



REVISED FLORAL AND FAUNAL ASSEMBLAGES FROM LATE PLEISTOCENE DEPOSITS OF THE GÁNOVCE-HRÁDOK NEANDERTHAL SITE – BIOSTRATIGRAPHIC AND PALAEOECOLOGICAL IMPLICATIONS

MARTIN SABOL^{1,*}, DIANA SLYŠKOVÁ¹, SILVIA BODORIKOVÁ², TOMÁŠ ČEJKA³, ANDREJ ČERŇANSKÝ⁴, MARTIN IVANOV⁵, PETER JONIAK¹, MARIANNA KOVÁČOVÁ¹, CSABA TÓTH⁶

¹ Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University in Bratislava, Ilkovičova Str. 6, SK-84215 Bratislava, the Slovak Republic; e-mail: sabol@fns.uniba.sk, slyskova@fns.uniba.sk, joniak@fns.uniba.sk, kovacova@fns.uniba.sk.

² Department of Anthropology, Faculty of Natural Sciences, Comenius University in Bratislava, Ilkovičova Str. 6, SK-84215 Bratislava, the Slovak Republic; e-mail: bodorikova@fns.uniba.sk.

³ Institute of Botany, Plant Science and Biodiversity Center, Slovak Academy of Sciences, Dúbravská cesta 9, SK-84523, Bratislava, the Slovak Republic; e-mail: tomas.cejka@savba.sk.

⁴ Department of Ecology, Faculty of Natural Sciences, Comenius University in Bratislava, Ilkovičova Str. 6, SK-84215 Bratislava, the Slovak Republic; e-mail: cernansky@fns.uniba.sk.

⁵ Department of Geological Sciences, Faculty of Science, Masaryk University, Kotlářská 267/2, Brno, the Czech Republic; e-mail: mivanov@sci.muni.cz.

⁶ Central Slovakia Museum, SNP Square 4, SK-97590 Banská Bystrica, the Slovak Republic; e-mail: toth@ssmuzeum.sk.

*corresponding author

Sabol, M., Slyšková, D., Bodoriková, S., Čejka, T., Čerňanský, A., Ivanov, M., Joniak, P., Kováčová, M., Tóth, Cs. (2017): Revised floral and faunal assemblages from Late Pleistocene deposits of the Gánovce-Hrádok Neanderthal site – biostratigraphic and palaeoecological implications. – Fossil Imprint, 73(1-2): 182–196, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: Revisory research of floral and animal assemblages from the Neanderthal site of Gánovce-Hrádok confirmed the previous stratigraphic division of the travertine mound to five horizons on the basis of different petrological and palaeontological contents, indicating climatic and palaeoenvironmental changes in the vicinity, from the Saalian termination to the Holocene. At least two species of molluscs and approximately 20 taxa of vertebrates have been determined, and at least 8 endocasts of large mammals have been re-discovered. Revised floral record contained 570 specimens, but no more than 20% were suitable for taxonomic revision.

Key words: Gánovce-Hrádok Neanderthal site, Slovakia, travertine, Pleistocene, Flora, Mollusca, Reptiles, Aves, Mammalia

Received: March 13, 2017 | Accepted: May 22, 2017 | Issued: August 15, 2017

Introduction

The Gánovce-Hrádok Neanderthal site is one of the most important Late Pleistocene archaeological and palaeontological localities in Central Europe, famous mainly for a specific Neanderthal find – travertine cranial endocast (Vlček 1969, 1995). The site (49° 1' 49" N, 20° 19' 15" E), consisting of the travertine mound rest, is situated about 3 km SE from Poprad town in northern Slovakia (Text-fig. 1).

Scientists have occasionally investigated this site since the time of its opening as a travertine quarry, in the 1880s. Although intensive travertine exploitation continued here until the 1920s, all mining activities ended just before World War II. During this exploitation, many fossils were discovered, but also destroyed. Some of these fossil remains, including also several cranial endocasts of large

mammals and Neanderthal man, were saved by Bohemian teacher and amateur palaeontologist Jaroslav Petrbok (1881–1960) in 1926, and housed in the National Museum in Prague (the Czech Republic). He also published a record of bird feather impression, probably belonging to common crane (Petrbok 1937, 1939), and a turtle shell internal core saved by him was described by Štěpánek (1934) as a fossil remnant of *Emys orbicularis*.

Even before initiation of systematic site research (1955–1960), two preliminary surveys were carried out, in 1949 and 1953. During five years of systematic research, the scientist team headed by František Prošek (1922–1958) and Emanuel Vlček (1925–2006), consisting of specialists from the Archaeological Institute of the Slovak Academy of Science in Nitra, the Archaeological Institute of Czechoslovak Academy of Science in Prague, and from the Geological Survey in Prague, found a large quantity of

new fossils, including casts of Neanderthal left radius and left fibula. Results of this research were summarized in a final report (Vlček 1958), and published in several papers (e.g., Ložek 1955, Vlček 1956, 1959, 1961, Fejfar 1958, Kneblová 1958b, 1960, Musil 1972, Horáček and Sánchez Marco 1984). General results were presented in a monograph (Vlček 1969). The Neanderthal finds were later dated to ca. 105 ka BP (from $131,800 \pm 3,900$ – $4,100$ to $85,200 \pm 3,200$ – $3,300$ BP) on the basis of petrographic and stratigraphic analysis, fluorine index and U-Th dating of the surrounding travertine (Jäger 1989). From an archaeological point of view, these remains fall within the cultural layer (complex III, Taubachian, 130,000–83,000 years BP) that contained finds of chipped stone industry (86 artefacts made of quartz, radiolarite, and undetermined raw material) (Kaminská 2014).

In 1969, a separate exhibition focused on the environment of Neanderthals in the Spiš area was established in the Podtatranské Museum in Poprad, representing the only specialized exhibition of this type in Slovakia (currently undergoing reconstruction). The presence of some so far unstudied fossils in the exhibition and depositories of the museum led to the submission of a new research project, focused on the revision on the entire preserved palaeontological record from the site. During this project (2012–2015), some fossils saved by Prošek, including also some mammalian endocasts were restudied in the National Museum, Prague.

Locality and geological settings

Gánovce village is situated in the southern part of the Poprad basin, the territory of which consists predominantly of Paleogene deposits of Central Carpathian Flysch (slates and sandstones). Large travertine mounds are spread from Poprad town to Hôrka village, along faults of the Podtatranská tectonic line aligned E–W, and their existence is connected with mineralized hot springs. Although travertine formations have aggraded in this area since the end of Tertiary Period, most of them were formed from the Pleistocene to the Holocene, mainly during the Eemian Interglacial.

The travertine mound of Hrádok in Gánovce village belongs to the Late Pleistocene travertine formations. The original travertine mound was about 170 m in diameter and 20 m high, the central crater was about 20 meters in diameter. After intensive exploitation, only a torso of the central crater was preserved from the large heap (Text-fig. 1).

Initially, Prošek (1958) presented eight petrographically different layers in two profiles of the mound (profile in the crater margin and profile in the crater centre). Although the sedimentological situation in both profiles was slightly different, their main layers could be mutually correlated. Kukla (1958) recapitulated the whole structure of the Gánovce-Hrádok site into five petrographic associations: (1) Bottom layers of travertine sands, marls and clays form an underbed of the compact travertine. These lowermost



Text-fig. 1. Location of Gánovce-Hrádok Neanderthal site in northern Slovakia and the rest of the travertine mound (map source: <https://commons.wikimedia.org> and Google Earth; 2017).

layers, formed at the end of the Saalian Glacial Stage, were affected by cryoturbation. (2) Compact, stratified travertine with occasional intercalations of marls was deposited in the following Eemian Interglacial Stage. The travertine contained many fossil remnants of flora and fauna, which allowed a good observation of changes in the site-surrounding environment during the time of the travertine development. (3) Younger, crumbling travertine with soil layers was observed in overlying beds. Abundant mollusc fauna together with remains of mammals and plants document the cooler climate, in comparison to the interglacial maximum. (4) Last Glacial sediments consist of bottom soils, loess layer, and stony-sandy clay soils at the top. Fragments of travertine often occurred in all layers. Remains of typical cold mammalian and molluscan species were found in loess, indicating subarctic climatic and environmental conditions. (5) Travertine heap was covered with Holocene soils with artefacts from Neolithic, Aeneolithic, Bronze Age, Hallstatt, and Roman Period, whereas Late Pleistocene deposits contained archaeological artefacts from the Middle and Upper Palaeolithic (Mousterian and Gravettian stone tools) (Vlček 1995).

Material

The revised fossil material is housed in the National Museum, Prague (the Czech Republic), in the Podtatranské Museum in Poprad, and at the Department of Geology and Palaeontology, Comenius University in Bratislava (temporarily, before being stored in a museum). Whereas Prague collections contain Gánovce fossil remains from the period before World War II, collected predominantly by Petrbok in the 1920s (labelled NM-R and NM-Rv numbers), finds deposited in Bratislava (labelled OF numbers; originally a collection of Oldřich Fejfar) and Poprad (labelled P numbers) were found mostly in the second half of the 1950s during the systematic research. However, the institutional deposition of many fossils from this last field campaign is unknown, since only a small part of the whole collection is housed in the Podtatranské Museum. Maybe these were a part of Vlček's collections, originally housed in the Archaeological Institute of the Slovak Academy of Science in Nitra during his employment in this scientific institution, and later moved to Prague. Its current location is unknown. Additionally, a few samples housed in the Podtatranské Museum bear labels from 19th/20th centuries.

The state of preservation of revised osteological material from assumed individual layers varied. Finds from clay-soil sediments are well preserved, whereas fossils from travertine are rather disintegrated. No fossils of micromammals (except for beavers), the accumulation of which was caused probably by exhalations of thermal waters or the activity of raptors (predators), have been revised. Gnawed bones of large herbivorous mammals, hunted by humans and large predators (such as cave lions), are evidence of the scavenging of cave hyenas, wolves and possibly bears.

Floral and faunal assemblages

Floral record

The floral fossil record from the site (Text-fig. 2), consisting of leaf imprints in travertine, pollen, seeds and woods, was originally evaluated by Knebllová (1958a, b, 1960, 1961) and later Knebllová-Vodičková (1961). Revision of the Gánovce floral record was based mainly on 570 specimens deposited in the Podtatranské Museum in Poprad. Unfortunately, no more than 20% of the fossil material (mainly *Quercus* sp., *Salix rosmarinifolia*, *Carpinus betulus*, and *Alnus* sp.) was suitable for taxonomic revision, due to the state of preservation.

