

Late Neogene–Quaternary exhumation of the Tisza unit basement carbonates based on paleontological data: Villány Hills, SW Pannonian Basin

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A Tiszai-egység aljzati karbonátjainak késő neogén – kvarter kitakaródása őslénytani adatok alapján a Villányi-hegységben

Összefoglalás

A Pannon-medence miocén végétől máig tartó inverziója többek között területileg eltérő függőleges mozgásokban nyilvánul meg, emelkedési ütemek azonban leginkább csak a medence északnyugati részéről ismertek. Jelen munkában a Villányi-hegység őskarsztos üregeiben található késő pliocén – kvarter gerincesegyütteseket vizsgáltuk, hogy képet kapjunk a hegység pannóniai üledékek alól való kitakaródásáról és a neotektonikus emelkedés üteméről. A rétegzetlen, részben valószínűleg légi szállítás útján érkezett, gerincesmaradványokban dús üregkitöltések az egykori erózióbázis fölött halmozódtak fel. Megjelenésük azt mutatja, hogy az adott ponton a mezozoos alaphegység már felszínen, üledékes fedő nélkül volt. A viszonylag pontosan korolható ősmaradvány-együttesek magassági eloszlása alapján az első leőhely kialakulásának idejére, 3,5 millió évvel ezelőttre a hegységről már közel a mai állapotig lepusztultak a pannon-tavi üledékek. A 3,5 millió évtől máig tartó időszakban a hegység fő vonulatának emelkedési üteme legfeljebb 35 m/Ma lehetett, míg a Beremendi-rögé legfeljebb ~15 m/Ma. Ezt megelőzően, a késő miocén – kora pliocén (~6–3,5 Ma) során a kitakaródás üteme a hegység fő tömbjében legalább 76–92 m/Ma körülire becsülhető, és biztosan meghaladta a 12 m/Ma-et. A Beremendi-blokkban ezek az értékek legalább 97–111 m/Ma és 37 m/Ma lehettek, de nagyobb bizonytalansággal, mert ez a rög akár süllyedhetett is valamennyit a vizsgált időszakban. Az emelkedési ütemek pliocén–kvarter csökkenésének fő oka a Dráva-vető pliocénben kezdődő transzpressziós működése lehet, ami felveszi az Adria és Európa közeledése által okozott deformáció jelentős részét a tágabb területen. Emellett litoszféraléptékű folyamatok is közrejátszhatnak. Az ősmaradvány-együtteseket tartalmazó hasadékok legtöbbje nem közvetlen tektonikai hatásra jött létre, így a korábbi felvetésekkel ellentétben a feszültségviszonyok rekonstruálására nem használhatók. A tanulmány bemutatja, hogy a nem az erózióbázis szintjében keletkezett karsztos üregek is használhatók emelkedési ütemek behatárolására.

Tárgyszavak: paleokarszt, gerincesfauna, emelkedés, lepusztulás, Pannon-tó

Abstract

The latest Miocene – Quaternary inversion of the Pannonian Basin is manifested among others in spatially differential vertical movements. However, uplift rates are mostly available from the NW part of the basin. Paleokarst cavities with Late Pliocene and Quaternary vertebrate assemblages were studied in the Villány Hills, a low range in the SW, in order to track exhumation from under Upper Miocene Lake Pannon deposits and thus obtain numerical constraints on neotectonic uplift rates. Filled mostly with unstratified sediments, probably partly of aeolian origin, and enriched in vertebrate fossils, the studied fossiliferous cavities represent sites above the coeval base level. The accumulation of a vertebrate assemblage indicates the subaerial exposure of the Mesozoic carbonates at the given site. Based on the analysis of the elevation distribution of datable vertebrate sites, most of the Villány Hills had been exhumed from under Lake Pannon sediments before the accumulation of the first assemblages, 3.5 Ma, almost to its modern state. Base level lowering rate between 3.5 Ma and present was maximum 35 m/Ma for the main range and max. ~15 m/Ma for the Beremend block in the south. Latest Miocene – Early Pliocene (~6–3.5 Ma) minimum exhumation rates are estimated to be probably around 76–92 m/Ma for the main range and certainly above 12 m/Ma. Respective numbers for the Beremend block are 97–111 m/Ma and 37 m/Ma, carrying more uncertainty because this block might have suffered minor subsidence as well. Decreasing uplift rates in the Pliocene and Quaternary are tentatively attributed to the transpressional activity of the Drava Basin boundary fault from the Early Pliocene, which now accommodates a major portion of deformation in the region induced by

the Adria-Europe convergence. The majority of the fossiliferous fissures was not a direct product of tectonic deformation, therefore they cannot be used in stress field reconstructions. This study shows that even caves not formed at the paleo-base level can be used to constrain uplift rates.

Keywords: paleokarst, vertebrate fauna, uplift, denudation, Lake Pannon

Introduction

In the Pannonian Basin, a major back-arc basin in the Alpine orogenic belt in Europe, the post-rift subsidence phase with extensive sediment accumulation was followed by neotectonic inversion in the Late Miocene – Quaternary due to convergence between the Adria microplate and Europe (FODOR et al. 1999, 2005; HORVÁTH et al. 2006; BADA et al. 2007). Inversion is manifested among others in spatially differential vertical movements, with uplifting mountain ranges and subsiding sub-basins. Uplift rates are mostly available from the NW part of the basin, calculated from river terrace incision and base level lowering from caves (SZANYI et al. 2012; RUSZKICZAY-RÜDIGER et al. 2020, and references therein).

The Villány Hills, a low range of Mesozoic carbonates in the SW, belong to the Tisza tectonic unit comprising the SE half of the Pannonian basement. They host more than 50 vertebrate fossil sites in paleokarst cavities dated to the Late Pliocene and Quaternary (KRETZOI 1956, JÁNOSSY 1986, CSÁSZÁR & KORDOS 2007, PAZONYI 2011, MINDSZENTY & SEBE 2022). Before that, in the Late Miocene, the range was covered with sediments of Lake Pannon. This offers the possibility to obtain data on the relatively young denudation/uplift history of the area. Paleokarst fissures filled with sediment and fossils indicate that the Mesozoic carbonates forming the pre-neogene basement were subaerially exposed at the time of infilling, and karstification and sediment input could take place. If exhumation of the basement from under the Upper Miocene sedimentary cover happened during the accumulation of the vertebrate assemblages, then the age of the faunas should be related to the elevation, with the oldest fossil sites located at highest elevations. This does not mean that cavities can only form at the lower boundary of exhumed carbonates, near the base level, because the entire limestone surface already uncovered can karstify, but it does mean that old cavities should only be found at the highest elevations. To test this assumption, we examined the age-elevation relationship of the fossil sites in order to draw conclusions on the evolution of the area during neotectonic inversion.

