising 1.2 smooth whorls; transition to teleoconch marked by axial furrow. Spire slightly gradate; whorls with slightly flattened, narrow subhorizontal ramps and convex flanks. Last whorl about 70% of total shell height. Aperture ovate with weak lip; extended columellar lip partially covering umbilicus. Umbilicus deep and narrowly open.

Remarks. *Galba truncatula* is restricted to samples B4 and C3 where it occurs in considerable numbers (53 spec. in sample C3). The available shells agree fully with the specimens from the Early Pleistocene of Bojnice (Slovakia) (Ložek 1964), the Preboreal of Abri von Elsbethen and Hohenberg "Steinbruch" and the Boreal of Gumpoldskirchen (Austria) (Frank 2006). Small specimens of *G. truncatula* are reminiscent of juvenile shells of *Stagnicola* species. Nonetheless, these differ from the specimens herein treated as *Galba truncatula* in the less gradate spire and the more flattened whorl flanks, a drop-like aperture and a narrower umbilicus.

Habitat. *Galba truncatula* is a freshwater species, that can survive long dry periods (Kendall 1965). It lives on submerged plants and stones of small and very small water bodies as well as in springs and puddles (Welter-Schultes 2012). It can be found outside the water on wet and moist meadows or in swampy woodland. In the Alps, it is present up to 2600 m (Frank 2006) and it has been found in small lakes up to 2800 m (Lencioni & Maiolini 2006).

Distribution. It is a Holarctic species living in Central Europe, N Africa, W and N Asia, and N America, up to the Arctic Circle (Frank 2006; Welter-Schultes 2012).

Superorder **Eupulmonata** Haszprunar & Huber, 1990

Order **Stylommatophora** A. Schmidt, 1855

Superfamily Succineoidea Beck, 1837

Family Succineidae Beck, 1837

Subfamily Succineinae Beck, 1837

Genus *Succinella* Mabille, 1871

Type species: *Succinea oblonga* Draparnaud, 1801. Recent; Eurasia. Type by subsequent designation by Boettger (1947).

Succinella oblonga (Draparnaud, 1801)

Pl. 1, fig. D–F

1801 *S.[uccinea] oblonga* Draparnaud, p. 56.

1964 *Succinea* (S.) *oblonga* Draparnaud, 1801 - Ložek, p. 230, pl. 12, figs. 7, 8.

1983 *Succinea* (*Succinella*) *oblonga* Draparnaud, 1801 - Kerney et al., p. 79, pl. 2, fig. 2.

1998 *Succinella oblonga* (Draparnaud 1801) - Turner et al., p. 231, unnumbered text-fig. 231.

2006 *Succinella oblonga* (Draparnaud 1801) - Frank, p. 123, pl. 11, figs. 4-8.

Material: 2 spec. (NHMW 2017/0041/0002), 1 spec., 4 fragments (NHMW 2017/0042/0001), 3 fragm. (NHMW 2017/0044/0004), 2 fragm. (NHMW 2017/0045/0003), 1 spec. (NHMW 2017/0046/0005), 1 spec., 1 fragm. (NHMW 2017/0047/0001), 5 spec., 1 juv. (NHMW 2017/0048/0002, NHMW 2017/0063/0003), 9 spec., 8 juv. fragm., 9 adult fragm. (NHMW 2017/0065/0002), 1 juv. fragm. (NHMW 2017/0066/0002), 6 fragm. (NHMW 2017/0069/0001).

Dimensions: NHMW 2017/0046/0005 (Pl. 1, fig. D–F): H 5.5 mm, W 3.2 mm; Lw 4.3 mm; NHMW 2017/0065/0002: H 6.7 mm, W 3.4 mm, Lw 5.5 mm; NHMW 2017/0048/0002 H 6.0 mm, W 2.8 mm, Lw 4.5 mm; NHMW 2017/0048/0002 H 5.3 mm, W 2.5 mm, Lw 4.2 mm.

Description. Drop-shaped, whitish shell composed of about 3 whorls with coarse and densely spaced growth lines. Last whorl elongated, attaining about 80% of total shell height. Protoconch consisting of less than one bulbous whorl, bearing very faint, irregularly hammered sculpture. Transition into teleoconch marked by gradual onset of growth lines. Suture deep, whorl flanks strongly convex. Aperture broadly ovoid to almost elliptical, peristome thin. Umbilicus fully covered.

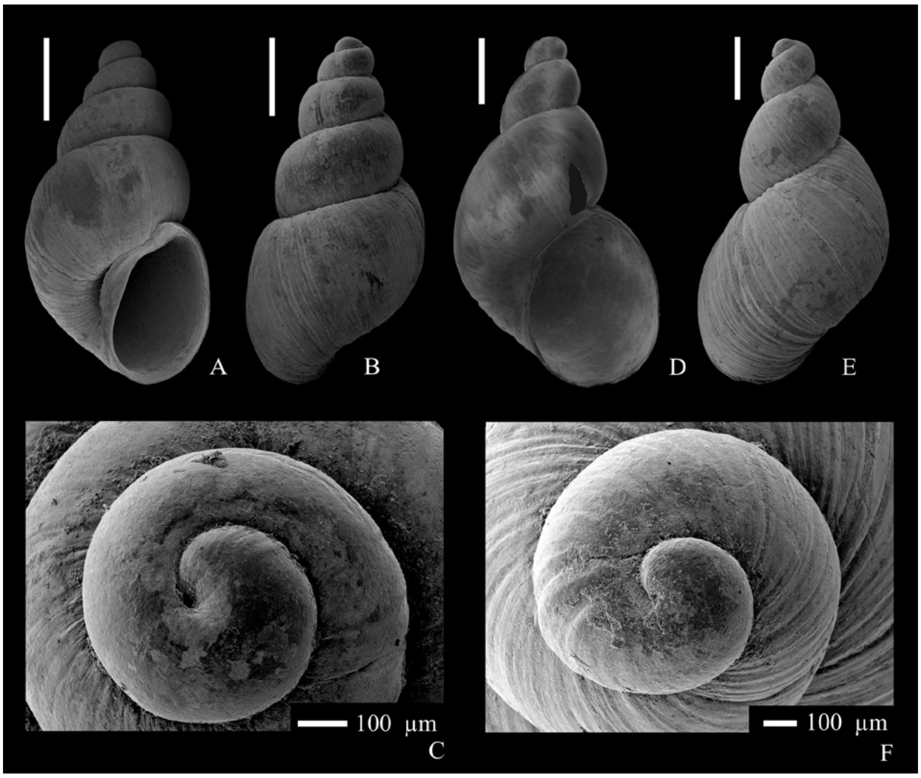
Remarks. *Succinella oblonga* occurs in most samples but is most frequent in samples C3 (26 spec.) and C7 (6 spec.). The specimens fit well with the material from the Late Pleistocene of Dolní Věstonice (Czech Republic) (Ložek 1964) and the ones illustrated by Frank (2006) from Austria. The morphotype *elongata* is frequently reported from Pleistocene deposits such as loess, loess-like clays, and slope sediments formed in the periglacial zone of Germany, Austria, and Czech Republic (Sandberger 1875; Ložek 1964; Łopuszyńska 2002; Frank 2006). However, a morphometric analysis of the shells from several loess localities in Central Europe did not reveal any statistically significant difference between *Succinella oblonga* and *Succinella o. elongata* (Łopuszyńska 2002). *Succinella oblonga* might easily be mistaken for *Quickella arenaria* (Potiez & Michaud 1838), which is slightly wider than *S. oblonga* and shows more convex whorls and asymmetric embryonic whorls (Ložek 1964). Moreover, *S. oblonga* has more whorls than *Q. arenaria* at the same size (Ložek 1964; Welter-Schultes 2012).

Habitat. It occurs in humid and open habitats, in muddy areas and under stones and plants. It can be found on river banks but also in moderately dry places (Ložek 1964; Frank 2006; Welter-Schultes 2012).

Distribution. *Succinella oblonga* is a common component of "loess faunas" throughout Central and Eastern Europe. During the Pleistocene, it

Plate 1

A-C - *Galba truncatula* (Müller, 1774) apertural (A), dorsal (B) and apical (C) views of an adult specimen from NHMW 2017/0039/0001;
D-F - *Succinella oblonga* (Draparnaud, 1801) apertural (D), dorsal (E) and apical (F) views of an adult specimen from NHMW 2017/0046/0005.
Scale bars correspond to 1 mm (A, B, D, E), 100 µm (C, F). All SEM images.



was more common in glacial periods but is also known from interglacials (Frank 2006). This species is often found in Holocene sediments, particularly those which accumulate in relatively humid environments such as calcareous tufas and alluvial sediments (Łopuszyńska 2002). Ložek (1964) and Frank (2006) provide comprehensive lists of Pleistocene and Holocene occurrences from Austria, Czech Republic and Slovakia. Today, this species is widespread throughout Europe and W-Asia (Frank 2006).

Superfamily Pupilloidea Turton, 1831
Family Pupillidae Turton, 1831
Genus *Pupilla* Fleming, 1828

Type species: *Pupa marginata* Draparnaud, 1801 [= *Pupilla muscorum* (Linnaeus, 1758)]. Recent; Northern Hemisphere. Type species by monotypy.

Pupilla loessica **Ložek, 1954**

Pl. 2, fig. A–C

1954 *Pupilla loessica* sp. n. Ložek, p. 341, pl. 1, figs. 4, 5.
1964 *Pupilla loessica* Ložek, 1954 - Ložek, p. 217, pl. 9, fig. 3.
1976 *Pupilla loessica* Ložek, 1954 - Puisségur, pl. 24, figs. 1, 2, pl. 25, fig. 4.
2006 *Pupilla loessica* Ložek 1954 - Frank, p. 236, pl. 18, figs. 6, 7.

Material*:* 8 spec., 4 fragm. (NHMW 2017/0040/0001), 8 spec., 3 fragm. (NHMW 2017/0044/0006), 13 spec. (NHMW 2017/0046/0015), 12 spec. (NHMW 2017/0048/0012), 7 spec., 1 fragm. (NHMW 2017/0063/0008), 1 spec. (NHMW 2017/0070/0001).

Dimensions*:* NHMW 2017/0039/0002 (Pl. 2, fig. A–C): H 3.1 mm, W 1.6 mm, Lw 1.3 mm; NHMW 2017/0040/0001: H 3.0 mm, W 1.6 mm, Lw 1.3 mm; NHMW 2017/0040/0001: H 3.1 mm, W 1.6 mm, Lw 1.4 mm; NHMW 2017/0040/0001: H 2.9 mm, W 1.7 mm, Lw 1.3 mm; NHMW 2017/0040/0001: H 2.9 mm, W 1.7 mm, Lw 1.4 mm; NHMW 2017/0040/0001: H 2.9 mm, W 1.4 mm, Lw 1.2 mm.

Description. Tiny, cylindrical-ovate, pupiform light pinkish-brown shell comprising about 4.5 strongly convex teleoconch whorls with sculpture of dense, somewhat prominent, prosocline growth lines. Last whorl about 45% of total shell height. Suture initially deep, weakening abapically. Protoconch consisting of about 1.4 whorls, transition between protoconch and teleoconch abrupt, marked by appearance of growth lines. Last whorl ending in wide semi-elliptical aperture with slightly projecting lip. Aperture without teeth. Umbilicus narrow and moderately deep.

Remarks. The morphology of the herein studied material resembles highly the holotype and the paratype from the Late Pleistocene of Předmostí u Přerova (Czech Republic) (Ložek 1954) and the specimens from the middle Würm of Dolní Věstonice (Czech Republic) (Ložek 1964) and the Late Pleistocene of Stillfried (Austria) (Frank 2006). *Pupilla loessica* is reminiscent of *Pupilla sterrii* (Voith in Forster, 1840), but the first species lacks apertural teeth and has a weakly developed peristome.

Habitat. The extant *Pupilla loessica* lives in steppe environments, steppe meadows and high mountain forb tundra with mean annual temperatures below 0°C (Meng & Hoffmann 2009; Moine 2014).

Distribution. The species is a typical element of glacial loess deposits and characteristic of the so-called *Pupilla*-fauna and the *Columella*-fauna in Central Europe (Frank 2006). According to Ložek (1954), *Pupilla loessica* is a typical loess-steppe species of the Late Pleistocene. Its mass occurrences are often associated with the coldest phases of glacial, and particularly with the period of intensive aeolian accumulation (Alexandrowicz et al. 2013, 2014). It was extirpated in Europe with the onset of the Holocene but is still present today in Siberia and the Altai region of Central Asia (Meng & Hoffmann 2009; Moine 2014; Nekola et al. 2015).

Pupilla muscorum (Linnaeus, 1758)

Pl. 2, fig. D–F

1758 *Turbo muscorum* Linnaeus, p. 767.
1964 *Pupilla muscorum* (Linné, 1758) - Ložek, p. 215, pl. 9, figs. 1, 7.
1976 *Pupilla muscorum* (Linné, 1758) - Puisségur, pl. 23, figs. 2-4, pl. 25, fig. 3.
1983 *Pupilla* (*Pupilla*) *muscorum* (Linnaeus, 1758) - Kerney et al., p. 118, unnumbered text-fig. 118.
1998 *Pupilla* (*Pupilla*) *muscorum* (Linnaeus 1758) - Turner et al., p. 162, unnumbered text-fig. 162.
2006 *Pupilla muscorum* (Linnaeus 1758) - Frank, p. 211, pl. 17, figs. 10, 11.

Material: 10 spec., 5 fragm. (NHMW 2017/0040/0001), 5 spec., 7 fragm. (NHMW 2017/0041/0003), 1 spec. (NHMW 2017/0043/0001), 21 spec., 8 fragm. (NHMW 2017/0044/0005), 31 spec., 1 frag. (NHMW 2017/0046/0010), 21 spec. (NHMW 2017/0048/0009), 10 spec., 2 fragm. (NHMW 2017/0063/0005), 7 spec. (NHMW 2017/0065/0006), 1 spec. (NHMW 2017/0066/0001).

Dimensions: NHMW 2017/0039/0003 (Pl. 2, fig. D–F): H 3.7 mm, W 1.7 mm, Lw 1.5 mm; NHMW 2017/0040/0003: H 3.6 mm, W 1.8 mm, Lw 1.8 mm; NHMW 2017/0040/0003: H 3.8 mm, W 1.7 mm, Lw 1.9 mm; NHMW 2017/0044/0005: H 3.6 mm, W 1.8 mm, Lw 1.7 mm; NHMW 2017/0044/0005: H 3.6 mm, W 1.9 mm, Lw 1.6 mm; NHMW 2017/0044/0005: H 3.5 mm, W 1.8 mm, Lw 1.6 mm.

Description. Elongate, cylindrical, light rose-coloured to brownish shell composed of 5 to 6 somewhat convex teleoconch whorls with irregular, prosocline, weak growth lines. Conical apex and slightly impressed suture. Last whorl about 45% of total shell height. Protoconch comprising 1.5 whorls; transition to teleoconch marked by onset of thin and faint growth lines. Aperture semicircular and narrowed posteriorly. Peristome with well-developed, projecting lip and thickened cervical callus. Some specimens with straightened outer lip and subtriangular aperture. Pointed parietal tooth present at some distance from aperture; larger palatal tooth sometimes present deep inside aperture. Umbilicus small and moderately deep.

Remarks. The slender outline distinguishes this species from other members of *Pupilla*. The described material matches the specimens from the middle Würm of Předmostí (Czech Republic) (Ložek 1964) and the late Würm of Stillfried/Hausberg (Austria) (Frank 2006). They share the elongate outline, pointed apex and slightly convex flanks. Some specimens display rather convex whorls similar to the material from Dolní Věstonice (Czech Republic) illustrated by Ložek (1964). Both *P. muscorum* and *P. sterrii* (Voith in Forster, 1840) bear apertural teeth, but *P. sterrii* is typically smaller, has a much deeper suture and more convex flanks than *P. muscorum*. However, specimens of *P. sterrii* with moderately convex whorls might be misidentified with *P. muscorum*.

Habitat. *Pupilla muscorum* is an extant species ranging from relatively moisty meadows to dry and sunny habitats, such as rocks, debris and sand dunes. It occurs in hills and up to 2400 m in the Alps (Ložek 1964; Welter-Schultes 2012).

