A middle Miocene vertebrate assemblage from the Czech part of the Vienna Basin: Implications for the paleoenvironments of the Central Paratethys

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ABSTRACT

Czujan's sandpit is an abandoned quarry in the Vienna Basin (Mikulov, Czech Republic) that has yielded an important middle Miocene vertebrate assemblage. Here we re-describe the site from the perspective of sedimentology, taphonomy, and paleoenvironments, and further review the biochronology of the fauna to clarify the age. The updated faunal list includes two testudines (one trionychid and one medium-sized testudinid), and 12 species of terrestrial mammals (three proboscideans, four perissodactyls, four artiodactyls, and one carnivoran), consistent with an early Astaracian (MN6) age. The position of the Wielician/Kosovian boundary just below the floor of Czujan's sandpit, and our new biostratigraphic data, further allow us to constrain the fossil assemblage to the latest MN6 (late Badenian, ~13.6 Ma) and resolves a longstanding controversy about the age of the site. The site exposes a coarsening-upward succession deposited in a braid delta environment, and comprises three facies association: from bottom to top, pelagic sediments (FA1); prodelta and delta slope sediments (FA2); and distributory channel infills of the delta front and delta plain (FA3), the latter containing all the studied terrestrial vertebrates. We propose two taphonomic explanations for the genesis of the vertebrate assemblage: (1) a time-averaged assemblage generated by riverine transport, or (2) a transported assemblage from a mass death site(s), with mass death episode(s) caused by seasonal droughts in the river catchment. Our new findings allow the more precise reconstruction of late Badenian terrestrial paleoenvironments in the northwest area of the Vienna Basin and adjacent Carpathian Foredeep Basin. This region comprised a mosaic of continental habitats dominated by woodlands but also including forest patches and more open environments.

1. Introduction

The intramontane Vienna Basin is among the best explored Paratethyan basins, where decades of research of both marine and brackish sedimentary deposits have greatly contributed to the understanding of paleoenvironmental changes during the middle to late Miocene (e.g., Jiříček, 2002; Kováč et al., 2007, 2018; Harzhauser et al., 2011, 2018). Paleoenvironmental reconstructions of the middle Miocene environment are largely based on the marine fauna (e.g., Harzhauser et al., 2011) or palynoflora (e.g., Kvaček et al., 2006; Kováčová et al., 2011; Kovar-Eder and Teodoridis, 2018). Middle Miocene sites with terrestrial vertebrates are rather scarce with only two well-documented localities,

comprising Kleinhadersdorf (former spelling also Klein-Hadersdorf), Austria (e.g., Thenius, 1948, 1951; Böhme et al., 2012) situated close to the studied site in western part of the Vienna Basin; and Devínska Nová Ves, Slovakia (e.g., Zapfe, 1949, 1954, 1979, 1993; Estes, 1969; Sabol and Holec, 2002; Sabol and Kováč, 2006) situated at the southeastern margin of the Vienna Basin. A detailed paleoenvironmental analysis based on the complete spectrum of the terrestrial taphocoenosis has been conducted only for the Devínska Nová Ves-"Bonanza" site (Sabol and Kováč, 2006).

Here we revise the evidence from another, less known, vertebrate site called Czujan's sandpit (sand quarry), which is situated close to the Carpathian Foredeep Basin at the northwestern margin of the Vienna

Basin (Fig. 1). This site has yielded a high concentration of fossil macrovertebrates. However, this relatively diverse assemblage has remained largely unpublished, even though it constitutes one of the most important middle Miocene mammal assemblages from the Central Paratethys. The importance of this site increased in the 1950s, when Thenius (1951) established it as a type locality of the bovid *Tethytragus stehlini*. Later, the description of the proboscidean fauna (Holec, 1985; Seitl, 1985) highlighted this locality as one of the most important occurrences of the relatively rare proboscidean *Zygolophodon turicensis*. Despite the significance of the studied site, the fossil fauna, its taphonomy and sedimentology has never been studied comprehensively. Accordingly, the research carried out since the 1930s did not provide a clear agreement on the stratigraphical position of this site (e.g., Seitl, 1985; Čtyroký et al., 1990; Stráník et al., 1999). Moreover, late Miocene mammals are known from other abandoned sandpits (Fig. 1B) in the southern area of Mikulov as well. Although multiple sites near Mikulov have been grouped as a single locality, Mikulov (= Nikolsburg), and considered contemporaneous (e.g., Abel, 1910; Rzehak, 1922; Stejskal, 1934; Thenius, 1959; Fejfar, 1990; Böhme et al., 2012), middle and late Miocene vertebrates have been found in various sites of the Mikulov area (Čtyroký, 1989; Čtyroký et al., 1990; Březina, 2019). Therefore, studied sites in the Mikulov area must be always clearly specified.

Here we provide the first taxonomic review of the fossil vertebrates from the former Czujan' sandpit. In addition, the combination of sedimentological, taphonomic and taxonomical characteristics allows us to (1) determine the age of the site; and (2) provide a reconstruction of the late Badenian terrestrial paleoenvironment of the northwestern part of the Vienna Basin and adjacent southeastern part of the Carpathian Foredeep Basin, in areas where the paleobotanical fossil record is rather poor.

2. Czujan's sandpit and overview of research on Neogene vertebrates from the Mikulov area

The former Czujan's sandpit (also called Furstenälle, Fürstenwegfeld, Teichäcker or Na Rybníkách) was a psephitic and psammitic quarry located 2 km east of Mikulov (Fig. 1A–B; GPS: 48°47′49″ N, 16°40′18″ E) in the South Moravian Region, Czech Republic. The mining activity began in the 1930s, reaching a maximum extension of 250 × 120 m and 7–10 m in depth. Exploitation of sands and gravels progressed from south to northwest and the abandoned southern parts of the sandpit were gradually filled with garbage (Březina, 2019). During the 1980s, Czujan's sandpit was filled to the top and leveled completely, being currently part of a vineyard.

Czujan's sandpit stands out as the oldest Miocene vertebrate site of the Mikulov area, which is located close the Carpathian Foredeep Basin. Indeed, vertebrate fossil remains have been known from sandpits in the Mikulov area since the 19th century (e.g., Hörnes, 1848; Alth, 1850). However, their contribution to a broader understanding of the European middle Miocene paleoenvironments and faunas has been hampered by different conceptions about the age of the various sites. Abel (1910) advocated an early Pliocene age, given the faunal similarities with Eppelsheim (currently late Miocene, Pannonian), including the presence of *Deinotherium giganteum*, *Chalicotherium* aff. *goldfussi*, *Hipparion gracile*, and *Chalicomys jaegeri*. Stejskal (1934) agreed with the early Pliocene age suggested by Abel (1910), whereas Rzehak (1922) dated it to the late Pliocene based on the absence of Pannonian mollusks (*Congeria* and melanopsids). Jüttner (1938) first noted that the Mikulov area included several Miocene vertebrate sites of different ages. In particular, Jüttner (1939a) interpreted Czujan's sandpit as being Sarmatian in age, given petrographical similarities with the sands from Chrastiny Hill, near
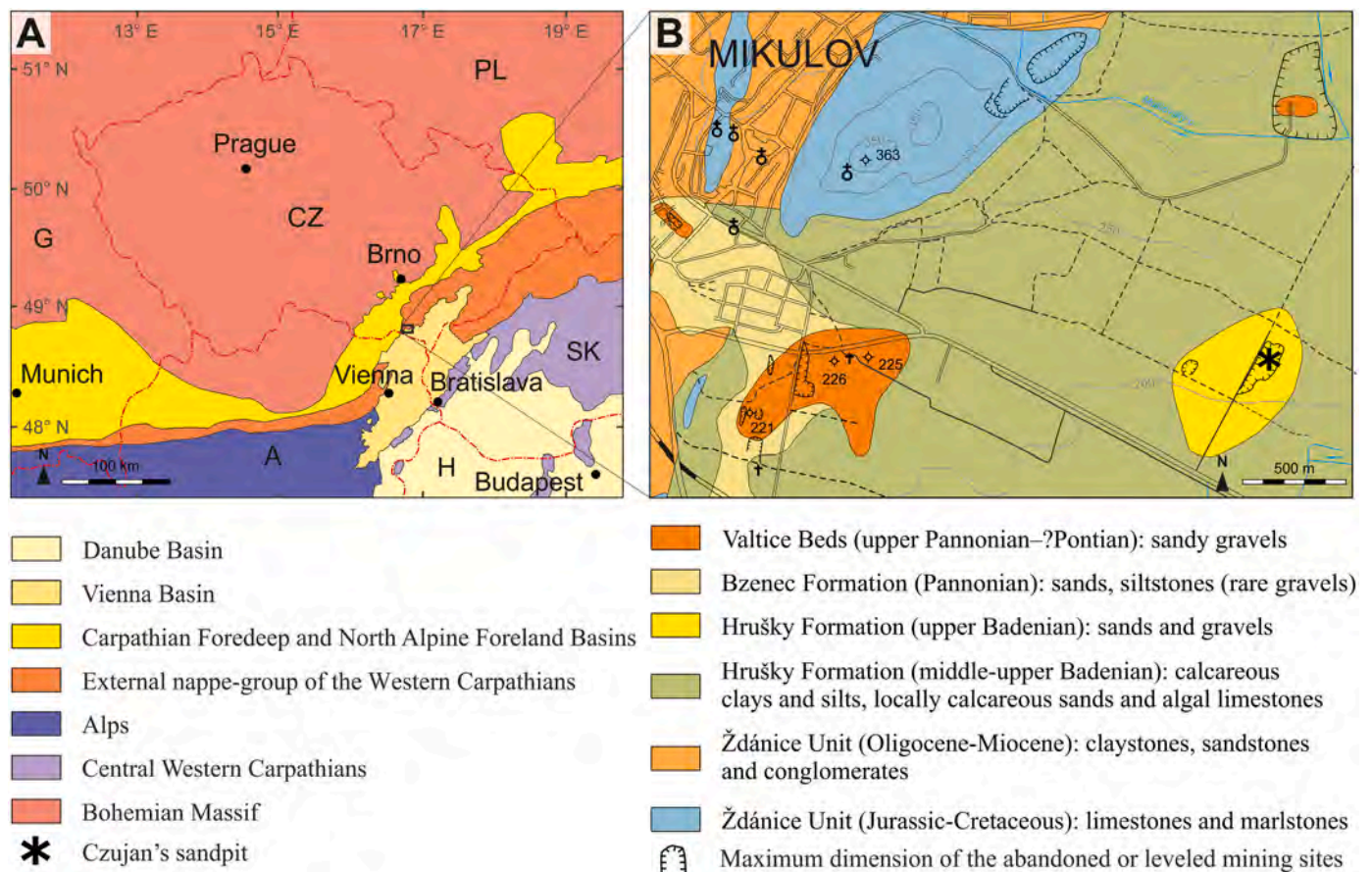

Fig. 1. A: Simplified geological map of Central Europe (A: Austria, CZ: Czech Republic, G: Germany, H: Hungary, PL: Poland, SK: Slovakia). B: Geological map of Mikulov area where the location of Czujan's sandpit is denoted by an asterisk (based on Jüttner, 1939b; Čtyroký et al., 1995).

Valtice, where Sarmatian mollusks are present. Such interpretation was followed by many subsequent authors (e.g., Musil, 1956; Thenius, 1959; Seitl, 1985). However, Buday et al. (1964) considered Czujan's sandpit as the highest strata of the late Badenian (Kosovian substage) based on the foraminifers and mollusks. A Kosovian age was later confirmed by comparison with nearby (800 m away) Nové Mlýny-2 borehole (Čtyroký, 1989; Fejfar, 1990; Čtyroký et al., 1990). Alternatively, some authors advocated that Czujan's sandpit is "middle" Badenian (Wielician substage) in age, but such proposals were not substantitated (Kuklová, 1978; Stráník et al., 1999; Jiříček, 2002), and changes in the Badenian subdivision during time (see Kováč et al., 2018) make this assertion doubtful as well.

