

Holocene palaeoecological changes recorded in mollusc-bearing cave sediments, the Cave above the Słupska Gate (southern Poland)

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ABSTRACT

The Cave above the Słupska Gate (southern Poland) contains about 2m depth of mollusc-bearing deposits. Radiocarbon and archaeological dating indicate that these deposits accumulated during the Holocene (Preboreal to Subatlantic), although the earliest layers may date from the end of the Pleistocene. Eight layers of silts, sands and loess-like deposits were distinguished at the site. Seven of them contained identifiable snail shells, sometimes in large numbers, and sparse remains of vertebrates and archaeological artefacts. The molluscan assemblages retrieved from the cave contain over 40 taxa and 1,200 specimens. The balance of species distributed among 11 zoogeographical groups enabled us to identify four assemblages which differ in their ecological structure and in the composition of the fauna. The oldest fauna (Late Glacial/Preboreal and/or Preboreal) with many shade-loving species is typical of a cool climate. Episodes of drying are evidenced by the loess-like deposits and the occurrence of open-country snails such as the glacial relic *Vallonia tenuilabris*. This species disappeared in the younger part of the Early Holocene, which is the most distinctive feature of the Shupsko Hill sequence. The Middle Holocene climatic optimum is characterised by abundant and diverse fauna which is typical of mixed and deciduous forests with distinct oceanic influences. The critical *Discus ruderatus* and *Discus rotundatus* succession reflects the general trends in European malacofaunas. The Late Holocene record may bear some hiatuses, but the shift away from a complete forest fauna is evident.

KEYWORDS Malacofauna. Cave sediment. Early Holocene. Middle Holocene. Palaeoenvironment.

INTRODUCTION

The Pleistocene/Holocene transition and the Early Holocene were a time of important climatic and environmental changes in Central Europe, which marked a transition from glacial to interglacial conditions. Significant changes, mostly connected with the increase

of temperature and varying humidity, can be seen in plant cover, the development of water bodies and transformation of terrestrial environments.

Molluscs are one of the best indicators of environmental change. They document changes of many habitats, starting from the freshwater to dry land conditions. An excellent record

of development of water bodies during the Late Vistulian/Holocene boundary and the Holocene was provided by the malacofaunas of many lakes of northern Poland. The abundant profiles of lacustrine chalk and calcareous gyttja yielded characteristic mollusc assemblages and their succession could be associated with certain climate and environmental conditions (e.g. Wojciechowski, 2000; Alexandrowicz, 2013a). In terrestrial environments, molluscan records from the late Quaternary come mainly from the calcareous tufas and loess deposits of southern Poland (e.g. Alexandrowicz, 1983; 2001a, 2004, 2013b, 2014; Alexandrowicz *et al.*, 2014). In Poland, loess sequences usually document severe conditions of the Late Vistulian (or older) with characteristic species *Pupilla loessica*, *Pupilla muscorum*, *Vallonia tenuilabris*, *Semilimax kotulae*, *Columella columella*, *Succinea oblonga* and the others (Alexandrowicz and Alexandrowicz, 1995a, b; Kruk *et al.*, 1996), whereas those from tufas and travertines reveal faunas typical of different parts of the Holocene and the Pleistocene/Holocene transition. One of the best defined boundaries of these periods in Poland was noted in Groń (the Podhale Basin) (Alexandrowicz, 2013b), but abundant comparative material of that age is also available at many profiles throughout Europe (e.g. Limondin-Lozouet and Rousseau, 1991; Meyrick and Preece, 2001; Meyrick, 2002; Gedda, 2001; Limondin-Lozouet and Preece, 2004; Limondin-Lozouet, 2011).

Despite the many malacofauna sequences reported from cave sediments, few of these go back as far as the final part of last glaciation (Stworzewicz, 1973, 1988; Alexandrowicz *et al.*, 1992; Svoboda *et al.*, 2000; Alexandrowicz and Stworzewicz, 2003; Ložek, 2012). In southern Poland most such stratigraphic profiles are only a few dozens of centimetres thick, covering the middle or just the youngest part of the Holocene (e.g. Bocheński *et al.*, 1985; Alexandrowicz, 1992, 1997, 2000a, b, 2001b; Alexandrowicz and Rudzka, 2006).

Hence, the relatively thick sequence of mollusc-bearing sediments from the Cave above the Słupska Gate can provide a more complete account of local environmental changes over the whole of the Holocene. Here, we characterise the succession of mollusc assemblages of the Cave above the Słupska Gate and relate them to the conditions of their development and the accumulation of cave deposits. Finally, the palaeoenvironment of surrounding area and the climate variability is reconstructed and compared with regional trends. The interpretation is supplemented by analysis of vertebrates.

GEOLOGICAL SETTING

The Cave above the Słupska Gate (N: 50°35'27.8" E: 19°34'15.2") is situated on the western slope of Słupsko, the easternmost hill of the Kroczyckie Rocks ridge in the central part of the Cracow-Częstochowa Upland, ca. 40 km south-east of Częstochowa (Fig. 1). It was not mentioned in literature before the excavation in 2011-2012. Its name (*Jaskinia nad Bramą Słupską* in Polish) was proposed by spelaeologist K. Mazik during the spelaeological symposium in Olsztyn, Poland, in 2013 (Krajcarz *et al.*, 2014a). The area is built of the Upper Jurassic massive limestone, partially covered by the red desert sands and loams dated to Paleogene/Neogene (Gradziński, 1977) and sandy deposits attributed to the fluvio-periglacial facies of the Middle Pleistocene (Lewandowski, 1994). The karstic cavities and caves are filled with the Late Pleistocene and Holocene cave and colluvial sediments. The Cave above the Słupska Gate is not an isolated site in the region, but several others are known from the Kroczyckie Rocks, including Deszczowa Cave, Shelter on Słupsko Hill, Cave Wisielców and Krucza Skała Rockshelter (Cyrek, 1994; Madeyska, 1996; Cyrek *et al.*, 2000; Nadachowski *et al.*, 2009; Krajcarz and Madeyska, 2010; Krajcarz *et al.*, 2014b).

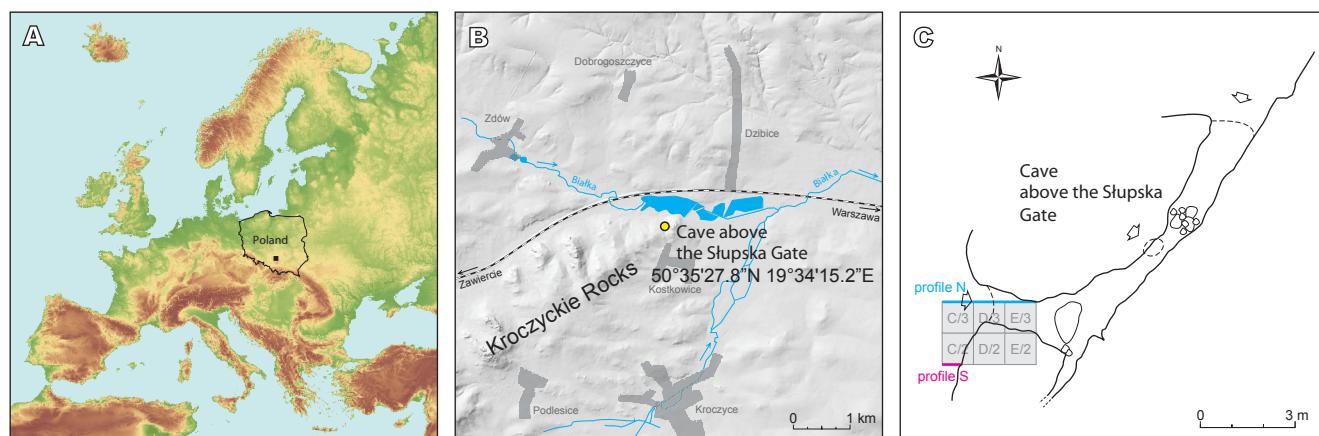


FIGURE 1. A, B) Localisation of the Cave above the Słupska Gate. C) Plan of the cave with situation of archaeological trench in 2012.

The sedimentary sequence in the Cave above the Słupska Gate is up to 2m thick. Altogether 8 layers of silts, sands and loess-like deposits were distinguished (Fig. 2). Seven of them bear abundant and diverse malacofauna and sparse remains of vertebrates. The sediments under study represent only near-entrance facies of sedimentary fill, with intercalations of colluvial sediments. The lithology and stratigraphy of sediments is presented in Table 1. The chronology of deposition is shown in Table 2.