Distribution. It is a Holarctic species. In Austria, it is widespread from Vienna to Lake Neusiedl, and in Carinthia (Frank 2006). *Pupilla muscorum* occurred throughout the Pleistocene but was most common during glacials; it is a typical element of loess-assemblages (see Ložek 1964 and Frank 2006 for extensive lists of Pleistocene occurrences). Wenz (1923) listed also occurrences from the late Miocene of Hungary and several Pliocene occurrences from England. These, however, need confirmation.

Pupilla alpicola (Charpentier, 1837)

Pl. 2, fig. G–I

1837 *Pupa alpicola* Charpentier, p. 16, pl. 2, fig. 5.
1871 *Pupa muscorum* var. *pratensis* Clessin, p. 101.
1954 *Pupilla muscorum densegyrata* subsp. n. - Ložek, p. 340, pl.1, figs. 2, 3.
1964 *Pupilla m. densegyrata* V. Ložek, 1954 - Ložek, p. 215, pl. 9, fig. 4.
2006 *Pupilla alpicola densegyrata* (Ložek 1954) - Frank, p. 205, pl. 17, fig. 9.

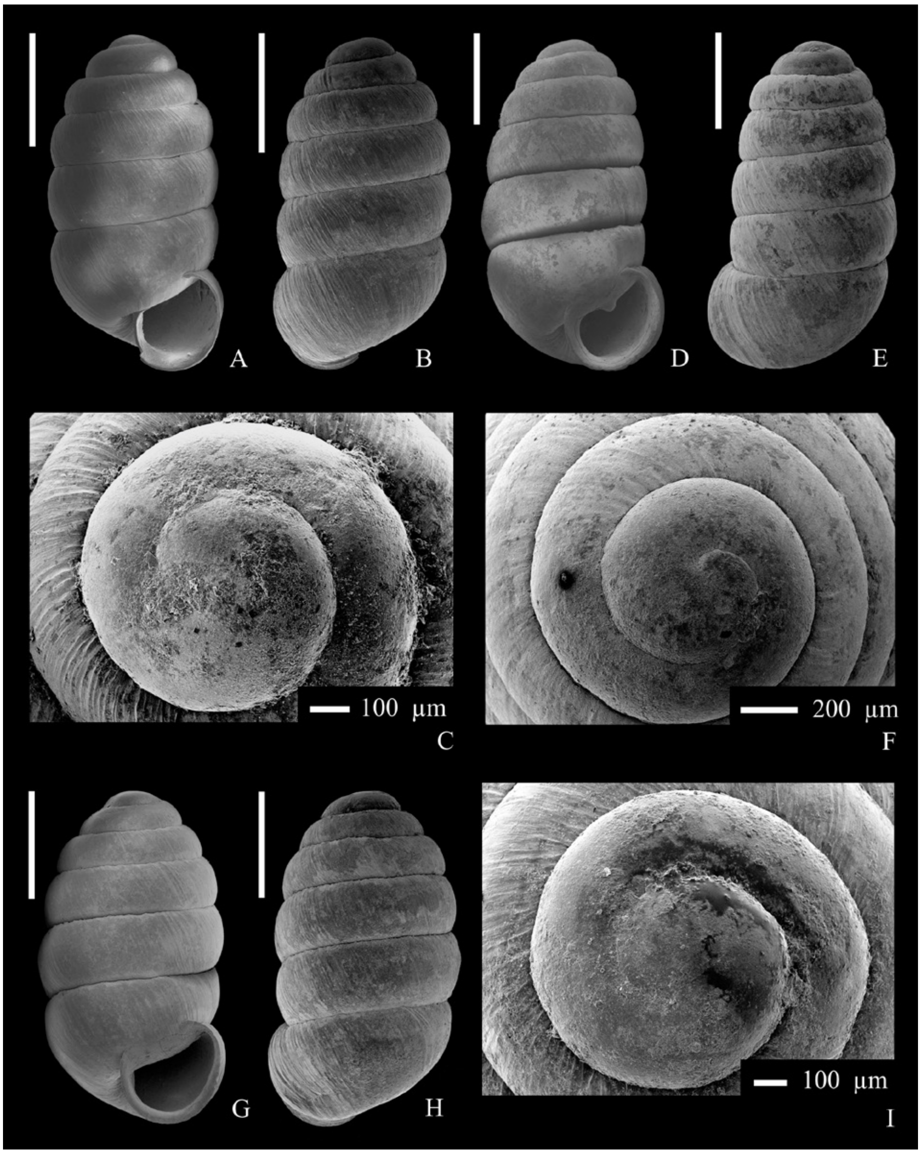


Plate 2

A-C - *Pupilla loessica* Ložek, 1954 apertural (A), dorsal (B) and apical (C) views of an adult specimen (specimen broken after imaging) from NHMW 2017/0039/0002;

D-F - *Pupilla muscorum* (Linnaeus, 1758) apertural (D), dorsal (E), apical (F) views of an adult specimen from NHMW 2017/0039/0003;

G-I - *Pupilla alpicola* (Charpentier, 1837) apertural (G), dorsal (H) and apical (I) views of an adult specimen (specimen broken after imaging) from NHMW 2017/0039/0004.

Scale bars correspond to 1 mm (A, B, D, E, G, H), 100 µm (C, I), 200 µm (F). All SEM images.

2009 *Pupilla pratensis* (Clessin, 1871) - von Proschwitz et al., p. 317, figs. 1 a-f.
2010 *Pupilla alpicola* (Charpentier, 1837) - Horsák et al. 2010, p.1016, figs. 12, 13.
2012 *Pupilla pratensis* (Clessin, 1871) - Welter-Schultes, p. 131, unnumbered text-fig. 131.
2012 *Pupilla alpicola* (Charpentier, 1837) - Welter-Schultes, p. 130, unnumbered text-fig. 130.

Material: 12 spec. (NHMW 2017/0040/0002), 1 spec. (NHMW 2017/0041/0005), 1 spec. (NHMW 2017/0042/0005), 15 spec., 2 fragm. (NHMW 2017/0044/0008), 10 spec. (NHMW 2017/0046/0014), 13 spec. (NHMW 2017/0048/0011), 5 spec. (NHMW 2017/0063/0008), 3 spec. (NHMW 2017/0065/0007), 1 spec. (NHMW 2017/0068/0002).

Dimensions: NHMW 2017/0039/0004 (Pl. 2, fig. G–I): H 3.1 mm, W 1.8 mm, Lw 1.3 mm; NHMW 2017/0040/0002: H 3.4 mm, W 1.8 mm, Lw 1.7 mm; NHMW 2017/0040/0002: H 3.4 mm, W 1.9 mm, Lw 1.5 mm; NHMW 2017/0040/0002: H 3.7 mm, W 1.9 mm, Lw 1.5 mm; NHMW 2017/0040/0002: H 3.3 mm, W 1.8 mm, Lw 1.4 mm; NHMW 2017/0040/0002: H 3.6 mm, W 1.9 mm, Lw 1.4 mm.

Description. Rather elliptical, rose-coloured to brownish shell consisting of 6 whorls with coarse prosocline growth lines and moderately convex flanks. Apex rounded, suture slightly incised. Protoconch consisting of 1.5 whorls. Transition from protoconch to teleoconch indicated by onset of prominent growth lines. Last whorl about 40% of total shell height. Aperture broad, lacking teeth and showing poorly thickened lip and thin cervical callus. Umbilicus small and narrow.

Remarks. Charpentier (1837) described *Pupilla alpicola* as slightly wider than *P. muscorum*. In addition to the greater width of the shell, the herein described specimens show a broader and less developed peristome compared to *P. muscorum*. According to von Proschwitz et al. (2009), there are some resemblances between Charpentier's species and *Pu-*

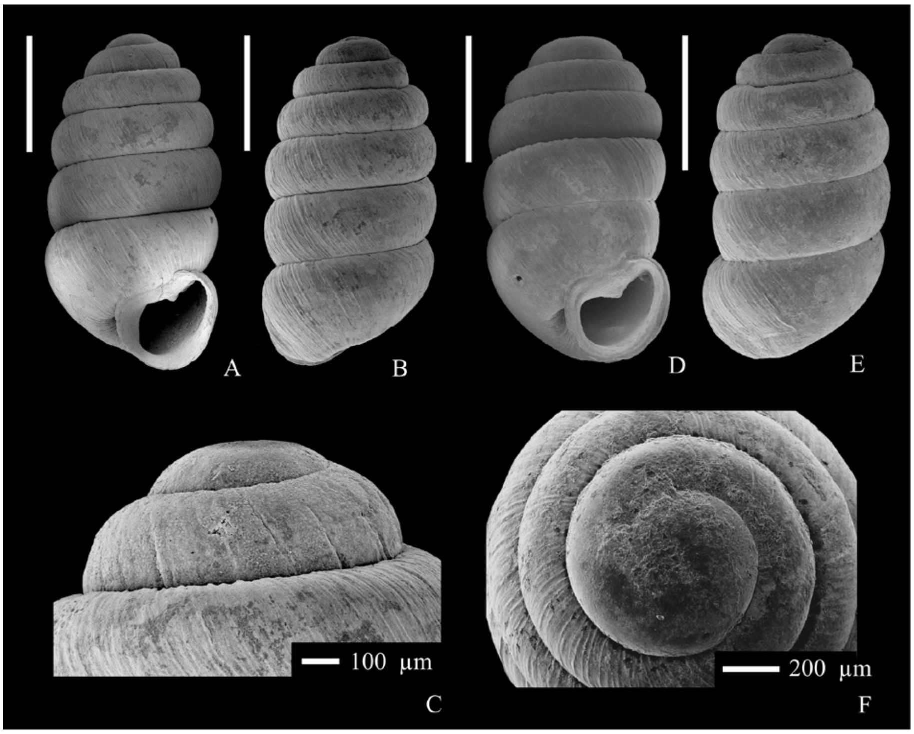


Plate 3

A-C - *Pupilla sterrii* (Voith in Forster, 1838) apertural (A), dorsal (B), and apical (C) views of an adult specimen from NHMW 2017/0039/0005;
D-F - *Pupilla triplicata* (Studer, 1820) apertural (D), dorsal (E) and apical (F) views of an adult specimen from NHMW 2017/0039/0006.
Scale bars correspond to 1 mm (A, B, D, E), 100 µm (C), 200 µm (F). All SEM images.

pilla pratensis (Clessin, 1871). In fact, Clessin (1876) synonymized his variety *pratensis* with *Pupa muscorum* var. *madida* Gredler, 1856, a junior synonym of *Pupilla alpicola* but he subsequently went back to his former point of view and considered *Pupilla pratensis* as an ecophenotype of *P. muscorum* (von Proschwitz et al. 2009). However, *Pupilla pratensis* was recently confirmed as a species distinct from *P. muscorum* based on morphological, ecological and molecular evidence (von Proschwitz et al. 2009). *Pupilla alpicola* and *Pupilla pratensis* resemble each other in the greater width of the shells and also in ecological requirements. According to von Proschwitz et al. (2009), they differ in other general conchological features: *P. alpicola* shows a shorter and more cylindrical shell with a rather pronounced apex as compared to *P. pratensis*. Additionally, *Pupilla alpicola* presents a depression or flattening on the palatal wall of the aperture. However, a multidimensional analysis showed that *P. pratensis* specimens are mostly impossible to distinguish from *P. alpicola* in terms of shell measurements (Horsák et al. 2010). Furthermore, recent DNA sequence analysis by Nekola et al. (2015) indicates that *Pupilla pratensis* and *Pupilla alpicola* are not phylogenetically separated and represent a monophyletic clade for both nDNA and mtDNA (Nekola et al. 2015). The synonymy between the two taxa has been accepted also by Horsák et al. (2015). The form *Pupilla muscorum densegyrata* was introduced by Ložek (1954), who suggested its possible affinity with *Pupilla alpicola* and smaller specimens of *Pupilla pratensis*. Horsák et al. (2015) stated that the subspecies *densegyrata* is a form of *Pupilla alpicola* characteristic of the younger loess sediments in Central Europe (e.g. Ložek 2001) and should be therefore considered as a Late glacial relict. Our material resembles fully the syntype and the other specimens of *P. pratensis* documented by von Proschwitz et al. (2009), as well as the paratype of *P. muscorum densegyrata* from the Late Pleistocene of Zamarovce (Slovakia) (Ložek 1954) and specimens from the Late Pleistocene of Stillfried (Austria) identified as *P. alpicola densegyrata* by Frank (2006). In the view of the latest studies (e.g. Horsák et al. 2011, 2015; Nekola et al. 2015), we consider our material as representative of *Pupilla alpicola* and its ecophenotype *P. alpicola densegyrata*. As already pointed out (von Proschwitz et al. 2009; Horsák et al. 2015; Nekola et al. 2015), further molecular and morphological analyses are required for accurate species assignment in this genus, along with a revision of Pleistocene specimens attributed in the past to *Pupilla pratensis/alpicola/muscorum*.

Habitat. *Pupilla alpicola* lives in moss of wet meadows in high alpine regions, mostly in calcareous fens with sparce herbal vegetation characterized by extremely high calcium carbonate precipitation (tufa) (Horsák et al. 2011; Welter Schultes 2012; Horsák et al. 2015).

Distribution. The species occurs in Central Europe and extends continuously northwest into southern Scandinavia and Ireland and east into central Asia. During the Pleistocene, its ecomorphological form *P. alpicola densegyrata* occurred in numerous central European loesses localities (Ložek 1964, 2001; Frank 2006; Horsák et al. 2015).

Pupilla sterrii (Voith in Forster, 1840)

Pl. 3, fig. A–C

1838 *Pupa Sterrii* de Voith Forster, p. 469.
1964 *Pupilla sterri* (Voith, 1838) - Ložek, p. 216, pl. 9, fig. 2.
1976 *Pupilla sterri* (Voith, 1838) - Puisségur, pl. 23, figs. 5, 7, pl. 25, figs. 5, 6.
1983 *Pupilla* (*Pupilla*) *sterrii* (Voith, 1838) - Kerney et al., p. 120, unnumbered text-fig. 120.
1998 *Pupilla* (*Pupilla*) *sterrii* (Voith 1840) - Turner et al., p. 167, unnumbered text-fig. 167.
2006 *Pupilla sterrii* (Voith 1840) - Frank, p. 230, pl. 18 figs. 3-5.

Material: 3 spec. (NHMW 2017/0040/0004), 1 spec. (NHMW 2017/0041/0004), 2 spec. (NHMW 2017/0044/0007), 11 spec. (NHMW 2017/0046/0011), 3 spec. (NHMW 2017/0047/0010), 8 spec. (NHMW 2017/0048/0010), 3 spec. (NHMW 2017/0063/0006), 1 spec. (NHMW 2017/0068/0002).

Dimensions: NHMW 2017/0039/0005 (Pl. 3, fig. A–C): H 3.1 mm, W 1.4 mm; Lw 1.3 mm; NHMW 2017/0048/0010: H 3.1 mm, W 1.5 mm, Lw 1.3 mm; NHMW 2017/0048/0010: H 3.3 mm, W 1.7 mm, Lw 1.4 mm; NHMW 2017/0046/0011: H 3.2 mm, W 1.4 mm, Lw 1.4 mm; NHMW 2017/0046/0011: H 3.2 mm, W 1.5 mm, Lw 1.4 mm; NHMW 2017/0046/0011: H 3.2 mm, W 1.45 mm, Lw 1.4 mm.

Description. Slender, cylindrical, light brownish-reddish shell with 5 strongly convex whorls and impressed suture. Last whorl about 40% of shell height. Protoconch comprising 1.5 whorls; onset of teleoconch marked by slightly protruding, regular and prosocline growth lines. Aperture semi-elliptical to nearly semi-circular. Thickened peristome bearing developed cervical callus, rounded parietal tooth and less prominent palatal tooth. Umbilicus small and moderately deep.

Remarks. The convex flanks with prominent growth lines and the apertural teeth characterize the individuals from Bullendorf. The shells agree fully with material from the middle Würm of Banka (Slovakia) (Ložek 1964), the late Würm of Stillfried/Hausberg (Austria) (Frank 2006) and the Preboreal of Abri von Elsbethen (Austria) (Frank 2006). The Recent specimen figured by Turner et al. (1998) differs from our material in having a broader aperture and a much more reflected lip.