Geological setting

The Villány Hills are an isolated outcrop of Mesozoic carbonates in SW Hungary, close to the Croatian border (Fig. 1). They belong to the Tisza tectonic unit comprising the southeastern half of the Pannonian Basin basement. The low range has a peak elevation of 442 m a.s.l. The hills show an imbricate structure that formed in the middle Cretaceous, with six north-vergent thrust sheets in the main body of the

range, and the southernmost one at Beremend underlain by thrust faults on both the northern and southern sides (RAKUSZ & STRAUZS 1953, WEIN 1969). Above the Cretaceous deposits the next sediments are small patches of Late Miocene sands (Pannonian in Central Paratethys regional stratigraphy) (RAKUSZ & STRAUZS 1953). These are followed by Late Pliocene – Quaternary fossiliferous red clays and Pleistocene loess. Because of the large stratigraphic gap, little is known about the Cenozoic history of the range.

In the Late Miocene the range was most probably flooded by Lake Pannon (Fig. 1). The presence of the lacustrine environment is shown by sporadic patches of sands attributable to Lake Pannon on the highest hill of the range (Szársomlyó or Harsány Hill), both on the surface of the Mesozoic rocks and in fissures within them (RAKUSZ & STRAUZS 1953; DEZSŐ et al. 2007, and references therein), up to an elevation of 240 m. Given that the nearby Mecsek Mts., only ~30 km to the north, were flooded by the lake up to elevations higher than 400 m a.s.l. (SEBE et al. 2013), the Villány Hills were probably entirely or almost entirely buried under the lacustrine sediments. This was also suggested based on the interpretation of seismic reflection profiles (CSONTOS et al. 2002). No data more precise than this are available on the thickness of Upper Miocene cover over the range. The accumulation of the Plio-Quaternary fossiliferous red clays started 3.5 Ma ago (PAZONYI 2011), while at ~1 Ma loess became the dominant sediment (MARSI & KOLOSZÁR 2004, PAZONYI et al. 2018a).

Inversion in the area driven by (N–S to) NW–SE compression occurred from the late Pannonian (Late Miocene), from ~7 Ma (TOMLJENOVIC & CSONTOS 2001, CSONTOS et al. 2002). This event resulted in thrusting of the Mesozoic succession of the Villány Hills into and onto Lake Pannon sedi-

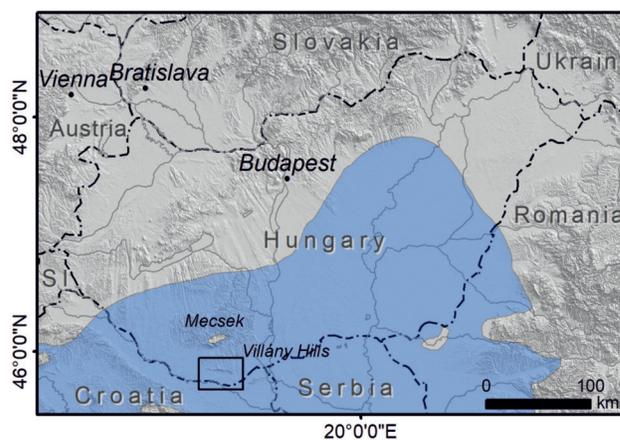


Figure 1. Location of the study area within the Pannonian Basin. Blue indicates the extent of Lake Pannon ~8 Ma ago (from MAGYAR et al. 1999).

1. ábra. A vizsgált terület helyzete a Pannon-medencében. A kék szín a Pannon-tó ~8 millió évvel ezelőtti kiterjedését jelöli (MAGYAR et al. 1999 alapján).

ments, in uplift of the range, and is responsible for the present topography of the region. Somewhat in contrast, PETRIK (2010) reconstructed a N–S transpressional stress field for the late Pannonian and NE–SW transpression for the Pliocene–Quaternary. The latter is in accord with the present-day stress field in the region (BÉKÉSI et al. 2023). KRETZOI (1955, 1956) proposed a stress field change in the Quaternary, because E–W oriented fissures contained older faunas than N–S ones. He attributed the fragmentary character of fossils in the E–W fissures (Villány 3, 5) to „rock pressure” (N–S compression).

Methods

Location and age data of all dated Pliocene–Quaternary fossil sites of the range were gathered, then based on the locations the elevation of the sites was retrieved from high-resolution maps. For sites that had been exposed through quarrying, original elevations a.s.l. were reconstructed from archive maps and aerial photos (source: fentrol.hu, geo-shop.hu, Lechner Nonprofit Kft.). In case of some old sites quarried off in the early 20th century, the locations are approximate due to imprecise documentation, meaning a few tens of metres of uncertainty in the horizontal directions and a few metres vertically. For vertical fissures the elevation of the top was considered, since that is where the fossils could get into the cavity. For two sites the previously published ages were re-evaluated based on the small mammal, mainly vole fauna. The small mammal fauna of the site Villány 5 belongs to the *Allophaiomys deucalion* – *Borsodia* Biozone (with an age of around 2000 ka; TESAKOV 2004, MAYHEW 2012, PAZONYI & VIRÁG 2025), in contrast to the 1100 ka age published in PAZONYI (2011). At Nagyharsányhegy 4, the *Microtus voles* (VAN DER MEULEN 1973) and the absence of *Mimomys pusillus* suggest that the site belongs to the early part of the *Mimomys savini* zone (ca. 750 ka), and its age is intermediate between Villány 6 and Villány 8 (PAZONYI et al. 2018b).

In case of fissures containing fossil assemblages of multiple ages, the oldest one was considered, since this marks the first time when the cavity (and thus the Mesozoic basement) was certainly open to the surface. Where the age of the site had been identified as an interval (e.g. Beremend14, Beremend Cave), because it was not possible to give an exact age based on the fossil species ranges, the centre of the interval was used in the graph. As additional data, the Villány cable car cut, interpreted to represent a Late Middle Pleistocene base level (SZUJÓ et al. 2017), and two fissures filled with Lake Pannon sands in the Nagyharsány quarry were considered. Age and elevation data were plotted in a point graph to help interpretation. The shape and orientation of the fossiliferous cavities was characterised based on the documentations, in order to gain information on possible tectonic control and check the proposal of KRETZOI (1956) on stress field change in the light of the new age data. Most of the still accessible sites were also visited in the field.

Results

It was possible to gather 19 fossil sites with well confined age data (Table 1, Fig. 2). With one exception, Palkonya, which represents the paleosurface, they are infills of paleokarst cavities and fissures. Their age distribution gives a good, relatively even coverage of the time interval after 3.5 Ma (Fig. 3). The elevation of the fossil sites ranges between 130 m a.s.l., close to the local base level, to 440 m, almost the peak of the range. The local base level lies at ~90 m a.s.l. near Beremend, at the southeastern tip of the range (Drava plain in the west and Karasica valley in the east), and at ~95 m a.s.l. near Csarnóta in the west (Drava plain).

The relationship between age and elevation data is shown in Fig. 3. Remarkably, the points do not show a trend referring to ongoing uplift, with older sites lying at higher elevations. Instead, all but one points fall in a 100 m wide elevation interval, between 130 and 230 m a.s.l. The higher levels of the range are devoid of known fossil paleokarst sites, while one locality lies very close to the peak.

