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Miocene crocodylian and marine turtle from Kienberg: First record from the Moravian part of the Vienna Basin

JAKUB BŘEZINA[1,✉], MILAN CHROUST[2],
TOMASZ SZCZYGIELSKI[2] and VLADIMÍR HRAZDIL[3]

[1]Moravian Museum, Department of Geology and Paleontology, Zelný trh 6, 659 37 Brno, Czech Republic
[2]Polish Academy of Sciences, Institute of Paleobiology, Twarda 51/55, 00-818, Warsaw, Poland
[3]Moravian Museum, Department of Mineralogy and Petrography, Zelný trh 6, 659 37 Brno, Czech Republic

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Abstract: Kienberg (Middle Miocene, upper Badenian) represents one of the richest and most significant paleontological localities of the marine Miocene in the Czech Republic. Despite the fact that Kienberg has been known since the 19th century and provided remains of hundreds of taxa, recently it became a rather overlooked locality. Therefore, we provide a current overview of geological and paleontological research at the locality. Fossil marine invertebrates are the most common, and the vertebrate fossil record is represented mainly by bony fishes, sharks, and rays. Rare remains of a crocodylian and a sea turtle are newly identified. A tooth of *Crocodylia* indet. and a proximal fragment of a left femur of *Pan-Cheloniidae* indet. are described and compared within spatiotemporally co-occurring forms. The presence of a sea turtle fits well within the context of the strict marine fauna documented from Kienberg, whereas the crocodylian tooth in the marine section could imply a saltwater tolerant crocodylian species or a transport of this only crocodylian remain from more distant brackish/freshwater environment.

Keywords: Kienberg, Mikulov, Miocene, Vienna Basin, Crocodylia, Testudines

Introduction

The early upper Badenian locality of Kienberg represents one of the richest paleontological localities in the Vienna Basin. Kienberg has been known since the 19th century (Reuss 1848; Hoerness 1856, 1870) for its rich fossil record of invertebrates, especially mollusks deposited in many institutions of Central Europe. Historical research of the locality was summarized in detail by Tomaštík (1981). In addition to private collecting activities, several paleontological excavations were organized in the sandpit and vineyard terraces. Sieving of tons of sediments provided tens of thousands of specimens of fossil mollusks (Kroupa 1991; Brzobohatý et al. 2007). Vertebrate finds have been limited to fishes only (Schubert 1902, 1905, 1906; Brzobohatý et al. 2007). Despite this large amount of prospected material, no fossil amniotes have been reported.

Unexpectedly, in 1985, an isolated crocodylian tooth was found in the fossiliferous strata with the marine fauna. Subsequently and surprisingly, a turtle femur was identified in 2023 in the collections of the Department of Geology and Paleontology of the Moravian Museum labelled as Kienberg without further information.

The aim of this paper is the description of the above mentioned fossil crocodylian tooth and incomplete turtle limb bone from the fossil site of Kienberg. The material described here represents very rare finds in the Middle Miocene marine deposits from the Moravian part of the Vienna Basin.

Abbreviations

IRSNB – Royal Belgian Institute of Natural Sciences, Rue Vautier 29, 1000 Brussels, Belgium.

MZM – Moravian Museum, Zelný trh 6, 659 37 Brno, Czechia.

OP – private collection of Pavel Opravil, Hradčany 95, 751 11 Hradčany, Czechia.

Geological setting of the studied locality

Kienberg (presented in German and Czech transcriptions as Kienberk, Kinberk, Kimberk, Kimberg, and sometimes generalized as the closest town Mikulov = Nikolsburg) is located approximately 3 km east from Mikulov (Fig. 1). The locality is an elevation with several outcrops located on its western slope and represented by vineyard terraces and an abandoned sandpit. Paleogeographically it is located on the northwestern edge of the Vienna Basin, close to the active margin of the Carpathian Foredeep Basin.

The oldest Neogene deposits in the Mikulov area are the lower Badenian calcareous marine clays of the Lanžhot Formation and conglomerates of the Sedlec Beds, which lie on the Mesozoic and Paleogene flysch bedrock of the Ždánice

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✉ corresponding author: Jakub Březina
jbrezina@mzm.cz