The oldest findings of plants from basal layers are known only on the basis of the palynological record, which documents a cold steppe vegetation with a prevalence of pine (*Pinus*; approximately 83%), with a relatively developed herbaceous layer with *Artemisia*, *Helianthemum*, *Ephedra*, and other small plants from families Cyperaceae, Poaceae, Chenopodiaceae, Silenaceae, Ranunculaceae, Daucaceae or Asteraceae.

The floral record from the overlaying travertine indicates a climate change without the stratigraphic hiatus from a cold phase through the vegetation optimum to the next cooling. In the early, cold phase of travertine sedimentation, small-leaved willows (*Salix rosmarinifolia* and *S. helvetica*) dominated. Birches (*Betula* cf. *humilis*, *B. carpatica*, *B. pendula*) together with *Vaccinium* cf. *uliginosum* were only poorly presented. The whole assemblage was supplemented by other species (such as *Hippophae rhamnoides* or *Juniperus sabina*) and sporadic occurrence of pines. Climate change connected with the incoming so-called warmer climatic phase (Eemian vegetation optimum) was reflected in increased diversity of plant communities with meadow grasses (*Poa* sp.), willows (*S. cinerea*, *S. caprea*, *S. hastata*), elms (*Ulmus* sp.), oaks (*Quercus petraea* and *Q. robur*), alder buckthorns (*Frangula alnus*), lindens (*Tilia* sp.), hazel (*Corylus avellana*), ashes (*Fraxinus excelsior*), dogwoods (*Cornus mas*), and boxwood (*Buxus sempervirens*). The cold *Pinus-Betula* assemblage was thus replaced by a thermophilous forest, with sporadic occurrence of holly (*Ilex aquifolia*). With gradual cooling, hornbeam (*Carpinus betulus*), maple (*Acer pseudoplatanus*), and elm (*Ulmus* cf. *scabra*) appeared, together with the first firs (*Abies excelsa*), spruces (*Picea abies*), and sporadic alders (*Alnus* sp.).

The overlaying travertine breccia contained only a few remains of *S. rosmarinifolia* and *B. cf. humilis* in some places, accompanied by fossils of spruce needles.

Based on the all palaeobotanical analyses, the complete absence of beech (*Fagus* sp.) can be considered a typical character for the above-mentioned Interglacial floral assemblage(-s) from Gánovce.

Molluscan record

Ložek (1955, 1958) originally described five mollusc assemblages (A to E) from the site. The oldest assemblage A from the most basal level consists only of *Radix balthica*, representing a glacial mollusc element with no stratigraphic importance.



Text-fig. 2. Floral record from the travertine of Gánovce-Hrádok Neanderthal site. a–c) *Salix* L.; d–f) *Quercus* L.; g) *Fraxinus excelsior* L.; h) *Pinus* L.; i) Poaceae, stem of cf. *Poa* sp.; j) *Betula* L.; k) *Salix rosmarinifolia* L., leaf detail; l) *Salix rosmarinifolia* L. All scale bars (except “g”) are 20 mm, for “g” 50 mm.

The following assemblage B (*Stagnicola palustris/turricula*, *Galba truncatula*, *R. balthica*, *Anisus leucostoma*, *Vertigo pygmaea*, *V. genesii*, *Pupilla* cf. *alpicola*, *Vallonia costata*, *V. pulchella*, *Succinella oblonga*, *Oxyloma elegans*, *Euconulus fulvus*) from the unconsolidated travertine sands is a mollusc fauna of calcareous swamps, indicating a tundra environment without a forest in the vicinity of Gánovce during this period.

Taphocoenosis of assemblage C contained index Interglacial mollusc taxa, such as *Soosia diodonta*, *Perforatella dibothryon*, *Pseudalinda stabilis*, *Helicodonta obvoluta*, *Cepaea vindobonensis*, *Helix pomatia*, and *Drobacia banatica*.

Another rich molluscan fauna (assemblage D) from the period of travertine sedimentation subsiding shows a considerable decrease in forest elements, while genera of open habitats (such as *Pupilla* cf. *alpicola*, *Vallonia tenuilabris*, and *V. pulchella*) dominated. However, it indicates an important climate cooling, resembling more climate conditions known today from the Carpathian

highlands (800 to 1,500 m), central Sweden and southern Finland, than glacial climate conditions.

The youngest assemblage E from the overlying layers is similar to loess taphocoenoses. The composition of this molluscan fauna with *Columella columella* indicates conditions of cold subarctic steppe to tundra.

A revision of mollusc finds housed in the Podtatranské Museum in Poprad detected the presence of two Interglacial taxa – *Helix pomatia* (P-14283; originally determined as *Helicigona banatica*) and *Cepaea vindobonensis* (P-14287–14290; originally undetermined) (Text-fig. 3). Fossilised shells of all these re-determined terrestrial snails were found in pieces of compact travertine, coming in all likelihood from petrographic association 2, dated to the Eemian Interglacial Stage.

Non-mammalian vertebrate record

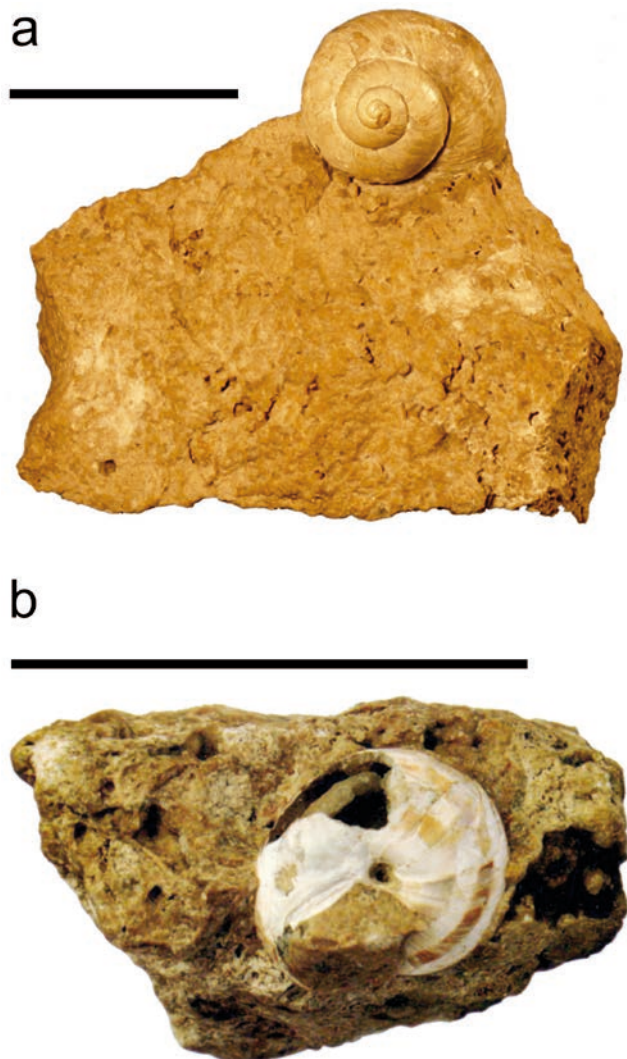
The non-mammalian vertebrate fossil record from Gánovce is documented by remains of **reptiles** and **birds**. Besides the above-mentioned internal core of a shell (NM-Rv 21001) of *Emys orbicularis* sensu lato (see e. g., Štěpánek 1934, Ullrich and Młynarski 1978, Fritz 1995), an unusually well preserved snake skeleton (P-14297) is also now known from the site (Text-fig. 4a–b). It is partly embedded in a firm travertine plate, and consists of skull elements separated from partly articulated vertebral column and ribs. It is determined as *Vipera berus* (Ivanov and Čerňanský 2017). Circumstances of the find indicate a possibility of connecting this fossil record with the latest phase of the sedimentation of petrographic association 2 (firm tabular travertine), dated probably to the Eemian Interglacial; however, Early Weichselian (interstadial) climatic conditions cannot be excluded (e.g., Młynarski and Szyndlar 1989). On the other hand, *Emys orbicularis*, which is a typical member of warm interglacial assemblages (Böhme 1996) is unambiguously connected with the Eemian sedimentation phase of the travertine mound.

Gánovce bird fossils (feather impressions in compact travertine) are also connected with this Interglacial period. Some impressions have already been determined by Petržok (1937, 1939) as *Grus* sp. cf. *cinerea* (an younger synonym of *G. grus*) (probably specimens NM-Rv 21002a and NM-Rv 21002b), whereas the other is so far referred to *Aves* gen. et sp. indet. only (P-14292) (Text-fig. 4c–e).

