



AN EARLY PLEISTOCENE VERTEBRATE AND MOLLUSC FAUNA FROM DREVENÍK (NORTHERN SLOVAKIA), WITH REMARKS ON THE EARLY/LATE BIHARIAN TRANSITION

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Abstract: The first abundant vertebrate and mollusc fauna from a travertine complex Dreveník (northern Slovakia) is preliminarily reported. The greatly diversified community of small mammals (580 MNI, 38 spp.) is characterized by the simultaneous appearance of elements otherwise restricted to the earliest Biharian stage (such as *Petenya*, *Pitymimomys pitymyoides*), those related to the late Biharian clades (*Mimomys savini*, *Cricetus c. runtonensis*), and the typical elements of the late early Biharian (such as *Pliomys episcopalis*, *Mimomys pusillus*, *Pliomys hollitzeri*, including a derived form of *Pliomys coronensis*). A rich assemblage of early *Microtus* (s. l.) clade exhibiting an extreme phenotype diversity covering a broad spectrum of diverse transitional morphotypes is compared with the situation in other European sites of assumed age along the early/late Biharian transition. The common biostratigraphic characteristics of these sites and the stratigraphic setting of the transitional period between the early and late Biharian (Q 1 and Q 2 zones in terms of Horáček and Ložek 1988) are discussed. The record of non-mammalian vertebrates and particularly the molluscs assemblage (2,452 MNI, 51 spp.), supposedly the richest reported for that stage in Europe, further supplement the report with detailed paleoenvironmental reconstructions.

Key words: early/late Biharian, vertebrates, molluscs, biostratigraphy, paleoenvironment, *Microtus*

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Introduction

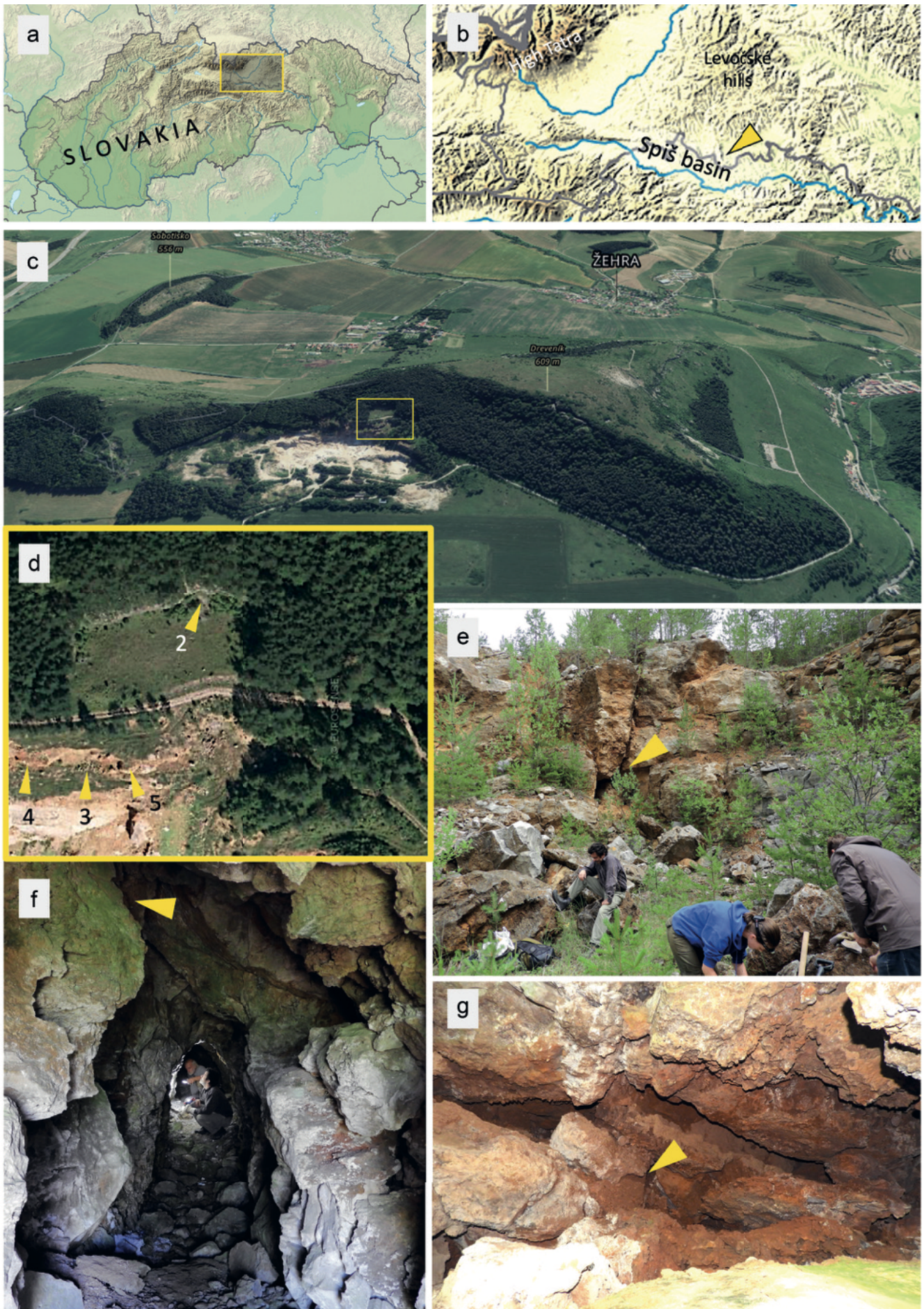
Dreveník Hill, located in Spiš Basin (northern Slovakia) near the town Spišské Podhradie (Text-fig. 1a–c), represents perhaps the largest travertine complex in Central Europe. Travertines form a 2 km long strip extending from NNW to SSE, reaching 1 km in width, covering with thickness up to 80 m the underlying flysch deposits of the Central Carpathian Paleogene Basin (Gross et al. 1999, Wroblewski et al. 2010).

The age of the travertine lithofacies is indicated first of all by a rich leaf flora, reported from Dreveník by Němejc (1967). It covers at least 43 taxa with the dominant representation of exotic trees (*Torreya*, *Ginkgo*, *Parottia*, *Liquidambar*, *Pterocarya*, *Carya*, *Zelkova*, *Rhododendron*, *Styrax*, *Diospyros*) supplementing ancient clades of extant thermophilous European elements (*Picea*, *Cupressus*, *Fagus*, *Quercus*, *Carpinus*, *Alnus*, *Populus*, *Juglans*, *Ulmus*,

Daphne, *Acer*, *Buxus*, *Cornus*), all suggesting a Pliocene age. Rare vertebrate remains found in the travertine proper (cast of a tooth of a mastodon, “*Mammut*” *borsoni* (HAYS, 1834) or *Anancus arvernensis* (CROIZET et JOBERT, 1828), cast of a turtle carapace, *Testudo* sp.; Holec 1985, 1992, Krempaská 1993, Holec and Krempaská 2007, Tóth and Krempaská 2008, Danilov et al. 2012) are in accord with that dating.

The travertine complex has been exposed to a plethora of post-diagenetic and tectonic alternations, resulting in diverse erosion processes, gravitationally induced mass movements, and karstification (Füssgänger 1985, Tometz 1997, Tulis and Novotný 2008, Wroblewski et al. 2010, Pivko and Vojtko 2021).

The cracks and veins in the travertine body are often associated with corrosion karstification either of an interstratal appearance or enlarged sub-vertical spaces with speleothems. Surface erosion produced even smaller rock



Text-fig. 1. Dreveník hill: geographical position (a, b) and western aerial view of travertine hill (c), position of fossiliferous sites reported in this paper (d), detailed view of main site, no. 2 (e, f, g).

towns along plateau margins, and several subhorizontal caves reaching up to 120 m in length, some with important archeological records (Horváthová and Soják 2012).

A number of such phenomena, mostly diverse fissures infilled by loose terra rossa deposits (supposedly of the Late Pliocene and Early Pleistocene age; Wroblewski et al. 2010), are preserved at upper benches of the main quarry at the western slope of the hill (Text-fig. 1c), denoted here as bench 0. The occasional sampling for fossil remains in these sites (undertaken by IH in 1986, 1994, 2020, 2021) were mostly negative except for three (Text-fig. 1d):

- Site 03 – *Myotis bechsteinii* (KUHL, 1817) (MNI 5), *M. cf. blythii* (TOMES, 1857) (1), *M. cf. nattereri* (KUHL, 1817) (2), *M. cf. exilis* HELLER, 1936 (7), *Pliomys episcopalis* MÉHELY, 1914 (1), *Mustela* sp. (1).

- Site 04 – *M. cf. bechsteinii* (1), *Hypolagus* DICE, 1917 seu *Lepus* LINNAEUS, 1758 (1).

- Site 05 – *M. bechsteinii* (3), *M. cf. nattereri* (1), *M. cf. frater* ALLEN, 1923 (1), *M. cf. exilis* (4).

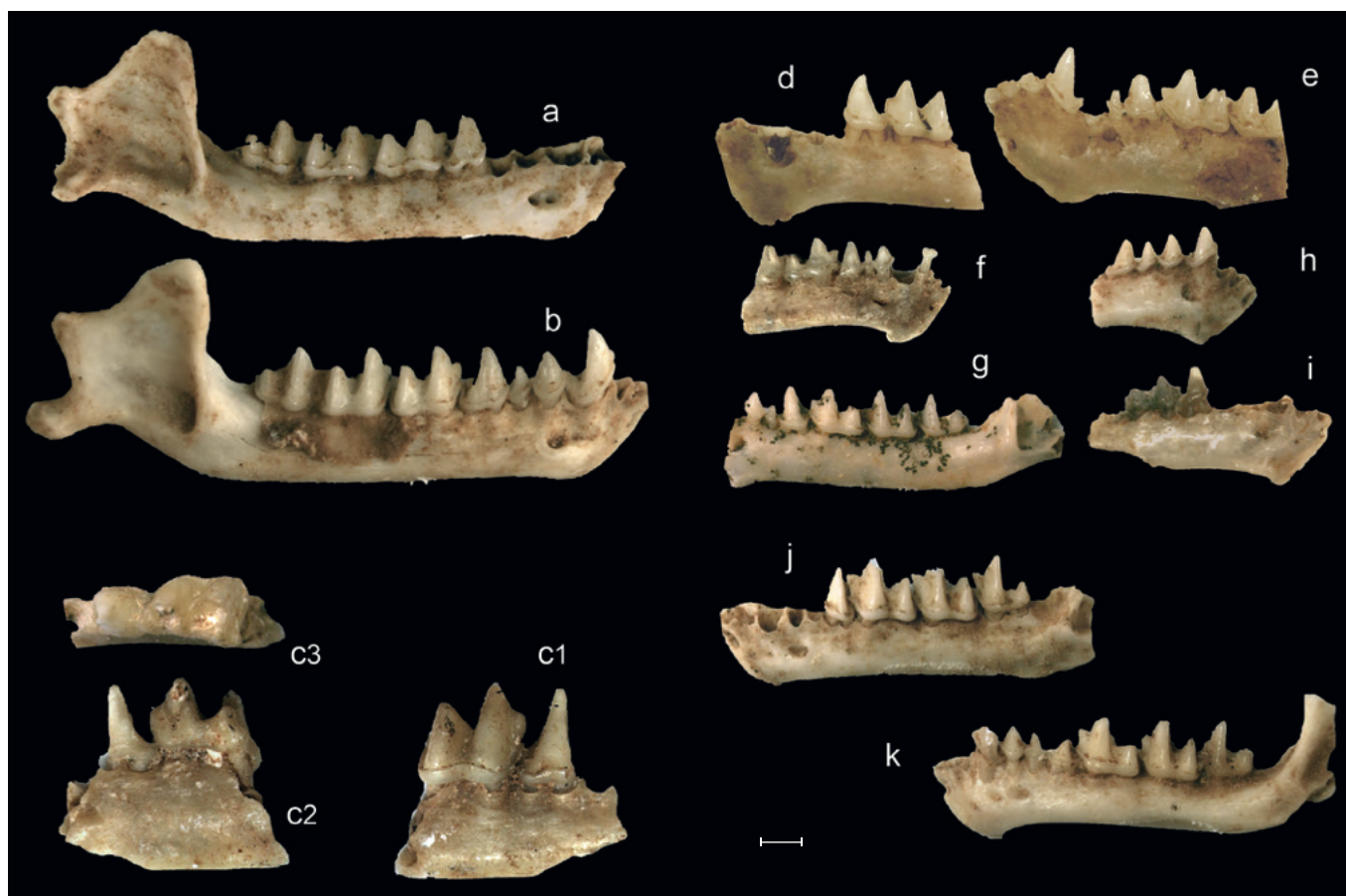
Here we report a recent discovery of the first record of a rich mammal and mollusc fossil assemblages discovered in 2020 in a small, abandoned quarry situated at the surface slope of the travertine plateau, ca. 500 meters N of the hilltop (Text-fig. 1d–g). The surprisingly diversified fauna obviously comes from a period along the Q 1/Q 2, i.e., the early/late Biharian boundary, i.e., the quite important yet still the least comprehended stage in the Quaternary faunal evolution. At

least for that reason, the record is worth a brief preliminary report, before further additional sampling and detailed comparative analyses which are expected to substantially refine knowledge of the Q 1/Q 2 transition patterns.

The site 2 and sampling

A small gallery (ca. 30 m in length) in the eastern wall of the small, abandoned quarry disclosed in its ceiling a loose accumulation of travertine blocks infilling a deep base of a cavity concordant with E–W cracks apparent in a wall of the quarry above the gallery opening (Text-fig. 1e, f). The cavity might be somehow related to a sub-vertical vein mapped there by Pivko (2022). Most material was obtained from blocks of destructed infilling at the bottom of the gallery entrance (“Dreveník 2A”); the dark ochraceous sandy loam incompletely infilling the fissures in between the rock blocks at gallery ceiling (Text-fig. 1g) was sampled separately (“Dreveník 2B”).