There are multiple possibilities to interpret the graph. The most straightforward one is to consider all data points together and state that by ~3.5 Ma ago, the entire range had become uncovered nearly to the state it is now: Beremend 26, with its 3.3 Ma age, belongs to the lowest-lying locations, showing exhumation down to ~140 m a.s.l. by that time. Supposing steady uplift for this period from 3.3 Ma up to today (red line 1 in Fig. 3), the maximum uplift rate – more precisely the maximum rate of base level lowering – can be calculated from the site, which lies ~50 m above the local base level. This gives a lowering rate of 15.15 m/Ma or 0.015 mm/a. This is a maximum value, since Beremend 26, similarly to most of the fossil sites, was filled with red clay that formed over elevated terrain, i.e. not on floodplains (KOLOSZÁR 2004), so it was lying somewhat above the coeval base level when it accumulated.

It is also possible to suppose that the Beremend block, which is relatively isolated from the rest of the range, moved separately. While in the main body of the Villány Hills thrusting was north-vergent, in the Beremend block it is opposite (WEIN 1969), so it is possible that it behaved differently. If Beremend sites are disregarded (line 2 in Fig. 3), then the maximum exhumation rate for the past 3.5 Ma is 35 m/Ma.

Individual thrust sheets can be considered separately as well. During the formation of an imbrication zone, the normal (in sequence) succession of thrusting migrates towards the foreland, i.e. the uppermost thrust sheet forms first (FOSSEN 2010). Based on the fossiliferous cavities, this principle does not work for the rejuvenation of the thrust planes of the Villány Hills. The oldest fossil site is located in the lowermost thrust sheet. Exhumation of the uppermost unit (Beremend) happened earlier than that of the underlying one (Nagyharsány), but the next one (Villány) has again older sites. The western (lower) three examined thrust sheets have too few sites to draw conclusions on them. Viewing sites within a unit, none of the thrust sheets shows a younging trend towards lower elevations.

Table I. Data of the dated fossil sites of the Villány Hills*I. táblázat. A felhasznált ősmaradvány-lelőhelyek adatai*

Site	Abbr	Lat	Lon	Z	Age (ka)	Comment	Reference	Structural data
Palkonya	P	45.8904906	18.39227605	130	300	on palaeosurface of Triassic basement; >300 ka	SEBE et al. 2023	on palaeosurface, not tectonic
Beremend 26	B26	45.7930881	18.44026545	139	3300		MÁRSI & KOLOSZÁR 2001	oval, tens of metres wide and long, 20 m high, probably not tectonic
Beremend 5	B5	45.7886592	18.43803883	140	3100		KRETZOI 1956	fissure, orientation unknown
Beremend 11	B11	45.7911844	18.43921935	140	3000		JÁNOSSY 1979	shape unknown
Villány, cable car cut	Vcc	45.875328	18.44911108	140	1200	400–2000 ka; local base level at the given time	SZUJÓ et al. 2017	
Villány 8	V8	45.8749049	18.44906421	145	700		KRETZOI 1956, JÁNOSSY 1979	high N–S vertical fissure, downward widening
Beremend 15	B15	45.7899059	18.43901501	145	2700		JÁNOSSY 1987	fissure, orientation unknown
Villány 7		45.8749601	18.44928254	146	900	800–1000 ka	KRETZOI 1957	N–S fissure
Villány 3	V3	45.8756388	18.4517349	160	2000		KORMOS 1937, KRETZOI 1956, PAZONYI 2011	>10 m high, m wide N–S vertical fissure crosscutting bedding (KORMOS 1937); according to KRETZOI 1956 E–W
Villány 5	V5	45.8756388	18.4517349	160	2000		KRETZOI 1956, PAZONYI & VIRÁG 2025	E–W fissure, parallel with Villány 3 (? – see V3)
Villány 6	V6	45.8753959	18.45172467	162	770		KRETZOI 1956, PAZONYI et al. 2018b	high, m wide N–S vertical fissure
Beremend Crystal Cave	BC	45.7919251	18.44309448	163	1350	1200–1500 ka	TAKÁCSNÉ BOLNER 1985, 2003, PAZONYI et al. 2019	fossiliferous red clay in cave walls, not as infill; shape of original cavity unknown
Nagyharsány-hegy 2	N2	45.8557547	18.43112219	165	1200		KORMOS 1917, KRETZOI 1956, VAN DER MEULEN 1973	fissure dipping towards 120–130°
Nagyharsány-hegy 4	N4	45.8561587	18.43098888	166	750		VAN DER MEULEN 1973	small cavities, probably not tectonic
Beremend 14	B14	45.7912722	18.44379608	169	2350		PAZONYI et al. 2016	shape unknown
Somssich-hegy 2	So2	45.8740601	18.44253135	181	1000		PAZONYI et al. 2018a	probably not tectonic
Nagyharsány Crystal Cave	NC	45.8516354	18.39482834	190	400		PAZONYI et al. 2021	330/40 fissure at collection points, upwards more irregular; bones are being washed down from above, original location unknown
Siklós	Si	45.8811899	18.24986972	210	90	140–40 ka	SEBE et al. 2023	no data on cavity shape; if fissure, then extensional (gravitational?) and E–W trending
Csarnóta 2	Cs2	45.8865598	18.39232331	226	3500		KORMOS 1911, 1917, 1937; KRETZOI 1959; SZENTESI et al. 2015	KORMOS 1917: cone-shaped breccia column, cave infill, probably not tectonic
Nagyharsány-hegy 6	N6	45.8556353	18.41143933	440	250		JÁNOSSY 1979, PAZONYI et al. 2021	cave along lithological boundary

Exhumation rates for the time interval pre-dating the fossil record can be calculated accordingly for the first two scenarios. There are no certain data on the thickness of the Upper Miocene succession that once covered the range, various options can therefore be considered. The delta front of Lake Pannon passed the area ~6 Ma ago (based on MAGYAR et al. 2013), so exhumation of the range could start after-

wards. Accepting the complete burial of the range, as suggested by MAGYAR et al. (1999), the modern peak elevation (442 m a.s.l.) is indeed an arbitrary number to assess the original elevation of Lake Pannon deposits, but lacking other constraints on the thickness of Upper Miocene sediments overlying the range, it can be used. Exhumation from this elevation to the lowest old site, Beremend 26, gives ~300

