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On the present habitats and ecology of *Vertigo pseudosubstriata* Ložek, 1954 (Mollusca, Gastropoda, Vertiginidea) in Central Asia and its distribution history in Central and Eastern Europe

STEFAN MENG,[1]* PAVLO VASYLIEV,[2] IVAN KHOPTYNETS,[3] VITALII TKACH[4] and ANDREAS MAIER[5]
[1]Institute of Geography and Geology, University of Greifswald, Greifswald, Germany
[2]Institute of Archaeology, the National Academy of Sciences of Ukraine, Kyiv, Ukraine
[3]Department of Archaeology and Monumentology, State Scientific Center for Protection of Cultural Heritage from Industrial Disasters, Kyiv, Ukraine
[4]Dubno, Ukraine
[5]Institute for Prehistoric Archaeology, University of Cologne, Cologne, Germany

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ABSTRACT: The small terrestrial gastropod *Vertigo pseudosubstriata* Ložek, 1954 is one of the rarest glacial indicator species in the Pleistocene of Central and Eastern Europe. In all, this species has been found at only about 15 sites in Europe. *V. pseudosubstriata* was initially described as a fossil in Central Europe and was discovered only later alive in Central Asia. With regard to its modern distribution, 25 habitats with *V. pseudosubstriata* have been examined in Tien Shan and in the central and southern Altai. These findings seem to capture the contemporary distribution of the species and provide information on the boundaries of its ecological requirements. These data are of great significance for the interpretation of the fossil assemblages. Since the few fossil specimens in Europe date from very different glacial periods in the Elsterian, Saalian Complex and Weichselian, it can be concluded that *V. pseudosubstriata* apparently immigrated in at least three distinct waves. Most of the Pleistocene specimens in eastern Central Europe and Eastern Europe are reported from archaeological sites of the Upper Middle Weichselian (Gravettian), roughly between 33 and 29 ka cal BP. In this paper, we review all reported modern and fossil occurrences and discuss the species' ecological range.

KEYWORDS: Central Asia; climate conditions; Gravettian; Pleistocene Europe; *Vertigo pseudosubstriata*

Introduction

The snail *Vertigo pseudosubstriata* Ložek, 1954 was first detected as a fossil in the Weichselian loess at the archaeological site of Dolní Věstonice in Moravia, Czechia (Ložek, 1954). Following its first description, shells of this species were also detected at other findspots in Central and Eastern Europe (Ložek, 1954, 1964), before it was discovered alive in Central Asia (Schileyko, 1984; Meng, 2009; Horsák *et al.*, 2010, 2015).

Being one of the most famous glacial indicator species of Central and Eastern Europe, *V. pseudosubstriata* is also one of the rarest. To date – and in spite of thousands of published mollusc faunas in Europe (summaries in e.g. Ložek, 1964; Mania, 1973; Alexandrowicz, 1987; Fűköh *et al.*, 1995; Frank, 2006; Hošek *et al.*, 2017) – fossil occurrences have been reported from about 15 sites only, including the latest and north-easternmost discovery at the archaeological site of Myrohoshcha I in north-eastern Ukraine (Fig. 1). In addition to its scarcity, the density of *V. pseudosubstriata* specimens in the analysed samples was usually very low. Unsurprisingly, information about its glacial distribution, palaeo-ecology, or stratigraphic range is very limited and a comprehensive compilation is missing.

*Correspondence: S. Meng, as above.
E-mail: stefan.meng@uni-greifswald.de

The interpretation of fossil terrestrial gastropod fauna is an important tool for palaeo-ecological reconstructions in the Quaternary, since molluscs can provide information about important parameters both for the climate and landscape history of a site. Well-known examples are, for instance, *Vallonia tenuilabris* (A. Braun, 1843), *Vertigo parcedentata* Braun, 1847 or *Pupilla loessica* Ložek, 1954, which have discovery histories similar to *V. pseudosubstriata* and today are likewise found in habitats in Central Asia (Gerber, 1996; Meng 2008, 2009; Meng and Hoffmann, 2009; Horsák *et al.*, 2010, 2015; Haase *et al.*, 2021). *V. parcedentata* was also discovered alive in Norway (Pokryszko, 1993). These findings lead to the conclusion that ecosystems similar to those of glacial Europe are today rather to be found in the continental regions of Central Asia than in the arctic or subarctic biomes of Europe or northern Eurasia (Ložek, 1999); an opinion also held for other species (Chytrý *et al.*, 2019).

Using fossil molluscs to reconstruct environmental conditions during the Quaternary requires knowledge about the species' ecological preferences. In this regard, observations from current habitat preferences of *V. pseudosubstriata* become an important source of information. Between 1995 and 2014, one of us (SM) was able to identify this species in 25 modern mollusc assemblages from Tien Shan (Kyrgyzstan) and the central and southern Altai (Fig. 2).

The first indications of modern occurrences of *V. pseudosubstriata* in Central Asia were provided by P.-V.

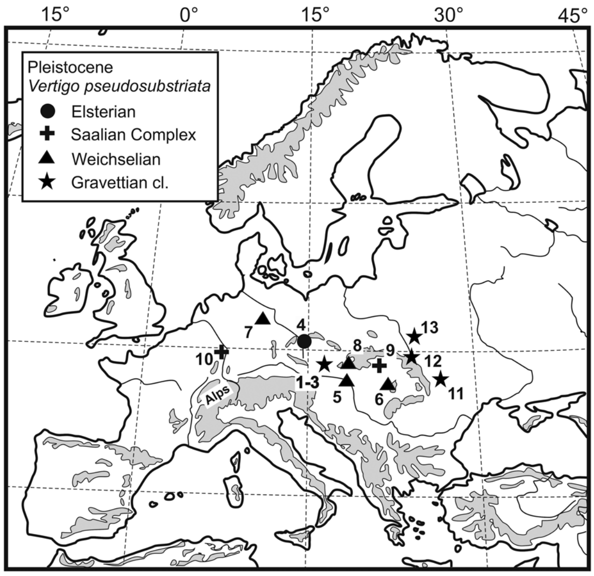

Figure 1. Map with Pleistocene locations of *Vertigo pseudosubstriata* in Europe. **1** Type locality Dolni Věstonice, Moravia, Czechia (Ložek, 1954, 2001), **2** Milovice near Dolni Věstonice, Moravia, Czechia (Kovanda, 2009), **3** Pavlov near Dolni Věstonice, Moravia, Czechia (Ložek, 1967), **4** Horky nad Jizerou, on the Isar river, Bohemia, Czechia (Ložek, 1956), **5** Buda hills (Budai-hegység), near Budapest, Hungary (Krolopp, 1958), **6** Nyírábrány, eastern Hungary (Krolopp and Sümegi, 1992b), **7** Erfurt-Riethnordhausen, Thuringia, Germany (Meng, 1995), **8** Bíňa, Danube lowland, south-western Slovakia (Hošek *et al.*, 2017), **9** Brehov, south of Trebišov, eastern Slovakia (Schmidt *et al.*, 1978), **10** Mainz-Weisenau, Rheinland-Pfalz, Germany (Bibus *et al.*, 1996), **11** Molodova V, Dnjestr valley, Chernõvtsy province, western Ukraine (Ložek, 1976), **12** Halych I, Dnjestr valley, south-east Lviv, western Ukraine (Alexandrowicz *et al.*, 2014), **13** Myrohoshcha I, south-west Rivne, Ukraine (Maier *et al.*, 2020a).