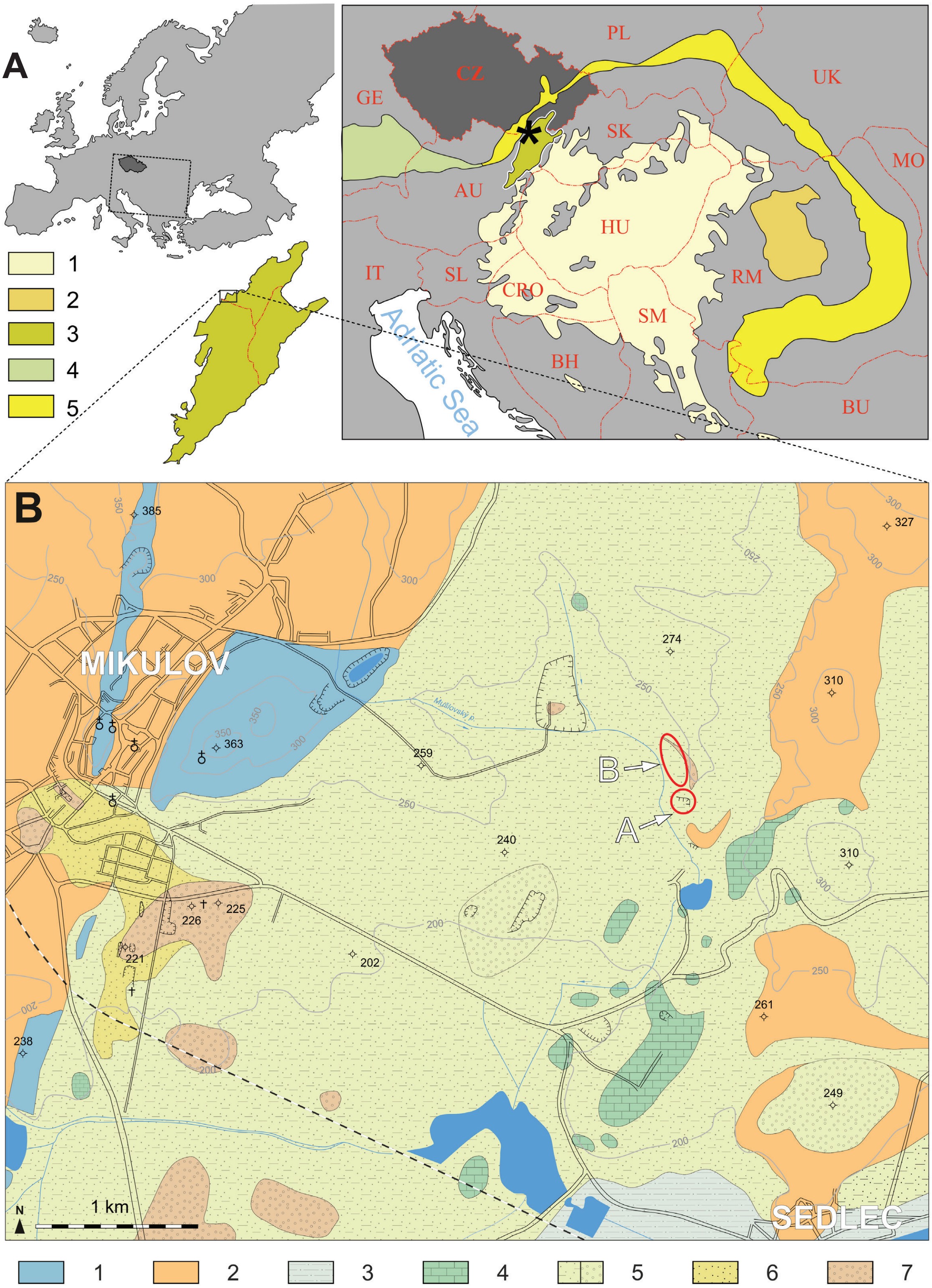

Fig. 1. A — Location of Kienberg within the Central Paratethys and the Vienna Basin (1 – Panonian Basin, 2 – Transylvanian Basin, 3 – Vienna Basin, 4 – Alpine Foreland Basin, 5 – Carpathian Foredeep Basin). **B** — Location of Kienberg (A – sandpit, B – vineyard) in uncovered geological map of the northwestern margin of the Viena Basin between Mikulov and Sedlec. 1 – Ždánice Unit (Jurassic–Cretaceous): limestones and marlstones, 2 – Ždánice Unit (Oligocene–Miocene): claystones, sandstones, and conglomerates, 3 – Lanžhot Beds (lower Badenian): calcareous clays and sands, 4 – Hrušky Formation (middle Badenian): algal limestones, 5 – Hrušky Formation (middle–upper Badenian): calcareous clays and sands, locally with gravels, 6 – Bzenec Formation (Pannonian): sands, silts, locally gravels, 7 – Valtice Beds (upper Pannonian–?Pontian): sandy gravels. Interpretation of uncovered geological map follows Jüttner (1939), Čtyroký et al. (1995), and Březina et al. (2021).

Unit (Stráník et al. 1999; Brzobohatý et al. 2007). As a result of the Badenian salinity crisis (see, e.g., Hohenegger et al. 2014), sedimentation in the southern part of the Carpathian Foredeep Basin in Moravia was interrupted at the end of the early Badenian. However, sedimentation continued, forced by new overlying deposits, in the Vienna Basin. Its sedimentation in the Mikulov area is represented by variegated beds of marine clays, sands and algal sandstones, and limestones of the upper Badenian Hrušky Formation (Stráník et al. 1999). During the deposition of the Hrušky Formation, the delta prograded east of Mikulov with topset facies of gravel-sand fluvial deposits containing a terrestrial assemblage of reptiles and mammals (Seitl 1985; Březina et al. 2021; Březina 2022). Badenian clays and flysch deposits south of Mikulov are overlaid by silts and sands corresponding to the Bzenec Formation (lower–middle Pannonian), which are often discordantly overlaid by gravels and sands of the Valtice Beds (probably upper Pannonian–?Pontian). After that, the Miocene sedimentation in the Mikulov area ended (Čtyroký 1989, 1999; Čtyroký et al. 1990; Březina 2019).