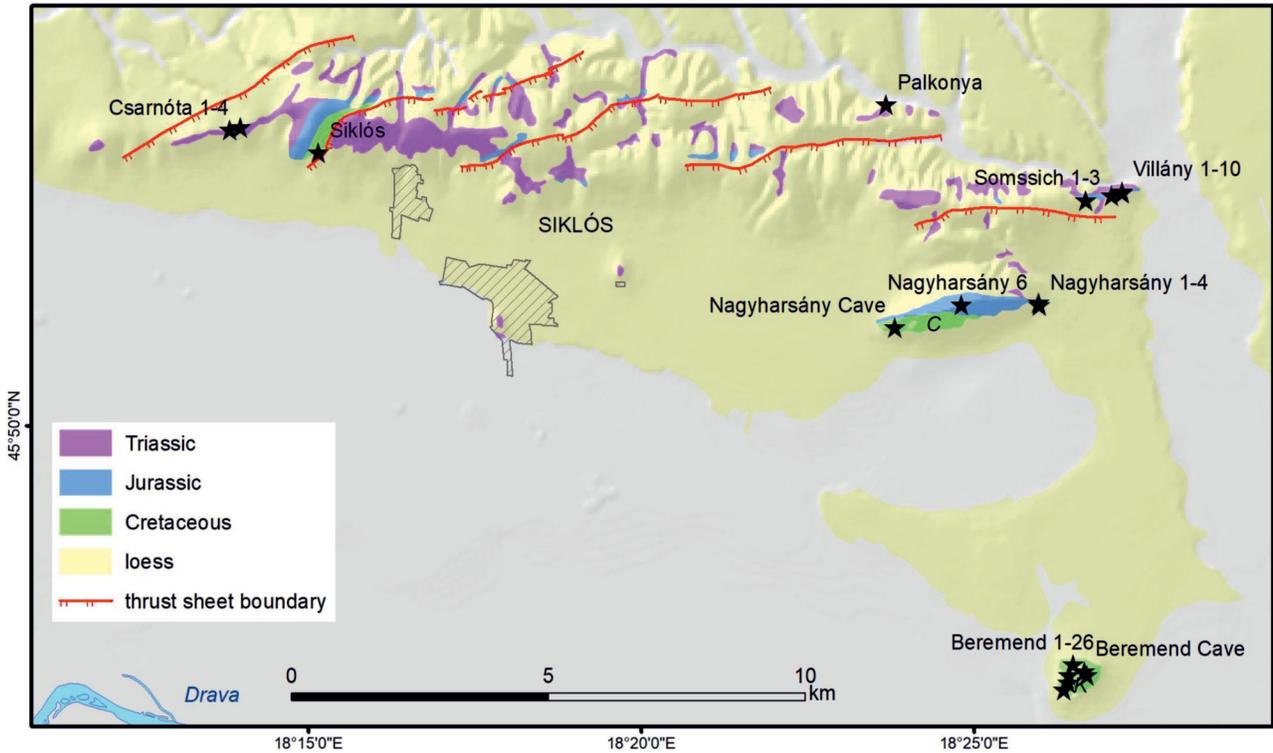


Figure 2. Location of paleokarst cavities with dated vertebrate fossil assemblages. Surface lithology after GYALOG & SÍKHEGYI (2005), tectonic boundaries after RAKUSZ & STRAUZ (1953)

2. ábra. A korolható gerincesegyütteseket tartalmazó őskarsztos üregek elhelyezkedése. Felszíni földtan GYALOG & SÍKHEGYI (2005), pikkelyhatárok RAKUSZ & STRAUZ (1953) alapján

m/2.7 Ma, i.e. 111 m/Ma (0.111 mm/a). Supposing burial up to 400 m a.s.l. like in the Mecsek Mts. (SEBE et al. 2013) would slightly lower the rate: 261 m/2.7 Ma, which is 96.7 m/Ma. If only the uppermost preserved occurrence of Upper Miocene sands at 240 m a.s.l. (DEZSŐ et al. 2007) is accepted as certain burial height, then exhumation rate would be 101 m/2.7 Ma = 37.4 m/Ma.

For only the main range, line 2 should be considered, which lies at ~210 m a.s.l. at 3.5 Ma. Counting from complete burial results in ~230 m/2.5 Ma, i.e. 92 m/Ma (0.092 mm/a). From 400 m a.s.l. the exhumation rate will be ~190 m/2.5 Ma = 76 m/Ma, while from 240 m very low, 30 m/2.5 Ma = 12 m/Ma.

These are all minimum rates, because the coeval base

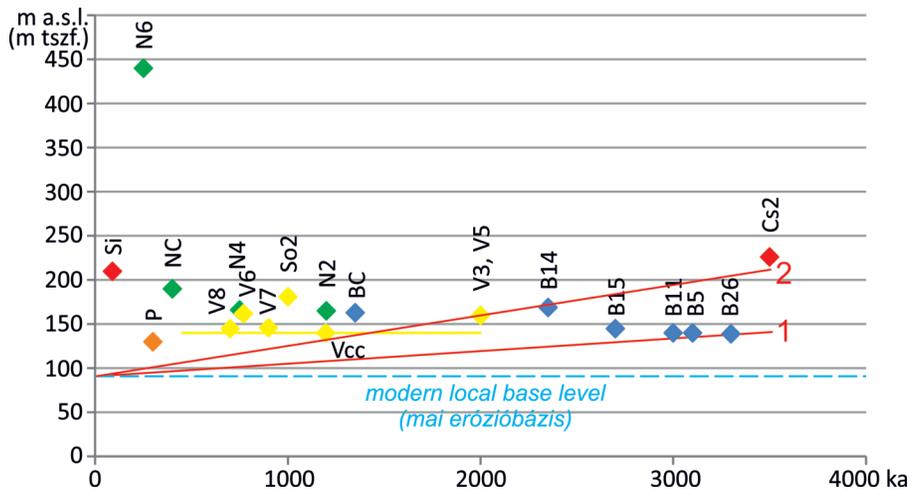


Figure 3. Age vs. elevation plot of dated vertebrate fossil sites of the Villány Hills and lines of base level change for the two scenarios described in the text. Different colours indicate different thrust sheets. For site name abbreviations see Table I

3. ábra. A Villányi-hegység ismert korú ősmaradvány-lelőhelyeinek kora és magassága, valamint az erózióbázis süllyedését leíró görbék szövegben bemutatott két változata. Az eltérő színek eltérő pikkelyt jeleznek. A lelőhelyek nevének rövidítései lásd az I. táblázatban

level could have been somewhat lower than the fossil sites used in the calculations. In addition, with complete burial, the range could have been covered with Lake Pannon deposits higher than its modern peak, the higher thickness still increasing the rate. In a new seismic stratigraphic study, a younger, ~5.4 Ma old date is proposed for the passage of the Lake Pannon delta at the Villány Hills, though the dating of seismic horizons carries large uncertainties in the area (BAGOLY ÁRGYELÁN et al. 2025). If true, this would result in even higher exhumation rates for the Early Pliocene.

Structural data

Considering the shape of fossiliferous cavities, 8 out of 18 were linear fissures crosscutting bedding, which had been probably fracture-controlled (*Table I*). In two cases the orientation was unknown already when the site was found. In the other six cases orientations were given in the publications, sometimes with quite large differences (*Fig. 4*).