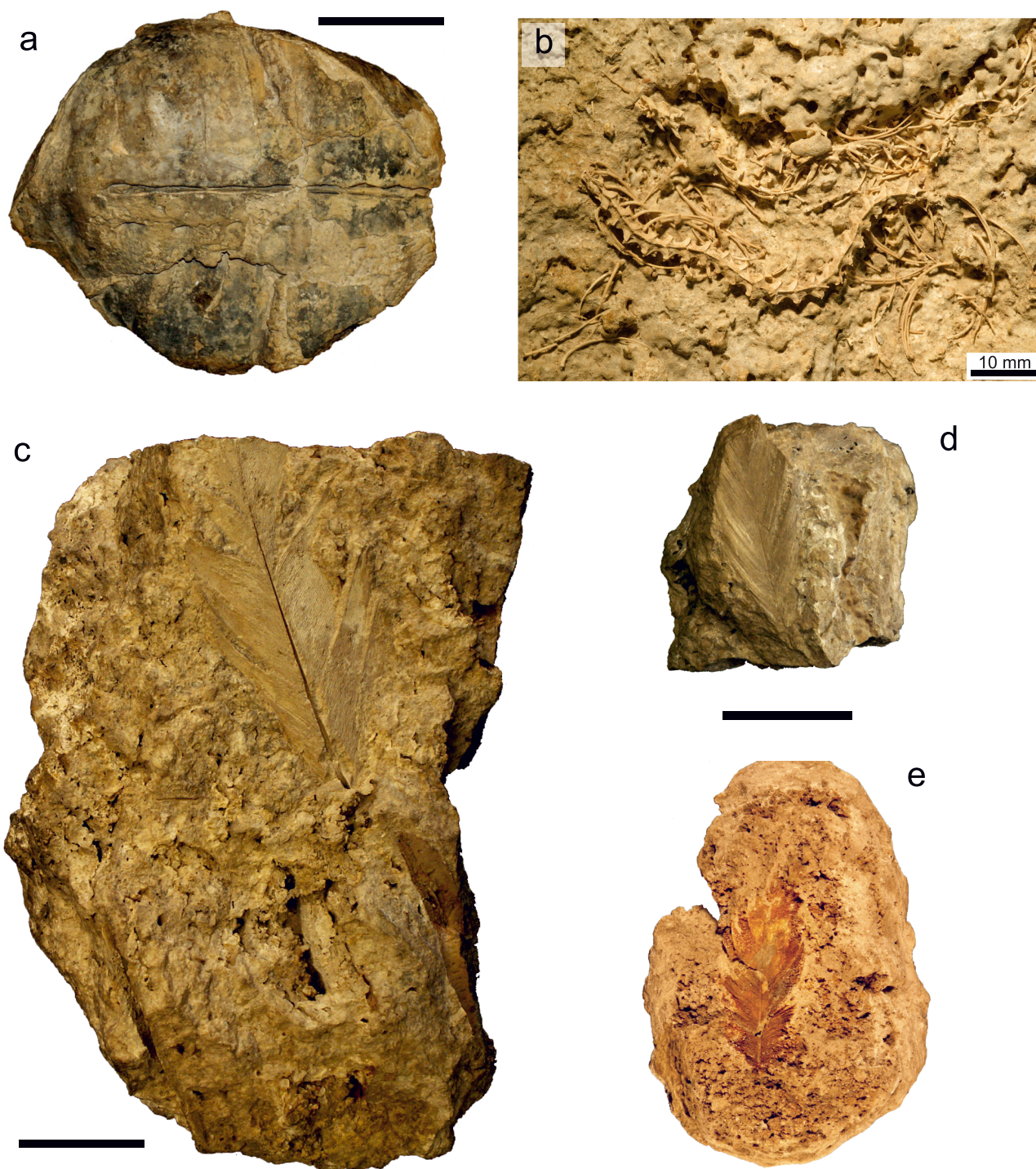
Mammals record

During the re-evaluation of the mammalian fossil record from Gánovce, dental and osteological remains of rodents (beavers), carnivores (felids, hyenids, and ursids), perissodactyls (equids and rhinos), artiodactyls (bovids and cervids), and proboscideans (elephantids) were determined (Text-fig. 5).

Rodents are represented in the revised material by fossil remains of at least three individuals of *Castor fiber* (2 mandible dext. et sin. with incisors and p4–m3 (OF 6664–6665 and OF 6666–6667) (Text-fig. 5a), one fragment of left toothless mandible (without a number), and at least six isolated teeth without numbers (incisor fragments, P4 dext., M1 dext., M3 dext., p4 sin., and m3 dext.), probably connected with the record of mandibles), found in a grey layer (pit I, section E–F) in the overlying of travertine (Last Glacial).



Text-fig. 3. Two re-determined gastropod species from the travertine of Gánovce-Hrádok Neanderthal site in collections of the Podtatranské Museum in Poprad. a) *Helix pomatia* (P-14283); b) *Cepaea vindobonensis* (P-14288). Scale bars 50 mm.



Text-fig. 4. Non-mammalian record from travertine of Gánovce-Hrádok Neanderthal site. a) *Emys orbicularis* s. l. (NM-Rv 21001), internal core of shell in dorsal view; b) *Vipera berus* (P-14297), partly articulated skeleton in dorsal view; c–e) Aves gen. et sp. (c: NM-Rv 21002a, d: NM-Rv 21002b; e: P-14292), feather impressions in travertine. All scale bars (except “b”) are 50 mm, for “b” 10 mm.

The material is relatively homogeneous as to size, and fits into the variability range of *C. fiber*. However, it reaches the upper size limit of recent beavers. From a morphological point of view, the beaver teeth from Gánovce also represent a relatively homogenous sample. The known morphological variability of *C. fiber* is relatively wide, and therefore often causes a different taxonomical interpretation. Some authors

distinguish a subspecies *C. fiber plicidens* on the basis of accessory folds on the enamel (Barisone 2003, Barisone et al. 2006). On the other hand, some others consider this character insufficient for subspecies separation (Mayhew 1979, Stefen 2009, Wessels et al. 2011), indicating only the stage of abrasion (Mayhew 1979). The geographic distribution of *C. fiber plicidens* is limited only to southern Europe (Italy) and

stratigraphically restricted only for the Early Biharian. Fine accessory enamel folds are present in available material from Gánovce only in specimens OF 6666 and OF 6667. Another distinguishing morphological character is the length of striae (folds on inner and outer tooth margin). Some researches (Kretzoi 1977, Heinrich 1989) consider the distance between tooth base and striae base as indicative for relative age determination. The variability of this character has been demonstrated for homogenous recent populations, and depends mainly on ontogeny stage (Stefen 2009). Depéret (1897) described the species *C. praefiber* from Pliocene deposits of Roussillon in France. This identification was subsequently disputed by various authors (Schreuder 1928, Van de Weerd 1978), since the morphological variability of *C. fiber* is quite wide, and unambiguous morphological criteria for the species distinguishing are missing. *C. praefiber* is therefore considered a younger synonym of *C. fiber*. The development of teeth roots in material from Gánovce can be observed only on the isolated M1 dext. Other teeth are rootless. The presence of roots is, however, typical only for individuals older than four year (Stefen 2009). The cross-section of preserved incisors corresponds with the incisor cross-sections of *C. fiber*. Based on the morphological and metric characters, the fossil remains of beavers from Gánovce can be unambiguously attributed to *C. fiber*, and minor morphological differences from recent populations can be interpreted as intraspecific variability.

The **carnivoran guild** in the revised material contains fossils of representatives from three families: Felidae, Hyaenidae, and Ursidae. The felid record consists of imprints of five lumbar vertebrae with typical long transverse processes in travertine, belonging to a big felid (NM-Rv 21003), probably a cave lion (*Panthera* cf. *spelaea*). Their “preservation” in the consolidated rock indicates rather the petrographic association 2 (compact Eemian travertine) than the petrographic association 3 (crumbling Early Weichselian travertine), although the latter is not fully excluded, since Fejfar (1958) reported fossil remains probably belonging to this big felid from Late Eemian to Late Weichselian deposits.

Hyanids are represented in the Gánovce fossil record by six isolated teeth (2 c dext., p2 dext., p3 sin., 2 p4 sin.) of *Crocota crocota spelaea* (P-14304 – P-14309), maybe from earlier fossil collecting at the site. Light tooth crowns, if preserved entirely, are mainly unworn or only slightly worn, indicating young animals (juveniles to sub-adults; MNI = 2). From morphological and metric viewpoints, the teeth fully correspond with characters and metric ranges determined for cave hyenas from the Last Glacial. This may also be supported by circumstances of the find, when hyenid teeth (unlike felid fossil record) were probably found in unconsolidated sediments situated in the overburden of the Eemian compact travertine, and likely connected with petrographic association 3 (more likely) or maybe 4.

Another Last Glacial carnivore fossil from the site is a right mandible fragment with m1 to m3 (stored in the Podtatranské Museum without a number) assigned to cave bear (*Ursus* ex gr. *spelaeus*), probably also found in overlying unconsolidated sediments like hyenid remains (Text-fig. 5b). Although m2 and m3 measurements (m1 is not preserved completely) are in the lower part of the metric range for these types of cave bear teeth, these are

distinctly larger than molars of brown bears. Also from the morphological viewpoint, the found teeth indicate cave bear molars, distinctly differentiated from teeth of brown bears, in spite of the heavy abrasion of their occlusal surface. This abrasion corresponds with the VIth wear stage according to Stiner (1998), indicating an older prime adult individual. The Gánovce ursid record is also supplemented by finds of two endocasts (see below).

All three taxa of carnivores have already been mentioned by Fejfar (1958), who even lists fossil remains of brown bear (*Ursus arctos*), canids (*Canis lupus*, *Vulpes vulpes*, *V. lagopus*), and mustelids (*Mustela* sp., *Mustela (Putorius)* sp., *Meles meles*). Horáček and Sánchez Marco (1984) also mention *Mustela* cf. *nivalis* from the site.

Perissodactyls were represented by two families in the revised material – Equidae and Rhinocerotidae. Equid fossils (left mandible fragment with p3 to m3? (P-14311) in travertine, P3–M3 dext. (P-14302) in travertine, fragment of Mt sin. (OF unnumbered), and skull with broken-off P3–M3 dext. and P2–M3 sin. (NM-Rv 21004) in travertine) have been assigned to *Equus* sp. I and II only (Text-fig. 5d–e), because of their fragmentary preservation or fossilization in compact travertine with no possibility to determine characters on the occlusal surface of teeth or skull. Fejfar (1958) reported three equid taxa (*Equus caballus taubachensis*, *E. caballus germanicus*, and *Asinus* cf. *hydruntinus*) from the site, which were later revised by Musil (1972). He determined only a lesser species from Middle Weichselian deposits (*E. germanicus*) and older horse remains from Interstadial sediments of the Early Weichselian, more similar to equid fossils from Taubach than from Ehringsdorf (*E. cf. taubachensis*). Revised fossils found in the travertine (upper teeth, mandible fragment, and skull probably of young animals, MNI = 2) could be correlated with these remains that were originally attributed by Musil to horses from the *taubachensis*-group and dated to the Eemian/Early Weichselian Period – *Equus* sp. I (cf. *taubachensis*). On the other hand, an isolated record of adult metatarsal fragment from unconsolidated sediments (“grey mud”) could represent a different horse species – *Equus* sp. II (cf. *germanicus*). The dental and osteological finds are accompanied by three endocasts, which probably also belong to horses (Equidae gen. et sp. indet.; see below).