Matiokin (in Ložek, 1964; Matiokin, 1966; according to Schileyko, 1984) from Tien Shan, where it was found in high mountain meadows at up to 3500 m a.s.l. Uvalieva (1967) discovered this species later in the southern Altai (northern Kazakhstan) and described it initially as *V. laevis* (synonym for *V. pseudosubstriata*) (compare also Schileyko, 1984; Uvalieva 1990). According to currently available data, the distribution of *V. pseudosubstriata* extends to Tien Shan (Kyrgyzstan, southern Kazakhstan, western China) and to the central and southern Altai (southern Russia, northern Kazakhstan) (Schileyko, 1984; Schileyko and Rymzhanov, 2013; Uvalieva, 1990; Egorov, 2008; Sysoev and Schileyko, 2009; Meng, 2008; Horsák *et al.*, 2010, 2015; Nekola *et al.*, 2018).

To date, there is no information about *V. pseudosubstriata* from the Pamir-Altai mountain system (see also Uvalieva, 1990); an expedition to the neighbouring Hissar range by one of us (SM) in 2015 likewise brought no evidence of this species. In addition, the Himalayan region (Pakistan, northern India, Nepal) remains problematic. In the case of Pakistan, Pokryszko *et al.* (2009) mentioned only one specimen of *V. pseudosubstriata* among thousands of *Vertigo* shells. This information requires further confirmation. The extensive material of U. Bößneck (publication in preparation), from seven expeditions in the Nepalese Himalayas (1997–2017) also contains no *V. pseudosubstriata*. The evidence reported from Sakhalin Island in East Asia (Prozorova and Berezhok, 2004) must also be considered questionable, since no figures or further description of these findings exist and confusion is likely.

The shells of *V. pseudosubstriata* are about 2.1–2.2 mm high and 1.2 mm wide, dextral, subovate with about five convex whorls, of brownish colour and their surface is relatively smooth. The aperture is semi-elliptical. The outer edge is slightly indented at about two thirds of its height. The crest is only very weakly indicated or missing. There are five lamellar denticles (one parietal, one angular, one columellar and two palatal) which are deeply embedded in the aperture. Besides the strong parietal denticle, an angular denticle is also developed, which is only half as high and lies a bit further forward. The columellar denticle and the parietal denticle are also strong. The lower palatal denticle is a little deeper in the aperture than the upper one (Ložek, 1954, 1964; Schileyko, 1984). Overall, the shells of *V. pseudosubstriata* are dimensionally very stable (Fig. 3).

In this paper, we present a comprehensive compilation of all currently known occurrences, fossil and modern, of *V. pseudosubstriata* to assess its past and current extent and use data from weather stations in the vicinity of the modern findspots to infer its ecological range. Based on these inferences, we discuss possible reasons for the conspicuous

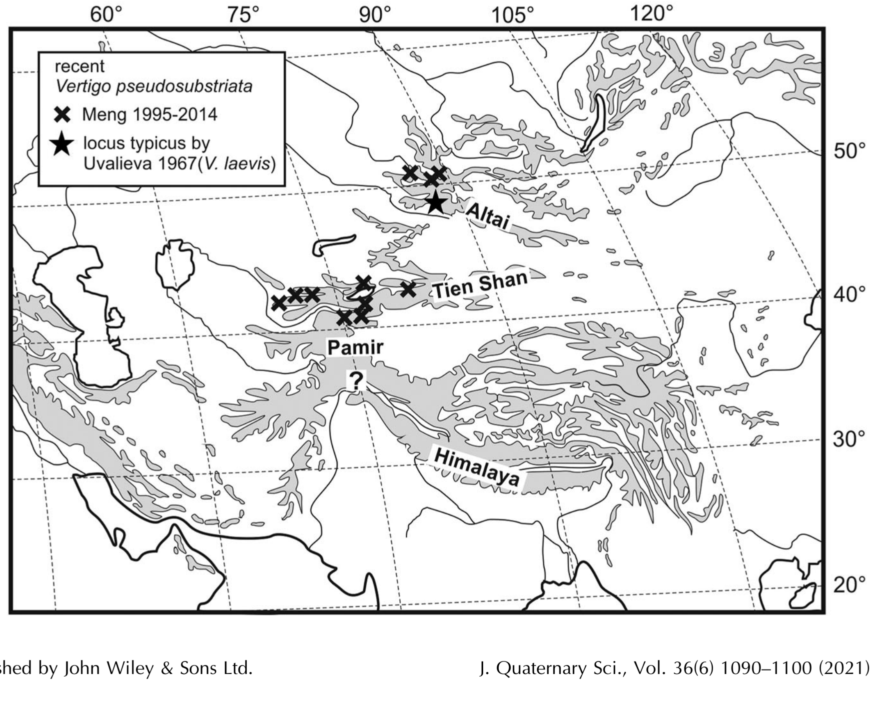

Figure 2. Map with recent locations of *Vertigo pseudosubstriata* in Central Asia (Supplement 1), collections of Meng (1995–2014) and type locality of the synonym *Vertigo laevis* in the southern Altai (Uvalieva, 1967).