Habitat. *Pupilla sterrii* lives on dry meadows of calcareous substrate, on limestones, south-facing rocks and between stones (Ložek 1964; Frank 2006; Welter-Schultes 2012).

Distribution. It occurs in Central and S Europe, in Asia from Anatolia through Turkestan to N-China, in the Alps, Carpathians and Balkans (Frank 2006; Welter-Schultes 2012). It was widespread during the Pleistocene in Europe and it was a typical element of the loess-assemblages (see Ložek 1964 and Frank 2006 for a long list of Central European occurrences).

Pupilla triplicata (Studer, 1820)

Pl. 3, fig. D–F

1820 *Pupa triplicata* Studer, p. 89.
1964 *Pupilla triplicata* (Studer, 1820) - Ložek, p. 214, pl. 9, fig. 6.
1983 *Pupilla* (*Pupilla*) *triplicata* (Studer, 1820) - Kerney et al., p. 119, unnumbered text-fig. 119.
1998 *Pupilla* (*Pupilla*) *triplicata* (Studer 1820) - Turner et al., p. 166, unnumbered text-fig.166.
2006 *Pupilla triplicata* (S. Studer 1820) - Frank, p. 224, pl. 18 fig. 2.

Material: 2 spec. (NHMW 2017/0040/0005), 1 spec. (NHMW 2017/0042/0006), 6 spec. (NHMW 2017/0046/0012).

Dimensions:NHMW 2017/0039/0006 (Pl. 3, fig. D–F): H 2.6 mm, W 1.4 mm; Lw 1.2 mm; NHMW 2017/0046/0012: H 2.9 mm, W 1.5 mm, Lw 1.3 mm; NHMW 2017/0047/0011: H 2.8 mm, W 1.4 mm, Lw 1.2 mm; NHMW 2017/0047/0011: H 2.5 mm, W 1.3 mm, Lw 1.1 mm; NHMW 2017/0047/0011: H 2.8 mm, W 1.4 mm, Lw 1.3 mm.

Description. Tiny, cylindrical, light brownish-yellowish shell of about 5 moderately rounded whorls separated by deep suture. Protoconch made of 1.4 whorls; onset of teleoconch marked by axial edge and fine, regular and oblique growth lines. Last whorl about 45% of shell height, terminating in nearly semi-circular aperture. Peristome with well developed, projecting lip and three teeth: a pointed parietal tooth, a flattened palatal tooth and a less prominent columellar tooth. Umbilicus small and moderately deep.

Remarks. *Pupilla triplicata* represents one of the smallest species of the *Pupilla* complex. It is similar to *P. sterrii* in shell shape, but differs by its flatter apex, shallower suture and three apertural teeth instead of two. The specimen from the Late Pleistocene of Předmostí (Czech Republic) (Ložek 1964, pl. 9, fig. 5) represents a dwarf form of *P. triplicata*. It resembles the present material regarding the shape of the peristome and whorl outline, but it is egg-shaped and much smaller.

Habitat. This species occurs in dry and ex-

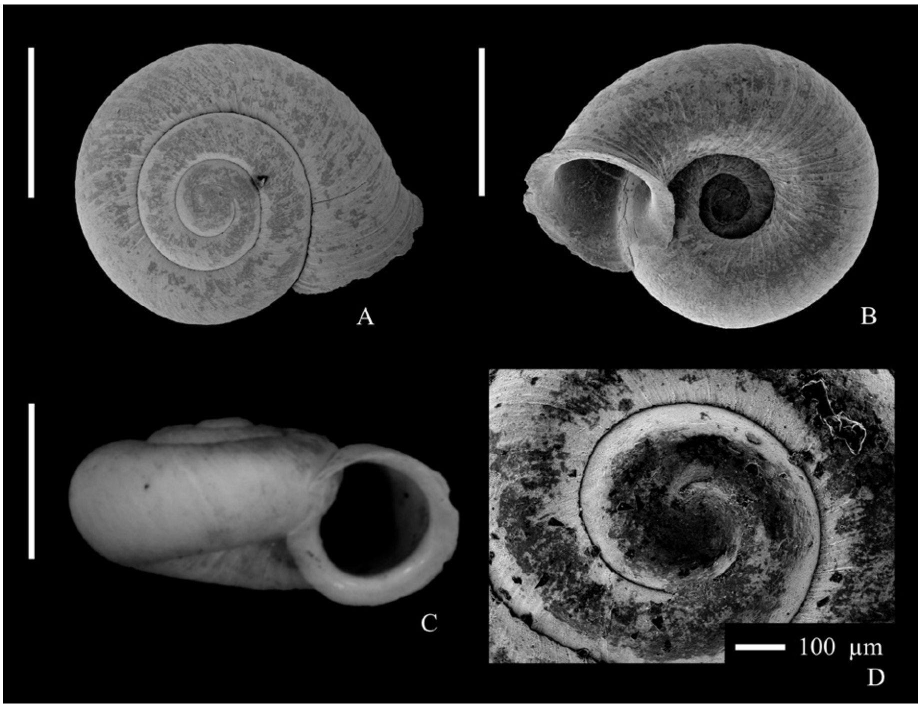


Plate 4

A-D - *Vallonia costata* (Müller, 1774) apical (A), umibilical (B), views and detail of the protoconch (D) of an adult specimen from 2017/0040/0012 and apertural (C) of an adult specimen from NHMW 2017/0039/0008. All SEM images except for C macrophotograph.

Scale bars correspond to 1 mm (A, B, C) and 100 µm (D).

posed habitats, often in grass at calcareous outcrops and at rock debris with xerothermic grasslands. It occurs in hilly and submontane areas, from 220 to 1550 m (Frank 2006; Welter-Schultes 2012).

Distribution. It is present in the Alps and southern Europe, from Spain to Transcaucasia. It occurred throughout the Pleistocene but is most characteristic for the warmer phases (Frank 2006).

Family Valloniidae Morse, 1864
Subfamily Valloniinae Morse, 1864
Genus *Vallonia* Risso, 1826

Type species: *Vallonia rosalia* Risso, 1826 [= *Vallonia pulchella* Müller, 1774]. Recent; Northern Hemisphere. Type by monotypy.

Vallonia costata (Müller, 1774)

Pl. 4, fig. A–D

1774 *Helix costata* Müller, p. 30.
1964 *Vallonia costata* (Müller, 1774) - Ložek, p. 219, pl. 10, figs. 3 a-c
1976 *Vallonia costata* Müller - Puisségur, pl. 7, figs. 1,4.
1983 *Vallonia costata* (Müller, 1774) - Kerney et al., p. 125, unnumbered text-fig. 126.
1996 *Vallonia costata* (Müller, 1774) - Gerber, p. 156, pl. 62, figs. a-c.
1998 *Vallonia costata* (Müller 1774) - Turner et al., p. 170, unnumbered text-fig. 170.
2006 *Vallonia costata* (Müller 1774) - Frank, p. 170, pl. 14, figs. 6-13.

Material: 1 spec. (NHMW 2017/0040/0012), 1 spec. (NHMW 2017/0063/0002), 3 spec. (NHMW 2017/0046/0018).

Dimensions: NHMW 2017/0039/0008 (Pl. 4, fig. C): H 1.2 mm, W 2.4 mm; NHMW 2017/0040/0012 (Pl. 4, fig. A, B, D): H 1.3 mm, W 2.3 mm.

Description. Tiny, flat, whitish shell comprising 3 rounded whorls. Suture well impressed. Sculpture consisting of widely, regularly spaced, prominent collabral ribs and much finer threads in interspaces. Sculpture visible mostly on last whorl. Protoconch smooth delimited from teleoconch by onset of axial ribs. Terminal part of last whorl turning slightly down and terminating in quite circular, oblique and flaring peristome with thick and well-developed lip. Umbilicus wide and open.

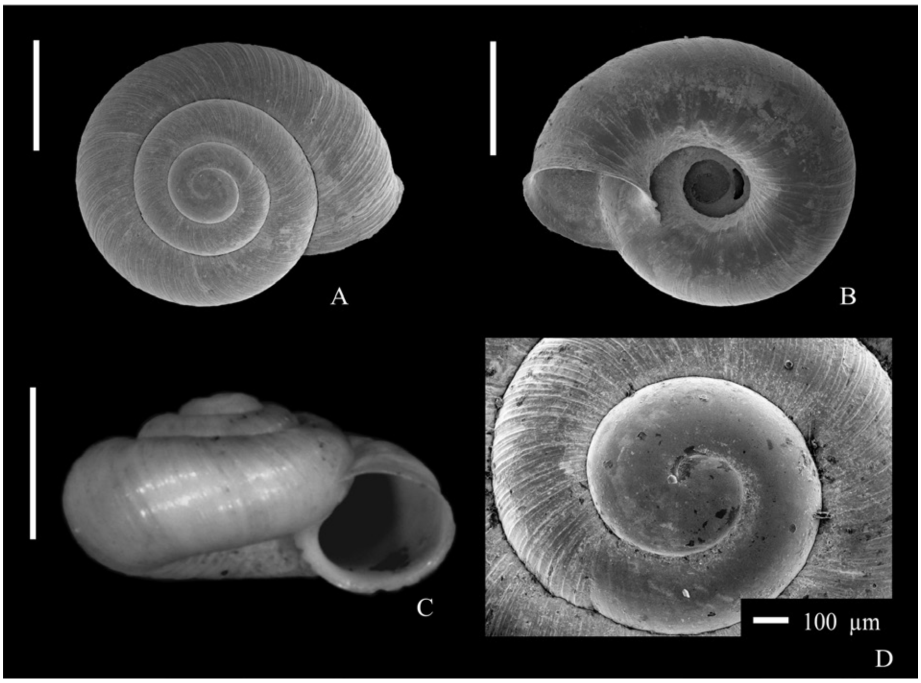
Remarks. *Vallonia costata* resembles *Vallonia enniensis* (Gredler, 1856) in shell shape but differs from it in the stronger descending last whorl and more widely arranged ribs. Specimens from the Late Pleistocene of Hinterbrühl, Schletz and Gauderndorf (Austria) (Frank 2006) and Gánovce-Hrádok (Ložek 1964) correspond fully to our material. Compared to the Preboreal material of Abri von Elsbethen (Austria) (Frank 2006) and the recent shell of Täuffelen (Switzerland) (Turner et al. 1998), the Bullendorf material shows less prominent growth lines on the flanks.

Habitat. *Vallonia costata* is characteristic for open habitats on calcareous substrate, occurring on dry rocky slopes, sandy dunes and relatively humid meadows, sometimes in sparse forests. In the Alps, it is present up to 2200 m (Ložek 1964; Welter-Schultes 2012).

Distribution. The taxon is present in N Africa and Europe to Central Asia (Frank 2006;

Plate 5

A-D - *Vallonia tenuilabris* (A. Braun, 1843) apical (A), umibilical (B), apertural (C) views and detail of the protoconch (D), of an adult specimen from NHMW 2017/0039/0009. All SEM images except for C macrophotograph.
Scale bars correspond to 1 mm (A, B, C) and 100 µm (D).



Welter-Schultes 2012). The species was common during the Pleistocene in Europe (Frank 2006). Miocene records, cited by Frank (2006), are based on misidentifications (e.g. Harzhauser & Binder 2004). Wenz (1923) did not list this species from any Miocene or Pliocene locality.

Vallonia tenuilabris (A. Braun, 1843)

Pl. 5, fig. A–D

1843 *Helix pulchella* var. *tenuilabris* Braun: p, 143
1996 *Vallonia tenuilabris* (A. Braun, 1843) - Gerber, p. 191, pl. 77
1964 *Vallonia tenuilabris* (A. Braun, 1843) - Ložek, p. 223, pl. 10, figs. 1 a-c
2006 *Vallonia tenuilabris* (A. Braun 1843) - Frank, p. 181, pl. 15, figs. 1-6

Material: 3 spec. (NHMW 2017/0040/0011), 2 spec. (NHMW 2017/0041/0007), 4 spec. (NHMW 2017/0044/0003), 5 spec., 1 juv. (NHMW 2017/0046/0017), 5 spec. (NHMW 2017/0047/0006), 5 spec. (NHMW 2017/0048/0006), 4 spec. (NHMW 2017/0063/0001), 4 spec. (NHMW 2017/0065/0003).

Dimensions: NHMW 2017/0039/0009 (Pl. 5, fig. A–D): H 1.3 mm, W 2.5 mm; NHMW 2017/0047/0006: H 1.5 mm, W 3.0 mm; NHMW 2017/0047/0006: H 1.4 mm, W 2.9 mm; NHMW 2017/0047/0006: H 1.6 mm, W 2.9 mm; NHMW 2017/0047/0006: H 1.8 mm, W 3.1 mm; NHMW 2017/0047/0006: H 1.6 mm, W 2.9 mm.

Description. Small-sized, almost circular, whitish shell comprising about 3.4 rounded and convex whorls. Protoconch consisting of about 1.4 smooth whorls, separated from teleoconch by axial rim. Suture deep, spire elevated. Whorls covered by densely but irregularly spaced, delicate, prosocline growth lines, more prominent on last whorl. Moderately descending last whorl ending in enlarged, circular aperture with thin and projecting lip. Umbilicus wide and deep.

Remarks. *Vallonia tenuilabris* differs from other *Vallonia* species by its more elevated spire, irregularly sculptured whorls and weak apertural lip. Moreover, *V. tenuilabris* has a larger and thinner shell, as already discussed by Braun (1843). The specimens from Bullendorf agree with the material from the Late Pleistocene of Dolní Věstonice (Czech Republic) (Ložek 1964) and Stillfried/Hausberg, Stillfried and Willendorf (Austria) (Frank 2006).

Habitat. *Vallonia tenuilabris* lives in taiga and tundra habitats, between grass and leaf litter and under stones (Frank 2006).

Distribution. The recent representatives of the species live in cold climates of N Asian, Siberia, N and NW China, Tibet and Mongolia (Ložek 1964; Frank, 2006). Consequently, *Vallonia tenuilabris* was also typical for cold phases during the Pleistocene of Central and Northern Europe (Frank 2006).

Family Vertiginidae Fitzinger, 1833
Subfamily Vertigininae Fitzinger, 1833

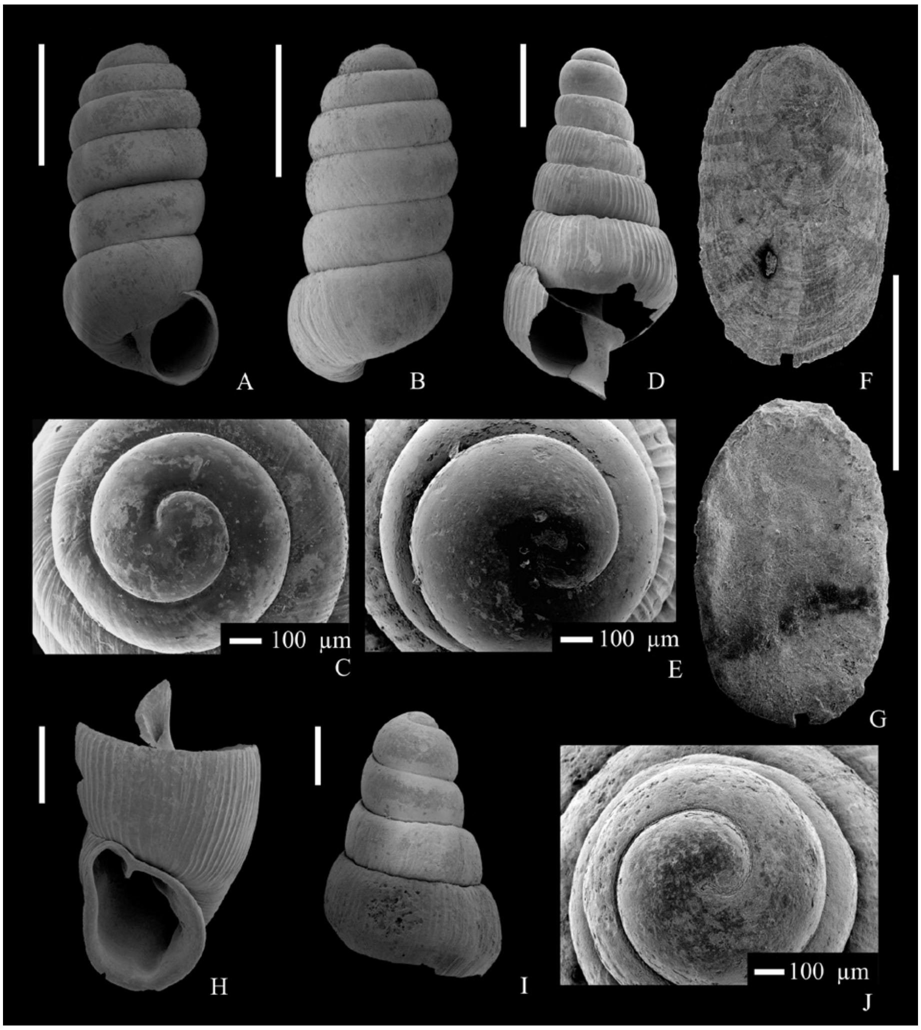


Plate 6

A-C - *Columella columella* (Martens, 1830) apertural (A), dorsal (B) and apical (C) views of an adult specimen (specimen broken after imaging) from NHMW 2017/00039/0007;
D-E - *Macrogastra* cf. *ventricosa* (Draparnaud, 1801) lateral (D) and apical (E) views of a fragmentary specimen from NHMW 2017/0047/0003;
F-G - Milacidae gen. et sp. Indet, dorsal (F) and ventral (G) views of a fragmentary juvenile specimen from NHMW 2017/0040/0008;
H - *Clausilia dubia* Draparnaud, 1805 apertural view of a fragmentary specimen from NHMW 2017/0063/0004.
I-J - *Clausilia* cf *dubia* Draparnaud, 1805 lateral (I) and apical (J) views of a fragmentary specimen from NHMW 2017/0046/0013.
Scale bars correspond to 1 mm (A, B, D, F, G, H, I) and 100 µm (C, E, J). All SEM images.