The revised fossil record of rhinoceroses outnumbers the equid remains. It consists of fragmented P3 dext. (OF 6793–6794/4364), fragmented M2 dext. (OF /4364), and fragmented lower right premolar (p3–4?, OF /4364), all from grey mud under the compact travertine (pit PI); p2 sin. (OF unnumbered) from cultural loamy layer of the E–F section in pit I; a slightly worn crown fragment of lower cheek tooth (OF 7196) from grey clay of the E–F section in pit I; the left maxilla fragment with damaged P2 to M1 (NM-Rv 21005) in travertine; two fragments of the juvenile left mandible with p2 (OF 7188; Text-fig. 5c) and two fully unerupted cheek teeth (OF 7187) from grey layer of the E–F section in pit I; two fragments of the left mandible – molar part with roots of cheek teeth (P-14314) and posterior part (P-14316); right mandible fragment with m2 – m3 roots (P-14315); two (cervical?) vertebra and two ribs (P-14279) in travertine; and 28 tooth fragments from at least two (prime adult) upper and one (senile) lower cheek teeth (OF unnumbered)

from cultural loamy layer of the E–F section in pit I. Thus, at least four fossiliferous horizons with the fossil record of rhinoceroses are known from the site. The geologically oldest fossils (P3 dext., M2 dext., and p3–4 dext.; MNI = 1) come from the bottom grey layers dated to the end of the Saalian Glacial Stage. According to Fejfar (1958), these remains are exceptionally rare proof of *Coelodonta antiquitatis* occurrence during the Saalian in the Central European territory. Somewhat younger findings (left maxilla fragment with partly uncovered P2–M1 and vertebra with ribs; MNI = 1) are situated in the compact travertine, and these may correspond with Eemian (petrographic association 2) or Early Weichselian deposits (petrographic association 3). In the case of the stratigraphically former position, these could be assigned to the Merck's rhinoceros ("*Dihoplus kirchbergensis*"), mentioned from Gánovce also by Fejfar (1958) in association with *Palaeoloxodon antiquus*. All remaining revised fossil rhino remains (p2 sin., lower cheek tooth fragment, two fragments of left mandible with teeth, two fragments of toothless left mandible, right mandible fragment with molar roots, and tooth fragments; MNI = 2) probably belong to *Coelodonta antiquitatis* from the Last Glacial, found in the clayey and loamy layers of the overlying unconsolidated deposits (petrographic association 4).

Other unpreserved findings of rhinoceroses (2 maxilla fragments with teeth) are reported from the site by Schmidt (1980).

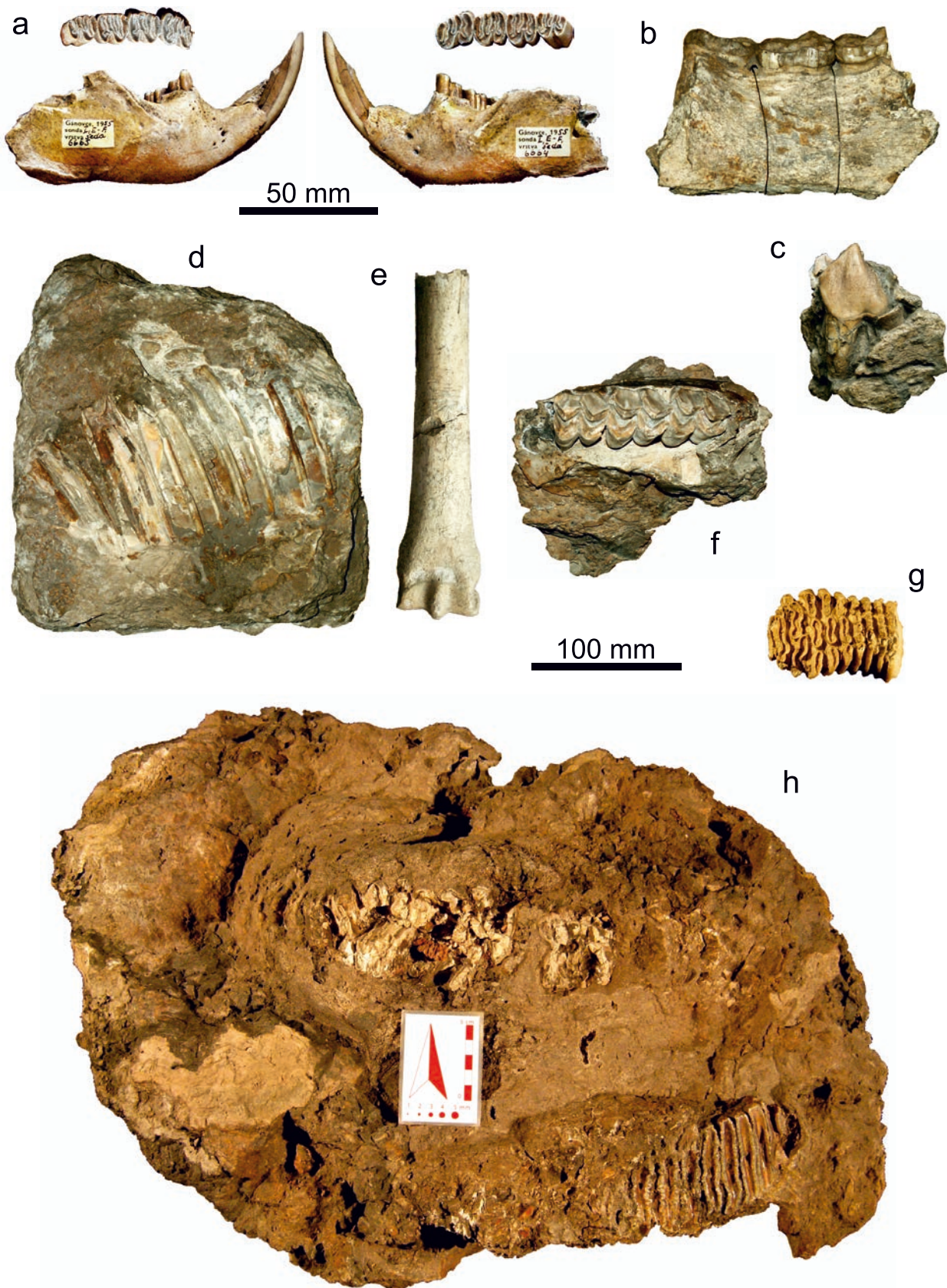
Like perissodactyls, the **artiodactyls** are also represented by two families – Bovidae and Cervidae – in the revised fossil material. The bovid record (MNI = 3) consists only of a left mandible fragment with m1 and m3 (P-14310) in grey compact travertine, and an undetermined fragment of (lower?) jaw with the first two molars (P-unnumbered) in the bone-travertine breccia, accompanied by an endocast (see below). Although Ďurišová assigned the toothed left mandible fragment (P-14310) preliminarily to *Bos primigenius* in unpublished inventory cards of the Podtatranské Museum in Poprad from 1992, the preservation stage of this fossil find (badly damaged, but not very worn teeth, partly covered by the travertine) does not allow a more exact determination. Since the aurochs was not the only large bovid in Central Europe during the Late Pleistocene (another was *Bison priscus*), the fossil remain is classified only as Bovidae gen. et sp. indet. (or *Bos primigenius* seu *Bison priscus* resp., previously also reported by Fejfar (1958) from the site) at the current stage of the revisory study. The same conclusion can be drawn for the unnumbered toothed jaw fragment.

The cervid record is better preserved, and enables determination of at least two taxa – *Alces alces* and Cervidae gen. et sp. indet. The presence of elk at the site was confirmed by the dental record of probably two young adult animals, although the possibility that these dental remains are from only one individual cannot be fully excluded. However, the left maxilla fragment with M1 to M3 and P4 alveolus (P-14303) in travertine (Text-fig. 5f) was found in 1898, whereas the unnumbered right tooth row (P4–M3 dext.) in travertine was labelled in 1906. The upper cheek teeth are larger than the same teeth of *Cervus cervus*, and morphologically different from P4 and upper molars of *Megaloceros giganteus*, especially in the occlusal pattern of P4 and M3, fully corresponding to the morphology of modern

European *Alces alces*. Fejfar (1958) reports the elk fossils from the assemblage C found in the compact travertine from the Eemian Interglacial (petrographic association 2), which could also indicate the stratigraphic position of revised dental remains. Although recent elk populations typically inhabit boreal and temperate broadleaf-mixed forests of the Northern Hemisphere in temperate to subarctic climates, the occurrence of these were recorded also further south, in Georgia, Iran, and Turkey in the past. The fossil remains of elks in Slovakia are also known from Late Eemian to Early Weichselian deposits of the travertine mound near Bojnice (Bojnice III Neanderthal site). The rest of the cervid fossils (antler fragment in travertine (P-14280) and unnumbered, longitudinally split left mandible fragment with deciduous (dp3 and dp4?) and permanent (molar) dentition in travertine) belonged probably to a cervid smaller than elk and so far are determined only as Cervidae gen. et sp. indet. Their connection with the hard grey travertine can indicate the age of these fossils and the possible classification to some of thermophilous cervid species.

A significant part of the large herbivorous mammal remains from the Gánovce site belongs to fossil **elephantids**. Nonetheless, they have not been studied in detail. The majority of elephantid bones and teeth were collected at the end of 19th and the beginning of 20th century, so unfortunately there is no precise taphonomic record. According to the brief report by Fejfar (1958), two elephantid species were determined. The remains of *Palaeoloxodon antiquus* have been found in the mammalian faunal assemblage C, and *Mammuthus primigenius* fossils are known from mammalian faunal assemblages B, D, and E, but without any specific data about the fossil material. Therefore, examination of the lithology (literature data) and the subsequent correlation of a colour, as well as the preservation character of the studied remains were necessary. Several postcranial elements, mainly limb bones, were excavated from various travertine horizons. White to grey bones are damaged on the surface, possibly with gnawing marks in several samples. Some cracks indicate that bones were fractured before the fossilization process. Fossil remains were previously determined by A. Ďurišová in 1992 (unpublished inventory cards of the Podtatranské Museum in Poprad). Methods of measurements and indices (LF – lamellar frequency, HI – hypsodonty index) calculation of teeth follow Lister (1996).

