Chapter 5

# Ice Age Terrestrial and Freshwater Gastropod Refugia in the Carpathian Basin, Central Europe

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**Abstract**

Thanks to its unique microclimatic, geomorphological , hydrological conditions forming a mosaic-like environment present at all scales, numerous Late Tertiary and Pleistocene warmth-loving gastropod taxa managed to find refugee within the Carpathian Basin during the major-minor cold spells of the Ice Age. This complex system of refugia have been continuously functioning and evolving since the Late Tertiary through the entire Pleistocene and the Holocene. To understand the spatial and temporal evolution of refugia, detailed paleoecological investigations have been implemented, results of which are summed here. The high-grade fractal-like complexity of the environment led to the emergence of a so-called dual refugia, which is a unique feature of the Carpathian Basin. This temporally parallel but spatially differing presence of habitats for taxa of contrasting ecological needs was noted for paleotemperature gradients and temperate woodland and steppe habitat types as well. Furthermore, detailed geological and paleoecological analysis of a small Pleistocene hot-spring fed pond revealed information about the evolution of endemic thermophylous freshwater gastropod taxa within this microrefugia. This chapter is aimed to give an overview of the nature, evolution of temperate terrestrial and freshwater gastropod refugia present in the Carpathian Basin during the Ice Age.

**Keywords:** gastropods, refugia, evolution of mollusk biota, ice age, Carpathian Basin, Central Europe

## 1. Introduction

Embraced by the rugged peaks of the Carpathians, Alps, and Dinaride Mts lies the Carpathian Basin covering an area of ca. 300,000 km$^2$ at the boundary of Central and Southeast Europe

(**Figure 1**). During the ice ages, glaciers were strictly restricted to the Alps with only sporadic occurrences in the adjacent Carpathians leaving the entire basin ice-free [1]. Moreover, permafrost was restricted to the northern rim alone [2–4]. Numerous scientific postulations emerged from as early as the late nineteenth and early twentieth centuries, according to which several Late Tertiary and Pleistocene warmth-loving (thermophilous) gastropods could have found refugee within the Carpathian Basin during the major-minor cold spells of the ice age. This proposed system of refugia must have been continuously functioning and evolving from the Late Tertiary through the entire Pleistocene up to the Holocene. Most of these postulations were made about a single member of a gastropod family, whose representatives were widespread in Europe during the Tertiary: the Melanopsidae. This taxon was first reported during the mid-nineteenth century by the Austrian geologist, von Bregrath Franz Ritter Hauer, from a hot-water spring-fed thermal lake (Lake St. Ladislaus, Püspökfürdő) (**Figure 2**) found near the city of Nagyvárad (today Oradea) [5]. It must be noted though that the German natural scientist Phillippi who gave the first taxonomic description of the gastropod taxon *Melanopsis parreyssii* in his seminal volume from 1847 [6] (page 176 and Table 4, Figure 15) mentions Hungary as the type locality and the Austrian naturalist von Mühlfeld as the collector. Unfortunately, not a single word is given about the exact locality or the time and area of von Mühlfeld's visit. No further details on how the specimen described were attained.

Although there is no exact way to prove that the referred specimen was collected from Püspökfürdő (Baia Mai 1, Romania today), this assumption cannot be fully refuted either, as modern occurrences of this taxon are strictly restricted to a single locality, the referred thermal lake, with no others known. The first detailed geological description of the lacustrine deposits and the embedded Melanopsis taxa comes from the Austrian geologist von Heinrich Wolf [7].

His profile, located at the lakeshore, starts with an embryonic humus layer [7]. The lack of a map displaying the exact location, orientation of his work, as well as the environmental changes of the past centuries hampered the later comparative use of his first description. Yet his work is by no means futile as the major geological units identified and described by him were clearly traceable in later works on the lacustrine deposits as well. So, the referred gastropod taxa appear in later publications from the late nineteenth century as well [8]. Despite the promising start, the first detailed presentation on the Quaternary mollusk fauna of Püspökfürdő, including morphological changes observed on the shells of Melanopsidae, was given only in 1890 by the Hungarian amateur naturalist Mihály Tóth on the 25th Congress of Hungarian Medical Doctors and Naturalists held in Nagyvárad (Oradea) [9]. He presented a series of mollusk shells collected via singling from a 2-m-deep profile. In addition, based on the observed variations, he lined up an evolutionary series with numerous members. In his view, the lake harboring the *Melanopsis* taxa is older than the so-called Old Alluvial (presently known as the Holocene epoch). Thus, these gastropods must derive from a Tertiary ancestor, whose descendants managed to survive the cold periods of the Diluvial (Pleistocene epoch). His work is the first presentation of the referred ice age refugia hypothesis in Central Europe. Considering the formerly accepted relatively short time