Reports about Villány 3 are most contradictory. KORMOS (1937) wrote about a N–S fissure, but his photo (fig. 2. in p. 1075) suggests a roughly E–W orientation. KRETZOI (1956) described it as an E–W fissure, together with Villány 5. According to J. DEZSÓ (in DEZSÓ et al. 2002) the fissure orientation is 40–220°, closer to N–S than E–W. The remnants of Villány 3 are still visible in the field. The general orientation of the fissure is vertical, trending 55–235°, but its lowermost part turns toward the south. Its walls are highly irregular, uneven, and downward the fissure divides into multiple curving branches. Because of the thick flowstone incrustation the wall surfaces are not visible, but their undulating and not angular shape refers to formation by dissolution rather than by fracturing. Along the presently upper part of the fissure, which is not the original top but some metres lower, a fracture with a 330/72° dip bounds short intervals, for some part on the northern, for the other part on the southern side of the karst fill, with the opposite boundaries being irregular. The shape and preservation of vertebrate fossils does not differ

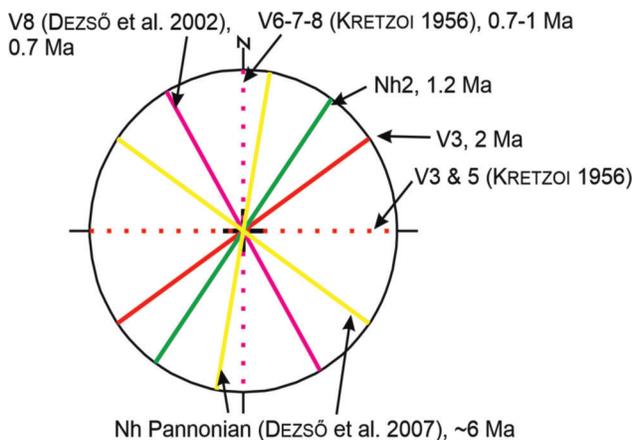


Figure 4. Reported orientations of dated fissures (for references see text)

4. ábra. Ősmaradvány-tartalmú karstos hasadékok irányjai. Hivatkozások a szövegben

from those of other sites, do not seem to be deformed by pressure.

The younger sites of Villány 6, 7 and 8 were described as N–S trending (KRETZOI 1956). According to DEZSÓ et al. (2002) the remains of the fissure of Villány 8 trend 150–330° and have dissolved walls, without speleothems (flowstone). At the location of Villány 6 an 8 m high, 10–15 cm wide, N–S trending fissure was visible recently, with a 10 cm thick flowstone crust and a loess-like infill with small mammal fossils (DEZSÓ et al. 2002). Nagyharsány 2 was described as a steep fissure dipping towards 120–130° (KRETZOI 1956).

Two fissures filled with sand originally deposited by Late Miocene Lake Pannon (DEZSÓ et al. 2007) in the Nagyharsány quarry are among the very few occurrences of Miocene sediments within the Villány Hills. The lower one is 8 m thick (CSÁSZÁR 2002) and trends 125–305° according to DEZSÓ et al. (2007). It is probably identical to the occurrence mentioned by RAKUSZ (1937) as „fine, mica-bearing sand above the Nagyharsány cemetery at an elevation of ~170 m a.s.l., which overlies the karstified surface of the Lower Cretaceous limestone and intrudes into its fissures”. The artificial exposure of the quarry showed that infill was not homogeneous sand, but mostly sandstone debris, as reported already by FÜLÖP (1966). The northern half is filled with sub-angular to angular sandstone blocks up to a metre size, with silty sand between them, and thick coarse sparry calcite crusts covering some of the blocks (*Fig. 5 A, B*). In the middle a large flowstone sheet covers the entire height of the outcrop. The southern half is mainly sand, with sandstone blocks. According to the grain size curves (DEZSÓ et al. 2007) all samples both from sandstone blocks and their matrix have their peaks in the coarse silt fraction, in contrast with the field observations. The mineralogy of the samples is similar, they are all dominated by quartz and clay minerals. The uppermost sample from the matrix differs from the others in containing chlorite instead of kaolinite. CSÁSZÁR (2002, table 6, 7) provided a mineral composition for the matrix dominated by clay minerals and subordinate amounts of quartz. On the wall of the fissure slickenlines referring to horizontal movement were observed (PETRIK 2009). The northern half of the infill, the sandstone debris, must have got into the fissure after the lithification of the Lake Pannon sands, when the fissure opened to the surface. The fallen blocks were then draped by flowstone, showing that the cave passage was filled with air and not water, so this must have happened already after the regression of Lake Pannon, when base level and the karst water table had already lowered. The other half of the cavity was filled up with less consolidated material, mostly sand, with some sandstone, so the sand was still available on the surface when this accumulated. Therefore the age of the opening of the fissure and its filling up with clastics and speleothems has to be between ~6 Ma, the disappearance of Lake Pannon, and ~3.5 Ma, when already red clay was depositing and the range was devoid of Upper Miocene sands.

The upper outcrop lies about 70 m higher. The fissure trends 10–190° according to DEZSÓ et al. (2007). In 2000 no



Figure 5. Paleokarst cavities with Lake Pannon sediments in the Nagyarsány quarry. A, B) Lower outcrop; C, D) upper outcrop; hammer for scale circled. Photos A and C courtesy of Gábor CSILLAG

5. ábra. Pannon-tavi üledéket tartalmazó őskarsztos üregek a nagyarsányi kőfejtőben. A, B) alsó feltárás; C, D) felső feltárás; a méretarányul szolgáló kalapács jelölve. A és C kép: CSILLAG Gábor

fissure was visible in the field, rather irregular cavity walls, partly with (hemi)spherical shapes (Fig. 5 C, D). Walls are dissolved, with fossils of the Cretaceous limestone weathered out. The infill was laminated fine sand, in patches cemented with calcite, with frequently changing dip angles and directions. No speleothems were observed. The spherical cavity remnants suggest a hypogenic origin for this paleocave. Hypogene karstification has been active in the Villány Hills and was proposed among others for several Beremend fossil sites (DEZSŐ & TÓTH 2006, DEZSŐ et al. 2007). As the cavity is filled solely by Lake Pannon sands (DEZSŐ et al. 2007) and does not contain e.g. red clay, it probably opened to the surface around the deposition time of the sands: either before flooding by Lake Pannon and sand was

washed into the cavity by the lake, or after the accumulation of the sands and the sands got redeposited into the cave. So the cavity filled up probably in the latest Miocene or possibly in the earliest Pliocene.

Discussion

The elevation range of the fossil sites may suggest at first sight that their vertical distribution does not represent the natural conditions but instead is restricted by good exposures, as most sites have been discovered in quarries which lie at low elevations. However, there exist sites that are unrelated to quarrying and were still found, for instance the

highest one (Nagyharsány 6). Another argument against this is that the Nagyharsány quarry reaches as high as 320 m a.s.l., but no fossiliferous cavities were found in its upper levels. We therefore now do not consider the possibility of detection bias and handle the data as representing the natural situation.

Position of the fossil sites relative to base level

The gravel outcrop in the cable car cut of Villány was included in this study as supplementary data representing a paleo base level. The age of the gravel could be bracketed between ~400 and 2000 ka (SZUJÓ et al. 2017). In the graph of Fig. 3 it is included with the mean of the age interval, similarly to the fossil sites, but the entire interval is also marked. The mean age falls above both lines indicating the hypothesised maximum position of the lowering base level. If the gravel really represents the floodplain of the trunk stream of the range foreland, as supposed (SZUJÓ et al. 2017), then its age must fall below one or both base level lines. This condition is only fulfilled in case of line 2, supporting the exhumation scenario when the Beremend block moved independently of the bulk of the Villány Hills. In this case, the age of the gravel should be in the older portion of the proposed interval, between ~1.4 and 2 Ma. Another resolution to the contradiction would be if the gravel had been deposited by a minor, steeper watercourse (even intermittent stream) discharging into the trunk stream. Given the exclusively local provenance of the clast material, this could also be a possibility, though the clast sizes are too large for the small watershed such a stream branch could have.