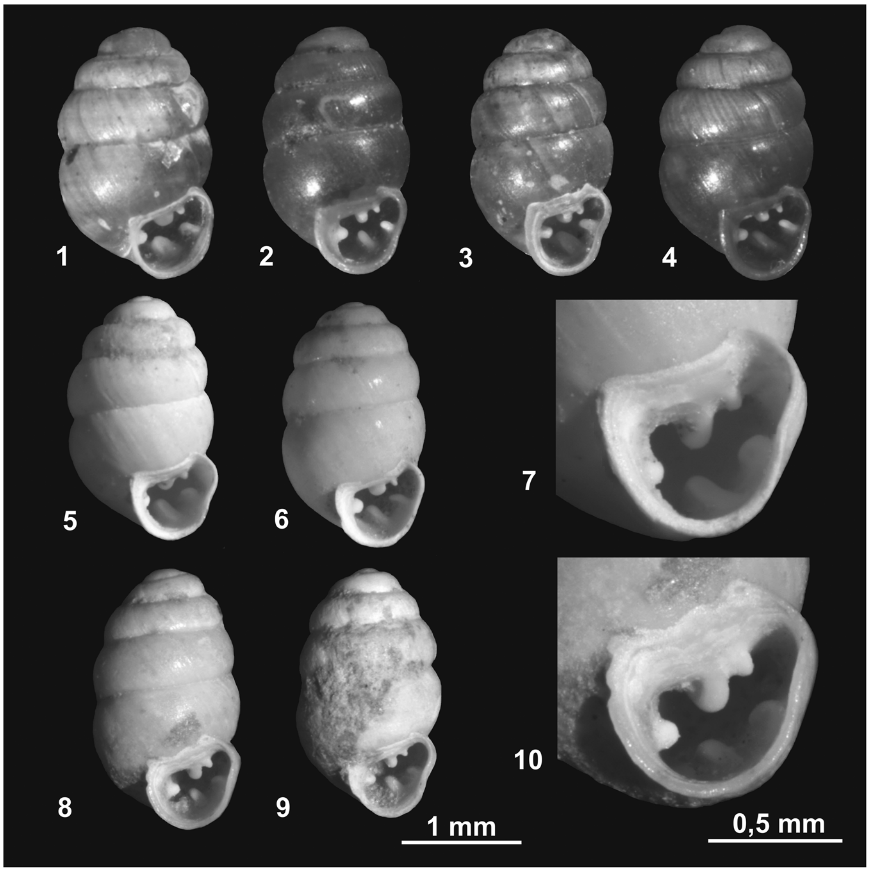

Figure 3. *Vertigo pseudosubstriata*; recent 1–4, **1** Russia, Altai, Severo Chujskiy Khrebet (SM 2562), **2** Russia, Altai, west of Onguday (SM 4682), **3** Kyrgyzstan, Tien Shan, Khrebet Terskey (SM 4843), **4** Kyrgyzstan, Tien Shan, Kungey Alatau (SM 4849), Pleistocene 5–10, **5–7** Germany, Thuringia, Erfurt-Riethnordhausen, Early Weichselian (SM 292/1), **7** aperture from 5, **8–10** Western Ukraine, south-west of Rivne, Myrohoshcha I, Upper Weichselian loess deposit, archaeological Gravettian cultural layer, **10** aperture from 8.

clustering of *V. pseudosubstriata* between 33 and 29 k cal a BP and its apparent demise thereafter.

Material and methods

The following analyses and reflections on *V. pseudosubstriata* are based on a literature survey (about 13 sites with fossil finds) as well as on field surveys (two sites with fossil finds and 25 modern find locations) by us (SM = Collection Stefan Meng).

The 25 samples from Central Asia (Altai, Tien Shan) can be considered representative for the contemporary distribution of this species. Hence, they can be used to reliably infer the boundaries of the species' ecological requirements (Supplement 1).

Ecological boundary conditions (macroclimate: temperature and precipitation) of the modern population were derived using data from representative weather stations (Walter and Lieth, 1967; Walter and Breckle, 1994; Bolch, 2006, 2007; https://en.climate-data.org; http://www.klimadiagramme.de/Asien; http://meteo.infospace.ru).

The weather stations provide the primary data. Since these stations are not always in the immediate vicinity of the habitats of *V. pseudosubstriata*, but often at lower altitudes, the temperature and rainfall had to be estimated using established altitude gradients, already applied in previous studies (e.g. Bolch, 2006, 2007). In addition, we attempt to incorporate information from weather stations located in neighbouring mountain ranges at corresponding topographic positions (Table 3). Therefore, homogeneous conditions can be assumed for the elevation gradients. However, small-scale relief-related variations cannot be taken into account. For example, the weather station Tien Shan, which is located in a relatively isolated high mountain valley, shows clearly deviating climatic conditions (Table 3).

In line with previsions studies, the decrease in temperature with increasing altitude was assumed to be c. 0.58°C/100 m for the Altai (Modina, 1997; Hoffmann *et al.*, 2011), 0.51°C/100 m (altitude gradient) Northern Tien Shan and c. 0.64°C/100 m for central Tien Shan (Bolch, 2006, 2007).

Estimating shifts in precipitation is less straightforward. Generally, the climate of Tien Shan and the Altai is markedly continental. Nevertheless, the development of the rainfall is extremely complex. On the one hand, precipitation depends on altitude, ranging from the arid lowlands to the humid high mountain ranges exposed to orographic and relief precipitation. On the other, it depends on exposition with more humid northern slopes and drier southern slopes. Further complicating matters are the position of the valleys or the source of the water underground (e.g. glacier water or permafrost islands).

While high annual rainfall (>1000 mm) is possible in western and northern Tien Shan depending on the altitude, the mountain interior of central Tien Shan is considerably more arid and more continental, due to its relatively sheltered position. The mean annual precipitation in Tien Shan thus ranges from 100 mm in the western Issyk-Kul basin (1700 m a.s.l.) to 1200 mm in Zailijski Alatau (3500 m a.s.l.) in northern Tien Shan. In central and northern Tien Shan, the mean annual precipitation which increases with height due to orographic precipitation is specified with an altitude gradient of about 25 mm/100 m (Bolch, 2006, 2007).

While the north-western Altai is ocean-influenced with annual rainfall up to 1500 mm, its climate becomes increasingly continental towards the east and south-east, where annual rainfall decreases to a mere 100 mm (Walter and Breckle, 1994).

Of the Pleistocene occurrences of *V. pseudosubstriata* in Europe, only 15 records could be researched. To create a frame of reference for the ecological preferences of the fossil populations, their stratigraphic position, accompanying mollusc fauna with known habitat requirements, and specimen counts of *V. pseudosubstriata* specimens have been recorded whenever possible (Table 1). Special emphasis is given to the latest finding of *V. pseudosubstriata* in 2019 during an archaeological excavation at the site of Myrohoshcha I (Table 2), western Ukraine,

Table 1. Pleistocene sites of *Vertigo pseudosubstriata* Ložek, 1954 in Europe with terrestrial accompanying mollusc fauna, total individuals or only proofs (X).

	1.1	**1.2**	**2.1**	**2.2**	**2.3**	**2.4**	**3**	**4**	**5***	**6***	**7**	**8.1**	**8.2**	**9.1**	**9.2**	**10.1**	**10.2**	**11**	**12**	**13**
Carychium minimum O.F. Müller 1774											1									
Carychium tridentatum (Risso 1826)											2									
Succinella oblonga Draparnaud 1801	x	98	x	x	x	x	12		x		287	x	x	210	257	704	264	x	22	8
Succinea/Oxyloma									x		150	x	x							
Cochlicopa lubrica (O.F. Müller 1774)	x			x					x		92	x	x							
Columella columella (G. v. Martens 1830)	x	8	x	x	x	x	4	14				x	x	1	46	276	104	x	31	9
Columella edentula (Draparnaud 1805)											1									
Columella sp.											1									
Vertigo parcedentata Braun 1847	x	2	x	x	x	x	4							1		149	53			
Vertigo pseudosubstriata **Ložek 1954**	**x**	**5**	**x**	**x**	**x**	**x**	**2**	**1**	**x**	**x**	**8**	**x**	**x**	**2**	**42**	**1**	**198**	**x**	**14**	**12**
Vertigo genesii (Gredler 1856)											5									
Pupilla muscorum (Linnaeus 1758)	x	14	x	x	x	x	1	44	x		235	x		8	69	320	277		30	
*Pupilla alpicola** (Charpentier 1837)		48						7				x	x	6				x		19
Pupilla sterrii (Voith 1838)								5	x			x	x		2	1				
Pupilla loessica Ložek 1954		20	x	x	x	x	12	7			1	x		143	120				97	
Pupilla triplicata (Studer 1820)							1	2				x		1	7					
Vallonia pulchella (O.F. Müller 1774)											125	x					1			
Vallonia costata (O.F. Müller 1774)	x							4	x		278				6	140	209			
Vallonia tenuilabris (Braun 1843)	x	6	x	x	x	x	3	35	x		30	x	x	40	99		1	x	105	4
Punctum pygmaeum (Draparnaud 1801)	x			x					x		9					1				
Discus rotundatus (O.F. Müller 1774)											1									
Zonitoides nitidus (O.F. Müller 1774)											2									
Semilimax cf. *kotulae* (Westerlund 1883)			x	x																
Vitrea subrimata (Reinhardt 1871)											1									
Nesovitrea hammonis (Ström 1765)											10				2	2			1	
Euconulus fulvus (O.F. Müller 1774)	x			x				3						2				x		
*Euconulus alderi** (Gray 1840)											4	x								
Agriolimacidae/Limacidae											3					75	35			
Clausilia rugosa (Draparnaud 1801)								37								8	91			
Clausilia dubia Draparnaud 1805			x	x	x	x	3	1					x		27			x	10	
Clausilia pumila C. Pfeiffer 1828											3	x	x							
Clausilia bidentata (Ström 1765)											1									
Macrocastra attenuata (Rossmässler 1835)											1									
Helicopsis striata (O.F. Müller 1774)			x					1			2	x	x							
Arianta arbustorum (Linnaeus 1758)	x	11	x	x	x	x	11					x	x			1		x	12	
Pseudotrichia rubiginosa (A. Schmidt 1853)												X	X							
Trochulus hispidus (Linnaeus 1758)		19	x	x	x	x	18	8			9	x	x		3	369	298	x	34	
Fruticicola fruticum (O.F. Müller 1774)											1									
Cepaea hortensis (O.F. Müller 1774)											1									