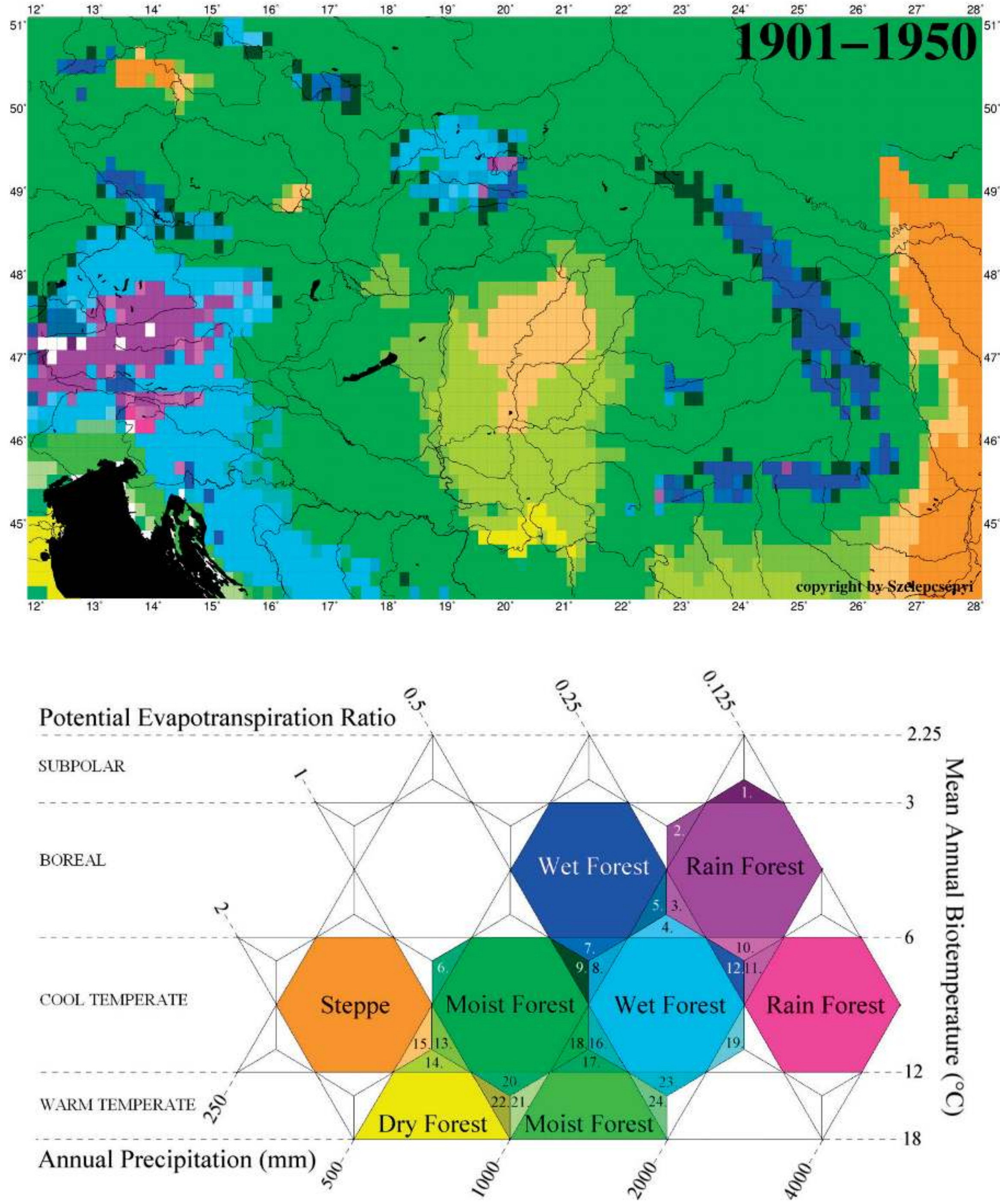


**Figure 1.** Location of the sites mentioned in this study on the Holdridge-type bioclimatological map of Szelepcsényi et al. [69]: (1) Lake St. Ladislaus, Püspökfürdő-Nagyvárad (Baia Mai 1, Oradea, Romania); (2) Petény rock shelter (Bükk Mts, Hungary); (3) Rejtek rock shelter (Bükk Mts, Hungary); (4) protected marshland, Bátorliget (Nyírség, Hungary); (5) Selyemrét, Ócsa (Danube-Tisza interfluve, Hungary); and (6) brickyard (Crvenka, Serbia).

span of the Pleistocene at ca. 600 Ky [10–11] compared to the modern known value of 2.58 My [12–16], his postulation is rather remarkable considering our modern understanding of speciation and macroevolution.

**Figure 2.** View of thermal Lake St. Ladislaus near Nagyvárad-Püspökfürdő (Oradea, Bai 1 Mai, Romania) in 1999 preceding its complete desiccation.

Tóth's work gave a major impetus to further detailed malacological studies on the mollusk fauna of the lake in the forthcoming decades involving the two internationally known malacologists of the Austro-Hungarian Monarchy: the Croatian Spiridon Brusina and the Hungarian Tivadar Kormos as well [17–21]. Their work included the genera *Melanopsis* and *Theodoxus* as well. Brusina examined the shells collected by Tóth, in addition to the ones collected by himself from the surficial deposits alone [17]. No profiles or boreholes were deepened to yield him stratigraphically reliable data and samples, which had serious consequences leading to erroneous observations and statements in the future. In his work Brusina identified eight different taxa of the *Melanopsis* genus, including the first described *Melanopsis parreyssii*. In addition, 23 varieties were mentioned. Unfortunately, his work is lacking a detailed taxonomic description and figures, having only a short diagnosis of each taxa in two or three sentences [17]. Brusina, based on his readings of the works of a paleobotanist Móric Straub [22, 23] describing a special waterlily from the thermal lake, considered the mollusks as representatives of a remnant Subtropical Tertiary oasis. Tivadar Kormos on the other hand prepared a new 11-m-deep composite profile near the one by Tóth after careful consideration of the geology and geomorphology of the area and the available publications [8–9]. Kormos gave a detailed description of the stratigraphy and geology in addition to the identified *Theodoxus* and *Melanopsis* taxa including the ones described by Brusina [18–21]. What is more a geological compilation of regionally available boreholes is also given along with maps displaying the exact location of these including his own and Tóth's profile as well. Thus, Kormos' seminal work could have been considered as a reliable foundation for our future research. The most important bullet points of his work are:

- Taxa of the genera *Melanopsis* and *Theodoxus* (*Neritina)* identified in the lacustrine deposits must have a Tertiary common ancestor. In his view, this ancestor must be found in the Late Tertiary mollusk fauna of the southern parts of the Carpathian Basin.
- Some taxa of the genus *Melanopsis* from Lake St. Ladislaus have clear evolutionary relationship with certain taxa of the genus *Fagotia* (considered as *Melanopsis* by him), especially the ones of *Fagotia acicularis* and *Fagotia esperi* [20]. These latter two taxa now known as *Esperiana* (*Microcolpia*) *daudebartii acicularis* (Férussac, 1823) and *Esperiana* (*Fagotia*) *esperi* (Férussac, 1823) are considered to be Pontian from a biogeographical point of view by certain researchers [24]. However, cyclical recurrence of these taxa in the malacofauna of the Carpathian Basin is connected to the warmer periods of the Pleistocene, that is, interglacials, and by no means to the Neogene Period (Tertiary) [25, 26].

It must be emphasized though that the presence of a special waterlily *Nymphaea lotus thermalis* in Lake St. Ladislaus leads numerous botanists to the conclusion that the area is a true subtropical relict of a former geological period [22, 23, 27, 28] despite a clear objection of other botanists, who were highly skeptic regarding the origin and age of immigration of the referred plant taxon [29, 30]. So Kormos simply adopted the generally accepted scientific notion of his era along with another famous malacologist studying the modern mollusk fauna of the region: Lajos Soós [31, 32].