After initial sampling in 2020, field excavations in 2021 and 2022 provided about 600 kg of sediments, which were wet washed at 0.5 mm mesh. The fossils were manually extracted, sorted, and examined with the aid of standard laboratory equipment. The material is deposited in the collection of the Faculty of Science, Charles University, Prague.



Text-fig. 2. Selection of vertebrate fossils from Dreveník 2: bats. a, b: *Myotis bechsteinii*, mandible. c: *Myotis cf. myotis*, p4–m1; c1 – labial view, c2 – lingual view, c3 – occlusal view. d, e: *Myotis cf. schaubi*, mandible fragment. f, g: *Myotis exilis/mystacinus*, mandible fragment. h, i: *Myotis cf. helleri*, mandible fragment. j, k: *Plecotus auritus*, mandible fragment. Scale bar 1 mm.

The fauna

Mammalia

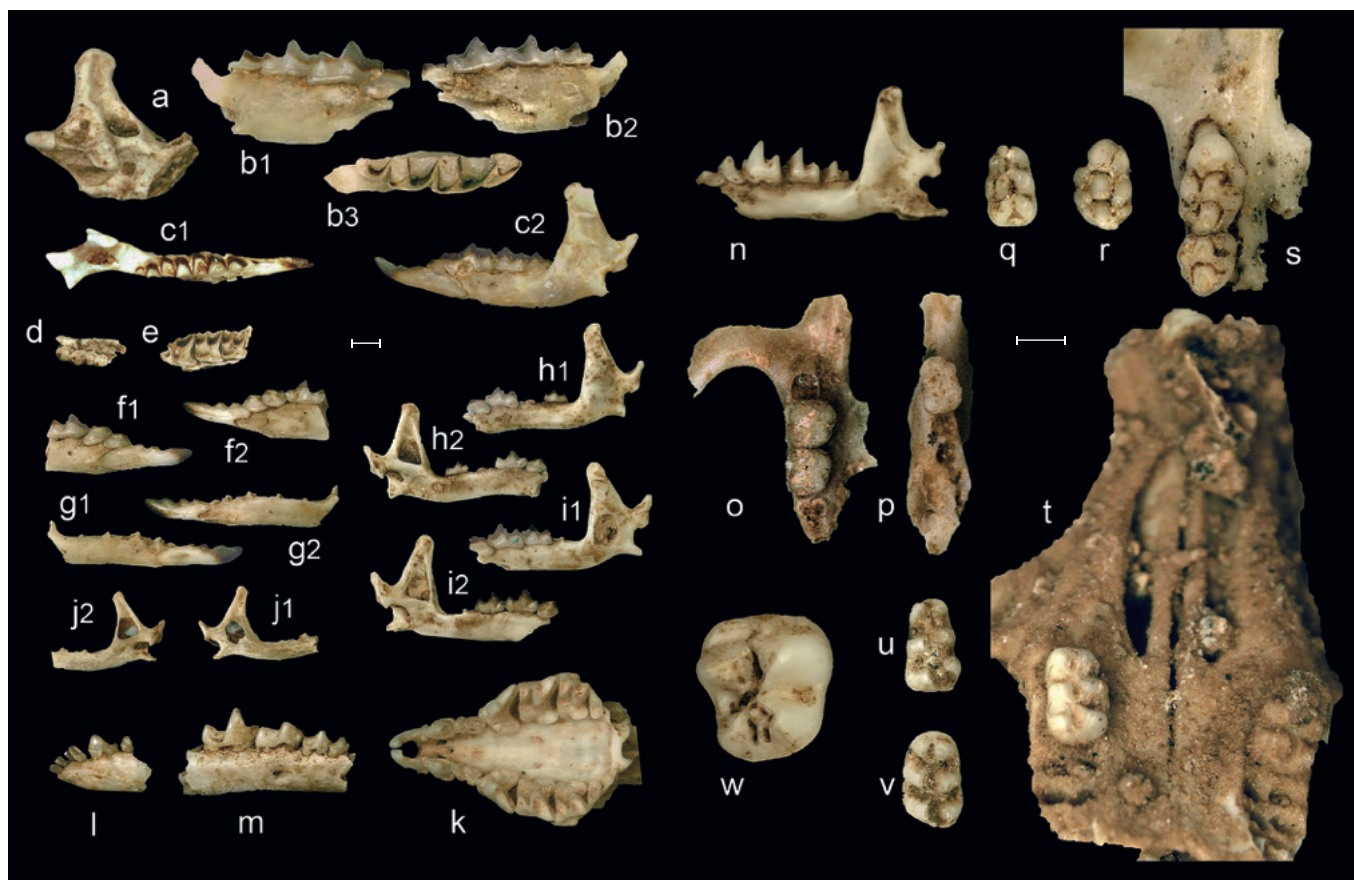
At the present stage of the study, we collected the material of about 5,000 bone and teeth fragments providing ca. 1,200 NISP (number of identified specimens), representing at least 600 individuals (MNI – minimum number of individuals) of 43 species of vertebrates, mostly mammals (580 MNI, 34 spp.), and remains of at least 2,452 (MNI) individuals of land snails representing 51 species and two families of slugs that cannot be determined to a species level. The list of records is in Table 1 and Table 2.

Remains of large vertebrates are invariantly absent; the dominant items of the vertebrate community are bats. The preservation of the bat material (as well as its composition) corresponds to a thanatocenosis, supposedly in situ dying individuals from communities of bats hibernating in the underground cavity before its destruction. In contrast, numerous fragmentary remains of small ground mammals presumably represent a taphocenosis supposedly accumulated by pellets of owls roosting at the cavity entrance sedimented synchronously with thanatocenosis of molluscs.

A preliminary view of the fauna is given below, supplementary sampling and more detailed analyses will

follow. Since we did not recognize significant differences between samples 2A and 2B, in the following text we mostly take them as a single faunal unit.

Bats represent the most common component of Dreveník 2 vertebrate fossil assemblages (Text-fig. 2). The vast majority of the bat remains (74 % in NISP, 70 % in MNI) belong to *Myotis bechsteinii*, a dominant element of the European bat communities throughout the Late Pliocene and Quaternary (Horáček et al. 2000). The subdominant elements are *Myotis mystacinus/exilis*, a small *Myotis* bat with considerably reduced p3, *Plecotus auritus* (LINNAEUS, 1758), slightly larger than the extant form, and *Myotis nattereri*, another characteristic element of the Pleistocene bat communities, including a large *Myotis schaubi* KORMOS, 1934, restricted in Europe to Early and early Middle Pleistocene sites (Horáček and Hanák 1984). Two other forms of the assemblages *Myotis emarginatus* (E. GEOFFROY, 1806), and *Barbastella barbastellus* (SCHREBER, 1774), have been also recorded in more European sites of that age. However, the remaining two are worth a special comment. One is a small *Myotis* bat with rather unreduced premolars closely resembling *Myotis helleri* KOWALSKI, 1962, described from the MN 15 site of Gundersheim (Heller 1936) and reported in several Pliocene localities. The other is a fragment of p4–m1 of a very large myotodont bat. Its robust m1 trigonid (with particularly thick



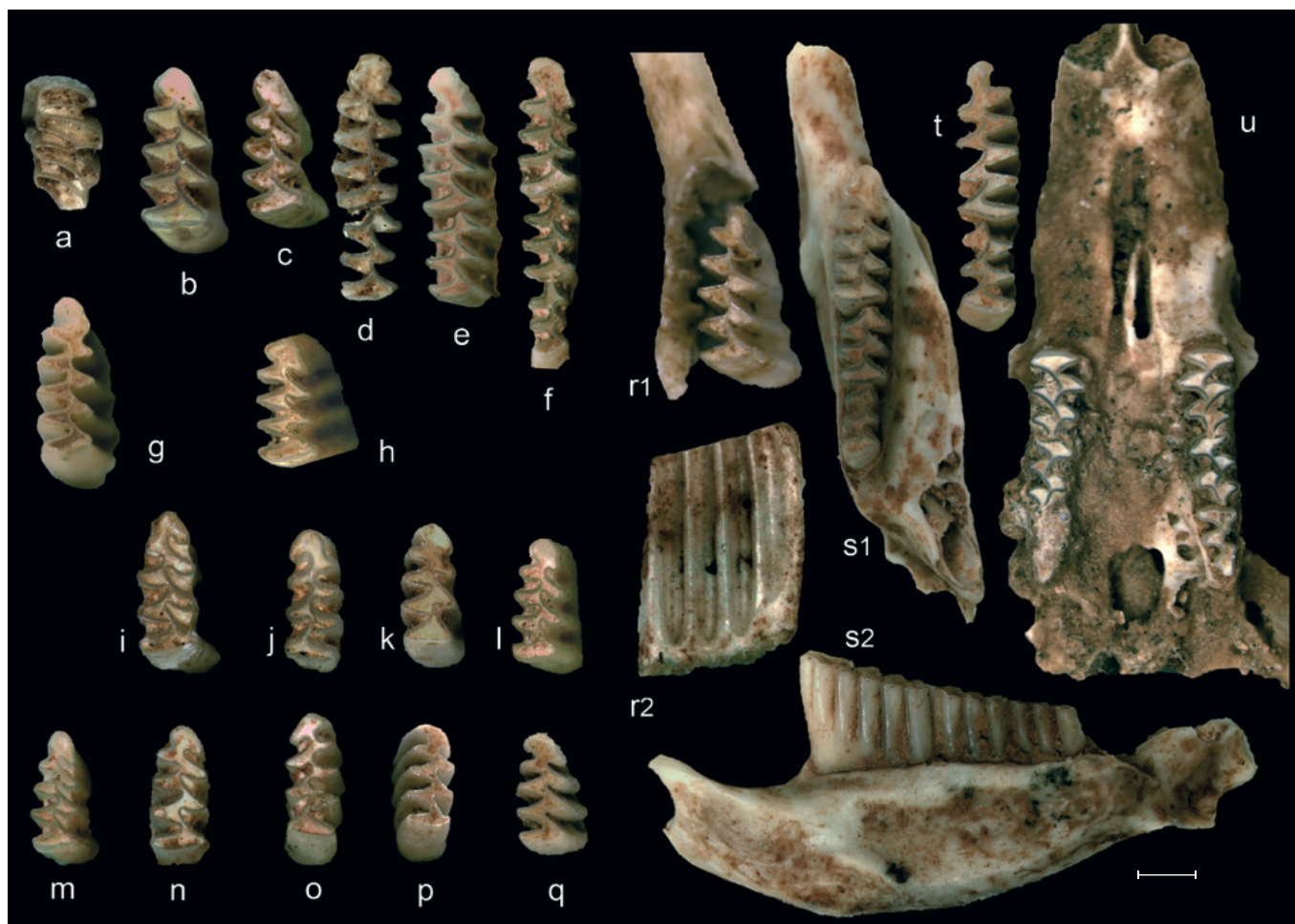
Text-fig. 3. Selection of vertebrate fossils from Dreveník 2: Eulipotyphla (a–n) and non-arvicoline rodents (o–w). a, b: *Beremendia fissidens*, mandible ramus (a), p4–m3 (b); b1 – labial view, b2 – lingual view, b3 – occlusal view. c: *Petenyia hungarica*, complete mandible; c1 – occlusal view, c2 – labial view. d–i: *Sorex runtonensis*, Z1–Z4 (d), P4–M2 (e), mandibles (f–i); f1, g1, h1, i1 – labial views, f2, g2, h2, i2 – lingual views. j: *Sorex minutus*, mandible fragment; j1 – labial view, j2 – lingual view. k: *Crocidura leucodon*, complete rostrum. l, m: *Talpa* cf. *fossilis*, i1–p2 (l), p3–m2 (m). n: *Crocidura leucodon*, mandible. o, p: *Sicista praeloriger*, M1–M2 (o), m1 (p). q–s: *Apodemus* (*Sylvaemus*) cf. *sylvaticus*, m1 (q), M1 (r), maxilla fragment with M1–M2 (s). t–v: *Allocricetus bursae*, rostral fragment with M1 (t), m1 (u), M1 (v). w: *Cricetus cricetus runtonensis*, M3. Scale bars 1 mm (left: a–n; right: o–w).

paraconid) excludes a possible identification as *Eptesicus serotinus* (SCHREBER, 1774), and suggests its belonging to *Myotis blythii*-*M. myotis* clade, recorded by poor fragmentary items from just a few mid-European Early Pleistocene sites (Horáček 1976, Jánossy 1986). They have been referred to a smaller *M. blythii*, yet the present specimen suggests rather *M. myotis* (BORKHAUSEN, 1797), the Mediterranean element which, to our knowledge, has not been recorded so far in the mid-European Pleistocene.

Insectivores (Eulipotyphla) are represented by five species of shrews and one mole (Text-fig. 3a–n). *Beremendia fissidens* PETÉNYI, 1864 is a regular element in almost all communities from Early Pliocene to the Early Pleistocene age. Yet in numerous late Biharian sites throughout central Europe it is absent, except for few (Chlum 4B, Horáček and Ložek 1988; Villány 6 and 8, Kretzoi 1956) which represent the last appearance data of the clade in the region. *Petenya hungarica* KORMOS, 1934, an index element of Villányian (MN 16, MN 17) communities, is consistently absent in the late Biharian assemblages. Its last appearances seem to take place in the sites associated with the Q 1/ Q 2 boundary, particularly in the Pannonian region (Somssichhegy 2, Nagyarsányhegy 2, Včeláre 4A). *Sorex minutus* LINNAEUS, 1766 and *Sorex runtonensis* HINTON, 1911 are both constant elements of the Biharian communities. The latter species exhibits a gradual increase in body size

during that stage (Horáček 1985). In Dreveník 2, its metric characteristics (comp. e.g., height of processus coronoideus, CrH: 3.70–4.00, 3.87 on average) clearly exceeds the variation span in the closely related Villányian form *S. fejfari* HORÁČEK et LOŽEK, 1988 (3.25–3.75), or in the earliest Biharian sites (Žabia, Včeláre 5, Mokrá 1), being at the same time distinctly smaller than the form recorded by abundant samples of the late Biharian age (3.70–4.55), including the type of the species from UFB West Runton (CrH 3.96 on average, 3.70–4.20). The medium-sized form of the species corresponding to the population from Dreveník 2 has been reported from Podumci, Les Valerots, Kövesvárad, Untermassfeld and Včeláre 4 (comp. Maul 2001).