The larger quantity of proboscidean finds belongs to the straight-tusked elephant (*Palaeoloxodon antiquus*). These consist of a palate fragment with M3 dext. et sin. (P-14281; Text-fig. 5h), a proximal fragment of a right humerus (P-14300), a left humerus fragment (P-14278), a right femur (P-14277), a distal fragment of left tibia (P-14276), and two fragments of undetermined long bones (P-14298 and P-14299), originally attributed to a rhinoceros on labels from the 19th/20th centuries. All elephant fossils (apart from undetermined fragments) are situated in blocks of compact travertine, indicating the second petrographic association from the (Late) Eemian Interglacial (MIS 5e). A badly preserved palate (P-14281) with both damaged M3 in situ and isolated, not complete m3 most probably belongs to the same individual. Unfortunately, this lower tooth has been lost and is known only from the publications by Vlček (1953, 1969). Except for the relatively narrow crown – 70 mm (therefore



Text-fig. 5. Fossils of some mammalian taxa from Gánovce-Hrádok Neanderthal site. a) *Castor fiber* – mandible dext. et sin. with incisors and p4 – m3 in lateral (mandible) and occlusal (cheek teeth) views (OF 6664–6665); b) *Ursus ex gr. spelaeus* – right mandible fragment with m1 – m3 in lateral view (P-unnumbered); c) *Coelodonta antiquitatis* – p2 sin. in buccal view (OF 7188); d) *Equus* sp. I (cf. *taubachensis*) – P3 – M3 dext. in travertine, buccal view (P-14302); e) *Equus* sp. II (cf. *germanicus*) – Mt sin. fragment in anterior view (OF unnumbered); f) *Alces alces* – left maxilla fragment with M1 – M3 in occlusal view (P-14303); g) *Mammuthus primigenius* – m2 sin. in occlusal view (P-14312); h) *Palaeoloxodon antiquus* – palate fragment with M3 dext. et sin. in occlusal view (P-14281). 50 mm scale is for a–c, 100 mm scale is for d–h.

it has an unusually high value of HI for m3) and not well marked loxodont patterns, these teeth are morphometrically comparable to the dentition from German Eemian sites Taubach and Burgtona (Guenther 1977, 1978). Also the teeth from Slovakian localities Šaľa, Malé Leváre (Ďurišová 1981, 1984) and Okoč (unpublished) are similar to this m3, but these were collected from poorly dated fluvial sediments.

The remaining proboscidean fossils (molar fragment (m1?; P-14301), m2 sin. (P-14312), m3 dext. (P-14313), tusk fragment (P-14317), and right humerus (P-14282)) are attributed to mammoths (*Mammuthus* sp. and *M. primigenius*). A longitudinally broken anterior part of a tooth, probably m1 (P-14301) of a mammoth is deeply embedded in a greyish brown travertine. It was obviously collected from the bottom of a compact stratified travertine horizon dated to the boundary of the Saalian and the Eemian cold phase (MIS 6–5e). Although incomplete preserved, according to the low LF (7.52) this tooth is rather more primitive than m1 of *M. primigenius* from LGM Moravian site Předmostí (Musil 1968). It is similar to those from the locality Ehringsdorf (MIS 5?) (Guenther 1975), and to the teeth assigned to re-evaluated, but still problematic species *M. intermedius*, characteristic for the end of the Middle Pleistocene (Labe and Guérin 2005). This tooth fragment was originally determined as *Elephas primigenius* (old museum label dated to 1903), but in the museum catalogue (Bekessová 2009) it was erroneously referred to *P. antiquus*. This incomplete molar is tentatively determined as *Mammuthus* sp. nov. Fragmentary, but well preserved m2 (P-14312) of *M. primigenius* has a slightly reddish colour, but it was certainly not found in travertine (Text-fig. 5g). The sediment samples preserved between the lamellas suggest that tooth was found in the overlaying clay soil layer, dated most plausibly to the Weichselian (MIS 5a–4), and thus presumably belongs to the mammalian assemblage E (cold open landscape mammals). According to the LF (8.80) and quite elevate HI (1.79), this m2 is more progressive than those from Ehringsdorf (Guenther 1975), and corresponds to teeth from Předmostí (Musil 1968). On the base of the dental material in mammalian assemblage D, the occurrence of *M. primigenius* is not confirmed. However, regarding several undetermined bone fragments, its presence cannot be ruled out. Incomplete and damaged m3 (P-14313) of *M. primigenius* was most probably collected from the upper loess layer dated to the late part of the Last Glacial. Its precise assignation to mammalian fauna E or F is uncertain. However, the poor state of preservation (entirely different than m2 P-14312) most likely indicates the younger mammalian fauna F. Advanced morphometry of this lower tooth corresponds to *M. primigenius* teeth of the Last Glacial Maximum. Also the right humerus, presumably assigned to *M. primigenius*, was found in an unspecified Weichselian layer. The bone is damaged on the surface, with marks of taphonomic agents – the lateral epicondyle is bitten off and the bone head was probably gnawed by hyenas.

Although the number of taxonomically significant teeth from the Gánovce site is relatively small, they provide important data to the discussion about the Late Pleistocene proboscidean biostratigraphy and evolution. Most probably all fossil material of *Palaeoloxodon antiquus* has been found in travertine of Late Eemian age. Less frequent

mammoth remains were excavated from sediments both before and after this phase. Thus, coexistence of straight-tusked elephants and mammoths at this site is not proven. Only one fragmentary tooth of mammoth (*Mammuthus* sp.) was preserved in travertine (Saalian/Eemian boundary), two more incomplete molars of *M. primigenius* were collected from different Last Glacial sediments. A major turnover in European woolly mammoth evolution occurred earlier, but knowledge concerning the taxonomy of pre- and post-Eemian mammoth populations is still incomplete. These preliminary results require further research, together with the complete re-examination of all proboscidean postcranial elements.

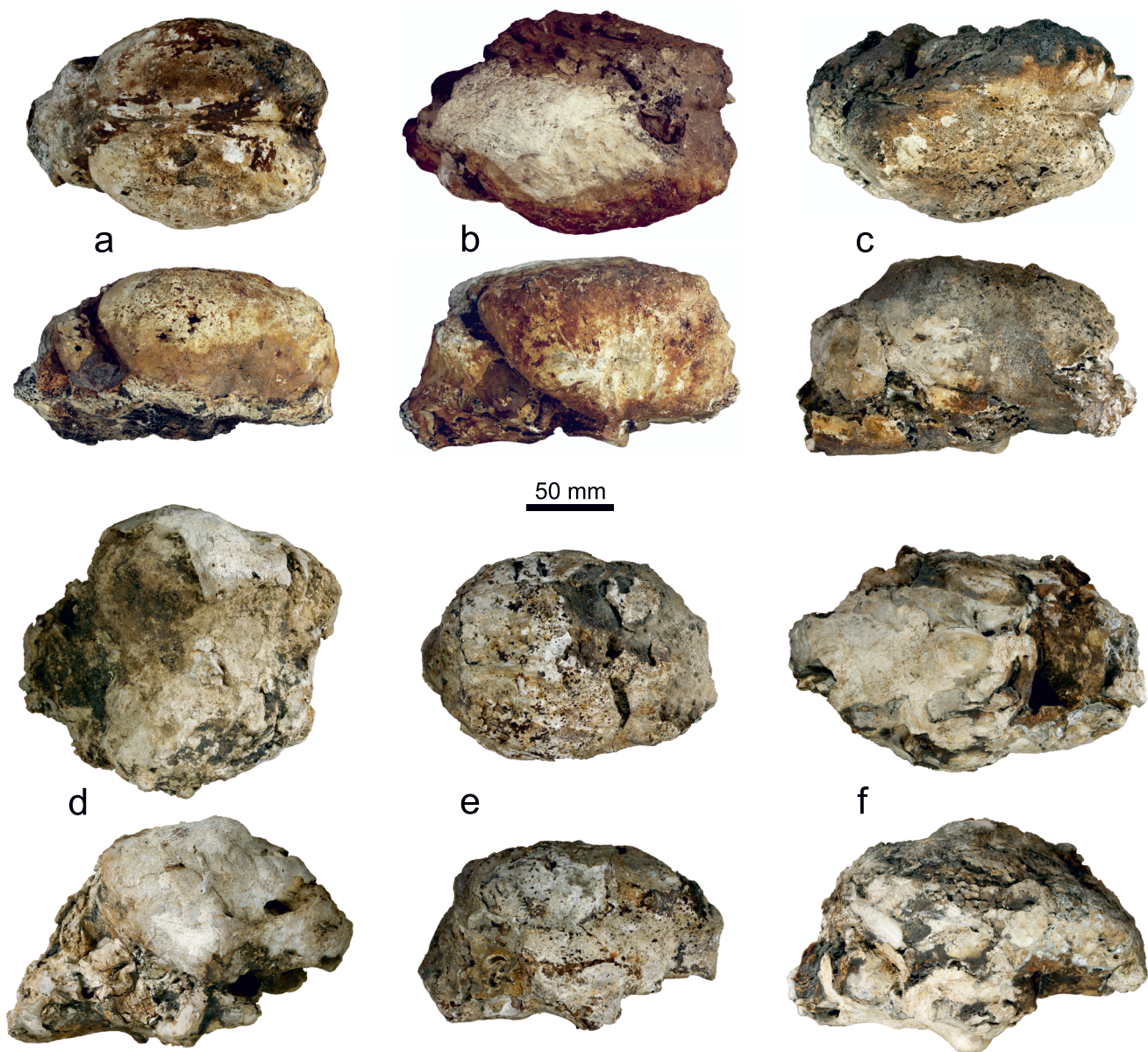
Hominine record

Apart from the important fossil record of Late Pleistocene mammalian assemblages (Fejfar 1958, Musil 1972, Schmidt 1980), a travertine cranial endocast (originally found by gypsy stonemason Koloman Koki and saved by J. Petrbok in 1926, and later determined by E. Vlček), and the long bone casts of *Homo neanderthalensis* are among the most valuable fossil finds at the site. Originally, these were found in a top position of the compact travertine (Vlček 1995), with date about 105,000 years BP (Jäger 1989). Whereas travertine casts of gracile long bones (left radius and fibula) come from a non-adult or gracile adult individual, the endocast probably belonged to an adult female. The cranial capacity reaches approximately 1,320 cm³. From the lateral view, the endocast is markedly low, with a receding forehead and rounded occiput, with typical Neanderthal's occipital bun. Imprints of gyri and dural venous sinuses, and fragments of some skull bones (temporal, parietal, and frontal ones) are also visible on the endocast surface (Thurzo 1998).