Deposition of the Kienberg section began with lower Badenian conglomerates of the Sedlec Beds (Čtyroký 1993), followed by an approximately 12-m-thick section of fine-grained sands with the fossil record of algae and bivalves (*Chlamys flava*, *Linga collumbella*, and *Corbula gibba*) to coarse grained sands with the mollusks genera *Glycimeris*, *Flabellipecten*, *Ostrea*, *Diloma*, and *Ancilla*. Subsequently, the deposition ended by alternating coralline algae sandstones and "oyster and *Pecten* layers" observed at the abandoned sandpit (Tejkal 1956, 1968; Brzobohatý et al. 2007; Schultz et al. 2010).

Although the fossil record of mollusks in the sandpit section is characterized by predominant bivalves, sections of the vineyard terraces (see Fig. 2) predominantly yield gastropods (Tejkal 1956; Tomaštík 1981). The most common are *Ancilla glandiformis*, *Apporhais pespelecani alatus*, several species of *Conus*, *Turritella*, *Natica*, *Nassa*, *Clavatula*, and others (see Tomaštík 1981). This laterally variable section of the vineyard terraces continues with fine-grained calcareous sands rich in the bivalve *Megacardita jouanneti* and other mollusks. These sands pass to sandy and silty calcareous clays and unlaminated calcareous clays with the bivalve *Amussium* sp. and gypsum. The vineyard fossiliferous section grade into fine-grained sands with abundant mollusks often as lumachelle (Brzobohatý et al. 2007). Cross-bedded sands alternate with gravels rest discordantly on the marine section and contain only reworked mollusks (Tomaštík 1981; Brzobohatý et al. 2007).

Fundamentally all types of sediments of the Hrušky Formation can be found at Kienberg and therefore represent sedimentation related to an algal bioherm located between Mušlov and Kienberg (Jiříček 2002, Fig. 2). The algal bioherm environments generated highly diverse assemblages of fauna (Harzhauser et al. 2024). Mollusks are the most diverse, with 98 bivalve and 107 gastropod recorded species (Hoernes 1856, 1870; Tejkal 1956, 1968; Steininger et al. 1978; Švagrovský 1981; Tomaštík 1981). Other abundant fossils include 17 ostracod species (Brestenská & Jiříček 1978), 35 bryozoan species (Zágoršek et al. 2004, 2007), several echinoid species (Kalabis 1938, 1948; Kroh 2005), snapping shrimps and crabs (Hyžný et al. 2018). The presence of polychaetes and Porifera is documented by the ichnological record (Pek & Mikuláš 1999). Vertebrate finds from Kienberg are limited to anamniotes, namely 63 otolith-based taxa of bony fishes, 15 shark species, and 7 ray species (Brzobohatý et al. 2007; Schultz et al. 2010).

The Kienberg sandpit section was first placed at the base of the upper Tortonian (=upper Badenian in the concept of Kováč et al. (2018) as algal limestone facies (Buday 1963). The vast majority of authors (e.g., Tejkal 1968; Papp et al. 1978; Tomaštík 1981) interpreted Kienberg (more specifically the sandpit) on the basis of foraminifers and ostracodes as "middle" Badenian (*sensu* Wieliczian; Cicha et al. 1998). Recent research confirms the "middle" Badenian (*sensu* Wieliczian) age based on biostratigraphy (especially foraminifers) of the terraces, whereas the sandpit section may extend to the uppermost lower Badenian (Brzobohatý et al. 2007; Schultz et al. 2010, Fig. 2).

The sites have not yet been sedimentologically studied. Therefore, interpretation of the environment is possible only on the basis of the fossil record. Mollusks indicate a well-oxygenated euryhaline shallow sublittoral environment not far from a flat coast where the sandpit section was deposited in the shallowest environment (Tomaštík 1981; Tejkal 1968). Based on the otoliths, an infralittoral environment with a depth of 30–60 m and subtropical climate with gradual cooling during deposition is assumed (Brzobohatý et al. 2007; Schultz et al. 2010).

Material and methods

The original bone MZM Ge33513 from the Kienberg locality is stored in the Department of Geology and Paleontology of the Moravian Museum (MZM). The crocodylian tooth was studied firsthand and is stored in the private collection of Pavel Opravil (OP Ge33514), whereas its gypsum cast cataloged as MZM Ge33514 is stored in the Department of Geology and Paleontology of the Moravian Museum. For comparisons, photographs of a femur of *Eochelone brabantica* (IRSNB R 0001), published data on the femoral morphology in fossil pan-cheloniids (Weems 1974: pl. 2.6–8; 5.7; Weems 1988: fig. 11G–H; Lynch & Parham 2003: fig. 7; Lapparent de Broin et al. 2014: fig. 10F1–F4; Weems & Sanders 2014: figs. 8A–C, S1F–J, S5C–E) and crocodylian teeth (Schlögl & Holec 2004: fig 3; Nojima & Itoigawa 2017: fig. 5; Iijima et al. 2018: figs. 2F, 11A–B; Nicholl et al. 2020: figs. 4–5; Chroust et al. 2021: fig. 6; Massonne & Böhme 2022: fig. 3C–E; Venczel et al. 2023: figs. 2–8) were used.