WWI brought a sudden halt to malacological investigations. The only exception is perhaps an article published by Pauca [33] following the 1933 conservation of the site. Pauca kept only two taxa *Melanopsis parreissi* and *Melanopsis sikorai* from the ones listed by the former researchers providing highly questionable justification for his choice. In addition, no reason was given why these two were considered to be relict taxa from the Late Tertiary. His views were systematically adopted in later studies on the Romanian mollusk fauna [34] as well as the malacofauna of the region [24, 35] despite Diaconesa and Popa's works from the 1960s [36, 37], who clearly justified a Holocene timing of waterlily the invasion into the thermal lake. The origin and evolution of the Melanopsidae of Lake St. Ladislaus are far from settled and are a constant subject of scientific debates [38–42]. Yet, as it is an important hallmark in the question of Carpathian Basin refugia, a brief discussion based on our latest findings is presented in the next chapter.

WWI meant an end not only to malacological research done on the unique Melanopsidae of Lake St. Ladislaus but on the question of refugia in Hungary and Central Europe as well. Not long after, however, studies implemented on the woodland mollusk fauna of a species-rich marshland near Bátorliget, NE Hungary initiated another debate regarding a potential refugia for temperate mollusk taxa in the basin during the ice age [43, 44]. Evidence for the survival of temperate woodlands in the Carpathian Basin during the Pleistocene was first presented between 1956 and 1969 by the paleobotanist József Stieber based on his detailed anthraconomical studies of wood remains deriving from cave sites in the Bükk Mts and loess/paleosol profiles from different parts of Hungary [45–48]. Thirty years after Stieber's seminal work, members of a British-Hungarian research group managed to independently corroborate the idea of Stieber on the presence of temperate woodland refugia in the Carpathian Basin [49–56]. Besides the presence of woodland refugia, ice age refugia for several temperate grassland elements have also been recently identified [57–61]. Detailed malacological studies starting from the 1980s and the accompanying reconstruction of Late Glacial and Holocene vegetation changes have brought the question of ice age refugia into focus again [54, 55, 62–65]. Complementing comprehensive paleoecological investigations of loess/paleosol sequences from various parts of the basin using numerous biotic proxies (mollusks, phytoliths, alkanes) clearly highlighted the presence of temperate grassland refugia in the southern parts of the Great Hungarian Plain and its wider surroundings [53, 54, 66–70]. In the following chapters, a short overview of the results of these works is also presented in addition to those of freshwater and woodland mollusk refugia.

## 2. Ice age refugia in hot-water springs and lakes: Lake saint Ladislaus, Nagyvárad-Püspökfürdő (Lake Petea, Oradea region)

In 1999, following the works of Kormos [18–21] and Tóth [9], a new 2-m-deep geological profile was created in the littoral part of Lake St. Ladislaus adjacently to the one of Tóth by members of our Geoarcheological and Quaternary Paleoecological research group. In addition, numerous undisturbed cores were also taken to delineate the spatial distribution of the identified stratigraphic horizons. Another 8.4-m-deep profile was dug next to that of Kormos in 2012 as part of a bilateral Romanian-Hungarian project, this time in the fully dried-up lakebed. The first geological profile spans the interval from the Late Glacial, while the 2012 one dates back to the last glacial maximum (LGM) of the last glacial.

Lithological observations made on the shorter profile are fully congruent with the one made by Tóth [9]. The profile starts with coarse silt-rich clayey lacustrine silts followed by lacustrine carbonate muds ending in highly altered peats representing the final desiccation of the lakebed. The stratigraphy of the longer, more recently established profile is much more complex recording several sedimentary changes. Nevertheless, the ice age part here is likewise represented by clayey, fine-silty coarse silts similarly to the bottom part of the shorter profile. A significant increase in the carbonate content is recorded only from the Late Glacial part of the profile, which also means that the more complex lithology is restricted to the upper Holocene parts. Samples from both profiles are fossiliferous yielding representatives of the

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gastropod taxon *Melanopsis*. However, for our final evaluation, the material of the longer profile was used. Here a larger volume of samples (ca. 30 l) yielded several thousand shells yielding better representativity of the original mollusk fauna. The forms and varieties described by Tóth [9], Brusina [17], and Kormos [18–21] were all present in the studied samples from both profiles [38, 39]. The identified taxa were further investigated using X-ray photographs of the shells (**Figure 3**) as this way even minor morphological and size differences could have been noted as well.

After a meticulous study of shell variations from different parts of the profile, a clear evolutionary lineage could have been outlined. In the layers corresponding to the LGM as well as the Heinrich 1 event [71–73], smooth shelled forms prevailed, displaying a close affinity to the taxon *Fagotia acicularis* [*Esperiana* (*Microcolpia*) *daudebartii acicularis*]. Other morphological varieties or taxa were clearly missing from these horizons. This horizon and its dominant taxon were missed in the works of Neubauer and his colleagues [41, 42], because their analysis was restricted to museum specimens representing those of the surficial collections made by Brusina [17] and the 2-m-deep profile of Tóth [9]. So the projection of their findings to our 8.4-m-deep profile [38, 39] is highly misleading, similarly to their delineation of the Pleistocene–Holocene boundary [41]. According to the recorded 14C age of a charcoal piece from the depths of 596–600 cm in our profile (10,789–11,185 cal BP years), the majority of the profile can be dated to the Holocene. The Pleistocene/Holocene boundary could have