Mammalian endocasts

During the revisory research, other mammalian endocasts have also been revised, originally probably collected at the site by J. Petrbok in 1926. Overall, eight endocasts and their fragments have been distinguished among re-studied Gánovce fossils (Text-fig. 6). Most found endocasts are preliminarily assigned to horses (Equidae gen. et sp. indet.), represented by three almost entirely preserved endocranial casts, with well-preserved brain surface structures and adjacent soft tissues (NM-Rv 21006, NM-Rv 21007, NM-Rv 21008). Another ungulate endocast in all likelihood belongs to a big bovid (Bovidae gen. et sp. indet., NM-Rv 21009). It is not as well preserved as the horse endocasts, but basic morphology and shape indicate its preliminary bovid affinity. The carnivore endocast record consists of two, so far most-examined fossils that are determined as endocasts of spelaeoid bears (NM-R 604, NM-Rv 21010), and prepared for more detailed analysis with implications for ursid taxonomy. The remaining two endocranial remains (NM-Rv 21011, NM-Rv 21012) are undetermined endocasts of large mammals in travertine, probably belonging to an ungulate. Based on their fossilisation, all rediscovered endocasts were found in deposits older than the unconsolidated overlying Last Glacial sediments, and are most probably connected with the forming of petrographic association 2 (Eemian) or 3 respectively (Early Weichselian, lesser probable).

The endocast record from the site is still supplemented by a soft tissue cast (medulla oblongata?) of a large mammal.



Text-fig. 6. Fossil endocasts of large mammals from Gánovce-Hrádok Neanderthal site. a) Equidae gen. et sp. indet. (NM-Rv 21008); b) Equidae gen. et sp. indet. (NM-Rv 21007); c) Equidae gen. et sp. indet. (NM-Rv 21006); d) Bovidae gen. et sp. indet. (NM-Rv 21009); e) *Ursus* ex gr. *spelaeus* (NM R-604); f) *Ursus* ex gr. *spelaeus* (NM-Rv 21010); lateral and dorsal (except for f: ventral) views; lateral view for d and f are inverted.

Biostratigraphic and Palaeoecological implications

Based on petrographic and palaeontological data from previous researches of the site (Štěpánek 1934, Ložek 1955, Fejfar 1958, Kukla 1958, Prošek 1958, Kneblová 1958b, 1960, Vlček 1969, Musil 1972, Horáček and Sánchez Marco 1984) in connection with the revised fossil findings (in bold), the following stratigraphic and palaeoecological scheme can be summarized (Tab. 1):

1) Late Saalian Glacial Stage (MIS 6?)

The oldest horizon consists of underlying layers of grey travertine sands, marls and clays affected by cryoturbation

with fossil elements indicating an open landscape (steppe to tundra environment) with the cold climate.

Palaeobotanical record: *Pinus* sp., *Artemisia* sp., *Helianthemum* sp., *Ephedra* sp., Cyperaceae indet., Poaceae indet., Chenopodiaceae indet., Silenaceae indet., Ranunculaceae indet., Daucaceae indet., and Asteraceae indet.

Molluscan assemblage A and B: *Stagnicola palustris/turricula*, *Galba truncatula*, *Radix balthica*, *Anisus leucostoma*, *Vertigo pygmaea*, *V. genesii*, *Pupilla* cf. *alpicola*, *Vallonia costata*, *V. pulchella*, *Succinella oblonga*, *Oxyloma elegans*, *Euconulus fulvus*, and *Pisidium* cf. *casertanum*.

Vertebrate assemblage A: *Mustela* sp. and *Coelodonta antiquitatis*.

2) Eemian Interglacial (MIS 5e)

During the Last Interglacial period, a hard, compact, stratified grey travertine with occasional marl intercalations was deposited. Found floral and faunal remains indicate a climate change without the stratigraphic hiatus from a colder phase through the vegetation optimum to the next cooling. From palaeoenvironmental and palaeoclimatic views, the cold *Pinus-Betula* assemblage was replaced by thermophilous forest, which was finally replaced by assemblage with elements adapted more to gradual cooling.

Palaeobotanical record (cold phase): *Salix rosmarinifolia*, *S. helvetica*, *Betula* cf. *humilis*, *B. carpatica*, *B. pendula*, *Vaccinium* cf. *uliginosum*, *Hippophae rhamnoides*, and *Juniperus sabina*.

Palaeobotanical record (Eemian vegetation optimum): *Poa* sp., *Salix cinerea*, *S. caprea*, *S. hastata*, *Ulmus* sp., *Quercus petraea*, *Q. robur*, *Frangula alnus*, *Tilia* sp., *Corylus avellana*, *Fraxinus excelsior*, *Cornus mas*, *Buxus sempervirens*, and *Ilex aquifolia*.

Palaeobotanical record (final cooling phase): *Carpinus betulus*, *Acer pseudoplatanus*, *Ulmus* cf. *scabra*, *Abies excelsa*, *Picea abies*, and *Alnus* sp.

Molluscan assemblage C: *Cochlicopa lubricella*, *Vallonia costata*, *Ena montana*, *Succinella oblonga*, *Punctum pygmaeum*, *Discus ruderratus*, *D. rotundatus*, *Aegopinella nitens/minor*, *Vitrea diaphana*, *Limacidae* sp. div., *Euconulus fulvus*, *Cochlodina orthostoma*, *C. cerata*, *C. laminata*, *Clausilinae* sp., *Pseudalinda stabilis*, *Fruticicola fruticum*, *Monachoides incarnatus*, *M. vicinus*, *Perforatella dibothryon*, *Euomphalia strigella*, *Helicodonta obvoluta*, *Soosia diodonta*, *Drobacia banatica*, *Isognomostoma isognomostoma*, *Cepaea vindobonensis*, and *Helix pomatia*.

Vertebrate assemblage B (cold phase): *Mammuthus* sp.

Vertebrate assemblage C (Eemian optimum): *Emys orbicularis*, *Aves* gen. et sp. indet. (incl. cf. *Grus cinerea*), *Microtus arvalis-agrestis*, *Ursus arctos*, *Panthera* cf. *spelaea*, *Palaeoloxodon antiquus*, “*Dihoplus*” *kirchbergensis*, *Capreolus capreolus*, and *Alces alces*. This assemblage indicates a woodland with typical forest species, such as *Palaeoloxodon antiquus*, “*Dihoplus*” *kirchbergensis*, and cervids.

Vertebrate assemblage D (final cooling phase): *Vipera berus*, *Aves* gen. et sp. indet., *Talpa europaea*, *Homo neanderthalensis*, *Lepus* sp., *Castor fiber*, *Arvicola amphibius*, *Microtus subterraneus*, *M. arvalis-agrestis*, *M. oeconomus*, *Canis lupus*, *Vulpes vulpes*, *Ursus ex gr. spelaeus*, *Panthera* cf. *spelaea*, *Mustela (Putorius) sp.*, *Meles meles*, *Crocota crocota spelaea*, *Mammuthus primigenius*, *Equus* sp. I (cf. *taubachensis*), *Equidae* gen. et sp. indet., *Asinus* cf. *hydruntinus*, *Coelodonta antiquitatis*, *Cervus elaphus*, *Bison priscus*, *Bos primigenius*, and *Bovidae* gen. et sp. indet.

It is not fully excluded that this rich vertebrate assemblage does not belong to the Late Eemian, but may correspond to Early Weichselian interstadials (MIS 5d–b?).

3) “Early” Weichselian (MIS 5d–3)

Younger, crumbling travertine to travertine breccia with soil layers deposited in the overburden of the Eemian compact travertine contains abundant molluscan fauna, together with remains of mammals and plants. The fossil

record from this sequence of the travertine mound formation document a cooler climate, in comparison to the interglacial maximum, and probably represents a Weichselian period before the LGM. The number of forest elements decreased and taxa of open habitats began to dominate.

Palaeobotanical record: *Salix rosmarinifolia*, *Betula* cf. *humilis*, and *Picea* sp.

Molluscan assemblage D: *Carychium minimum*, *C. tridentatum*, *Stagnicola palustris/turricula*, *Galba truncatula*, *Radix balthica*, *Anisus leucostoma*, *Cochlicopa lubricella*, *Cochlicopa* sp., *Truncatellina cylindrica*, *Vertigo angustior*, *V. pusilla*, *V. antivertigo*, *V. pygmaea*, *V. alpestris*, *Pupilla muscorum*, *P.* cf. *alpicola*, *Vallonia costata*, *V. pulchella*, *V. excentrica*, *V. tenuilabris*, *Succinella oblonga*, *Oxyloma elegans*, *Punctum pygmaeum*, *Discus ruderratus*, *Nesovitrea hammonis*, *Aegopinella nitens/minor*, *Oxichylus depressus*, *Vitrea crystallina*, *Zonitoides nitidus*, *Euconulus fulvus*, *Cochlodina cerata*, *Clausillia pumila*, *Fruticicola fruticum*, *Monachoides vicinus*, and *Euomphalia strigella*.

Vertebrate assemblage E: *Aves* gen. et sp. indet., *Talpa europaea*, *Sorex* cf. *araneus*, *Crocidura* cf. *suaveolens*, *C. gr./cf. russula*, *Lepus* sp., *Castor fiber*, *Citellus citelloides*, *Cricetus cricetus*, *Arvicola amphibius*, *Microtus subterraneus*, *M. arvalis*, *M. cf. agrestis*, *M. oeconomus*, *Canis lupus*, *Vulpes vulpes*, *Ursus ex gr. spelaeus*, *Panthera* cf. *spelaea*, *Mustela* cf. *nivalis*, *Mustela (Putorius) sp.*, *Meles meles*, *Crocota crocota spelaea*, *Mammuthus primigenius*, *Equus* sp. II (cf. *germanicus*), *Asinus* cf. *hydruntinus*, *Coelodonta antiquitatis*, *Cervus elaphus*, *Bison priscus*, *Bos primigenius*, and *Bovidae* gen. et sp. indet.

The fairly monotonous occurrence of micromammals in assemblages D and E is probably a result of either the inorganic origin of their accumulation (by exhalations) or the activity of raptors (predators). Mammalian taxa of both these assemblages indicate an open landscape with sporadic occurrence of open forest surrounding the site. The occurrence of beavers is also interesting. These are semi-aquatic animals, inhabiting larger water sources with well-developed bank woods that form an important component of their food.

4) “Late” Weichselian (MIS 2)

This phase of the travertine mound formation consists of Last Glacial sediments (soil, loess layer, stony-sandy clay) with fragments of travertine. Found remains of cold steppe to tundra mammalian, and molluscan species indicate subarctic climatic and environmental conditions of LGM. No floral fossils are known from this horizon.