A single specimen of *Crociodura* WAGLER, 1832 (rostrum and mandible; Text-fig. 3k, n) shows perfect correspondence with the extant *C. leucodon* (HERMANN, 1780). The Biharian *Crociodura* specimens (rather rare north of Pannonia) are mostly identified as *C. kornfeldi* KORMOS, 1934. A larger form, *C. obtusa* KRETZOI, 1938, was described from Q 2 Gombasek. However, the type is lost and Mészáros et al. (2020) established a neotype from Q 1/Q 2 site Osztramos 8. Following Kretzoi (1938), they stress the difference from extant *leucodon* in a larger and prolonged first mandibular antemolar (a1). Nevertheless, our specimen seems to correspond in this character rather to the extant species. As



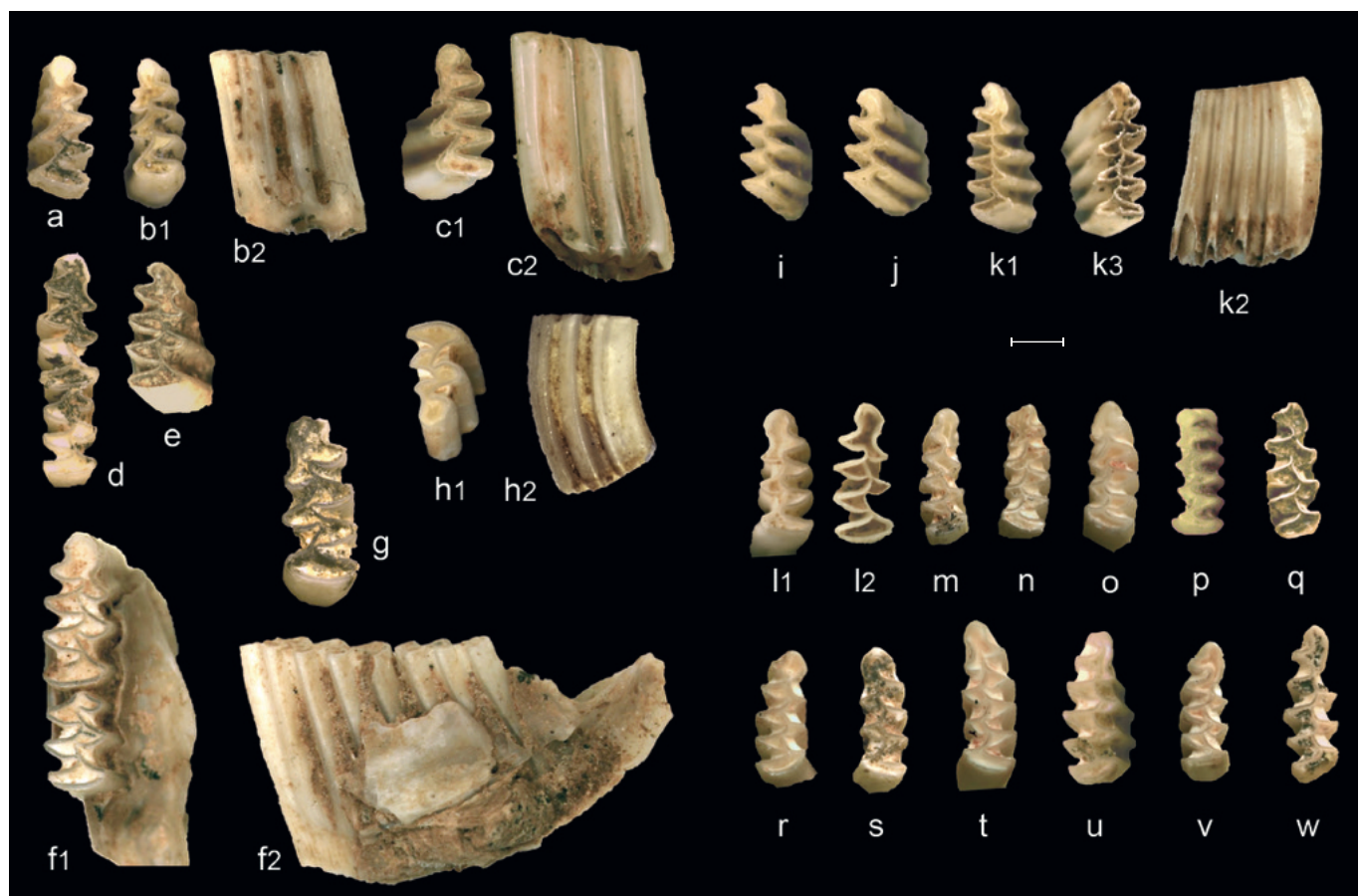
Text-fig. 4. Selection of vertebrate fossils from Dreveník 2: arvicoline rodents 1. a: *Lemmus* cf. *kowalskii*, M3. b–g: *Pliomys episcopalis*, m1 (b, c, g), m1–m2 (d, e), m1–m3 (f). h: *Pliomys hollitzeri*, m1. i–l: *Clethrionomys* cf. *acrorhiza*, m1. m–q: *Clethrionomys hintonianus*, m1. r–u: *Pliomys coronensis*, m1 (r), mandible with m1–m3 (s), m1–m2 (t), rostrum with M1–M3 (u). r1, s1 – occlusal views, r2 – labial view, s2 – lingual view. Scale bar = 1 mm.

in other cases recalled from this preliminary report, further comparative analysis will follow in a consecutive paper. This also concerns several specimens of *Talpa* LINNAEUS, 1758 (two humeri, four clavicles, two femurs; Text-fig. 3l, m) not essentially differing from the extant *T. europaea* LINNAEUS, 1758, except for somewhat smaller size, yet larger than in Q 2 *T. minor* FREUDENBERG, 1914. Tentatively we identify them as *T. cf. fossilis* PETÉNYI, 1864.

Except for a generalized murid, *Apodemus* (*Sylvaemus*) *cf. sylvaticus* (LINNAEUS, 1758), the non-arvicoline rodents are represented with just a few specimens (Text-fig. 3o–w). Despite that, the group also shows a considerable diversity – besides *Glis sackdillingensis* HELLER, 1930 and *Allocricetus bursae* SCHAUB, 1930, both index taxa of Biharian communities, it includes a rare zapodid, provisionally attributed to *Sicista cf. praeloriger* KORMOS, 1930, and a conspicuously large specimen of *Cricetus cricetus* LINNAEUS, 1758 (m3; Text-fig. 3w), which in its dimensions (L = 3.05, W = 2.85) even exceeds the variation span of most middle and late Biharian specimens (*C. c. runtonensis* NEWTON, 1909 sensu Horáček and Lebedová 2022).

We identified nine clades of rhizodont arvicolids. *Pliomys episcopalis* (Text-fig. 4b–g) was the most common of them. Worth mentioning is its tendency to mesial prolongation of anteroconid complex, apparent particularly

in juvenile specimens (Text-fig. 4g). At least two small specimens showed a different morphology (Text-fig. 4h), corresponding to *Pliomys hollitzeri* RABEDER, 1981 described from Deutsch Altenburg 4B. Also within the genus *Clethrionomys* TILESIIUS, 1850 we recognized two distinct morphotypes: a more common, close to extant *C. glareolus* (VON SCHREBER, 1780), differing from it by a laterally undulated anteroconid complex, preliminarily co-identified with *C. acrorhiza* KORMOS, 1933, and a smaller form with narrower synclinales and mesially compressed anteroconid complex, corresponding to *C. hintonianus* KRETZOI, 1958 (= *C. hintoni* KORMOS, 1934) from Nagyarsányhegy 2 or Deutsch Altenburg 2 and 4, the form supposedly related to extant *C. rufocanus* (SUNDEVALL, 1846) (comp. Rabeder 1981). Perhaps the most exciting is the appearance of a highly derived form of *Pliomys coronensis* (MÉHELY, 1914) (= *P. lenki* HELLER, 1930), somehow a mysterious clade with sparse records (often reported as separate species or subspecies: *praeivius*, *progressus*, *chalconi*, *relictus*, *ultimus*, *orghidani* etc.) dispersed throughout Europe from the early Biharian to the Late Pleistocene (Bartolomei et al. 1975, Kowalski 2001). The asymmetric, distinctly separated, anteroconid complex in the Dreveník specimens even resembles the situation of the most derived Middle Pleistocene form *P. coronensis relictus* CHALINE, 1975.



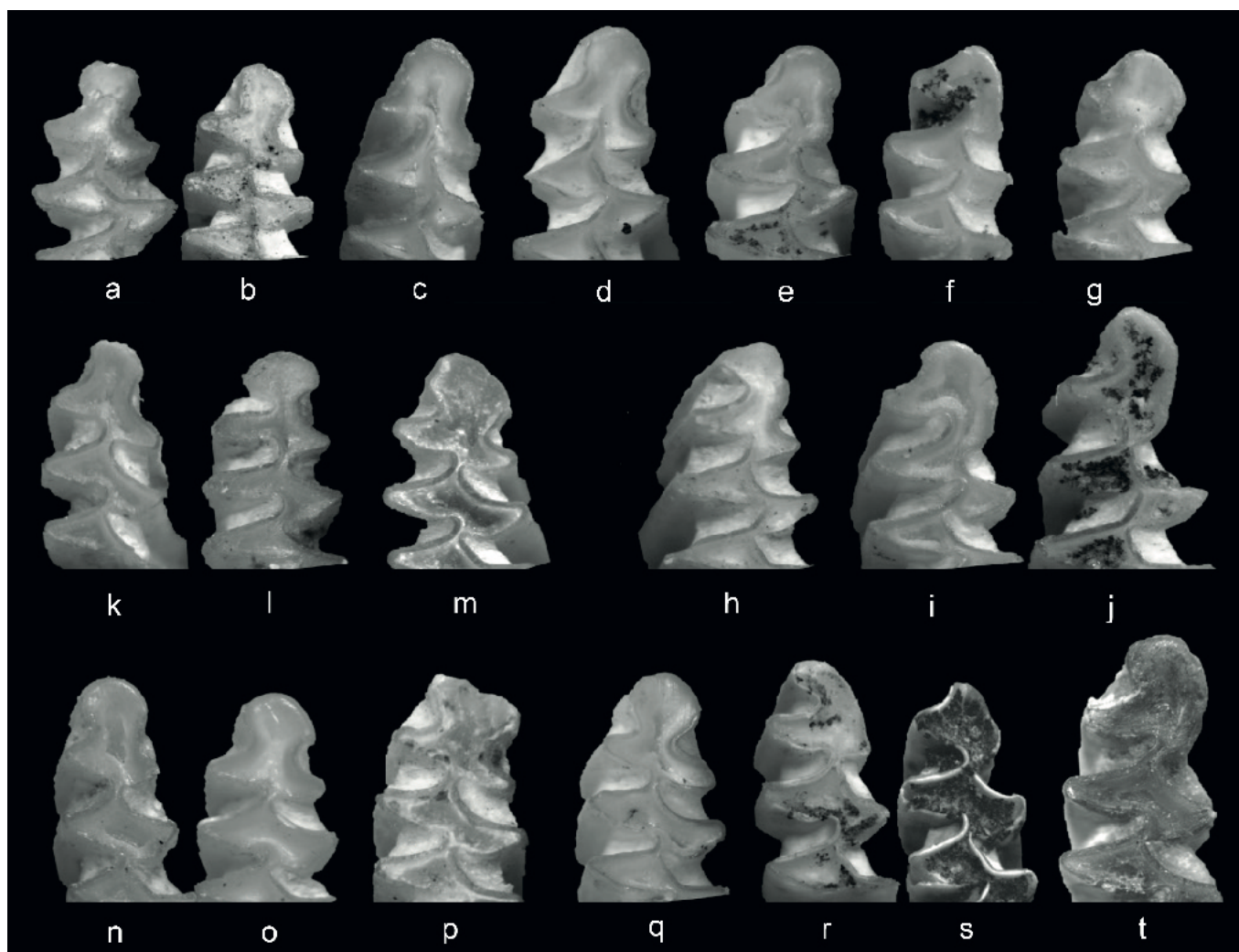
Text-fig. 5: Selection of vertebrate fossils from Dreveník 2: arvicoline rodents 2. a–b: *cf. Pitymimomys pitymyoides*, m1; b1 – occlusal view, b2 – labial view. c: *Borsodia cf. hungarica*, m1; c1 – occlusal view, c2 – labial view. d, e: *Mimomys pusillus*, m1–m2 (d), m1 (e). f–h: *Mimomys ostramosensis/savini*, mandible fragment with m1–m2 (f), m1 (g), M3 (h); f1, h1 – occlusal views, f2, h2 – labial views. i–k: *Lagurus arankae*, m1; k1 – occlusal view, k2 – labial view, k3 – root view. l–w: *Microtus* spp., m1; l – *Microtus (Allophaiomys) pliocaenicus deucalion/superpliocaenicus* (l1 – occlusal view, l2 – root view), m–r – *Microtus pitymyoides/thenii*, s – *nivaloides*, t – *coronensis*, u, v – *ratticepoides*, w – *gregalis*. Scale bar = 1 mm.

