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First record of *Diplocynodon ratelii* Pomel, 1847 from the early Miocene site of Tušimice (Most Basin, Northwest Bohemia, Czech Republic)

Premier signalement de Diplocynodon ratelii *Pomel, 1847 dans le site du Miocène inférieur de Tušimice (bassin de Most, Bohême du Nord-Ouest, République tchèque)*

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ABSTRACT

The early Miocene deposits of Bohemia (Czech Republic) contain numerous fragmentary crocodylian remains. Despite this abundance, a detailed taxonomical assignment of these remains was impossible due to the absence of diagnostic cranial elements. Here, we report two partially preserved skulls together with some osteoderms and a partially preserved vertebra from the Tušimice site (MN3, Most Basin, Northwest Bohemia). Though the specimens were from Bohemia, the exact placement of this site was lost during the last century. Our results confirm that the coal from the reported specimens is consistent with the Tušimice site. Based on the detailed cranial description of the new material, the crocodylian remains from the above-mentioned locality can be referred to the extinct alligatoroid *Diplocynodon ratelii* with confidence. Our data extend the known spatial distribution of this taxon to Central Europe.

RÉSUMÉ

Les gisements du Miocène inférieur de la région de Bohême (République tchèque) contiennent plusieurs restes fragmentaires de crocodiles. Malgré cette abondance, une assignation taxonomique détaillée de ces restes était impossible à réaliser, du fait de l'absence d'éléments diagnostiques crâniens. Nous rapportons ici deux crânes partiellement

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préservés ainsi que des ostéodermes et une vertèbre incomplète du site de Tušimice (MN3, bassin du Most, Bohême du Nord-Ouest). Bien que les spécimens soient originaires de Bohême, l'emplacement exact de ce site a été perdu au cours du siècle dernier. Nos résultats ont confirmé que le charbon des spécimens signalés est compatible avec le site de Tušimice. Sur la base de la description crânienne détaillée du nouveau matériel, les restes de crocodiles du site de Tušimice peuvent être rapportés avec certitude à l'alligatoroïde éteint *Diplocynodon ratelii*. De plus, nos données étendent la distribution spatiale connue de ce taxon, révélant sa présence en Europe centrale.

1. Introduction

Historically, Neogene crocodylian remains in the Czech Republic were ascribed to Crocodilia Owen, 1842 (Jokély, 1858; Štúr, 1873) or even the extant genera *Crocodylus* Laurenti, 1768 (e.g., Štúr, 1879) and *Alligator* Daudin, 1802 (Becker, 1882). Despite its fragmentary nature, subsequent works (Dvořák et al., 2010) placed new material recovered from this area to the genus *Diplocynodon* (Dvořák et al., 2010; Fejfar and Schleich, 1994; Frič, 1903; Laube, 1901, 1910; Liebus, 1936; Redlich, 1902; Schlosser, 1910; Schlosser and Hibsch, 1902; Zázvorka, 1966). The crocodylian fossil record in Bohemia is quite rich, yielding more than 600 remains to date. Most of them, including the new material described here, were recovered from the same area (Most Basin, Eger Graben). The first reports of these reptiles date back to the 19th century and were based on isolated teeth and osteoderms from the village of Vintířov (close to Kadaň) and Tušimice site (Josef-Oswald mine) both in the Most Basin (Jokély, 1858; Štúr, 1873, 1879). Additional fragmentary remains were published at the beginning of the 20th century from the village of Lukavice and Tušimice (Laube, 1901). The latter consisted of a partial jaw, an isolated tooth, osteoderms, and postcranial bones. In contrast, the crocodylian fossil record from the nearby Sokolov Basin is rather fragmentary and less abundant than in the Most Basin (Redlich, 1902). Only isolated teeth, vertebrae and other postcranial bones are known from Friedrich-Anna mine in the Sokolov Basin (Redlich, 1902). Other than a natural mold of a mandible and one osteoderm element from Břešt'any (Most Basin), Frič (1903) mentioned a complete skull, which was sent to Vienna to some unknown coal magnate. This specimen has never been figured nor described in detail, and unfortunately, its location is unknown after checking the three most important paleontological institutions in Vienna (see § *Materials and Methods*) by two of us (À.H.L and M.C.). Similarly, only preliminary finds of fragmentary fossil crocodylian occurrences have been reported from the Most Basin during the 20th century. Most of them are isolated teeth (Fejfar and Schleich, 1994; Laube, 1910; Schlosser, 1910; Zázvorka, 1966), postcranial bones (Liebus, 1936), skull bones or skeletal fragments (Dvořák et al., 2010) or indirect evidences such as coprolites, bitemarks or tracemarks (Mikuláš and Dvořák, 2010; Mikuláš et al., 2006; Radoň, 2001; Štamberg, 1970). The most recently recovered crocodylian specimens (skull fragments and skeletal bones) were collected during the 1990s from the Ahníkov site and stored, until very recently, in Dvořák's private collection (Dvořák et al., 2010). Fortunately, specimens from Ahníkov have been transferred to the National Museum in Prague, though they have never been published nor figured in detail.