A list of fossil mammals from Czujan's sandpit was first reported by Thenius (1951), who erected the nominal species *Gazella stehlini* on the basis of a set of horn cores from Czujan's sandpit (type locality) and Kleinhadersdorf (Austria), some of which are currently housed at the Paleontological Institute of the University of Vienna (Weinfurter collection). In addition, Thenius (1951) provided a faunal list from the site, including chelonians, proboscideans, rhinocerotids, cervids, and chalicotheriids. Later on, Thenius (1979) erected the genus *Caprotragoides* to accommodate ?*Pseudotragus potwaricus* (middle Miocene of Fort Ternan, Kenya) as type species, as well as "*Gazella*" *stehlini* from Czujan's sandpit. Subsequently, Azanza and Morales (1994) tentatively included *Caprotragoides stehlini* in *Tethytragus* as ?*Tethytragus stehlini*. Some proboscidean molars from Czujan's sandpit have also been described (Holec, 1985; Seitl, 1985) and ascribed to *Zygolophodon turicensis* and *Gomphotherium angustidens*.

3. Geological background

Czujan's sandpit belongs to the Pannonian Basin System and is located on the northwest margin of the Vienna Basin (Fig. 1A). In the Mikulov area, Neogene sedimentation began by the deposition of marine lower Badenian clays (Lanžhot Beds) on the Mesozoic and Paleogene flysch basement (Ždánice Unit). At that time, the Vienna Basin was connected with the Carpathian Foredeep Basin by a narrow marine channel known as the "Mikulov Gate" (Brzobohatý and Stráník, 2012). From a tectonic viewpoint, the Vienna Basin was transformed into a pull-apart basin at the beginning of the "middle" Badenian (sensu Harzhauser et al., 2018). The rivers flowed into the basin from the west through the Mikulov area and apparently eroded the Lanžhot Beds (Stráník et al., 1999; Jiříček, 2002).

During the "middle" Badenian, the Sedlec Gravels were deposited discordantly on the Ždánice Unit in the Mikulov area (Čtyroký et al., 1990). The overlying "middle" to "upper" Badenian (sensu Harzhauser et al., 2018) marine deposits belong to the Hrušky Formation, which has yielded a rich marine fauna (e.g., Kienberg locality; Brzobohatý et al., 2007). The uppermost part of the Hrušky Formation terminates with alternating continental sands and gravels, which contain the terrestrial vertebrate remains uncovered in Czujan's sandpit (Čtyroký, 1989; Čtyroký et al., 1990).

In the Mikulov area, no Sarmatian deposits are known. The closest occurrences of marine Sarmatian deposits are found at Chrastiny Hill near Valtice (Stráník et al., 1999). Therefore, uppermost parts of the Hrušky Formation in the area of Mikulov were eroded during the Sarmatian to the early Pannonian. Then, sands and silts (Bzenec Formation, Pannonian; Fig. 1B) were deposited overlying the Badenian clays of the Vienna Basin and the flysch basement (Ždánice Unit). Miocene sedimentation in the Vienna Basin terminates with the uppermost Pannonian and Pontian sediments, mainly composed of gravels and cross-bedded fluviatile sands (Valtice Beds; Čtyroký, 1989, 1999; Čtyroký et al., 1990). Generally, Miocene sequences are covered by Quaternary deposits, such as fluvial and eolian sediments, as well as paleosols (Čtyroký et al., 1990; Stráník et al., 1999).

The Czujan's sandpit deposits are constituted by fine- to coarse-grained sands displaying a trough cross-stratification (Jüttner, 1939a).

They are light gray to yellow in color and mainly composed of quartz, quartzite, feldspar, and intercalated eolian quartz and diverse pebbles (Patočková, 1966). Cerha (1987) noted that sands contain an admixture of gravels and clays up to 50% (Fig. 3). According to Kuklová (1970), deposits overlying the Hrušky Formation (i.e., Bzenec Formation and Valtice Beds, respectively, interpreted as Pannonian and Pontian) have never been recorded from the borehole samples in the surroundings of Czujan's sandpit (see also Čtyroký, 1989; Březina, 2019).

4. Materials and methods

4.1. Studied material

The fossil vertebrate material from Czujan's sandpit consists of 464 identified remains collected between 1930 and 1970. They include teeth, skulls, postcranial bones, and turtle shell remains (see complete list in the Supplementary Table 1). The studied material is currently housed in the following institutions: PIUW, Paleontological Institut University Vienna (Weinfurter collection), Austria; MZM, Moravian Museum, Brno, Czech Republic; RMM, Regional Museum in Mikulov, Mikulov, Czech Republic; ÚGV, Department of Geological Sciences, Faculty of Sciences, Masaryk University, Brno, Czech Republic. The material housed in MZM includes the research collection of Rudolf Musil from the 1950s and the remains gathered by private collectors between 1956 and 1959 (V. Solařík) and in 1965 (J. Maňák). The material housed in MZM was prepared for this study by one of the autors (J.B). However, a detailed description of the available material is beyond the scope of this paper, which focuses instead on the most informative specimens from taxonomic, biostratigraphic, and/or paleoecological viewpoints.

4.2. Sedimentology, taphonomy and biostratigraphy

Sedimentological and taphonomic analyses of Czujan's sandpit are restricted because the site is no longer accessible and also field documentation is lacking. Sedimentological interpretations were based on Jüttner's (1938, 1939a, 1940) lithological descriptions; associated information preserved on labels; unpublished reports from the Czech Geological Survey (Geofond, Prague); and old photos from the photoarchive of the Department of Geology and Paleontology, MZM. As for the micropaleontological analysis, some samples of clay and silt preserved in bone and tusk cavities were washed using a sieve with a mesh diameter of 0.062 mm, and inspected using a stereomicroscope NIKON SMZ 1.

Given that fossil remains were recovered from the surface or the profiles of former Czujan's sandpit without systematic excavation techniques or any documentation of their provenance or spatial distribution, taphonomical analyses are restricted to the study of the assemblage and bone modification data (see Eberth et al., 2007). A bias toward the collection of the most complete fossils during fieldwork is unlikely, given the high number of rounded, fragmentary and otherwise poorly preserved specimens available among the studied material from MZM. The taphonomic analysis is focused on the degree of abrasion, corrosion, and weathering of the bones. We mainly considered the completeness of the bones and their degree of anatomical articulation with other elements to evaluate their preservation state. The taphonomical terminology and practical approach follows Behrensmeyer (1991). We quantified the minimum number of individuals (MNI) and the minimum number of elements (MNE). Other aspects that were taken into account, include differences in tooth wear, epiphyseal fusion, and morphology of fossil bones.

The European Neogene Land Mammal Units (Mein, 1975, 1990, 1999; de Bruijn et al., 1992) do not display consistent boundaries throughout the Europe (e.g. Hilgen et al., 2012; Koufos, 2016). Mammal zonation applied for the Central European area was modified according to Steininger (1999), Becker (2003) and Hilgen et al. (2012). Age limits for well dated Central European Miocene localities with their fossil

record follows works listed in the Supplementary Information.

5. Results

5.1. Sedimentology

The reconstruction of a composite profile was made using data obtained from the individual boreholes in close proximity of the Czujan's sandpit (Fig. 2), which allow us to define three facies associations (FAs; Fig. 3). The lower part of the composite profile (~80 m thick) corresponds to FA1 (Wielician to Kosovian), constituted by clays with occasional sand layers. FA2 (Kosovian) reaches a thickness of ~20 m and overlies FA1. Sporadic layers of gravel appear at the base of the FA2, whereas its upper part consists of interbedded sand and clay layers. The upper part of the profile corresponds to FA3 (Kosovian), which almost reaches 20 m in thickness. It is characterized by the highest portion of coarse-grained deposits (sands and gravels) over the clays. This facies association (FA1–FA3) represents a coarsening-up sequence belonging to the Hrušky Formation. Czujan's sandpit was opened in the uppermost part of the FA3, which contains the coarsest deposits. Both FA2 + FA3 constitute a gravel-sand body up to ~600 m wide and ~45 m thick. This body is deposited within clay-dominated deposits. Clayey sediments overlying FA3 (Fig. 3) and recovered in the uppermost borehole S164 (Fig. 2) were not described and interpreted in detail due to the cursory description of Cerha (1987).

The sedimentary architecture of the Hrušky Formation can only be studied in FA3 based on two historical photographs of the Czujan's sandpit profiles taken by R. Musil in 1964. The first profile shows co-sets of sand and gravelly sand with trough cross-stratification (St, SGt; Fig. 4A) and co-sets of sand and gravelly sand with horizontal stratification (Sh, SGh; Fig. 4A). Strongly eroded bases are recognized in the co-sets of facies (St, SGt) and the individual sets (red and blue lines respectively; Fig. 4A). Some sections show the cross strata onlap to the rising bases (white arrows; Fig. 4A). The individual sets (blue lines, Fig. 4A) and the co-sets of facies Sh, SGh (green lines; Fig. 4A) have either subhorizontally or planar bases. In contrast, the second profile (Fig. 4B) shows a sequence of two sedimentary units. The lower unit is formed by co-set of planar cross-stratified sand (Sp facies), where individual sets are separated by either planar or variously inclined surfaces (blue lines; Fig. 4B). A large body of clay (yellow arrow) is discerned in facies Sp (Fig. 4B). This lenticular clay body was originaly placed horizontally in the profile, but in fact it is partially deformed due to a partial sliding of the sandpit wall (Fig. 4B). In turn, the upper unit is formed by co-sets of sand and gravel with low-angle cross stratification (co-sets of facies Sl, Gl; Fig. 4B), where the bases of the sets are faintly scoured (red lines; Fig. 4B).

5.2. The faunal assemblage from Czujan's sandpit

The following sections report on the fossil vertebrates from Czujan's sandpit (see updated faunal list with MNI in Table 1).

5.2.1. Reptiles

The herpetological assemblage only includes nine specimens of Testudines, of which one belongs to a soft-shelled turtle and the remaining ones to a middle-sized testudinid. PIUW-8 × 1939 (Fig. 5A) is a costal plate fragment, as shown by the presence of a rib on the visceral part. Dorsally, the distinctive sculpturing consisting of small rounded pits, separated from one another, allows us to refer the specimen to Trionychidae indet. (Marmi and Luján, 2012; Vitek and Joyce, 2015). Thenius (1951) reported from Czujan's sandpit the presence of *Trionyx* sp. However, given that the sculpturing pattern does not allow distinguishing between the two genera of soft-shelled turtles recorded from the Miocene of Central Europe (i.e., *Rafetus* and *Trionyx*; Georgalis and Joyce, 2017), identification at the genus rank is not possible.

The remaining Testudines remains belong to a medium-sized

testudinid, which was reported as *Testudo* sp. by Thenius (1951). Four specimens have three-dimensionally preserved carapace. The most complete shell (MZM Ot7877; Fig. 5B–C) is slightly elongated and preserves the xiphiplastra (Fig. 5C), which indicates the lack of a hypoxiphiplastral hinge (Delfino et al., 2012). The peripherals 1–3 are not crossed by the pleuromarginal sulcus, unlike in geoemydids (Luján et al., 2014). Peripherals 3–7 are completely involved in the shell bridge and not elevated relative to overall shell height. Peripherals 8–10 are well developed posteroventrally (Figs. 5B, 6G), but not curved medially as in *Testudo canetoniana* (see Lapparent de Broin, 2000). The complete pygal shows that the supracaudal scute is not divided by a sagittal groove. The anterior plastral lobe is trapezoidal and the anterior edge is truncated (it does not protrude from the carapace contour). The neural 1 is subrectangular and not constricted posteriorly. Based on these features, the *Testudo* specimens from Czujan's sandpit are referred to *Testudo (Chersine) kalksburgensis*, which is only known from its type locality (Wien-Kalksburg, Vienna Basin), dated to the middle Miocene (MN5–MN6; Toula, 1896; Bachmayer and Młynarski, 1981; Luján, 2015; Luján et al., 2016, in press).