Genus *Columella* Westerlund, 1878

Type species*: Pupa inornata* Michaud, 1831 [= *Columella edentula* Draparnaud, 1805]. Recent; Holartic. Type species by monotypy.

Columella columella (Martens, 1830)

Pl. 6, fig. A–C

1830 *Pupa Columella* Benz. Martens, 1830, p. 171.
1964 *Columella columella* (Martens, 1830) - Ložek, p. 198, pl. 6, fig. 3.
1976 *Columella columella* (Martens, 1830) - Puisségur, pl. 24, figs. 4-6.
1983 *Columella columella* (Martens, 1830) - Kerney et al., p. 87, unnumbered text-fig. 87.
1998 *Columella columella* (Martens 1830) - Turner et al., p. 179, unnumbered text-fig. 179.
2006 *Columella columella* (Martens 1830) - Frank, p. 268, pl. 22, figs. 2, 3.

Material: 1 spec. (NHMW 2017/0040/0017), 1 spec. (NHMW 2017/0046/0009), 1 spec. (NHMW 2017/0047/0008), 14 spec. (NHMW 2017/0048/0003), 2 spec. (NHMW 2017/0063/0009), 8 fragm. (NHMW 2017/0065/0005).

Dimensions: NHMW 2017/0039/0007 (Pl. 6, fig. A–C): H 2.5 mm, W 1.2 mm, Lw 0.9 mm; NHMW 2017/0048/0003: H 2.7 mm, W 1.3 mm, Lw 1.2 mm; NHMW 2017/0048/0003: H 2.8 mm, W 1.2 mm, Lw 1.1 mm; NHMW 2017/0048/0003: H 2.6 mm, W 1.2 mm, Lw 1.1 mm; NHMW 2017/0048/0003: H 2.6 mm, W 1.2 mm, Lw 1.1 mm; NHMW 2017/0048/0003: H 2.7 mm, W 1.3 mm, Lw 1.1 mm.

Description. Slender, irregularly cylindrical, reddish to brownish shell of about 6 strongly convex and rounded whorls. Suture deep. Enlarged last whorl consisting of about 40% of shell height. Apex slightly rounded; smooth protoconch of 1.4 whorls; transition into teleoconch marked by onset of weak growth lines. Penultimate and antepenultimate whorls of same height. Ovate aperture with weakly developed peristome and slightly reflected columellar lip. Umbilicus small and moderately deep.

Remarks. Among the *Columella* species, *C. columella* stands out for its cylindrical, slender shell and somewhat flatter apex. Juveniles and fragmentary specimens are morphologically reminiscent of *Columella edentula* (Draparnaud, 1805), which differs from *C. columella* by the less cylindrical shell and more pointed apex. Our material corresponds fully to the specimens from the Late Pleistocene of Hornsburg (Austria) (Frank 2006) and of Dolní Věstonice (Ložek 1964). The individual from Schletz figured by Frank (2006) seems to have a smaller and less elongated aperture compared to the specimens from Bullendorf.

Habitat. The species lives in grasslands on calcareous substrate, between stones and reeds, on swampy meadows, in wet subarctic forest and in willow scrub (Frank 2006; Welter-Schultes 2012).

Distribution. *Columella columella* is a Holarctic species; in Europe, it is restricted to boreo-alpine areas (Frank 2006). During the Pleistocene, it was common in Central Europe, where it was typical of glacial phases (Frank 2006).

Superfamily Clausilioidea Gray, 1855
Family Clausiliidae Gray, 1855
Subfamily Clausiliinae Gray, 1855
Tribe Clausiliini Gray, 1855
Genus *Clausilia* Draparnaud, 1805

Type species: *Pupa rugosa* Drapanaurd, 1801. Recent; Europe. Type fixed by ICNZ under the plenary powers in ICZN Opinion 1455.

Clausilia dubia Draparnaud, 1805

Pl. 6, fig. H–J

1805 *C.*[*lausilia*] *dubia* Draparnaud, p. 70, pl. 4, fig. 10.
1964 *Clausilia dubia* Draparnaud, 1805 - Ložek, p. 269, pl. 20, figs. 10, 11.
2006 *Clausilia* (*A.*) *dubia* Draparnaud 1805 - Frank, p. 352, pl. 28, figs. 9-14; pl. 29, figs. 1-9, pl. 30, figs. 1-11.
2012 *Clausilia dubia* Draparnaud, 1805 - Welter-Schultes, p. 297, unnumbered text-fig. 297.

Material: 2 aperture fragm. (NHMW 2017/0063/0004).
Dimensions: NHMW 2017/0063/0004 (Pl. 6, fig. H): W 2.5.

Remarks. The Bullendorf material consists of only three fragmentary specimens of taxa of Clausiliidae: two apertural fragments and one spire fragment. Since the identification of Clausiliidae species is mostly based on the apertural features, only the apertural fragments can be safely identified as *Clausilia dubia*. The aperture shows two columellar folds, a parietal and a frontal upper palatal fold; the outer lip is straight. The specimens correspond to the individuals from the middle Würm of Zamarovce (Slovakia) and from the Atlantikum of Dzeravá skala (Slovakia) (Ložek, 1964), as well as to the Austrian material studied by Frank (2006). In addition, the specimens were compared with *Clausilia dubia* specimens stored in the mollusc collection of the Natural History Museum of Vienna. The spire fragment (NHMW 2017/0046/0013: H 2.7 mm, W 1.5 mm) is tentatively affiliated with *Clausilia dubia*. It consists of a high protoconch of 2 smooth, bulbous, dome-like rose-whitish whorls and 2 slightly convex teleoconch whorls, covered by evenly spaced thin collabral ribs. The sutures are strongly incised, sloped and sub-parallel.

Habitat. *Clausilia dubia* is a calciphile species that lives on moisten shady rocks, tree trunks, mosses covered walls, in cavities and ground litter of wet forests. Sometimes, it can be found in open and xerothermic habitats (Frank 2006; Welter-Schultes 2012).

Distribution. The species is widespread throughout Europe (Welter-Schultes 2012). The species had a similar distribution during the Pleistocene like today (Frank 2006).

Genus *Macrogastra* Hartmann, 1841

Type species: *Pupa ventricosa* Draparnaud, 1801. Recent; Europe. Type species by monotype.

Macrogastra* cf. *ventricosa (Draparnaud, 1801)

Pl. 6, fig. D–E

cf. 1801 *P.*[*upa*] *ventricosa* Draparnaud, p. 62.
cf. 2006 *Macrogastra ventricosa* (Draparnaud 1801) - Frank, p. 339, pl. 27, figs. 5, 6.
cf. 2012 *Macrogastra ventricosa* (Draparnaud, 1801) - Welter-Schultes, p. 324, unnumbered text-fig. 324.

Material: 1 spire fragm. (NHMW 2017/0047/0003).
Dimensions: NHMW 2017/0047/0003 (Pl. 6, fig. D–E): H 4.5 mm, W 2.2 mm.

Remarks. A single fragment of an elongate, reddish sinistral shell with slightly coeloconoid spire and densely and regularly ribbed whorls is available. The high protoconch consists of 2 smooth, bulbous whorls. The transition to the teleoconch is characterised by a thickened collabral rim. The sutures are deep, sloped and sub-parallel. The flanks are poorly convex. The specimen resembles the material illustrated by Frank (2006) in terms of outline and ornamentations, as well as specimens stored in the collection of the Natural History Museum of Vienna. Nevertheless, due to the poor preservation the identification of the specimen available is uncertain.

Habitat. *Macrogastra ventricosa* lives in the underbrush of humid woodlands, between ground and leaf litter and stones. It occurs under moist conditions also on tree trunks and rocks (Frank 2006; Welter-Schultes 2012).

Distribution. The species lives in Europe from northern Spain to southern Norway and Central Russia (Frank 2006; Welter-Schultes 2012). It had a similar distribution during the Pleistocene with occurrences also in England (Frank 2006).

Superfamily Parmacelloidea Fischer, 1856
Family Milacidae Ellis, 1926
Milacidae gen. et sp. indet.
Pl. 6, fig. F–G

Material: 1 juv. fragm. (NHMW 2017/0040/0008).
Dimensions: NHMW 2017/0040/0008 (Pl. 6, fig. F–G): H 1.8 mm, W 1.2 mm.

Description. Shell lenticular and longitudinally symmetrical, very thin and slightly convex, with elliptical to subrectangular outline. Commarginal growth lines starting from nucleus placed close to posterior margin. Ventral side smooth and pearly.

Remarks. According to Wiktor & Likharev (1979) and Reuse (1983), the taxonomic assignment of Milacidae based on the internal shells is problematic even at genus and family level. Moreover, the material from Bullendorf consists of only a single juvenile specimen. The lentil-like shape, the commarginal growth lines and the symmetry of the embryonic shell are reminiscent of Milacidae as described by Frank (2006).

Habitat. The majority of milacid species lives in xerothermic habitats, while several species occur also in moist mountain forests, but never in swamps or near water bodies. Many species dwell on leaf litter (Wiktor 1987; Frank 2006).

Distribution. Milacidae have a Palearctic distribution (Wiktor 1987).

Superfamily Helicoidea Rafinesque, 1815
Family Hygromiidae Tryon, 1866
Subfamily Hygromiinae Tryon, 1866
Tribe Trochulini Lindholm, 1927
Genus *Trochulus* Chemnitz, 1786
Type species: *Helix hispida* Linnaeus, 1758. Recent; Europe except Greece, Italy, S Spain, Portugal and N Scandinavia.
Type by monotypy.

Trochulus hispidus (Linnaeus, 1758)
Pl. 7, fig. A–D

1758 *Helix hispida* Linnaeus, p. 771.
1964 *Trichia* (*T.*) *hispida* (Linné, 1758) - Ložek, p. 300, pl. 25, figs. 1 a-c.
2006 *Trichia hispida* (Linnaeus 1758) - Frank, p. 528, pl. 48, figs. 2-10.
2009 *Trochulus hispidus* (Linnaeus, 1758) - Prockow, p. 128, figs. 88-95.
2012 *Trochulus hispidus* (Linnaeus, 1758) - Welter-Schultes, p. 562, unnumbered text-fig. 562.

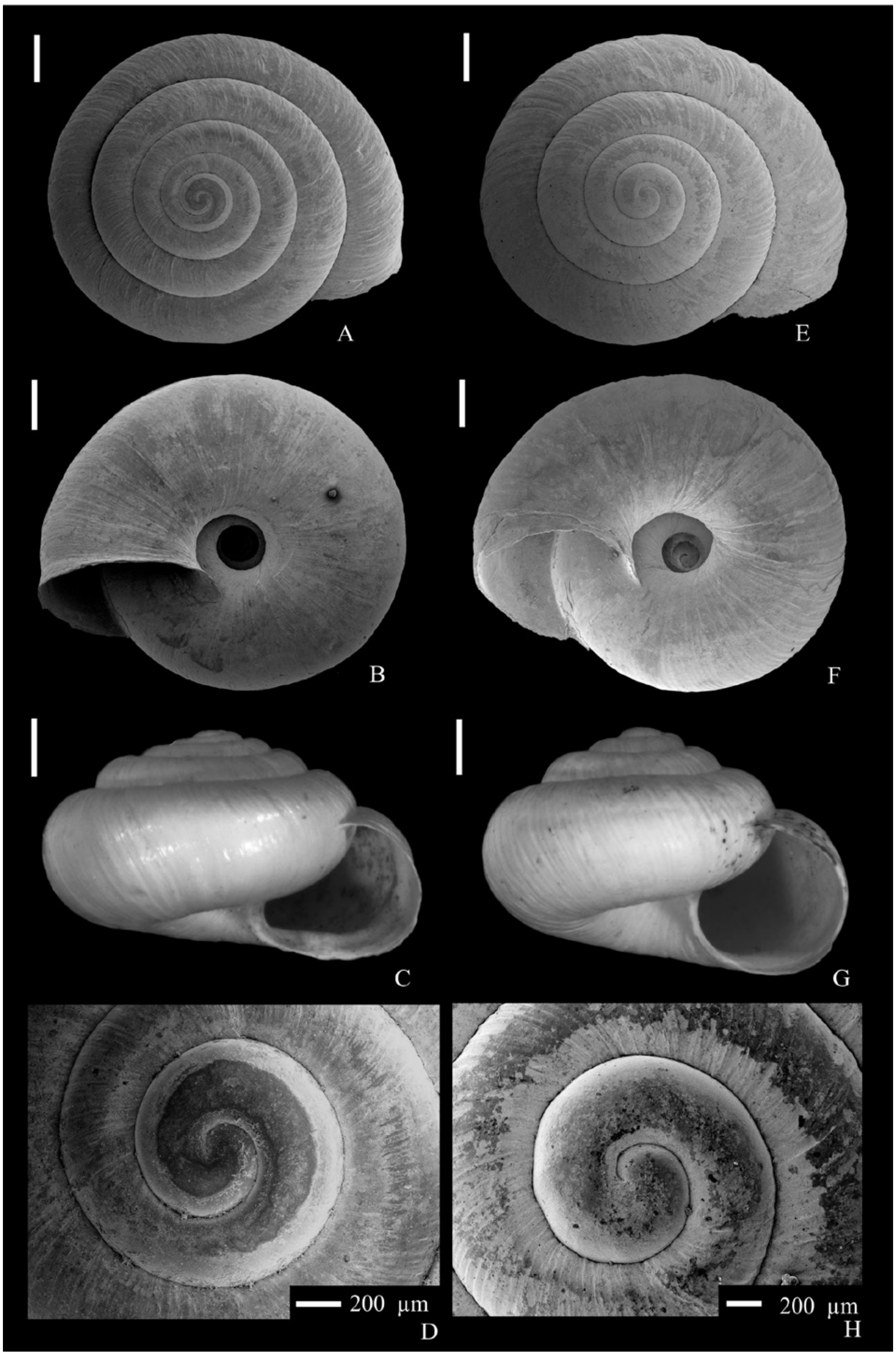
Material: 1 spec., 1 fragm. (NHMW 2017/0040/0013), 1 spec. (NHMW 2017/0042/0004), 2 spec., 3 juv. (NHMW 2017/0044/0002), 2 spec., 1 juv. (NHMW 2017/0046/0019), 1 spec. (NHMW 2017/0047/0005), 23 spec., 5 juv. (NHMW 2017/0048/0005), 4 spec. (NHMW 2017/0065/0004).
Dimensions: NHMW 2017/0039/0010 (Pl. 7, fig. A–D): H 4.5 mm, W 6.7 mm; NHMW 2017/0048/0005: H 3.5 mm, W 6.5 mm; NHMW 2017/0048/0005: H 4.3 mm, W 6.8 mm; NHMW 2017/0048/0005: H 4.6 mm, W 6.8 mm; NHMW 2017/0048/0005: H 3.9 mm, W 6.3 mm; NHMW 2017/0048/0005: H 4.1 mm, W 6.2 mm.

