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PALEOENVIRONMENTAL AND NEOTECTONIC INSIGHTS FROM THE PLIOCENE FOSSIL RECORD OF VELIKA PASICA CAVE, SLOVENIA: IMPLICATIONS FOR KARST SYSTEM EVOLUTION

VPOGLED V PALEOOKOLJE IN NEOTEKTONSKE PROCESE NA PODLAGI PLIOCENSKEGA FOSILNEGA ZAPISA IZ JAME VELIKA PASICA, SLOVENIJA: POMEN ZA RAZVOJ KRAŠKEGA SISTEMA

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Abstract UDC 551.442:551.3.051:592/595(24+28)(497.4)
Andrej Mihevc, Ivan Horáček, Nadja Zupan Hajna, Jon Woodhead & Anton Brancelj: Paleoenvironmental and neotectonic insights from the pliocene fossil record of Velika Pasica Cave, Slovenia: Implications for karst system evolution
Velika Pasica Cave, situated on a karst plateau at an altitude of 665 meters above sea level, offers a unique record of paleontological, speleological, and tectonic processes. The cave, predominantly filled with allogenic sediments and speleothems, contains fossilized remains of the aquatic cave invertebrate *Marifugia cavatica* and terrestrial small mammals, characteristic of the early Pliocene (MN15–16). Paleontological dating estimates the cave sediments to be approximately 4 Ma old, while U/Th dating of the overlying flowstone indicates deposition at 410 ± 21 ka. These findings suggest that stagnant phreatic conditions prevailed prior to tectonic uplift and basin subsidence, which reshaped the karst landscape. This study highlights the dynamic interplay between neotectonics, karst system evolution, and biodiversity changes. By integrating speleobiology, geomorphology, and biostratigraphy, it provides valuable insights into the environmental history of the northern Dinarides and the impact of geological processes on karst ecosystems.
Keywords: paleontology, *Marifugia cavatica*, small mammals, karst geomorphology, cave sediments dating, tectonic.

Izvleček UDK 551.442:551.3.051:592/595(24+28)(497.4)
Andrej Mihevc, Ivan Horáček, Nadja Zupan Hajna, Jon Woodhead & Anton Brancelj: Vpogled v paleookolje in neotektonske procese na podlagi pliocenskega fosilnega zapisa iz jame Velika Pasica, Slovenija: pomen za razvoj kraškega sistema
Jama Velika Pasica, ki leži na kraški planoti na nadmorski višini 665 metrov, nudi edinstven zapis paleontoloških, speleoloških in tektonskih dogajanj. Jama, pretežno zapolnjena z alogenimi sedimenti in sigami, vsebuje fosilne ostanke vodnega jamskega nevretenčarja *Marifugia cavatica* ter kopenskih malih sesalcev, značilnih za zgodnji pliocen (biocona MN15–16). Paleontološke analize kažejo, da so sedimenti stari približno 4 milijone let, medtem ko U/Th datacije na njih odložene sige kažejo na odlaganje pred približno 410 ± 21 tisoč leti (ka). Ti rezultati nakazujejo, da so v jami pred tektonskim dvigom in pogrezanjem bazena prevladovali mirni freatični pogoji, kar dokazuje prisotnost *M. cavatica*. Študija izpostavlja dinamično prepletanje neotektonskih procesov, razvoja kraškega sistema in sprememb v biotski raznovrstnosti. Z združevanjem spoznanj iz speleobiologije, geomorfologije in biostratigrafije prispeva dragocena spoznanja o okoljski zgodovini severnih Dinaridov ter o vplivu geoloških procesov na kraške ekosisteme.
Ključne besede: paleontologija, *Marifugia cavatica*, mali sesalci, kraška geomorfologija, datacija jamskih sedimentov, tektonika.

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1. INTRODUCTION

This study focuses on Velika Pasica Cave (Velika Pasica), located on a karst plateau above the Ljubljansko Barje plain (i.e. Ljubljana Marsh, Ljubljana Basin) in central Slovenia (Europe; 45° 55'7.87" N 14° 29'34.97" E), in the northernmost part of the Dinaric Mountains (i.e. Dinaric Karst, Dinarides). This region forms the characteristic karst landscape and is also the predominant relief type in southern Slovenia.

The Dinarides extend in a southeast to northwest direction along the northern edge of the Adriatic Sea. The main features of the karst relief are the levelled surfaces and plateaus subdivided by surface karst forms and caves. Their correspondence with tectonic units suggests a major influence of tectonic displacements on the present relief formation (e.g. Mihevc, 2007).

The study of the Velika Pasica Cave offers important insights into the interplay of tectonic uplift, karst system evolution, and paleoenvironmental dynamics. By integrating paleontological, geomorphological and geochronological data, this research not only contributes to the understanding of karst hydrology, but also emphasises the global significance of neotectonic processes in shaping biodiversity and landscapes during the Pliocene and Quaternary.

Understanding the paleoenvironmental and neotectonic history of karst systems such as Velika Pasica is crucial for interpreting the broader impacts of tectonic uplift and climatic fluctuations on karst hydrology and biodiversity. As highly sensitive systems, karst landscapes play a critical role in regional water resources and serve as biodiversity hotspots, making them essential for global research on ecosystem evolution and environmental changes.

The main questions concern the timing of the development of the area and whether the observed adaptations are due to the gradual disintegration of a single large area or to the formation of levelled surfaces at different elevations shaped by local geological settings. The tectonic evolution of the area, i.e. the Dinarides, is characterized by rotations of the Adriatic microplate (Adria), causing contractional deformations since the late Tertiary. The counterclockwise rotation (CCW) started about 6 Ma ago, and was accompanied by multistage regional tectonic uplift, folding and the formation of basins along strike-slip faults (Vrabec and Fodor, 2006).

Extensive speleobiological, meteorological and hydrological studies in the period between 2006 and 2014

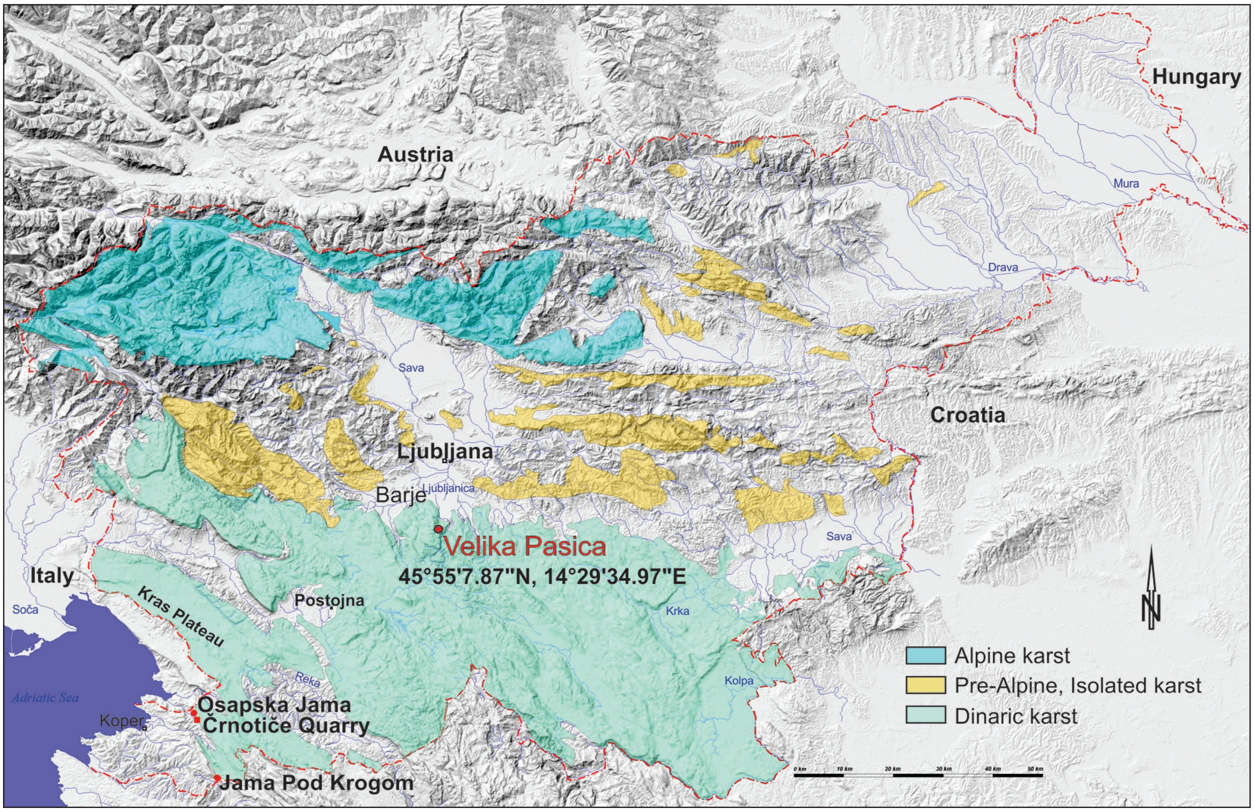

Figure 1: Location of Velika Pasica and other caves with Marifugia cavatica tubes (red dot - recent, red square - fossil) on the DEM of Slovenia with the main karst regions, karst types, and rivers. Source of Lidar data: Geodetski oddelek ARSO.