Only the crocodylian tooth can be located within the sedimentary sequence from Kienberg. It was found by VH in coarse-grained sands of the sandpit (Fig. 2). The turtle speci-

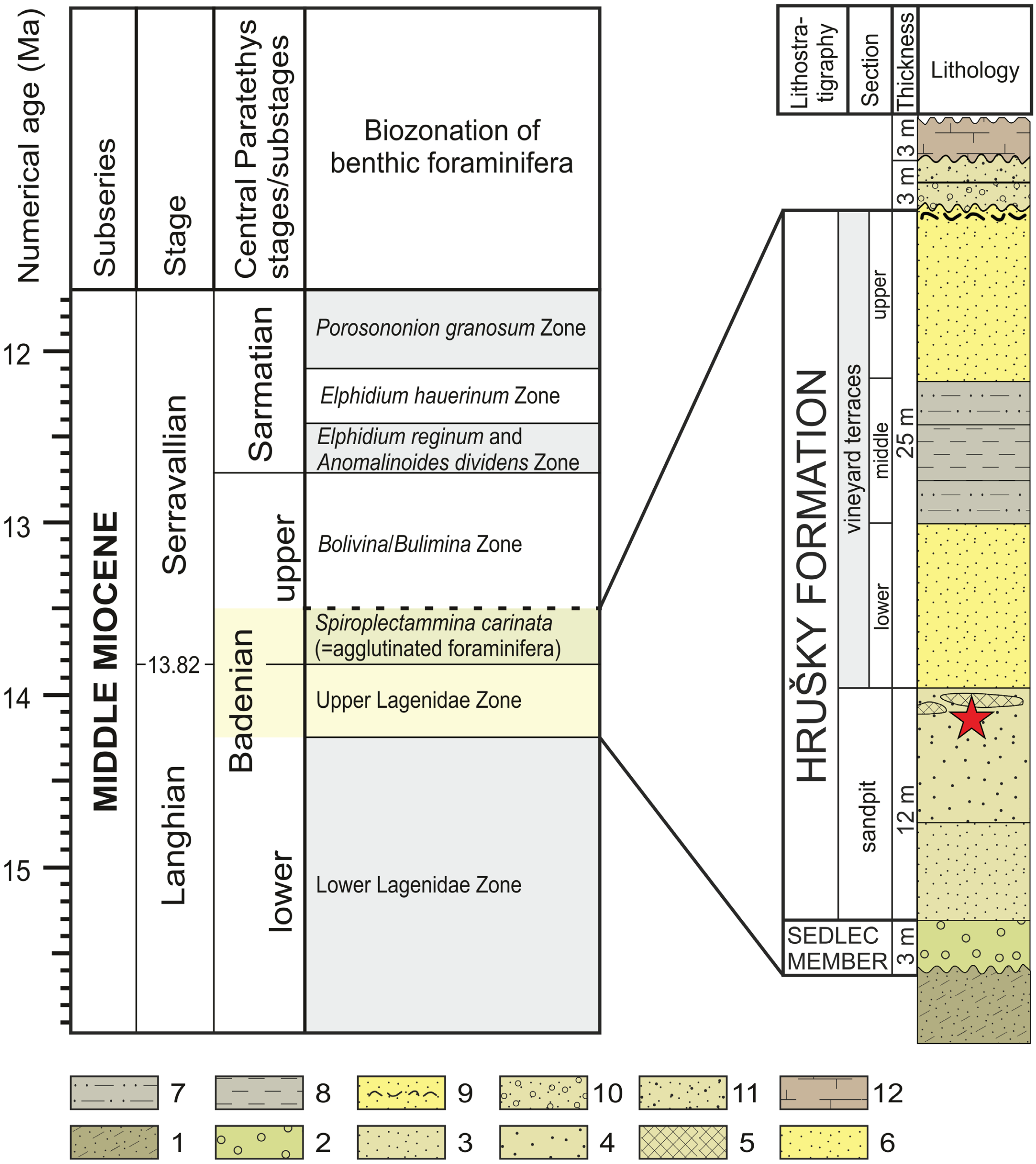

Fig. 2. Stratigraphic position, lithostratigraphy, and lithology of Kienberg according to Brzobohatý et al. (2007) and Schultz et al. (2010). The red star indicates the position of the studied crocodylian tooth within the profile. 1 – micaceous sandstones of Ždánice–Hustopeče Formation, 2 – chaotic coarse and block conglomerates, 3 – fine-grained yellowish-gray sands, 4 – coarse-grained sands and sandstones, 5 – coralline algae incrustations, 6 – fine-grained yellowish calcareous sands, 7 – gray silty calcareous clays, 8 – gray nonlaminated calcareous clays, 9 – lumachelle, 10 – chaotic gravels/cross bedded sands, 11 – gray-yellow fine/coarse sands with reworked Mollusca, 12 – Quaternary loess and loam.

men unfortunately lacks any stratigraphic information, and the sediment residues provide no clues as to its original provenience.