5.2.2. Mammals

Proboscidean remains belong to three genera from different families — *Prodeinotherium* (Deinotheriidae), *Zygolophodon* (Mammutidae), and *Gomphotherium* (Gomphotheriidae) — of which only the last one was mentioned by Thenius (1951). Deinotheres are only represented by a single M3 (MZM Ot7526; Fig. 5D), which displays a bilophodont occlusal pattern with a distally tapering contour, a moderately developed distal cingulum, and a distinct convolute (postmetaloph ornamentation) close to the distal cingulum at about crown midline. The small dimensions of this tooth (62 cm in length and 59 cm in width) overlap with *Prodeinotherium* (Ginsburg and Chevrier, 2001; Gasamans et al., in press) and enable to rule out the assignment to a species of *Deinotherium*. Although the two European species of *Prodeinotherium* cannot be distinguished based on M3 morphology (Ginsburg and Chevrier, 2001; Gasamans et al., in press), *Prodeinotherium cuvieri* is only recorded from the early Miocene (Ginsburg and Chevrier, 2001; Böhme et al., 2012; Pickford and Pourabrishami, 2013; Gasamans et al., in press) so that a tentative assignment to *Prodeinotherium* cf. *bavaricum* is warranted.

In turn, mammutid remains are the most abundant, being represented by dental as well as cranial and postcranial remains. This is very exceptional for Mammutidae, which is much less common than Deinotheriidae and Gomphotheriidae in the European Miocene (see Göhlich, 2010). We concur with previous authors (Holec, 1985; Seitl, 1985) that *Zygolophodon turicensis* is the only mammutid species recorded at Czujan's sandpit, as supported by the morphological features displayed by the M3 (MZM Ot7519; Fig. 5E), namely mesiodistally compressed lophs with well defined zygodont crests, long interlophs, well-developed cingula, a disctinctly lower and narrower fourth loph, and a rhombic wear pattern in the pretritte (Tobien, 1975, 1996; Tassy, 1977). Finally, only an M2 (MZM Ot7524; Fig. 5F) and an upper tusk fragment (MZM Ot7505; Fig. 5G) testify to the presence of a gomphothere. The M2 crown is trilophodont and displays a typical bunodont pattern (Tobien, 1973), with relatively thick enamel, an asymmetrical trefoil wear pattern in the pretritte, a reduced lingual cingulum, massive cusps, and narrow interlophs that are blocked by enlarged central conules. These characters allow us to discount the assignment of the material to the early diverging species of the *Gomphotherium* (*annectens*) species group, and further distinguish the Czujan's M2 from the subtapiroid dental pattern of the more derived species *Gomphotherium subtapiroideum* and *Gomphotherium steinheimense* (see Göhlich, 2010; Tassy, 2014). The tusk fragment has a pyriform cross section and is twisted, with a helicoidally oriented enamel band. The latter morphology is characteristic of *G. angustidens*, whereas the upper tusks of *G. subtapiroideum, G. steinheimense*, and *Archaeobelodon filholi* lack torsion (Göhlich, 1998, 2010; Tassy, 2014). We therefore concur with Seitl (1985) that the Czujan's
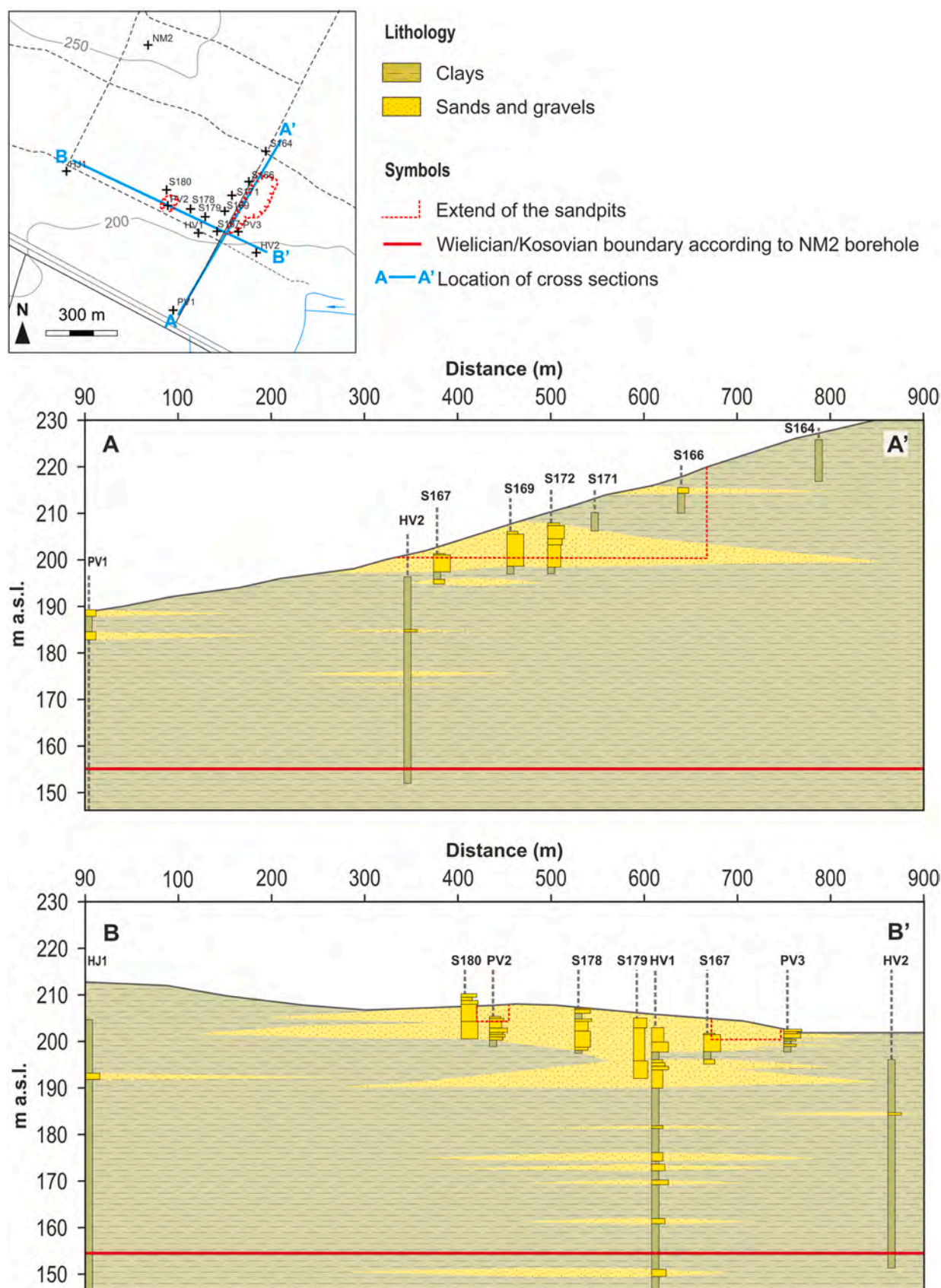
Fig. 2. Geological cross sections through the area of Czujan's sandpit reconstructed from drill cores and boreholes: HV1 and HJ1 (Kuklová, 1970, 1978); PV1 and PV3 (Seitl, 1985); S164-180 (Cerha, 1987). The red line indicates the border between successive upper Badenian substages Wielician and Kosovian according to the borehole NM2 (Bimka et al., 1983). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
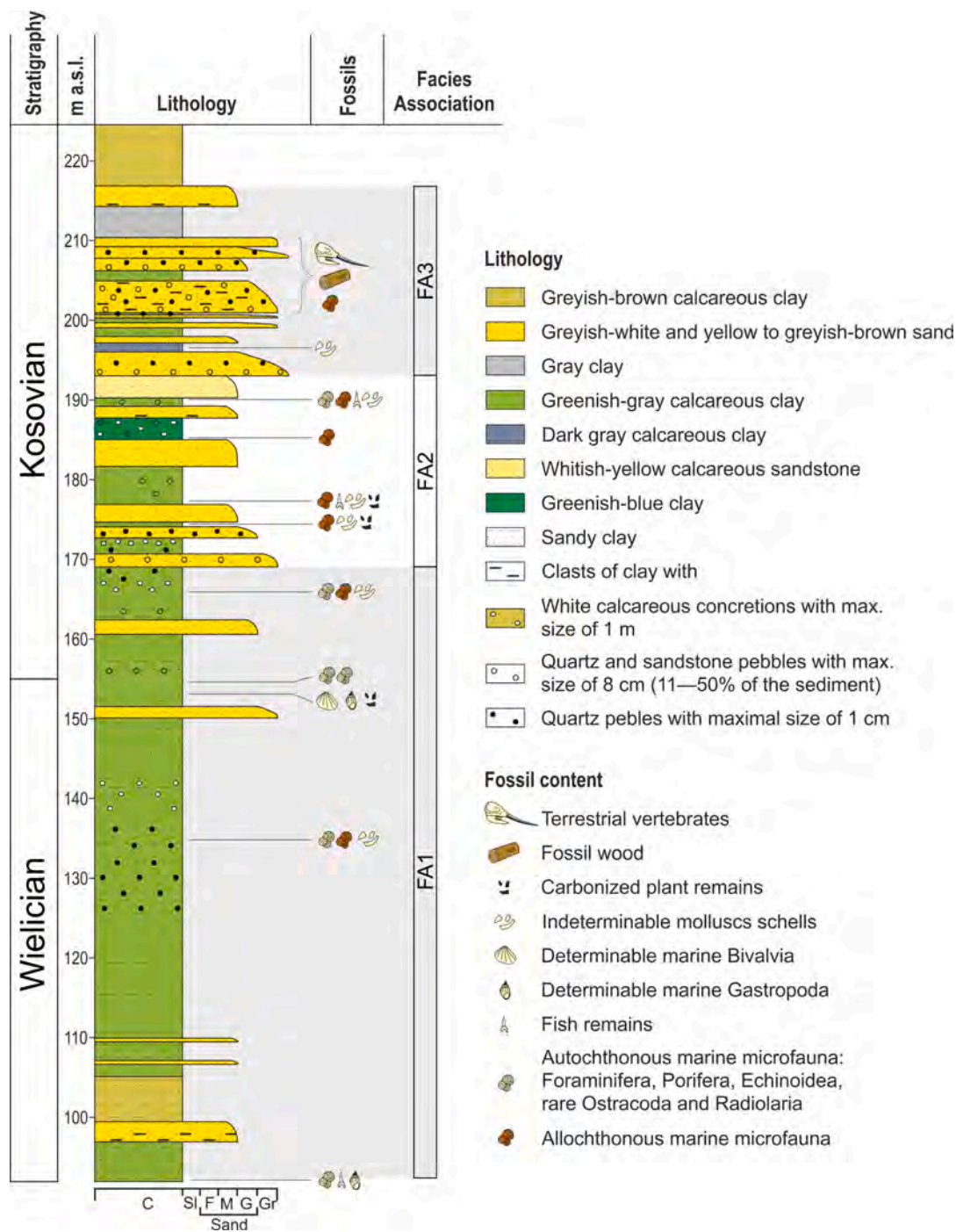
Fig. 3. Composite stratigraphic log of the Hrušky Formation in the studied area, including the fossil content recovered from the borehole samples (Kuklová, 1970, 1978; Seitl, 1985; Cerha, 1987) and stratigraphic boundary between successive upper Badenian substages Wielician and Kosovian in Nové Mlýny 2 borehole (Bimka et al., 1983).

gomphothere is attributable to *G. angustidens*.

Three perissodactyl families are represented at Czujan's sandpit: Chalicotheriidae, Rhinocerotidae, and Equidae. Thenius (1951) already reported the presence of *Chalicotherium grande* (currently in *Anisodon*; Anquetin et al., 2007), but the original material has not been found. The currently available most complete material is represented by a fourth metacarpal (MZM Ot7766; Fig. 5H). It displays a roundish distal facet and a deep lateral ligament fossa, and the shaft is lateromedially compressed but widens distally. The dorsal side of the shaft is straight, whereas the palmar side is concave. The concave palmar side and the presence of a single facet for metacarpal III in the Czujan specimen

distinguish it from the morphology displayed by the schizotheriines, which display a more massive and dorsoventrally compressed metacarpal IV with two separate facets for the metacarpal III (Zapfe, 1979). MZM Ot7766 fits well in size and shape with the remains of *Anisodon grande* from Devínská Nová Ves - Zapfe's fissure (Zapfe, 1979) and Sansan (Guérin, 2012), whereas *Chalicotherium goldfussi* shows slightly larger dimensions (Guérin, 2012).