in Velika Pasica have also revealed the presence of fossils of the cave bear (*Ursus spelaeus* Rosenmüller, 1794) (Brancelj, 2015), several species of small mammals and fragmented tubes of aquatic cave animals, e.g. *Marifugia cavatica* Absolon & Hrabě 1930 (Annelida: Polychaeta) were found. The discovery of *Marifugia cavatica* fossils highlights stagnant phreatic conditions that preceded significant neotectonic uplift, which reshaped the karst landscape. Detailed studies of such caves contribute to our understanding of the dynamic interplay between geological processes and biodiversity over millions of years. Velika Pasica provides a unique opportunity to explore these dynamics in a region where neotectonic activity has profoundly reshaped the karst landscape. Therefore, we aimed to study the cave sediments in more detail, and the results are presented in this paper.

2. CAVE AND RECENT FAUNA

2.1. CAVE SETTINGS AND SEDIMENTS

Velika Pasica is located about 350 m above the Ljubljansko Barje on the edge of the Iška Valley on the northwestern edge of a karst plateau at an altitude of 665 m (Figure. 2) in the Upper Triassic dolomitized limestone (Pleničar, 1970). To the west of the cave, the plateau

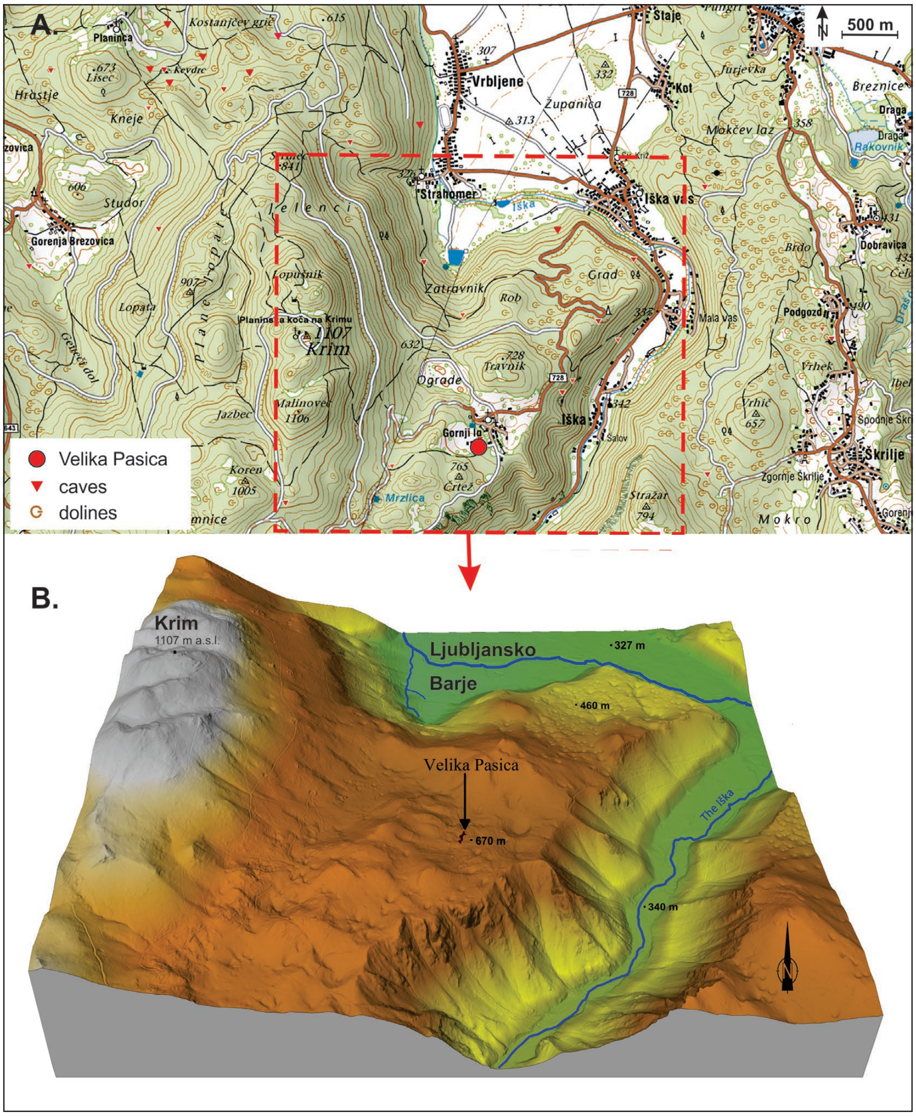

Figure 2: Location of Velika Pasica on a topographic map and a DEM hillshade. A) Cave location (red dot) on the karst plateau above the Iška Valley, together with other caves (red triangles) and dolines (circles), the red rectangle marks the area shown in the 3D terrain model (B).; and B) Hillshade DEM of the plateau with the cave location. Source of Lidar data: Geodetski oddelek ARSO.

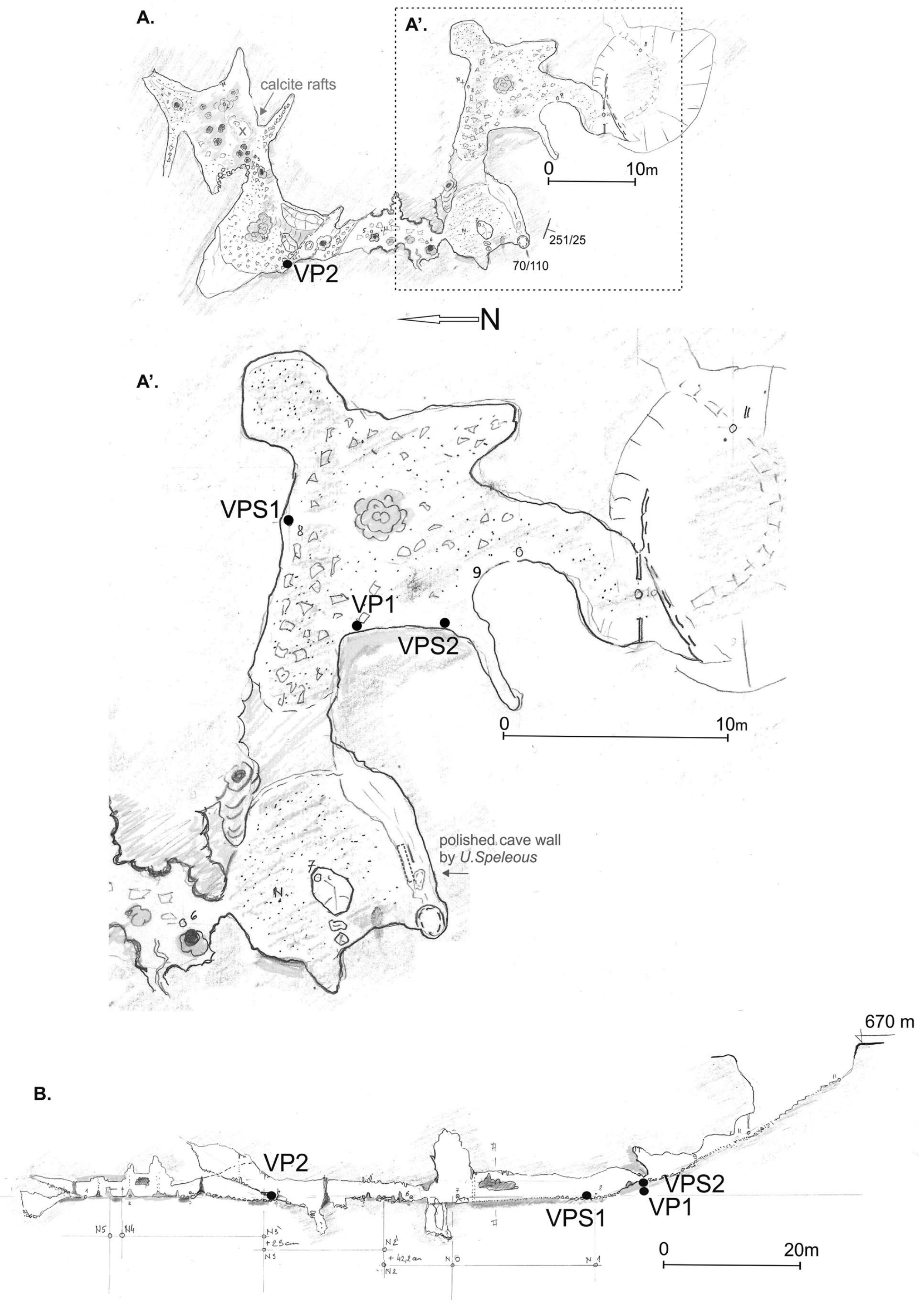

Figure 3: Map of Velika Pasica with marked measuring points and sampling points. A) ground plan of the cave; A') enlarged section of the entrance chamber; B) extended cross-section of the cave (measured by A. Mihevc, J. Koren and A. Brancelj, December 2017; drawn by A. Mihevc). VP1, VP2 – sampling points for microfossils; VPS1, VPS2 – sampling points for dating.