The specimens were measured using a digital caliper. Photographs were taken with a Canon PowerShot G7 X Mark II camera. Obtained images were then used for the reconstruction of a 3D photogrammetric model of MZM Ge33513 using Agisoft Metashape Standard, version 2.0.1. The 3D model was uploaded to the MorphoSource data archive, Media 000655735, ark:/87602/m4/655735, available under the link: https://www.morphosource.org/concern/media/000655735. Our taxonomical approach follows the International Code of Phylogenetic Nomenclature (PhyloCode; Cantino & Queiroz 2020).

Systematic Paleontology

Eusuchia Huxley, 1875 [Brochu, 1999]
Crocodylia Gmelin, 1789 [Benton & Clark, 1988]
Crocodylia indet.
Fig. 3

Description: The tooth OP Ge33514 is conical, slender, and lingually curved. As preserved, it is 33.8 mm long, but approximately 5 mm of its apex is broken and the basal part of the root is missing with 16.7 mm in maximal diameter and 15.6 mm in minimal diameter. The diameter of crown at the basal termination of carinae is maximally 11.9 mm and minimally 11 mm. The tooth is infilled with non-lithified coarse-grained sand with shell fragments. The enamel is smooth and quite thin, varying between 0.5 and 1 mm in thickness (Fig. 3). Anterior and posterior carinae are present, more pronounced in the apical half of the tooth. The tooth itself is grooved by faint longitudinal striations and crossed by incremental bands of different colors (darker/lighter brown). Its original left/right orientation or precise position in the jaw is impossible to determine.

Remarks: According to several authors (e.g., Brochu 2000; Delfino et al. 2021), closer taxonomic attribution of crocodylian teeth is impossible and, therefore, OP Ge33514 can only be referred to *Crocodylia* indet. During the Miocene, the area near the Vienna Basin was occupied by two different genera of crocodylians, the genus *Diplocynodon* Pomel, 1847 and *Gavialosuchus* Toula & Kail, 1885 (Böhme 2002, 2003; Schlögl & Holec 2004). The size and proportions of the studied tooth fit adult representatives of the genus *Diplocynodon*, whereas in *Gavialosuchus*, the teeth are larger and more robust. We cannot exclude a possibility of a juvenile *Gavialosuchus*, but in *Gavialosuchus*, the teeth generally have rough enamel with distinct apicobasal ridges, whereas in *Diplocynodon* the enamel is generally smooth. Nevertheless, the distinctness of this characteristic depends on the fossilization process (abrasion rate during transport, diagenetic changes, etc.) and must be taken with caution. Even though the tooth OP Ge33514 is very similar to *Diplocynodon*, we cannot identify it with full confidence at the genus level, so we assign the material to *Crocodylia* indet.