Two rhinocerotid genera are recognized at Czujan's sandpit on the basis of different limb bone proportions: *Hoploaceratherium* and *Brachypotherium*. The right complete tibia MZM Ot7749 (Fig. 5I) displays more elongated proportions than in the teleoceratin *Brachypotherium*
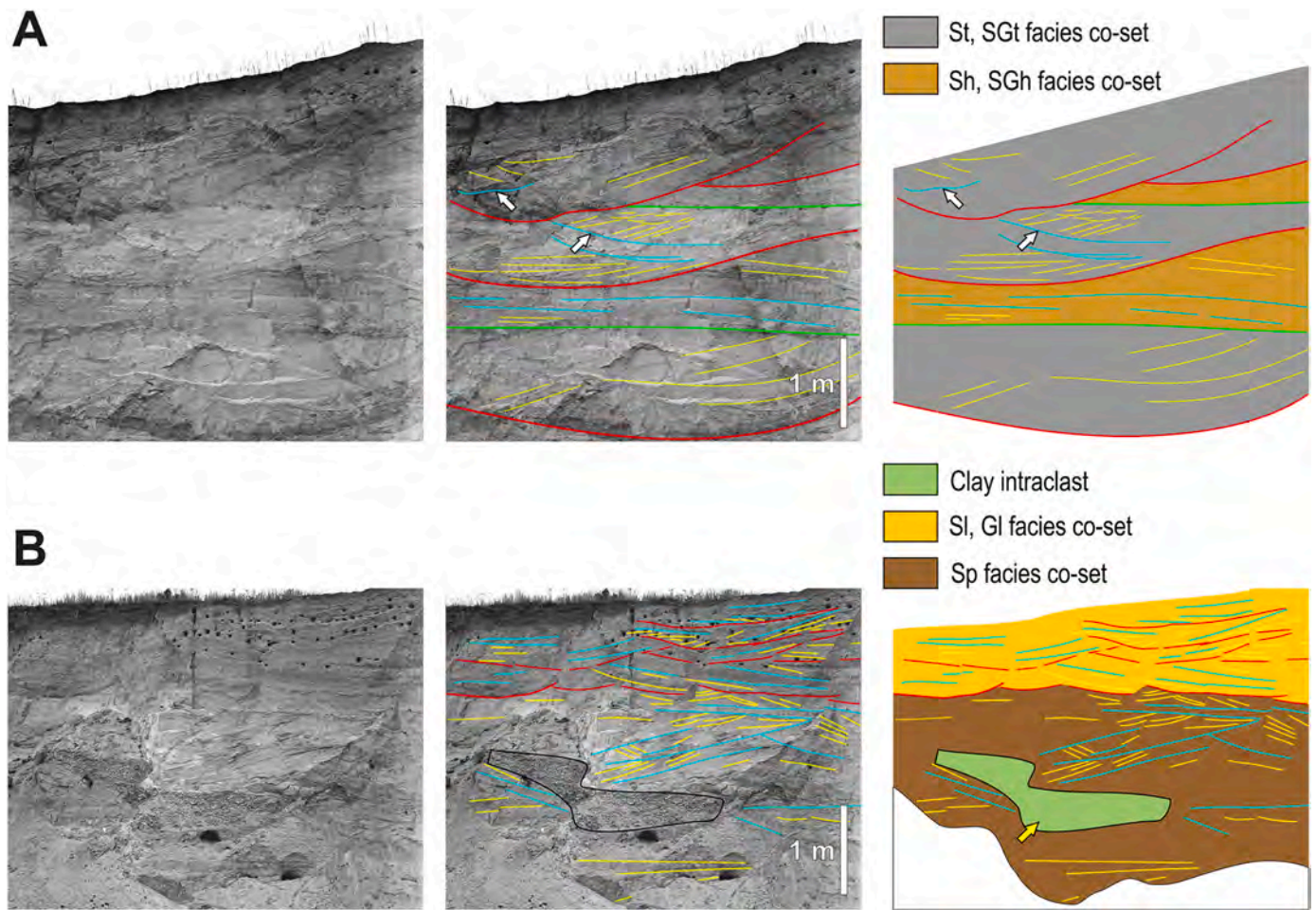
Fig. 4. Photographs taken by R. Musil in 1964 showing the uppermost part of the Hrušky Formation. Facies association 3 (FA3, Kosovian, modified with lines indicating the sedimentary architecture). A: sequence of two sedimentary units (St, SGt and Sh, SGh). B: sequence of two sedimentary units (Sp facies and Sl, Gl). The irregularity of the originally horizontally placed clay body is caused by a partial slide of the wall. Original in photoarchive of the Department of Geology and Paleontology, MZM; colored lines are explained in the text.

Table 1

Comparison of minimum numbers of individuals (MNI) recorded at Czujan's sandpit with recent mass death sites reported during drought in Zimbabwe (Haynes, 1988, counted in 1986).

Taxon	Czujan's sandpit	Shabi Shabi	Lememba	Shkawanki	Nehimba
Proboscidea	21	45	21	8	4
Non-equid Perissodactyla	7	–	–	–	–
Equidae	1	2	2	–	–
Non-bovid Ruminantia	4	–	3	1	–
Bovidae	11	11	8	1	2
Suidae	1	–	–	1	1
Carnivora	1	2	2	–	–
Aves	–	5	1	–	–
Testudines	4	4	–	–	1
Total MNI	50	69	37	11	8
Taxa represented	14	13	8	4	5

(Fig. 5J) and compared with other long-legged rhinocerotid genera, it more closely matches the morphology of *Hoploaceratherium* (Heissig, 2009, 2012). The shaft is slenderer than in *Aceratherium* and the distal epiphysis is broader than in *Lartetotherium* (Hünermann, 1989; Heissig, 2012). The caudal plane below the condyles is medially bounded by a sharp ridge, and the frontal groove of tuberositas tibiae is narrow and centrally located. These characters are typical for Aceratheriini and do not occur in *Lartetotherium* (Heissig, 2009, 2012).

In turn, the genus *Brachypotherium* is represented by dentognathic (an upper incisor and a maxillary fragment) and postcranial (tibia) remains. The slightly worn I1 (MZM Ot7700; Fig. 5K) displays a short blunt root and differs from those of *Aceratherium* and *Lartetotherium*, which are somewhat smaller and possess a pointed root (Heissig, 2012). In turn, an assignment to *Hoploaceratherium* can be excluded due to the lack of upper incisors in the latter genus (Heissig, 2012). The M2–M3 from the maxillary fragment MZM Ot7752 (Fig. 5L) display a brachyodont morphology, with a strong lingual cingulum surrounding the protocone and extending to the base of the hypocone; the M2 has a weak buccal cingulum and a well-developed crochet. These molars differ from those of Aceratheriini and Rhinocerotini by their greater dimensions and stronger cingulum (Heissig, 2012). The complete left tibia MZM Ot7752 (Fig. 5J) is relatively shorter and more robust than in the "long-legged" Aceratheriini and Rhinocerotini (Cerdeño, 1993; Heissig, 2012), supporting an assignment to *Brachypotherium*. The dimensions of M3 and tibia correspond well to those of *Brachypotherium brachypus* from Malartic (MN7+8, France; Cerdeño, 1993), in agreement with the previous report by Thenius (1951) of *B.* cf. *brachypus* from Czujan's sandpit based on unknown material.

As for the equids, only an anchitheriine maxillary fragment with fragmentary M1 and very worn M2 is available (MZM Ot7765; Fig. 5M). The molars are brachyodont and broader than long; the metaloph and protoloph hooked in distal direction, and only a vestigial lingual
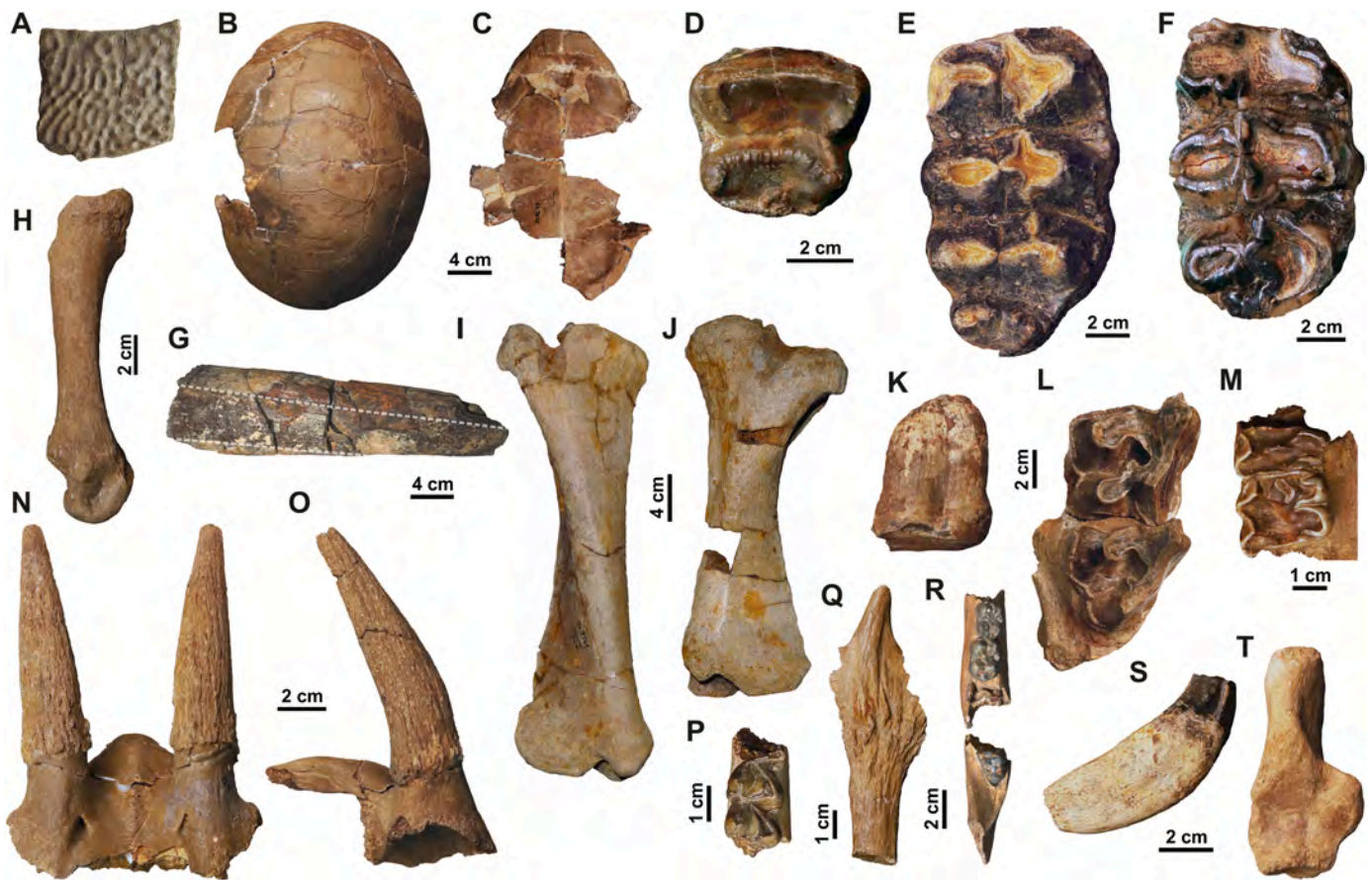
Fig. 5. Vertebrate remains from Czujan's sandpit. A: Trionychidae indet., costal plate (PIUW-8 × 1939) in dorsal view. B–C: *Testudo* (*Chersine*) *kalksburgensis*, carapace and plastron (Ot7875) in dorsal (B) and visceral (C) views. D: *Prodeinotherium* cf. *bavaricum*, left M3 (Ot7526), in oclusal view, E: *Zygolophodon turicensis*, right M3 (Ot7541), in oclusal view. F–G: *Gomphotherium angustidens*, right M2 (Ot7524) in (F) oclusal view; right I2 (Ot7505) in (G) lateral view. H: *Anisodon grande*, left fourth metacarpal (Ot7766) in lateral view. I: *Hoploaceratherium* sp., right tibia (Ot7749) in dorsal view. J–L: *Brachypotherium brachypus*, left tibia (Ot7752) in (J) dorsal view; right incisor (Ot7700) in (K) labial view; left maxillary fragment with M2–M3 (Ot7752) in (L) oclusal view. M: *Anchitherium* sp., right maxillary fragment with M1–M2 (Ot7765) in oclusal view. N–O: *Tethytragus stehlini*, frontoparietal with horn cores (Ot7786) in anterior (N) and left lateral (O) views. P: Palaeomerycidae indet., right mandibular fragment with m2–m3 (Ot7773) in oclusal view. Q: *Heteroprox larteti*, partial antler (Ot7771) in side view. R: cf. *Retroporcus matritensis*, right (with m3) and left (with m1) mandibular fragments (RMM P11) in oclusal view. S–T: *Amphicyon* cf. *major*, partial left canine (Ot7814) in (S) lingual view; left calcaneus (Ot7815) in (T) proximal view.

cingulum is present. Three anchitheriine species have been recorded from Central Europe: *Anchitherium aurelianense*, *Anchitherium hippoides*, and *Anchitherium steinheimense* (Abusch-Siewert, 1983; Rotgers et al., 2011). However, we refer MZM Ot7765 to *Anchitherium* sp. because the advanced degree of wear makes it impossible to ascertain occlusal details.