rises to Krim Mountain (1107 m a.s.l.), while to the east it descends steeply to the Iška Valley, which reaches the Ljubljana Barje north of the cave at an altitude of about 320 m a.s.l. With an average present-day discharge of about 0.5 m^3/s, the Iška River (the Iška) has incised a valley about 350 m deep into the plateau. The cave is located only 270 meters far from the edge of the valley. The Krim Massif and its surroundings form the northwestern part of the Dinarides and border the Classical Karst (in sense Gabrovšek et al., 2022) in the west. The tectonic subsidence of the Ljubljansko Barje probably began at Pliocene/Pleistocene boundary; it was strongest in the middle and upper Pleistocene and continues today (Gosar and Brenčič, 2012). The subsidence is mainly due to NW-SE faults that divide the surface into individual blocks. The bottom of the basin in the eastern part of the Ljubljansko Barje is deeper than in the western part (Mencej, 1989).

The cave is a 105 m long horizontal passage and lies shallow, mostly 12 m below the surface (Figure. 3). The passage is about 5 m wide and high, with a slightly larger chamber just after the entrance. At the end of the entrance chamber, about 30 m from the entrance, there are several rocks polished by cave bears, which rubbed their fur on the stones when they visited/hibernate in the cave (Figure. 3A'). In the rear part of the cave, the flowstone formed large gours (1.0 x 0.7 m) in which calcite rafts formed (Figure. 3A). It lies about 1.7 m above the present floor and is located exactly above the area where visitor signatures are located (Brancelj, 2015).

The preserved passage, part of a formerly more extensive epiphreatic cave system, appears to have been filled with sediment repeatedly during its existence. The oldest preserved filling consisted of red clay, which filled the cave completely and evenly. Most of this clay was later eroded, and then coarser-grained sediment was deposited. This gravel contained clasts up to 10 cm in size with a matrix of red clay and sand. It consisted of poorly rounded dolomite pebbles and sand lenses mixed with red clay, indicating a steeper stream gradient or a temporarily increased flow velocity/volume. The stream or river entering the cave transported a lot of material, especially after heavy rainfall. In some places, the passages were completely filled forming clogged sections that reduced water flow.

Over time, most of the sediment was removed from the cave. In certain areas, the sediments were cemented into conglomerate. Layers of flowstone, up to one m thick were then deposited on top of the conglomerate in some places. However, the inflow of carbonate-rich water was uneven, which led to an incomplete flowstone cover. When the clastic sediments were later removed, the flowstone crusts remained suspended, hanging freely in the open spaces, attached to the walls or even to the ceiling.

In the past, the cave was frequently visited by tourists and amateur entomologists who, while exploring the interior, destroyed the speleothems by physically removing them or using torches, leaving black soot stains on the walls. In 2006, the entrance to Velika Pasica was closed with an iron gate to prevent the collection of cave beetles and to protect the monitoring instruments used for hydrological and ecological studies in the cave (Brancelj, 2015).

About 110 m further north is the entrance to another cave, Mala Pasica Cave, which is a remnant of the same epiphreatic cave system. The two caves are now separated by a collapsed doline.

2.2. RECENT FAUNA RECORDS

Velika Pasica is particularly important from a speleobiological point of view, as it is a type locality of several invertebrate species, both stygobiont and troglobiont, nowithstanding numerous aditional record of other taxa of that kind (comp. e.g. Brancelj 2015).

Several specialized and endemic terrestrial (Mollusca and Coleoptera) and aquatic (Crustacea: Copepoda) obligatory cave-dwelling animals (= stygobionts) have been discovered in the cave. The semi-terrestrial snails (Gastropoda) include two members of the genus *Zospeum*, i.e. *Z. schmidti* (Frauenfeld, 1854) and *Z. amoenum* (Frauenfeld, 1856), whose distribution area in central Slovenia is relatively limited (ca 5,000 km^2). The beetle (Coleoptera) *Anophthalmus hirtus* Sturm, 1853 was described from the cave and is to date, known only from this locality (distribution area > 1 km^2). Four other species were also described for the first time from the cave, but have a slightly wider distribution area. Three well defined aquatic species living in the epikarst zone, *Morariopsis dumonti*, Brancelj, 2000, *Elaphoidella millennii* Brancelj, 2009 and *E. tarmani* Brancelj, 2009 were discovered there as narrow-local endemites (with > 10 km^2 distribution area). The presence of local endemites, both terrestrial and aquatic, indicates a long-lasting hydrological isolation of the area, at least of the epikarstic zone (Brancelj, 2015).

Fossil remains of small terrestrial mammals (= micromammalia), and fossil tubes of the aquatic freshwater invertebrate *Marifugia cavatica* were found in sediment samples in a chamber next to the present entrance and in the distal part of the cave. Living populations of *Marifugia* exist today in many caves along the Dinarides (about 600 km long; Kupriyanova et al., 2009), from Italy (NW) to Albania (SE), but Velika Pasica is the second record of the fossil tubes (Mihevc, 2000; Mihevc et al., 2001). No recent populations are known in the immediate vicinity.

3. MATERIALS AND METHODS

The cave was mapped with laser measuring devices for study purposes (Bosch, DLE 150 Laser, Germany). The cave was surveyed from the entrance to the outermost point of the cave with a tolerance of ± 0.1 m in both the vertical and horizontal directions.

Sediment samples (VP) were collected from two sites (VP1 and VP2; Figure. 3). These samples consisted of conglomerates and red clays containing microfossils, including *M. cavatica*, and were also used for mineralogical analyses. The samples were collected in two campaigns, in 2015 and 2017. A second group of samples comprised speleothems (VPS).

The studied conglomerate section VP1 (Figure. 4A), which contains red clay layers, is located in the entrance chamber on the west wall between measuring points 8 and 9 (Figure. 3). This section lies about 7 m below the surface and more than 5 m from the cave entrance. With a height of up to 1.5 m, it represents the largest conglomerate mass in the cave. Approximately 20 kg of conglomerate was sampled from the site. Due to the indistinct stratification of the conglomerate, the sample was taken over half a meter of the section. Because of the size of the conglomerate pebbles, it was not possible to determine exactly from which part of the conglomerate or at which level within the section the individual fossil remains originated. After the paleontological analysis, the section was divided into two units, B1 and B2 (Figure. 4A).

Another set of samples for paleontological analysis was taken from site VP2, which is located about 70 meters inside the cave (Figure. 3) and is covered with flowstone layers. The sample for fossil analysis (Figure. 4C) consists of a similar conglomerate sediment containing breccia fragments, gravel, sand and red clay. The sampling point is at approximately the same level as the sediment near the cave entrance.