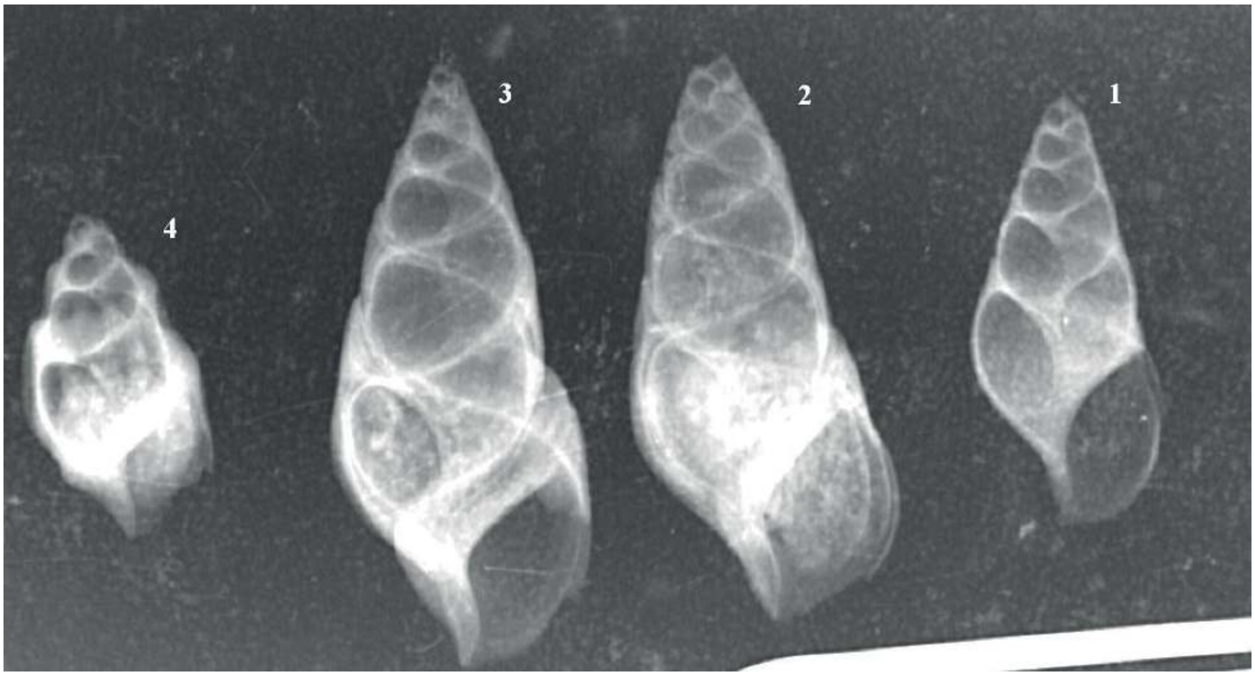


**Figure 3.** X-ray photographs of shells of various *Esperiana* (Microcolpia) taxa identified from Lake St. Ladislaus, Nagyvárad-Püspökfürdő (Oradea, Baia 1 Mai, Romania): (1) *Esperiana* (*Microcolpia*) *daudebartii acicularis* [*Fagotia acicularis*] (Férussac, 1823), (2) *Microcolpia parreyssii sikorai* (Brusina, 1903), (3) *Esperiana daudebartii daudebartii* (Prevost, 1821) [*Esperiana daudebartii acicularis F. thermalis*], and (4) *Microcolpia parreyssii parreyssii* (Philippi [6]).

been placed between 600 and 620 cm in our 8.4-m-deep profile. So, during the LGM, forms of the *Melanopsis* taxa displaying a close affinity to *Fagotia acicularis* [*Esperiana (Microcolpia) daudebartii acicularis*] were present. A longer type of this taxon with a thicker shell turns up in the Late Glacial part of the profile termed as *Fagotia acicularis F. thermalis* besides another smaller type which was described as *Melanopsis hazayi* by Brusina [17]. In addition, several other forms, taken to represent individual taxa by researchers during the late nineteenth and early twentieth centuries, turn up here as well (*sublanceolata*, *szontaghi*, *mucronifera*, *tothi*, *hazayi*, *staubi*, *franciscae*, *vidovici*, and *hazayi*) [9, 17, 18–21]. The appearance of these various new forms is clearly connected to a major environmental change noticed in a sudden increase in the carbonate content and water-soluble Ca and Mg content of the samples. This marked change in the geochemistry and the lithological character was so strong that it must signal a significant increase in the water temperature of the hot spring and the lake during the Late Glacial following the H1 event compared to temperatures characteristic for the LGM. It is also the horizon, where the first smooth, keeled, and shouldered shell forms of *Melanopsis* are recorded, though subordinately. These smooth, keeled, and shouldered shells having spiral striae running parallel with the suture are similar to the ones of the taxon *Melanopsis sikorai* (Brusina [17]). On the basis of these observations, we can postulate that the ecophenotypes leading to the evolution of the endemic taxon *M. parreyssi* inhabiting the modern lake must have emerged even during the Late Glacial. The opening of the Holocene marked the appearance of further sculpted, shouldered forms (*M. sublanceolata*, *M. staubi*), but the Late Glacial ecophenotypes were also preserved. The Early and Middle Holocene are characterized by an outstanding variety of shell forms. The Holocene also marks the disappearance of the smooth forms displaying close affinity to *Fagotia acicularis* [*Esperiana* (*Microcolpia*) *daudebartii acicularis*] including the taxa determined as *M. hazayi* and *Fagotia acicularis F. thermalis*. The Late Holocene corresponding to the last 2000 years is characterized by an increase in the organic content of the lacustrine deposits marking the transition to a marshland at the end of the Iron Age. By this time the presence of ribbed and shouldered forms can be attested representing the so-called *Melanopsis hungarica* assemblage (*M. hungarica*, *M. themaki*). It is also the time when the first representatives of the modern endemic taxon *Microcolpia* (*Melanopsis*) *parreyssii parreyssii* (Phillipi [6]) turn up. This endemic taxon represents the final member of an evolutionary lineage starting from the Late Pleistocene ancestor *Esperiana* (*Microcolpia*) *daudebartii acicularis* through various Late Glacial and Holocene ecophenotypes. Findings of detailed genetic analysis have independently corroborated our assumptions regarding the evolution of this taxon [74].

The final part of the story is rather heartbreaking as this unique Middle Pleistocene refugee forming a cradle for various endemic gastropod taxa, including *Theodoxus prevostianus*, is bound to fully disappear in a couple of years. The last members of the endemic *Microcolpia* (*Melanopsis*) *parreyssii parreyssii* (Phillipi [6]) are living among artificial conditions in the aquarium of a Hungarian research institute thanks to the quick response of dedicated zoologists to the human-induced desiccation of the lakebed of Lake St. Ladislaus. Although there have been measures taken to restore the previous conditions, the newly created artificial thermal lake system may not fully be capable to fulfill its preservational role as refugia in the future. Yet our records have clearly pointed to the importance of hot-water spring-fed thermal lakes in the preservation of mollusks even during the coldest periods of the ice age in the area of the Carpathian Basin. As several such systems are known from various parts of the basin as well as the transitional zone to the Carpathian Mts, one can presume that these also could have a significant role in the survival of warmth-loving mollusk taxa during the cold spells of the ice age.