MATERIAL AND METHODS

Mollusc analysis

Mollusc analysis was conducted using 35 samples (weight 3-5kg) taken at ca. 10cm intervals from 7 layers of the cave sediments during the archaeological excavation conducted in 2012. The excavation was conducted on a N-oriented archaeological metre grid (Fig. 1) and the material was collected from five square meters (C/2, C/3, D/2, D/3, E/3), excavated in the near-entrance facies of the sedimentary fill.

Malacological investigations were carried on in accordance with the schemes proposed by Ložek (1964, 1986, 2000) and Alexandrowicz and Alexandrowicz (2011). Samples were sieved on 0.5mm mesh and carefully cleaned. Mollusc remains, picked up from the samples, were taxonomically determined under a binocular microscope at magnifications up to 64x using taxonomical keys (Kerney *et al.*, 1983; Wiktor, 2004; Welter-Schultes, 2012) and comparative collection of the Department of Climate Geology, Faculty of Geology, University of Warsaw. All completely preserved shells and their identifiable fragments were picked from sediments and counted applying schemes for broken individuals (Ložek, 1964; Alexandrowicz and Alexandrowicz, 2011). Damaged specimens were determined only to the genus or family levels, and the calcareous plates of slugs were counted together under the heading of Limacidae.

Identification of vertebrate taxa

Larger remains of vertebrates were collected directly from the sediment during excavation. The small bones

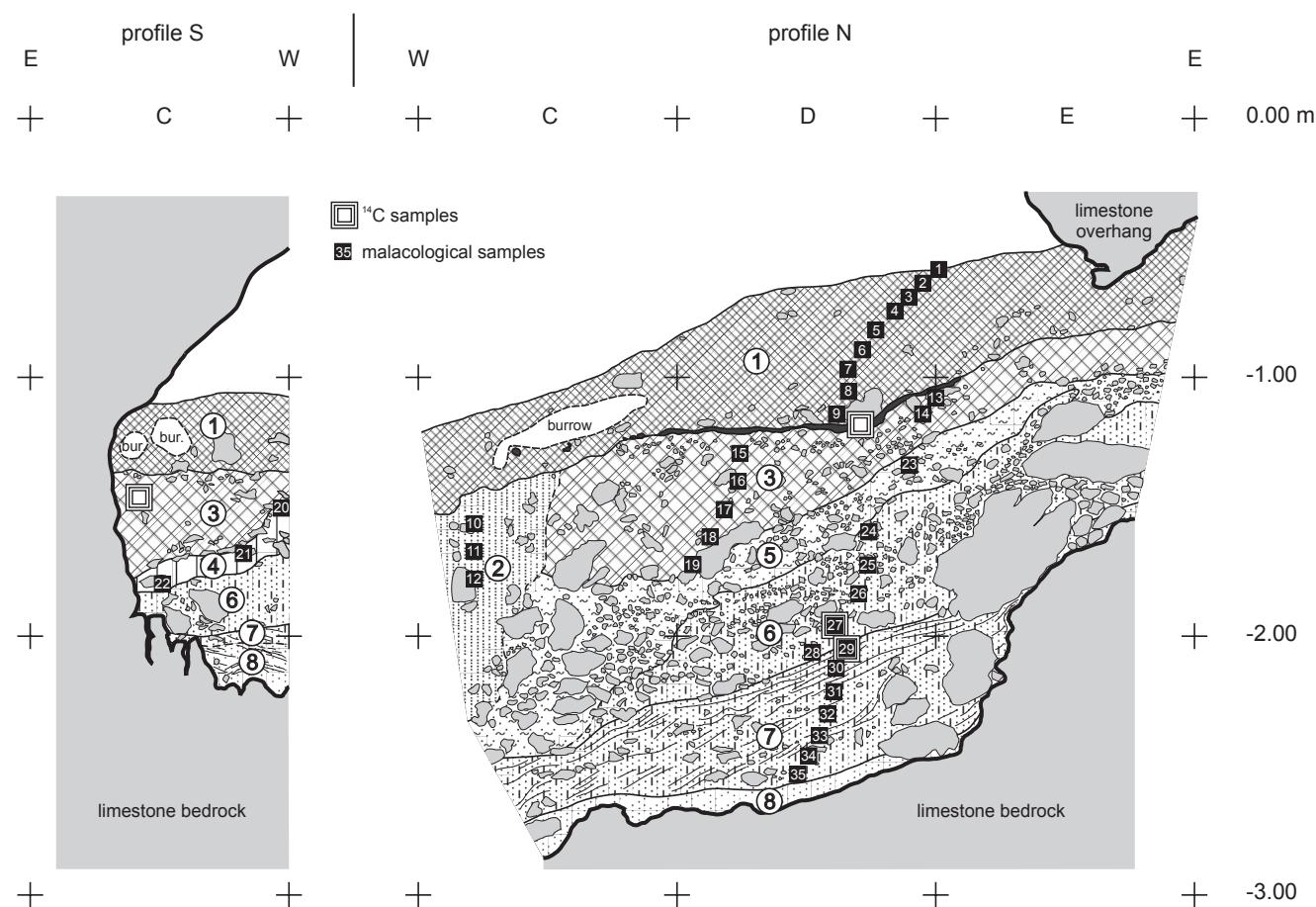


FIGURE 2. Geological cross-section through the sedimentary fill of the Cave above the Słupska Gate (profiles S and N of archaeological trench). For lithological description see Table 1.

TABLE 1. Lithological description and stratigraphy of sediments from the Cave above the Słupska Gate. Stratigraphic units according to Starkel *et al.* (2013). 10YR 4/1, etc.: colours referenced to Munsell colour codes

Layer	Lithology	Stratigraphy
1	Dark brown (10YR 4/1 dry, 10YR 2/2 moist) humic sandy silt with smoothed limestone rubble; the bottom is clear, erosional, and exhibits traces of human activity – it was prepared as a result of artificial leveling of cave bottom for fireplace; the remains of hearth with stone ring and pottery fragments are preserved.	Late Holocene (SA1–SA2); ¹⁴ C date of charcoal suggests pre-Medieval, while pottery fragments Early Medieval period
2	Very dark (10YR 3/1 dry, 10YR 2/1 moist) humic slightly clayey sand with smoothed limestone rubble; the layer occurs only outside the cave and partially forms a lateral variant of layer 3; it exhibits the features of illuviation horizon of cambisol developed in front of the cave entrance; sparse Neolithic artefacts occur.	Middle–Late Holocene (?)
3	Brown to dark brown or dark gray (10YR 5/1.5 dry, 10YR 4/1.5 moist) sandy silt with abundant limestone rubble; occurrence of smoothed clasts is prominent; sparse Neolithic artefacts.	Middle Holocene (at least AT3)
4	Pale brown to dark grayish brown (10YR 6/3 dry, 10YR 4/2 moist) sandy silt with sparse sharp-edged limestone rubble; it forms a small lens of loess-like sediment, occurring only in S part of the trench, between layers 3 and 6, with distinct inclination toward the cave interior.	Early–Middle Holocene (?)
5	Dark gray to grayish brown (10YR 5/2 – 2.5Y 5/2 dry, 10YR 4/1 moist) silty sand with medium amount of limestone rubble, fine in the upper part, coarse in the lower; sharp-edged clasts dominates, but in the middle part smoothed clasts are more abundant.	Early–Middle Holocene (?)
6	Dark gray (10YR 6/2 dry, 10YR 4/1 moist) sandy silt to clayey sand with abundant limestone rubble; coarser and sharp-edged clasts dominate in the upper part; toward the bottom the rubble becomes finer and slightly smoother; the remains of hearth are weakly preserved in the bottom part along with artificially worked flint testing pieces, probably connecting to Mesolithic.	Early Holocene (at least PB)
7	Grayish to yellowish brown and dark brown (10YR 5/2 – 6/4 dry, 10YR 4/3 moist) silty sand to sandy silt, laminated, with participation of limestone clasts varying between laminas; in the upper part clasts are sparse and the smoothed ones occur, while in the lower part clasts are abundant and only sharp-edged ones are present; the laminas of limestone debris with sand deposited by debris flow intercalate with well-sorted sands deposited by washing; the remains of washed hearth are preserved; the sedimentary structures and hearth are disturbed by subsidence.	Late Pleistocene (?)–Early Holocene (PB)
8	Yellowish brown (10YR 6/4 dry, 10YR 5/4 moist) sandy silt with sharp-edged limestone rubble, laminated.	Pleistocene

and teeth were extracted from the same sediment samples studied for molluscs. Specimens were identified to skeletal element and species where possible. The remains of birds were identified with the use of the comparative collection of bird bones of the Institute of Systematics and Evolution of Animals PAS (Kraków, Poland), and those of mammals using the comparative collection of mammalian bones of the Institute of Geological Sciences PAS (Warsaw, Poland). The quantification of examined material follows Lyman (1994,

2008). The abundance of fossil mammal and bird material is very low and it occurred mainly in the uppermost layers 1–3, and only single remains in the lower layers. Altogether, only 72 identifiable remains were discovered.