The first aim of this study is to clarify the geographic origin of the specimens stored at the University of Vienna, herein studied in detail, to confirm that these specimens were originally recovered from Tušimice (MN3, Most Basin, Northwest Bohemia). We investigated Tušimice using all available bibliographic sources as well as petrological analyses extracted from fossil crocodile remains. Secondly, we describe and figure in detail all of these remains and undertake a taxonomic assessment.

2. Age and geological background

The Most Basin is the largest of the four basins within the Eger Graben within the European Cenozoic Rift System. It is located in northwestern Bohemia (Czech Republic) and occupies an area of about 1400 km^2 (Grygar and Mach, 2013; Kvaček et al., 2004; Rajchl et al., 2009). Continental stratigraphic record extends from the upper Eocene (Priabonian) to the lower Miocene (Burdigalian: see Kvaček, 1998; Kvaček et al., 2004). The main filling phase had begun during the late Oligocene and continued into the early Miocene, when volcanoclastic and sedimentary deposits reached up to 550 m in thickness (Mach et al., 2014; Rajchl et al., 2009). Middle Miocene deposits are not preserved due to uplift and later erosion (Ziegler and Dèzes, 2007). The oldest unit in the sequence, the Staré Sedlo Formation, was formed during the upper Eocene, and is mostly comprised of fluviolacustrine clastic sediments (Pešek et al., 2014). During the early Oligocene, there was an important volcanic episode registered within the Střezov Formation, which produced alkaline volcanoclastic rocks such as tuffs and lava bodies (Ulrych et al., 2011). This is overlain by the Most Formation, which is mainly characterized by lacustrine, swamp, and fluvial sediments developed during the lower Miocene (Mach et al., 2013). Successively, the Most Formation can be divided into the following four Member successions: (1) the Duchcov Member, which comprises three different lithologies: neovolcanic, claystones, and sandstones (Pešek et al., 2014); (2) the Holešice Member, including the Main Coal Seam and subsequent deposition of clays made by the Žatec and Bílina river deltas and anastomosing streams (Grygar et al., 2017a, 2017b); (3) the

Libkovice Member, mainly formed by lacustrine deposits (Grygar et al., 2017a, 2017b); (4) the Lom Member with coal and mudstones (Grygar and Mach, 2013). Sedimentation of the Most Formation ended during the late early Miocene (Burdigalian), before the middle Miocene Climate Optimum (Grygar et al., 2014).

In the Most Basin, mining started in Tušimice area in the early 1800s, and during this century up to four mining enterprises exploited the coal. In particular, Josef-Oswald mine was opened at the end of the 1860s (Bílek et al., 1976). This mine, currently lost, was placed within the Holešice Member, southwest of the Most Basin, and more specifically at 6 km ENE of the town of Kadaň in the Chomutov district (Fig. 1A–C). The mine had a 70mdeep pit across three coal seams (Becker, 1882; Bílek et al., 1976). However, other mines of the time were more productive and produced higher-quality coal than mines from the Jirkov area. Consequently, Josef-Oswald coal mine was closed in 1888 due to economic reasons (Bílek et al., 1976).

Concerning the vertebrate paleontological record in the Tušimice area, the middle coal seam had a horizon rich in fossil crocodiles, containing up to 15 multiple fragments belonging to different individuals (Laube, 1901; Redlich, 1902). Just below this coal seam, a clay layer was rich in the snails: *Planorbarius cornu* (Brongniart, 1810), and femoral bones of an undetermined frog (Becker, 1882; Laube, 1901; Redlich, 1902; Štúr, 1873). This level has been inferred as a fluvio-lacustrine system of anastomosing rivers net (see Grygar et al., 2017a, 2017b; Kvaček et al., 2004; Laube, 1901; Redlich, 1902; Štúr, 1873). The data obtained from micromammals correlated the Tušimice fauna with the early Miocene MN3 Zone of the European Neogene Mammal biochronological system (Fejfar, 1989; Fejfar and Kvaček, 1993).

3. Materials and methods

Undescribed finds from the Tušimice site are currently housed at the Paleontological collection of the University of Vienna. In this paper, we describe complete material recovered from the above-mentioned site, although the postcranial bones such as vertebrae are not diagnostic at generic level. We focused our study on two individuals: (1) a partially preserved cranium (UW6526A1-A4) with a caudal vertebral body (UW6526A5); (2) and a posterior portion of a skull table (UW6526B1) together with the left angular (UW6526B2).