## 3. Ice age woodland refugia in highlands between the elevations of 500–700 m ASL: Petény cave and Rejtek 1 rock shelter, Bükk Mts, NE Hungary

Excavations starting in the 1950s as part of a collaborative work of vertebrate paleontologists, anthracologists, and archeologists in two cave systems found in the Bükk Mts in NE Hungary yielded outstanding records regarding the presence of ice age woodland refugia in a highland setting of the Carpathian Basin [45–48, 75–78]. One of the studied caves was formed in Triassic limestone at an elevation of 735 m ASL (Petény Cave) (**Figure 1**). The other, the Rejtek rock shelter, found at an elevation of 500 m ASL was formed in Jurassic limestone. Both cave systems are facing south. According to the retrieved vertebrate fauna and recovered archeology, sediment accumulation must have initiated from the terminal part of the last glacial in these karstic depressions. Fine-stratigraphic sampling of the identified lithological horizons yielded numerous charcoal pieces. The taxonomic composition of these charred plant remains indicated the emergence of mixed taiga woodland at this elevation during the last stage of the last glacial [45–48]. Besides the clear dominance of spruce and Scots pine, scattered patches of deciduous elements like elm, oak, lime, maple, beech, ash, as well as hazel were also present in these woodlands. On the basis of this information, József Stieber came up with the idea regarding the presence of ice age woodland refugia for temperate thermomesophylous trees in the Carpathian Basin for the first time [45–48]. Unfortunately, his observations were by no means welcomed by the majority of Hungarian botanists of his time. It was only in 1999 when a British-Hungarian research group managed to corroborate his presumption independently [49–52, 55, 56]. The samples taken by Stieber and his colleague Dénes Jánossy yielded numerous terrestrial mollusk shells, which were handed over for further evaluation to the late Endre Krolopp, an outstanding Quaternary malacologist of the late twentieth century. The malacological remains of both caves have been scientifically evaluated along with a revision of the charcoal remains complemented by 14C dating of the major stratigraphic units sampled in the 1950s [55, 56]. According to the results of these investigations, Central European woodland mollusk elements prevailed in this area from even the last glacial onward (**Figure 4**).

The prevailing taxon of the Late Glacial horizon is *Cochlodina cerata*. The modern distribution of this taxon's habitat is found in the area of the Northern, Northeastern Carpathian Mts ranging from the lower alpine woodlands of the foothills to the upper alpine woodlands to a height of ca. 1000 m [79–84]. Consequently, the studied region in the Bükk Mts, NE Hungary, between the elevations of 500–750 m ASL must have acted as an ice age

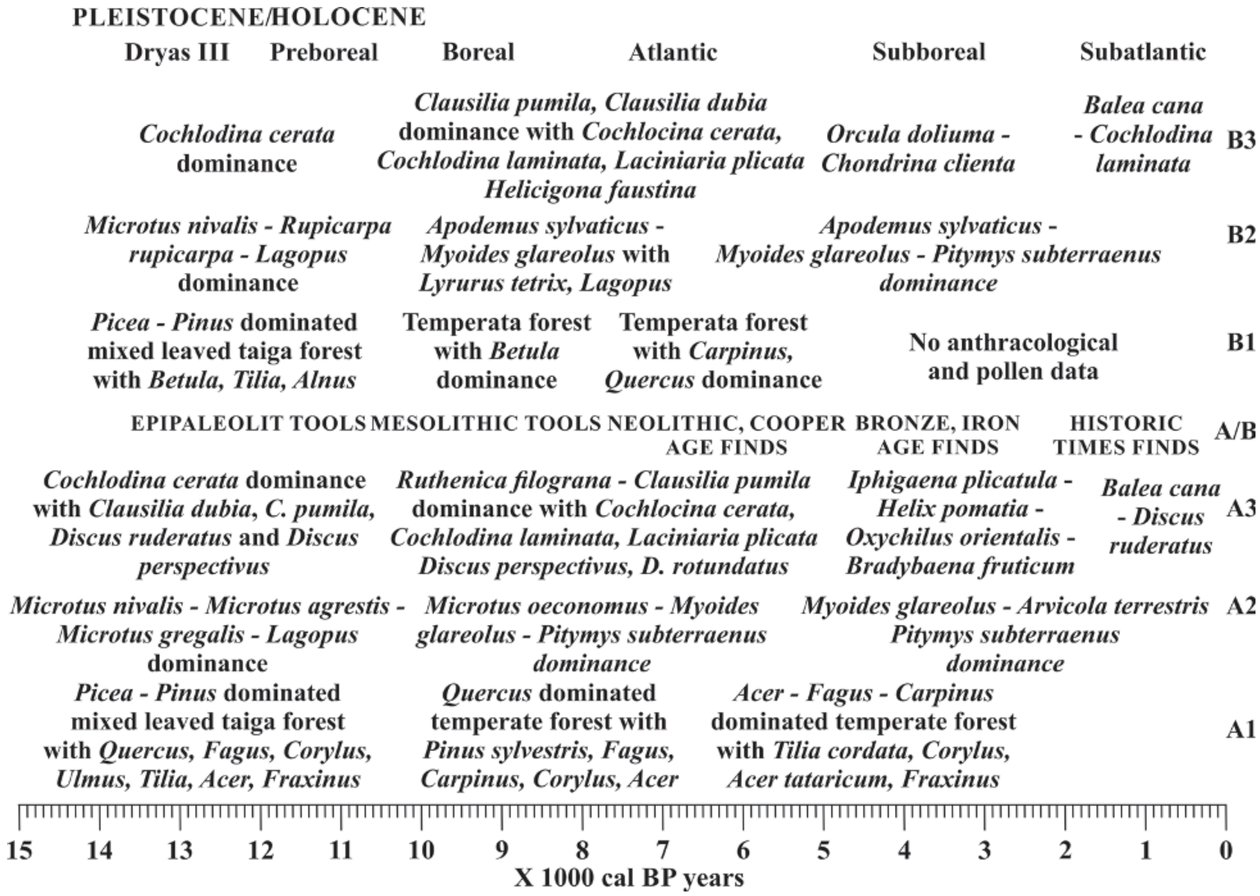


**Figure 4.** The radiocarbon-dated palaeoecological data from Petény (Peskő II) and Rejtek rock shelters A1 = anthracological-based vegetation phases of the sequence in the Rejtek site, A2 = mammalian phases of the sequence in the Rejtek site, A3 = local malacological zones of the sequence in the Rejtek site, A/B = archeological finds and times in the analyzed sites, B1 = anthracological- and pollen-based vegetation phases in the Petény site, B2 = mammalian phases of the sequence in the Petény site, and B3 = local malacological zones of the sequence in the Petény site.