Artiodactyls are represented at Czujan's sandpit by five taxa from four different families: Bovidae, Palaeomerycidae, Cervidae and Suidae. The bovid material includes a single frontoparietal with horn cores (MZM Ot7786; Fig. 5N–O). The horn cores are long, straight, and moderately divergent, and display a mediolateral uniform compression and weak longitudinal grooves from base to apex; the pedicels are tall (Fig. 5N–O). MZM Ot7786 represents the most complete material and fits well in size and shape with the material from Czujan's sandpit and Kleinhadersdorf used by Thenius (1951) to erect "*Gazella*" *stehlini* and subsequently assigned to ?*Tethytragus stehlini* by Azanza and Morales (1994; see also Bibi and Güleç, 2008). We note that MZM Ot7786 is more complete than the holotype (only a gypsum cast was inspected in PIUW) of *Te. stehlini*, which is represented by a single left horn core fragment.

A palaeomerycid mandibular fragment with right m2–m3 is preserved (MZM Ot7773; Fig. 5P). The lower molars display a rugose enamel surface (particularly on the lingual side) and a brachyselenodont morphology with strong deep valleys and pointed conids (Fig. 5P). This combination of features supports the attribution to Palaeomerycidae

indet., but does not enable a more refined assignment to a genus due to the absence of more complete cranial material.

Three cervid antler fragments with consistent morphology are preserved. MZM Ot7771 (Fig. 5Q) is the most complete cranial appendage, where only the anterior branch and proximal part of the pedicle are broken off. The antler is straight, laterally compressed and bifurcated, without burr, but with extended, strongly sculptered base with longitudinal grooves and ridges. The studied antlers clearly differ from coronate antlers of *Lagomeryx* and *Paradicrocerus* (previously *Stehlinoceros*, see Böhme et al., 2012). MZM Ot7771 is dichotomous and more closely resembles the antlers of *Heteroprox*, being distinguished from other European genera by the absence of a burr (e.g., Heckeberg, 2017; Rössner et al., 2021). The general morphology and dimensions of MZM Ot7771 only fit well with those of *Heteroprox*, which is known by three species in Europe. The appendage allows an assignment to *Heteroprox larteti* by the larger dimensions and stronger sculpture than those of *H. eggeri* (see Rössner, 2010). Its smaller dimensions, more ellipsoid cross section of the pedicle and short anterior prong, excludes an assignment to *Heteroprox moralesi* (see Rössner, 2010).

Suids are represented by two mandibular fragments that, based on their similar preservation, might belong to the same individual (Fig. 5R): a right fragment with m1–m2 (RMM P11a) and a left one with a partial m3 preserving the distal crown portion (RMM P11b). The moderately worn m1 (16.5 × 10.4 mm) and the less worn and larger m2 (19.0 ×
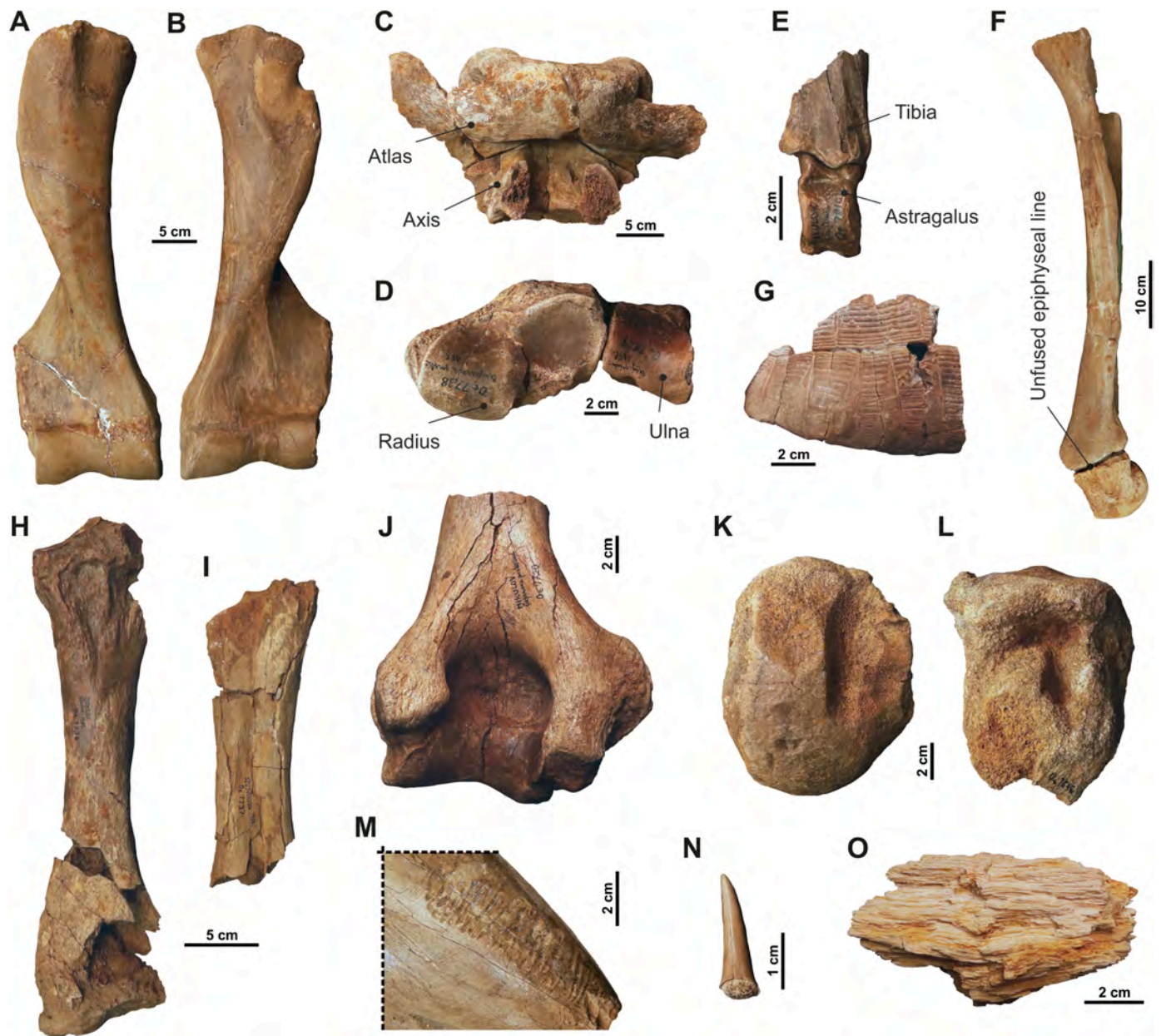
Fig. 6. Taphonomic features of fossil vertebrate remains from Czujan's sandpit. A–B: Proboscidean right (Ot7596) and left (Ot7599) humerus from a single individual in (A–B) cranial views. C: Proboscidea indet., atlas (Ot7545) and axis (Ot7547) in anatomical articulation, in dorsal view. D: *Hoploaceratherium* sp., radius (Ot7738) and ulna (Ot7829) in anatomical articulation, in distal view. E: Artiodactyla indet. (small size), tibia (Ot7810) and astragalus (Ot7808) in anatomical articulation, in plantar view. F: Proboscidea indet., right femur (Ot7647) with unfused distal epiphysis (Ot7650), in medial view. G: Right posterior carapace fragment with well preserved growth scute lines (Ot7877) in lateral view. H–I: Rhinocerotidae indet., comparison of a well preserved radius (Ot7736) with a deformed partial radius (Ot7737) as a possible result of trampling, in (H–I) caudal views. J: *Brachypotherium brachypus*, cracks in distal head of humerus (Ot7720), in caudal view. K–L: Proboscidea indet., proximal head of humerus (Ot7646) with gnawing traces of a large carnivore, in proximal (K) and caudal (L) views. M: Proboscidea indet., detail of gnawing traces of on the tip of tusk (Ot7483) possibly produced by a small rodent. N: *Isurus* sp., partial tooth (Ot7870), in labial view. O: wood fragment (Ot7871).

12.7 mm) display a similar morphology, with thick enamel, a similarly narrow subrectangular occlusal outline, conspicuous furrows between the main cusps and the central and distal pillars, a well developed mesiobuccal cingulum, and a distinct hypoectoconulid. The distal m3 fragment displays a relatively short talonid that is only slightly tilted buccally, with the hypoconulid surrounded by cingular cusplets. This morphology resembles the tetraconodont genera *Conohyus* and *Retroporcus*, which have been the subject of taxonomic revision during the last decade (Pickford and Laurent, 2014; Pickford, 2016) and are still a matter of debate (van der Made, 2020). Pickford and Laurent (2014) designated a lectotype for *Conohyus simorrensis* and provided an

emended diagnosis of the species, distinguishing the genus *Conohyus* from the new genus *Retroporcus* (see also Pickford, 2016), which includes material previously assigned to *C. simorrensis* by various authors (e.g., van der Made, 1989; van der Made and Salesa, 2004). Pickford and Laurent (2014) and Pickford (2016) interpreted *Retroporcus matritensis* as a senior synonym of *C. simorrensis goeriachensis*, whereas van der Made (2020) questioned the lectotype designation by Pickford and Laurent (2014) and considered *R. matritensis* a junior synonym of *C. simorrensis*. The suid mandibular fragments from Czujan's sandpit would be referrable to *C. simorrensis* sensu van der Made (2020), but until Pickford and Laurent's (2014) lectotype designation is proven

wrong, we prefer to follow their concept of *C. simorrensis* and distinguish *R. matritensis* as a distinct species. Although both species largely overlap in the size of their teeth, the proportions of the m1 and m2 from Czujan's sandpit do not fit well with those of *C. simorrensis* sensu Pickford and Laurent (2014), being relatively narrower and most closely resembling those of *R. matritensis* (Pickford, 2013, 2016). The slightly tilted m3 talonid also more closely resembles the latter species, since *C. simorrensis* is characterized by a less symmetrical talonid (Pickford and Laurent, 2014; Pickford, 2016). Although additional material (particularly the premolar series) would be required to confirm our identification, based on the aforementioned features we tentatively assign the material to cf. *R. matritensis*. Similarly to *C. simorrensis*, *R. matritensis* is known from European localities ranging from MN5 to MN9 (Pickford and Laurent, 2014; Pickford, 2016).