Description. Low trochiform, tightly coiled, whitish shell of 5 slightly protruding whorls with densely-spaced and irregular growth lines. Protoconch comprising 1.4 smooth whorls; demarcation between protoconch and teleoconch indistinct. Suture deeply incised. Last whorl large, widened, turning down slowly and ending in an enlarged, semilunar aperture. Continuous collabral internal swelling present closely behind peristome. Peristome projecting. Umbilicus open and wide.

Remarks. The present material corresponds well to specimens from the Late Pleistocene of Zamarovce (Slovakia) (Ložek 1954) and Lanzenkirchen (Austria) (Frank 2006). The specimens agree in outline, number of whorls and shape of aperture, even though small specimens and juvenile forms sometimes lack the internal collabral swelling. The *T. hispidus* complex comprises a great variety of morphotypes, differing in shell shape, width/height ratio and size of the umbilicus (Ložek 1964; Frank 2006; Welter-Schultes 2012; Duda et al. 2014). For instance, *Trochulus sericeus* (Draparnaud, 1801) has a trochiform shell consisting of five whorls covered by long and curved hairs; it has convex and much more coarsely sculptured flanks than *T. hispidus*. The peristome is thin and lacks the internal collabral swelling (Ložek 1964; Frank 2006). Both Prockow (2009) and Welter-Schultes (2012) agree in considering *T. sericeus* as a synonym of *T. hispidus*. Although Ložek (1964) and Frank (2006) treat *T. sericeus* as a separate species, they point out that, by considering its morphological plasticity, less closely coiled specimens of *T. sericeus* might range within the intraspecific variability of *T. hispidus*. Further-

Plate 7

A-D - *Trochulus hispidus* (Linnaeus, 1758) apical (A), umbilical (B) apertural (C) views and detail of the protoconch (D) of an adult specimen from NHMW 2017/0039/0010.
E-H - *Helicopsis striata* (Müller, 1774) apical (E), umbilical (F) apertural (G) views and detail of the protoconch (H) of an adult specimen from NHMW 2017/0039/0011. All SEM images except for C and G macrophotographs.
Scale bars correspond to 1 mm (A, B, C, E, F, G) and 200 μm (D, H).



more, also *Trochulus plebeius* (Draparnaud, 1805), showing a strongly sculptured shell with prominent swelling inside the aperture, is treated as synonym of *T. hispidus* by Prockow (2009). According to recent studies (e.g. Duda et al. 2014), the taxonomic status of *T. hispidus* complex remains debatable and the assignment of *T. hispidus* and *T. sericeus* to two distinct species requires further investigations.

Habitat. The taxon is present in different types of humid habitats: sparse forests, thickets and cultivated areas. It occurs under stones and woods, usually on vegetation near water bodies. In the Alps, it appears up to 2300 m (Ložek 1964; Frank 2006; Welter-Schultes 2012).

Distribution. It is found from N Spain to the Ural (Welter-Schultes 2012). *Trochulus hispidus* was also widespread throughout the Pleistocene of Europe and it is characteristic for glacials and associated loess deposits (Frank 2006).

Tribe Helicopsini H. Nordsieck, 1987
Genus *Helicopsis* Fitzinger, 1833
Type species*: Helix striata* Müller, 1774. Recent; Central and Eastern Europe to Iran. Type species by monotypy.

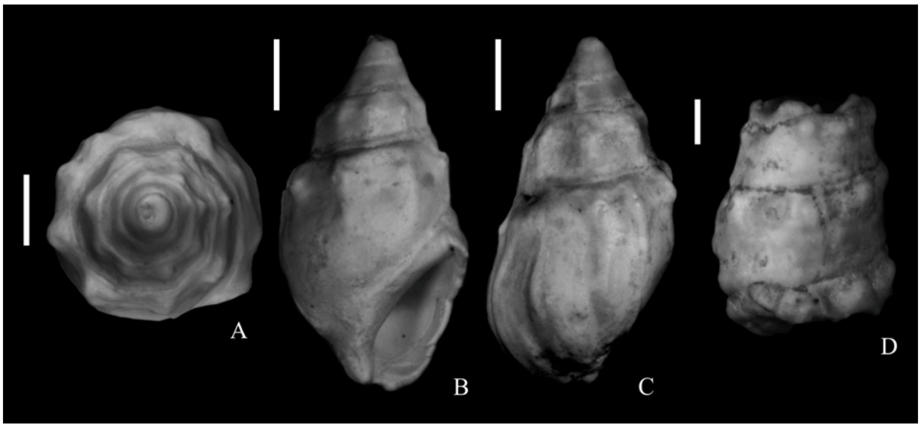


PLATE 8

A-C - *Melanopsis bouei* Férussac, 1823 apertural (A), dorsal (B) and apical (C) views of an adult specimen from NHMW 2017/0049/0001;
D - *Granulolabium bicinctum* (Brocchi, 1814) lateral view of a fragmentary specimen from NHMW 2017/0049/0005.
Scale bars correspond to 1 mm. All macrophotographs.

Helicopsis striata (Müller, 1774)

Pl. 7, fig. E–H

1774 *Helix striata* Müller, p. 38.
1964 *Helicopsis striata* (Müller, 1774) - Ložek, p. 289, pl. 22, figs. 2 a-c.
2006 *Helicopsis striata* (Müller 1774) - Frank, p. 552, pl. 50, figs. 5-9.

Material: 4 spec., 1 fragm. (NHMW 2017/0041/0008), 1 spec. (NHMW 2017/0046/0020), 6 spec. (NHMW 2017/0047/0004), 2 spec. (NHMW 2017/0048/0004), 1 spec. (NHMW 2017/0068/0001).

Dimensions: NHMW 2017/0039/0011 (Pl. 7, fig. E–H): H 4.2 mm, W 6.2 mm; NHMW 2017/0047/0004: H 4.3 mm, W 7.0 mm; NHMW 2017/0047/0004: H 3.9 mm, W 5.9 mm; NHMW 2017/0047/0004: H 4.9 mm, W 6.4 mm; NHMW 2017/0047/0004: H 3.9 mm, W 6.9 mm; NHMW 2017/0047/0004: H 4.1 mm, W 6.2 mm.

Description. Trochiform, whitish shell with up to 4 whorls with prominent and coarse growth lines. Protoconch comprising 1.2 slightly hammered whorls, separated from teleoconch by abrupt onset of growth lines. Whorls moderately convex with adapical shoulder; suture deep. Enlarged last whorl slightly inclined toward aperture. Peristome semicircular and poorly developed. Umbilicus open and rather wide.

Remarks. The specimens from the Late Pleistocene of Banka (Slovakia) illustrated by Ložek (1964) and the ones recorded by Frank (2006) from Austria develop a similarly enlarged peristome as the Bullendorf specimens. Three extant subspecies are known in Austria: *H. striata striata* (Müller, 1774), *H. striata austriaca* (Gittenberger, 1969) and *H. striata hungarica* (Soos & Wagner, 1935). *H. s. hungarica* has a tightly coiled, larger shell with less sculptured whorls than the nominal form. Its last whorl ends in a well-rounded aperture with poorly developed lip. This subspecies has been collected in Austria, Slovakia and Hungary. *H. s. austriaca* displays a small, rounded shell with prominent growth lines whorls. Based on preliminary molecular analysis, the three subspecies can be clearly distinguished (Eschner et al. 2014). Furthermore, the analysis indicates that *H. s. austriaca* is endemic to the southern Vienna basin and the eastern margins of the Alps in Lower Austria (Eschner et al. 2014).

Habitat. It is a steppe species of dry and open habitats, often found in calcareous stony places and grasslands (Ložek 1964; Welter-Schultes 2012).

Distribution. The species lives in Central and E-Europa (Frank 2006; Welter-Schultes 2012). The species had a similar distribution during the Holocene and Pleistocene, being typically found in loess deposits and associated soils (Ložek 1964).

ADDITIONAL TAXA REWORKED FROM MIDDLE AND UPPER MIOCENE BEDS

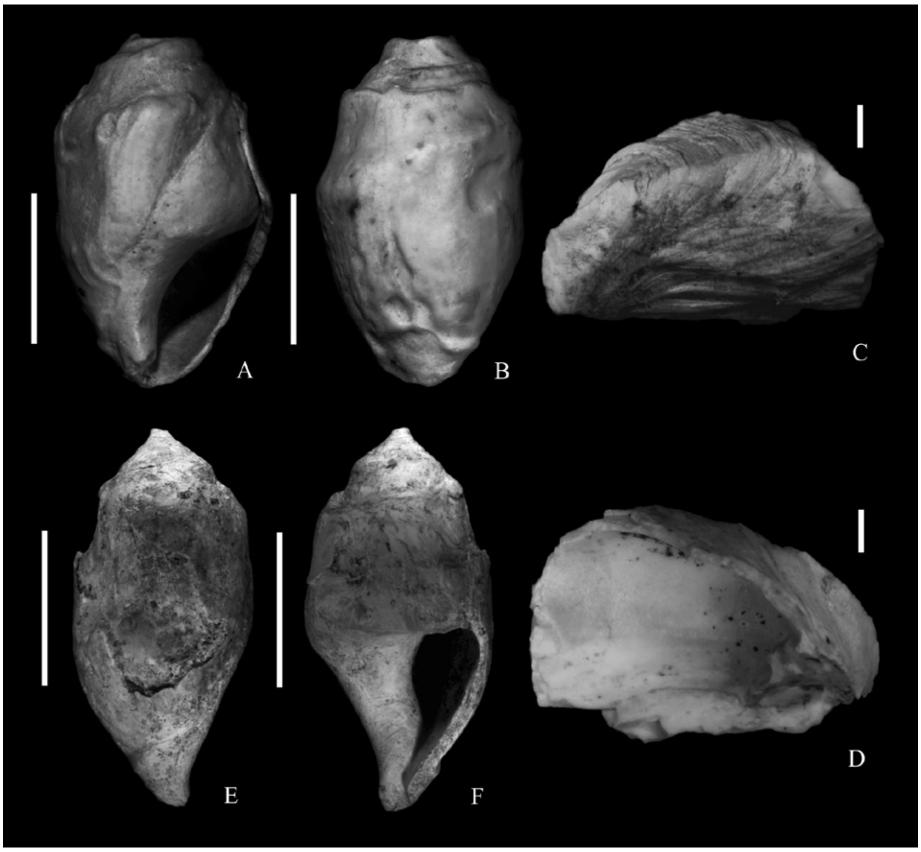
Granulolabium bicinctum (Brocchi, 1814) (Gastropoda, Batillariidae) – Pl. 8, fig. D
Melanopsis bouei Férussac, 1823 (Gastropoda, Melanopsidae) – Pl. 8, fig. A–C
Melanopsis impressa phenotype *pseudonarzolina* Papp, 1953 (Gastropoda, Melanopsidae) – Pl. 9, fig. A–B
Melanopsis impressa phenotype *posterior* Papp, 1953 (Gastropoda, Melanopsidae) – Pl. 9, fig. E–F
Trigonipraxis ornithopsis (Brusina, 1892) (Bivalvia, Dreissenidae) – Pl. 9, fig. C–D

TAXONOMIC COMPOSITION

The herein studied material comprises 19 species-level taxa. The samples contain mixed assemblages of autochthonous Pleistocene species with shells reworked from the underlying middle

Plate 9

A-B - *Melanopsis impressa* phenotype *pseudonarzolina* Papp, 1953 apertural (A) and dorsal (B) views of an adult specimens from NHMW 2017/0049/0004;
C-D - *Trigonipraxis ornithopsis* (Brusina, 1892) interior (C) and exterior (D) views of a fragmentary specimen from NHMW 2017/0049/0002.
E-F - *Melanopsis impressa* phenotype *posterior* Papp, 1953 dorsal (E) and apertural (F) views of an adult specimen from NHMW 2017/0049/0004;
Scale bars correspond to 1 mm. All macrophotographs.



and upper Miocene successions (not described herein; Tab. 1). The Pleistocene taxa are represented by 15 gastropod species of 9 genera, including one freshwater species (Lymnaeidae) and 14 terrestrial species (Succineidae, Pupillidae, Valloniidae, Vertiginidae, Clausiliidae, Milacidae, Hygromiidae). The freshwater species belongs to the genus *Galba* (Lymnaeidae), accounting for about 12% of the total number of 539 specimens. Among the terrestrial species, *Pupilla* (Pupillidae) is the most abundant genus (54%), comprising five species (*Pupilla loessica*, *P. muscorum*, *P. alpicola*, *P. sterrii* and *P. triplicata*). *Pupilla* is followed by *Succinella* (Succineidae) accounting for about 10% of the total fauna. Hygromiidae are represented by the two genera *Trochulus* (*Trochulus hispidus*) and *Helicopsis* (*Helicopsis striata*) representing 8% and 3% of the fauna, respectively. About 7% of the specimens are represented by *Vallonia* (Valloniidae), with the two species *Vallonia costata* and *Vallonia tenuilabris*. Only 5% of the specimens belong to the genus *Columella* (Vertiginidae) represented by *Columella columella*. Milacidae is represented by only one species, which accounts for 0.01% of the fauna. Finally, Clausiliidae are documented by the two genera *Clausilia* (0.75%) and *Macrogastra* (0.25%).

The reworked taxa are admixed from two

Taxa	Quantitative sampling	Qualitative collection	Specimens
Pleistocene taxa			
Freshwater elements			
Galba truncatula	56	8	64
Terrestrial elements			
Succinella oblonga	46	9	55
Pupilla loessica	32	25	57
Pupilla muscorum	77	53	130
Pupilla alpicola	40	23	63
Pupilla sterrii	10	22	32
Pupilla triplicata	3	6	9
Vallonia costata	2	3	5
Vallonia tenuilabris	17	16	33
Columella columella	11	16	27
Clausilia dubia	2	1	3
Macrogastra cf. *ventricosa*	0	1	1
Milacidae	1	-	1
Trochulus hispidus	12	32	44
Helicopsis striata	6	9	15
Total	**315**	**224**	**539**
Pannonian taxa			
Melanopsis bouei	-	2	2
Melanopsis impressa phenotype *pseudonarzolina*	-	1	1
Melanopsis impressa phenotype *posterior*	-	3	3
Trigonipraxis ornithopsis	-	2	2
Total		**8**	**8**
Sarmatian taxa			
Granulolabium bicinctum	-	1	1
Total		**1**	**548**

Tab. 1 - List of identified taxa.

Taxa	Temperature	Air humidity	Vegetation
Freshwater elements			
Galba truncatula	Cr	-	-
Terrestrial elements			
Succinella oblonga	Cr	H	O
Pupilla loessica	C	D	O
Pupilla muscorum	M	M	O
Pupilla alpicola	M	M	O
Pupilla sterrii	C	D	O
Pupilla triplicata	T	D	O
Vallonia costata	M	M	W/O
Vallonia tenuilabris	C	D	O
Columella columella	C	H	O
Clausilia dubia	M	Sh	W
Macrogastra cf. *ventricosa*	M	Sh	W
Milacidae	M	M	W
Trochulus hispidus	Cr	H	W/O
Helicopsis striata	T	D	O

Tab. 2 - Ecological preferences of identified taxa after Ložek (1964), Krolopp & Sümegi (1995) and Sümegi & Krolopp (2002). M: mesophilous, C: cryophilous, Cr: cold-tolerant, T: thermophilous, D: aridity-tolerant, H: hygrophilous, Sh: subhygrophilous, O: open habitats, W/O: intermediate habitats, W: woodland.

different stratigraphic levels. The documented species of *Melanopsis* (Melanopsidae) and *Trigonipraxis* (Dreissenidae) are all typical Lake Pannon elements from upper Miocene deposits (Papp 1953, 1985), whereas the batillariid *Granulolabium* is typically found in middle Miocene strata from the Sarmatian Sea (Harzhauser et al. 2011). Such complex reworking from various stratigraphic levels is a common phenomenon on the Mistelbach Block (Harzhauser et al. 2011). The exposure of different marine and lacustrine Miocene deposits during the Pleistocene may well have contributed to habitat heterogeneity. None of the Pleistocene species is also known from Miocene strata. Therefore, a reworking of these specimens can be excluded.