refugia for woodland mollusk taxa [49–55, 64]. These findings have been corroborated by later studies on the Quaternary mollusk fauna of the Hungarian Highland and the Western Carpathians [85–90]. It must be noted that in Ref. [90], radiocarbon results presented span the Holocene Epoch alone. Cold-loving and cold-resistant elements in the accessory fauna of the *Cochlodina cerata* horizon are represented by a single taxon, presently dwelling in beech and pine woodlands: *Discus ruderatus*. However, warmth-loving elements like *Bradybaena fruticum* and *Euomphalia strigella* have also been recorded in this part of the profiles. Consequently, the general composition of the mollusk fauna is clearly in line with the observations and conclusions made on the basis of charcoal remains. Namely, the presence of refugia for temperate thermophilous woodland taxa within a Late Glacial mixed taiga forest [45–52]. The Late Glacial presence of *Discus perspectivus* as well as the records of the mollusk taxa *Cochlodina cerata*, *Cochlodina laminata*, *Clausilia dubia*, *Clausilia pumila*, and *Laciniaria plicata* in the layers representing the Pleistocene/Holocene transition is a highly outstanding feature of the sites. The collective appearance of *Discus perspectivus* and *Discus ruderatus* indicates the development of a dual refugia in the study area [49], i.e., the collective presence of Pleistocene cold-resistant and cold-loving elements with warmth-loving

Holocene taxa during the Late Glacial in the Carpathian Basin as postulated earlier on the basis of paleoecological, geological, geochemical, and sedimentological observations made at the environmental historical site of Bátorliget marshland discussed in the next chapter [55]. According to our findings, rock walls and rock surfaces with a southern exposure in the inner Subcarpathian zone of the Carpathian Mts at suitable heights between 800 and 500 m ASL must have had special microclimatic conditions (angle of incoming radiation, minimal height for air humidity condensation), which allowed for the emergence of temperate woodland refugia [53–56, 67], even during the coldest periods of the ice age [91, 92]. Similar woodlands could have developed at the ecotone of floodplains and foothill areas of island-like hills in the heart of the basin as well [93, 94].

## 4. Ice age refugia at the interface of windblown sand dunes and floodplains: examples from the Bátorliget marshland, Nyírség region, NE Hungary, and the Ócsa marshland, Danube-Tisza interfluve, Central Hungary

The highly protected area of the Bátorliget marshland is situated on the NE part of the Great Hungarian Plain (GHP) approximately 2 km west of the state border with Romania in the area of the Nyírség alluvial fan covered by windblown sands (**Figure 1**). The Ócsa marshland is on the other located at the NW part of the GHP at the fringe of the Danube Lowland in an area of scattered windblown sand dunes. Both sites are located in an interdune depression hosting initially an oligotrophic lake during the ice age, which developed into a calcareous lake system finally evolving into a eutrophic lake then a marshland. According to the available absolute chronology, the emergence of an oligotrophic lake initiated around 20–22 ka during the coldest period of the last glacial: the last glacial maximum (LGM). However, the first mollusk remains turn up in deposits dated to the Late Glacial only. Shells of the Pontian *Pomatias rivulare*, the Central European woodland dweller *Discus perspectivus*, as well as the Boreal woodland dweller *Discus ruderatus*, presently populating the alpine woodlands of the Carpathian Mts, turn up as early as the transitional zone between the Late Glacial and the Postglacial in the profile of the Bátorliget marshland. This paleoassemblage composed of cold-loving and thermophilous elements can be clearly synchronized by the findings of pollen analysis indicating the presence of a mixed taiga hosting stands of pine and various temperate arboreal elements [55, 95]. These records thus indicate the development of a mixed taiga woodland at the interface of windblown sand and floodplain areas in the NE part of the GHP during the ice age, whose composition was the same as the mixed taiga woodlands of the foothill areas mentioned in the previous chapter. A significant difference in the mollusk faunas is the appearance of a Pontian gastropod taxon, which evolved during the Tertiary in the Carpathian Basin [96, 97], in the marshland sequence. This gastropod taxon, the *Pomatias rivulare*, has a clear preference for milder climatic conditions (**Figure 5**).

A similar paleoassemblage was identified in the Postglacial/Holocene deposits of the Ócsa marshland. However, in this latter profile, the Pontian *Pomatias rivulare* is substituted by


**Figure 5.** The European distribution of *Pomatias elegans* and *Pomatias rivulare* and their Hungarian fossil, pre-modern and modern occurrences. Horizontal black line = European distribution of *Pomatias elegans*; vertical black line = European distribution of *Pomatias rivulare*; white cross = Hungarian Pleistocene distribution of *Pomatias elegans*, Vértesszőlős, Tata, and Budai Várhegy; white stars = Hungarian modern distribution of *Pomatias elegans*, Bérbaltavár, Tihany, Őrtilos, Zákány, and Zákányfalu; white circle = Hungarian Holocene distribution of *Pomatias elegans*, Szurdokpüspöki, Esztergom, Budapest—Rákos-patak, Ócsa, Kiskörös, Fehérvárcsurgó, and Keszthely—Fenékpuszta, Kisapáti, Tapolca, Celldömölk, Ménfőcsanak, Balf, and Fertőboz; white pentagon = modern Hungarian distribution of *Pomatias rivulare*, Bátorligeti marshland, Szekszárd Sötét-valley, and Nagymányok; white rectangle = Hungarian Holocene and subrecent distribution of *Pomatias rivulare*, Bátorligeti marshland, Bátorliget Fényi-forest, and Vámospércs Jónás region.

its Atlanto-Mediterranean vicariant counterpart: *Pomatias elegans*. The radiocarbon-dated appearance of these latter taxa in the Ócsa profile is the oldest recorded one in Europe several thousand years before the first Atlantic distribution records of the taxon [98, 99]. On the basis of this record, the assumption that the Atlantic and Central European distribution of this taxon is connected to the Middle Holocene [100] must be refuted. The appearance of *Pomatias* *elegans* coevally with our Hungarian records was noted in the Early Mesolithic cultural layer of the Italian Grotta di Latronico Cave as well. Shells of this taxon have been retrieved in deposits older than 9000 cal BP years and those dated to the Postglacial and Early Holocene as well [101]. Representatives of this taxon with similar ages have been reported from Iberia [102] as well as Southern France [103]. In these latter examples, the first representative of the gastropod taxon *Pomatias elegans* likewise appears in layers older than the Mesolithic horizon dated at 9000 cal BP years.