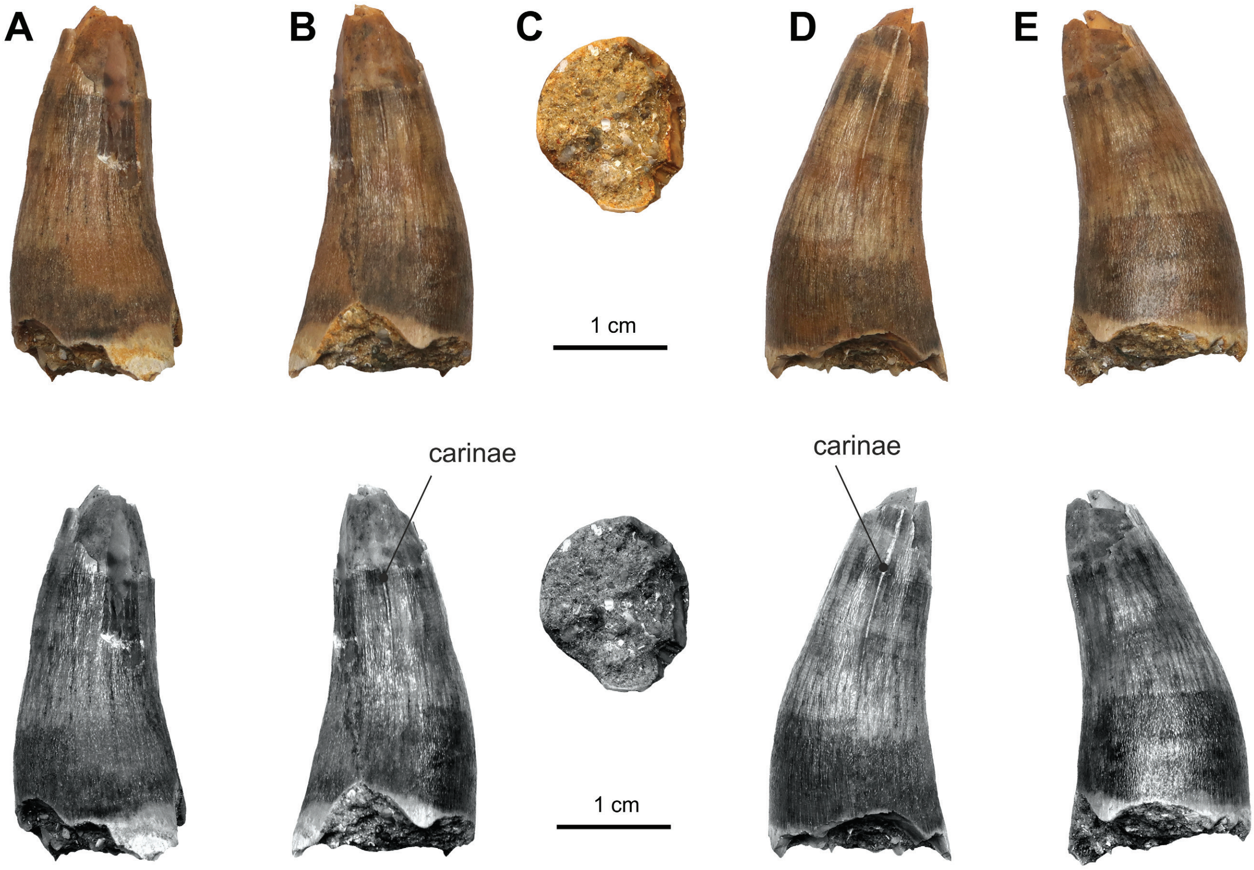

Fig. 3. Tooth of *Crocodylia* indet. PO Ge33514 from the Kienberg locality. A – lingual view, B – mesial/distal view, C – basal view, D – distal/mesial view, E – labial view.

Testudines Batsch, 1788 [International Turtle Nomenclature Committee et al., 2020]
Cryptodira Cope, 1868 [International Turtle Nomenclature Committee, 2020]
Chelonioidea Baur, 1893 [Joyce et al., 2021]
Pan-Cheloniidae Joyce et al., 2004 [Joyce et al., 2021]
Pan-Cheloniidae indet.
Fig. 4

Description: The left femur, MZM Ge33513, preserves only the proximal part, whereas most of the diaphysis and the whole distal part are missing. The fragment is 38.5 mm long. The proximal part consists of the femoral head and the trochanter major and minor. In the anteroposterior aspect, the femoral head is deflected dorsally from the shaft. The head is generally oval and is prolonged anteroposteriorly (longer than wide). The articular surface of the head itself is damaged by abrasion and is distinctly porous in the areas formerly covered by cartilage. The neck of the femoral head is not well-defined due to the lack of a distinct constriction and the absence of any distal overhang of the articular surface. The bridge between the femoral head and the trochanter major is gently concave and slightly constricted in proximal view.

The trochanter major is roughly parallel to the long axis of the shaft and extends proximally beyond the femoral head. The trochanter minor is very short and directed predominantly anteriorly. Its tip is partially eroded but the preserved portion of the cartilage-covered, porous surface indicates that not much of that structure is missing. A bowed, sharp, thin edge connecting both trochanters is nearly as tall as the trochanter minor. The edge between the femoral head and trochanter minor is twice as thick as the ridge connecting both trochanters and together these structures create a pit-like concavity of the intertrochanteric fossa, well enclosed posteriorly and only slightly enclosed ventrally and anteriorly. The anterior (facing towards the intertrochanteric fossa) surface at the base of the trochanter major bears two distinct foramina (presumably nutrient foramina), the proximal one is larger than the distal one. The diaphysis is slender and oval in the cross-section (wider anteroposteriorly than dorsoventrally), infilled with spongiosa.