Notes: **1** Type locality Dolni Věstonice (Moravia, Czechia), Gravettian archaeological layer (al), tundra gley, younger Middle Weichselian (Würmian), base WIII loess, 29.9 ka cal BP (Antoine *et al.*, 2016). **1.1** Ložek (1953, 1954, 1964); **1.2** Ložek (2001). **2** Milovice near Dolni Věstonice (Moravia, Czechia), Gravettian al, younger Middle Weichselian (Würmian), loess (Kovanda, 2009), Gravettian layer c. 30 ka cal BP (Oliva, 2009). **2.1** Section A, under al; **2.2** Section A, above al.; **2.3** Section G, above al.; **2.4** Section L, above al. (Kovanda, 2009). **3** Pavlov near Dolni Věstonice (Moravia, Czechia), lower Gravettian al, younger Middle Weichselian (Würmian) (Ložek, 1967). **4** Horky nad Jizerou (Iser), Mladá Boleslav, brickyard (Bohemia, Czechia), Elsterian (Mindel) loess (Ložek, 1956, 1964, 1965, 2001, Bibus *et al.*, 1996). **5** Buda Hills (Budai-hegység), west of Budapest (Hungary), Upper Pleistocene, Weichselian (Würmian) loess (Krolopp, 1958, Ložek, 1964, Krolopp and Sümegi, 1992a, 1992b, 1993, 2000); a mixed fauna with cold-period (e.g. *Vallonia tenuilabris*) and interglacial indicator species (e.g. *Aegopis verticillus*). **6** Nyírábrány (eastern Hungary), Weichselian (Würmian) loess (Krolopp and Sümegi, 1992b); no information on accompanying fauna. **7** Erfurt-Riethnordhausen, gravel pit (Thuringia, Germany), Early Weichselian interstadial (Brørup or Odderade?), gravel of the River Gramme, in silt lentils, Weichselian low terrace (Niederterrasse), covered with loess (Meng, 1995, added 1997). **8** Bíňa, Danube lowland (south-western Slovakia), Early Pleniglacial 'Middle Weichselian' (MIS 4). **8.1** Profile 2 (samples 12–13 b summarised), sandy silt, OSL 62.9 ± 4.3 ka BP; **8.2** Profile 3, over it the following swamp loess (Hošek *et al.*, 2017). **9** Brehov (south of Trebišov, eastern Slovakia), loess, upper Saalian Complex (younger Rissglacial) under Eemian soil (Schmidt *et al.*, 1978). **9.1** Brehov S-1; **9.2** Brehov S-2. **10** Mainz-Weisenau (Rheinland-Pfalz, Germany), Saalian (Riss) Complex, loess palaeosol complex (Bibus *et al.*, 1996). **10.1** 'Unterster Nassboden' (lowest wet soil); **10.2** 'Dritter Nassboden' (third wet soil). **11** Molodova V, Dnjestr River valley (Chernõvtsy province, Western Ukraine), Weichselian loess, archaeological cultural layer 7 (Gravettian), wet soil (gley horizon) (Kahlke, 1967; Ložek, 1976; Ivanova, 1987), 23.7 ka ^{14}C BP (Haesaerts *et al.*, 2003), Ložek (1976) after I. K. Ivanova (verbal communication or examined material from Ložek). **12** Halych I, Dnister River valley, (south-east of Lviv, western Ukraine), Late Pleistocene loess, gley horizon = archaeological cultural layer (Alexandrowicz *et al.*, 2014), for example, after Cyrek and Sytnyk (2012) cl. (Gravettian) under Rivne soil in Halych I 30-29 ka cal BP. **13** Myrohoshcha I, south-western Rivne (western Ukraine), Weichselian loess, Gravettian cl 5, subgley, ^{14}C >33.4–33.0 ka cal BP (^{14}C dates from cl. 4) (Vasyliev *et al.*, 2020, Maier *et al.*, 2020b).
*Pupilla alpicola** - summarised (=*P. muscorum densegyrata, alpicola densegyrata, pratensis*) – see Haase *et al.* (2021)
Euconulus alderi *- compare Horsáková *et al.* (2019)
5* - only selection
6* - no information on accompanying fauna

Table 2. Myrohoshcha I (western Ukraine): terrestrial molluscs, total individuals, for sample correlation see Fig. 4.

Mollusc samples	**1–4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Archaeological cultural layer		**1**	**2**	**3**	**4**	**5**			**6**
Succinella oblonga Draparnaud 1801				16	11	8	1	6	51
Cochlicopa lubricella (Porro 1838)					1				
Columella columella (G. v. Martens 1830)				4		9		2	27
Vertigo pseudosubstriata **Ložek 1954**						**12**			
Pupilla muscorum (Linnaeus 1758)								12	56
Pupilla alpicola (Charpentier 1837)				6		19	1		
Pupilla loessica Ložek 1954								2	6
Pupilla sp.			1	4					
Vallonia tenuilabris (Braun 1843)				18	3	4		5	61
Euconulus fulvus (O.F. Müller 1774)									2
Trochulus hispidus (Linnaeus 1758)		2		8	1				2
Total species (10)	**0**	**1**	**1**	**6**	**4**	**5**	**2**	**5**	**7**
Total individuals (361)	**0**	**2**	**1**	**56**	**16**	**52**	**2**	**27**	**205**

representing to date the north-easternmost findspot of this species in Europe.