Further, rhizodont arvicolids (Text-fig. 5a–g) represent four distinct clades. One is a large form, obviously close to the late Biharian index species *Mimomys savini* HINTON, 1910. Despite a nearly identical morphology of M3 (Text-fig. 5h), m1 seems to differ in somewhat smaller size and a low broad anteroconid complex, resembling the situation of derived forms of *Mimomys ostramosensis* JÁNOSSY et MEULEN, 1975, as reported from Deutsch Altenburg 4 by Rabeder (1981) and Döppes and Rabeder (1997). It possesses dental cementum in synclines, similar to a small form (Text-fig. 5d, e) that we identified as *Mimomys pusillus* (MÉHELY, 1914), an index species of the early Biharian (Q 1). Another hypsodont form (Text-fig. 5a, b) is characterized by a gracile morphology, a prolonged anteroconid complex with well-marked *Mimomys*-Kante and T3-T4 confluency. A detailed revision of the clade including *M. pitymyoides* JÁNOSSY et MEULEN, 1975, by Tesakov (1998) resulted in its classification as a separated genus *Pitymimomys* TESAKOV, 1998. This species was reported from at least 40 sites throughout Europe, all of the late Villanyian or (quite rarely) earliest Biharian age. The last item of that group is a form with an extreme degree

of hypsodonty, yet without cementum, a relatively long m1 anteroconid complex but without a marked undulation at its lingual wall. Just tentatively we identified it as *Borsodia* cf. *hungarica* (KORMOS, 1938) in correspondence to references from multiple Villanyian and early Biharian sites of Central Europe. Whether the mid-European form could be directly synonymized with the late Villanyian *Mimomys newtoni* FORSYTH MAJOR, 1902, as proposed by Mayhew and Stuart (1986) should be carefully re-examined.

Three clades of arhizodont arvicolids were recorded, viz. *Lemmus* LINK, 1795 (Text-fig. 4a), *Lagurus* GLOGER, 1841 (Text-fig. 5i–k), and *Microtus* SCHRANK, 1798 (Text-figs 5l–w, 6). A few items of the first clade (M3, m3 and a fragment of M2) show characters of an extant European Lemmini (*Lemmus*, *Myopus* MILLER, 1910); we tentatively identify them as *Lemmus* cf. *kowalskii* CARLS et RABEDER, 1988 sensu Arbez et al. (2024).

Lagurus: rootless molars without cementum with the predominance of juvenile teeth showing a closed anteroconid complex, mesially tapered and undulated. In these characters, the Dreveník 2 population seems to exceed



Text-fig. 6. Variation in shape of m1 anteroconid complex in population of *Microtus* from Dreveník 2 site and alternative interpretation of particular morphotypes (in terms of Chaline 1972, Rabeder 1981, Fejfar and Horáček 1983, Maul 2001). a–j: *nivaloides* (sensu Pazonyi et al. 2017); a, b – *arvalinus/arvalis*, c, d – *coronensis*, e–g – *nivalinus*, h, i – *ratticepoides*, *praeratticepoides*, j – *gregalis*. k–t: *pitymyoides/thenii* (sensu Fejfar and Horáček 1983); k, l – *pitymyoides-prearvalidens*, m, p – *thenii*, n – *mesoarvalidens*, o, q – *arvalidens/maskii*, r – *preahenseli/henseli*, s – *preahintoni/hintoni*, t – *gregaloides*.

variation both of *L. arankae* KRETZOI, 1954, from other sites and extant *L. lagurus* PALLAS, 1773. However, it cannot be ruled out that some of these items represent juvenile teeth of *Pliomys coronensis* (MÉHELY, 1914).

The remains of *Microtus* s. l. (for the reasons of this naming, see Horáček (in press); we do not follow the current splitting *Microtus* in a number of separate genera – comp. Abramson et al. 2021, Kryštufek and Schenbrot 2023) form the major components of the community, and not only for that reason, they are worth a more detailed comment below.

A dominant representation of the genus *Microtus*, easily distinguished by arhizodont molars with a cementum infill in recentrant angles, is an index characteristic of small ground mammal communities of the Biharian and post-Biharian age. In the earliest stage of the Biharian (Q 1 sensu Horáček and Ložek 1988), the populations of the genus exhibit a pronounced predominance of ancestral phenotype with a broad undifferentiated m1 anteroconid, attributed to the subgenus *Allophaiomys* KORMOS, 1932. In contrast, since the late Biharian (Q 2), *Allophaiomys* phenotypes are invariably absent while the genus is represented by more or less well defined taxa (in most instances clearly related to extant species groups), distinguished by the specific arrangement of m1 anteroconid complex, combined with either confluency of T4-T5 m1 triangles (*hintoni-gregaloides*, *arvalidens-subterraneus*), or the absence of that ancestral arrangement (*arvalinus-arvalis*, *ratticepoides-oeconomus*, *nivaloides-nivalis*, *coronensis-agrestis*). The situation recorded in Dreveník 2 differs significantly from both these patterns. With a single tooth, it included the phenotype corresponding to the most ancestral morphotype of the genus, *Microtus* (*Allophaiomys*) *deucalion* (KRETZOI, 1969) (Text-fig. 5I), while the remaining items cover an enormously broad spectrum of phenotypes. They cover, besides unique transitional morphotypes, the items corresponding to all Q 2 species, some even to the extant forms not appearing during Q 2 stage (*M. gregalis* (PALLAS, 1779)). Enormous diversity in m1 morphology and predominance of transitional morphotypes makes a proper taxonomic interpretation of *Microtus* population of that stage an extremely hard task.

Perhaps Chaline (1972) and Van der Meulen (1973) were the first who stressed this topic in detail. The latter demonstrated different phenotype variations within particular horizons in Monte Peglia, the upper one bearing a derived form with a predominance of diverse transitional morphotypes. He denoted it as *Allophaiomys* sp. B, and later co-identified it with *M. (A.) burgondiae* CHALINE, 1972, from Les Valerots, another site with a derived form of *Allophaiomys*. The more recent analyses by Laplana et al. (2000) identified in Les Valerots three clades reported as separate species (despite considerable overlaps among them): *burgondiae* (assumed ancestor of *Chionomys* MILLER, 1908), *valerotensis* LAPLANA, MONTUIRE, BRUNET-LECOMTE et CHALINE, 2000, (assumed ancestor of *Stenocranius* KASTSCHENKO, 1901), and *nutiensis* CHALINE, 1972, (an ancestor of *Iberomys* CHALINE, 1972), which they attributed as a subspecies to *hintoni* KRETZOI, 1941. Yet, *hintoni* s. str. is a widespread index fossil of the early Biharian, from Russia to France, transforming during the late Biharian via *gregaloides* HINTON, 1923, to *gregalis*, i.e., subgenus *Stenocranius* or *Lasiopodomys* LATASTE, 1887 (Kowalski 2001, Krokhmal et al. 2023).

Corresponding patterns of variation were reported, of course, with quite different taxonomic interpretations, from several other sites bearing relevant population samples, for instance, Atapuerca Sima del Elefante (Laplana and Cuenca-Bescós 2000, Cuenca-Bescós et al. 2013). Rabeder (1981) reports it from Deutsch Altenburg 4, distinguishing here three separate species: *praehintoni* RABEDER, 1981, *hintoni* KRETZOI, 1941, *superpliocenicus* RABEDER, 1981, and a number of transitional morphotypes. In Somssichhegy 2, where *Allophaiomys* morphotypes form a mere 2 % of individuals, Pazonyi et al. (2017) and Pazonyi and Virág (2025), using techniques of geometric morphometry, identified three distinct clades co-identified with the widespread late Biharian taxa: two arranged by m1 T4-T5 confluence in the subgenus *Terricola* FATIO, 1867, viz. *hintoni* and *arvalidens* KRETZOI, 1958 (assumed ancestor of *subterraneus*), and *nivaloides* HINTON, 1929 lacking the T4-T5 confluence (assumed as an ancestor of *arvalis-agrestis* and *oeconomus*). In some sites, the form with T4-T5 confluence clearly predominates, yet instead of a distinct difference between *hintoni* and *arvalidens*, it shows rather a dominance of the transitional morphotypes, sharing characters of both. It was described as a separate species *pitymyoides* CHALINE, 1975 from Bourgade, and *thenii* MALEZ et RABEDER, 1984 from Podumci, reported also from Untermassfeld by Maul (2001) or as *pitymyoides* from Včeláre 4D by Fejfar and Horáček (1983).

In any case, the controversial taxonomies suggest for *Microtus* from the Q 1/Q 2 transitional period (i) considerable enlargement of phenotype variation, (ii) incipient appearances of the morphotypes resembling the late Biharian or even extant clades, (iii) pronounced between-site/between-population differences in the representation of particular morphotypes, including appearances of unique phenotypes not reported from other sites. Yet obviously there is little chance to decide whether they indeed represented real crown taxa – separate biological species with a restricted stratigraphic or geographic distribution, and/or ancestors of modern species in statu nascendi – or just temporal offshoots of abrupt swelling of incipient adaptive dynamics from a common stem group.

In these regards, the approach proposed by Fejfar and Horáček (1983), considering whole *Microtus* populations of individual sites as primary OTUs (operational taxonomic units), seems to be quite substantiated. It revealed gradual enlargements of variation since the beginning of Biharian, retaining a unimodal variation pattern in all scored dental characters in the populations dated to the early stage of Q 1, contrasting to populations dated to the late stage of Q 1 (Chlum 6, Holštejn, Včeláre 4D), which show clear bimodalities in some characters, indicating the presence of distinctly separated clades. The population from Dreveník 2 seems to fall in the former variation type. Besides the specimens exhibiting T4-T5 confluence, tentatively presented here as *pitymyoides/thenii*, those lacking the confluence include a plethora of intermediate morphotypes, excluding the possibility to consider them as a single separate taxon (such as *nivaloides* in sense of Pazonyi et al. 2017). In these regards, we propose to consider the *Microtus* assemblage found in Dreveník as an example of an advanced stem clade, whose variation prefigured the morphogenetic potential of

Table 1: List of mammalian records from Dreveník 2 site.

Dreveník 2	NISP		MNI			NISP	MNI	%
	B	A	B	A		Total		
Small ground mammals								
<i>Talpa</i> cf. <i>fossilis</i> PETÉNYI, 1864 / <i>europaea</i> LINNAEUS, 1758	6	7	2	2		13	4	2.03
<i>Crocidura leucodon</i> (HERMANN, 1780) / <i>obtusa</i> KRETZOI, 1938		1		1		1	1	0.51
<i>Petenyia hungarica</i> KORMOS, 1934	1		1			1	1	0.51
<i>Sorex minutus</i> LINNAEUS, 1766		3		1		3	1	0.51
<i>Sorex runtonensis</i> HINTON, 1911	30	21	11	9		51	20	10.15
<i>Beremendia fissidens</i> (PETÉNYI, 1864)	2	5	1	2		7	3	1.52
<i>Glis sackdillingensis</i> HELLER, 1930	1	1	1	1		2	2	1.02
<i>Sicista praeloriger</i> KORMOS, 1930	1	1	1	1		2	2	1.02
<i>Apodemus</i> cf. <i>sylvaticus</i> (LINNAEUS, 1758)	7	41	4	11		48	15	7.61
<i>Allocricetus bursae</i> SCHAUB, 1930	1	4	1	2		5	3	1.52
<i>Cricetus cricetus runtonensis</i> NEWTON, 1909		1		1		1	1	0.51
<i>Mimomys ostramosensis</i> JÁNOSSY et MEULEN, 1975 / <i>M. savini</i> HINTON, 1910		9		3		9	3	1.52
<i>Mimomys pusillus</i> (MÉHELY, 1914)	5	11	4	7		16	11	5.58
<i>Pitymimomys</i> cf. <i>pitymyoides</i> (JÁNOSSY et MEULEN, 1975)		6		5		6	5	2.54
<i>Borsodia</i> cf. <i>hungarica</i> (KORMOS, 1938)		1		1		1	1	0.51
<i>Lemmus</i> cf. <i>kowalski</i> CARLS et RABEDER, 1988		3		2		3	2	1.02
<i>Lagurus</i> cf. <i>arankae</i> KRETZOI, 1954		12		6		12	6	3.05
<i>Pliomys episcopalis</i> (MÉHELY, 1914)	5	33	3	14		38	17	8.63
<i>Pliomys hollitzeri</i> RABEDER, 1981		2		2		2	2	1.02
<i>Pliomys</i> cf. <i>coronensis</i> (MÉHELY, 1914) / <i>lenki</i> HELLER, 1930	12	18	4	7		30	11	5.58
<i>Clethrionomys hintonianus</i> KRETZOI, 1975	4	14	3	10		18	13	6.60
<i>Clethrionomys</i> cf. <i>acrorhiza</i> KORMOS, 1933	9	55	6	19		64	25	12.69
<i>Microtus</i> s. l. altogether						142	48	24.37
<i>Microtus</i> morphotypes								
<i>Microtus</i> morphotype <i>plioaenicus</i>						1	1	2.08
<i>Microtus</i> morphotype <i>arvalidens</i>						16	10	20.83
<i>Microtus</i> morphotype <i>hintoni</i>						11	9	18.75
<i>Microtus</i> morphotype <i>gregaloides</i>						1	1	2.08
<i>Microtus</i> morphotype <i>nivalinus</i>						8	8	16.67
<i>Microtus</i> morphotype <i>arvalinus</i>						14	10	20.83
<i>Microtus</i> morphotype <i>ratticepoides</i>							6	12.50
<i>Microtus</i> morphotype <i>coronensis</i>						2	2	4.17
<i>Microtus</i> morphotype <i>gregalis</i>						1	1	2.08
Chiroptera								
<i>Myotis bechsteinii</i> (KUHL,1817)	71	454	48	222		525	270	70.50
<i>Myotis</i> cf. <i>nattereri</i> (KUHL, 1817)	4	33	4	21		37	25	6.527
<i>Myotis schaubi</i> KORMOS, 1934		2		2		2	2	0.522
<i>Myotis emarginatus</i> (E. GEOFFROY, 1806)		10		6		10	6	1.567
<i>Myotis</i> cf. <i>exilis</i> HELLER, 1936 / <i>mystacinus</i> (KUHL, 1817)	22	71	15	32		93	47	12.27
<i>Myotis</i> cf. <i>helleri</i> KOWALSKI, 1962		2	2	2		2	4	1.044
<i>Myotis</i> cf. <i>myotis</i> (BORKHAUSEN, 1797)		1		1		1	1	0.261
<i>Plecotus auritus</i> (LINNAEUS, 1758)	3	29	3	20		32	23	6.005
<i>Barbastella</i> cf. <i>barbastellus</i> (SCHREBER, 1774)		6		5		6	5	1.305
Total Small ground mammals	84	249	42	107		475	197	
Total Chiroptera	100	608	72	311		708	383	
Total Mammals	184	857	114	418		1,183	580	

the early *Microtus* population, later canalized into distinct morphotypes of the modern late Biharian taxa. In terms of a degree of anteroconid complex differentiation (a common morphocline in *Microtus* evolution) expressed by A/L ratio, the Dreveník 2 population with an average value 46.5 (38.2–53.3) fall in between the variation in Chlum 6 (35.7–49.2) or Deutsch Altenburg 4 (39.6–50) and Somssichhegy 2 (41–55) or Včeláre 4D (45.6–53), respectively. These relations conform to the stratigraphic interpretation suggested below (Text-figs 7, 8).