The carnivoran remains from Czujan's sandpit consist only of two partial lower canines (ÚGV Pal297, Fig. 5S; MZM Ot7814) and a calcaneum (MZM Ot7815; Fig. 5T). The more complete canine (>8.2 cm in height) preserves the entire root and most of the crown (except for the apex; ÚGV Pal297; Fig. 5S). The base of the crown is labiolingually compressed and preserves a distinct wide lingual wear facet to accommodate the I3 (Fig. 5S). In mesiodistal view, ÚGV Pal297 is slightly sigmoidal, which is typical for several groups of carnivorans. According to Viranta (1996), two valid amphicyonid genera are known from the middle Miocene of Europe: *Megamphicyon giganteus* (MN3–MN5), until recently included in *Amphicyon* (Siliceo et al., 2020); and *Amphicyon major* (MN4–MN9). The canine root of ÚGV Pal297 is less robust than in *Megamphicyon giganteus* (see Kuss, 1965). Based on size and root proportions, both canines are thus referred to *Amphicyon* (Ginsburg, 1961; Ginsburg and Antunes, 1968). The calcaneum MZM Ot7815 (Fig. 5S) is slightly abraded, especially the tuber calcanei, but it preserves enough diagnostic features to further support the assignment to *Amphicyon*. It is relatively short (8 cm long) and displays a robust tuber calcanei. The ectal facet is convex, craniocaudally elongated, and completely separated from the sustentacular facet. The latter is rather flat, semicircular in outline, and medially protruding. The referral to *Amphicyon* is based on size as well as the robustness of the tuber calcanei and the shape of the ectal facet (Argot, 2010). Given the restricted available material, we only tentatively assign the material to *Am.* cf. *major*.

5.3. Taphonomy

Despite the lack of field documentation, many fragmentary remains could be joined into complete bones during material preparation. This fact, and the presence of fresh fractures on the bone fragments, indicate that they were well-preserved and generally complete in the field, but that they were not adequately collected due to the "rescue" character of the excavations. Bones and teeth without any sign of transportation include 91% of the studied material, and 31% of the studied material represents complete skeletal elements from various parts of skeletons: teeth, skull fragments, mandibles, vertebrae, ribs, scapula, humerus, ulna, radius, and autopodial bones. The preservation of the vertebrate remains from Czujan's sandpit may be summarized as follows: 1) there is a high number of complete bones and teeth, being the former more frequent than the latter; 2) teeth are preserved both as dentognathic fragments (Fig. 5G, L, M, P, R) and isolated tooth crowns with roots (e.g., Fig. 5D, E, F, K, S); 3) we identified up to 29 cases of antimere bones (e. g., right and left humerus: Fig. 6A–B) and teeth; 4) in 10 cases, different bones appear to belong to the same individual and have been preserved in articulation or close spatial association, based on anatomical congruence, preservation state and/or information from labels (Fig. 6C–E), while in four cases unfused epiphyses matched with the corresponding diaphysis (Fig. 6F); 5) as pointed out by Jüttner (1938), there were well-preserved proboscidean skulls in Czujan's sand pit (either not recovered or subsequently disintegrated); 6) four of the seven testudinid specimens preserved well their 3D morphology and growth scute lines are discernible in some carapace plates (Figs. 5B, 6G). The

presence of antimeres and articulated specimens among the proboscidean sample, coupled with similar preservation, indicates that most of the bones come from a single individual—as further supported by information from the museum label of the proboscidean atlas RMM P34, according to which it was articulated with the skull in situ.

Generally, all bones and teeth are strongly mineralized in a similar way (Březina, 2019), and the mineralization of the more rounded and abraded bones is comparable with most of the better preserved ones, suggesting the lack of reworking and resedimentation of fossils from older deposits. Bone cavities are filled by quartzose sands, gravels, and clays. Finally, some specimens (e.g., MZM Ot7497 and MZM Ot7694) may contain remnants of soil or plant roots. Most of the fossil bones are fresh and angular (Figs. 5B–C, G, H–J, N–O; 6A–D, G–H) and only rarely are deformed (Fig. 6I). Prediagenetic traces of bone corrosion are infrequent. Only weathering stage 1 (sensu Behrensmeyer, 1978) modifications were observed, although longitudinal cracks in diaphyses and articular facets are often present (Fig. 6I–J). Two gnawing traces, probably produced by some large carnivores (Fig. 6K–L) and a rodent, were identified (Fig. 6M). However, we cannot exclude that some gnawing traces were alternatively produced by a ruminant, as they show a similar pattern to those produced by rodents (Hutson et al., 2013).

Most of the studied material belongs to terrestrial vertebrates and shows no signs of redeposition. In contrast, rare marine fossils indicate redeposition (Seitl, 1985). In particular, the analyzed pelitic matrix taken from the fossil bones only sporadically contains microfaunal marine remains, including: a single placoid shark scale; and the following foraminifera (*Arenobulimina* sp., *Ammodiscus* cf. *glabratus*, *Paragloborotalia acrostoma*, *Heteroleppa dutemplei*, and Globigerinida indet.), which must have been redeposited from the lower Badenian deposits and older deposits of Ždánice Unit (R. Brzobohatý and M. Bubík, pers. comm. to J.B.) as well as a single isolated shark tooth crown (Fig. 6N) referred to *Isurus* sp. The macroflora is represented by non-redeposited scarce wood remains (Fig. 6O), whereas palynomorphs were not present in the analyzed sediment samples.

All recovered testudinids from Czujan's sandpit are adult individuals, not only based on size, but further because the sutures between plates are completely fused or poorly visible in some cases. Based on the third molar eruption and/or epiphyseal fusion, mammals from Czujan's sandpit are adult individuals, with the only exception of proboscideans. Ontogenetic analysis, based on dental wear stages in the proboscidean samples (see Tassy, 1996, 2013), revealed different ontogenetic stages, including three juveniles, two mature subadults and fifteen midlife adults (Table. 2).

Table 2

Age profile of studied proboscideans (*Zygolophodon turicensis* and *Gomphotherium angustidens*) from Czujan's sandpit. Dental ages follow Tassy (1996, 2013, 2014), whereas ontogenetic age follow Haynes (2017).

Dental ages	MNI		Approximate age (years)
	Zygolophodon turicensis	*Gomphotherium angustidens*	
I-II.			0–1
III.	1		1–1.5
IV-VI.			1.5–5.5
VII.	1		5.5–7
VIII-IX.			7–10
X.	1		10–13
XI-XII.			13–18
XIII.	1		18–20
XIV.	3	1	20–22
XV.	2		22–24
XVI.	4		24–27
XVII.	1		27–28
XVIII-XIX.			28–32
XX.	2	1	32–35
XXI.			35–37
XXII.		1	37–42

6. Discussion

6.1. Sedimentological interpretation

From a sedimentological viewpoint (Figs. 3–4), the original outcrops of Czujan's sandpit were formed by tabular bars (Sh, SGh) and channel infills (St, SGt, Sp), which fill the distributary channels of both deltaic plain and deltaic front of a shallow water fluvial dominated delta (Postma, 1990; Chen et al., 2015; Zhang et al., 2017). The onlaps of cross strata arise during migration of climbing dunes in mouth bars of a delta front (Dasgupta et al., 2016), whereas the superposition of co-set facies Sl, Gl over co-set facies Sp can be interpreted as delta plain deposits overlapping mouth bar sediments (Francírek, 2018). The clay body (Fig. 4B) is most probably interdistributary bay infill (Zhu et al., 2017). As is typical for braid deltas, the delta plain is composed only by distributary channel infills (McPherson et al., 1988). Both the coarsening-upward sequence of facies association FA1–FA3 and the lens shape of megascale body FA2 + FA3 reflect a delta progradation into a marine basin. According to this interpretation, three facies associations are recognized: FA1, composed by pelagic sediments; FA2, prodelta sediments (suspension clays plus occasional sand turbidites) up to the delta slope sediments (sand turbidites plus suspension sediments of quiet phase on delta slope); FA3, sediments of delta front (mounth bars and interdistributary bays) and delta plain (subaerial distributary channels) infills. The latter interpretation is supported by the occurrence of wood fragments (Fig. 6O), which are common in distributory channels or their mouth along the delta front (Olariu and Bhattacharya, 2006), as well as by the presence of terrestrial fauna. Based on the sedimentary architecture, Czujan's sandpit can be interpreted as a shallow-water river delta with braid delta plain and with mouth bars in distributary outlets and interdistributary bays on delta front (Nemec, 1990; Postma, 1990; Zhu et al., 2017).

6.2. Taphonomical interpretation

The bone concentration from Czujan's sandpit is characterized by the relatively diverse assemblage of terrestrial vertebrates, the presence of complete and associated bones (skull bones, mandibles, vertebrae, ribs, limb bones), a low degree of weathering, and a predominance of fresh and angular specimens. These aspects, and the absence of polished or otherwise discrepant bone of terrestrial vertebrates characteristic for exhumation or redepositions (Rogers and Kidwell, 2007), unequivocally indicates that the terrestrial vertebrate assemblage is not mixed with reworked older terrestrial fossils. In contrast, the rare marine fossils represent redepositions from the Ždánice Unit, Lanžhot Formation and lower parts of Hrušky Formation (Seitl, 1985). Reworked, allochthonous marine fossils have been already documented by Kuklová (1970, 1978) from the Wielician-Kosovian clays in boreholes (Figs. 2, 3).

The presence of bones and teeth from more than a single individual and with multiple species represented allows us to classify at least the sands and gravels of FA3 (vertebrate remains are not documented from sands and gravels of FA1–FA2) as a macrofossil multitaxic bonebed (Behrensmeyer, 2007; Eberth et al., 2007; Rogers and Kidwell, 2007). Because mining extraction in Czujan's sandpit from the 1930s to the 1980s progressed from south toward north and east, and abandoned parts of the sandpit were gradually filled by waste as extraction progressed, new and relatively small outcrops (in comparision with the whole mining area) were accessible in each mining phase (Březina, 2019). This implies that more than a single bone bed was present in the Czujan's sandpit profiles. The different types of rocks represented by the matrix adhered to the fossils as well as the presence of recent soil remnants on some specimens suggest that the fossil remains came from different stratigraphic positions. This is further supported by the old label of PIUW 4501–4503, which clearly describes the find at 6.5 m depth, and corresponds well with Seitl's (1985) observation that bones and teeth were vertically scattered along the whole profile. Therefore,

from a finer scale perspective, we can conclude that the bone accumulations of FA3 were located in more than one chanel infill, probably as a result of gradual or periodical fluvial sedimentation. In the absence of field documentation, it is impossible to confidently establish whether the fossil bones originated from a time-averaged accumulation of carcasses randomly transported from the river basin and deposited due to the loss of water energy along the mouth of distributary channels into the sea. Alternatively, the assemblage might have originated by the progressive accumulation from a preexisting source of mass death accumulation. However, the high concentration of terrestrial taxa is outstanding in the context of surrounding marine deposits, and the low number of carnivorans and the presence of a single specimen of a freshwater taxon (trionychid) rule out either a flooding event or a miring mortality (Rogers and Kidwell, 2007). Moreover, multitaxic fossil assemblages, formed by immature individuals as well as gnawing traces, do not occur in mass drowning (Rogers and Kidwell, 2007; Backwell et al., 2018). Both the presence of cracks and the gnawing traces suggest that some carcasses were laying for some time on the surface before sediment deposition.