The VPS1 sample was taken for dating from the broken base of a stalagmite near polygon measurement point 8 (Figure. 3). The diameter of the stalagmite was about 12 cm. The base of the broken stalagmite grows over pebble, sand and clay sediments, which also contained small mammal remains and *Marifugia* tubes. The original shape of the upper part of the stalagmite is unknown, as it was broken off and removed from the cave at an earlier date. The cross-section of the stalagmite (Fig-

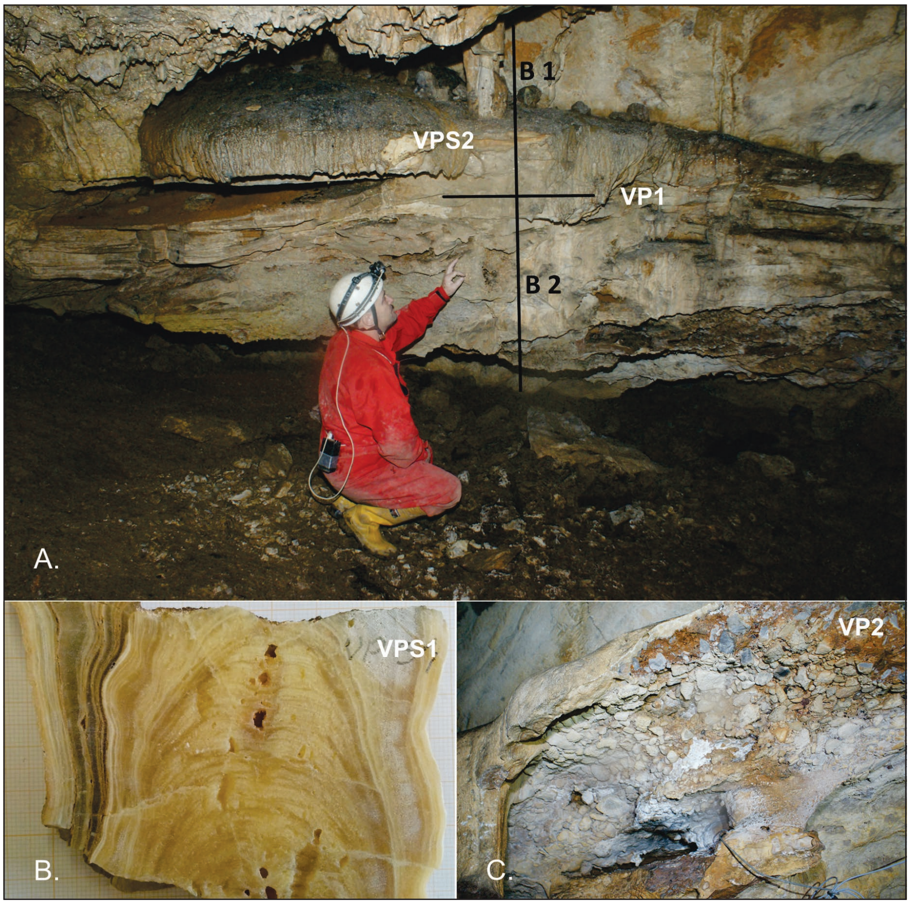

Figure 4: Conglomerate and flowstone samples from Velika Pasica: A) The studied section VP1 in the entrance chamber, showing the location of the two distinct taphonomical units B1 and B2 and the position of the flowstone crust sample VPS2. B) A broken stalagmite sample VPS1, cut for dating purposes. C) Remains of the clayey sediments of the original cave fill on the passage wall, located under the conglomerate with large clasts, marked as VP2 (photos A. Mihevc).

ure. 4B) shows two different growth phases. Light brown calcite with clearly defined incremental lamellae can be seen in the core. This central part is porous and contains cavities up to one centimeter in size. There are thicker lamellae around this core, suggesting a significant increase in water inflow and subsequent deposition of $CaCO_3$. The central section in the lower part of the stalagmite was sampled and dated using the U/Th method.

The VPS2 sample was taken just above fossil-bearing conglomerate site (VP1) covered by a flowstone crust up to 2 cm thick (Figure. 4A). The crust consisted of thin light and dark calcite layers.

Blocks of the conglomerate collected for the paleontological studies were etched in the laboratory with 10 % acetic acid. The leached debris was removed daily and then sieved on a 0.7 mm sieve and washed several times in water to remove acid and fine-grain sediment. Some teeth of small mammals had to be hardened later with acrylic resin dissolved in ether. Small mammal remains (bones and teeth) were obtained from a section by wet sieving from VP1 of unconsolidated clay deposits.

The insoluble residual of the conglomerate, pebbles, silt and clay, were analyzed for mineralogical composition of the allogenic sediments. The composition was determined by X-ray diffraction (XRD), using standard procedures for randomly oriented powder of the bulk sample on the Bruker D2 PHASER diffractometer with CuKα anode, 30 kV, current 10 mA, and a LynxEye XT-T in Cu_High Resolution mode. The samples were scanned in the 2θ range: 3–83° with a scan speed of 0.02° 2θ/0.2 s. Bruker's EVA 5.1 software was used to acquire and process the data.

In the Isotope and Trace Element Geochemistry Research Group Laboratory at the University of Melbourne, five subsamples were dated using the U/Th method. The preparation and analytical procedures followed the protocols established by Hellstrom (2006). However, only the samples from VPS1 and VPS2 yielded reliable results. VPS1 was taken from the base of the broken stalagmite, while VPS2 represented the flowstone crust covering the conglomerate fill.

Abbreviations and characters: *cf.* is used for specimens that appear identical to the named taxon at first sight, but require further comparison; *aff.* indicates a form that is related to, but not identical with the named taxon; brackets around the author's name indicate that the original description was published under a different generic name; *asterisks denote taxa discussed further in the text.

4. RESULTS

4.1. MINERALOGY

The semi-quantitative XRD analysis revealed that the sample of the less-soluble residue of the conglomerate (i.e. the calcite cement was dissolved) consists mainly of dolomite (87%), magnesium calcite (8%), quartz (2.5%), and boehmite (bauxite mineral) and hematite in traces (Figure. 5). Sediment composition indicates that Velika Pasica was influenced by a small sinking river flowing

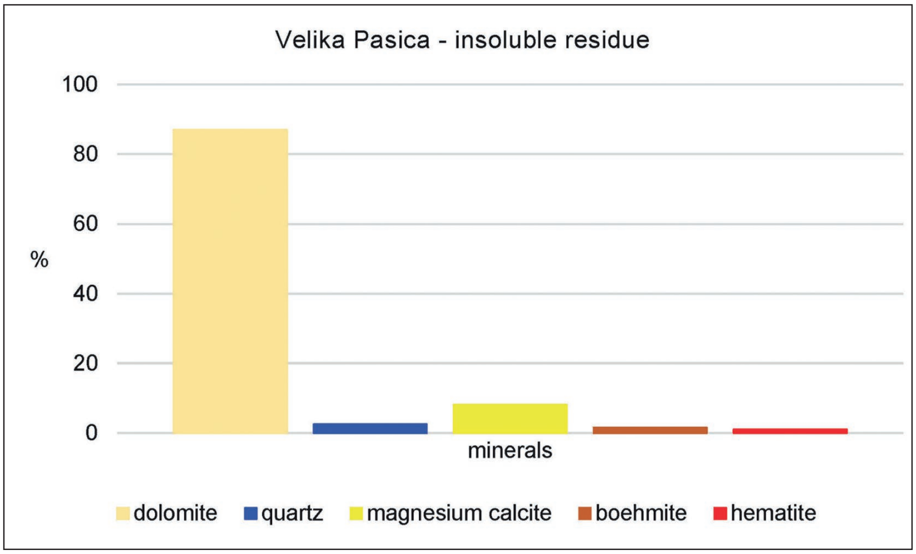

Figure 5: Mineralogical composition of the fine fraction of conglomerate residues after dissolution of calcite cement from Velika Pasica.

from the southeast to the northwest. The water flowed from the Upper Triassic dolomite, which is enriched in boehmite.

4.2. SPELEOTHEM DATING

Two samples yielded a U/Th age (Table 1). VPS1, the base of a broken stalagmite, was dated at 129 ± 1 ka. It was growing on top of flowstone crust covering pebbles, sand and clayey sediments containing approximately 2 Ma old faunal remains (small mammals and *Marifugia* tubes). VPS2, a flowstone crust deposited directly over clastic sediments, was dated at 410 ± 21 ka.

Table 1*: U/Th dating results of two speleothem samples from Velika Pasica, VPS1 = base of stalagmite, and VPS2 = flowstone crust.*

sample ID	U cont. [ppb]	corr. age [ka]
VPS1	330 ppb	129 ± 1
VPS2	492 ppb	410 ± 21

4.3. PALEONTOLOGY

4.3.1. Freshwater fauna

Three small fragments of *M. cavatica* tubes (Figure. 6) were identified in VP1 sediments, mixed with fine-grained gravel and red clay. The largest fragment measured 3.5 mm, while the others were 2.5 mm long. These fossils indicate low-energy phreatic conditions in the cave before tectonic uplift disrupted the hydrological regime.

Figure 6: The fragments of fossilized tubes of Marifugia cavatica Absolon & Hrabě, 1930 from Velika Pasica. The tubes are covered by a thin calcite crust (photo A. Mihevc).