Amphibia and Reptilia

The amphibian and reptile community from Dreveník 2 consists of at least nine species, including caudates (*Triturus cristatus* (LAURENTI, 1768), *Lissotriton* cf. *vulgaris* (LINNAEUS, 1758)), frogs and toads (*Rana arvalis* NILSSON, 1842, *Bufotes* cf. *viridis* (LAURENTI, 1768)), anguid lizards (*Anguis fragilis* LINNAEUS, 1758), and snakes (*Zamenis* cf. *longissimus* (LAURENTI, 1768), *Coronella austriaca* LAURENTI, 1768, *Natrix natrix* (LINNAEUS, 1758), *Vipera berus* (LINNAEUS, 1758)). An indeterminate colubrid (Colubridae gen. et sp. indet. 1) is different from snakes recently inhabiting Central Europe, and might represent an invader from southern European regions. The presence of “Mediterranean” snake taxa (sensu Szyndlar 1984, Ivanov 2007) in early Biharian (Q 1) of Central Europe is not surprising. For example, whip snakes of the genera *Hierophis* FITZINGER, 1834 or *Dolichophis* GISTEL, 1868, currently inhabiting large areas of southern Europe (e.g., Heimes 1993, Ščerbak and Böhme 1993) have been documented from Deutsch Altenburg 2 and 4 and Malá Dohoda Quarry (Ivanov 1996, 2007). Ivanov (2007) considered the Q 1/Q 2 transition an important boundary, beyond which “Mediterranean” taxa of amphibians and reptiles no longer occurred in the Central European fossil record. However, a recent study of a small mammal assemblage from Mladeč – excavation II, where an unusually diversified snake community has been described, including multiple “Mediterranean” taxa (Ivanov 1997, 2007), now appears to be of Middle Pleistocene age, and most probably corresponding to the early warm stage of the Saalian complex (Děkanovský 2018).

The most thermophilic species, *Zamenis* cf. *longissimus*, is typical for the interglacial phase of the Quaternary climatic cycle (Böhme 1996). Its occurrence indicates warm and moderately humid climate and forest or bush complexes, with rocky ravines in close proximity to the site (Rehák 1992a, Musilová et al. 2015). The common European adder (*Vipera berus*), which is strongly dominant in Dreveník 2 community (90 %) is a forest species well adapted to temperature fluctuations, and usually inhabiting exposed biotopes in humid habitats (Rehák 1992b, Fric and Moravec 2015). The presence of semi-open humid to dry habitats is documented by the occurrence of the common slow worm (*Anguis fragilis*) (Kminiak 1992, Gvoždík and Moravec 2015). The smooth snake (*Coronella austriaca*) prefers semi-open to open landscapes with xerotherm rocky outcrops (Rehák 1992c, Moravec 2015). The grass-snake (*Natrix natrix*) indicates the presence of water reservoirs with shrub-covered banks (Rehák 1992d, Kabisch 1999, Berec et

al. 2015). Permanent water reservoirs are also documented by the occurrence of newts (*Triturus cristatus*, *Lissotriton* cf. *vulgaris*). However, European green toad (*Bufotes* cf. *viridis*) and moor frog (*Rana arvalis*) can inhabit even open and dry steppe environments (Rehák 1992e).

An amphibian and reptile community documents a warm and moderately humid climate with a mosaic of various, mostly semi-open or open environments, where sometimes rather dry surface conditions alternated with local occurrences of more humid biotopes around stagnant to slow-flowing water reservoirs.

Molluscs

The mollusc communities found consist of 51 species of land snails and indeterminate representatives of two families of slugs (Tab. 2), which makes the site one of the richest in species diversity from the Q 1, Q 2 periods. Localities of comparable age from Slovakia, Nové Mesto n. Váhom – Skalka/Bzince (Ložek 1962, Ložek and Horáček 1984) or Plešivec – Cöpke (Ložek 1958), do not have even half the number of species. The Hungarian locality Somssichhegy 2 is also poorer in species, and the forest communities do not correspond to the interglacial climatic optimum conditions that existed at Dreveník (Krolopp 2000, Pazonyi et al. 2018). Only the classical locality Deutsch Altenburg 4B (Frank and Rabeder 1997, Döppes and Rabeder 1997) is richer (66 species), which is given by the species that perhaps never extended their ranges north of the Donau River (*Archaeogypsis acutus* H. BINDER, 1977, *Helicopsis hungarica* (Soós et H. WAGNER, 1935), *Helix* aff. *lutescens* ROSSMÄSSLER, 1837, *Neostyriaca corynodes* (HELD, 1836), *Pseudoklikia altenburgensis* (H. BINDER, 1977)).

The mollusc assemblages of Dreveník 2 are characteristic of the fully developed fauna of the interglacial climatic optimum. Mollusc shells did not undergo such major morphological changes in the Pleistocene as did mammalian teeth, and are therefore less useful for stratigraphic purposes. Nevertheless, there are several species of significant stratigraphic value. In the case of Dreveník 2, these are mainly *Campylea capeki* PETRBOK, 1922, which became extinct around the Early-Middle Pleistocene transition. Other stratigraphically important species are *Aegopsis klemmi* SCHLICKUM et LOŽEK, 1965 (two sites in Slovakia, Q 2 Nové Mesto n. Váhom (= Skalka-Bzince) – Ložek 1962, Ložek and Horáček 1984, and Dreveník representing the easternmost known site of the species) and *Zonitoides sepultus* LOŽEK, 1964, which are considered characteristic of the Early Pleistocene in Austrian and Hungarian localities (Füköh et al. 1995, Frank 2006). In the Czech Republic and Slovakia, however, they survive into the Middle Pleistocene (Ložek 1964, Horáček and Ložek 1988). Interesting is the first and oldest site in Slovakia of the South Carpathian species *Mastus bielzi* (M. KIMAKOWICZ, 1890), previously known from Central Europe only from the EMTP.

The vast majority of species found (76 %) and individuals found (85 %) are species of humid canopy forests with a high proportion of Carpathian endemics. *Vestia gulo* (E. A. BIELZ, 1859) was previously known only from Remeniny (Harčár and Kovanda 2012), which was later dated to MIS 3 (Juříčková

Table 2: List of molluscs records from Dreveník 2 site. Ecological characteristics: General ecological groups: A – woodland (in general); B – open country; C – woodland/open country. Ecological groups: 1 – woodland (sensu stricto); 2 – woodland, partly semi-opened habitats; 3 – damp woodland; 4 – xeric open habitat; 5 – open habitats in general (moist meadows to steppes); 6 – predominantly dry; 7 – mesic or various. Biostratigraphic characteristics: + – characteristic loess species; (+) – local or occasional loess species; ! – species of warm phases; (!) – eurythermic species of warm phases; !! – index species of warm phases; G – species surviving glacial out of loess zone; (G) – ditto as relics.

Dreveník 2			B	A	Total	Total	
Ecol. group	Biostratigraphy	Species	n	n	n	%	%
A	1	<i>Aegopis klemmi</i> SCHLICKUM et LOŽEK, 1965	9	32	41	1.67	54.28
		!! <i>Aegopis verticillus</i> (A. FÉRUSSAC, 1819)	2		2	0.08	
		! <i>Aegopinella nitens/epipedostoma</i> LINDHOLM, 1927	2		2	0.08	
		! <i>Aegopinella pura</i> (ALDER, 1830)		6	6	0.24	
		!! <i>Campylea capeki</i> PETRBOK, 1922	30	95	125	5.10	
		<i>Bulgarica cana</i> (HELD, 1836)	10	23	33	1.35	
		! <i>Cochlodina laminata</i> (MONTAGU, 1803)	63	387	450	18.35	
		! <i>Cochlodina orthostoma</i> (MENKE, 1828)		15	15	0.61	
		!! <i>Gonyodiscus perspectivus</i> (MEGERLE VON MÜHLFELD, 1816)	2		2	0.08	
		(G) <i>Discus ruderatus</i> (W. HARTMANN, 1821)	4		4	0.16	
		! <i>Helicodonta obvoluta</i> (O. F. MÜLLER, 1774)	18	117	135	5.51	
		(!) <i>Faustina faustina</i> (ROSSMÄSSLER, 1835)	5	11	16	0.65	
		! <i>Isognomostoma isognomostomos</i> (SCHRÖTER, 1784)	10	18	28	1.14	
		!! <i>Macrogastra borealis</i> (O. BOETTGER, 1878)		3	3	0.12	
		! <i>Macrogastra plicatula</i> (DRAPARNAUD, 1801)	3	8	11	0.45	
		!! <i>Mastus bielzi</i> (M. KIMAKOWICZ, 1890)	6	7	13	0.53	
		(G) <i>Mediterranea depressa</i> (STERKI, 1880)	25	143	168	6.85	
		!! <i>Pagodulina pagodula</i> (DES MOULINS, 1830)		1	1	0.04	
		! <i>Perforatella dibothrion</i> (E. A. BIELZ, 1860)	39	156	195	7.95	
		! <i>Platyla polita</i> (W. HARTMANN, 1840)		2	2	0.08	
		! <i>Ruthenica filigrana</i> (ROSSMÄSSLER, 1836)	4	21	25	1.02	
		0 <i>Semilimax semilimax</i> (J. B. FÉRUSSAC, 1802)		2	2	0.08	
		!! <i>Soosia diodonta</i> (A. FÉRUSSAC, 1832)	1	16	17	0.69	
		! <i>Sphyradium doliolum</i> (BRUGUIÈRE, 1792)		9	9	0.37	
		! <i>Vitrea diaphana</i> (S. STUDER, 1820)	3	11	14	0.57	
		! <i>Vitrea subrimata</i> (REINHARDT, 1871)	2	2	4	0.16	
		!! <i>Zonitoides sepultus</i> LOŽEK, 1964		8	8	0.33	
	2	! <i>Aegopinella minor</i> (STABILE, 1864)		33	33	1.35	7.75
		! <i>Gonyodiscus rotundatus</i> (O. F. MÜLLER, 1774)	3	35	38	1.55	
		(!) <i>Fruticicola fruticum</i> (O. F. MÜLLER, 1774)	8	80	88	3.59	
		! <i>Helix pomatia</i> LINNAEUS, 1758	1	12	13	0.53	
		! <i>Perforatella incarnata</i> (O. F. MÜLLER, 1774)	3	14	17	0.69	
		(+) <i>Vitrea crystallina</i> (O. F. MÜLLER, 1774)		1	1	0.04	
	3	!! <i>Drobacia banatica</i> (ROSSMÄSSLER, 1838)	61	155	216	8.81	23.41
		(G) <i>Clausilia pumila</i> (C. PFEIFFER, 1828)	20	19	39	1.59	
		(G) <i>Perforatella vicina</i> (ROSSMÄSSLER, 1842)	51	249	300	12.23	
		(+) <i>Vestia turgida</i> (ROSSMÄSSLER, 1836)		3	3	0.12	
		! <i>Macrogastra ventricosa</i> (DRAPARNAUD, 1801)		12	12	0.49	
		! <i>Urticicola umbrosus</i> (C. PFEIFFER, 1828)		3	3	0.12	
		! <i>Vestia gulo</i> (E. A. BIELZ, 1859)		1	1	0.04	
B	4	!! <i>Caucasotachea vindobonensis</i> (C. PFEIFFER, 1828)	1	3	4	0.16	0.77
		(+) <i>Granaria frumentum</i> (DRAPARNAUD, 1801)		2	2	0.08	
	5	+ <i>Pupilla muscorum</i> (LINNAEUS, 1758)		1	1	0.04	
		G <i>Vallonia pulchella</i> (O. F. MÜLLER, 1774)		7	7	0.29	
		(+) <i>Vallonia costata</i> (O. F. MÜLLER, 1774)	1	4	5	0.20	
C	6	(!) <i>Euomphalia strigella</i> (DRAPARNAUD, 1801)	4	85	89	3.63	13.78
		<i>Limacidae</i> BATSCH, 1789	48	106	154	6.28	
		<i>Milacidae</i> ELLIS, 1926	3	4	7	0.29	
		(+) <i>Clausilia rugosa parvula</i> (A. FÉRUSSAC, 1807)	5	15	20	0.82	
	7	(+) <i>Nesovitrea hammonis</i> (STRØM, 1765)		2	2	0.08	
		(+) <i>Orcula doliolum</i> (DRAPARNAUD, 1801)	2	1	3	0.12	
		! <i>Vitrea contracta</i> (WESTERLUND, 1871)	1	2	3	0.12	
		(+) <i>Clausilia dubia</i> DRAPARNAUD, 1805	11	49	60	2.45	
Number of species			35	49			
Total			461	1,991	2,452		

et al. 2025), making Dreveník 2 its oldest and second known site. The East Carpathian endemic *Perforatela dibothrion* (E. A. BIELZ, 1860) is also a significant find, as this is the second locality of this species from the Early Pleistocene (Ložek 1958). Another Carpathian endemic, *Macrogastra borealis* (O. BOTTGER, 1878), was previously known only from an early Middle Pleistocene interglacial assemblage in Mladečské Cave 2 (Horáček and Ložek 1984), apart from two Eemian localities. It is therefore the oldest known find. The Alpine element *Pagodulina pagodula* (DES MOULINS, 1830) is also the oldest known find in the Carpathians.