For some vertebrate sites it has been proposed that they contain remains of (semi)aquatic animals and therefore they represent water-linked, e.g. floodplain, locations, or indicate the presence of a permanent water body in the close proximity of the site. If true, these would be the best candidates to quantify exhumation and uplift. At site Somssich-hegy 2, KROLOPP (2000) found a few fluvial snails in many samples. This led him to suppose that the site was not a closed shaft but a re-entrant open to the north (towards the mountain front watercourse), which lay at the level of the floodplain and floods transported aquatic molluscs into the site. From this he also inferred considerable uplift of the range since the early Pleistocene. However, excavations in 2014 disproved this idea by exposing the Jurassic host limestone all around the fossil-bearing Pleistocene sediment (BOTKA & MÉSZÁROS 2015). For the same site and also for the Late Pliocene Csarnóta 3, a permanent water surface was assumed nearby based on moisture-loving herpetofaunal elements (SZENTESI et al. 2015, SZENTESI 2016, PAZONYI et al. 2018a).

However, the presence of water-linked taxa does not mean that the site was located on a floodplain. If floodwater transported fossils into a cavity, then fluvial or swamp sediments and signs of water flow should be observed, which is not the case at these sites (PAZONYI et al. 2018a). Instead, most aquatic animals probably got into the cavities as prey,

of raptors, large snakes or mammals. Owl pellets were reported to have contributed to the accumulation of the vertebrate assemblages (Villány 5: KRETZOI 1956; Somssich-hegy 2: PAZONYI et al. 2018a). As a modern example, at a cave entrance in the Mecsek Mts., fish remains have been found at 700 m straight line distance (more than a km through the cave passages) from the nearest lake where fish of this size live and at ~70 m higher elevation. These must have been carried there by foxes or otters, both observed to dwell in the cave (BAUER et al. 2023). Members of the herpetofauna can also fall into elevated cavities related to their annual breeding migrations (KOVAR et al. 2009, PAZONYI et al. 2018a).

For the topographic position of the fossil-bearing cavities denudation surfaces were also put forward. For the Beremend vertebrate sites it was proposed that the limestone block hosting them was part of the piedmont of the Villány Hills during the Late Pliocene, and the karst infill material was transported from the main range on this surface into the fissures (KOLOSZÁR 2004, MARSÍ & KOLOSZÁR 2004). KRETZOI (1956) was also on the opinion that the range used to be part of an extensive karst surface in the early Pleistocene that could provide sediment into the fissures. These reconstructions also seem unlikely. Similarly to the floodplain situation, on a piedmont surface a fissure would rapidly fill up with water-transported sediment. In case of the fossiliferous cavities, the enrichment of the fossils refers to a low sediment accumulation rate, which is only possible with a very small catchment area with aquatic transport or a different – e.g. aeolian – mode of sediment input. Even if accumulated on the (paleo)surface, the Tengelic Red Clay is usually thin, reflecting low sedimentation rates, and recently it has been proposed that the bulk of its material has an aeolian origin (KOVÁCS 2008, VARGA 2011). Among the paleokarst infills a wind-blown origin has been proposed for the Somssich-hegy 2 site (PAZONYI et al. 2018a), then for Beremend and Csarnóta localities (KOVÁCS et al. 2020). For some cavity infills with a good fossil record it was shown that they accumulated over hundreds of thousands of years (Beremend 26: MARSÍ & KOLOSZÁR 2004; Csarnóta 2: KRETZOI 1959), meaning that they were active for a relatively long time without filling up. Obviously, this does not mean that aquatic sediment transport is entirely excluded, just that it is not the dominant mode of sediment supply. Actually, layered intervals in Beremend 26 (MARSÍ & KOLOSZÁR 2001) point to short-term deposition from water, but they only form a small portion of the karst infill, even though climate was not dry based on paleoecological reconstructions (MÉSZÁROS et al. 2021). Nevertheless, a provenance of the Beremend 26 red clay from bauxite was excluded based on mineralogical investigations (DEZSŐ et al. 2007).

The Mesozoic basement rocks do not get exhumed in a uniform manner: peaks, ridges and valley/gully floors get uncovered first, and flat hillslopes last. This is well reflected in the present state of the Cenozoic cover: red clay and loess thin out, then disappear upslope and below gullies and intermittent streams (RAKUSZ & STRAUSZ 1953, CZIGÁNY 1998).

As a result, subaerially exposed carbonates available for karstification at any time will not be located at the base level but at somewhat higher elevations.

To sum up, typical fossil assemblages known so far in the Villány Hills cannot be used as precise indicators of a paleo base level, but they do confine base level position from above, giving a maximum possible elevation.

Paleokarst cavity morphology and stress field orientations

Morphologically, several of the fossiliferous paleokarst cavities are fracture-controlled: they have planar walls and are narrow compared to their length and height. No wonder they invoke tectonic interpretations, and actually so it happened. KRETZOI (1956) observed in Villány that fissures with older, Villányian age faunas (Villány 3, 5) trend E–W, while the younger, Biharian ones (Villány 6–7–8) N–S, and from this he concluded on a change in the stress field. On p. 35 he wrote that it was N–S compression, related to late thrusting, that closed the older E–W fissures and opened the younger N–S ones. In contrast, on p. 93 he gave the interpretation that during the Villányian, N–S compression loosened and opened the E–W fissures, then later (in the Biharian) compression turned to E–W and opened the N–S fissures.

Actually, both options are possible: the first one in case of simple compression, the second one in case of folding (anticline formation) above a thrust and the related local extension, although with the north-vergent thrust planes of the Villány Hills it is hard for anticlines to form with E–W compression, at least pre-existing low-angle faults with proper orientations are missing. Fractures parallel and perpendicular to anticline hinges can even form coevally. In these cases the fossiliferous fissures are interpreted as extension cracks. But fissures can also form through faulting. By dissolution along fractures as well, as supposed by KOLOSZÁR (2004) for Beremend, and this is a very common phenomenon in all karst areas of the world. These are most often pre-existing fractures and can be significantly older than the fissure fill. On steep slopes cracks can also open due to gravitational mass movements. In order to use fissures for stress field reconstruction, it is necessary to know their formation mechanism.

From the various types, striated fault planes could be best used to infer on the stress directions, provided it can be shown that the opening of the fissure happened as a result of displacement along the fault and not later, in a different stress field. Among the sites mentioned so far, slickenlines have only been reported on the wall of the lower fissure of the Nagyharsány quarry (PETRIK 2010). No striation data are known from fossiliferous fissures, and as most of them have long been destroyed by quarrying, there is no more hope to obtain them. The fissures of Villány, interpreted by KRETZOI as tectonic, have dissolved walls and do not seem to represent single fractures. They were probably controlled by fractures, but it seems that dissolution created the open spaces, some unknown time after the formation of fractures. As a

result, no well-founded conclusions can be drawn from them on the paleo-stress fields due to the unknown age and type of the controlling fractures.