4.3.2. Vertebrate remains

The vertebrate remains were collected from the conglomerate samples (VP1, VP2), including fragmentary specimens extracted by wet sieving from the unconsolidated red clay deposits. The fauna remains compose two distinct taphonomic units: B1 and B2 (Figure. 4A). Unit B1 comprises well-preserved fragments of medium-sized bones and remains of extant living forms, obtained from section VP1. In contrast, unit B2 consists of fragmentary specimens, mainly isolated teeth and enamel fragments, which differ from B1 in both fossilization patterns and species composition.

Unit B1 (Figure. 7 and 8), including the remains of taxa listed below:

* ***Glis glis*** (Linnaeus, 1766)
Fig. 8/10
In sample VP1: complete mandible p4-m2, isolated m3; inner chamber (VP2) clay matrix: two molar teeth, mandible with isolated m2, m3.

* ***Cricetus cricetus*** (Linnaeus, 1758)
In sample VP1: complete mandible m1-m3, a mandibular fragment m2-m3; in samples from inner chamber (VP2) clay matrix: fragmentary left mandible, conglomerate matrix, entrance hall: fragments of i1 and m2, left mandible with m1-m3.

* ***Dinaromys bogdanovi*** (V. Martino & E. Martino, 1922)
Figure. 7/1
in sample VP1: a complete mandible m1-m3;

* ***Microtus*** sp. - a fragment of molar tooth.

* ***Arvicola*** sp. – in sample from inner chamber (VP2) clay matrix: a large sized m2 cemented in a breccia.

The situation with the other unit (B2) is much more complicated. Unit B2 consists of about 35 fragments, most of which do not allow a clear identification. In total, 12 of them are enamel wall fragments of diverse arvicolid molars, all with roots and indistinct undulation of the *linea sinuosa* (*sensu* Rabeder, 1981). 20 pieces (mostly figured in Figures 7 and 8) are more complete and allow some tentative identifications, indicating an ancient age of these fossils and a surprisingly high species diversity.

The following forms were identified in the assemblage of fragmentary remains obtained from the sample of the unit B2:

* ***Sorex* cf. *bor*** (Reumer, 1984)
Figure. 8/1-2
Two mandibular fragments of a small-sized *Sorex*, one with m1-m3. With m1-3 length: 3.6 mm, tooth row proportions (length m1:m2:m3 = 1.49:1.25:1.02) and by

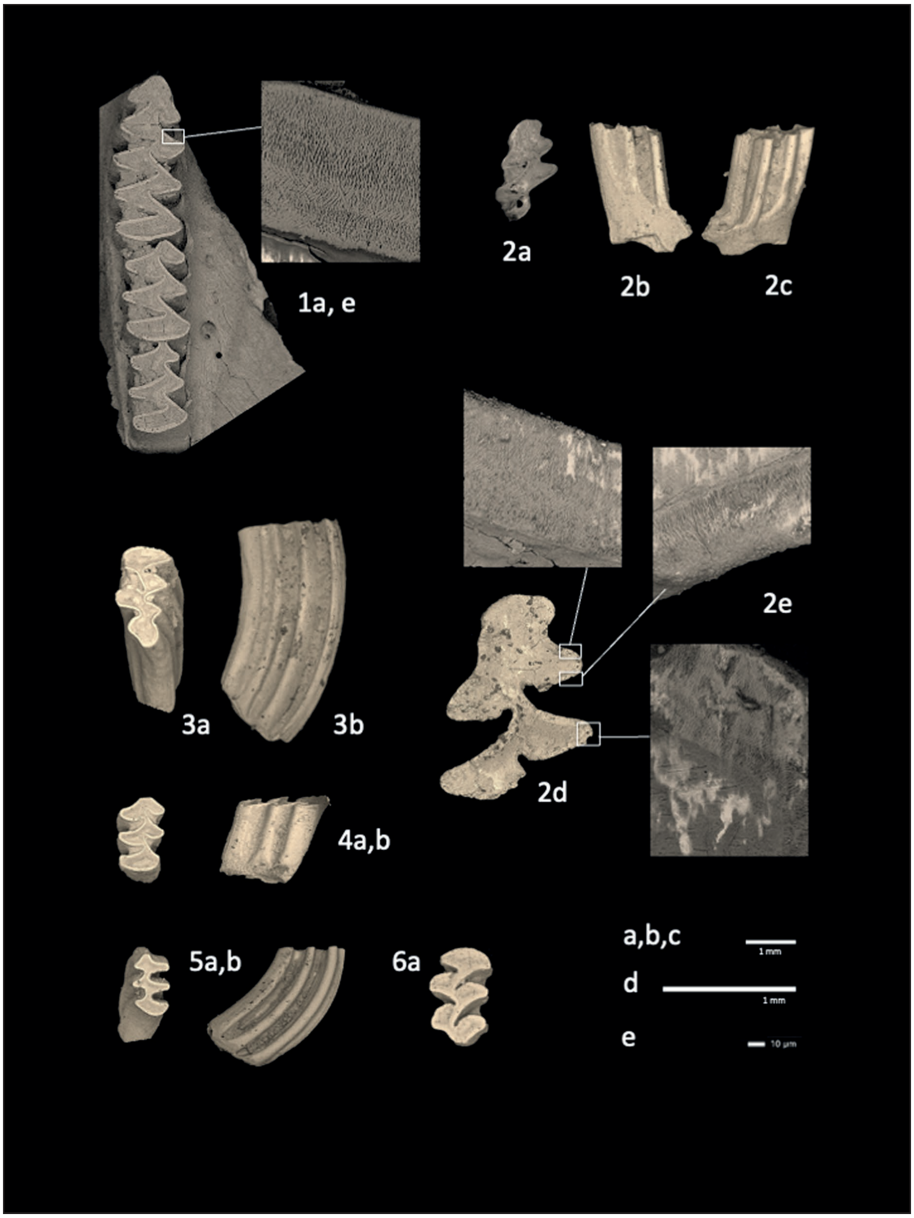

Figure 7: Small mammals remains in Velika Pasica conglomerates: 1 - Dinaromys bogdanovi (Late Pleistocene fossil) – md. dext. m1-m3, a – occlusal view, e – enamel pattern; 2 – Propliomys aff. hungaricus m1 sin. a,d – occlusal view, b – bucal, c – lingual view, e – enamel pattern; 3 – Mimomys cf. osztramosensis m3 sin.; 4 – Mimomys sp. 2 – m2 dext.; 5 – Borsodia cf. petenyi – m3 sin; 6 – Mimomys cf. osztramosensis (?) – m1 of a senile individual.

robust talonids (TrW/TalW m1 0.7/0.8, m2 0.71/0.71, m3 0.51/0.51) it differs from *S. minutus*, yet corresponds well to *Sorex bor*, the form reported from several MN14-MN17 sites (Osztramos 1,7,9, Podlesice, Węże, Kadzielna) by Reumer (1984) and Rzebik-Kowalska (1975).

At the same time, it is smaller than MN17-Q1 *Sorex fejfari* Horáček et Ložek, 1988 and Q2 *Sorex runtonensis* Hinton, 1911. By an unreduced m3 talonid it differs from *S. polonicus* Rzebik-Kowalska, 1994 from MN16 Rębielice Królewskie 1A, to which corresponds in other metrical characters.

* ***Petenyia* aff. *hungarica*** Kormos, 1934
Figure. 8/4

A single m2, quite robust tooth (L 1.4. trW 0.77, tlW 0.8 mm) with a very dark pigmentation, broad talonid and well pronounced mesial trigonidal cingulid. It resembles tooth shape in *Petenyia hungarica*, yet it is somewhat smaller and differs also in a weak labial cingulid, similarly as in the form from MN14 Osztramos 9 (comp. Reumer 1984).

* ***Beremendia fissidens*** (Petényi, 1864)
Figure. 8/3

A large sized dark pigmented i1 corresponding in all characters to the indicated species, widespread from MN14 to Early Pleistocene (LAD Q2).