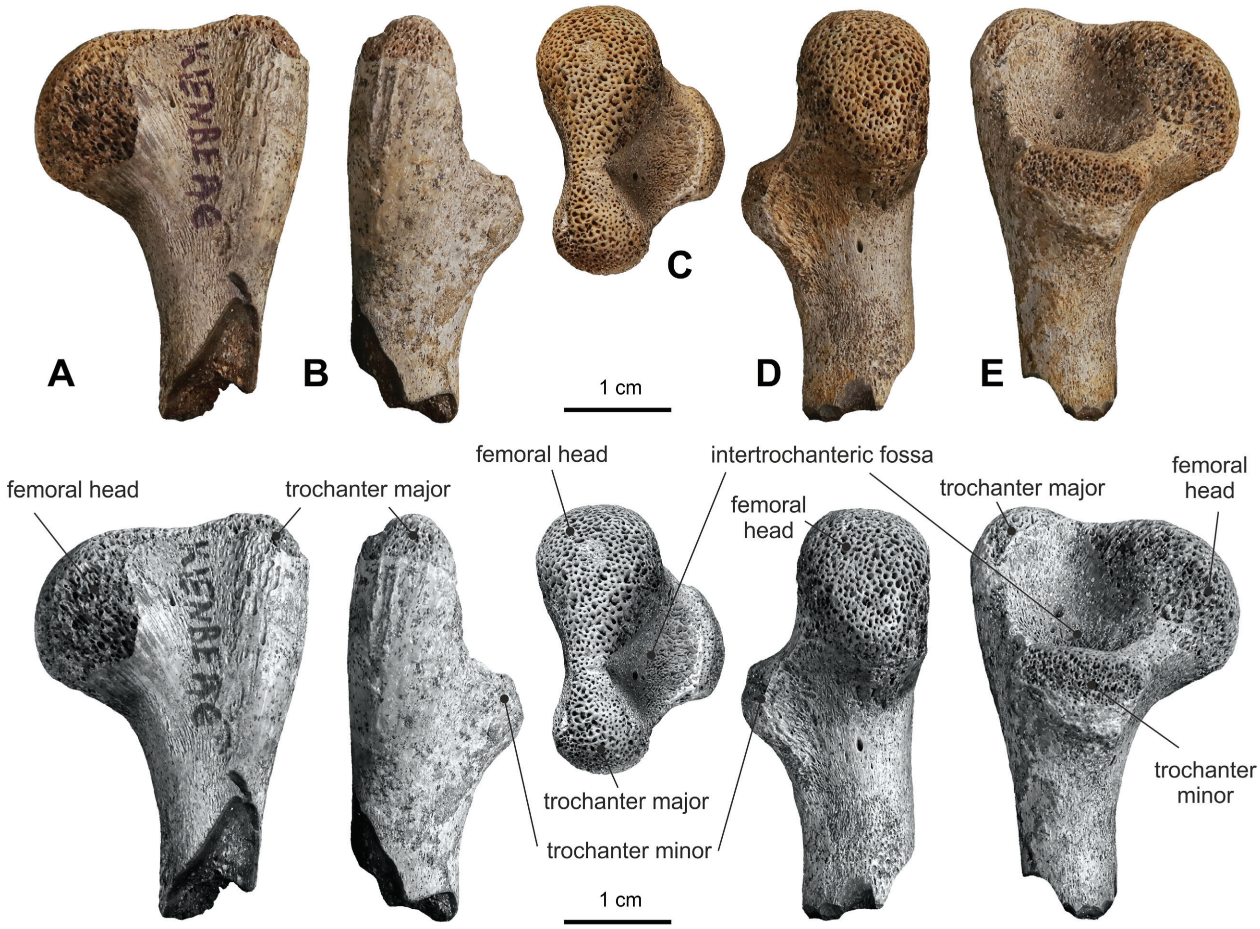

Fig. 4. Left femur MZM Ge 33513 of *Pan-Cheloniidae* indet. from the Kienberg locality. A – posterior view, B – ventral view, C – proximal view, D – dorsal view, E – anterior view.

Remarks: The morphology of the femur MZM Ge33513 and, in consequence, its taxonomic affinities are puzzling. The region of modern-day Central and Western Europe was inhabited in the Middle Miocene by the dermochelyid *Psephophorus polygonus* (von Meyer 1847; Seeley 1880; Delfino et al. 2013). There is no comparative material of the femora of that species, however, based on the general shape of the proximal part and the diaphysis, we can exclude the affinity of MZM Ge33513 to the *Dermochelyidae*, which typically have a distinctly hourglass-shaped diaphysis and a more advanced enclosure of the intertrochanteric fossa (Völker 1913; Seago 1979). The proportions and general morphology differ from the typical derived cheloniid femora most notably in the presence of a well-developed intertrochanteric fossa, lack of its anterior and ventral enclosure, and the short, anteriorly deflected trochanter minor (Koolstra et al. 2019; Joyce et al. 2021). Therefore, the specimen is best interpreted as a stem cheloniid.