The main taphonomic features of the Czujan's sandpit assemblage (i. e., wearing stage 1 sensu Behrensmeyer, 1978, a minimal number of gnawed bones, and evidence for articulated skeletons) are often reported from drought mass death sites (Haynes, 1985, 1988, 1991, 2018; Backwell et al., 2018). The structure and MNI of taxa such as proboscideans, bovids or testudines from Czujan's sandpit (Table 1) further resemble those from extant sites from Africa, where drought mass death implies a higher mortality of proboscideans and bovids (Haynes, 1988). Predominance of large herbivores such as proboscideans (Table 1), which are characterized by high mortality during dry periods, might support this idea (Haynes, 1985, 1991, 2017; Haynes and Klimowicz, 2015). Variously old proboscidean individuals have been recovered from Czujan's sandpit fossil record, including juveniles (Table 2), which are characteristic in recent drought mass death sites (Haynes, 1985, 1991, 2017; Haynes and Klimowicz, 2015). Based on our findings, a progressive secondary accumulation from preexisting drought mass death accumulations into FA3 seems most likely. This interpretation would be in agreement with the strong decrease of humidity in Central Europe during the late Badenian, as well as the presence of seasonality in the Vienna Basin accompanied by periodic drought conditions (e.g., Böhme et al., 2011; Harzhauser et al., 2011), supported by documented braid delta. This delta type occurs in areas with arid climate and limited vegetation, fed by flows with unbalanced flow rate (McPherson et al., 1988; Miall, 1996). However, poor field data do not allow to clearly determine if the fossil assemblage is a time-averaged abiotic accumulation or whether it was deposited following drought mass death accumulation. Taking in account the dispersal capabilities of large mammals, the studied taphocoenosis probably mixes taxa from various biotopes concentrated in one place of the river basin for both possible intepretations. In the analogy with recent elephant populations whose home ranges reach up to ~3000 km^2 (Haynes, 1991), we assume that animals might have inhabited area from the Vienna Basin coastline, including delta platform to the eastern slopes of Bohemian Masiff, which is largely formed by the soutwestern part of the Carpathian Foredeep Basin (see Fig. 1).

6.3. Biostratigraphy

All mammal taxa identified in the Czujan's sandpit have been reported from the European early Astaracian (MN6) localities. Although the mammal community as a whole displays a wide biostratigraphic range from MN3 up to MN10, the first occurrence of *R. matritensis* and *Hoploaceratherium* in Göriach, Austria (late MN5, ~14.5 Ma; Aiglstorfer et al., 2014), and *Te. stehlini* in Kleinhadersdorf, Austria (MN5-MN6, ~14.2 Ma; sensu Böhme et al., 2012) together with the last known occurrence of *P. bavaricum* from Devínska Nová Ves-Zapfe's fissures, Slovakia (early MN6; Fejfar, 1990) restrict the biostratigraphic age of

the Czujan's sandpit assemblage within the late MN5 to late MN6 (Fig. 7). Given by the fossil record of mammals from well-dated Central European localities, the above mentioned biostratigraphic age is supported by the coeval first appearance of *R. matritensis* and *Te. stehlini* and the last appearance of *P. bavaricum*, *Retroporcus matritensis*, *H. larteti* and *Am. major* (Fig. 7). The Badenian age of the vertebrate assemblage is also partially supported by the presence of a testudinid *T. kalksburgensis* reported from Wien-Kalksburg, Austria (MN5–MN6; Bachmayer and Młynarski, 1981).

The biostratigraphical age (late MN5 to late MN6; late early to late Badenian; Fig. 7), based exclusively on the vertebrate assemblage, is generally in agreement with the late Badenian age of the Czujan's sandpit, as previously suggested based on marine and brackish microfauna (Kosovian: Buday et al., 1964; Čtyroký, 1989; Čtyroký et al., 1990; Fejfar, 1990; and Wielician: Kuklová, 1978; Stráník et al., 1999; Jiříček, 2002). These authors did not verify the age on the basis of vertebrate fauna, such as Thenius (1951) and Musil (1956), who adopted Jüttner's (1938, 1940) exclusively petrographic correlation with the Sarmatian sands. However, a Sarmatian age is highly improbable, because Sarmatian sediments have not been documented from the Mikulov area (Fig. 1B). The presence of the *Ammonia beccarii* ecozone, laterally

replaced by the *Bulimina-Bolivina* Zone in the Nové Mlýny-2 borehole (Bimka et al., 1983), proves that both FA3 and FA2, together with the uppermost section of FA1, correspond to the Kosovian substage (Figs. 2–3). The lower limit of the Kosovian substage varies within the range of 13.6–13.1 Ma (Hohenegger et al., 2014) and therefore, Czujan's sandpit assemblage cannot be older than ~13.6 Ma. This corresponds to the upper MN6 boundary in Central Europe (base of C5ABn sensu Steininger, 1999, but see different MN zonation in Western Europe, Fig. 7).

According to the Nové Mlýny 2 borehole (Bimka et al., 1983), the section of Kosovian continues minimally for at least ~40 m above the sandpit; however, the original thickness of Kosovian section was most probably greater but subsequently reduced by Sarmatian and Quarternary erosions. Therefore, both the close proximity to the Wielician/Kosovian boundary (Figs. 2, 3) and mammal biochronology (Fig. 7) support a latest MN6 (~13.6 Ma) age of the Czujan's sandpit. *Prodeinotherium* and possibly also *Am. major* from Czujan's sandpit are among the youngest records of these taxa from Central Europe (late MN6, Kosovian substage; Fig. 7).
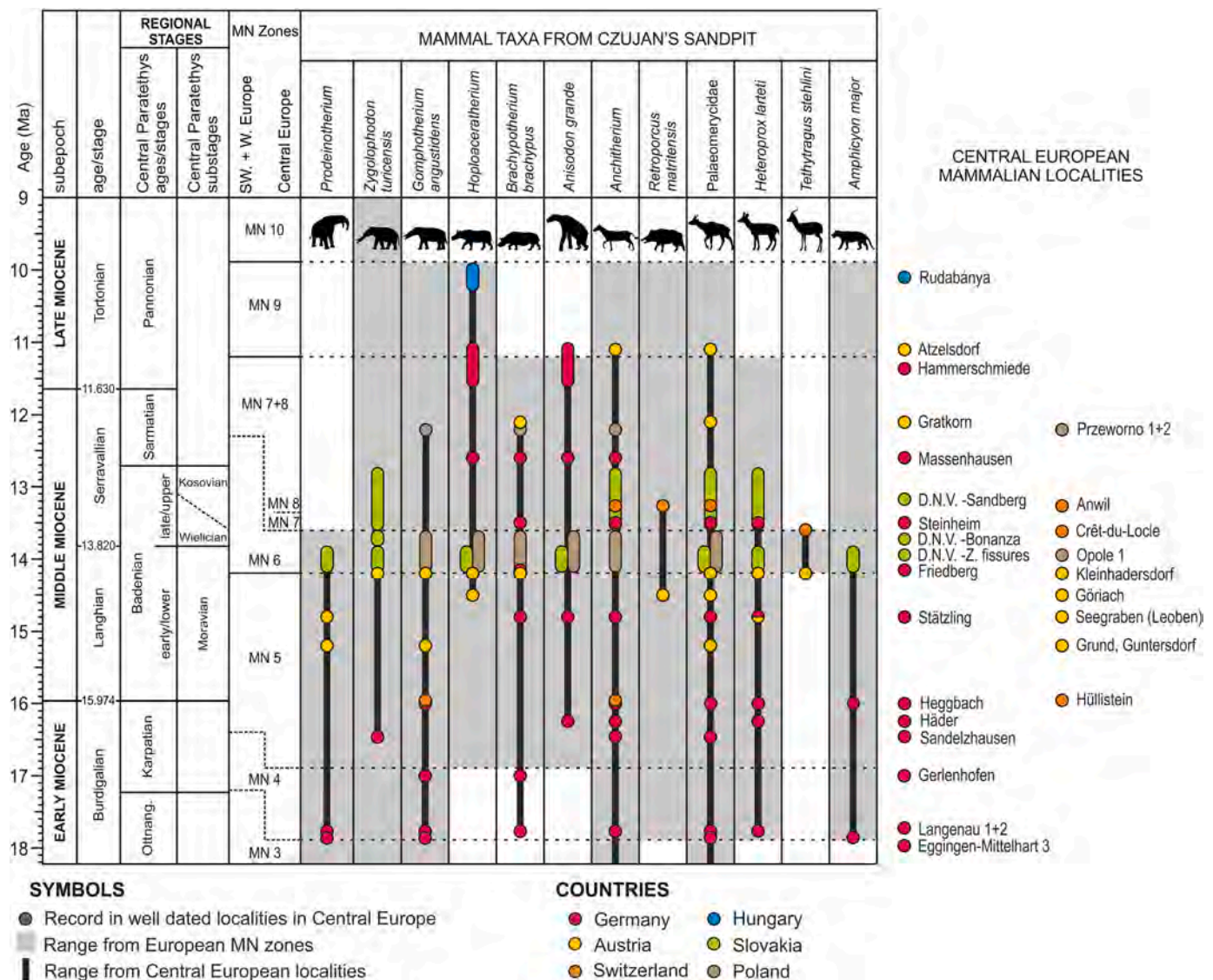

Fig. 7. Stratigraphic distribution of the studied taxa in Central Europe. Age boundaries for the Badenian stage follow Kováč et al. (2018). Modified MN zonation in Western and Southwestern Europe follows Hilgen et al. (2012), Central European MN zonation modified according to Steininger (1999), Becker (2003) and Hilgen et al. (2012). The taxa ranges and ages of localities are based on various sources (see Supplementary Information).

6.4. Paleoecological implications

The vertebrate assemblage from Czujan's sandpit comes from various paleohabitats. A closed woodland habitat is indicated by proboscideans (*Prodeinotherium* cf. *bavaricum* and *Zygolophodon turicensis*), rhinos (*Brachypotherium brachypus* and *Holoaceratherium* sp.), chalicotheres (*Anisodon grande*), palaeomerycids, suids (*Retroporcus matritensis*) and carnivorans (*Amphicyon* cf. *major*; Fig. 8). The dental morphology and the still rather limited number of δ^{13}C values from tooth enamel of *P. bavaricum* (Seegraben; Aiglstorfer et al., 2014) and *B. brachypus* (Steinheim; Tütken et al., 2006) indicate that both species might have inhabited a closed woodland environment. Mammutids of the genus *Zygolophodon* browsed in forest habitats as well (e.g., Lambert and Shoshani, 1998) but based on zygolophodont dentition their dietary spectrum was most probably different from that of bunodont gomphotheres and lophodont deinotheres. This assumption is indirectly supported by feeding preferences of conifers (*Taxodium*) in closely related American mastodons (*Mammut americanum*) from the Pleistocene of Florida (Green et al., 2005), where *Taxodium* swamps are comparable to those documented from the Miocene of Central Europe (e.g., Kvaček et al., 2004; Kázmér, 2008). The brachyodont teeth of palaeomerycids, as well as their isotopic data from middle Miocene localities of Germany and Spain, support a folivorous diet in woodlands (Tütken et al., 2006; Tütken and Vennemann, 2009; Domingo et al., 2012). A woodland habitat is also favored by the chalicotheriid *A. grande*, which is considered a specialized browser (Schulz et al., 2007), as well as the amphicyonid *Am. major*, which was an active omnivorous predator (Argot, 2010) anatomically well-adapted for climbing trees and chasing preys (Argot, 2010).

The presence of mixed-feeders such as *Gomphotherium*, *Anchitherium*, *Heteroprox* and *Tethytragus* suggest, in addition, the existence of more open environments. The genus *Gomphotherium* has been considered an inhabitant of open environments similar to recent African savannas (Tassy, 1977; Lambert, 1996; Lambert and Shoshani, 1998). The isotopic data for subtapiroid species of *Gomphotherium* from the latest early and early middle Miocene of Germany suggests the consumption of C3 vegetation in woodland environments, as documented by δ^{13}C values in *G. steinheimense* (−10.7‰ up to −10.1‰; Tütken et al., 2006) and *G. subtapiroideum* (−11.9‰ to −10.2‰; Tütken and Vennemann, 2009). However, dental microwear studies of both species indicate a mixed-feeding, with *G. subtapiroideum* likely favoring more open woodlands (Calandra et al., 2008, 2010). In contrast, the rather high δ^{13}C values for *G. angustidens* from the middle Miocene localities of the Madrid Basin,

Spain (−10.65‰ to −6.21‰; Domingo et al., 2009, 2012) indicate that *Gomphotherium* might have intruded into open and grassland environments. Although data from the Central European populations of *G. angustidens* are missing, this species most probably favored more open environments than the other proboscidean species recorded from Czujan's sandpit (i.e., *P. bavaricum* and *Z. turicensis*), which most probably occupied a different ecological niche in more closed woodland (Fig. 8). *Anchitherium* might also have inhabited open woodland environments, as suggested by results from dental mesowear (Kaiser, 2009) and isotopic studies (Tütken et al., 2006; Tütken and Vennemann, 2009) of *A. aurelianense* populations from Sandelzhausen and Steinheim (Germany), as well as more open environments as suggested by δ^{13}C values (−12.7‰ to −6.49‰; Domingo et al., 2012) from populations of Spanish MN5–MN6 localities.