The occurrence of two thermophilous species indicates the presence of dry open scree in the forest. For *Caucasotachea vindobonensis* (C. PFEIFFER, 1828), Dreveník together with Q 2 Nové Mesto (Ložek and Horáček 1984) are the only Early Pleistocene record of this species in the Slovakian Carpathians.

All of the above-mentioned findings make the Dreveník 2 a highly significant site for the Early Pleistocene mollusc record.

Concluding remarks

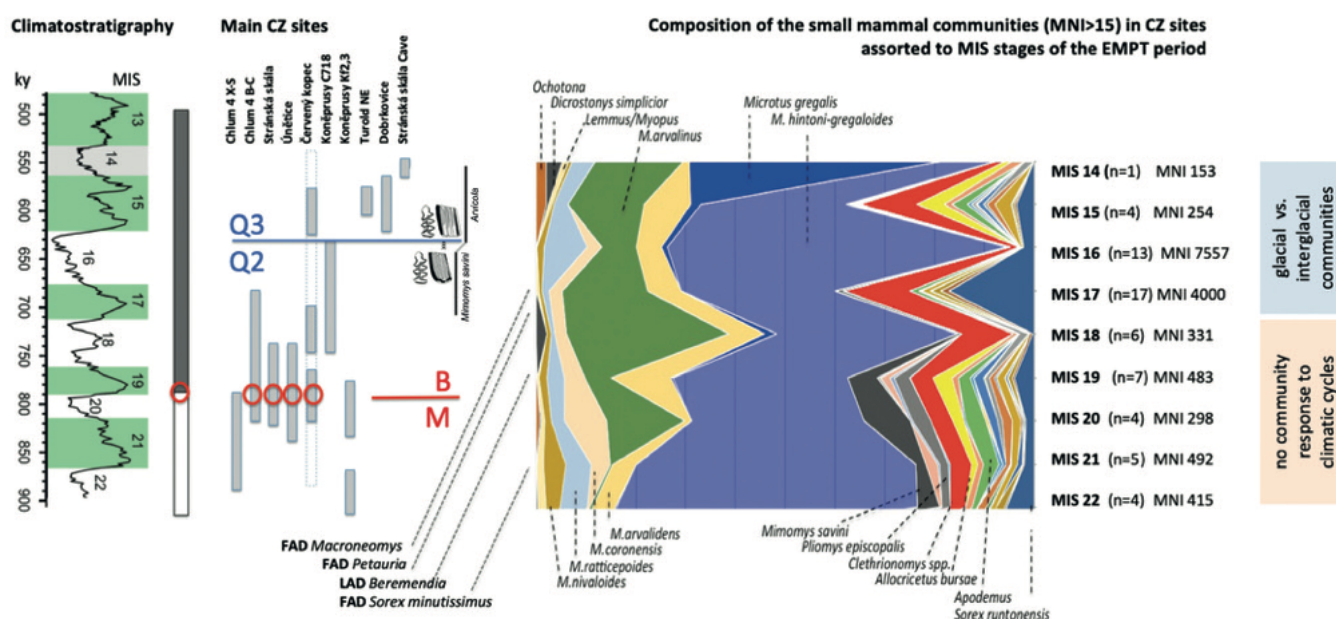
Stratigraphy and faunal setting

Not only in the pattern of *Microtus* phenotype diversity, but also in the composition of the mammal community, the above surveyed faunal sample differs distinctly from typical communities of either the early or late Biharian (Q 1, Q 2) communities, conforming to a stage of Q 1/Q 2 transition. It includes forms otherwise disappearing during the early Biharian (*Petenya hungarica*, *Pitymimomys pitymoides*,

Borsodia hungarica), and at the same time, some elements characterizing rather the Q 2 stage (*Mimomys savini*, *Cricetus c. runtonensis*), notwithstanding a subdominant representation of several clades otherwise less numerous both in the early and late Biharian assemblages (*Pliomys* MÉHELY, 1914, *Clethrionomys*, *Apodemus* KAUP, 1829).

Some of the curious faunal characteristics recorded in Dreveník 2 (in particular, the appearance of the early Biharian elements) might even be understood as locally specific phenomenon. The Spiš Basin, where the site is situated, an islet of a middle altitude undulated landscape surrounded by belts of the Carpathian high mountains (comp. Text-fig. 1b), has been steadily disposed to act as an isolated refugium. It could provide conditions suitable for the survival of clades already disappearing elsewhere, and at the same time, those promoting locally specific phenotype divergences (comp. curious items in *Lagurus*, *Pliomys coronensis*, etc.). In any case, in further comparisons, such hypotheses should also be taken into account.

The faunal record from Dreveník 2 shows clear similarity to other sites of the Q 1/Q 2 stage (for a detailed list of them see Maul 1990, 2001, Maul and Markova 2007). Thus, we can hypothesize that the drivers patterning the common characteristics proposed for *Microtus* diversity here above attributed also to patterning the structure and composition of mammalian communities of that stage in general. Namely the Q 1/Q 2 assemblages exhibit (i) relatively high alpha diversity due to the presence of the early Biharian clades largely missing in the late Biharian (*Beremendia* KORMOS, 1930, *Petenya* KORMOS, 1934, *Pitymimomys*, *Borsodia* JÁNOSSY et MEULEN, 1975, *Mimomys pusillus*), increased taxonomic diversity in the genera forming subdominant elements of the community (*Pliomys*, *Clethrionomys*),



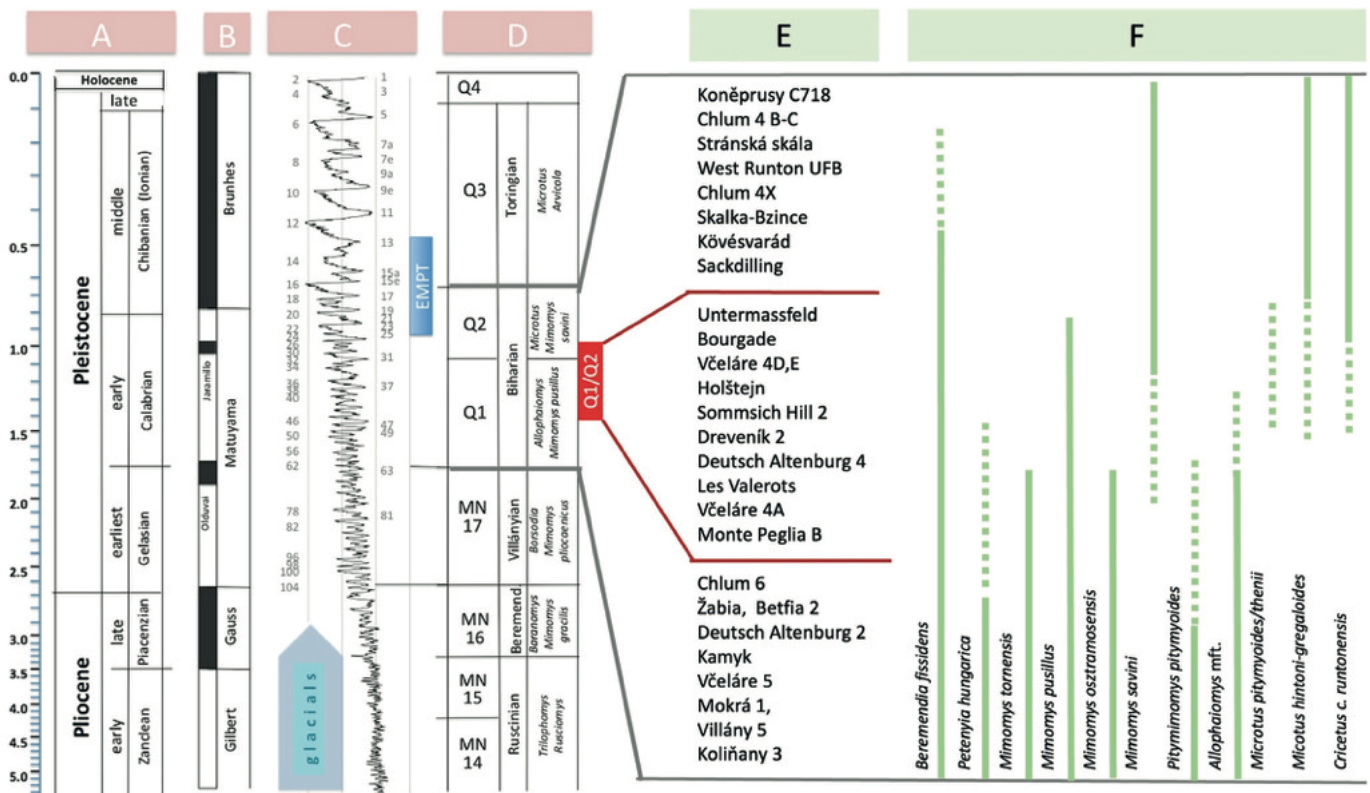
Text-fig. 7. Synoptic survey of EMPT (Early/Middle Pleistocene Transition) small ground mammal communities in Czech Republic. Left: sketch of time slots covered by major sites (mostly multilayered sedimentary sequences) fixed by records of Brunhes/Matuyama boundary and/or Q 2/Q 3 biozones, and lithostratigraphic interpretations of particular series (soil/loess colluvia, etc.). Central panel: Mean dominances of particular taxa arranged in groups of community samples corresponding to individual MIS units (right: with data on number of included communities = n, and total MNI of covered records).

and appearance of novel clades prefiguring the late Biharian faunal pattern (*Microtus* spp., *Mimomys savini*, *C. c. runtonensis*). (ii) In frame of Central Europe, one meets at that stage the morphotypes or clades which phenotypes exceed the variation of their relatives reported from both the early and late Biharian (*Lagurus* cf. *arankae* in Dreveník, *Dimylosorex tholodus* RABEDER, 1972 and *Dimylosorex leptoklon* RABEDER, 1982 in Deutsch Altenburg 2, 4 etc.). (iii) The beta diversity among Q 1/Q 2 assemblages seems to be particularly well pronounced – the above-mentioned characteristics exhibit a considerable between-site and between-region variation. In short, it can be hypothesized that the putative environmental changes accompanying the Q 1/Q 2 transition established a situation of ecological release, promoting multiple adaptive rearrangements in community structure and in phenotype dynamics of its members, both with diverse local and regional variations.

Regarding these specificities, a common biostratigraphic signal compared to that which separates the early and late Biharian assemblages (comp., e.g., Horáček and Ložek 1988) can barely be identified for the Q 1/Q 2 transition period. Last but not least, the essential uncertainties concerning the chronology of the Q 1/Q 2 transition must be mentioned. Besides biostratigraphic estimates, no sufficiently robust instrumental dating is available for the vast majority of European Q 1/Q 2 sites. The records from the loess series (Krems) are biased by massive erosion events (Kovanda et al. 1995). Thus, Untermassfeld, one of the few sites for which

a reliable magnetostratigraphic record is available (a reversal interpreted as the onset of Jaramillo event), is to be taken as the most relevant fixing point (Maul 2001). However, its validity was disproved by records of much less derived *Microtus*, including *Allophaiomys pliocaenicus* KORMOS, 1933, from sequences of fluviatile deposits in Eastern Europe accompanied by magnetostratigraphic records interpreted as the Brunhes/Matuyama reversal (comp. Maul and Markova 2007). Nevertheless, a particularly rich faunal record along the Brunhes/Matuyama boundary, available from the Czech Republic for all cycles of EMPT (MIS 22–14) (comp. Text-fig. 7, shows invariantly the fauna which reveals the index characteristics of Q 2 biozone (comp. Horáček and Ložek 1988, Horáček et al. 2018), i.e., distinctly different from the situation associated with Q 1/Q 2 transition. This obviously provides a robust support against the latter interpretation (see also Discussion in Maul and Markova op. cit.). Concerning the East European record, consideration should be given to the possible stratigraphic hiatus caused by large-scale erosion of the late Matuyama terrace deposits as a result of massive global uplift during the early stage of EMPT.

A tentative estimation of the stratigraphic context of the Q 1/Q 2 transition corresponding to these issues is presented in Text-fig. 8. The Q 1/Q 2 transition is expected to be correlated with the stage of relatively stable warm climate, with minute amplitudes of glacial-interglacial cycles that took part from MIS 47 to MIS 26, i.e., 1.4–1.0 Ma.



Text-fig. 8: Summary of stratigraphic context of early/late Biharian (Q 1/ Q 2) transition. A: chronology and standard subdivision; B: magnetostratigraphy; C: climatostratigraphy: $\delta^{18}\text{O}$ paleotemperatures and MIS units after Lisiecki and Reymo (2005); D: Biostratigraphy, MN and Q stages after Mein (1975, 1989) and Horáček and Ložek (1988), hierarchical subdivision after Fejfar and Heinrich (1990); E: assumed stratigraphical position of selected European sites; F: assumed stratigraphic distribution of selected clades contributing to Q 1/Q 2 communities. EMPT – Early/Middle Pleistocene Transition, Q 1/Q 2 – early/late Biharian transition.

Paleoenvironmental implications

The composition of the mammal community covers the elements indicating either a subxerothermic arboreal vegetation (*Clethrionomys*, but note the low percentage of glirids) or semi-open habitats (comp. cricetids, *Pliomys* spp., *Microtus*, *Lemmus*, *Lagurus*), including habitats rich in diversified herbal cover (*Sicista* GRAY, 1827, *Apodemus*, *Sorex* spp.). Elements characterizing wetland habitats are invariantly absent. *Dreponosorex margaritodon/savini* and *Asoriculus/Neomys* are worth mentioning, as they appear fairly regularly in other Biharian sites (Botka and Mészáros 2016, 2018, Pažitková and Horáček 2024). Also, reptiles (*Zamenis*, *Coronella*, *Anguis* LINNAEUS, 1758) and frogs (*Bufo viridis*, *Rana arvalis*) suggest warm and dry surface conditions, far from the fluid water. However, newts and grass-snakes suggest at least a small water reservoir, perhaps canopy-covered, in a more distant vicinity.