Exhumation in a regional geodynamic framework

As presented above, various exhumation rates can be calculated for the Villány Hills from the latest Miocene to the present, considering different options of blocks moving together and various burial heights:

scenario	exhumation rate (m/Ma)			3.5–0 Ma
	6–3.5 Ma			
	from complete burial (442 m a.s.l.)	from burial elevation of Mecsek Mts. (400 m a.s.l.)	from highest preserved M3 sand (240 m a.s.l.)	
Villány Hills as a single block (controlled by Beremend sites)	min. 111	min. 96.7	min. 37.4	max. 15.15
main range without Beremend block	min. 92	min. 76	min. 12	max. 35

From the two scenarios, the condition that the Villány cable car cut as a paleo base level should be below the exhumation line obtained from the fossil sites supports the second one, the main range moving separately from the Beremend block. Consequently, rates of the first scenario apply to the Beremend block only.

The examination of fossil sites by individual thrust sheets does not refer to foreland-vergent propagation of thrusting in the studied time interval, after 3.5 Ma. The fact that the oldest locality of the main range (Csarnóta 2) lies in the lowermost thrust sheet, and its coordinates control the exhumation line of the range (*Fig. 3*), suggests that since its formation the six north-vergent thrust sheets were probably moving together. Seismic sections clearly show that thrust sheets of the Villány Hills experienced differential displacement during or after Lake Pannon sedimentation and moved relative to each other when thrusting into the Upper Miocene succession of the northern foreland (CSONTOS et al. 2002). This must have increased the relief of the basement rocks, still, there is no sign of it in the exhumation data shown by the paleokarst cavities (i.e. exhumation of the upper thrust sheets does not precede that of the lower ones). The reason behind this might be that the bulk of internal deformation happened before the time interval covered by the fossil sites. This could be approximately coeval with Late Miocene syn-sedimentary compressional deformation reported from the Mecsek Mts. and Mórág block (CSONTOS et al. 2002, KONRÁD & SEBE 2010, SEBE et al. 2016, KOVÁCS et al. 2018, BUDAI et al. 2019).

The uplift rate calculated from the cable car cut at Villány for the past 0.4–2 Ma was 50–10 m/Ma (SZUJÓ et al. 2017). If the age of the fluvial gravel is 1.4–2 Ma, as discussed above, then the uplift rate falls between 14.3–10 m/Ma. These numbers are the same order of magnitude and in agreement with that calculated for the past 3.5 Ma.

For the preceding interval (6–3.5 Ma) considerably higher exhumation rates were obtained for almost all variations of burial. Only one of them is in accord with the more recent

rate, for the main range, if very shallow Upper Miocene burial is supposed, what is less probable. That thin cover would imply that the Mecsek Mts. underwent at least 160 m more uplift than the Villány Hills. This is not excluded, but seismic sections (CSONTOS et al. 2020) do not show marked differences in vertical displacement between the two ranges, though it is difficult to precisely assess these values from the sections. Obviously, we do not suppose one single breakpoint in the exhumation or uplift curve, the change in the pace of movement must have been gradational. Still, most of the presented scenarios mean that movement definitely slowed down in the Late Pliocene and Quaternary.

There are few data to compare the obtained exhumation rates to. For the present day, satellite-based positioning measurements do not help to increase the precision of geological data. The Villány Hills are part of a regional GPS monitoring network (Western Mecsek GPS geodynamic network), with stations at Csarnóta and Villány. Vertical movements in the network since 1998 were below measurement error (~ 0.5 mm/a) (GRENERCZY & KÖRMENDY 2014). Global navigation satellite system (GNSS) measurements only show general subsidence in the wider region, admittedly in contrast with geological data (PORKOLÁB et al. 2023).

The geographically nearest numerical uplift rates have been published for the Western Mecsek Mts., a maximum incision and uplift rate of 8–35 m/Ma for the later Quaternary (since 1 Ma – 231 ka to present day) (SEBE et al. 2025), which are in the same range as those obtained in the Villány Hills. More to the north, in the Transdanubian Range, fairly constant incision rates of ~ 50 m/Ma of the Danube were reconstructed for most of the past 3 Ma (RUSZKICZAY-RÜDIGER et al. 2020), higher than in the Villány Hills. An apparent, partly climate-induced acceleration of incision to ~ 200 m/Ma was reported for the latest Quaternary (since 140 ka) (RUSZKICZAY-RÜDIGER et al. 2020). In the same range, the analysis of paleosurfaces related to Pliocene – Quaternary volcanoes and related paleosurfaces gave similar long-term rates of 70–100 m/Ma (FODOR et al. 2022) as well as the dating of aeolian landforms (40–80 m/Ma for the past 1.5 Ma; RUSZKICZAY-RÜDIGER et al. 2011). In a geodynamically different setting, in the orogenic belt surrounding the Pannonian Basin, at the transition between the Alps and Carpathians, uplift/incision similarly increased towards the present has been observed: the 36–42 m/Ma rates for the past 4.1–4.6 Ma increased to max. 162 m/Ma for the past 0.31–0.34 Ma (NEUHUBER et al. 2020). Quite close by, in the westernmost Carpathians, a relatively low, 26 m/Ma maximum uplift rate was obtained for the past 1.7 Ma (ŠUJAN et al. 2017). It is interesting that higher strain (shortening) rates are calculated for the Villány Hills area than for more northern/northwestern parts of the Pannonian Basin (PORKOLÁB et al. 2023), and the uplift rate still seems to be lower here.

To the south, on the opposite side of the Drava Basin, much higher rates were reported. According to MATOŠ et al. (2016, 2017, and references therein), the Bilogora Mts. underwent more than 400 m of differential uplift during the Pliocene and Quaternary, due to transpressional rejuvena-

tion of the dextral strike-slip Drava Basin boundary fault. The same authors gave uplift rates between ca. 0.38 and 0.71 mm/yr (380–710 m/Ma) for the oldest Lower to Middle Pleistocene Drava River terrace in the Bilogora area, and this points to intensification of uplift in the later Quaternary when compared to 400 m uplift from the beginning of the Pliocene. Luminescence dating of the same terrace provided minimum ages (>359 ka and >450 ka). Based on them, WACHA et al. (2018) calculated incision rates of 0.22 and 0.09 mm/a (220 and 90 m/Ma) for the Drava river since terrace formation in the NW and SE of the Bilogora, respectively. Since luminescence data are minimum ages, the incision rates should be considered maximum values, especially that the terrace contained macroflora typical of the Pliocene (MRINJEK et al. 2006), so can be considerably older than the minimum ages. Besides the Drava Basin boundary fault, originally Miocene normal faults between the North Croatian Mountains and the Sava Basin got inverted as well in the Pliocene, accommodating further shortening (PRELOGOVIĆ et al. 1998, USTASZEWSKI et al. 2014).