Palaeoecological analysis

All mollusc species and specimens were grouped according to their environmental preferences (Table I,

TABLE 2. Radiocarbon dating of material from the Cave above the Słupska Gate

Layer	material	radiocarbon determination years BP	calibrated age (probability 95.4%) acc. to OxCal 4.2.4	Lab code
1 (lower part)	Charcoal	1,670 ± 30	1,693–1,666 cal a BP (6.0%)	Poz-51106
			1,660–1,655 cal a BP (0.4%)	
			1,629–1,523 cal a BP (89.0%)	
3	bone (<i>Martes martes</i>)	6,480 ± 40	7,470–7,310 cal a BP	Poz-51107
6	shell (<i>Discus ruderatus</i> , 2 specimens), sample 27	9,210 ± 40	10,496–10,450 cal a BP (13.1%) 10,445–10,252 cal a BP (82.3%)	Poz-61243
7 (upper part)	shell (<i>Discus ruderatus</i>), sample 29	9,570 ± 50	11,125–10,724 cal a BP	Poz-61242

after Kerney *et al.*, 1983; Wiktor, 2004; Alexandrowicz and Alexandrowicz, 2011; Welter-Schultes, 2012) and zoogeographical distribution (Table 3, after Alexandrowicz and Alexandrowicz, 2011). The structure of malacocoenoses was presented on the Malacological Spectra of Species (MSS) and Individuals (MSI) (Fig. 3). Because the spectra are affected by discrepancies in numbers of shells in each sample, the average percentages were also drawn for molluscan assemblages (Fig. 3). Malacological succession was illustrated by the frequency bar diagram (Fig. 4) providing the picture of environmental and climatic changes during the deposition. For samples with more than 50 specimens a percentage of the total sum was calculated, whereas for those containing less than 50 specimens only absolute numbers of shells were declared (Fig. 4). Mollusc assemblages were distinguished subjectively on the basis of their structure and composition. Statistical clustering appeared inadequate due to variable numbers of recorded shells. Zoogeographical distribution was illustrated by diagram of absolute number of species for each zoogeographical group (Fig. 5). Species with corresponding ranges were listed in Table 3. Both the character and succession of the assemblages were used in the palaeoecological and palaeoclimatic reconstructions.

Radiocarbon dating

Radiocarbon dating was conducted in the Poznań Radiocarbon Laboratory (Poznań, Poland) to establish the chronology of the stratigraphic profile. The Accelerator Mass Spectrometry (AMS) method was applied to shells of the snail *Discus ruderatus* representing layers 7 and 6 (samples 29 and 27), the bone of pine marten *Martes martes* from layer 3 (sample SŁ W-26) and the charcoal from the

fireplace found on the boundary of layers 2 and 1 (sample SŁ P-6) (Table 2). Analysed snail shells were composed of aragonite, with no measurable admixture of calcite evidenced by X-ray diffraction analysis, thus the negative effect of recrystallisation was excluded. In case of bone the extracted collagen was dated. All dates presented were calibrated with OxCal v. 4.2.4 (Bronk Ramsey and Lee, 2013) versus the IntCal'13 radiocarbon calibration curve (Reimer *et al.*, 2009).

RESULTS

Mollusc assemblages

Altogether 46 taxa of land snails, including 40 species, 4 genera, one family (Clausiliidae) and a collective group of Limacidae were recognised in the Cave above the Słupska Gate (Table I). They are represented by 1,226 specimens classified in three ecological groups, F: shade-loving taxa (25 species), O: open-country taxa (7 species), M: mesophilous taxa (8 species). The number of taxa and specimens varies between 1 and 24 and 1 and 208 per sample, respectively, with the greatest abundance in layer 3 (Fig. 3; Table I). Four molluscan assemblages can be identified (Fig. 4), differing in their ecological profile.

The assemblage with *Discus ruderatus* and *Semilimax kotulae* (DrSk) occurs between samples 35 and 21 (layers 7, 6, 5 and the lower part of layer 4) (Fig. 4). The concentration of mollusc shells is rather low with one peak in sample 27 (layer 6), mostly related to large numbers of these two species. They are forest species characteristic of a cool, continental climate. The occurrence of glacial relic *Vallonia tenuilabris* is characteristic of this assemblage.

TABLE 3. Mollusc species from the Cave above the Słupska Gate with corresponding zoogeographical ranges (after Alexandrowicz and Alexandrowicz, 2011)

Zoogeographical groups	Corresponding species
Holarctic species	<i>Euconulus fulvus</i> , <i>Cochlicopa lubricella</i> , <i>Vallonia pulchella</i> , <i>Vallonia costata</i>
Palearctic species	<i>Discus ruderatus</i> , <i>Punctum pygmaeum</i> , <i>Nesovitrea hammonis</i>
European species	<i>Vitrea crystallina</i> , <i>Aegopinella pura</i> , <i>Cochlodina laminata</i> , <i>Macrogastera ventricosa</i> , <i>Macrogastera plicatula</i> , <i>Fruticicola fruticum</i> , <i>Carychium tridentatum</i>
Euro-Siberian species	<i>Vallonia tenuilabris</i>
Central-European upland species	<i>Platyla polita</i> , <i>Discus rotundatus</i> , <i>Aegopinella minor</i> , <i>Oxychilus depressus</i> , <i>Cochlodina orthostoma</i> , <i>Balea bispinata</i> , <i>Monachoides incarnatus</i> , <i>Isognomostoma isognomostomos</i> , <i>Clausilia dubia</i> , <i>Laciniaria plicata</i>
Central-European mountain species	<i>Semilimax kotulae</i> , <i>Oxychilus glaber</i> , <i>Macrogastera latestriata</i> , <i>Clausilia cruciata</i> , <i>Monachoides vicinus</i> , <i>Helicigona faustina</i>
Ponto-Caspian and Balkan species	<i>Chondrula tridens</i> , <i>Cepaea vindobonensis</i>
South-European species	<i>Sphyradium dololum</i> , <i>Vitrea diaphana</i>
Atlantic species	<i>Cepaea hortensis</i> , <i>Helicigona lapicida</i>
Boreal-Alpine species	<i>Vertigo substriata</i>
East-European species	<i>Ruthenica filograna</i> , <i>Euomphalia strigella</i>

This is typical loess species usually connected with the severe climatic conditions and open areas of so-called “cold-steppes” (Ložek, 1964), but based on recent data from Asia, it may also occur in alpine grasslands, taiga, hemiboreal forest and wooded fens (Schileyko, 1984; White *et al.*, 2008; Horsák *et al.*, 2010, 2015). Its highest frequency is noted in sample 21, layer 4. The assemblage is composed mainly of shade-loving gastropods, with the proportion of 53 and 74% of all species and all individuals, respectively (Fig. 3). In the middle of the layer 6, the meadow species *Vallonia pulchella* and some mesophilous species of wide tolerance occur frequently – *Nesovitrea hammonis*, *Euconulus fulvus* and the thermotolerant, calciphile *Clausilia dubia*, common on shady and humid rocks. The occurrence of a single shell of a species of higher thermal demands, *Discus rotundatus*, in this assemblage is also noteworthy (Fig. 4; Table I). Two radiocarbon dates relating to this assemblage indicate that it is of Preboreal age (Table 2).

The assemblage dominated by *Discus ruderatus* (Dr) occurs in samples 20–18 (the uppermost part of layer 4 and the lowermost of layer 3). *D. ruderatus* is characteristic of taiga-type coniferous forests. It is accompanied by other shade-demanding gastropods (53% of species and 68% of individuals) *Balea bispinata*, *Fruticicola fruticum*, *Isognomostoma*

isognomostomos and others (Figs. 3; 4). Gastropods of open habitats constitute averagely 16% of all species and 17% of all individuals (Fig. 3), with the most numerous being *Vallonia pulchella*, *Cochlicopa lubricella* and *Euomphalia strigella*. Amongst mesophilous species, *N. hammonis* dominates. From this assemblage upwards *V. tenuilabris* does not occur in studied cave deposits (Fig. 4; Table I).