3.1. Institutional abbreviations and anatomical terminology

3.1.1. Institutions and fossil collections

ICP: Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Spain); IPS: acronym of the ICP collections (given the former name of the ICP: Institut de Paleontologia de Sabadell); IGUW: Institut für geologische Wissenschaften, Universität Wien (formerly Institut für Geologie), Vienna, Austria. UW: acronym of the collections of IGUW. MNHN SG: Muséum national d'histoire Naturelle, Paris (France), collection from Saint-Gérand-le-Puy.

3.1.2. Anatomical abbreviations

Anatomical abbreviations employed in the present work are the following: an, angular; bo, basioccipital; bs, basisphenoid; ch, choanae; cqg, cranioquadrate groove; dt3, third dentary tooth; dt4, fourth dentary tooth; den, dentary; do, dorsal osteoderm; dss, dorsal splenial suture; dt, dentary tooth; ect, ectopterygoid; exo, exoccipital; f, frontal; fa, foramen aereum; fs: frontal step; if, incisive foramen; itf, infratemporal fenestra; j, jugal; l, lacrimal; lk, longitudinal keel; mt4, fourth maxillary tooth; mt5, fifth maxillary tooth; mg, Meckelian groove; mhq, medial hemicondyle of the quadrate; mx, maxilla; n, nasal; na, naris; o, osteoderm; oc, occipital condyle; or, orbit; p, parietal; pal, palatine; pf, prefrontal; pmxt3, third premaxillary tooth; pmx, premaxilla; po, postorbital; pob, postorbital bar; pt, pterygoid; q, quadrate; qj, quadratojugal; soc, supraoccipital; sof, suborbital fenestra; sp, splenial; sq, squamosal; stf, supratemporal fenestra; vss, ventral splenial suture.

3.1.3. Analysis of organic petrology

In order to confirm the provenance of the studied material, a series of petrographic analyses on coal samples were carried out. They were extracted from both the dorsal and ventral surfaces of the two partial skulls. The polished sections were made following the standard ISO 7404-2 (ISO, 2009a). For the present study, composition (ISO, 2009b) and rank (ISO, 2009c) of organic matter measurements were taken by optic microscopy (Olympus BX51 with a Zeiss MK3 photomultiplier) both in normal light and fluorescent system. Here, for the analyses we used: (1) immersion lenses with focus 10×, 40× and 100× with PELCON (automatic point calculator for maceral composition: see further standard ISO 7404-3) (ISO, 2009b): (2) photomultiplier, monochromatic light ($\lambda = 546$ nm), software SpectraVision, calibration standards spinel ($R = 0.422\%$) and sapphire ($R = 0.596\%$: ISO, 2009c). All optic characters and coal fragment analyses conform to international standards (ICCP, 2001; Pickel et al., 2017; Sýkorová et al., 2005; Taylor et al., 1998).

4. Results

4.1. Historical revision and palynological and geochemical results

Crocodylian material here studied is currently stored at IGUW (Vienna, Austria). During a first-hand study of these remains in 2016, two of us (À.H.L and M.C) realized that these exquisite materials had never been reported in detail, possibly due to the lack of information about the site where the remains were recovered. However, both original labels (UW6526A and UW6526B) and the record book of the IGUW collections confirmed that the remains came from "Böhmen" (German name of Bohemia, Czech Republic) and had been referred to *Diplocynodon* aff. var. *ebertsi*. K. A. Redlich made similar referrals for specimens recovered from Friedrich-Anna mine (see above, and Redlich, 1902), but it is unknown who ascribed the IGUW specimens to