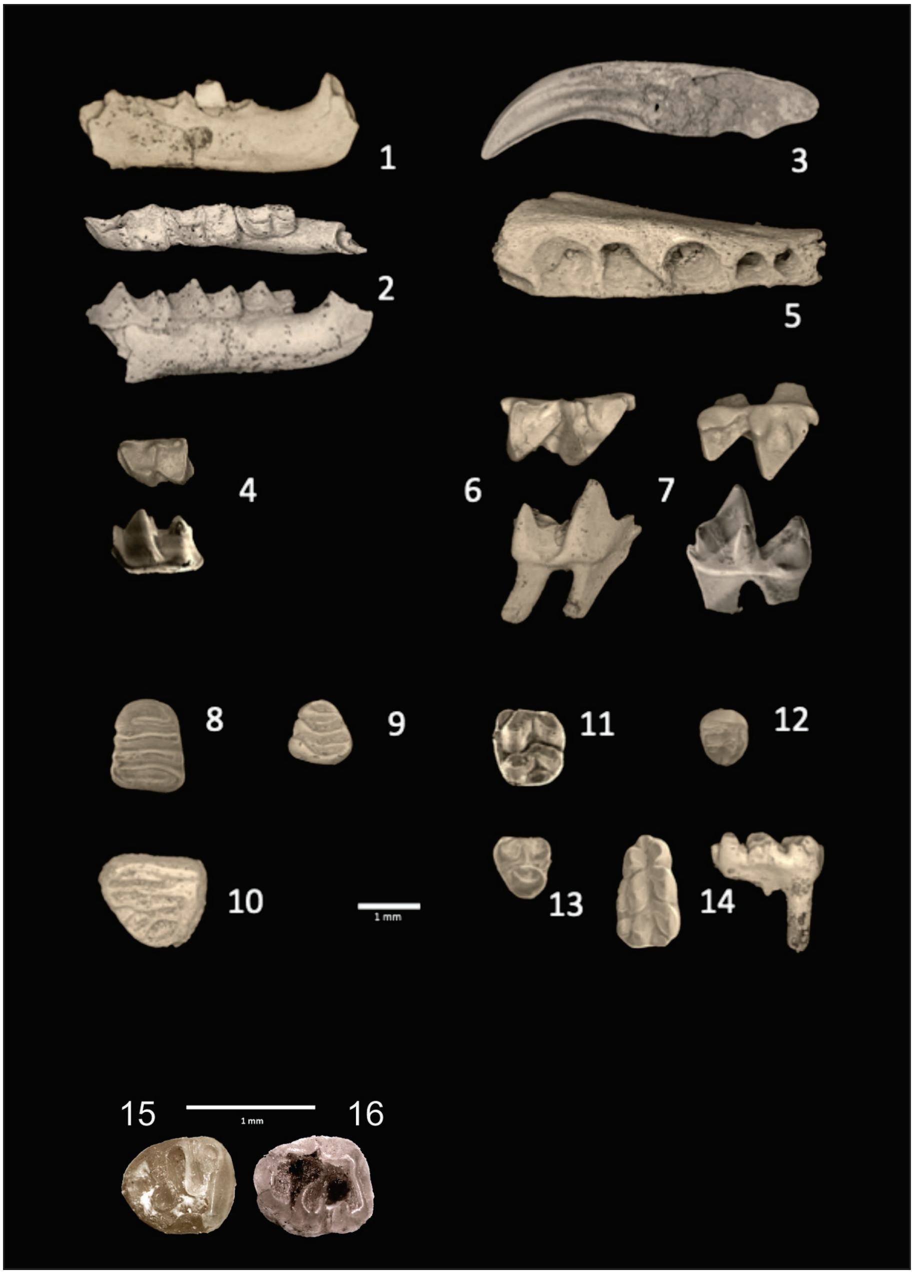

Figure 8: Remains of small mammals in Velika Pasica: 1, 2 - Sorex cf. bor, mandible sin; 3 - Beremendia fissidens - i1sin.; 4 - Petenyia aff. hungarica - m2 sin.; 5 - 7: Talpidae - cf. Skoczenia sp.; 5 - mandible fragment (p4-m2) sin., 6 - m1 dext., 7 - m3 dext.); 8 -Muscardinus pliocaenicus - m1 sin.; 9- Glis minor p4 sin.; 10 - Glis glis m3 (a late Pleistocene fossil); 11- Apodemus cf. atavus - m2 sin.; 13 - Apodemus cf. atavus - m3 sin; 14 - Apodemus cf. atavus - m1 sin; 12, 15 - Apodemus cf. atavus - M3 sin.; 16 - Apodemus cf. atavus - m3 dext.

* **Talpidae - cf. *Skoczenia*** sp.
Figure. 8/5-7

Material of moles consist of a fragment of a very robust mandible with enlarged m1 alveoli, isolated m1 (L 2.1 mm) and m3 (L 2.02 mm) with moderately reduced talonid, and a fragment of lower molar trigonid. All are larger than both *Talpa minor* or *T. fossilis* and correspond well to the characters diagnosing the genus (*Skoczenia* Rzebik-Kowalska, 2014; type locality MN17 Kadzielna 1).

* ***Glis minor*** Kowalski, 1956
Figure. 7/9

A single p4 sin. falling with its dimension (L 1.1 mm) to lower part of variation range of *Glis minor* (as in MN15 Węże, Rębielice Królewske or Sonderhausen (MIS 15) (Hellmond and Ziegler, 2012).

* ***Muscardinus pliocaenicus*** Kowalski, 1963
Figure. 8/8

A single m1 (L 1.52 mm, W 1.15) differing both from *M. avellanarius* and *M. dacius* but corresponding well both in dimension and morphology to the *M. pliocaenicus* from MN14-15 sites Węże or Podlesice (MN15–14) (comp. Daoud, 1993; Kowalski, 2001).

* ***Apodemus* cf. *atavus*** Heller, 1936
Figure. 8/11-16

Four teeth (m1: 1.8×1.0, two m3 1.0×0.95, 0.98×0.88, m2) with massive cingular cuspids on m1 and elongated anteroconid complex show identity with the phenotype traits of *Apodemus atavus* from MN 15 sites Gundersheim (type locality) and Vitošov (both MN15/16), by a direct comparison. The m2 seems to be a bit more robust than expected (L 1.25, W 1.15), it might belong to another murid species, eventually. Two teeth supposedly considered M3 of this species are the most confusing items in the collection. One is heavily worn, the other is a broken crown enamel coat of an unworn tooth. They differ distinctly from murid M3 by a prolonged rectangular shape, relatively high crown, high and narrow perpendicular anterior crest, and occlusal tapering of individual crests.

Alternatively, they could be (also in regard to their extremely small size: L 0.93, W 0.83, and L0.97 W 0.81) tentatively attributed (as d4 teeth) to Eomyidae, an extinct family greatly diversified during the Miocene, but rare in Early and Middle Pliocene assemblages (with the last European appearances in early MN17). Yet, compared to rarely figured d4 teeth of the Pliocene eomyids (*Estramomys simplex, Eomyops bodvanus*) – (comp. Daxner-Höck & Höck, 2009; Prieto, 2012), they differ in some respects, e.g. in a continuity of lateral crest. In short, we feel confused from the specimens and correct identification of the respective items remains unclear.

* ***Propliomys* aff. *hungaricus*** (Kormos, 1934)
Figure. 7/2

A fragment of m1 of a medium sized arvicolid, rhizodont, without cementum. In contrast to most taxa with these characters (*Mimomys, Borsodia* etc.) it shows (i) a broad and short anteroconid complex (anteroconid L 1.1, W 0.81) without insula or deeper lateral incisions; (ii) rather deep and mesially tappered synclinales both in distal margins of anteroconid complex and t3; (iii) conspicuously thick enamel cover at mesial walls while the distal walls of particular triangles are remarkably thin; (iv) correspondingly, distal walls are composed of a simple radial enamel without lamelar or tangential decusations, while the mesial walls shows the pattern well developed, like e.g. in *Pliomys* or *Dinaromys*, characterized by appearance of a distinct layer of lamellar enamel at ca 1/3 of the enamel thickness. In contrast to the mentioned genera, arrangement of that layer shows distinct irregularities, which as a rule are associated with early stages of arvicolid phylogeny. Summing up it seems quite probably that the specimen in question is a member of *Pliomys-Dinaromys* clade, supposedly closer to the root of their divergence than MN16–17 *Propliomys hungaricus*.

* ***Mimomys* cf. *osztramosensis*** Jánossy & van der Meulen, 1975
Figure. 7/3,6

A juvenile M3 (at beginning of root formation) of a larger-sized rhizodont arvicolid (Figure. 7/3) with relativelly advanced pattern of occlusal design: elogated posteroconid complex lacking insula or spatial separation of distal part of the posteroconid loop but without cementum and relatively low undulation of *linea sinuosa*. By larger size and its generalized morphology (L 2.13, W 1.1, tooth height 4.6, protosinus height 3.4, Lp/L = 0.54) it corresponds to diagnostic characters of the subgenus *Mimomys sensu* Rabeder (1981) exhibiting at the same time a more advanced stage than *M. pliocaenicus.* In these regards (as well as e.g. in absence of insula) it corresponds well to *M. osztramosensis* either from MN16 Osztramos 3 or MN17 Schernfeld (comp. Tesakov, 1998).

A robust m1 of a senile individual with thick enamel not interrupted by *linea sinuosa* undulation (Figure. 7/6) might belong to that form as well.