The trochanter minor appears to be smaller and more abbreviated than in *Carolinochelys wilsoni* (Eocene–Oligocene of the USA), *Eochelone brabantica* (IRSNB R 0001; Eocene of Belgium), *Euclastes wielandi* (‘*Dollochelys coatesi*’; Cretaceous–Eocene of the USA, Morocco, and Belgium), *Pacifichelys* (‘*Euclastes*’) *hutchisoni* (Miocene of the USA), and *Procolpochelys charlestonensis* (Oligocene of the USA) (Weems 1988; Lynch & Parham 2003; Weems & Sanders 2014; Ullmann & Carr 2021; see also Parham & Pyenson 2010). This results in a more pronounced anterior opening of the intertrochanteric fossa of MZM Ge33513, particularly when compared to *C. wilsoni*, *Eo. brabantica*, *Eu. wielandi*, and *P. hutchisoni*, although those species also seem to either lack the low but distinct ridge delineating the ventralmost perimeter of the fossa in MZM Ge33513, or this ridge is located deeper (more dorsally) than the ventralmost surfaces of the trochanters (Weems 1988; Lynch & Parham 2003; Weems & Sanders 2014; Ullmann & Carr 2021). Both trochanters also seem shorter than in *Syllomus aegyptiacus* (Miocene–Pliocene of the USA), including the juvenile illustrated by Weems (1974: pl. 2.7), although MZM Ge33513 seems to resemble that species in the size and shape of the intertrochanteric fossa. The size and inclination of the trochanter minor is comparable to that in *Osonachelus decorata* (Eocene of Spain) but the trochanter major in MZM Ge33513 is significantly slenderer in ventral view due to its much lesser anteroposterior expansion (Lapparent de Broin et al. 2014). The morphology of the preserved part is the most resemblant of *Procolpochelys grandaeva* (Cretaceous–Miocene of the USA) and *Ashleychelys palmeri* (Oligocene of the USA) when it comes to the general proportions, form and size of the trochanters, and the degree of the anterior and ventral opening of the intertrochanteric fossa (Weems 1974; Weems & Sanders 2014). Because these two genera were found to be closely related and they either form a clade or occupy successive nodes on the stem leading to crown *Cheloniidae* (Weems & Sanders 2014; Weems & Brown 2017; Ullman & Carr 2021), it seems possible that MZM Ge33513 may represent either that clade or grade of pan-cheloniids. The only named Neogene Southern European cheloniid, *Trachyaspis lardyi*, lacks preserved femora (Chesi et al. 2007; Villa & Raineri 2015; Zoboli et al. 2023), precluding direct comparisons. The femoral morphology of fossil cheloniids has never been the focus of thorough studies and remains poorly understood. Therefore, due to the lack of described femoral material, we cannot identify MZM Ge33513 at the genus or species level and so we assign the material to *Pan-Cheloniidae* indet.

Taphonomical and paleoenvironmental interpretation

The exact stratigraphic position of the finds within the profile of Kienberg is important for their paleoenvironmental interpretation because the entire sedimentary section may not be of marine origin, in particular the uppermost sands and gravels which are most likely of fluvial origin (see Fig. 2).

The crocodylian tooth was found in coarse-grained sands of the sandpit (Fig. 2), which represents the stratigraphically oldest Miocene outcrop in Kienberg with abundant marine bivalves and other marine fauna (e.g., Tejkal 1956; Brzobohatý et al. 2007; Schultz et al. 2010). Because the fossil tooth comes from the sequence with only marine mollusks and fishes, it suggests that the crocodylian inhabited the marine environment together with other marine fauna. On the other hand, due to the lack of other crocodylian finds at the site, it is also likely that the studied tooth is allochthonous and was transported into the marine sediments from the land or nearby brackish/freshwater environment. Such allochthonous elements transported from the land were already documented from Kienberg in the form of fossil wood with *Teredolites clavatus* burrows (Pek & Mikuláš 1999). Concerning the paleoenvironment at Kienberg, interpretation is limited to the proxies from macrofauna, because the site has not yet been studied sedimentologically. Because there are no taxa indicating the brackish environment, the presence of a permanent river flow or estuary proposed by Jiříček (2002) in Mikulov during “middle” Badenian is highly unlikely. The deltaic sediments with strictly terrestrial fossil record opened in the former Czujan’s sandpit, located about 1 km SW of Kienberg, seem to be slightly younger than the marine deposits of Kienberg (Seitl 1985; Březina et al. 2021; Březina 2022). According to Seitl (1985), the non-fossiliferous gravels and sands discordantly overlying the autochthonous malacofauna-rich sands in the vineyard section of Kienberg most probably represent an equivalent of the delta-plain deposits documented from the Czujan sandpit. On the contrary, Jüttner (1939) interprets them as an equivalent of Late Miocene gravels located south of Mikulov (Fig. 1B). In fact, findings of proboscidean enamel fragments and bone fragments of large and medium-sized mammals could come from the uppermost horizon of the vineyard terraces at Kienberg (pers. observ. in the private collection of J. Šamánek and T. Turek, 2018). However, these denthognathic and bone fragments always represent surface collections without a known stratigraphic position (T. Turek pers. comm. 2024) and, therefore, can represent material redeposited by post-middle Miocene rivers.

Although we do not know the exact position of the turtle femur within the profile at Kienberg, its identification as a sea turtle agrees well with the predominantly marine fauna known from both the sandpit and the vineyard sedimentary sequences. Thus, it seems more likely the turtle fragment comes from the marine sequence of Kienberg without the possibility of a more precise localization within the profile.

Conclusions

The material described here represents the first discovery of fossil crocodylian and turtle from the Kienberg locality as well as the entire Moravian part of the Vienna Basin. The material consists of a single crocodylian tooth and an incomplete left femur of a sea turtle. In both cases, it is a rare find at the fossil site predominantly rich in invertebrates. The tooth is attributed to *Crocodylia* indet., whereas the turtle bone is referred to *Pan-Cheloniidae* indet. In the context of the marine deposition at Kienberg, the presence of a crocodylian in the fully marine section could imply a saltwater tolerant crocodylian species or a transport of this only remain from a more distant brackish/freshwater environment.

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