To get a better idea about the timing of the occurrences of *V. pseudosubstriata* in the Weichselian, all available radiocarbon dates have been compiled. Calibration followed the IntCal20 calibration curve (Reimer *et al.*, 2020) as implemented in CalPal Version 2020.11 (Weninger *et al.*, 2014). We then use the findings on the ecological requirements of *V. pseudosubstriata* to assess the habitat suitability during its presence in Europe and towards its potential demise as inferred from the youngest attested occurrence.

Results

Current occurrences of Vertigo pseudosubstriata Ložek, 1954 in Central Asia and ecological parameters of its habitat

With regard to its modern distribution, 25 habitats with *V. pseudosubstriata* have been examined in Tien Shan and in the central and southern Altai (Supplement 1, Fig. 2). These data include the present-day distribution of the species and provide information about the limits on the ecological requirements. This is of great significance for the interpretation of the fossil assemblages.

Taking account of the gradients of temperature and rainfall related to altitude (e.g. Modina, 1997; Bolch 2006, 2007; Hoffmann *et al.*, 2011), the following conditions for the habitats of *V. pseudosubstriata* can be derived from the data of the weather stations (Table 3).

In the Altai, *V. pseudosubstriata* was found at four locations with heights of 1100–2100 m a.s.l. The habitats comprise a mean annual temperature of about -5.5 to -2.5°C (January -22 to -18°C, July 9 to 17°C) and a mean annual precipitation of about 450–700 mm (Table 4). In addition to these four sites from the Altai, Horsák *et al.* (2010) report another three sites at 1354–1994 m a.s.l., with a mean annual temperature of -7.5 to 1°C (January -21.4 to -18°C, July 6.4 to 11.4°C) and an annual rainfall of 522–821 mm.

The specimens from the 21 localities in the Tien Shan Mountains cover a wide topographic and climatic range (Table 4): 1800–3600 m a.s.l., annual precipitation of about 400–850 mm, and annual temperature of about -7 to 6°C (January -21 to -8°C, July 5 to 18°C).

The habitats of *V. pseudosubstriata* in the Altai and Tien Shan thus also encompass a total climate range of about 400–850 mm annual precipitation and an annual temperature of about -7 to 6°C (January -22 to -8°C, July 5 to 18°C).

In its present environment, the species prefers somewhat humid habitats, such as alpine meadows (partly alpine tundra), forest-meadow complexes, usually near bodies of water, moister shrublands, swamps and, at lower elevations, floodplain forests. The species is not found on dry steppes (Supplement 1).

Pleistocene fauna with Vertigo pseudosubstriata Ložek, 1954 in Central and Eeastern Europe

The glacial indicator species *Vertigo* could be found in Central and Eastern Europe in a very diverse Quaternary geological and archaeological context, which is re-examined and re-evaluated in this study.

Elsterian (Mindel)

At the only Elsterian findspot, the loess sequence of Horky (Bohemia, Czechia), apparently only one specimen of *V. pseudosubstriata* has been found (Ložek, 1956, 1964, 1965; Bibus *et al.*, 1996). The glacial mollusc assemblage (Table 1) with e.g. *Columella columella*, *Vallonia tenuilabris* or *Clausilia rugosa*, indicates somewhat more humid glacial conditions. In contrast, in the high glacial loess steppes in Central Europe, assemblages with very few species of *Pupilla* spp. and *Succinella oblonga* clearly predominate (Ložek, 1964; Mania, 1973). The glacial indicator species *V. tenuilabris,* in particular, also prefers somewhat more humid habitats in Central Asia in modern times (Meng, 2009).

From the localities of Bulhary and Milovice (Moravia, Czechia) *V. pseudosubstriata* is also described from the older Pleistocene, but with unclear stratigraphy (Havlíček and Kovanda, 1985). Therefore these localities are not considered in the locality list.

Saalian (Riss)

Only a few sites with *V. pseudosubstriata* are known from the Saalian glacial period. For example, the species is described from the Saalian Complex, namely the loess-palaeosol sequence of Mainz-Weisenau (Rheinland-Pfalz, Germany), where about 200 specimens, the highest reported quantity in the entire data set, were found (Bibus *et al.*, 1996). The faunal composition (Table 1) also suggests more moderate glacial conditions. The predominance of *Vallonia costata*, which avoids high glacial periods, is striking, for example. In addition to *V. pseudosubstriata*, *Vertigo*

Table 3. Find regions of *Vertigo pseudosubstriata* in Central Asia (Supplement 1) with climate data from adjacent weather stations (Walter and Lieth, 1967; Walter and Breckle, 1994; Bolch, 2006, 2007; Hoffmann *et al.*, 2011; https://en.climate-data.org; http://www.klimadiagramme.de/Asien; http://meteo.infospace.ru).

Region	Altitude (m)	No. of plots/shells	Weather station	Altitude (m)	Mean annual temp (°C)	January temp (°C)	July temp (°C)	Mean annual precipitation (mm)
Central Altai								
West of Onguday	1100	1/3	Onguday N 50° 44′/E 086° 07′	833	-1.1	-22.1	16.2	345
			Ust Kan N 50°55′39″/E 084°45′39″	1042	0.4	-14.9	16.4	567
South central Altai								
Severo Chujskiy Khrebet,	1700–2100	3/18	Ak-Tash N 50° 18′/E 087° 36′	1349	-0.3	-17.5	16.0	323
			Čibit N 50 19′/E 087° 30′	1170	0.5	-17	17.1	333
Northern Tien Shan								
Kungey Alatau	2000–2310	4/20	Kyrchin N 42°49′/E 077°30′	2305	2.9	-9	12	592
Central Tien Shan								
Khrebet Terskey Alatau	2500–3600	5/55	Tamga (Lake Issyk Kul) N 42° 08′/E 077° 32′	1690	7.5	-3	19	242
			Karabatak glacierN 42° 12′/RE 078° 29′	3415	-3.5	-15	6	819
			Tien Shan N 41° 51′/E 078° 07′	3614	-7.6	-21	5	311
Sary-Jaz river valley	>3000	1/7	Karakol N 42° 30′/E 078° 22′	1714	6.2	-6	18	430
			Karabatak valley N 42° 18′/E 078° 28′	2550	0.1	-12	10	613
South central Tien Shan								
Khrebet At Bashy	2620–3200	5/20	At Bashy N 41° 10′/E 075° 48′	2056	3.6	-15.2	17.7	270
Khrebet Naryn Tau	2430–3020	3/20	Naryn N 41° 25′/E 076° 00′	2041	3.5	-15	17	291
Western Tien Shan								
Khrebet Talasskiy Alatau	1950–2790	3/15	Talas N 42° 31′/E 072° 14′	1235	7.8	-7.2	21.5	350
Chatkalskij Khrebet	1830	1/12	Kurulush N 41° 39′/E 070° 47′	1758	6	-10.8	19.7	389

Table 4. Summary of climate data from *Vertigo pseudosubstriata* sites in the Altai and Tien Shan (Supplemenet 1).

Climate parameters	Found regions					
	Central Altai	South central Altai	Northern Tien Shan	Central Tien Shan	South central Tien Shan	Western Tien Shan
Altitude (m)	1100	1700–2100	2000–2310	2500–3600	2430–3200	1830–2790
Mean annual temp (°C)	0	-5.5 to -2.5	2 to 4	-7 to 0	-3.5 to 2.5	0 to 6
January/July temp (°C)	-18/17	-22 to -20/9 to 13	-9 to -8/12 to 14	-21 to -12/5 to 10	-20 to -15/8 to 13	-16 to -11/12 to 18
Mean annual precipitation (mm)	450	500–700	500–600	500–850	400–600	400–700

parcedentata, another glacial indicator species which prefers humidity, is found in abundance.