Palaeoecological constrains of the fauna

The terrestrial malacofauna provides detailed insights into palaeoenviromental and palaeoclimatological conditions (Ložek 1964, 1990, 2001; Krolopp & Sümegi 1995; Rousseau 2001; Sümegi & Krolopp 2002; Frank 2006; Alexandrowicz 2014). The majority of Quaternary mollusc species are still living. Thus, their environmental requirements are partly well known (e.g. Welter-Schultes 2012) and can be used as constrains for the fossil assemblages. Species composition and abundance of certain taxa in each assemblage depend on climatic conditions and local ecological factors, such as vegetation cover (Sümegi & Krolopp 2002). Based on their palaeoenviromental preferences, the identified species have been classified following Ložek (1964, 1990), Krolopp & Sümegi (1995), Sümegi & Krolopp (2002) and Welter-Schultes (2012).

Freshwater species are represented only by *Galba truncatula*, which lives in both temporary and permanent aquatic environment (Chapuis et al. 2007). The absence of other freshwater species and the broad environmental tolerance of *G. truncatula* might suggest that only ephemeral ponds and puddles might have been present at Bullendorf, rather than a large perennial lake, in which other lymnaeids and planorbids might be expected. On the other hand, its occurrence is a clear indication of

Quantitative collection												
Sample name	B2	C1	B3	C3	B4	C4	B5	B6	C6	B7	C7	C8
Galba truncatula	-	-	-	53	3	-	-	-	-	-	-	-
Succinella oblonga	-	1	2	26	5	1	-	3	-	2	6	-
Pupilla loessica	12	8	-	-	-	-	-	11	-	-	-	1
Pupilla muscorum	15	12	12	7	-	1	1	29	-	-	-	-
Pupilla alpicola	12	5	1	3	1	-	-	17	1	-	-	-
Pupilla sterrii	3	3	1	-	-	-	-	2	1	-	-	-
Pupilla triplicata	2	-	-	-	1	-	-	-	-	-	-	-
Vallonia costata	1	1	-	-	-	-	-	-	-	-	-	-
Vallonia tenuilabris	3	4	2	4	-	-	-	4	-	-	-	-
Columella columella	1	2	-	8	-	-	-	-	-	-	-	-
Clausilia dubia	-	2	-	-	-	-	-	-	-	-	-	-
Milacidae	1	-	-	-	-	-	-	-	-	-	-	-
Trochulus hispidus	2	-	-	4	1	-	-	5	-	-	-	-
Helicopsis striata	-	-	5	-	-	-	-	-	1	-	-	-
Total	52	38	23	105	11	2	1	71	3	2	6	1

Tab. 3 - Quantitative distribution of continental molluscs in the samples of the Bullendorf section.

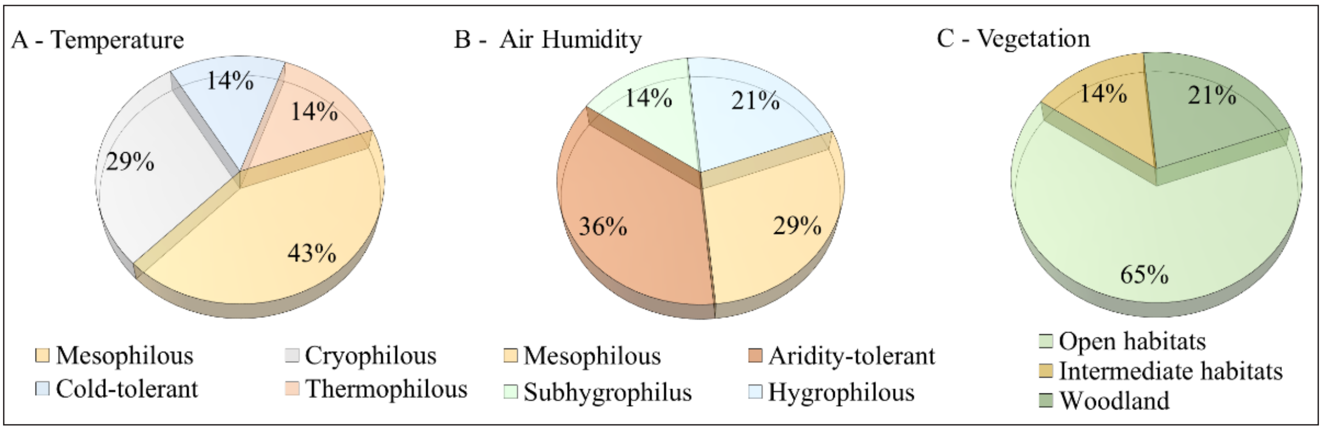


Fig. 3 - Percentage distribution of temperature (A), air humidity (B) and vegetation (C) demands of the identified species.

the presence of at least small water bodies.

Following Ložek (1964, 1990), Krolopp & Sümegi (1995), Sümegi & Krolopp (2002) and Welter-Schultes (2012), continental gastropods have been classified according to three ecological factors: temperature, air humidity and vegetation (Tab. 2):

1. Temperature: cryophilous (C), cold-tolerant (Cr), mesophilous (M) and thermophilous (T).

2. Air humidity: hygrophilous (H), subhygrophilous (Sh), mesophilous (M) and aridity-tolerant (A).

3. Vegetation: species preferring open environment (O), intermediate habitat (W/O) and woodland (W).

With respect to temperature, *mesophilous* species (43% of the identified species) and *cryophilous* species (29%) are the most abundant groups, followed by *thermophilous* (14%) and *cold-tolerant* species (14%) (Fig. 3, A). In terms of air humidity, *aridity-tolerant* and *mesophilous* species account for 65% of the species. *Hygrophilous* (21%) and *subhygrophilous* (14%) species are less abundant (Fig. 3, B). Finally, the majority of species (65%) are indicative of open habitats, ranging from dry to more humid environments; 14% live in the transitional zones between open and closed vegetation and three taxa (21%) usually dwell in woodland (Fig. 3, C).

Molluscan assemblages

The quantitative analysis has been conducted on the 12 samples representing 315 specimens attributed to 13 terrestrial species and 1 freshwater species (Tab. 3).

The Principal Component Analysis reveals a clear grouping of the samples (Fig. 4). Component 1, which accounts for 47.4% of the variability in the data set, separates samples with the aquatic *Galba truncatula* (B4, C3) and with the semiaquatic *Succinella oblonga* (B7, C7) clearly from *Pupilla*-dominated samples. Component 2 (28.1%) suggests a subgrouping of these samples which is supported by the visualisation of Component 3 (14.3%) in (Fig. 4). Samples dominated by *Pupilla muscorum* and *P. loessica* form a subcluster (B5, C4, C8), which is clearly separated from a subcluster including *Pupilla alpicola, P. sterrii* and *Helicopsis striata* (C1, B2, B3, B6, C6). In the following, we treat these clusters and subclusters as *Galba truncatula* assemblage, *Succinella oblonga* assemblage, *Pupilla muscorum/loessica* assemblage and *Pupilla alpicola/sterrii* assemblage, respectively. Although the species number in some samples is very low, which weakens our statistic treatment, the resulting assemblages correspond largely to those described by Klima et al. (1962), Ložek (1964, 1965, 1990, 2001), Puisségur (1976), Rousseau (1987, 2001), Alexandrowicz et al. (1989), Krolopp & Sümegi (1995), Frank (1997a, 1997b), Frank & Rabeder (1997), Sümegi & Krolopp (2002), Moine et al. (2005, 2008), Moine (2008), Alexandrowicz et al. (2013, 2014), Antoine et al. (2013) and Alexandrowicz (2014) from other European Pleistocene sections.

The diversity index of dominance clearly shows that the *Galba truncatula* assemblage (7 species, 116 specimens in total) and the *Pupilla alpicola/sterrii* assemblage (11 species, 187 specimens in total) have lowest dominance values representing comparatively balanced faunas compared to the

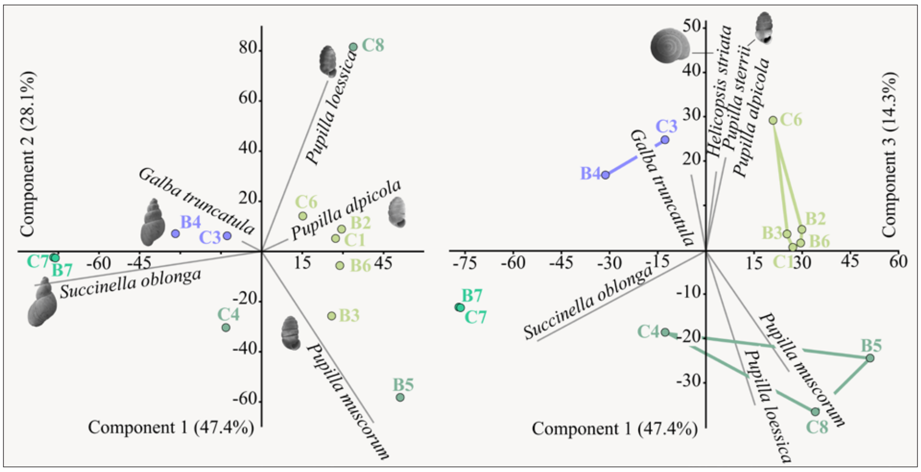


Fig. 4 - Principal component analysis of the Bullendorf molluscan fauna. The PCA is based on 12 samples with 14 species (see Table 3).

Succinella oblonga assemblage (1 species, 8 specimens in total) and *Pupilla muscorum/loessica* assemblage (2 species, 3 specimens in total). This indicates a repeated change of the palaeoenvironment with two phases of environmental amelioration (section meters 0–3 and 5–6 in Fig. 5).

The *Galba truncatula* assemblage was identified in samples B4 and C3. Apart from the nominal species, the major components are *Succinella oblonga*, *Trochulus hispidus* and *Columella columella*, with *Pupilla* species being less common. This assemblage occurs in environments characterized by moderately cold climate conditions and increased habitat humidity (Klima et al. 1962; Krolopp & Sümegi 1995; Antoine et al. 2013). Likewise, the high presence of *Galba truncatula* denotes the occurrence of small water bodies.

The *Succinella oblonga* assemblage occurs in samples B7 and C7. It is characterized by the total dominance of *Succinella oblonga*, recording rather cold and moist environmental conditions (Krolopp & Sümegi 1995; Łopuszyńska 2002; Moine 2008). A *Succinella oblonga* assemblage accompanied by *Pupilla* species indicates the occurrence of cold phases with a progressive increase of humidity (Alexandrowicz 2013). On the contrary, a *Succinella oblonga* assemblage with few *Pupilla* species and the presence of *Vallonia tenuilabris* indicates a climate-warming interval with an increase of moisture (Alexandrowicz 2014, Alexandrowicz et al. 2014). Based on the ecological demands of the nominal species, the *Succinella oblonga* assemblage documents an environment characterized by moderately cold temperature, high humidity and sparse vegetation cover (Kerney 1971).

The *Pupilla muscorum/loessica* assemblage occurs in samples B5, C4 and C8. The assemblage is extremely poor in terms of species composition and abundance, including only specimens of the nominal taxa. According to the ecological preferences of the species, this assemblage documents a period characterized by cold and relatively dry climate conditions (Ložek 1964, 1990; Krolopp & Sümegi 1995; Sümegi & Krolopp 2002). The rare occurrence of specimens might be a further hint to harsh environmental conditions.

The *Pupilla alpicola/sterrii* assemblage was detected in samples in C1, B2, B3, B6 and C6. The assemblage is marked by the predominance of *Pupilla* species: *Pupilla alpicola*, *P. sterrii*, *P. muscorum* and *P. loessica*. *Vallonia tenuilabris* often accompanies the assemblage, while other species are rare. This association typically dwelled in dry and cold steppe-like environments and, therefore, it is usually considered to represent the coldest climate periods (mean annual temperature -2°/0°C) during glacial/stadial maxima (Ložek 1964, 1990, 2001; Alexandrowicz 2014). Samples B3 and C6 include specimens of *Helicopsis striata,* a thermophilous species recording drier environment conditions as compared to pure *Pupilla* assemblage.

Overall, the assemblages identified at Bullendorf can be considered representatives of *Pupilla*-Fauna as described by Ložek (1964, 1990, 2001). This attribution is supported by the presence of *Pupilla* species (*Pupilla loessica*, *P. muscorum*, *P. alpicola*, *P. sterrii*), *Vallonia tenuilabris*, *Succinella oblonga* and *Trochulus hispidus. Helicopsis striata* records drier conditions within this assemblage, and *Columella columella*, as index loess species, has often been recorded accompanying this assemblage (Alexandrowicz et al. 1989; Alexandrowicz 2014). *Pupilla triplicata*, *Val-*

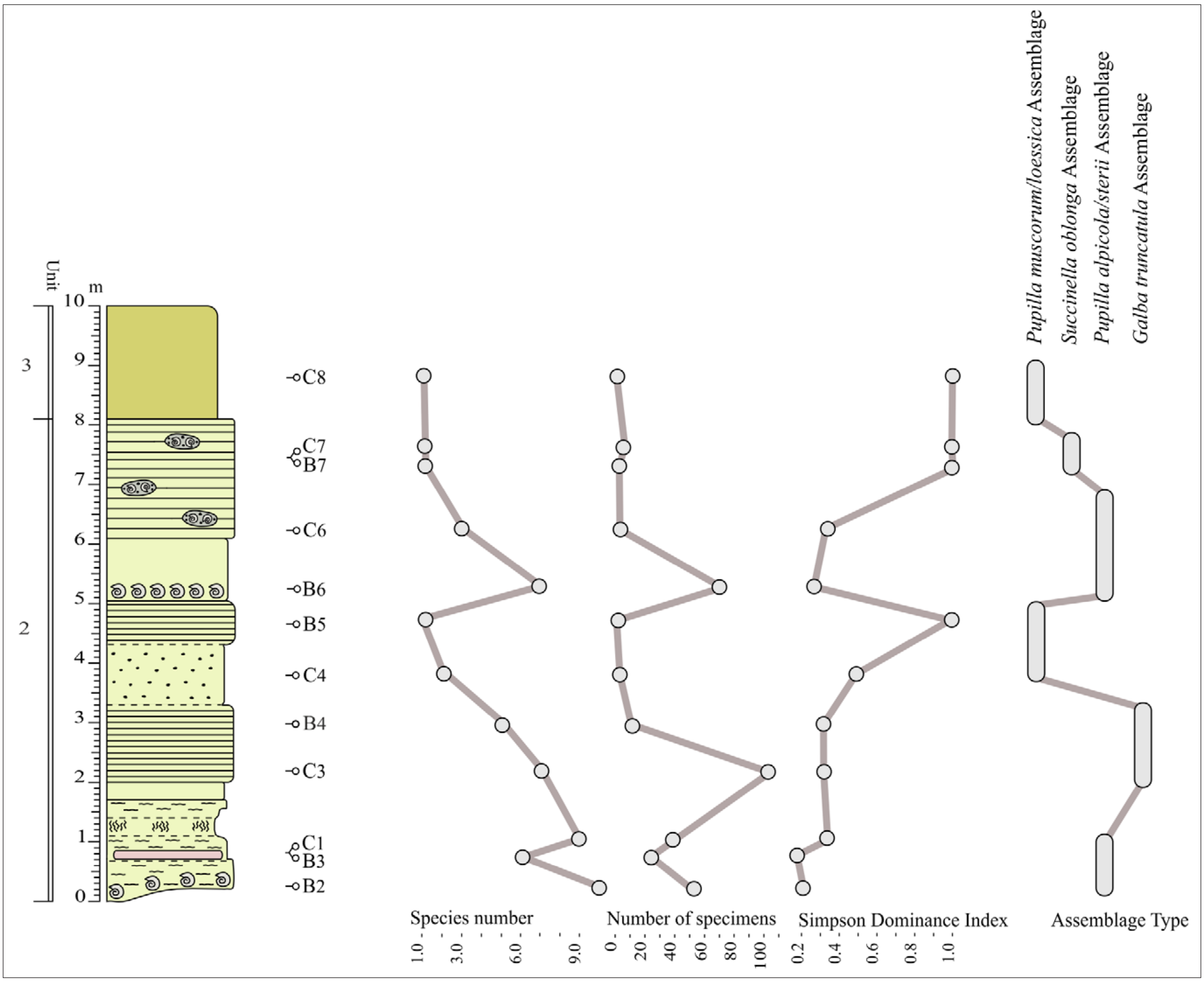


Fig. 5 - Species abundance, individual abundance, Simpson Dominance Index from Bullendorf samples and assemblages distribution throughout the section.

lonia costata, *Clausilia dubia* and *Galba truncatula* are usually abundant in loesses within certain areas or occur sporadically in low numbers throughout the loess zone (Ložek 2001).