The driving force for the exhumation of the Villány Hills is without question the basin inversion, starting around 8 Ma in the wider area and considered to be ongoing up to the present day (FODOR et al. 1999, 2005; TOMLJENIĆ & CSONTOS 2001; CSONTOS et al. 2002; UHRIN et al. 2009; SEBE et al. 2020). It is more difficult to explain the decrease in uplift rate in the Pliocene. HORVÁTH et al. (2006) mention a regional compression event from ~ 3 Ma ago until today, with widespread upwarping of basement units from below the Neogene cover. Based on data presented in this paper, it seems that in the Villány Hills this exhumation happened earlier, before 3 Ma. In Slovenia, partly in the Pannonian Basin and partly in the Alpine realm, major strike-slip and contractional deformation between the Adriatic microplate and the Periadriatic fault started at the Miocene–Pliocene transition (VRABEC & FODOR 2006), temporally close to basin inversion in the SW Pannonian Basin. In central Slovenia, uplift and river incision was documented around the Pliocene/Quaternary boundary, but later, during the Quaternary rivers reached steady state, without incision (MENCIN GALE et al. 2024). The exact tectonic drivers behind declining incision are unknown as of now, they may lie in local factors. These events are close in time to the period of relatively fast, then diminishing exhumation of the Villány Hills, but geographically and considering the structural units a bit far away.

As shown by the GNSS measurements, recent horizontal movement velocities abruptly decline at the Drava Basin towards the inner Pannonian Basin (PORKOLÁB et al. 2023). This means that a considerable part of the deformation induced by convergence is accommodated along the Drava Basin boundary fault, and explains the uplift differences between N Croatia and SW Hungary. In addition, uplift rates in the Bilogora are lower in the SE, closer to the Villány Hills, than in the NW (WACHA et al. 2018). The old Drava terrace dissected by the Drava Basin boundary fault shows significantly more subsidence basinward of the boundary fault than up-

lift on the outer side, in the Bilogora (WACHA et al. 2018). As the boundary fault has a north vergent reverse component during its neotectonic activity since the Early Pliocene (PRELOGOVIĆ et al. 1998, LUČIĆ et al. 2001, MATOŠ et al. 2016), in the generally compressional regime of inversion the Drava basin subsidence exceeding margin uplift might even be a consequence of flexural subsidence (downwarping) in front of the reverse fault, caused by the thrusting of the North Croatian Mountains onto the northern foreland. This way the lowering of the Drava Basin basement might contribute to the relatively low exhumation rates of the Villány Hills along its northern, not fault-bounded margin.

A further factor in the low rate of base level lowering in the Villány Hills, just next to the Drava plain, could be the increase of sediment production in the higher, East Alpine reaches of the river catchment. Growing sediment delivery was shown to slow down river incision in the Quaternary in the lower reach of the tributary Mur, and even to stop it more downstream along the Drava (in the Pohorje dome) despite the fact that there is evidence for ongoing uplift there (WAGNER et al. 2010).

The listed data add up to a quite coherent evolution history of the area. Basin inversion started to act in the SW Pannonian Basin in the Late Miocene, around 8–7 Ma ago, when the region was still flooded with Lake Pannon. It caused syn-sedimentary and also possibly post-sedimentary compressional or transpressional deformation in the Mecsek Mts. and the Villány Hills as well as in the wider area including North Croatia as well. With continuing convergence between Adria and Europe, the Pannonian Basin experienced further ~N–S shortening. In the Early Pliocene the Drava Basin boundary fault started to act as a dextral reverse fault, and the uplift of the southern basin margin including Bilogora began. This might have been coeval with the formation of the marginal unconformities between the Lake Pannon succession and the overlying fluvial deposits in the Drava Basin, dated to the beginning of the Pliocene based on seismic section analysis (SEBE et al. 2020). Much of the compressional deformation got transferred to this fault zone from more interior (northern) parts of the Pannonian Basin, and exhumation of the Villány Hills slowed down. This might be an example of propagation of inversion towards basin margins forecasted by numerical modelling (ORAVECZ et al. 2024). Tectonic loading and flexural downwarping of the Drava Basin basement could contribute to the lowering of exhumation rates, especially in case of the Beremend block due to its more southern position. In fact, the low present position of the Beremend block might even be the result of some relatively recent minor subsidence after inversion-related uplift and exhumation. This would be in agreement with recent local extension observed in Beremend (GERNER 1992). Further factors governing uplift rates, shown to act in basin scale but not possible to quantify in the study area yet, can lay in deep lithospheric and mantle processes as well as surface denudation and large-scale sediment redistribution (RUSZKICZAY-RÜDIGER et al. 2020, ORAVECZ et al. 2024). Depending on the relative proportion of these factors, in re-

gions with low convergence rates, contraction-driven localized uplift may be hindered by the thermal sag effects, resulting in basin subsidence even in an inversional setting (ORAVECZ et al. 2024). With the ~3 mm/year shortening in the transition zone of the Dinarides and the SW Pannonian Basin (PORKOLÁB 2003), the study area counts as having low convergence rates.

Exhumation could also influence karstification processes in the area, as supposed by HEGEDŰS-CSONDOR et al. (*accepted*). Among other effects, inversion related compression induced upwelling of basinal thermal waters towards the Villány Hills (CSONDOR et al. 2020), creating favourable conditions for hypogene cave formation. With the exhumation of the range, meteoric infiltration increased and these waters could meet upwelling basinal fluids, leading to mixing corrosion and again the formation of hypogene caves (HEGEDŰS-CSONDOR et al., *accepted*). Later, as direct precipitation infiltration became more and more prominent, epigene karstification took over. In this framework, the upper cavity in the Nagyarsány quarry, at 240 m a.s.l., which bears spherical cavities, could be the highest-lying and oldest hypogene (paleo)cave in the Villány Hills, which formed during the early part of basin inversion and opened to the surface due to the denudation of the range shortly after, in the latest Miocene or Early Pliocene. In the Beremend block, which lies at a lower elevation, hypogene karstification could continue longer and have impact on some of the Late Pliocene or Quaternary fossil sites as well. Nevertheless, most fossiliferous cavities with Pliocene and Quaternary fauna formed through epigene karstification, due to the work of meteoric waters.

Conclusions

Filled mostly with unstratified sediments, probably partly of aeolian origin, and enriched in vertebrate fossils, the studied fossiliferous paleokarst cavities represent sites above the coeval base level. The accumulation of a vertebrate assemblage indicates the subaerial exposure of the Mesozoic carbonates at the given site. Based on the analysis of the elevation distribution of datable fossil sites, most of the Villány Hills had been exhumed from under Lake Pannon sediments before the accumulation of the first assemblages, 3.5 Ma, almost to its modern state. Base level lowering rate between 3.5 Ma and present was maximum 35 m/Ma for the main range and max. ~15 m/Ma for the Beremend block in the south. Latest Miocene – Early Pliocene (~6–3.5 Ma) minimum exhumation rates are estimated to be probably around 76–92 m/Ma for the main range and certainly above 12 m/Ma. Respective numbers for the Beremend block are 97–111 m/Ma and 37 m/Ma, carrying more uncertainty because later this block might have suffered minor subsidence as well. The denudation of Upper Miocene lacustrine deposits is a result of the neotectonic inversion of the Pannonian Basin. Decreasing uplift rates in the Pliocene and Quaternary are tentatively attributed to transpressional deformation along the Drava Basin boundary fault from the Early Pliocene, which now

accommodates a major portion of deformation in the region induced by the Adria–Europe convergence, but deep lithospheric processes may also play a role. The majority of the fossiliferous fissures was not a direct result of tectonic deformation, therefore they cannot be used in stress field reconstructions.

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