Molluscan assemblage E: *Stagnicola palustris/turricula*, *Galba truncatula*, *Radix balthica*, *Anisus leucostoma*, *Cochlicopa lubrica*, *Columella columella*, *Pupilla triplicata*, *P. muscorum*, *P.* cf. *alpicola*, *Vallonia costata*, *V. pulchella*, *Succinella oblonga*, *Oxyloma elegans*, *Punctum pygmaeum*, *Nesovitrea hammonis*, *Aegopinella nitens/minor*, *Trochulus hispidus*, and cf. *Arianta arbustorum*.

Vertebrate assemblage F and G: *Aves* gen. et sp. indet., *Dicrostonyx torquatus*, *Microtus oeconomus*, *M. gregalis*, *Vulpes lagopus*, *Panthera* cf. *spelaea*, *Equus germanicus*, *Coelodonta antiquitatis*, *Rangifer tarandus*, and *Bovidae* gen. et sp. indet. These assemblages, with the presence of reindeer and a small form of horse are typical for a subarctic steppe up to steppe-tundra habitat.

Table 1. Correlation stratigraphic scheme of the Gánovce-Hrádok Neanderthal site (data source: Ložek 1955, Fejfar 1958, Kukla 1958, Kneblová 1960).

GEOLOGICAL AGE	MIS	PETROLOGY	FLORA	MOLLUSCS	VERTEBRATES	REVISED RECORD	CLIMATE
Holocene (< 11.7 ka)	MIS 1	Petrographic Association 5					warm
Weichselian (115–11.7 ka)	MIS 2	Petrographic Association 4		Assemblage E	Assemblage G Assemblage F	<i>Coelodonta antiquitatis</i>	LGM
	MIS 5d–3	Petrographic Association 3	<i>Salix-Betula-Picea</i> Assemblage	Assemblage D	Assemblage E	<i>Castor fiber</i> , <i>Ursus ex gr. spelaeus</i> , <i>Crocota crocuta spelaea</i> , <i>Mammuthus primigenius</i> , <i>Equus</i> sp. II, <i>Coelodonta antiquitatis</i>	cold
Eemian (130–115 ka)	MIS 5e	Petrographic Association 2	<i>Carpinus-Acer-Ulmus-Abies-Picea</i> Assemblage	Assemblage C	Assemblage D	<i>Vipera berus</i> , <i>Ursus ex gr. spelaeus</i> , <i>Equus</i> sp. I, Equidae indet., Bovidae indet.; <i>Helix pomatia</i> , <i>Cepaea vindobonensis</i> , <i>Emys orbicularis</i> , <i>Aves</i> indet., <i>Panthera</i> cf. <i>spelaea</i> , <i>Palaeoloxodon antiquus</i> , " <i>Dihoplus</i> " <i>kirchbergensis</i> , <i>Alces alces</i> ;	Eemian final cooling phase
			Thermophilous forest Assemblage		Assemblage C	<i>Helix pomatia</i> , <i>Cepaea vindobonensis</i> , <i>Emys orbicularis</i> , <i>Aves</i> indet., <i>Panthera</i> cf. <i>spelaea</i> , <i>Palaeoloxodon antiquus</i> , " <i>Dihoplus</i> " <i>kirchbergensis</i> , <i>Alces alces</i> ;	Eemian climatic optimum
			<i>Salix-Betula</i> Assemblage		Assemblage B	<i>Mammuthus</i> sp.	Eemian "cold" phase
Late Saalian (> 130 ka)	MIS 6?	Petrographic Association 1	<i>Pinus</i> Assemblage with herbaceous layer	Assemblage B Assemblage A	Assemblage A	<i>Coelodonta antiquitatis</i>	cold

5) Holocene (MIS 1)

The youngest horizon is formed by Holocene soils, with archaeological artefacts from the Neolithic up to the Slavic Period. It covers the travertine heap, where remnants of medieval fortification were once situated. According to data from the period before the travertine exploitation, the Gánovce mound was fortified by ramparts. The climatic and environmental conditions were similar to congruent with present-day ones.

Conclusion

During the revisory research of the fossil record from the Neanderthal site of Gánovce-Hrádok, single floral and animal assemblages were once again studied and evaluated from biostratigraphic and palaeoenvironmental points of view. Moreover, the occurrence of at least two species of land snails (*Cepaea vindobonensis* and *Helix pomatia*) and approximately 20 taxa of vertebrates (*Emys orbicularis* s. l., *Vipera berus*, cf. *Grus cinerea*, *Aves* gen. et sp. indet., *Castor fiber*, *Panthera* cf. *spelaea*, *Crocota crocuta spelaea*, *Ursus ex gr. spelaeus*, *Equus* sp. I (cf. *taubachensis*), *Equus* sp. II (cf. *germanicus*), Equidae gen. et sp. indet., cf. "*Dihoplus*" *kirchbergensis*, *Coelodonta antiquitatis*, *Bos primigenius* seu *Bison priscus*, Bovidae gen. et sp. indet., *Alces alces*, Cervidae gen. et sp. indet., *Palaeoloxodon antiquus*, *Mammuthus* sp., and *M. primigenius*) was confirmed in museum collections, attended by restudy of eight mammalian endocasts. These are preliminarily assigned to ursids, horses and bovids.

The research also confirmed the previous stratigraphic division of the travertine mound into five horizons on the basis of different petrological and palaeontological contents, mirroring climatic and palaeoenvironmental changes from

the Saalian termination through the Eemian Interglacial, and the Weichselian Glacial up to the Holocene.

A more exact determination of some species and the exact position of vertebrate assemblage D are still open, needing a more detailed study and comparison with close relative forms and data from the same periods for specification of such information.

Acknowledgements

Research for this paper was carried out with financial support from the Grant Agency of the Slovak Ministry of Education (VEGA 1/0080/16) and the Slovak Research and Development Agency (APVV-16-0121). The research was also financially supported by the Ministry of Culture of the Slovak Republic and Central Slovakia Museum in Banská Bystrica. The authors thank to D. Mlynárčiková and M. Bekessová (Podtatranské Museum in Poprad), J. Wagner (National Museum in Prague), M. Hyžný (Comenius University in Bratislava), A. Ďurišová (Slovak National Museum – Natural History Museum in Bratislava), R. Hradecký and E. Martincová (Central Slovakia Museum in Banská Bystrica) for the contribution to this study, as well as to M. Poljak for taking photos of plant fossils.

References

Barisone, G. (2003): Neogene and Quaternary *Castor* (Castoridae, Rodentia) of Central and Western Europe: systematics, palaeobiogeography and patterns of evolution; Ph.D. Thesis. – MS, University Roma Tre, Italy, 153 pp. (copy in library of the Università degli Studi Roma Tre, Rome)

- Barisone, G., Argenti, P., Kotsakis, T. (2006): Plio-Pleistocene evolution of the genus *Castor* (Rodentia, Mammalia) in Europe: *C. fiber plicidens* of Pietrafitta (Perugia, Central Italy). – *Geobios*, 39(6): 757–770. <https://doi.org/10.1016/j.geobios.2005.10.004>
- Bekessová, M. (ed.) (2009): Gánovce nálezisko neandertálskeho človeka a jeho životné prostredie. Katalóg špecializovanej expozície 1969 – 2009 [Gánovce site of Neanderthal man and his environment. Catalogue for specialized exposition 1969 – 2009]. – Podtatranské múzeum v Poprade, Poprad, 64 pp. (in Slovak)
- Böhme, G. (1996): Zur historischen Entwicklung der Herpetofaunen Mitteleuropas im Eiszeitalter (Quartär) [On the historical development of the Herpetofauna of Central Europe in the Ice Age (Quaternary)]. – In: Günther, R. (ed.), *Die Amphibien und Reptilien Deutschlands*. Gustav Fischer Verlag, Jena, pp. 30–39.
- Depéret, Ch. (1897): Animaux pliocènes de Roussillon [Pliocene animals of Roussillon]. – *Mémoires de la Société géologique de France*, 4(7): 165–194.
- Ďurišová, A. (1981): *Palaeoloxodon antiquus* (Falconer et Cautley, 1847) z Malých Levár [Palaeoloxodon antiquus (Falconer et Cautley, 1847) from Malé Leváre]. – *Acta Rerum Naturalium Musei Nationalis Slovaci*, 27: 3–10. (in Slovak)
- Ďurišová, A. (1984): Nálezy slonovitých chobotnáčov v mladopleistocénnej terase rieky Moravy pri Malých Levároch, okres Senica [Elephantid finds in the Late Pleistocene terrace of Morava River near Malé Leváre, Senica District]. – *Acta Rerum Naturalium Musei Nationalis Slovaci*, 30: 7–26. (in Slovak)
- Fejfar, O. (1958): Die fossilen Säuger aus den Travertinen in Gánovce bei Poprad [Fossil mammals from travertine in Gánovce near Poprad]. – In: Vlček, E. (ed.), *Zusammenfassender Bericht über den Fundort Gánovce und die Reste des Neandertalers in der Zips (ČSR)*. Archeologický ústav ČSAV, Praha, pp. 50–52.
- Fritz, U. (1995): Kritische Übersicht der Fossilgeschichte der Sumpfschildkröten-Gattung *Emys* A. Duméril, 1806 [Critical review of the fossil history of the tortoise genus *Emys* A. Duméril, 1806]. – *Zoologische Abhandlungen, Staatliches Museum für Tierkunde Dresden*, 48: 243–264.
- Gunther, E. W. (1975): Die Backenzähne der Elefanten von Ehringsdorf bei Weimar [The molars of elephants from Ehringsdorf near Weimar]. – *Abhandlungen des Zentralen Geologischen Instituts, Paläontologische Abhandlungen*, 23: 399–452.
- Gunther, E. W. (1977): Die Backenzähne der Elefanten von Taubach bei Weimar [The molars of elephants from Taubach near Weimar]. – *Quartärpaläontologie*, 2: 265–304.
- Gunther, E. W. (1978): Die Elefantenmolaren aus den Travertinen von Burgtonna in Thüringen [The molars of elephants from travertine in Burgtonna in Thuringia]. – *Quartärpaläontologie*, 3: 139–150.
- Heinrich, W.-D. (1989): Biometrische Untersuchungen an Fossilresten des Bibers (*Castor fiber* L.) aus thüringischen Travertinen [Biometric research on fossil remains of beaver (*Castor fiber* L.) from Thuringian travertine]. – *Ethnographisch-Archäologische Zeitschrift*, 30: 394–403.
- Horáček, I., Sánchez Marco, A. (1984): Comments on Weichselian small mammal assemblages in Czechoslovakia and their stratigraphic interpretation. – *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1984(9): 560–576.
- Ivanov, M., Čerňanský, A. (2017): *Vipera berus* (Linnaeus, 1758) remains from the Late Pleistocene of Slovakia. – *Amphibia-Reptilia*, 38(2): 133–144. <https://doi.org/10.1163/15685381-00003095>
- Jäger, K.-D. (1989): Aussagen und Probleme radiometrischer Untersuchungen zur Datierung des Travertins von Bilzingsleben (Kreis Artern) [Statements and problems of radiometric investigations on the dating of travertine in Bilzingsleben]. – *Ethnographisch-Archäologische Zeitschrift*, 30: 664–672.
- Kaminská, Ľ. (2014): Staré Slovensko 2 – Paleolit a mezolit [Ancient Slovakia 2 – Palaeolithic and Mesolithic Age]. – AÚ SAV, Nitra, 366 pp. (in Slovak)
- Kneblová, V. (1958a): Die paläobotanische Erforschung der Travertine des «Hrádok» in Gánovce [Palaeobotanic exploration of “Hrádok” travertine in Gánovce]. – In: Vlček, E. (ed.), *Zusammenfassender Bericht über den Fundort Gánovce und die Reste des Neandertalers in der Zips*. Archeologický ústav ČSAV, Praha, pp. 45–49.
- Kneblová, V. (1958b): Flora interglacialnych trawertynów w Ganowciach [Flora of the Interglacial travertine in Gánovce]. – *Acta Biologica Cracoviensis, Ser. Botanica*, 1: 1–4. (in Polish)
- Kneblová, V. (1960): Paleobotanický výzkum interglaciálních travertínů v Gánovcích [Palaeobotanical research of Interglacial travertine in Gánovce]. – SAV, Bratislava, 42 pp. (in Czech)
- Kneblová, V. (1961): Die paläobotanische Erforschung der Travertine der „Hrádok“ in Gánovce [Palaeobotanical research of travertine in Gánovce]. – In: *Die Pflanzenwelt der Tschechoslowakei. Ergebnisse der 12. Internationalen Pflanzengeographischen exkursion (IPE) durch die Tschechoslowakei 1958*. Veröffentlichungen des Geobotanischen Institutes der Eidg. Tech. Hochschule, Stiftung Rübel, in Zürich, 36: 164–170.
- Kneblová-Vodičková, V. (1961): Flora – Survey of Czechoslovak Quaternary. – *Czwartorzęd Europy Środkowej i Wschodniej, Warszawa*, 34: 125–132.
- Kretzoi, M. (1977): Die *Castor*-Reste aus den Travertinen von Taubach bei Weimar [Remains of *Castor* from travertine of Taubach near Weimar]. – *Quartärpaläontologie*, 2: 398–400.
- Kukla, J. (1958): Předběžné výsledky petrografického výzkumu travertínů na Hrádku v Gánovcích [Preliminary results of the petrographic research of the travertine in Gánovce-Hrádok]; Preliminary report. – MS. (in Czech) (copy in library of Institute of Archaeology of the CAS, Prague, v. v. i.)
- Labe, B., Guérin, C. (2005): Rehabilitation de *Mammuthus intermedius* (Jourdan, 1861), un mammoth (Mammalia, Elephantidae) du Pleistocene moyen recent d'Europe [Rehabilitation of *Mammuthus intermedius* (Jourdan, 1861), a mammoth (Mammalia, Elephantidae) of the Middle Pleistocene Europe]. – *Comptes Rendus Palevol*, 4(3): 235–242. <https://doi.org/10.1016/j.crpv.2005.01.001>