Another finding place is Brehov, south of Trebišov (eastern Slovakia), loess, upper Saalian Complex (younger Rissglacial) (Schmidt *et al.*, 1978). Brehov also provided typical cold-period associations with *V. tenuilabris*, *P. loessica* or *C. columella* (Table 1).

Weichselian (Würm)

For the often quoted Weichselian findings of *V. pseudosubstriata* at Csordakút in the Buda Hills (Budai-hegység), west of Budapest, Hungary (Krolopp, 1958; Ložek, 1964; Krolopp and Sümegi, 1992a, 1992b, 1993, 2000), hardly any verifiable data are available. Krolopp (1958) describes a mixed fauna with glacial (e.g. *Vallonia tenuilabris*) and interglacial indicator species (e.g. *Aegopis verticillus* or *Orcula dolium*). No information concerning the exact stratigraphic or chronological position is available.

With regard to the findings in the Weichselian loess at Nyírábrány, eastern Hungary (Krolopp and Sümegi, 1992b), the situation is similar. The authors give no information about the accompanying fauna or more precise stratigraphic conditions.

The earliest Weichselian evidence of *V. pseudosubstriata* in Germany was found in the gravel pit Erfurt-Riethnordhausen (Thuringia, Germany; Fig. 3: 5–7; Meng, 1995). The gravel of the River Gramme forms a Weichselian low terrace up to 8 m thick which is covered by a thin layer of loess. The molluscs were found in silt layers. Today, the pit is closed. The deposition conditions and the unusual mollusc fauna (Meng, 1995; Böhme, 1998) seem to indicate an Early Weichselian interstadial (Brørup or Odderade). The average temperatures of the warmest month (July), reconstructed for this interstadial, amount to about 15 to 17°C for northern Central Europe. However, the winters were apparently considerably colder (annual temperature in January -15 to -12°C) and longer, so that only boreal forests could develop in Central Europe (Behre and Lade, 1986; Lang, 1994; Litt, 1994; Litt *et al.*, 2007; Wohlfarth, 2013). The wide variety of the accompanying terrestrial mollusc fauna (Table 1) in part recalls temperate conditions and glacio-fluvial redeposition of mollusc shells cannot be ruled out. On the other hand, there is a lack of clearly interglacial indicator species. For instance *Carychium minimum* and *Carychium tridentatum*, *Vitrea subrimata*, *Discus rotundatus*, *Clausilia pumila* and *bidentata* are found today not only in the European lowlands, but can also penetrate alpine regions and far to the north into Scandinavia (Welter-Schultes, 2012). As in typical glacial faunas, the assemblage is dominated by *Succinella oblonga*, *Pupilla muscorum* or *Vallonia costata* and, with *Vallonia tenuilabris* and *Vertigo genesii*, also comprise glacial indicator species.

The site Bíňa (south-western Slovakia) can be dated into the Early Pleniglacial, OSL 62.9 ± 4.3 ka BP (MIS 4) (Hošek *et al.*, 2017). The cold-period molluscan fauna of Bíňa is also relatively species abundant, e.g. with *Pseudotrichia rubiginosa*, *Clausilia pumila*, *Vallonia tenuilabris* or *Pupilla alpicola* (Table 1), which also indicates living conditions favourable for *V. pseudosubstriata*.

Most of the specimens of *V. pseudosubstriata* were found in the east of Central Europe and in Eastern Europe in the Upper Middle Weichselian in the context of archaeological layers attributed to the so-called Gravettian. The Gravettian (ca. 33–25 ka cal BP) coincides with the cooling period before the Last Glacial Maximum (LGM, sensu Mix *et al.*, 2001), characterised by several stadial–interstadial cycles. In Central Europe, the period between 33 and 29 ka cal BP coincides with the demographic maximum of hunter-gatherers (Maier and Zimmermann, 2017; Schmidt *et al.*, 2021), diversification in projectiles (Maier *et al.*, 2020b), and comparatively large campsites with an intense and potentially year-round occupation (Svoboda, 2007; Fišáková, 2013). It appears that *V. pseudosubstriata* reached its maximum distribution during this period in Europe (Fig. 1, Table 1).

The type locality for *V. pseudosubstriata* is the well-known archaeological site of Dolní Věstonice (Moravia, Czechia). The species was found in a tundra gley at the bottom of W III loess in the archaeological main layer (Ložek, 1953, 1954, 1964). Apparently no later findings were made (cf. Antoine *et al.*, 2016). The layer of the archaeological findings is roughly dated to between 32.5 and 30 ka cal BP (Table 5). Comparable sites in the surroundings of Dolní Věstonice (Moravia, Czechia) are Milovice (Kovanda, 2009) and Pavlov (Ložek, 1967).

The first specimen of *V. pseudosubstriata* in Ukraine was found in the Dniester River valley, at the site of Molodova V (Chernõvtsy province), in a gley horizon in Weichselian loess (unit 12) in the context of archaeological layer 7 (Ložek, 1976; after I. K. Ivanova). During later investigations (e.g. Motuz, 1987) the species was apparently not found again (Table 1). The find layer (culture layer 7) was dated to 27.5 ka cal BP (Table 5; Ivanova, 1987; Haesaerts *et al.*, 2003).

Also in the Dniester River valley, southeast of the city of Lviv, lies the site of Halych I, from where Alexandrowicz *et al.* (2014) report the finding of *V. pseudosubstriata* in connection with an archaeological cultural layer. However, different information is given on the age estimation of the embedding loess. Alexandrowicz (2014) refers to Fedorowicz, (2006) who thermoluminescence dated the culture layer to between 19 and 17.4 ka BP. Cyrek and Sytnyk (2012) described the profile

Table 5. Radiocarbon dates from fossil sites with *Vertigo pseudosubstriata*.