* ***Mimomys* sp.** 2
Figure. 7/4

An arvicolid m2 of an older individual (L 1.51, W 0.81) with traces of cementum in synclinales yet with relatively low undulation of *linea sinuosa* (crown height 1.5, anterosinuid 1.0).

* ***Borsodia* cf. *petenyi*** (Méhely, 1914)
Figure. 7/5

A juvenile m3 of a small sized rooted arvicolid (1.3×0.51) without cementum and low level of *linea sinuosa* undulation (in lower third of tooth height). A narrow-shaped triangles and relatively thin enamel layer equal in both mesial and distal walls suggest situation in the clade Lagurini, which ancestral rhizodont forms composed the genus *Borsodia,* first appearing during MN16. Regarding the state of the above-mentioned characters in our specimen, the most ancient form of the clade, i.e. MN 15/16 *Borsodia petenyi* (type locality Beremend 1-3) come particularly in account.

5. DISCUSSION

5.1. AQUATIC FOSSILS AND HYDROLOGY

The discovery of a diverse and rich tanatocenosis in a small cave, combining both aquatic and terrestrial representatives of the local fauna, sheds new light on the knowledge of geomorphological and environmental development and change in a small, but geologically and evolutionarily very dynamic part of Slovenia (Europe). From many aspects of its unique aquatic and terrestrial fauna, it seems that the Krim Massif represents an isolated local outcrop and a "time-capsule" as a result of rapid and localized geological uplift. Several terrestrial and aquatic organisms are known only from this massif and recognized as clearly defined species (Brancelj, 2015), although their relatives have also been found in nearby regions.

Marifugia cavatica, the only freshwater member of the Serpulidae family (Polychaeta), is a rare and specialized organism inhabiting stagnant or very slow-flowing waters. While extant populations are limited to caves in the western littoral karst of Slovenia, the fossilized tubes in Velika Pasica provide evidence of its past distribution in central Slovenia. As noted by Kupriyanova et al. (2009), the species requires calm hydrological conditions with suspended organic material, which were likely present in Velika Pasica before tectonic uplift disrupted the system and increased sediment transport.

Fossils of *M. cavatica* were previously discovered in the Črnotiče Quarry (Mihevc, 2000). In Velika Pasica, *M. cavatica* was found about 300 m above the current level of the saturated (phreatic) zone of karst groundwater. In the Črnotiče Quarry, fossil remains of *Marifugia* were found about 400 m above the springs of the Osapska Reka (River), where a vital population still exits. Both altitude differences are due to tectonic uplift/subsidence. The fossil remains of *Marifugia* in the Črnotiče Quarry have been indirectly dated as older than 3.6 Ma (Bosák et al., 2004; Horáček et al., 2007; Zupan Hajna et al., 2020). *Marifugia cavatica* represents an ancient inhabitant of inland waters, with the same geographic distribution as the cave salamander (i.e. olm; *Proteus anguinus* Laurenti, 1768) and the cave-dwelling mussels (*Congeria kusceri* Bole, 1962). Both *Marifugia*, and *Congeria* have a similar life history. Both are sessile as adults. They feed on suspended organic material that is regularly or occasionally transported into the caves, and both have juvenile stages (larvae) unable survive in water currents. They can move around in stagnant water to a limited extent, but are easily swept away by the current – either into inner parts of the cave with more limited food resources or out of the cave where ecological conditions do not support their survival.

From this aspect, the species is a good environmental marker, as it lives exclusively in water caves with stagnant or very slow-flowing water. The adult animals can survive short dry periods. Adult specimens of *M. cavatica* are surrounded by a calcite tube attached to the substrate (rock or other members of the colony). The tube is rather fragile; therefore, it can only survive in relatively low-energy water.

Fossil finds in the interior of the country show that the species also colonized the continental part of Slovenia in the past, but then became extinct in some places due to climatic, hydrological and geological changes. The main reason for this was probably the tectonic uplift of individual blocks, which could not provide enough water for the specific aquatic fauna, and the lack of suspended organic matter as food. The lowering of the groundwater level in karst due to the erosion of local streams is unlikely to create large enough water bodies to support the population of *M. cavatica*, which requires regular seasonal flooding for food and reproduction (Matjašič and Sket, 1966).

The *M. cavatica* tubes in Velika Pasica were probably eroded from their original substrate and redeposited between large pebbles. This suggested that the population thrived in the cave when it was still part of a larger, lower-altitude karst aquifer, before red clay was deposited. The fossilized tubes of *Marifugia cavatica* offer valuable insights into the hydrological conditions of the cave during their life span. These organisms thrived in calm, low-energy phreatic waters where suspended organic matter supported their colonies. However, as tectonic uplift began to alter the karst landscape, energy in the system increased, leading to erosion and sediment transport. This shift in hydrological conditions probably caused the tubes to detach from the cave walls and become redeposited as fragments in the conglomerates. The redeposition of these fossils indicates a significant environmental transition, from stagnant phreatic to more dynamic hydrological conditions associated with tectonic activity. Consequently, the fossilized tubes reflect not only the original habitat but also the subsequent processes of erosion, transport and sedimentation, illustrating the complex interplay between biological and geological factors in the karst system.

Their presence indicates that at a certain period there were pools or oxbows with stagnant water occasionally filled by a swallowed stream which brought some organic material from surface. This surface-derived allogenic material supported existence of *Marifugia* colonies within the cave, as elsewhere with present-day populations (Matjašič and Sket, 1966). *Marfugia* became extinct when the water flow ceased (i.e. there is the decline/extinction of population on its type locality in Herzegovina, when sinking river was regulated and dammed and natural flow was disrupted (Kupriyanova et al., 2009)).

Later, the hydrological conditions in the karst changed. The displacement of tectonic units increased the stream gradients. The water began to erode the red clay fillings and then deposited gravels into the cave. The water also carried the bones of small mammals. These may have been brought from the surface in the upstream sections or may have lived in a vicinity of the cave. Their age therefore does not necessarily correspond to the age of the *Marifugia* fossils, which can be older.

Velika Pasica was filled with water from at least the Miocene until the regional uplift, as suggested by Zupan Hajna et al. (2020) for other areas in the Classical Karst of Slovenia. This environment supported a diverse and highly specialized aquatic fauna inhabiting the vadose and epikarst zones (the uppermost layer of the karst; Bakalowicz, 2005), along with a rich assemblage of specialized cave-dwelling species (Brancelj, 2000, 2002, 2009, 2015). It can be assumed that such species had better survival conditions in extensive areas at lower altitudes with voluminous karst groundwater. The adaptation of aquatic animals from epigean freshwater lakes and rivers to subterranean rivers could only occur under these conditions, as seen in the Dinarides before and during the formation of the Dinaric Lake System, when freshwater lakes in the Upper Miocene (Mandic et al., 2012) were located in much lower reliefs and altitudes compared to today.

5.2. SMALL MAMMALS AND BIOSTRATIGRAPHIC INFERENCES

The paleontological items composing the taphonomic unit B1 are mostly well preserved. With the exception of *Microtus*, they are even represented with complete mandibles, so that there is no doubt in their species identifications. *Glis glis* ranks among the most common arboreal