To sum up briefly, the mollusk fauna dated to the opening of the Holocene in the areas of the Ócsa and Bátorliget marshland was a woodland dweller one characterizing temperate closed woodlands. This Early Holocene fauna is marked by the appearance of such taxa, which are restricted to the areas of the Carpathians, the Transylvanian Mid-Mountains, and the Hungarian Mid-Mountains and unique to the Great Hungarian Plains, serving as outstanding indicator species in both the stratigraphy and the paleoenvironmental conditions because they tended to appear in the mildest interglacial periods enjoying the greatest rainfall during the Pleistocene [25, 26]. The exuberant woodland malacofauna is made up of highly tolerant species appearing in uniform quantities in the closed woodland environment, which inhabit the mountains of Central Europe and are widespread in the area extending from the Balkan Peninsula up to the Baltics. The most characteristic elements of this community are the following: the Carpathian-Baltic *Ruthenica filograna*, *Macrogastra latestriata*, and *Bulgarica cana*; the Carpathian *Perforatella vicina*; the Central European *Acicula polita*, *Laciniaria plicata*, and *Perforatella bidentata*; the Central and Southern European *Discus perspectivus* and *Oxychilus glaber*; the European *Carychium tridentatum*, *Vertigo pusilla*, *Ena obscura*, *Vitrea crystallina*, *Aegopinella pura*, and *Cochlodina laminata*; and the Euxinic *Pomatias rivulare* or Atlanto-Mediterranean *Pomatias elegans*.

Both regions hosting the referred marshland had direct connections with the foothill areas of the surrounding mid-mountains, the south facing escarpments via the river valleys based on our subfossil distribution data of the mentioned woodland elements. It was these foothill areas which functioned as refugia for woodland elements from the Postglacial onward [55, 56].

## 5. Ice age refugia of temperate forest steppe and steppe gastropods: The results of quaternary malacological investigations on the loess/paleosol sequence of the Crvenka brickyard, northern Vojvodina, Serbia

The findings of Quaternary mollusk analyses implemented on radiocarbon-dated loess/paleosol sequences from the eastern half of the Carpathian Basin in the 1980s have clearly revealed that the Late Pleistocene environment of the Carpathian Basin was far from being uniform [54, 55, 64]. These observations gave an impetus to further comparative paleobiogeographical investigations using our malacological records deriving from different parts of the basin and covering the period of the Late Pleistocene. To highlight the environmental conditions characteristic of the southern part of the basin, our findings on the mollusk fauna of a Northern

Vojvodinian loess/paleosol sequence at the brickyard of Crvenka are presented in the following part [69, 104, 105]. The observed features of the malacofauna are in line with the ones made at other loess/paleosol profiles from the Southern GHP, spanning the same time period [54, 55, 67, 68]. A comparative analysis of these profiles with that or Crvenka enabled us to reconstruct the Late Glacial paleobiogeography of the southern part of the basin and tackle the spatial distribution of refugia for temperate forest steppe and steppe gastropod elements. Changes observed in the mollusk fauna of the Crvenka loess/paleosol profile are in line with climatic fluctuations recorded in the NGRIP Greenland ice core. The presence of numerous interstadial horizons representing the Greenland Interstadials between GI17 and GI2 could have been identified (**Figure 6**). The relatively low resolution of sampling hampered the identification of all GI events at the centennial scale. Based on our malacological data, the milder periods were characterized by higher temperatures and decreasing humidity resulting in a fixation and expansion of short grassland vegetation and the accompanying steppe-dwelling mollusk elements, while the cooler periods experienced only a minor drop in temperature and increasing humidity favoring the expansion of high grasses and some arboreal elements (scattered trees and bushes).

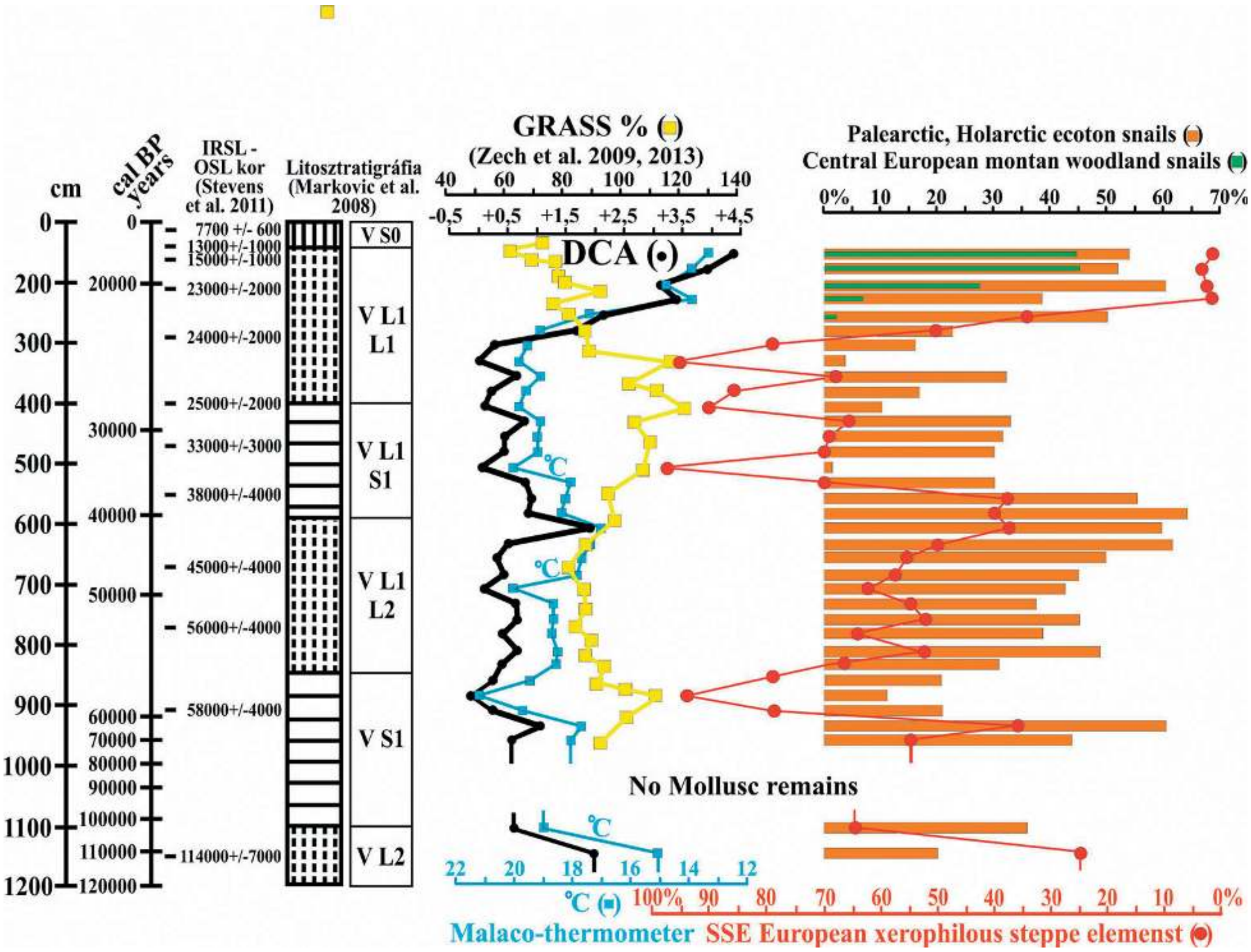


**Figure 6.** Fluctuations of different palaeoecological indicator groups on the late Pleistocene loess/paleosol sequence of the brickyard at Crvenka (northern Vojvodina, Serbia).