Above the layer bearing Dr fauna there is a rich assemblage with *Discus rotundatus* (Dro) in the middle and upper part of layer 3 (samples 17–13) (Fig. 4). It is the richest and most abundant assemblage in the succession. *D. ruderatus* still dominates, but forest species requiring humid- and warm conditions: *D. rotundatus*, *Oxychilus depressus*, *Monachoides incarnatus*, *Helicigona faustina* and *Cochlodina orthostoma* become commoner. The assemblage is supplemented by abundant taxa of wide ecological tolerance, which represent 17% of all species and 25% of all individuals (Fig. 3). The most frequent *Laciniaria plicata* and *Helicigona lapicida* become a main component of the fauna in the uppermost part of the profile (Fig. 4; Table I). Distinct reduction in numbers of shells of open-country taxa from 17 to 1% is noteworthy (Fig. 3). The radiocarbon age of a pine

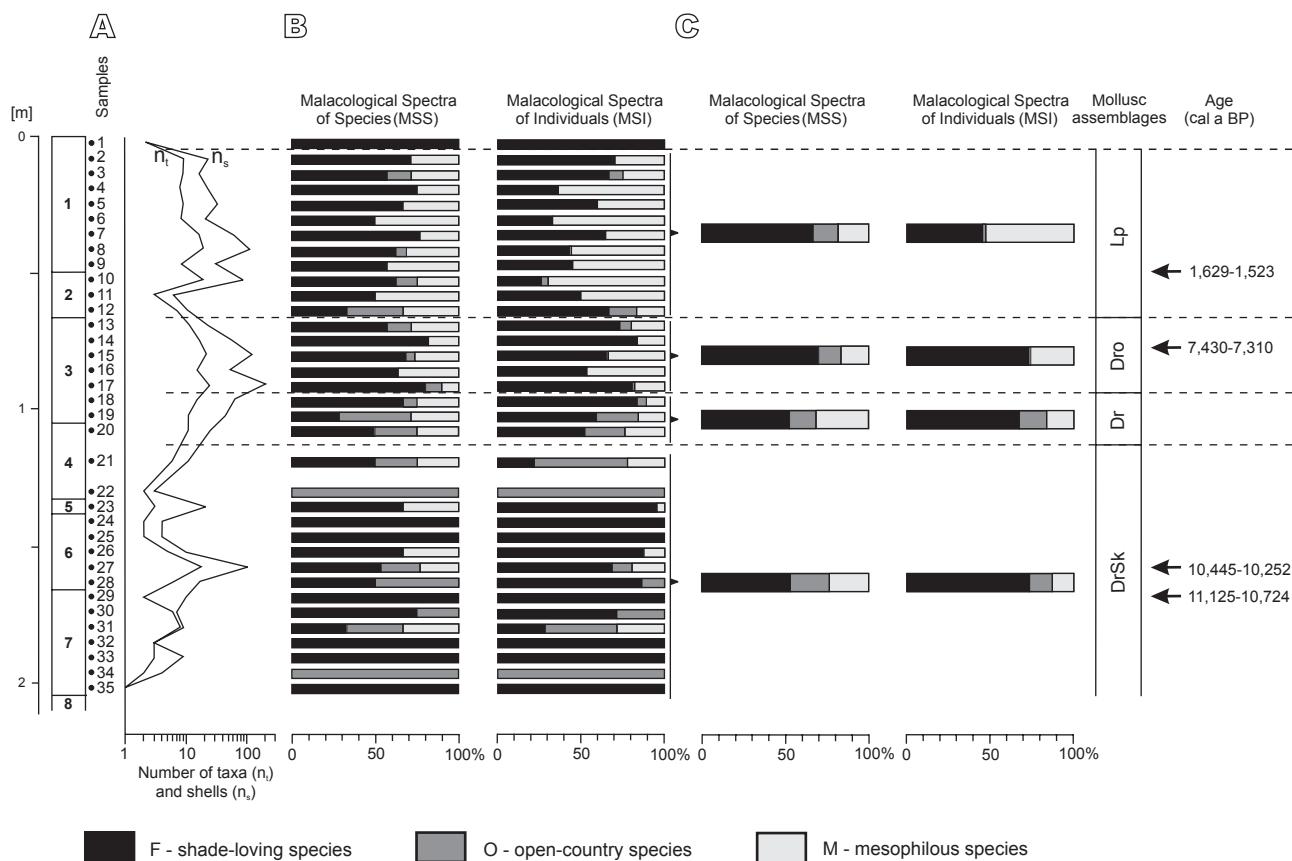


FIGURE 3. Ecological composition of molluscs in the Cave above the Słupska Gate. A) Numbers of taxa and shells per sample. B) Malacological spectra of individual samples. C) Malacological spectra of mollusc assemblages. Mollusc assemblages, DrSk: assemblage with *Discus ruderatus* and *Semillimax kotulae*; Dr: assemblage with *Discus ruderatus*; Dro: assemblage with *Discus rotundatus*; Lp: assemblage with *Lacinaria plicata*.

marten from this layer (Table 2) indicates that this assemblage corresponds to the climatic optimum of the Holocene, the Atlantic phase.

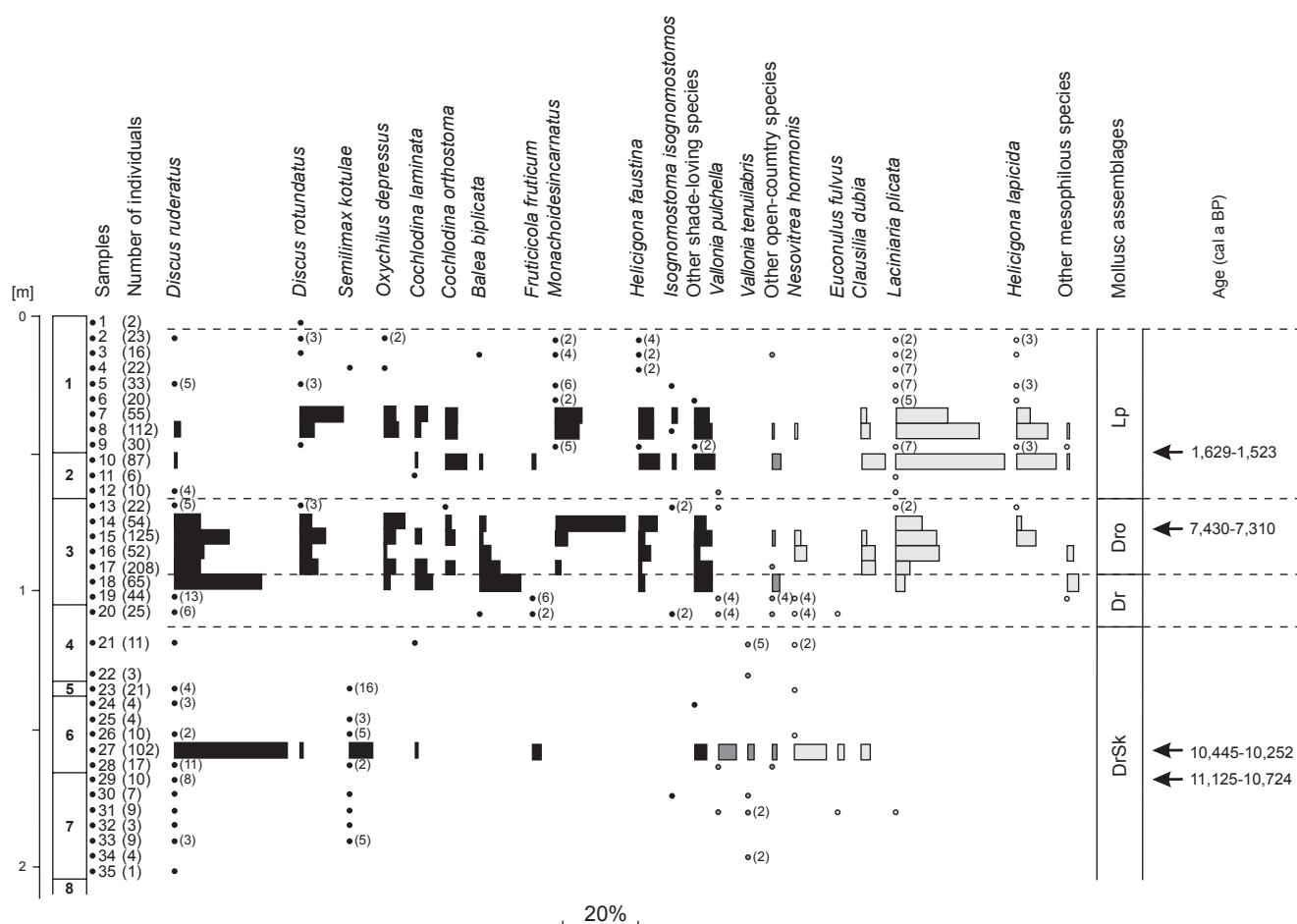
There is a significant change in the character of the mollusc assemblages in the uppermost part of layer 2, and in the whole of layer 1 (samples 11–2) (Fig. 4). These tend to be dominated by *Lacinaria plicata* (Lp). The assemblage is quite rich. The most characteristic of the association is expansion of mesophilous snails (52% of all individuals, Fig. 3) represented mostly by *L. plicata* and *H. lapicida*, most frequent in the humid rocks in open environments and deciduous forests and a shady rocky substrate, respectively. Among shade-loving species the most numerous are *M. incarnatus*, *H. faustina* and *D. rotundatus* also connected with humid rocks and humid forest communities. *D. ruderatus*, characteristic of continental conditions, is still present but in low numbers (Fig. 4; Table I). Sample 1, at the top of the succession, is very poor. The single shell of *D. rotundatus* found cannot be interpreted. Charcoal from the lowest part of layer 1 yields a radiocarbon age of ca. 1,650BP (1,629-1,523cal a BP; Table 2) indicating that layer 1 was deposited within the Subatlantic phase.