Mixed-feeding *Heteroprox* species usually inhabited forests or woodlands in Central Europe (specifically Seegraben, Austria and Sandelzhausen, Germany) during the Langhian, as documented by δ^{13}C values (−12.0‰ to 10.4‰; Tütken and Vennemann, 2009; Aiglstorfer et al., 2014). However, the dental microwear study of *H. larteti* populations from central Spain (DeMiguel et al., 2011), contrary to isotopic studies of Domingo et al. (2012), revealed a high degree of grazing interpreted as an adaptation to seasonal arid periods during the Serravallian. A similar variation in paleohabitat is recorded in *Tethytragus*. Isotope data of *Tethytragus* sp. from Gratkorn, Austria (MN7+8; Aiglstorfer et al., 2014) indicate a woodland environment, whereas isotope data of *Tethytragus langai* from Paracuellos 3, Spain (MN6; Domingo et al., 2012) show a mixed-feeding diet related to more open conditions. Augustí and Antón (2002) pointed out that *Tethytragus* was capable of inhabiting different habitats with a diet comprising a variety of vegetation. This was confirmed by micro- and mesowear analysis of *Tethytragus langai* from the Serravallian of Spain (DeMiguel et al., 2011). Hence, seasonal variations of dietary composition in Central European populations (e.g., those from Gratkorn) could have occurred as well (Aiglstorfer et al., 2014). The omnivorous *Retroporcus matritensis* also preferred a more open woodland environment based on isotopic studies (Tütken et al., 2006; Domingo et al., 2009).

Among rhinocerotids, *Brachypotherium brachypus* has been traditionally considered a semiaquatic species of open environments (Heissig, 1999; Augustí and Antón, 2002; Costeur et al., 2012). However, its brachyodont dentition, and the isotopical data of *Brachypotherium* from Steinheim (MN7+8, Germany) and Eichkogel (MN11, Austria), suggest browsing in closed woodland environment (Tütken et al., 2006; Aiglstorfer et al., 2014) unlike *Hoploaceratherium*, which most likely favored
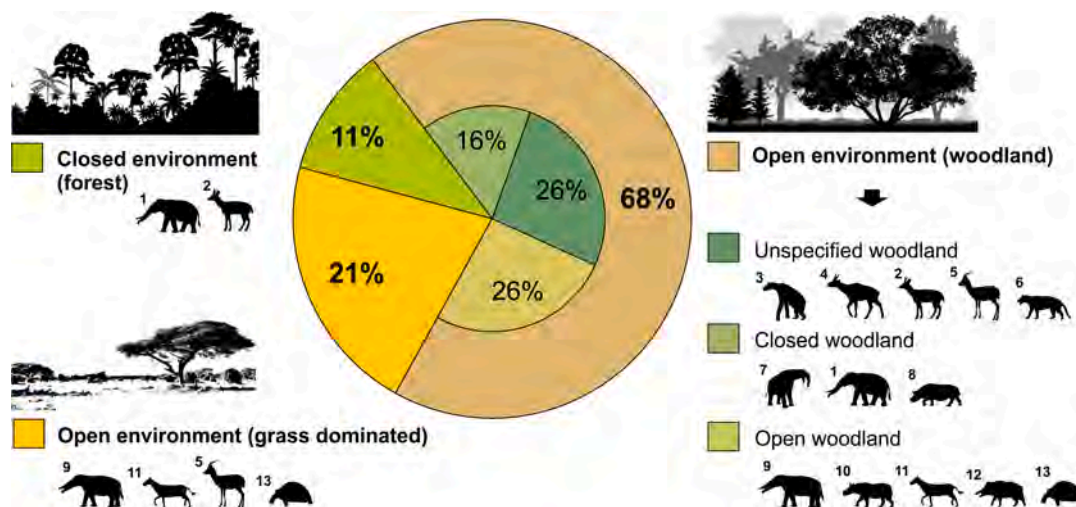

Fig. 8. Paleoenvironments derived for Czujan's sandpit taxa. Taxa silhouettes are not in scale: 1) *Zygolophodon turicensis*; 2) *Heteroprox larteti*; 3) *Anisodon grande*; 4) Palaeomerycidae; 5) *Tethytragus stehlini*; 6) *Amphicyon major*; 7) *Prodeinotherium bavaricum*; 8) *Brachypotherium brachypus*; 9) *Gomphotherium angustidens*; 10) *Hoploaceratherium*; 11) *Anchitherium* sp.; 12) *Retroporcus matritensis*; 13) *Testudo kalksburgensis*.

more open environments based on δ¹³C values from the middle Miocene (MN5–MN6) localities from the Madrid Basin, Spain (−11.15‰ to −9.02‰; Domingo et al., 2012). The different paleoecological preferences of these two rhinocerotids are as well manifested with their anatomical differences, as *Hoploaceratherium* has long legs and is better adapted for a cursorial locomotion in an open landscape, whereas *B. brachypus* is a short-limbed and hippo-like species (Cerdeño, 1993; Heissig, 2012).

The indeterminate trionychid turtle is indicative of the presence of permanent freshwater reservoirs, whereas the testudinid *Testudo kalksburgensis* inhabited open woodland, or even more open environments. Medium-sized testudinids are well adapted to dry conditons, and can inhabit a wide variety of open environments ranging from clearings with low vegetation to semiarid habitats (Miklas-Tempfer, 2003, 2005; Čerňanský et al., 2012; Luján et al., in press). The aquatic trionychid turtle, semiaquatic *Brachypotherium* together with the rich fossil record of proboscideans at Czujan's sandpit, (whose recent representatives are well known for water seeking; e.g., Haynes, 1991), further indicates the presence of permanent freshwater bodies occurring in the northwest area of the Vienna Basin coastline to the adjacent Carpathian Foredeep Basin. Middle Miocene changes in the Central Paratethyan terrestrial environments were conditioned by increased tectonic activity which resulted in uplifting mountains in the east and two marine transgressions, one during the early Badenian and second one in the late Badenian (Kováč et al., 2007). The extensive areas around the Vienna Basin were divided by the uplift of its eastern part into western lowlands and eastern steep highlands in the late Badenian (e.g., Kvaček et al., 2006; Kováč et al., 2007). The late Badenian paleobotanical record from eastern Central Europe indicate that the highland situated southeast of the Vienna Basin was covered by a mixed mesophytic forest with extrazonal (mountain) vegetation (i.e., Devínska Nová Ves, Slovakia; Kvaček et al., 2006; Kováčová et al., 2011; Kovar-Eder and Teodoridis, 2018). The dominance of forest environments is also documented in this area by the late Badenian mammal assemblages from Devínska Nová Ves locality - Zapfe's Fissures, "Bonanza" and Sandberg (Sabol and Kováč, 2006). Although paleobotanical record from lowlands situated in the Carpathian Foredeep Basin, (i.e., northwest of the Vienna Basin) is rather incomplete, recent analyses from the early late Badenian to early Sarmatian low altitude (0–300 m a.s.l.) localities of the Carpathian Foredeep Basin, together with the data obtained both south and west of the Vienna Basin, point to the presence of subhumid sclerophyllous vegetation (Kovar-Eder and Teodoridis, 2018). The paleoecological analysis of the late Badenian Czujan's sandpit revealed a mosaic of habitats represented by forests, close to open woodlands, more open environments, and stagnant or slowly flowing freshwater reservoirs in the continental northwestern area of the Vienna Basin to the adjacent Carpathian Foredeep Basin (Fig. 8). This mosaic of local habitats could be understood as restricted riparian and floodplain forests surrounded by widespread woodland which opened inland, locally passed into the more open environments (grass dominated).

Subhumid sclerophyllous forests documented from the Central Paratethys suggest a more marked precipitation seasonality for the late Langhian to early Serravalian period (Kovar-Eder and Teodoridis, 2018). The predominance of open habitats, both west of the Vienna Basin and in the southwestern part of the Carpatian Foredeep Basin (see also Section 5.3.; Tables 1 and 2) is in agreement with increase in precipitation seasonality reported since the early Badenian. This climatic change was mainly result of tectonically inferred sea-level falls in West Carpathian-North Pannonian Basins (Kováč et al., 2001), as well as a possible decrease of moist air mass production during the early Badenian (Böhme, 2003). The second period of increased precipitation seasonality 14.7–14.5 Ma (Böhme, 2003), which most probably persisted in the northwestern part of the Vienna Basin up to the early/late Badenian transition, was followed by a late Badenian steep decrease of humidity in Central and Eastern Europe. This drop in humidity culminated during the latest Badenian and Sarmatian stages (~13–12 Ma; Böhme et al.,

2008) as also documented by the dramatic succession of dry years with irregular precipitation events recorded from isotopic record of Serravallian oyster shells from the Vienna and Korneuburg Basins (Harzhauser et al., 2011).

7. Conclusions

Here we provide an updated faunal list of the middle Miocene vertebrate assemblage from Czujan's sandpit site as well as interpretation of the geological, taphonomical and paleoenvironmental data based on the osteological and dentognathic materials. A total of 14 vertebrate taxa were indentified, including two reptiles (**Testudines:** Trionychidae indet. and *Testudo kalksburgensis*) and 12 mammals (**Proboscidea:** *Prodeinotherim* cf. *bavaricum*, *Zygolophodon turicensis*, *Gomphotherium angustidens*; **Rhinocerotidae:** *Hoploaceratherium* sp., *Brachypotherium brachypus*; **Chalicotheriidae:** *Anisodon grande*, **Equidae:** *Anchitherium* sp.; **Suidae:** cf. *Retroporcus matritensis*; Palaeomerycidae indet.; **Cervidae:** *Heteroprox larteti*; **Bovidae:** *Tethytragus stehlini* and **Carnivora:** *Amphicyon* cf. *major*). The taphonomic analysis indicates that terrestrial vertebrate fossils could not be redeposited. Fossil vertebrates from Czujan's sandpit come from deposits of a braid delta plain to delta front deposited during the Kosovian substage (late Badenian). Based on the combination of biostratigraphic and geological data, we assume that Czujan's sandpit age can be dated to latest MN6 for Central Europe (close to Wielician/Kosovain substage boundary: ~13.6 Ma).

We conclude that there are two plausible explanations for the genesis of the fossil accumulation from Czujan's sandpit, including: 1) an abiotic time-averaged concentration generated by the transport energy of water; or 2) the gradual or periodical transport of remains from one or more (in the case of more time-averaged as well) mass death site accumulation. However, under both interpretations, the Czujan's sandpit vertebrate assemblage would reflect an averaged spectrum of species from the whole river basin flowing into northwest of the Vienna Basin. We suggest a mosaic of continental habitats in the area from northwestern coast of the Vienna Basin to the adjacent Carpathian Foredeep Basin. These habitats were represented by the restricted riparian and floodplain forests, surrounded by the widespread woodlands opening locally into more open environment, with enough freshwater sources that could eventually evaporate on a seasonal basis during droughts, leading to mass deaths of animals.

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Authors contributions

J.B. and M.I. conceived and designed the study. J.B. prepared and catalogued the material from MZM, compiled and analyzed data from all studied specimens, and prepared the initial manuscript draft (geology, taphonomy, paleoecology, biostratigraphy). J.B, M.I and À.H.L prepared figures and tables. D.M.A., M.I., M.H., and À.H.L. analyzed data and wrote additional sections of the manuscript (M.H.: sedimentology; D.M.A: Suidae and Deinotheriidae; À.H.L.: Testudines and Carnivora). All authors improved the initial manuscript draft equally and approved its final form.

Declaration of Competing Interest

The authors declare no conflicts of interest.

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