This type of change is especially pronounced in the horizon corresponding to the last glacial maximum. During this time an expansion of cold-loving, tundra-dweller mollusks is recorded in the northern and western ice-free areas of Europe. Conversely, this period is characterized by the appearance of closed woodland dwelling mollusks coevally with the cold-loving Arcto-Alpine elements. According to the trends observed, the southern parts of the GHP were characterized by fluctuating expansions and retreat of short grass and high-grass grasslands during the warmer and cooler periods of the late glacial. Thanks to the mosaic-like complexity of these habitats, mollusk taxa with contrasting ecological preferences regarding humidity, temperature, and vegetation cover could have existed side by side during the Late Pleistocene. Humidity increases during the coolings favored the expansion of mollusks resulting in a highly diverse fauna. Conversely, the warmer periods creating drier conditions decreased the diversity.

This unique feature of the southern part of the Carpathian Basin is by no means a newly described phenomenon. It has been known for ca. 30 years that compositional changes in the mollusk fauna of the southern parts of the basin are utterly different from those recorded in the other parts of the Carpathian Basin as well as in northern, western, and eastern Europe [54, 64, 67, 94, 106]. The most important difference is seen in the constant presence of xerothermophylous grassland elements (*Cochlicopa lubricella*, *Granaria frumentum*, *Pupilla triplicata*, *Chondrula tridens*, and *Helicopsis striata*) during the entire Late Pleistocene and their clear dominance in periods corresponding to the interstadials [67, 69]. It must be noted that the dominance peaks of the individual taxa in different profiles of the Southern GHP may not be fully coeval thanks to variations in local environmental and microclimatic conditions. Yet the general fluctuations of the similar warmth-loving paleoecological groups in time are synchronous between the individual profiles [67, 69].

It is also important to note that during the stadials characterized by only small temperature drops, the dominant elements of the mollusk fauna were those of the Holarctic forest steppe and high-grass-steppe dwellers, primarily members of the taxon *Vallonia costata*. During the interstadials, the fauna was prevailed by taxa characteristic of short grass Pontian grassland dwellers, which occupy the central driest Pannonian forest steppes of the Carpathian Basin (*Cochlicopa lubricella*, *Granaria frumentum*, and *Helicopsis striata* paleoassemblage). At the same time, elements of Holarctic forest steppes were also present in the malacofauna, although highly subordinately. Similarly, the Pontian grassland elements were likewise present in the mollusk assemblages of the stadials.

All these data indicate the presence of an ecotone of temperate Pannonian forest steppe-steppe areas composed of highly complex patches of short and high grassland types between 60,000 and 24,000 cal BP years. The recurring macroclimatic changes of the Late Pleistocene controlled a cyclical expansion and retreat of these environmental mosaics [67]. The best indicator element of temperate grasslands is *Granaria frumentum*. The largest aerial distribution of this taxon is recorded during the Late Glacial ca. 60 ka in the Carpathian Basin. During this time the presence of this taxon could have been observed in the areas of the Transdanubian Mid-Mountains in Western Hungary and the Sub-Carpathian alpine region as well besides that of the GHP. This spatial distribution must have developed during the last interglacial

(MIS 5), when this taxon expanded to almost all areas of Central Europe, including the Czech Basin [107], the Vienna Basin [108], as well as the Alps and the Carpathian Mts to a height of ca. 1000 m ASL [25, 26, 109]. All these indicate the expansion of temperate forest steppes to the foothill areas and the lower highlands during the drier periods of the last interglacial characterized by higher temperatures as well. After 60 ka, marking the onset of the last glacial, there is a gradual retreat in the distribution of *Granaria frumentum* to scattered habitats characterized by favorable microclimatic conditions. There is another major expansion of the referred taxon which can be dated between 40 and 30 ka. The highest dominances are recorded in the southern parts of the GHP with gradually decreasing northward trends. There is a major retreat between 30 and 24 ka to scattered refugia found in the southern part of the Carpathian Basin again, which hallmarked the start of the coldest phase of the last glacial. According to the findings of comprehensive studies done using our own mollusk data compiled into a database (Hungarian Quartermalacological Database), the southern part of the GHP, including the area of Vojvodina, Serbia, as well, was a transitional fluctuation zone between the refugia of the southern foothills of the Carpathians, the marginal area of the Dinarides and its northern island hills. This zone harbored an ecotone of temperate Pannonian grassland and forest steppe during the warmer, drier periods of the Late Pleistocene. Conversely, this vegetation complex was replaced by a boreal forest steppe during the cooler periods, similar to the taiga steppes of Southern Siberia today. This special evolution of the vegetation is utterly different from that of the northern parts of the Carpathian Basin as well as Northern, Western, and Central Europe. The difference is attributable to the regional and local higher temperatures of the ice age resulting in drier conditions in the former areas. Thus the most important ecological driver, regarding the evolution of both the vegetation and the mollusk fauna, in the southern areas of the basin was humidity. The higher aridity of this area during the Late Glacial is attributable partly to the high distance from the seas and oceans. In addition, the intensification of the so-called basin effect as a result of the uplift of the surrounding mountains.

## 6. Concluding remarks

The area of the Carpathian Basin is characterized by a large-scale environmental mosaicity present on the scale of the basin. This complexity increases downward to the regional and local scales. The major driving factor on the scale of the basin is the regional overlap of various climatic influences ranging from the Atlantic, Alpine, and Continental influences to the Sub-Mediterranean-Pontic climatic effects. According to our data, this type of mosaic-like complexity of the environment developed even during the ice age and controlled the evolution of the mollusk fauna both on the regional and local scales. Geomorphology, bedrock, groundwater table, exposition, as well as soil conditions further increased the macro-scale mosaicity on the regional and local scales. These regional environmental mosaics functioned as the ice age refugia for terrestrial and freshwater warmth-loving gastropods. Long-term conservation of these is the key to the preservation of the natural biota of the basin among changing climatic conditions.

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