While vertebrates characterize the wider environment of the site, molluscs indicate the environment directly surrounding the sedimentation site. The molluscs at Dreveník 2 clearly indicate a canopy forest, rather humid, with lots of fallen wood and rich herbaceous vegetation. Directly at the site, there was a drier, partly sun-exposed scree, which was indicated by *Granaria frumentum* (DRAPARNAUD, 1801). Although the differences in community structure between samples A and B are not clear, the former seems to indicate slightly wetter conditions than the latter, indicated by the species of ecological group 3, especially *Vestia gulo*, which occurs on forest seepages. Many species are thermophilic, indicating the temperatures that now prevail in the southern Carpathians, where they have their modern range limits (*Drobacia banatica* ROSSMÄSSLER, 1838, *Mastus bielzi*, *Soosia diodontia* (A. FÉRUSAC, 1832)).

The bat guild is dominated by dendrophilous forms foraging in spatially diversified arboreal or semi-opened habitats. They typically form dense hibernation clusters, often in rather small subterranean cavities (*M. bechsteini*, *Plecotus*, *M. nattereri*, *M. mystacinus*). The absence of thermophilous horseshoe bats or *Miniopterus*, regularly occurring in the Early Pleistocene bat assemblages of the Carpathian basin can be ascribed to the absence of spatial caves in the region.

All these issues suggest a densely patched mosaic of diverse arboreal and non-arboreal habitats, a climate warmer than today and perhaps with relatively shallow effects of seasonality.

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References

- Abramson, N. I., Bodrov, S. Y., Bondareva, O. V., Genelt-Yanovskiy, E. A., Petrova, T. V. (2021): A mitochondrial genome phylogeny of voles and lemmings (Rodentia: Arvicolinae): Evolutionary and taxonomic implications. – PLoS ONE, 16(11): e0248198 (28 pp.). <https://doi.org/10.1371/journal.pone.0248198>
- Arbez, L., Hadravová, T., Royer, A., Montuire, S., Fejfar, O., Horáček, I. (2024): Re-investigation of fossil Lemmini specimens from the early and Middle Pleistocene of Western and Central Europe: Evolutionary and paleoenvironmental implications. – Palaeogeography, Palaeoclimatology, Palaeoecology, 641: 112–128. <https://doi.org/10.1016/j.palaeo.2024.112128>
- Bartolomei, G., Chaline, J., Fejfar, O., Jánossy, D., Jeannet, M., Koenigsvald, W. v., Kowalski, K. (1975): *Pliomys lenki* (Heller 1930) (Rodentia, Mammalia) en Europe. – Acta Zoologica Cracoviensia, 21(10): 393–467.
- Berec, M., Moravec, J., Fric, Z. F. (2015): *Natrix natrix* (Linnaeus, 1758) – užovka obojková [*Natrix natrix* (Linnaeus, 1758) – Grass-snake]. – In: Moravec, J. (ed.), Plazi – Reptilia, Fauna ČR. Academia, Praha, pp. 337–362. (in Czech)
- Böhme, G. (1996): Zur historischen Entwicklung der Herpetofaunen Mitteleuropas im Eiszeitalter (Quartär). – In: Günther, R. (ed.), Die Amphibien und Reptilien Deutschlands. Gustav Fischer Verlag, Jena, pp. 30–39.
- Botka, D., Mészáros, L. (2016): *Sorex* (Mammalia, Soricidae) remains from the late Early Pleistocene Somssich Hill 2 locality (Villány Hills, Southern Hungary). – Fragmenta Palaeontologica Hungarica, 33: 135–154. <https://doi.org/10.17111/FragmPalHung.2016.33.135>
- Botka, D., Mészáros, L. (2018): Taxonomic and palaeoecological review of the Soricidae (Mammalia) fauna from the late Early Pleistocene Somssich Hill 2 locality (Villány Hills, Southern Hungary). – Fragmenta Palaeontologica Hungarica, 35: 143–151. <https://doi.org/10.17111/FragmPalHung.2018.35.143>
- Chaline, J. (1972): Les rongeurs du pléistocène moyen et supérieur de France: Systématique, biostratigraphie, paléoclimatologie. – Centre national de la recherche scientifique, Paris, 410 pp.
- Cuenca-Bescós, G., Rofes, J., López-García, J. M., Blain, H. A., Rabal-Garcés, R., Sauqué, V., Arsuga, J. L., Bermúdez de Castro, J. M., Carbonell, E. (2013): The small mammals of Sima del Elefante (Atapuerca, Spain) and the first entrance of *Homo* in Western Europe. – Quaternary International, 295: 28–35. <https://doi.org/10.1016/j.quaint.2011.12.012>
- Danilov, I. G., Čerňanský, A., Syromyatnikova, E. V., Joniak, P. (2012): Fossil turtles of Slovakia: New material and a review of the previous record. – Amphibia-Reptilia, 33(3–4): 423–442. <https://doi.org/10.1163/15685381-00002846>

- Děkanovský, O. (2018): Výzkum pleistocenních společenstev drobných savců v Mladečských jeskyních (Česká republika) [Research on Pleistocene micromammalian assemblages in Mladeč Caves (Czech Republic)]; MSc. Thesis. – MS, Masarykova univerzita Brno, the Czech Republic, 71 pp. (in Czech) (available online) <https://is.muni.cz/th/qmm9f/>
- Döppes, D., Rabeder, G. (1997): Pliozäne und Pleistozäne Faunen Österreichs. – Verlag der Österreichischen Akademie der Wissenschaften, Wien, 373 pp.
- Fejfar, O., Heinrich, W.-D. (1990): Muroid rodent biochronology of the Neogene and Quaternary in Europe. – In: Lindsay, E. H., Fahlbusch, V., Mein, P. (eds), European Neogene mammal chronology. Plenum Press, New York, pp. 91–117. https://doi.org/10.1007/978-1-4899-2513-8_7
- Fejfar, O., Horáček, I. (1983): Zur Entwicklung der Kleinsäugerfaunen im Villányium und Alt-Biharium auf dem Gebiet der ČSSR. – Schriftenreihe für geologische Wissenschaften, 19-20: 111–208.
- Frank, C. (2006): Plio-Pleistozäne und Holozäne Mollusken Österreichs 1., 2. – Verlag der Österreichischen Akademie der Wissenschaften, Wien, 860 pp. <https://doi.org/10.1553/0x0012664a>
- Frank, C., Rabeder, G. (1997): Deutsch-Altenburg 2-4-16-30. – In: Döppes, D., Rabeder, G. (eds), Pliozäne und Pleistozäne Faunen Österreichs. Verlag der Österreichischen Akademie der Wissenschaften, Wien, pp. 241–251.
- Fric, Z. F., Moravec, J. (2015): *Vipera berus* (Linnaeus, 1758) – zmije obecná [*Vipera berus* (Linnaeus, 1758) – Common European adder]. – In: Moravec, J. (ed.), Plazi – Reptilia, Fauna ČR. Academia, Praha, pp. 398–426. (in Czech)
- Füköh, L., Krollopp, E., Sümegi, P. (1995): Quaternary Microstratigraphy in Hungary. – Malacological Newsletter, Gyöngyös, Suppl. 1: 1–219.
- Füssgänger, E. (1985): Poznatky z terénneho výskumu plazivých svahových pohybov travertínových blokov na Spišskom hrade. – Mineralia Slovaca, 1: 15–24. (in Slovak)
- Gross, P., Buček, S., Ďurkovič, T., Filo, I., Karoli, S., Maglay, J., Nagy, A., Halouzka, R., Spišák, Z., Žec, B., Vozár, J., Borza, V., Lukáčik, E., Mello, J., Polák, M., Janočko, J. (1999): Geological Map of Popradská Kotlina Basin, Hornádska Kotlina Basin, Levočské Vrchy Mts., Spišsko-Šarišské Medzihorie Depression, Bachureň Mts. And Šarišská Vrchovina Highland, Scale 1 : 50 000. – Ministry of Environment of Slovak Republic and Geological Survey Slovak Republic, Bratislava.
- Gvoždík, V., Moravec, J. (2015): *Anguis fragilis* Linnaeus, 1758 – slepýš křehký [*Anguis fragilis* Linnaeus, 1758 – Common slow worm]. – In: Moravec, J. (ed.), Plazi – Reptilia, Fauna ČR. Academia, Praha, pp. 237–261. (in Czech)
- Harčár, J., Kovanda, J. (2012). Pleistocenní měkkýši od Remenin [The Pleistocene Molluscan faunas from Remeniny-village (Nízke Beskydy, East Slovakia)]. – Zprávy o geologických výzkumech v roce 2011: 213–218. (in Czech)
- Heimes, P. (1993): *Coluber viridiflavus* Lacepède, 1789 – Gelbgrüne Zornnatter. – In: Böhme, W. (ed.), Handbuch der Reptilien und Amphibien Europas. Schlangen (Serpentes) I. AULA-Verlag, Wiesbaden, pp. 177–198.
- Heller, F. (1936): Eine oberpliocäne Wirbeltierfauna aus Rheinhessen. – Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Band, Abt. B, 76: 99–160.
- Holec, P. (1985): Finds of mastodon (Proboscidea, Mammalia) relics in Neogene and Quaternary sediments of Slovakia (CSFR). – Západné Karpaty, Sér. Paleontológia, 10: 13–53.
- Holec, P. (1992): Teeth casts of mastodon species *Mammuthus borsoni* (Hays, 1834) from the Dreveník travertine near Spišské Podhradie. – Mineralia Slovaca, 24: 467–469.
- Holec, P., Krempaská, Z. (2007): Paleontological Finds of Some Vertebrata in Travertine Dreveník Site (Pliocene–Pleistocene) (near Spišské Podhradie, Slovakia). – In: 5th Meeting of the European Association of Vertebrate Palaeontologists, Carsassone-Esperaza, Abstract volume, pp. 36–37.
- Horáček, I. (1976): Přehled kvartérních netopýrů (Chiroptera) Československa [Review of Quaternary Bats in Czechoslovakia]. – Lynx, N. S., 18: 35–58. (in Czech)
- Horáček, I. (1985): Quaternary morphoclines and changes in community structure in European shrews (Mammalia: Soricidae). – In: Mlíkovský, J., Novák, V. J. A. (eds), Evolution and Morphogenesis. Academia, Praha, pp. 799–810.
- Horáček, I. (in press): History of European mammals. – In: Mitchell-Jones, A. et al. (eds), The 2nd European Mammal Atlas (EMMA2).
- Horáček, I., Hanák, V. (1984): Comments on the systematics and phylogeny of *Myotis nattereri* (Kuhl, 1818). – Myotis, 21(22): 20–29.
- Horáček, I., Fejfar, O., Ložek, V., Čermák, S., Wagner, J., Knitlová, M., Hošek, J. (2018): Early-Middle Pleistocene transition in Central Europe in a high-resolution record of karst deposits. – In: Zupan Hajda, N., Mihevc, A., Năpăruș-Aljančič, M. (eds), Program & Abstracts & Guide Book, Quaternary Stratigraphy in Karst and Cave Sediments (INQUA SEQS Symposium). ZRC Publishing, Ljubljana, pp. 30–31.
- Horáček, I., Hanák, V., Gaisler, J. (2000): Bats of the Palearctic region: A taxonomic and biogeographic review. – In: Wolszyn, B. W. (ed.), Proceedings of the VIIIth European bat research symposium, Vol. I. Institute of Systematics and Evolution of Animals PAS, Krakow, pp. 11–157.
- Horáček, I., Lebedová, K. (2022): Cricetinae in the Quaternary fossil record of the Czech Republic and Slovakia (Rodentia: Cricetidae). – Lynx, N. S., 53(1): 365–415. <https://doi.org/10.37520/lynx.2022.024>
- Horáček, I., Ložek, V. (1984): Z výskumu výplně Mladečské jeskyně u Litovle [Sedimentary fill of the Mladeč Cave near Litovel]. – Československý kras, 35: 98–100. (in Czech)
- Horáček, I., Ložek, V. (1988): Palaeozoology and the Mid-European Quaternary past: Scope of the approach and selected results. – Rozprawy Československé Akademie věd, Řada matematických a přírodních věd, 98(4): 1–106.
- Horváthová, E., Soják, M. (2012): Neolitické a eneolitické osídlenie Puklinovej jaskyne na Dreveníku pri Žehre [The Neolithic and Eneolithic settlement in the Puklinová jaskyňa Cave in Dreveník, near Žehra (eastern