Zoogeographical analysis

Species found in the malacofauna of the Cave above the Słupska Gate could be assigned to 11 zoogeographical groups (Fig. 5; Table 3). Although there are minor fluctuations in the proportions of individuals of species belonging to each even in neighbouring samples, there is a broadly bipartite division. The lower part of the profile (layers 7–4) contains mostly Palearctic and Central-European mountain taxa supplemented by Holarctic, European, South-European, East-European, Central-European upland and Euro-Siberian species represented by *Vallonia tenuilabris* (Table 3). In the upper part of the section (layers 3–1), by contrast, Central-European upland species dominate and Euro-Siberian species disappear being replaced by the Atlantic and Ponto-Caspian taxa connected with better climatic conditions (Fig. 5).

Vertebrates

Altogether, 14 mammal taxa and 7 bird taxa have been recognised in the Cave above the Słupska Gate (Table 4). Most of the mammal remains are of rodents.



The forest rodents are represented by 3 species of the family Gliridae (*Glis glis*, *Eliomys quercinus* and *Muscardinus avellanarius*) and Sciuridae with one taxa - *Sciurus vulgaris*. The remains of these species were found in layers 1 and 3, and at the boundary between these layers (1/3). The remains of voles are slightly more abundant. They are represented by woodland and bushy area species (*Clethrionomys glareolus*) and eurytopic species (*Microtus arvalis/agrestis* and *Microtus subterraneus*). Remains of *C. glareolus* and *M. arvalis/agrestis* are the only found in the lower part of the sequence (layers 7–4). Lagomorphs are represented by several remains of *Lepus* sp.

Larger mammals are represented by isolated teeth and fragments of bones. Among them are 4 forest species (*Cervus elaphus*, *Capreolus capreolus*, *Martes martes* and *Ursus* sp.) and one eurytopic species (*Vulpes vulpes*). The bird bones are sparse and represent forest species. Remains of birds and large mammals were found only in the upper part of sedimentary profile, in layers 1–3.

DISCUSSION

Age of deposition

Although we have no dated material from the lowest layer (8) in this cave, its composition of yellowish quartz sands is similar to those underlying Holocene deposits in other caves in the region. In Deszczowa Cave (Madeyska, 1996; Cyrek et al., 2000) these were dated at ca. 19,000BP, and in Krucza Skała Rockshelter to between 11,000 and 13,000BP (Nadachowski et al., 2009; Lorenc, 2013). Both radiocarbon dating and archaeological evidence (Krajcarz et al., 2014a) confirm that the sequence of layers 7–1 in the Cave above the Słupska Gate was accumulated during the Holocene from Preboreal to mid-Subatlantic times. Erosional boundaries and hiatuses are expected in the bottom of layers 7 and 1.

Palaeoecological changes of mollusc fauna

Although there are some discontinuities in the pattern of deposition in the cave, both radiocarbon dating and the

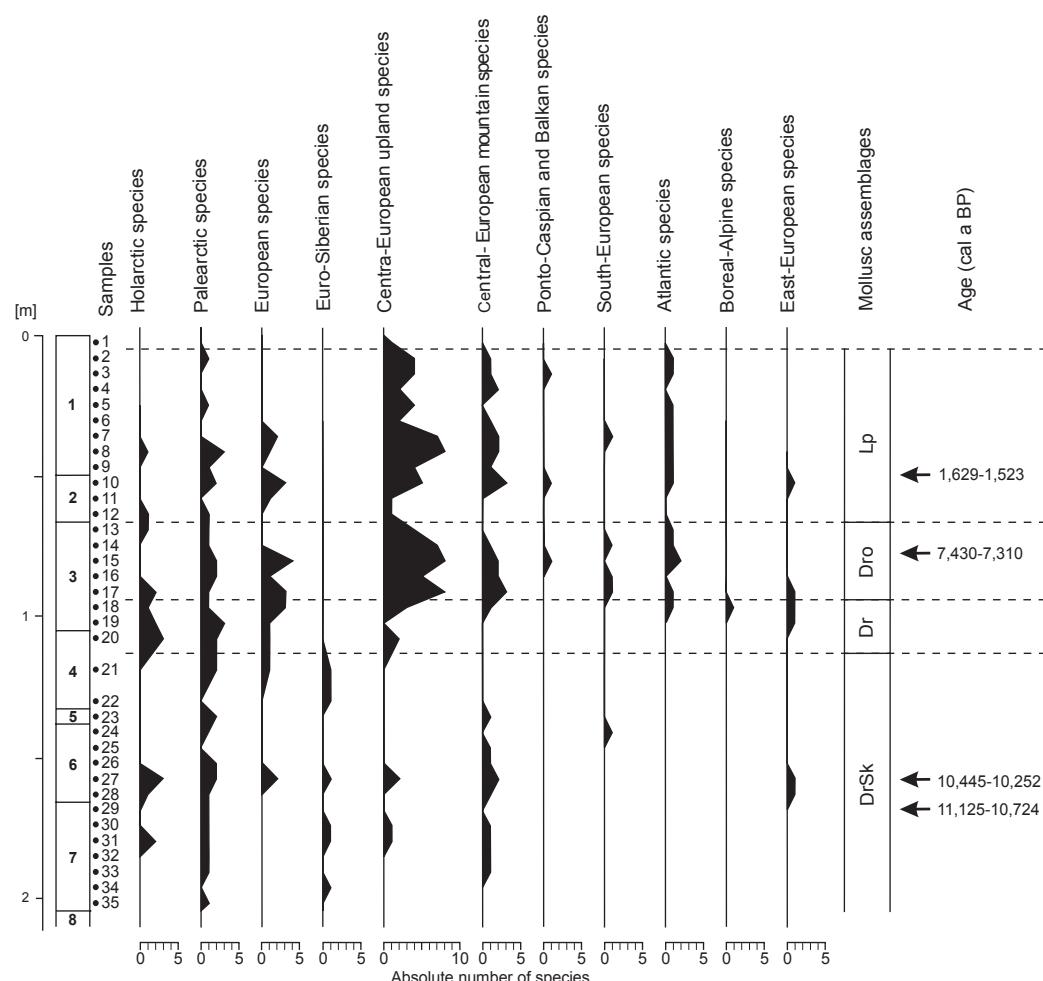


FIGURE 5. Zoogeographical distribution of molluscs from the Cave above the Słupska Gate. Zoogeographical groups after Alexandrowicz and Alexandrowicz (2011).

comparison with other cave deposits in the region (Krajcarz *et al.*, 2016) indicate that the sequence of changes in the malacofauna reflect a chronological sequence of local environmental changes. Despite their polygenetic character the studied thanatocoenoses appear to be representative of the sediments and stratigraphical levels where they occur. The deposits contain shells of some shade-loving species penetrating the cave, of those living in the surface near the cave entrance and shells dropped from the surrounding rocks during sedimentation. Some shells, especially those in laminated deposits (layer 7), might have been washed into the cave from the slope or blown with the wind, but these transports were rather short in time and distances (*cf.* Alexandrowicz and Alexandrowicz, 2011). The shells represent the closest neighbourhood being a good indicator of diversity of habitats around the cave (*cf.* Alexandrowicz *et al.*, 1985; Juřičková *et al.*, 2014). Intrusions from younger deposits caused by animal and/or human activities also occur, but are of minor importance as indicated by the rather environmentally coherent composition of the fauna.