Site	M	Lab number	^{14}C BP	Std	cal BP	Std	P%	^{14}C BP	Std	cal BP	Std	References
Dolní Věstonice II, brickyard, east wall	ch	n.s.	25 760	190	**30 036**	**176**						Fuchs *et al.*, 2013
Dolní Věstonice II, brickyard, east wall	ch	GrN-2002	28 300	300	**32 471**	**473**						Klima *et al.*, 1962
Molodova V, layer 7, unit 12	bo	GrA-9443	21 070	150	25 420	184						Haeserts *et al.*, 2003
Molodova V, layer 7, unit 12	ch	GrA-9455	23 000	170	27 348	155	*					Haeserts *et al.*, 2003
Molodova V, layer 7, unit 12	ch	MO-11	23 000	800	27 238	802	*					Ivanova, 1987
Molodova V, layer 7, unit 12	sol	GIN-10	23 700	320	27 949	364	*					Ivanova, 1987
weighted average							15.2	23 149	148	**27 448**	**146**	
Myrohoshcha I, layer 4	ch	OxA-38364	28 850	150	33 337	257	*					Maier *et al.*, 2020a
Myrohoshcha I, layer 3	ch	OxA-38142	28 910	210	33 382	323	*					Maier *et al.*, 2020a
Myrohoshcha I, layer 3	ch	OxA-38141	28 950	210	33 441	309	*					Maier *et al.*, 2020a
Myrohoshcha I, layer 4	ch	OxA-38424	29 470	550	33 776	610	*					Maier *et al.*, 2020a
Myrohoshcha I, layer 3	ch	OxA-X-3004-19	29 570	970	33 732	1144	*					Maier *et al.*, 2020a
Weighted average							79.3	28918	103	**33 431**	**198**	
Myrohoshcha I, layer 5										**>33 431**	**198**	

M: Material (bo: bone, ch: charcoal, sol: soil). P% Probability that all dates marked with * and used to calculate the weighted averages relate to the same occupation event (calculated in CalPal Version 2020.11). All calibrations according to the IntCal20 curve (Reimer *et al.*, 2020) as implemented in CalPal (Weninger *et al.*, 2014).

in more detail and dated the Gravettian culture layer to ^{14}C 30-29 ka cal BP. According to Cyrek and Sytnyk (2012), the archaeological horizon is believed to be below the Rivne soil horizon. The Rivne horizon is radiocarbon-dated to approximately 22.5 ka cal BP (Jary and Ciszek, 2013).

During archaeological excavations in the Late Pleistocene loess of Myrohoshcha I (south-west of Rivne, western Ukraine), a new site with *V. pseudosubstriata* was discovered in 2019. In the loess section, ten culture layers with charcoal and silex artefacts were examined (Fig. 4). The only find horizon with *V. pseudosubstriata* (Fig. 3: 8–10) is cultural layer 5, a subgley, which was dated to at least 33 ka cal BP (Table 5; Vasyliev *et al.*, 2020; Maier *et al.*, 2020a), which gives a rough estimate for layer 5 of between 34 and 33 ka cal BP. The layer of loess at the top of the stratigraphy is almost free of fossils and was probably deposited under drier, high glacial conditions. The mollusc fauna of Myrohoshcha I can well be compared with other archaeological sites in Ukraine or Czechia containing *V. pseudosubstriata* (Tables 1 and 2). In the subgley horizons at the base of the loess (Fig. 4), *Succinella oblonga*, *Columella columella*, *Vallonia tenuilabris*, *Pupilla alpicola* predominate, *inter alia*.

In all, the mollusc faunas from archaeological sites of the Gravettian with *V. pseudosubstriata* are very similar and form typical spectra, e.g. with *Columella columella*, *Vallonia tenuilabris*, *Succinella oblonga*, *Pupilla muscorum*, *P. alpicola* or *Clausilia dubia*. These compositions point towards rather humid cold conditions (Table 1). The currently oldest specimens of this cluster occur at Myrohoshcha I between 34 and 33 ka BP, followed by Dolní Věstonice between 32.5 and 29.5 ka BP, and Molodova V at 27.5 ka BP. Conspicuously, evidence for this cold-adapted species is lacking for the period of the LGM.

Discussion

Today, *V. pseudosubstriata* inhabits Central Asia (Altai, Tien Shan) where fossil evidence is lacking. Conversely, this species is no longer found in Central and Eastern Europe and only known from fossil sources. This indicates shifts in habitats, over larger areas, and is thus also the assumption for the past. Since small snails, especially juvenile animals or eggs, are ornithochores and can be transported in birds' feathers (Gittenberger *et al.*, 2006), high speeds for expansion over distance are possible. Transportation in the fur of large mammals is also conceivable. So these gastropods are likely able to comparatively quickly profit from favourable climatic developments and may shift their habitats accordingly. *V. pseudosubstriata* is generally extremely rare in the

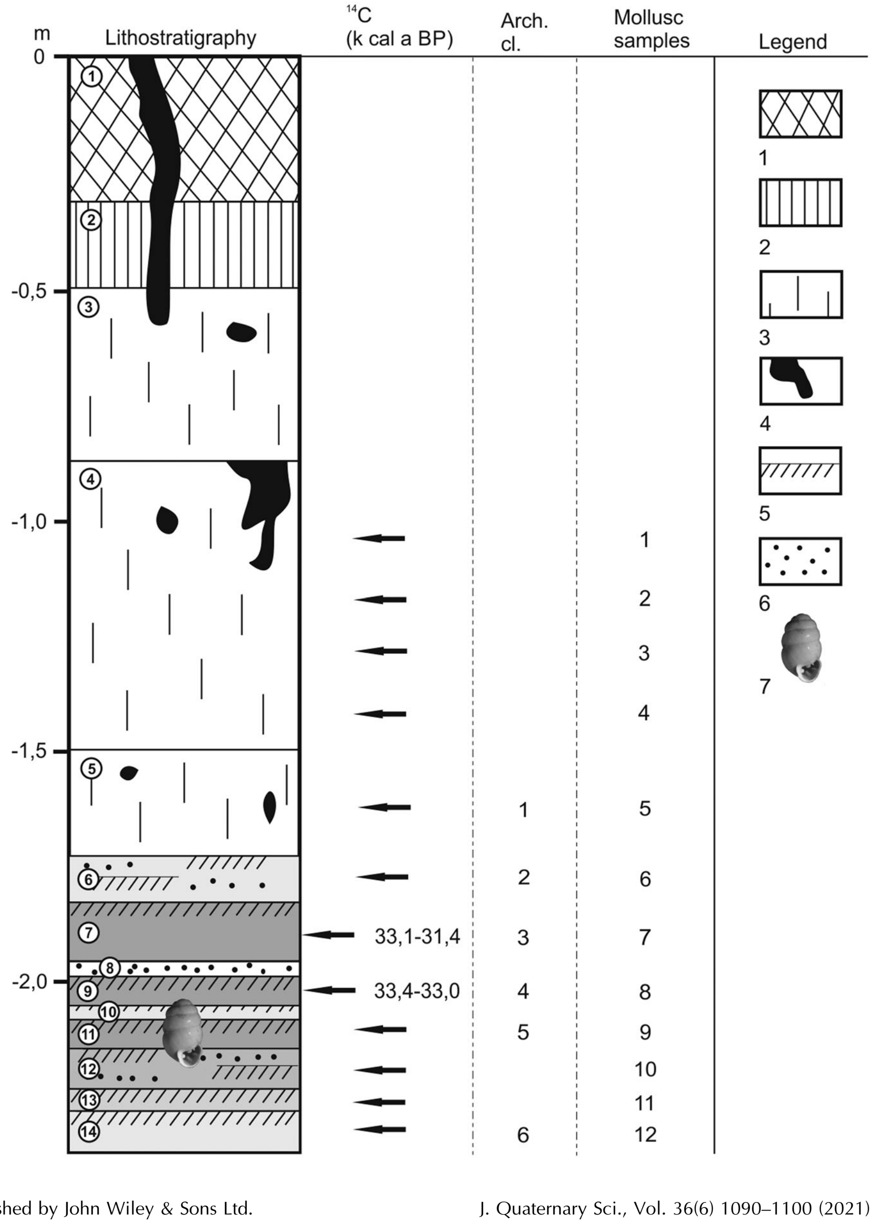

Figure 4. Myrohoshcha I (Ukraine): lithostratigraphy, radiocarbon dates, archaeology (cultural layer) and mollusc samples from 2019 (modified after Vasyliev *et al.*, 2020; Maier *et al.*, 2020a). Lithostratigraphy: **1** soil, A horizon, **2** soil, Bt horizon, **3** loess A, **4** loess B, **5** loess C, **6** loess mixed with subgley and sand, **7** subgley brown, **8** sand white, **9** subgley grey-brown, **10** subgley light brown, **11** subgley brown, **12** subgley red mixed with yellow sand, **13** subgley light brown, **14** subgley light grey. **1** soil, A horizon, **2** soil, Bt horizon, **3** loess, **4** krotovina, **5** subgley, **6** sand, **7** *Vertigo pseudosubstriata*.