- Slovakia)]. – Sborník prací Filozofické fakulty brněnské univerzity, M, Řada archeologická, 61(M17): 185–209. (in Slovak)
- Ivanov, M. (1996): Old Biharian Reptiles from the Malá Dohoda Quarry (Moravian Karst). – Scripta Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Geology, 24(1994): 9–26.
- Ivanov, M. (1997): Vývoj kenozoické hadí fauny [The evolution of European Cenozoic snake fauna]. – In: Hladilová, Š. (ed.), Dynamika vztahů marinního a kontinentálního prostředí. Masarykova univerzita, Brno, pp. 59–91. (in Czech)
- Ivanov, M. (2007): Herpetological assemblages from the Pliocene to the middle Pleistocene in Central Europe: Palaeoecological significance. – Geodiversitas, 29(2): 297–320.
- Jánossy, D. (1986): Pleistocene vertebrate faunas of Hungary. – Akadémiai Kiadó, Budapest, 208 pp.
- Juričková, L., Horáčková, J., Horsáková, V., Hájková, P., Hošek, J., Horsák, M. (2025, online): Persistence and dynamic of forest snails in the Western Carpathians over the last 40 thousand years. – Boreas, 12 pp. <https://doi.org/10.1111/bor.70019>
- Kabisch, K. (1999): *Natrix natrix* (Linnaeus, 1758) – Ringelnatter. – In: Böhme, W. (ed.), Handbuch der Reptilien und Amphibien Europas. Band 3/IIA: Schlangen II; Serpentes II: Colubridae 2 (Boiginae, Natricinae). Aula Verlag, Wiesbaden, pp. 513–580.
- Kminiak, K. (1992): 1. Druh *Anguis fragilis* Linnaeus, 1758 – Slepýš, Slepúch [1. Species *Anguis fragilis* Linnaeus, 1758 – Common slow worm]. – In: Baruš, V., Oliva, O. (eds), Plazi – Reptilia, Fauna ČSFR, Vol. 26. Academia, Praha, pp. 101–106. (in Slovak)
- Kovanda, J., Smolíková, L., Horáček, I. (1995): New data on four classic loess sequences in Lower Austria. – Sborník geologických věd, Antropozoikum, 22: 63–85.
- Kowalski, K. (2001): Pleistocene rodents of Europe. – Folia Quaternaria, 72: 1–389.
- Krepaská, Z. (1993): Paleontological finds of mastodon and cast of *Emys orbicularis* at Dreveník near Spišské Podhradie. – Zborník Východoslovenského Múzea v Košiciach, 34: 61–66.
- Kretzoi, M. (1938): Die Raubtiere von Gombaszög nebst einer Übersicht des Gesamtfauna. – Annales Historico-Naturales Musei Nationalis Hungarici, Pars Mineralogica, Geologica, Palaeontologica, 31: 88–157.
- Kretzoi, M. (1956). Die altpleistozänen Wirbeltierfaunen des Villányier Gebirges. – Geologica Hungarica, Ser. Palaeontologica, 27: 1–264.
- Krokhmal, O., Rekovets, L., Kovalchuk, O. (2023): Biochronological scheme of the Quaternary of the south of Eastern Europe and its substantiation based on arvicoline teeth morphometrics. – Quaternary International, 674–675: 5–17. <https://doi.org/10.1016/j.quaint.2022.12.003>
- Krolopp, E. (2000): Alsó-pleisztocén Mollusca-fauna a Villányi-hegységben [Lower Pleistocene mollusc fauna from the Villány Mts. (Southern Hungary)]. – Malacological Newsletter, 18: 51–58. (in Hungarian)
- Kryštufek, B., Schenbrot, G. I. (2023): Voles and Lemmings (Arvicolinae) of the Palaearctic Region. – University Press, Maribor, 449 pp. <https://doi.org/10.18690/um.fnm.2.2022>
- Kukla, J., Ložek, V., Bárta, J. (1962): Das Lößprofil von Nové Mesto im Waagtal. – Eiszeitalter und Gegenwart, 12: 73–91. <https://doi.org/10.3285/eg.12.1.08>
- Laplana, C., Cuenca-Bescós, G. (2000): Una nueva especie de *Microtus (Allophaiomys)* (Arvicolidae, Rodentia, Mammalia) en el Pleistoceno Inferior de la Sierra de Atapuerca (Burgos, España) [A new Early Pleistocene *Microtus (Allophaiomys)* species (Arvicolidae, Rodentia, Mammalia) from the Sierra de Atapuerca (Burgos, Spain)]. – Spanish Journal of Palaeontology, 15(1): 77–87. (in Spanish) <https://doi.org/10.7203/sjp.15.1.22088>
- Laplana, C., Montuire, S., Brunet-Lecomte, P., Chaline, J. (2000): Révision des *Allophaiomys* (Arvicolinae, Rodentia, Mammalia) des Valerots (Côte-d'Or, France). – Geodiversitas, 22(2): 255–267.
- Lisiecki, L. E., Raymo, M. E. (2005): A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}\text{O}$ records. – Paleoclimatology, 20(1): PA1003 (16 pp.). <https://doi.org/10.1029/2004PA001071>
- Ložek, V. (1958): Nové interglaciální fauny ze Slovenska [New interglacial faunas from Slovakia]. – Antropozoikum, 7: 37–45. (in Czech)
- Ložek, V. (1962): Interglaciální výplň ve Skalce u Nového Mesta nad Váhom [Interglacial infilling from the Skalka Cave near Nové Mesto nad Váhom]. – Krasový sborník, 3: 47–54. (in Czech)
- Ložek, V. (1964): Quartärmollusken der Tschechoslowakei. – Rozprawy Ústředního ústavu geologického, 31: 1–574.
- Ložek, V., Horáček, I. (1984): Staropleistocenní fauna z jeskyně na Skalce u Nového Mesta nad Váhom [Early Pleistocene fauna from the Skalka Cave near Nové Mesto nad Váhom]. – Českoslovený kras, 35: 65–75. (in Czech)
- Maul, L. (1990): Überblick über die unterpleistozänen Kleinsäugerfaunen Europas. – Quartärpaläontologie, 8: 153–191. <https://doi.org/10.1515/9783112760833-014>
- Maul, L. (2001): Die Kleinsäugerreste (Insectivora, Lagomorpha, Rodents). – In: Kalke, R.-D. (ed.), Das Pleistozän von Untermassfeld bei Meiningen, Teil 3. Monographien, Römisch-Germanisches Zentralmuseum, 4(3): 783–887.
- Maul, L. C., Markova, A. K. (2007): Similarity and regional differences in Quaternary arvicolid evolution in Central and Eastern Europe. – Quaternary International, 160(1): 81–99. <https://doi.org/10.1016/j.quaint.2006.09.010>
- Mayhew, D. F., Stuart, A. J. (1986): Stratigraphic and taxonomic revision of the fossil vole remains (Rodentia, Microtinae) from the Lower Pleistocene deposits of Eastern England. – Philosophical Transactions of the Royal Society of London, B, Biological Sciences, 312(1157): 431–485. <https://doi.org/10.1098/rstb.1986.0015>
- Mein, P. (1975): Resultats du Groupe de Travail des Vertébrés. – In: Report on Activity of the RCMNS Working Groups (1971–1975), Bratislava, pp. 78–81.
- Mein, P. (1989): Updating of MN zones. – In: Lindsay, E. H., Fahlbusch, V., Mein, P., European Neogene Mammal Chronology. Plenum Press, New York, pp. 73–90. https://doi.org/10.1007/978-1-4899-2513-8_6

- Mészáros, L., Botka, D., Gasparik, M. (2020): Establishing a neotype for *Crociodura obtusa* Kretzoi, 1938 (Mammalia, Soricidae): An emended description of this Pleistocene white-toothed shrew species. – *Palaeontologische Zeitschrift*, 94(2): 367–375.
<https://doi.org/10.1007/s12542-019-00458-x>
- Moravec, J. (2015): *Coronella austriaca* Laurenti, 1768 – užovka hladká [*Coronella austriaca* Laurenti, 1768 – Smooth snake]. – In: Moravec, J. (ed.), *Plazi – Reptilia, Fauna ČR*. Academia, Praha, pp. 283–300. (in Czech)
- Musilová, R., Zavadil, V., Kotlík, P., Moravec, J. (2015): *Zamenis longissimus* (Laurenti, 1768) – užovka stromová [*Zamenis longissimus* (Laurenti, 1768) – Aesculapian snake]. – In: Moravec, J. (ed.), *Plazi – Reptilia, Fauna ČR*. Academia, Praha, pp. 304–333. (in Czech)
- Němejc, F. (1967): Paleofloristické studie v neogénu Slovenska [Palaeofloristical studies in the Neogene of Slovakia]. – *Sborník Národního muzea v Praze*, B, 23(1): 1–32. (in Czech)
- Pazonyi, P., Virág, A. (2025, online): Tracking evolutionary changes within *Allophaiomys*, *Terricola* and *Microtus* voles revealed by a landmark point-based geometric morphometric study on molars from Hungary. – *Historical Biology*, 12 pp.
<https://doi.org/10.1080/08912963.2025.2454648>
- Pazonyi, P., Virág, A., Gere, K., Botfalvai, G., Sebe, K., Szentesi, Z., Korecz, L. (2018): Sedimentological, taphonomical and palaeoecological aspects of the late early Pleistocene vertebrate fauna from the Somssich Hill 2 site (South Hungary). – *Comptes Rendus Palevol*, 17(4–5): 296–309.
<https://doi.org/10.1016/j.crpv.2017.06.007>
- Pazonyi, P., Virág, A., Podani, J., Pálfi, J. (2017): *Microtus (Microtus) nivaloides* from the Somssich Hill 2 site (southern Hungary): An Early Pleistocene forerunner of modern ‘true’ *Microtus* voles revealed by morphometric analyses. – *Quaternary International*, 481: 61–74.
<https://doi.org/10.1016/j.quaint.2017.07.019>
- Pažitková, B., Horáček, I. (2024): Shrews of tribe Nectogalini (Mammalia, Eulipotyphla, Soricidae) in the fossil record of the Czech Republic and Slovakia. – *Fossil Imprint*, 80(2): 190–228.
<https://doi.org/10.37520/fi.2024.017>
- Pivko, D. (2022): Evolution of the Dreveník and the Spiš Castle travertine plateaus in Slovakia (Late Pliocene to Holocene). – In: Hudáčková, N., Ruman, A., Šujan, M. (eds), *Abstract Book, Environmental, Structural and Stratigraphical Evolution of the Western Carpathians (12th ESSEWECA Conference)*. Comenius University Bratislava, Bratislava, pp. 112–113.
- Pivko, D., Vojtko, R. (2021): A review of travertines and tufas in Slovakia: Geomorphology, environments, tectonic pattern, and age distribution. – *Acta Geologica Slovaca*, 13: 49–78.
- Rabeder, G. (1981): Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. – *Beiträge zur Paläontologie von Österreich*, 8: 1–343.
- Rabeder, G. (1982): Die Gattung *Dimylosorex* (Insectivora, Mammalia) aus dem Altpleistozän von Deutsch-Altenburg (Niederösterreich). – *Beiträge zur Paläontologie von Österreich*, 9: 233–251.
- Rehák, I. (1992a): 1. Druh *Elaphe longissima* (Laurenti, 1768) – Užovka stromová [Species *Elaphe longissima* (Laurenti, 1768) – Aesculapian snake]. – In: Baruš, V., Oliva, O. (eds), *Plazi – Reptilia, Fauna ČSFR*, Vol. 26. Academia, Praha, pp. 141–149. (in Czech)
- Rehák, I. (1992b): 1. Druh *Vipera berus* (Linnaeus, 1758) – Zmije obecná [1. Species *Vipera berus* (Linnaeus, 1758) – Common European viper]. – In: Baruš, V., Oliva, O. (eds), *Plazi – Reptilia, Fauna ČSFR*, Vol. 26. Academia, Praha, pp. 154–172. (in Czech)
- Rehák, I. (1992c): 1. Druh *Coronella austriaca* Laurenti, 1768 – Užovka hladká [1. Species *Coronella austriaca* Laurenti, 1768 – Smooth snake]. – In: Baruš, V., Oliva, O. (eds), *Plazi – Reptilia, Fauna ČSFR*, Vol. 26. Academia, Praha, pp. 134–140. (in Czech)
- Rehák, I. (1992d): 1. Druh *Natrix natrix* (Linnaeus, 1758) – Užovka obojková [1. Species *Natrix natrix* (Linnaeus, 1758) – Grass snake]. – In: Baruš, V., Oliva, O. (eds), *Plazi – Reptilia, Fauna ČSFR*. Vol. 26. Academia, Praha, pp. 111–124. (in Czech)
- Rehák, I. (1992e): 5. Druh *Rana arvalis* Nilsson, 1842 – Skokan ostronosý [5. Species *Rana arvalis* Nilsson, 1842 – Moor frog]. – In: Baruš, V., Oliva, O. (eds), *Obojživelníci – Amphibia, Fauna ČSFR*, Vol. 25. Academia, Praha, pp. 239–256. (in Czech)
- Szyndlar, Z. (1984): Fossil snakes from Poland. – *Acta Zoologica Cracoviensia*, 28(1): 3–156.
- Ščerbak, N. N., Böhme, W. (1993): *Coluber caspius* Gmelin, 1789 – Kaspische Pfeilnatter oder Springnatter. – In: Böhme, W. (ed.), *Handbuch der Reptilien und Amphibien Europas*. Band 3/I Schlangen (Serpentes) I. Aula Verlag, Wiesbaden, pp. 83–96.
- Tesakov, A. S. (1998): Voles of the Tegelen fauna. – *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, 60: 71–134.
- Tometz, L. (1997): Inžinierskogeologické pomery travertínových kôp a ich širšieho okolia pri Spišskom Podhradí [Engineering-geological relations of travertine hills in the Spišské Podhradie area]. – *Acta Montanistica Slovaca*, 2: 167–176. (in Slovak)
- Tóth, C., Krempaská, Z. (2008): Pliocene Proboscidea remains from travertine Dreveník site (near Spišské Podhradie, Slovakia). – In: Krempaská, Z. (ed.), *Volume of Abstracts, 6th Meeting of The European Association of Vertebrate Palaeontologists, 30th June – 5th July 2008, Spišská Nová Ves, Slovak Republic*. Museum of Spiš, Spišská Nová Ves, p. 116.
- Tulis, J., Novotný, L. (2008): Geologické a geomorfologické pomery NPR Dreveník [Geological and geomorphological settings of the National Natural Reserve Dreveník]. – *Slovenský kras*, 46(1): 5–30. (in Slovak)
- Van der Meulen, A. J. (1973): Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). – *Quaternaria*, 17: 1–144.
- Wróblewski, W., Gradziński, M., Hercman, H. (2010): Suggestions on the allochthonous origin of terra rossa from Dreveník Hill (Spiš, Slovakia). – *Slovenský kras*, 48(2): 153–161.