Traces of zoogenic and anthropogenic disturbances were visible during excavation only in layer 1.

The oldest ages of ca. 11,125–10,724 cal a BP, corresponding to the Preboreal phase of the Holocene (Starkel *et al.*, 2013), are represented by the middle part of the assemblage dominated by *Discus ruderatus* and *Semilimax kotulae* (Fig. 6), in the transition between layers 7 and 6. Layer 7 was formed by slope wash, as shown by its lamination and inclination. Despite quick deposition in relatively high energy these sediments are devoid of shell detritus. The rather good state of preservation of shells suggests that they did not undergo intensive transportation, but were accumulated during the deposition. They represent the cave surroundings and it appears that the extremely poor assemblage resulted from severe condition for mollusc development (*cf.* Ložek, 2012; Lorenc, 2013), as Late Glacial origin of the base of this layer cannot be excluded. The latter is not unequivocal, especially in the light of colluvial character of deposits, but similar malacocoenoses

TABLE 4. Vertebrate remains from Quaternary sediments of the Cave above the Słupska Gate: Number of Identified Specimens/Minimum Number of Individuals (NISP/MNI). Slashed numbers among layer numbers (e.g. 1/2) are used for the boundaries between the layers

Taxon	Layer							
	1	1/2	1/3	3	2/3	5/6	6	6/7
small mammals								
<i>Lepus</i> sp.	4/1		1/1	4/1				
<i>Sciurus vulgaris</i> Linnaeus	1/1		1/1					
<i>Clethrionomys glareolus</i> (Schreber)	2/2		2/1	11/4		3/1		1/1
<i>Microtus arvalis/agrestis</i>	2/1			1/1		1/1	1/1	
<i>Microtus subterraneus</i> (de Selys-Longchamps)			1/1	1/1				
<i>Eliomys quercinus</i> (Linnaeus)	1/1							
<i>Glis glis</i> (Linnaeus)	2/1			1/1				
<i>Muscardinus avellanarius</i> (Linnaeus)				1/1				
large mammals								
<i>Ursus</i> sp.	2/2				2/1			
<i>Vulpes vulpes</i> (Linnaeus)	1/1							
<i>Martes marten</i> (Linnaeus)	1/1			1/1				
<i>Martes</i> sp.			1/1	2/1				
<i>Sus</i> sp.	8/2							
<i>Capreolus capreolus</i> (Linnaeus)				2/1				
<i>Cervus elaphus</i> Linnaeus					1/1			
Indeterminata	70/-	3/-	18/-	15/-	13/-			
birds								
<i>Garrulus glandarius</i> (Linnaeus)	1/1							
cf. <i>Garrulus glandarius</i>			1/1					
<i>Turdus merula</i> Linnaeus				1/1				
<i>Turdus</i> sp. (cf. <i>philomelos</i>)	1/1							
<i>Turdus</i> sp. (cf. <i>viscivorus</i>)	1/1							
<i>Periparus ater</i> (Linnaeus)	1/1							
<i>Parus</i> sp. (cf. <i>Poecile palustris</i>)			1/1					
<i>Sitta europaea</i>			1/1					
TOTAL	98/17	3/-	27/8	40/13	16/2	4/2	1/1	1/1

of Late Glacial/Holocene transition predominated by *D. ruderatus* and *S. kotulae*, with the occurrence of species of wide thermal tolerance (e.g. *Euconulus fulvus*) were noted in the landslide deposits and calcareous tufas of southern Poland during the Alleröd interphase (e.g. Alexandrowicz, 1997, 2001a, 2004; Alexandrowicz and Alexandrowicz, 1999). Within layer 6 the lamination disappears and limestone rubble becomes abundant, indicating a change from slope processes to the accumulation of cave debris. The inclination exhibited by layers 6 and 4 suggests that slope processes, such as creep, were still active, but not intensive. The stratigraphy of layers 5 and 4 is uncertain but their position in the profile suggests correlation with the Boreal phase (Fig. 6). According to palaeobotanical data coniferous forests with pine, spruce and larch dominated in the Cracow-Częstochowa Upland of that time. During the periods of deterioration of the climate some transformations to sparse forests with larch and a “park tundra with abundant steppe-like communities” might occurred (Madeyska, 1998). These changes can be hardly interpreted in the poor mollusc assemblage of the sample

set 35–21, but some general environmental characteristic of these units may be defined, as malacocoenoses of the Early Holocene with high proportions of *D. ruderatus* and *S. kotulae* are also known from other sites (e.g. Alexandrowicz et al., 1985). Both species indicate taiga-type communities, relatively low temperatures and humid conditions. Rather cool climate is also evidenced by the glacial relic *V. tenuilabris* which usually disappeared in Central Europe in the Pleistocene/Holocene boundary (e.g. Dagnan-Ginter et al., 1992; Wiktor, 2004; White et al., 2008; Horsák et al., 2010, 2015), but here constitute very characteristic element of the fauna. Accumulation of loess-like deposits with the poor fauna with *V. tenuilabris* may indicate some transformation towards more open areas around the cave, but due to the occurrence of only few individuals this interpretation is open to discussion. Presence of single shells of *Cochlodina laminata* and *D. rotundatus* is not typical of such conditions nor their assumed age, and thus appears to result from re-deposition caused by the activity of burrowing animals. Small mammals in the DrSk assemblage are represented only

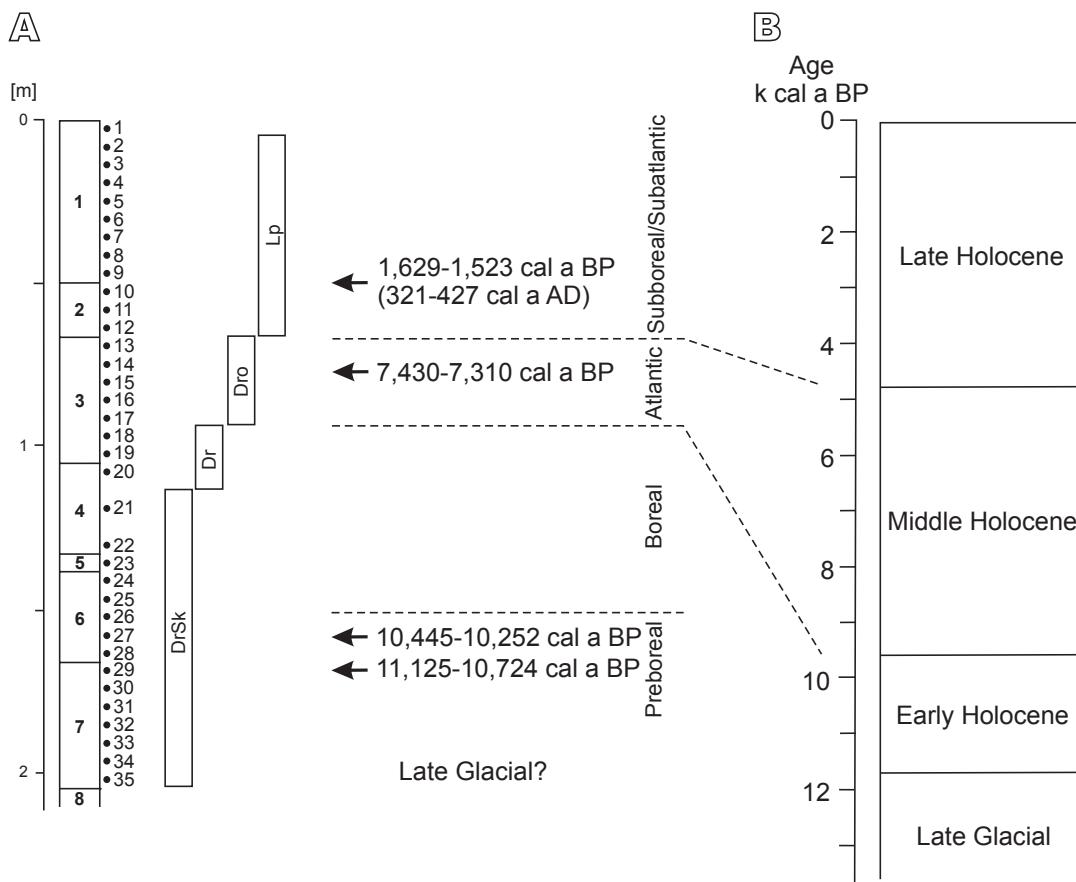


FIGURE 6. A) Stratigraphy and succession of molluscan fauna in the Cave above the Słupska Gate. B) Holocene subdivision according to Starkel et al. (2013). Mollusc assemblages, DrSk: assemblage with *Discus ruderatus* and *Semilimax kotulae*; Dr: assemblage with *Discus ruderatus*; Dro: assemblage with *Discus rotundatus*; Lp: assemblage with *Laciniaria plicata*.

by eurytopic *Microtus arvalis/agrestis* and *Clethrionomys glareolus* mostly associated with arboreal and shrub vegetation but not indicative for certain conditions. Although those species are not diagnostic, similar faunal compositions and biological disturbances are frequent in the Early Holocene cave deposits of the Moravian Karst in Czech Republic (Svoboda *et al.*, 2000).