Pleistocene mollusc record of Europe but, at the same time, has been reported from very different glacial periods (Elsterian, Saalian Complex, Early and Middle Weichselian). With regard to other dispersal scenarios assumed for more frequent glacial indicator species like *Vallonia tenuilabris*, *Pupilla loessica*, or *V. parcedentata* (Meng 2008, 2009; Meng and Hoffmann, 2009; Horsák *et al*., 2010, 2015; Haase *et al*., 2021), it seems reasonable to expect at least three to four distinct waves of migration into Europe for *V. pseudosubstriata*. Although past interglacial refugia are not known, Central Asia seems to be a possible candidate.

Most fossil occurrences of *V. pseudosubstriata* are reported from eastern Central and western Eastern Europe in archaeological context between 34 and 27.5 ka cal BP. Considering its general scarcity, this finding is in need of explanation. Given the low number of cases, this observation might just be a mere coincidence. A simple causal explanation could be that fine-meshed water screening meanwhile has become a standard procedure for Palaeolithic excavations, thus increasing the potential to also discover rather small molluscs. However, data from malacological surveys seem conspicuously underrepresented, particularly with regard to the fact that sieves with 1 mm meshes are even in modern excavations probably rather the exception than the rule. Regular water screening alone also does not explain why find layers containing *V. pseudosubstriata*, if dated, show a concentration between 34 and 27.5 ka BP. A potential explanation in line with the previous arguments could be a research focus in favour of sites of this period (Early Gravettian/Pavlovian). However, research on the Late Middle Palaeolithic and Early Upper Palaeolithic as well as on the period of the LGM and Late Glacial – i.e. on periods without any evidence for the presence of *V. pseudosubstriata* – has likewise been conducted over recent decades to quite a substantial degree (e.g. Alexandrowicz, 2014; Juřičková *et al*., 2014). Moreover, none of this explains why evidence for *V. pseudosubstriata* is absent from western Europe.

If chance and research biases are dismissed as explanations for the temporal pattern, shifts in climatic factors, particularly in temperature and precipitation, might be responsible.

In contrast to *Vallonia tenuilabris* or *Pupilla loessica* with preferences for annual mean temperatures below 0°C (Meng, 2009; Meng and Hoffmann, 2009; Horsák *et al*., 2010, 2015), *V. pseudosubstriata* shows a broader range of -7 to 6°C (January -22 to -8°C, July 6.4 to 18°C). This corresponds well with findings from pollen analysis for the occupation at Dolní Věstonice II, which shows 30 to 70% tree pollen, mainly with conifer combinations of *Pinus*, *Picea*, *Juniperus* and *Larix* (Antoine *et al*., 2016). Evidence of this is also provided by the charcoal found in the archaeological cultural layers. At other Moravian sites of this period, e.g. Předmostí, the reconstructed winter temperatures reached very low values of -23.4 to -17.8°C, whereas the summers were very mild with an average of 13.7 to 19.2°C in the warmest month (Musil, 2010). The climate was thus continental and the landscape was characterised by moderate tundra environments, especially in eastern Central Europe (Musil, 2010). Temperature conditions between 34 and 27.5 ka BP thus seem to have been quite favourable for *V. pseudosubstriata*. However, considering the snail's tolerance to cold, temperatures before that period and probably also during the LGM were likely not the limiting factor for its distribution.

This leaves increasing aridity as a major explanatory factor for its temporal distribution. Indeed, there is a reported increase of xerophilous mollusc species in the Pannonian Basin between 29 and 27 ka BP (Sümegi *et al*., 2016), as well as events of increased dust activities (Újvári *et al*., 2017) and a decline in arboreal pollen (Magyari *et al*., 2014), likely indicating generally more arid conditions towards and during the LGM. On the other hand, finds from arboreal macro remains from Central Europe dated to the LGM show that at least in sheltered places the moisture availability might have been sufficient for *V. pseudosubstriata*. Moreover, interstadials before 34 ka BP likewise should have provided sufficient moisture supply for its survival. Both temperature and moisture supply also fall short in explaining the absence of this species from western Europe.

Conclusion

The present study is the first comprehensive data synthesis on *V. pseudosubstriata*, a known Pleistocene indicator species from Central and Eastern Europe currently distributed across Central Asia.

In Central Asia, the species is currently found in the Altai and Tien Shan. In these regions, 25 habitats with *V. pseudosubstriata* could be investigated. The species prefers the humid habitats of high mountain regions, such as alpine meadows (partly alpine tundra), mostly near bodies of water, humid shrublands and swamps. Climatic spectra range from 400 to 850 mm annual precipitation and an annual temperature of about -7 to 6°C (January -22 to -8°C, July 6.4 to 18°C) with colder temperatures preferred.

V. pseudosubstriata is generally extremely rare in the Pleistocene molluscan record of Europe (a total of 15 localities in Germany, Czechia, Slovakia, Hungary and Ukraine), but at the same time it was reported from very different glacial periods (Elsterian, Saalian Complex, Early and Middle Weichselian). Thus, despite its rarity, we must also assume various waves of immigration from Central Asia to Europe. Similar areal shifts have been reported for the common cold-period indicator species *Vallonia tenuilabris*, *Pupilla loessica* and *Vertigo parcedentata*.

V. pseudosubstriata was most abundant during the Middle Weichselian between 34 and 27.5 ka cal BP. Several reasons can be hypothesised for this. With moderate tundra environments *V. pseudosubstriata* found appropriate living conditions in Europe. Moreover, also because of the important archaeological findings in these deposits, numerous excavations were carried out, during which the molluscs were also studied.

Why the species is so rare in the fossil record in Europe as a whole, although thousands of Pleistocene molluscan faunas have now been investigated, has not yet been clarified.

Temperature as a limiting factor in its distribution for *V. pseudosubstriata* seems rather unlikely. Thus, its absence from the LGM records is probably related to increasing aridity and adequate humid habitats during this period. This is also supported by the data collected in Central Asia.

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Data availability statement

The data that support the findings of this study are available in the supplementary material of this article.

Conflicts of interest—We have no conflicts of interest to declare.

Supporting information

Additional supporting information can be found in the online version of this article.

Supplement 1. List of recent locations of *Vertigo pseudosubstriata* in Central Asia, collections of Meng (1995–2014).

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