Environmental evolution

The species composition of the assemblages reveals shifts of the palaeoenvironment with two phases of more favourable climate conditions (Fig. 5).

The first flourishing period is attested by the rich and diversified *Pupilla alpicola/sterrii* (B2, C1, B3) and *Galba truncatula* assemblages (B4 and C3). The first assemblage indicates the development of a steppe-like environment in a cool and dry climate phase. A habitat characterized by more humid climate conditions coincides with the appearance of the *Galba truncatula* assemblage. The depleted *Pupilla muscorum/loessica* assemblage (B5 and C4) documents the onset of a harsh climatic interval, which seems to have hampered the development of a diverse mollusc biocenosis. The second favourable change is recorded by the reappearance of a *Pupilla alpicola/sterrii* assemblage (C6 and B6). Afterwards, the environment changed towards harsh climate conditions again, as documented by extremely poor *Succinella oblonga* (B7 and C7) and *Pupilla muscorum/loessica* assemblages (C8).

Based on sedimentological data (R. Roetzel pers. com.), the Bullendorf section represents an alluvial plain depositional environment, which might have favoured the preservation of lacustrine/flu-

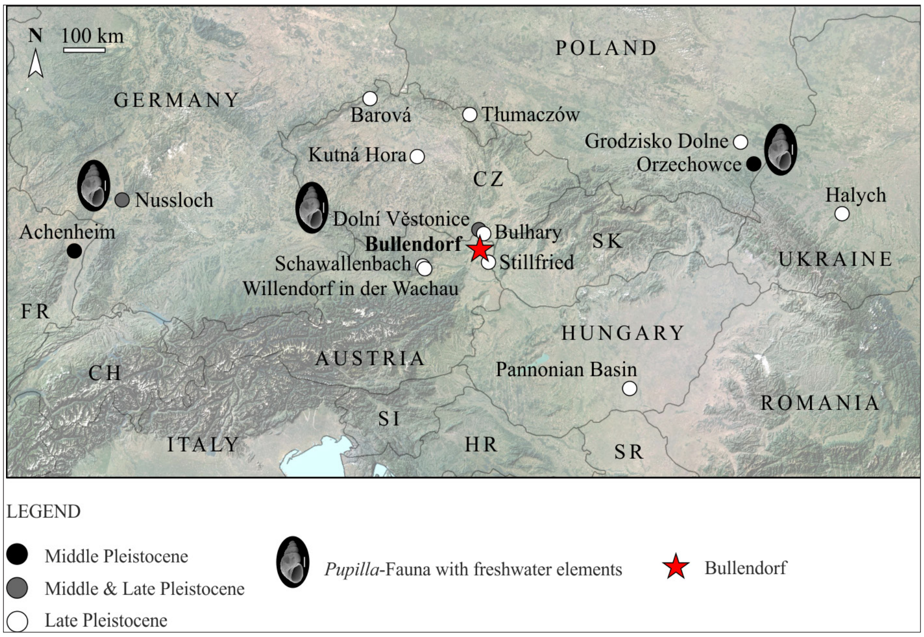


Fig. 6 - Map of European localities bearing a *Pupilla*-Fauna.

vial assemblages compared to pure open steppe/ tundra settings. Nevertheless, the species composition of the assemblages matches the *Pupilla*-Fauna composition of many other European localities (e. g. Klima et al. 1962; Ložek 1964, 1965, 1990; Alexandrowicz et al. 1989; Frank 1997a, 1997b; Frank& Rabeder 1997; Alexandrowicz et al. 2013, 2014; Antoine et al. 2013; Alexandrowicz 2014). This, as well as the occurrence of juvenile specimens of *Galba truncatula*, *Succinella oblonga*, *Pupilla* sp. and *Trochulus hispidus*, supports the hypothesis that the specimens actually lived nearby the locality. On the other hand, the gastropod assemblages from Bullendorf differ in abundance from many other European sites. The majority of the above-cited localities yielded a larger number of specimens. As no signs of aragonite dissolution can be detected on the shells, the low number of individuals seems to be a primary (not a diagenetic) feature. Thus, the reason for the rather impoverished assemblages remains unsolved. Maybe the local habitat heterogeneity in the alluvial plain environment was not ideal for the loess fauna.

Comparison with other European sites

The appearance of assemblages with a *Pupilla*-Fauna composition has been recorded by many authors from different sections in Europe (Klima et al. 1962; Ložek 1964, 1965, 1990, 2001; Puisségur 1976; Rousseau 1987, 2001; Alexandrowicz et al. 1989, Krolopp & Sümegi 1995; Frank 1997a, 1997b; Frank & Rabeder 1997; Sümegi & Krolopp 2002; Moine et al. 2005, 2008; Moine 2008; Alexandrowicz et al. 2013, 2014; Antoine et al. 2013; Alexandrowicz 2014) (Fig. 6). As Ložek (1964) and Alexandrowicz et al. (2014) documented, Early Pleistocene occurrences of the *Pupilla*-Fauna are restricted to few localities. Starting from the Middle Pleistocene, the *Pupilla*-Fauna becomes frequent in loess deposits, whose molluscan composition strongly resembles the loess assemblages of the Late Pleistocene (Ložek 1964). A typical *Pupilla*-Fauna has been found in the Saalian loess deposits of Orzechowce (SE Poland) (Alexandrowicz et al. 1989) and Dolní Věstonice (Czech Republic) (Klima et al. 1962). A rather depleted *Pupilla* assemblage was described in the Saalian loess deposits of Nussloch (Germany) (Moine et al. 2005). In France, Rousseau (1987) reports a *Pupilla*-Fauna in the Middle Pleistocene of the Achenheim sequence (Alsace). Nevertheless, the *Pupilla*-Fauna is best documented from the Late Pleistocene (Ložek 1964, 1990, 2001; Rousseau, 2001). It occurs especially in the Middle Pleniglacial (MIS 3) as well as the Upper Pleniglacial (MIS 2) and less often in the Lower Pleniglacial (MIS 4) and the Early Glacial (MIS 5a-d) (Alexandrowicz 2014). A *Pupilla*-Fauna has been detected in the Lower Pleniglacial of Bulhary (Czech Republic) (Ložek 1965), the Stillfried-Typesection (Austria) (Frank, 1997a) and the Barová Cave (Czech Republic) (Ložek 2001). *Pupilla*-like faunas appear in the Lower Pleniglacial of Schawallenbach (Austria) (Frank, 1997b) and Nussloch (Germany) (Moine et al. 2005). A

Pupilla-Fauna has been found in MIS 2-4 from both Grodzisko Dolne (S Poland) and Halych site (W Ukraine) (Alexandrowicz 2014; Alexandrowicz et al. 2014). The fauna occurs in the Upper Pleniglacial of Dolní Věstonice (Czech Republic) (Klima et al. 1962), Bulhary (Czech Republic) (Ložek 1965), Willendorf in der Wachau (Austria) (Frank & Rabeder 1997), Carpathian Basin (Hungary) (Sümegi & Krolopp 2002), Tłumaczów (SW Poland) (Alexandrowicz et al. 2013) and Kutná Hora (Czech Republic) (Ložek 2001).

Assemblages including *Pupilla* species as well as hygrophilous species (*Succinella oblonga, Trochulus hispidus*) and freshwater elements (e.g. *Galba truncatula*) have been often found in tundra gley horizons from the Lower Pleniglacial of Orzechowce (SE Poland) (Alexandrowicz et al. 1989) and Nussloch (Germany) (Moine et al., 2008) to the Upper Pleniglacial of Dolní Věstonice (Czech Republic) (Petrbok, 1951; Klima et al., 1962; Ložek, 1965; Antoine et al., 2013) and Halych site (W Ukraine) (Alexandrowicz, 2014).

Based on the high similarity with typical Upper Pleistocene assemblages from Austria, Czech Republic, Germany, Hungary and Poland, a Late Pleistocene, respectively Würmian, age is most plausible for the Bullendorf section. This age constraint is further supported by the preliminary OSL dating of the sediments indicating a time of deposition slightly younger than the LGM.

Acknowledgments: We are grateful to the ASFINAG and especially to Director Dr. Klaus Schierhackl for permission to perform field work during the road constructions and for support during the excavation. Many thanks to Reinhard Roetzel (Geological Survey, Vienna) and Ursula B. Göhlich (Natural History Museum, Vienna) for help during field work and discussions. The paper greatly benefited from the constructive comments by Thomas A. Neubauer (Justus Liebig University, Giessen) and an anonymous reviewer.

References

Adams H. & Adams A. (1853-1858) - The genera of Recent Mollusca arranged according to their organization. Van Voorst, London, 661 pp.

Alexandrowicz S.W., Butrym J. & Maruszczak H. (1989) - The malacofauna of the Younger and Older loess of the Przemyœl region, SE Poland. *Folia Malacologica*, 3: 7-21. http://dx.doi.org/10.12657/folmal.003.001

Alexandrowicz W. P. (2014) - Malacological sequence of Weichselian (MIS 5-2) loess series from a profile in Grodzisko Dolne (southern Poland) and its palaeogeographic significance. *Quat. Int.*, 319: 109-118. https://doi.org/10.1016/j.quaint.2013.08.048

Alexandrowicz W. P., Ciszek D. & Gołas-Siarzewska M. (2013) - Malacological characteristic of the Weichselian Upper Pleniglacial (MIS-2) loess profile in Tłumaczów (SW Poland). *Geol. Quart.*, 57: 433-442. https://doi.org/10.7306/gq.1104

Alexandrowicz W. P., Łanczont M., Boguckyj A. B., Kulesza, P. & Dmytruk R. (2014) - Molluscs and ostracods of the Pleistocene loess deposits in the Halych site (Western Ukraine) and their significance for palaeoenvironmental reconstructions. *Quat. Sci. Rev.*, 105: 162-180. https://doi.org/10.1016/j.quascirev.2014.10.008

Antoine P., Rousseau D. D., Degeai J.-P., Moine O., Lagroix F., Kreutzer S., Fuchs M., Hatté C., Gauthier C., Svoboda J. & Lisá L. (2013) - High-resolution record of the environmental response to climatic variations during the Last Interglacial-Glacial cycle in Central Europe: The loess-palaeosol sequence of Dolní Věstonice (Czech Republic). *Quat. Sci. Rev.*, 67: 17-38. https://doi.org/10.1016/j.quascirev.2013.01.014

Banak A., Mandic O., Kovacic M. & Pavelic D. (2012) - Late Pleistocene climate history of the Baranja loess plateau – evidence from the Zmajevac loess-paleosol section (northearn Croatia). *Geologia Croatica*, 65: 411-422.

Beck H. (1837−1838) - Index molluscorum praesentis aevi musei principis augustissimi Christiani Frederici. Hafniae, Copenhagen, 124 pp.

Bouchet P., Rocroi J.P., Hausdorf B., Kaim A., Kano Y., Nützel A., Parkhaev P., Schrödl M. & Strong E.E. (2017) - Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia*, 61: 1-526.

Braun A. (1843) - Vergleichende Zusammenstellung der lebenden und diluvialen Molluskenfauna des Rheinthals mit der tertiären des Mainzer Beckens. *Amtlicher Bericht über die zwanzigste Versammlung der Gesellschaft Deutscher Naturforscher und Aerzte zu Mainz im September 1842*: 142-150.

Brocchi G. B. (1814) - Conchiologia fossile subapennina con osservazioni geologiche sugli Apennini e sul suolo adiacente. Stamperia Reale, Milano, 712 pp.

Brusina S. (1892) - Fauna fossile terziaria di Markusevec in Croazia. Con un elenco delle Dreissensidae della Dalmazia, Croazia e Slavonia. *Glasnik Hrvatskoga naravoslovnoga društva*, 7: 113-210.

Burmeister H. (1837) - Handbuch der Naturgeschichte: zum Gebrauch bei Vorlesungen. Enslin, Berlin, 858 pp.

Chapuis E., Trouve S., Facon B., Degen L. & Goudet J. (2007) - High quantitative and no molecular differentiation of a freshwater snail (*Galba truncatula*) between temporary and permanent water habitats. *Mol. Ecol.*, 16: 3484-3496. https://doi.org/10.1111/j.1365-294X.2007.03386.x

Charpentier J. De. (1837) - Catalogue des mollusques terrestres et fluviatiles de la Suisse. Formant la seconde partie de la faune Helvétique. *Nouv. Mém. Soc. Helv. Sci. Nat.*, 1: 1-28.

Chemnitz J. H. (1786) - Neues systematisches Conchylien-Cabinet. Neunten Bandes zwote Abtheilung, enthaltend die ausführliche Beschreibung von den Land- und Fluß-schnecken, oder von solchen Conchylien, welche nicht im Meere, sondern auf der Erde und in süssen Wassern zu leben pflegen. Mit zwanzig nach der Natur gemalten und durch lebendige Farben erleuchteten Kupfertafeln. Raspe, Nürnberg, 194 pp.

Clessin S. (1871) - Die Mollusken-Fauna der Umgegend von Augsburg. *Bericht des Naturhistorischen Vereins in Augsburg*, 2: 81-126.

Cuvier G. (1795) - Second Mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an troisième. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts*, 2: 433-449.

Draparnaud J. P. R. (1801) - Tableau des mollusques terrestres et fluviatiles de la France. Montpellier, Paris, 116 pp.

Draparnaud J. P. R. (1805) - Histoire naturelle des mollusques terrestres et fluviatiles de la France. Ouvrage posthume. Montpellier, Paris, 134 pp.

Duda M., Kruckenhauser L., Sattmann H., Harl J., Jaksch K. & Haring E. (2014) - Differentiation in the *Trochulus hispidus* complex and related taxa (Pulmonata: Hygromiidae): morphology, ecology and their relation to phylogeography. *J. Molluscan Studies*, 80: 371-387. https://doi.org/10.1093/mollus/eyu023

Ellis A. E. (1926) -. British snails, a guide to the non-marine Gastropoda of Great Britain and Ireland, Pliocene to Recent. Clarendon Press, Oxford, 275 pp.

Eschner, A., Bieringer G., Duda M., Gobets G., Jaksch K. & Mrkvicka A. (2014) - Small steppe land species - big questions: First attempts to clarify the situation of *Helicopsis striata* and ssp. in Eastern Austria. In: Helmut Sattmann & Elisabeth Haring (Eds) - Report on the workshop alpine land snails 2014: 6. Verlag des Naturhistorishes Museums Wien, Vienna.

Esu D. & Girotti O. (1991) - Late Pliocene and Pleistocene assemblages of continenal molluscs in Italya. A survey. *Il Quaternario*, 4: 137-150.

Férussac A.E.J.P.J.F. d'Audebard de (1821-1822) - Tableaux systématiques des animaux mollusques classés en familles naturelles, dans lesquels on a établi la concordance de tous les systèmes; suivis d'un prodrome général pour tous les mollusques terrestres ou fluviatiles, vivants ou fossiles. A. Bertrand, Paris, 208 pp.

Férussac A.E.J.P.J.F. d'Audebard de. (1823) - Monographie des espèces vivantes et fossiles du genre mélanopside, Melanopsis, et observations géologiques à leur sujet. *Mémoires de la Société d'Histoire Naturelle de Paris*, 2: 132-164.

Fischer P. (1856) - Melanges de conchyliologie. *Actes de la Sociètè Linnèene de Bordeaux*, 20: 357-400.

Fitzinger L.I. (1833) - Systematisches Verzeichniß der im Erzherzogthume Oesterreich vorkommenden Weichthiere, als Prodrom einer Fauna derselben. *Beiträge zur Landeskunde Oesterreich's unter der Enns*, 3: 88-122.