The final retreat of *V. tenuilabris* population on the Słupsko Hill appears to be correlated with the Boreal phase and the expansion of *D. ruderatus*. This faunal shift is accompanied by many shade-loving species (*e.g.* *Fruticicola fruticum*, *Balea biplicata*, *Isognomostoma isognomostomos*), which indicate an increase of humidity and favourable thermal conditions. Occurrence of weathered, smoothed and pebble-like limestone rubble, starting at level 4, also points to climatic warming and moistening (Krajcarz and Madeyska, 2010). The composition of the assemblage resembles the *Ruderatus*-fauna described by Dehm (1967) and noted in many terrestrial deposits of Early Holocene across Europe between the Preboreal and the older part of the Atlantic phase (*e.g.* Ložek, 1964, 2000; Preece and Day, 1994;

Preece and Bridgland, 1999; Gedda, 2001; Meyrick, 2002; Limondin-Lozouet and Preece, 2004; Limondin-Lozouet, 2011).

The climatic optimum of the Holocene is represented by *Discus rotundatus* assemblage (Fig. 6). Large numbers of both species and shells result from abundant mollusc communities existing around the cave in favourable thermal and moisture conditions (*cf.* Svoboda *et al.*, 2000). Mixed or deciduous forests prevailed in the studied area, as evidenced among others by *Oxychilus depressus*, *Monachoides incarnatus*, *Helicigona faustina*, *Cochlodina orthostoma* and forest rodents *Glis glis* and *Muscardinus avellanarius*. This is in agreement with floristic changes in Central Europe described by, among others, Starkel (1977) and Ralska-Jasiewiczowa (1991). Gradual replacing of *D. ruderatus* by *D. rotundatus* indicates both the progressive warming of the climate and a transition from continental to oceanic circulation (*e.g.* Alexandrowicz, 2004, 2013b; Alexandrowicz and Rybska, 2013; Alexandrowicz *et al.*, 2014), supported in the profile by the expansion of Atlantic and Ponto-Caspian species. The structure of the assemblage

resembles *Discus rotundatus* and *Aegopinella pura* fauna typical of somewhat cooler periods during the climatic optimum of the Holocene, usually in the beginning or in its final part (e.g. Ložek, 1964; Alexandrowicz, 1983, 1992, 2004; Alexandrowicz and Alexandrowicz, 1995b). It may be also supported by still high frequency of *D. ruderatus*. The conditions around the cave were probably not suitable for development of characteristic warmth-demanding *Perspectivus*-fauna noted in many European sites (e.g. Ložek, 1964; Fuhrmann, 1973; Dehm, 1987; Füköh, 1995; Meyrick, 2002; Alexandrowicz and Rybska, 2013; Alexandrowicz *et al.*, 2014) or this part of the optimum is not recorded in the profile of the Cave above the Słupska Gate.

Significant reduction of sediment thickness above layer 3 suggests restricted deposition and/or possible hiatuses in the sequence of mollusc assemblages. Layer 2 may represent the lateral facies of layer 3, accumulated outside of the cave. However, its upper part is probably younger than layer 3. Layer 1, the youngest, originated after intensive human settlement in the cave (1,629–1,523 cal a BP; 321–427 cal a AD), and its lower boundary with layers 2 and 3 is anthropogenic (Krajcarz *et al.*, 2014a) and there is a hiatus between layers 2–3 and layer 1. Some burrows occur in the sediment of layer 1 but mollusc assemblage appears to be free of intrusive elements, as its composition, despite some irregular distribution of shells, is rather constant. Although gradual retreat of forest species noted in Lp assemblage is observed since Subboreal in Central Europe (e.g. Füköh, 1995), the detailed biostratigraphical subdivision for the Late Holocene is practically impossible due to lack of substantial changes in the composition of the mollusc assemblage. Compared to Dro assemblage, the transformation of fauna is evidenced by the expansion of gastropods of wide ecological tolerance with predominance of *Laciniaria plicata* in the Protohistorical and historical periods. Rodents and birds of woodland areas are still present in the assemblage, but abundant *L. plicata* indicates the exposing of open rocky walls near the site. More intensive human activity in the region is possible (Cyrek, 1994; Kruk *et al.*, 1996; Alexandrowicz, 2004; Rozmus *et al.*, 2006; Krajcarz *et al.*, 2014a), but estimation of its influence on malacofauna of the Słupsko Hill is not sufficiently evidenced.

Regional context and comparison with other records

Compared to other records of cave sediments and rocky shelters of Central Europe (Stworzewicz, 1973, 1988; Ložek, 1980, 2012; Alexandrowicz *et al.*, 1985; Bocheński *et al.*, 1985; Alexandrowicz, 1992, 1997, 2000a, b, 2001b; Füköh, 1995; Svoboda *et al.*, 2000; Alexandrowicz and Stworzewicz, 2003) the malacofauna from the Cave

above the Słupska Gate, with their over 40 taxa and 1,200 specimens, appears to be significant for palaeoecological studies of the Holocene and the Late Glacial of the Vistulian. Accumulations of ca. 2m of mollusc-bearing cave deposits is rather unique in the region and occurs only in few sites such as e.g. Veľká Drienčanská Cave in Slovakia (Ložek, 2012) and the Pekárna and Barová caves in the Moravian Karst in Czech Republic (Svoboda *et al.*, 2000). Among dozens of caves, rock-shelters and rocky niches of southern Poland, just a few have more than 20–50cm thick sedimentary fills with mollusc remains, usually corresponding to the Late Holocene (Alexandrowicz, 1997; Alexandrowicz, 2000a, b; Alexandrowicz, 2001b; Alexandrowicz and Rudzka, 2006). The local variability of shell-bearing deposits and of cave thanatocoenoses hinder the regional comparisons, but the main traits of malacofauna evolution over the central European region may be highlighted. Despite some considerable differences in mollusc composition of different regions, the environmental changes and mollusc succession of the Słupsko Hill correlates well with those inferred for Central-European uplands and karstic mountains (e.g. Starkel, 1977; Ralska-Jasiewiczowa, 1991; Alexandrowicz and Alexandrowicz, 1995a; Füköh, 1995; Madeyska, 1998; Alexandrowicz, 2000b; Svoboda *et al.*, 2000; Ložek, 2012). In the Early Holocene most of mid-European cave and other terrestrial records are characterised by low mollusc recoveries (Füköh, 1995; Svoboda *et al.*, 2000; Gedda, 2001; Ložek, 2012). The distinctive feature of Preboreal and Boreal assemblages is the occurrence of *Discus ruderatus*. At Słupsko Hill and in the cave in the Sobczański Gully (Pieniny Mts.) (Alexandrowicz *et al.*, 1985) it is accompanied by *Semilimax kotulae*, but many local variations occur in mollusc composition of that time throughout Europe (Füköh, 1995; Preece and Bridgland, 1999; Svoboda *et al.*, 2000; Gedda, 2001; Meyrick and Preece, 2001; Ložek, 2012). The mid-Holocene optimum in the Cave above the Słupska Gate with a quite rich Dro assemblage and declined open-country species is correlative with abundant forest communities of Moravian, Slovakian Hungarian and German records (Füköh, 1995; Svoboda *et al.*, 2000; Meyrick, 2002; Ložek, 2012). Well marked species-rich optimum is also characteristic of many British and French sequences, but the proportion of woodland species of those is considerably lower than in mid-European assemblages (Juřičková *et al.*, 2014). Those far distant sequences are usually hardly comparable with Central Europe, but record the most critical change of mollusc communities during the Atlantic period noted across many European land sequences. Starting from ca. 9000¹⁴C BP *Discus rotundatus* expanded throughout Europe and gradually replaced *D. ruderatus*, reaching its highest abundance at approximately 8000¹⁴C BP. This transformation was not synchronous and even a one-thousand-years delay may occur between several

countries (Preece and Day, 1994; Meyrick and Preece, 2001; Meyrick, 2002). In Cave above the Słupska Gate the upper part of *D. rotundatus* zone indicated by the date of 7,430–7,310 cal a BP (radiocarbon age of 6,480±40BP) occurs, but its detailed chronology stays open as its lower boundary have not been dated. It is noteworthy that *D. ruderatus* was still abundant around the cave and in smaller numbers survived until today. This is common in mid-European sequences, whereas in Britain it disappeared at radiocarbon age of ca. 7000BP and in France today occurs only in isolated sites in the Pyrenees (Preece and Bridgland, 1999; Welter-Schultes, 2012). The Late Holocene succession is characterised by the limited occurrence of shade-loving and expansion of mesophilous taxa (cf. Füköh, 1995; Svoboda et al., 2000; Ložek, 2012). The mollusc community with the most numerous *Laciniaria plicata* and *Helicigona lapicida* appears to be characteristic of the Słupsko Hill and at the moment is not correlated with any regional trends.