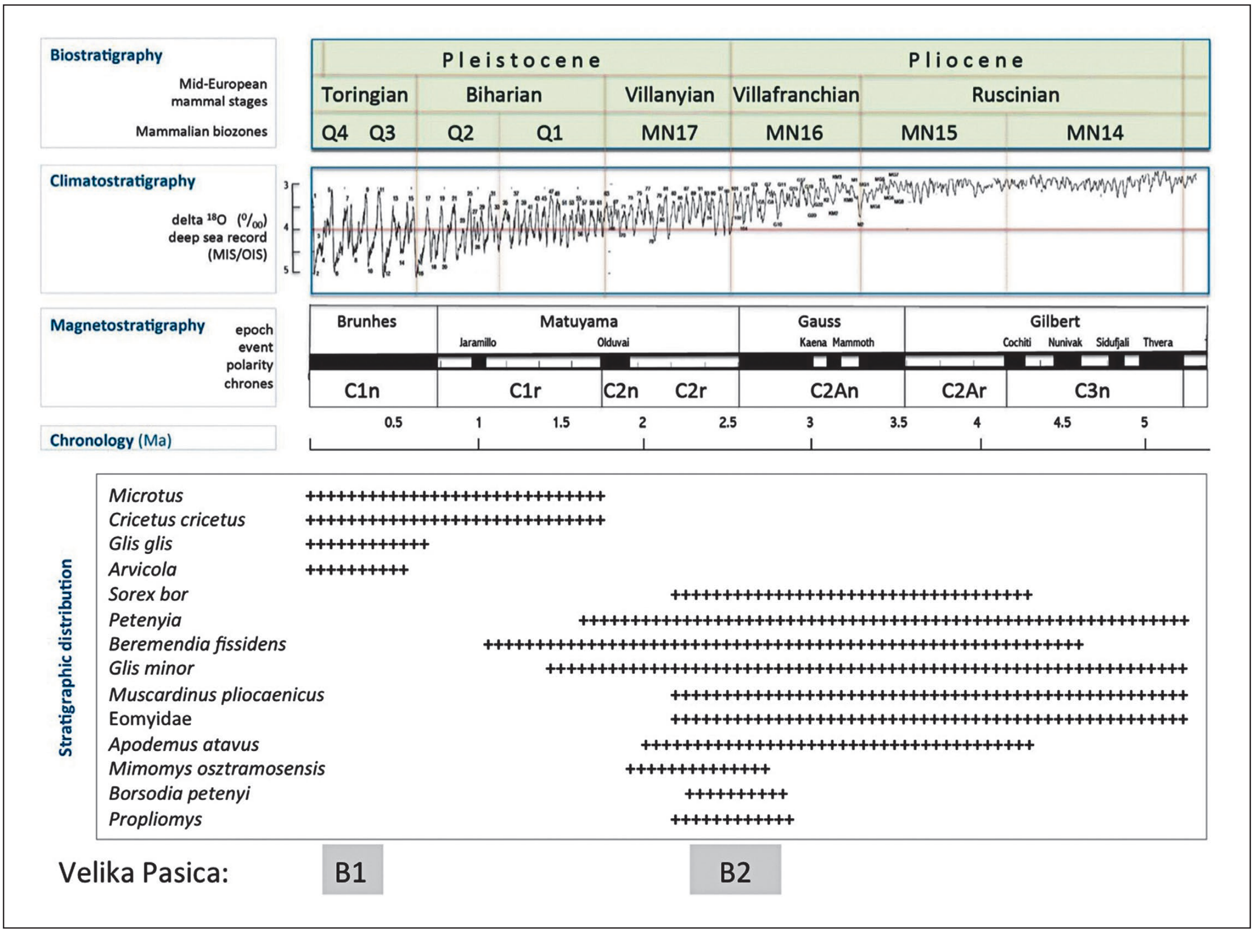

Figure 9: An overview of the stratigraphic distribution of taxa recorded in Velika Pasica, assumed stratigraphic position of taphonomical units B1 and B2 compared to stratigraphic standards of the European Late Cenozoic (after Horáček et al., 2013).

species in Slovenia, which nowadays hibernate in the caves in the karst habitats throughout Slovenia. *Cricetus cricetus* is linked to steppe-like open ground areas. In Slovenia it is today only restricted to very local populations in NE lowland, margin of the Pannonia lowland (Kryštufek, 1991). *Dinaromys bogdanovi*, recently restricted to the westernmost part of the Balkan Peninsula, has been recorded in Slovenia from several sites from the Late Pleistocene (caves Divje Babe, Dolarjeva Jama, Črni Kal; Pohar and Kralj, 2003; Toškan and Dirjec, 2011, own records) and also Holocene (*cf*. Toškan & Kryštufek, 2006). A single rootless molar of a large-sized *Arvicola* (unfortunately cemented in a breccia) excludes age of these items older than the Middle or Late Pleistocene. Tentatively we assume that the items of the unit B1 can be regarded as Late Pleistocene or even an early Holocene thanatocenosis, at least for taphonomic reasons (complete jaws, well-preserved fragments of postcranial bones, etc.).

In contrast, the assemblage composing the taphonomical unit B2 suggests quite a different picture. Although most items are fragmentary and poorly preserved (minute fragments of enamel, etc.) some of them allow a preliminary identification showing at the same time a remarkably high species diversity: at least 3 species of shrews, a mole and 8 species of rodents. None of the identified items are attributed to any index taxon suggesting a Quaternary age.

In surprisingly high diversity and composition of the fauna, the B2 unit resembles the MN15 sites like Beremend 1-4, Rębielice Królewskie or Sondershausen (Hellmund and Ziegler, 2012), yet the arvicolid species show clearly more advanced phenotype patterns conforming to forms reported from sites along MN16/MN17 boundary (Osztramos 3, Schernfeld, Kadzielna 1). Thus, combining the stratigraphic distribution of the taxa identified in unit B2 (Figure. 9), with particular regard to arvicolid species, the tentative assessments of stratigraphic age of the B2 assemblage can be concentrated on the period of late MN16 (i.e. ca 2.4 to 3 Ma B.P.).

5.3. RELIEF AND KARST SYSTEM EVOLUTION

The occurrence of *M. cavatica* in Velika Pasica underlines a complex history of karst hydrological evolution and landscape dynamics influenced by tectonic activities. The fragmented tubes found in Velika Pasica amidst coarse pebbles indicate a significant environmental change. Originally, these organisms inhabited deeper areas of the karst system, where calm, slow-flowing or occasionally stagnant river sections prevailed. However, tectonic uplift altered the hydrology of the cave and increased water flow, which eroded previous sediment deposits and triggered gravel transport, disrupting the habitat necessary for *Marifugia*.

In Velika Pasica, fossil *Marifugia* tubes were found 300 meters above the present-day karst groundwater level, the location of which can be attributed to tectonic uplift. The subsequent tectonic activity caused the original karst block to disintegrate into individual parts with different relief. The timing of this uplift could correlate with the uplift observed in the Črnotiče Quarry, western Slovenia (Horáček et al., 2007), where the proposed biostratigraphic dates for both sites of *M. cavatica* are almost identical and correspond to MN15 to MN16. However, in the Črnotiče Quarry, *Marifugia* populations were able to adapt to the lowering of the karst water level, and now survive in active karst springs or caves located about 300 m below the current karst plateau surface. In contrast, the *Marifuga cavatica* in the Velika Pasica area could not adapt to the evolving relief and changes in karst hydrology, which eventually led to their extinction. This difference in survival illustrates the local impact of karst topography and changes in groundwater levels on aquatic ecosystems. The radical reshaping of the hydrological network due to tectonic uplift in these areas can be traced back to the same phase in the tectonic history of the region and correlates with the significant regional uplift of the southern Kras Plateau after the Pliocene (e.g., Zupan Hajna et al., 2024). In addition, this latest uplift could be partly related to the subsidence of the Ljubljansko Barje, which started about 1.8 million years ago (Mencej,1989; Mihevc et al., 2015) and led to river incision in the wider area, including the Paleo-Iška River.

The dating from Velika Pasica provides valuable insights into two different phases of karst development. The biostratigraphic analysis of the mammal assemblages suggests that *Marifugia* existed until approximately 3 Ma, while the associated fluvial sediments could be older, dating back to about 4 Ma or more. In addition, the stalagmite base, dated to 410 ± 21 ka, suggests that speleothem deposition occurred after the time of gravel accumulation.

6. CONCLUSIONS

The study of the Pliocene fossil record in Velika Pasica, Slovenia, provides valuable insights into the ancient ecological and environmental dynamics of the region. The discovery of *M. cavatica*, a unique freshwater serpulid polychaete, together with fossils of small mammals, offers a rare insight into early Pliocene (MN15–16) life forms and their habitats, highlighting the ecological and hydrological conditions that existed prior to significant neotectonic activity.

Our results demonstrate that Velika Pasica, now a dry epikarst cave located well above the present-day karst water level, was once part of an active hydrological system that supported unique aquatic and terrestrial life forms. The fossil evidence underscores the cave's role as a dynamic ecological niche, shaped by geological processes such as uplift, subsidence, and valley incision over millions of years.

The fossil assemblages provide important biostratigraphic markers that contribute to the understanding of the evolutionary time and migration patterns of aquatic and terrestrial species in the Dinarides. The presence of small mammal remains alongside *M. cavatica* in a cave environment underlines the complex interplay between terrestrial and aquatic ecosystems during the Pliocene.

This study not only documents the persistence of ancient life forms such as *M. cavatica* in a changing karst environment, but also improves our understanding of the paleoenvironmental conditions that prevailed during the Pliocene. It emphasizes the crucial role of tectonic and hydrological changes in driving ecological changes and habitat evolution in karst systems. Velika Pasica Cave serves as a valuable case study to understand how such processes influence long-term biodiversity patterns and the preservation of paleoenvironments, with implications for similar karst systems worldwide. It also provides a robust foundation for future research on the impact of geological processes on biodiversity and habitat evolution in karst landscapes.

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