Fleming J. (1828) - A history of British animals, exhibiting the descriptive characters and systematic arrangement of the genera and species of quadrupeds, birds, reptiles, fishes, Mollusca, and Radiata of the United Kingdom; including the indigenous, extirpated, and extinct kinds, together with periodical and occasional visitants. Bell & Bradfute, Edinburgh, 565 pp.

Forster F. (1840) - Animalia mollusca. Mit Anmerkungen von I. v. Voith. In: Fürnrohr A. E. (Eds) - Naturhistorische Topographie von Regensburg. In Verbindung mit Forster, Herrich-Schäffer, Koch, v. Schmöger und v. Voith. Dritter Band, die Fauna von Regensburg enthaltend: 459-478. Regensburg, Manz.

Frank C. (1997a) - Stillfried-Typusprofile. In: Döppes D. & Rabeder, G. (Eds) - Pliozäne und pleistozäne Faunen Österreichs: 123-130. Verlag der Österreichischen Akademie der Wissenschaften, Wien.

Frank C. (1997b) - Schawallenbach. In: Döppes D. & Rabeder, G. (Eds): Pliozäne und pleistozäne Faunen Österreichs: 48-53. Verlag der Österreichischen Akademie der Wissenschaften, Wien.

Frank C. (2006) - Plio-pleistozäne und holozäne Molluscen Österreichs. Verlag der Österreichischen Akademie der Wissenschaften, Wien, 860 pp.

Frank C. & Rabeder G. (1997) - Willendorf in der Wachau. In: Döppes D. & Rabeder, G. (Eds) - Pliozäne und pleistozäne Faunen Österreichs: 68-74. Verlag der Österreichischen Akademie der Wissenschaften, Wien.

Georgopoulou E., Neubauer T.A., Harzhauser M., Kroh A. & Mandic O. (2016a) - Distribution patterns of European lacustrine gastropods – a result of environmental factors and deglaciation history. *Hydrobiologia*, 775: 69-82. https://doi.org/10.1007/s10750-016-2713-y

Georgopoulou E., Neubauer T.A., Strona G., Kroh A., Mandic O. & Harzhauser M. (2016b) - Beginning of a new age: How did freshwater gastropods respond to the Quaternary climate change in Europe? *Quat. Sci. Rev.*, 149: 269-278. https://doi.org/10.1016/j.quascirev.2016.07.034

Gerber J. (1996) - Revision der Gattung *Vallonia* Risso 1826 (Mollusca: Gastropoda: Valloniidae). *Schriften Malakozool.*, 8: 1-257.

Gray J. E. (1855) - Catalogue of Pulmonata or air-breathing Mollusca in the collection of the British Museum. Part 1. Taylor & Francis, London, 192 pp.

Gredler V. (1856) - Tirol's Land- und Süsswasser-Conchylien. I. Die Landconchylien. *Verhandlungen des Zoologisch-Botanischen Vereins in Wien (Abhandlungen)*, 6: 25-162.

Hammer Ø., Harper D.A.T. & Ryan P.D. (2001) - PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, 4: 1-9.

Hartmann J. D. W. (1844) - Erd- und Süsswasser-Gasteropoden der Schweiz. Mit Zugabe einiger merkwürdigen exotischen Arten. I. Band. Scheitlin & Zollikofer, St. Gallen, 227 pp.

Harzhauser M. & Binder H. (2004) - Pannonian Molluscs from the sections Richardhof and Eichkogel in the Vienna Basin (Austria, Late Miocene). *Archiv Molluskenkunde*, 133: 109-165.

Harzhauser M., Daxner-Höck G., Göhlich U. & Nagel D. (2011) - Complex faunal mixing in the early Pannonian paleo-Danube Delta (Late Miocene, Lower Austria). *An-*

nalen Naturhist. Mus. Wien, 113: 167-208.

Haszprunar G. & Huber G. (1990) - On the central nervous system of Smeagolidae and Rhodopidae, two families questionably allied with the Gymnomorpha (Gastropoda: Euthyneura). *J. Zool.* 220: 185-199.

Horsák M., Škodová J., Myšák J., Čejka T., Ložek V. & Hlaváč J. Č. (2010) - *Pupilla pratensis* (Gastropoda: Pupillidae) in the Czech Republic and Slovakia and its distinction from *P. muscorum* and *P. alpicola* based on multidimensional analysis of shell measurements. *Biologia*, 65: 1012-1018.

Horsák M., Škodová J. & Cernohorsky N. H. (2011) - Ecological and historical determinants of Western Carpathian populations of *Pupilla alpicola* (Charpentier, 1837) in relation to its present range and conservation. *J. Molluscan Studies,* 77: 248-254. https://doi.org/10.1093/mollus/eyr010

Horsák M., Chytrý M., Hájková P., Hájek M., Danihelka J., Horsáková V., Ermakov N., German D. A., Kočí M., Lustyk P., Nekola J. C., Preislerová Z. & Valachovič M. (2015) - European glacial relict snails and plants: environmental context of their modern refugial occurrence in southern Siberia. *Boreas*, 44: 638-657. https://doi.org/10.1111/bor.12133

Kendall S. B. (1965) - Relationships between the species of *Fasciola* and their molluscan hosts. *Adv. Parasitol.*, 3: 59-98.

Kerney M.P. (1971) - A Middle Weichselian deposit at Halling, Kent. *Proceedings of the Geologists' Association*, 82: 1-11. https://doi.org/10.1016/S0016-7878(71)80027-5

Kerney M.P., Cameron R.A. & Jungbluth J.H. (1983) - The Land Snails of North and Middle Europe. Paarey Verlag, Hamburg, 384 pp.

Klima B., Kukla J., Ložek V. & De Vries H. (1962) - Stratigraphie des Pleistozäns und Alter des paläolithischen Rastplatzes in der Ziegelei von Dolní Věstonice (Unter-Wisternitz). *Anthropozoikum*, 11: 93-145.

Krolopp E. & Sümegi P. (1995) - Palaeoecological reconstruction of the late Pleistocene, based on loess malacofauna in Hungary. *GeoJournal,* 36: 213-222. https://doi.org/10.1007/BF00813173

Lencioni V. & Maiolini B. (2006) - Invertebrates: zoobenthos. High-altitude lakes. Italian habitats. Italian Ministry of the Environment and Territory Protection, Friuli Museum of Natural History: 83-99.

Lindholm W. A. (1927) - Zur Systematik und Nomenklatur einiger Heliciden und ihrer Verwandten. *Archiv Molluskenkunde*, 59: 116-138.

Linnaeus C. (1758) - Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus 1. 10th edition. Laurentius Salvius, Holmiae, 824 pp.

Łopuszyńska M. (2002) - Differentiation of subfossil populations of snails from vistulian loesses of southern Poland. *Folia Quaternaria*, 73: 101-189.

Ložek V. (1954) - Neue Mollusken aus dem Tschechoslovakischen Pleistozän: *Vertigo pseudosubstriata* sp. a., *Pupilla muscorum densegyrata* ssp. n. und *Pupilla loessica* sp. n. *Anthropozoikum*, 3: 327-343.

Ložek V. (1964) - Quartärmollusken der Tschechoslovakei. Rozpravy Ústredního ústuvu geologického, Praha, 374 pp.

Ložek V. (1965) - Das Problem der Lössbildung und die Lössmollusken. *Eiszeit und Gegenwart*, 16: 61-75.

Ložek V. (1990) - Molluscs in loess, their paleoecological significance and role in geochronology e principles and methods. *Quat. Int.*, 7: 71-79.

Ložek V. (2001) - Molluscan fauna from the loess series of Bohemia and Moravia. *Quat. Int.*, 76-77: 141-156. https://doi.org/10.1016/S1040-6182(00)00098-7

Martens G. Von (1830) - Natur- und Vaterlandskunde. Ueber Würtembergs Fauna. *Correspondenzblatt des Würtembergischen Landwirthschaftlichen Vereins*, 17: 123-186.

Meng S. & Hoffmann M. H. (2009) - *Pupilla loessica* LOŽEK 1954 (Gastropoda: Pulmonata: Pupillidae) – "A Living Fossil" in Central Asia? *Quat. Sci. J.*, 58 (1): 55-69. http://doi.org/10.3285/eg.58.1.03

Moine O. (2008) - West-European malacofauna from loess deposits of the Weichselian Upper Pleniglacial: Compilation and preliminary analysis of the database. *Quaternaire*, 19: 11-29. https://doi.org/10.4000/quaternaire.1532

Moine O. (2014) - Weichselian Upper Pleniglacial environmental variability in North-Western Europe reconstructed from terrestrial mollusc faunas and its relationship with the presence/absence of human settlements. *Quat. Int.*, 337: 90-113. https://doi.org/10.1016/j.quaint.2014.02.030

Moine O., Rousseau D. D. & Antoine P. (2005) - Terrestrial molluscan records of Weichselian Lower to Middle Pleniglacial climatic changes from the Nussloch loess series (Rhine Valley, Germany): The impact of local factors. *Boreas*, 34: 363-380.

Moine O. Rousseau D. D. & Antoine P. (2008) - The impact of Dansgaard-Oeschger cycles on the loessic environment and malacofauna of Nussloch (Germany) during the Upper Weichselian. *Quat. Res.*, 70: 91-104. https://doi.org/10.1016/j.yqres.2008.02.010

Molluscabase (2016) - http://www.molluscabase.org/ [accessed 30 Jun. 2016]

Morse E.S. (1864) - Observations on the terrestrial Pulmonifera of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabitat the state. *Journal of the Portland Society to Natural History*, 1: 11-63

Müller O. F. (1774) - Vermivm terrestrium et fluviatilium, seu animalium infusoriorum, helminthicorum, et testaceorum, non marinorum, succincta historia. Volumen alterum. Heineck & Faber, Copenhagen & Leipzig, 214 pp.

Nekola J.C., Coles B.F. & Horsák M. (2015) - Species assignment in *Pupilla* (Gastropoda: Pulmonata: Pupillidae): integration of DNA-sequence data and conchology. *J. Molluscan Studies*, 81: 196-216. https://doi:10.1093/mollus/eyu083

Nordsieck H. (1987) - Revision des Systems der Helicoidea (Gastropoda: Stylommatophora). *Archiv Molluskenkunde*, 118: 9-50. https://doi.org/10.5962/bhl.title.141070

Papp A. (1953) - Die Molluskenfauna des Pannon des Wiener Beckens. *Mitt. geol. Gesell. Wien*, 44: 85-222.

Papp A. (1985) - Gastropoda (Neritidae, Viviparidae, Valvatidae, Hydrobiidae, Stenothyridae, Truncatellidae, Bulimidae, Micromelaniidae, Thiaridae) und Bivalvia (Dreissenidae. Limnocardiidae, Unionidae) des Pannonien. In: Papp, A., Jámbor, Á., Steininger, F. (Eds) - M6 Pannonien (Slavonien und Serbien): 276-339. Akadémiai Kiadó, Budpest.

Potiez V.L.V. & Michaud A.L.G. (1838) - Galerie des mollusques, ou catalogue méthodique, descriptif et raisonné des mollusques et coquilles du Muséum de Douai. Tome premier. Baillière, Paris, 560 pp.

Prockow M. (2009) - The genus *Trochulus* Chemnitz, 1786 (Gastropoda: Pulmonata: Hygromiidae) - a taxonomic revision. *Folia Malacologica*, 17: 101-176.

Puisségur J.J. (1976) - Mollusques continentaux quaternaries de Bourgogne. Significations stratigraphiques et climatiques. Rapports avec d'autres faunes boréales de France. Mémoires Géologiques de l'Université de Dijon 3, Paris, 241 pp.

Rafinesque C. S. (1815) - Analyse de la nature ou tableau de l'univers et des corps organisés. Aux dépens de l'auteur, Palerme, 244 pp.

Reuse C. (1983) - On the taxonomic significance of the internal shell in the identification of European slugs of the families Limacidae and Milacidae (Gastropoda, Pulmonata). *Biologisch Jaarboek Dodonaea*, 41: 180-200.

Risso A. (1826) - Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes. Tome quatrième. Levrault, Paris, 439 pp.

Rousseau D.D. (1987) - Paleoclimatology of the Achenheim series (Middle and Upper Pleistocene, Alsace, France). A malacological analysis. *Palaeogeogr., Palaeoclimatol., Palaeoecol.,* 59: 293-314.

Rousseau D.D. (2001) - Loess biostratigraphy: New advances and approaches in mollusk studies. *Earth-Sci. Rev.*, 54: 157-171. https://doi.org/10.1016/S0012-8252(01)00046-0

Sandberger C.L.F. (1875) - Die Land- und Süßwasser-Conchylien der Vorwelt. C. W. Kreidel, Wiesbaden, 675 pp.

Schmidt A. (1855) - Der Geschlechtsapparat der Stylommatophoren in taxonomischer Hinsicht gewürdigt. *Abhandlungen des Naturwissenschaftlichen Vereins für Sachsen und Thüringen in Halle*, 1: 1-52.

Schnabel W. (2002) - Geologische Karte von Niederösterreich 1:200.000. Legende und kurze Erläuterung, Vienna.

Schrank F. V. P. (1803) - Fauna boica: Durchgedachte Geschichte dere in Baiern einheimischen und zahmen Thiere. Krüll, Landshut, 272 pp.

Soós L. & Wagner H. (1935) - Faunánk egy új Helicella-fajáról. Állattani Közlemények, 32: 127-131.

Studer S. (1820) - Kurzes Verzeichniss der bis jetzt in unserm Vaterlande entdeckten Conchylien. *Naturwissenschaftlicher Anzeiger der Allgemeinen Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften,* 3: 83-90, 91-94.

Sümegi P. & Krolopp E. (2002) - Quatermalacological analysis for modeling of the Upper Weichselian palaeoenvironmental changes in the Carpathian Basin. *Quat. Int.*, 9: 53-63. https://doi.org/10.1016/S1040-6182(01)00102-1

Tryon G.W. (1866) - Monograph of the terrestrial Mollusca of the United States. *Am. J. Conchology*, 2: 306-327.

Turner H., Kuiper J. G. J., Thew N., Bernasconi R., Ruetschi J., Wuthrich M. & Gosteli, M. (1998) - Fauna Helvetica 2. Atlas der Mollusken der Schweiz und Liechtensteins. Centre suisse de cartographie de la faune, Schweizerische Entomologische Gesellschaft, Eidg. Forschungstalt für Wald, Schnee und Landschaft, Neuchatel, 527 pp.

Turton W. (1831) - A manual of the land and freshwater shells of the British Islands arranged according to the more modern systems of classification; and described from perfect specimens in the author's cabinet: with coloured plates of every species. Longman, Orme, Brown, Green & Longmans, London, 152 pp.

Von Proschwitz T., Schander C., Jueg U. & Thorkildsen S. (2009) - Morphology, ecology and DNA-barcoding distinguish *Pupilla pratensis* (Clessin, 1871) from *Pupilla muscorum* (Linnaeus, 1758) (Pulmonata: Pupillidae). *J. Molluscan Studies*, 75: 315-322.

Welter-Schultes F.W. (2012) - European non-marine molluscs, a guide for species identification. Planet Poster, Göttingen, 674 pp.

Wenz W. (1923–1930) - Fossilium Catalogus I: Animalia. Gastropoda extramarina tertiaria. W. Junk, Berlin, 17/1, 1–352 (1923), 18/2, 353–736 (1923), 20/3, 737–1068 (1923), 21/4, 1069–1420 (1923), 22/5, 1421–1734 (1923), 23/6, 1735–1862 (1923), 32/7, 1863 2230 (1926), 38/8, 2231–2502 (1928), 40/9, 2503–2886 (1929), 43/10, 2887–3014 (1929), 46/11, 3015–3387 (1930) pp.

Westerlund C. A. (1878) - Monografi öfver paläoarktiska regionens Clausilier. Lund, Berling, 184 pp.

Wiktor A. (1987) - Milacidae (Gastropoda, Pulmonata) - systematic monograph. *Annales Zoologici*, 41: 153-319.

Wiktor A. & Likharev I.M. (1979) - Phylogenetische Probleme bei Nacktschnecken aus den Familien Limacidae und Milacidae (Gastropoda, Pulmonata). *Malacologia*, 18: 123-132.