The most distinctive feature in the Cave above the Słupska Gate is the abundance and long occurrence of the glacial relic *Vallonia tenuilabris*, unknown both from the Holocene and most of the cave deposits of Central Europe. Nowadays this species occurs in Siberia, Central Asia and northern China (Dagnan-Ginter et al., 1992; Gerber, 1996; Meng, 2008, 2009; White et al., 2008; Horsák et al., 2010, 2015). It is common in the Late Vistulian loess and loess-loams of southern Poland, but in cave sediments has only been described in the Zawalona Cave and Duża Cave (southern part of the Cracow-Częstochowa Upland) (Alexandrowicz et al., 1992; Dagnan-Ginter et al., 1992; Alexandrowicz and Alexandrowicz, 1995a). In the latter it was accompanied by abundant forest species, thus some reworking and intermixing of the mollusc material was postulated (Dagnan-Ginter et al., 1992). It can never be excluded in cave sediments, but geological situation and sediment features in the Cave above the Słupska Gate do not indicate significant reworking of sediments and shell material, and a vast occurrence of *V. tenuilabris* from dry steppes to various woodland habitats in Asia, provides alternative ways of interpretation. Another appearance of this species in recently studied caves and shelters of the Cracow-Częstochowa Upland (Krajcarz et al., 2016) may confirm microclimate favourable for longer existence of this species in the Early Holocene and offers a perspective on further studies of the problem.

CONCLUSIONS

Sediments of the Cave above the Słupska Gate contain differentiated mollusc assemblages. Their composition and structure reflect the depositional conditions around the cave during the Holocene and possibly the final part of the

Late Vistulian. The detailed stratigraphic subdivision is not unequivocal, some hiatuses occur, but the Early, Middle and Late Holocene are quite well marked in the succession. The development of malacofauna indicates both the environmental and climatic changes of that time. The oldest, rather poor fauna (Late Glacial/Preboreal and/or Preboreal) is typical of a cold climate and light coniferous forests. The shade-loving taxa were the main component of mollusc assemblages, but episodes of drying and cooling of the climate are evidenced by the loess-like deposition and expansion of open-country snails with glacial relic *V. tenuilabris*. The latter disappeared in the younger part of the Early Holocene. The main phase of development of malacocoenoses correlates with the Middle Holocene. Radiocarbon dating provides age characteristic of the Atlantic phase. The climatic optimum is characterised by the abundant, differentiated fauna characteristic of mixed and deciduous forests and distinct oceanic influences. Malacological record of the Late Holocene may bear some gaps. Forests still existed in the surroundings of the site, but more areas appear to be relatively poorly vegetated, especially rocky walls around the cave. Gastropods of wide ecological amplitude dominated in the assemblage being the main component of the fauna during the Protohistorical and historical period noted in the uppermost part of the succession. The cave sequence on the Słupsko Hill corresponds to the malacological records of Central-European uplands bearing some individual characteristics, especially the long occurrence of glacial relic *V. tenuilabris*.

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ELECTRONIC APPENDIX I

TABLE I. Molluscs from Quaternary sediments of the Cave above the Słupska Gate. E: ecological groups (after Alexandrowicz and Alexandrowicz, 2011), F: shade-loving taxa, O: open-country taxa, M: mesophilous taxa

E	TAXON	LAYERS/SAMPLES																																				
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35		
F	<i>Platyla polita</i> (Hartman)																																					
F	<i>Sphyramidium doliolum</i> (Bruguière)																																					
F	<i>Discus ruderatus</i> (Férussac)	1																																				
F	<i>Discus rotundatus</i> (Müller)	1	3	1																																		
F	<i>Semilimax kotulae</i> Westerlund																																					
F	<i>Vitrea diaphana</i> (Studer)																																					
F	<i>Vitrea crystallina</i> (Müller)																																					
F	<i>Aegopinella pura</i> (Alder)																																					
F	<i>Aegopinella minor</i> (Stabile)																																					
F	<i>Oxychilus glaber</i> (Rossmässler)																																					
F	<i>Oxychilus depressus</i> (Sterki)	2	1																																			
F	<i>Cochlodina laminata</i> (Montagu)																																					
F	<i>Cochlodina orthostoma</i> (Menke)																																					
F	<i>Ruthenica filigrana</i> (Rossmässler)																																					
F	<i>Macrogaster ventricosa</i> (C. Pfeiffer)																																					
F	<i>Macrogaster plicatula</i> (Draparnaud)																																					
F	<i>Macrogaster latestriata</i> (Schmidt)																																					
F	<i>Clausilia cruciata</i> (Studer)																																					
F	<i>Balea biplicata</i> (Montagu)	1																																				
F	<i>Fruticicola fruticum</i> (Müller)																																					
F	<i>Monachoides incarnatus</i> (Müller)	2	4																																			
F	<i>Monachoides vicinus</i> (Rossmässler)																																					
F	<i>Helicigona faustina</i> (Rossmässler)	4	2	2																																		
F	<i>Isognomostoma isognomostomos</i> (Schröter)																																					
F	<i>Cepaea hortensis</i> (Müller)																																					
O	<i>Cochlicopa lubricella</i> (Porro)																																					
O	<i>Vallonia pulchella</i> (Müller)																																					
O	<i>Vallonia costata</i> (Müller)																																					
O	<i>Vallonia tenuilabris</i> (Braun)																																					
O	<i>Chondrula tridens</i> (Müller)																																					
O	<i>Euomphalia strigella</i> (Draparnaud)																																					
O	<i>Cepaea vindobonensis</i> (Férussac)																																					
M	<i>Carychium tridentatum</i> (Risso)																																					
M	<i>Vertigo substriata</i> (Jeffreys)																																					
M	<i>Punctum pygmaeum</i> (Draparnaud)																																					
M	<i>Nesovitrea hammonis</i> (Ström)																																					
M	<i>Euconulus fulvus</i> (Müller)																																					
M	<i>Clausilia dubia</i> Draparnaud																																					
M	<i>Laciniaria plicata</i> (Draparnaud)	2	2	7	7	5	10	32	7	33	1	1	2	5	17	8	11	2																				
M	<i>Helicigona lapicida</i> (Linnaeus)	3	1	3	1	3	12	3	12		1	1	9																									
TOTAL		1	17	12	11	25	9	40	88	20	76	2	6	15	37	95	28	125	37	32	21	9	1	21	4	3	8	83	15	8	4	7	2	8	2	1		
	<i>Vallonia</i> sp.																																					
	<i>Discus</i> sp.																																					
	<i>Monachoides</i> sp.	1																																				
	<i>Cepaea</i> sp.		1																																			
	<i>Limacidae</i>	5	2	3	3	3	3																															
	<i>Clausiliidae</i>	2	6	1	6	10	15	10	6	4	1	1	4	22	8	69	22	1																				
TOTAL		1	6	4	11	8	11	15	24	10	11	4	4	7	17	30	24	83	28	12	4	2	2	1	2	19	2	2	3	2	1	1	2					
TOTAL TAXA		2	9	9	8	9	8	16	19	8	19	3	7	11	16	22	15	24	15	11	6	2	3	2	2	5	18	6	2	6	8	3	3	2	1			
TOTAL INDIVIDUALS		2	23	16	22	33	20	55	112	30	87	6	10	22	54	125	52	208	65	44	25	11	3	21	4	4	10	102	17	10	7	9	3	9	4	1		