- Lister, A. M. (1996): Evolution and taxonomy of Eurasian mammoths. – In: Shoshani, J., Tassy, P. (eds), *The Proboscidea*. Oxford University Press, Oxford, pp. 203–213.
- Ložek, V. (1955): Měkkýši pleistocenních travertinů v Gánovcích [Molluscs of Pleistocene travertine in Gánovce]. – *Anthropozoikum*, 4(1954): 91–165. (in Czech with Russian and German summary)
- Ložek, V. (1958): Malakologické novinky z Československa IV [Malacological news from Czechoslovakia IV]. – *Časopis Národního Múzea (Praha), oddíl přírodovědný*, 127(2): 120–131. (in Czech with German summary)
- Mayhew, D. F. (1979): Evolution of a dental character in beaver *Castor fiber* L. (Mammalia: Rodentia). – *Zoological Journal of the Linnean Society*, 65: 177–184. <https://doi.org/10.1111/j.1096-3642.1979.tb01089.x>
- Młynarski, M., Szyndlar, Z. (1989): Plazy i gady – Amphibia et Reptilia [Amphibians and reptiles – Amphibia et Reptilia]. – In: Kowalski, K. (ed.), *Historia i ewolucje lądowej fauny Polski. Folia Quaternaria*, 59-60: 69–88. (in Polish)
- Musil, R. (1968): Die Mammutmolaren von Předmostí [Mammoth molars from Předmostí]. – *Paläontologische Abhandlungen, Abteilung A, Paläozoologie*, 3(1): 1–198.
- Musil, R. (1972): Die Pferdenähne aus der Lokalität Gánovce [Horse teeth from Gánovce site]. – *Acta Musei Moraviae*, 56-57: 139–146.
- Petrbok, J. (1937): Ptačí pero z doby ledové na Slovensku [A bird feather from the Ice Age in Slovakia]. – *Národní politika*, 28.8.1937. (in Czech)
- Petrbok, J. (1939): Jeřáb (*Grus* sp. cf. *cinerea* Bechst) v riss-würmienských travertinech na Slovensku. [Crane (*Grus* sp. cf. *cinerea* Bechst) from Riss-Würmian travertines in Slovakia]. – *Příroda*, 32(1): 42. (in Czech)
- Prošek, F. (1958): Stratigraphie und Altersstellung des Fundes von Gánovce [Stratigraphy and former position of finds from Gánovce]. – In: Vlček, E. (ed.), *Zusammenfassender Bericht über den Fundort Gánovce und die Reste des Neandertalers in der Zips (ČSR)*. Archeologický ústav ČSAV, Praha, pp. 43–45.
- Schmidt, Z. (1980): Fosílné nepárnokopytníky (Perissodactyla) Slovenska – Rhinocerotidae [Fossil perissodactyls (Perissodactyla) of Slovakia – Rhinocerotidae]; Čiastková záverečná správa [Partial final report]. – MS, Geologický ústav Dionýza Štúra, Bratislava, Slovak Republic, 94 pp. (in Slovak) (copy in library of the Geofond, Bratislava)
- Schreuder, A. (1928): *Castor praefiber* Depéret in der Fauna von Roussillon [*Castor praefiber* Depéret in fauna from Roussillon]. – *Paläontologische Zeitschrift*, 9(4): 374–378. <https://doi.org/10.1007/BF03041563>
- Stefen, C. (2009): Intraspecific variability of beaver teeth (Castoridae: Rodentia). – *Zoological Journal of the Linnean Society*, 155: 926–936. <https://doi.org/10.1111/j.1096-3642.2008.00467.x>
- Stiner, M. (1998): Mortality analysis of Pleistocene bears and its paleoanthropological relevance. – *Journal of Human Evolution*, 34: 303–326. <https://doi.org/10.1006/jhev.1997.0198>
- Štěpánek, O. (1934): Pleistocenní želva bahenní (*Emys orbicularis* L.) z travertinů v Gánovcích [Pleistocene European pond turtle (*Emys orbicularis* L.) from travertine in Gánovce]. – Bratislava, 8: 216–219. (in Slovak)
- Thurzo, M. (1998): Evolúcia človeka [Evolution of Man]. – Univerzita Komenského, Bratislava, 108 pp. (in Slovak)
- Ullrich, H. v., Młynarski, M. (1978): Reptilienreste aus dem Jungpleistozänen Travertin von Burgtonna in Thüringen [Reptile remains from Late Pleistocene travertine of Burgtonna in Thuringia]. – *Quartärpaläontologie*, 3: 97–102.
- Van de Weerd, A. (1978): Early Ruscinian rodents and lagomorphs (Mammalia) from lignites near Ptolemais (Macedonia, Greece). – *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. B*, 82(2): 127–170.
- Vlček, E. (1953): Lesní slon v Gánovcích na Slovensku [Forest elephant from Gánovce in Slovakia]. – *Vesmír*, 32(2): 47. (in Czech)
- Vlček, E. (1956): Záznam o paleontologickej komisii v Gánovciach dňa 10. X. 1956 [Report on the Palaeontological Commission in Gánovce, 10th of October, 1956]. – *Štúdijské zvesti AÚ SAV*, 1: 80–81. (in Slovak)
- Vlček, E. (ed.) (1958): Zusammenfassender Bericht über den Fundort Gánovce und die Reste des Neandertalers in der Zips (ČSR) [Comprehensive report on the locality of Gánovce and the remnants of Neanderthals in the Spiš (ČSR)]. – Archeologický ústav ČSAV, Praha, 81 pp.
- Vlček, E. (1959): Mezinárodní komise o nálezu neandertálskeho človeka v Gánovcích na Slovensku [International Commission on Neanderthal Man record from Gánovce in Slovakia]. – *Archeologické rozhledy*, 11: 361–370, 377–378. (in Czech)
- Vlček, E. (1961): K paleohistologickému vyšetření paleontologických nálezů z travertinů v Gánovcích [On the palaeohistological examination of palaeontological finds from travertine in Gánovce]. – *Anthropos*, 14: 139–140. (in Czech)
- Vlček, E. (1969): Neandertaler der Tschechoslowakei [Neanderthals of Czechoslovakia]. – *Academia*, Prag, 276 pp.
- Vlček, E. (1995): Kamenný mozek. Výlitek mozkovny neandertálce, Hrádok v Gánovcích na Spiši [Stone brain. A Neanderthal endocast, Gánovce-Hrádok in Spiš area]. – *Vesmír*, 74(11): 615–624. (in Czech)
- Wessels, W., Frieling, J., Fraaije, R. (2011): The oldest beaver from the Netherlands. – *Netherlands Journal of Geosciences*, 90(4): 311–314. <https://doi.org/10.1017/S0016774600000603>