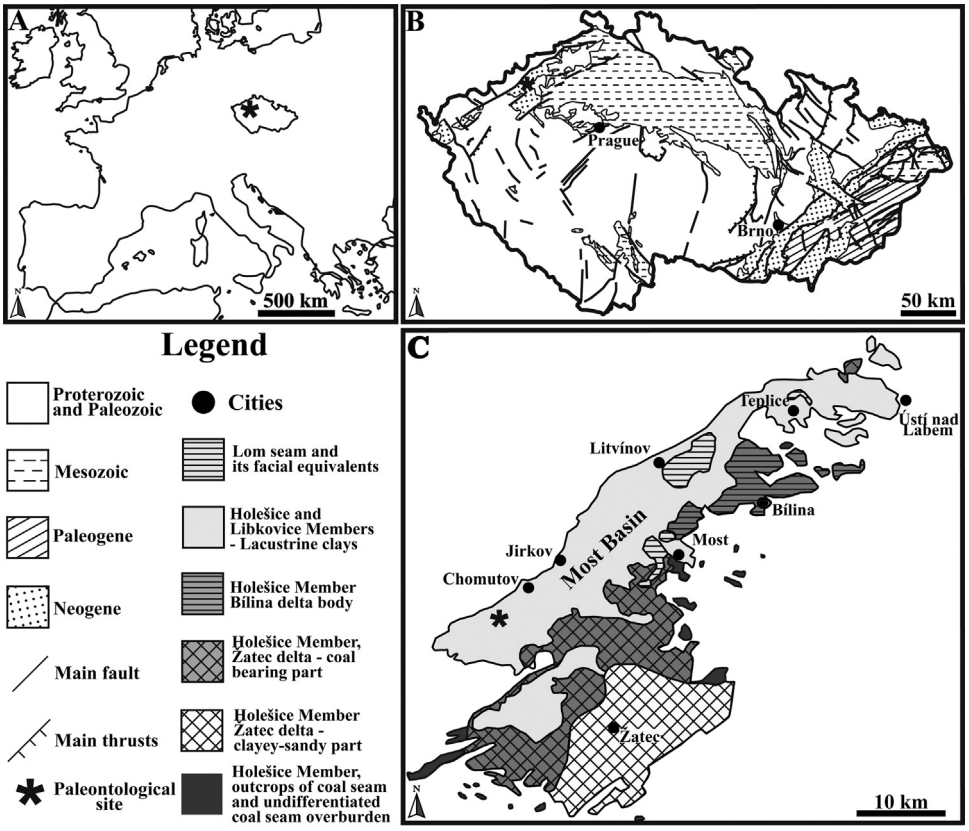

Fig. 1. Geographical location (**A–C**) and schematic geological maps of the Czech Republic and Most Basin (**B–C**) indicating the position of the Tušimice site. Geological map from the Most Basin (**C**) modified from Grygar et al. (2014).

Fig. 1. Localisation géographique (**A–C**) et cartes géologiques schématiques de la République tchèque et du bassin de Most (**B–C**) montrant l'emplacement du site de Tušimice. Carte géologique du bassin de Most, modifiée à partir de Grygar et al. (2014).

this taxon. Given that *Diplocynodon ebertsi* was erected by Ludwig in 1877, and taking into account the antiquity of the labels of the remains presented here (written before WWII, pers. com. K. Rauscher, curator of the IGUW), the *Diplocynodon* fossils were recovered and transferred to the IGUW before 1944.

Becker's long-neglected publication from 1882 merits comment. Becker was primary authority on studies on the stratigraphy close to Josef-Oswald mine. He documented coal seam and his associated deposits, and he collected fossil crocodiles from the Chomutov area that were later offered to D. Štúr (Štúr, 1873, 1879). However, the last alligatoroid remains reported by Becker, including "a jaw with teeth, vertebrae and osteoderms", were never studied in detail. Although we cannot be fully sure, these very likely correspond to the specimens herein reported. It is very probable that Becker's material has been saved for years to be studied posteriorly by D. Štúr. However, Štúr worked as a vice-head of the Imperial Geological Institute of Vienna at that moment (1877), and later he became director of this institution in 1885 (Barica, 2004). Hence, Štúr most probably offered this material, still unstudied, to the IGUW. For all these reasons, specimens discovered in Josef-Oswald mine (Tušimice) by Becker (1882) most probably represent the same material in Vienna described in our study.

The crocodylian fossil record from NW Bohemia only contains one Eocene locality from Kučlín, named Trupelník hill, (Dvořák et al., 2010). However, the deposits are formed by diatomites with no coal or similar lithological admixture (Kvaček, 2002). During the Oligocene, three areas in the Eger Grabenś basins have reported crocodile material. First locality is placed in Větruše (Ústí nad Labem) and includes claystones, diatomites and lava flows (Radoň, 2001). The second locality is situated within the Doupov volcanic complex (Doupov Mountains) formed by limestone and tuffites (Fejfar and Kvaček, 1993; Kvaček et al., 2014). Given that in both previous localities coal sedimentation does not exist, we can clearly discard them. In the Sokolov Basin a coal layer Rupelian in age exists, but it is sterile and does not contain fossil fauna (Rojík, 2004). In addition, there is no middle to late Miocene localities (neither fluvial nor limnic) in Eger Grabenś basins because sedimentation ended before the middle Miocene Climatic Optimum (Grygar et al., 2014). Consequently, only three localities fit well with the specimens herein studied, all of them roughly equal in age (early Miocene, MN3) and displaying a similar lithology and depositional environment: one from the Sokolov Basin (Friedrich-Anna mine; Redlich, 1902); and two from the Most Basin, Josef-Oswald mine (Laube, 1901) and Skyřice (Laube, 1910; Schlosser, 1910).

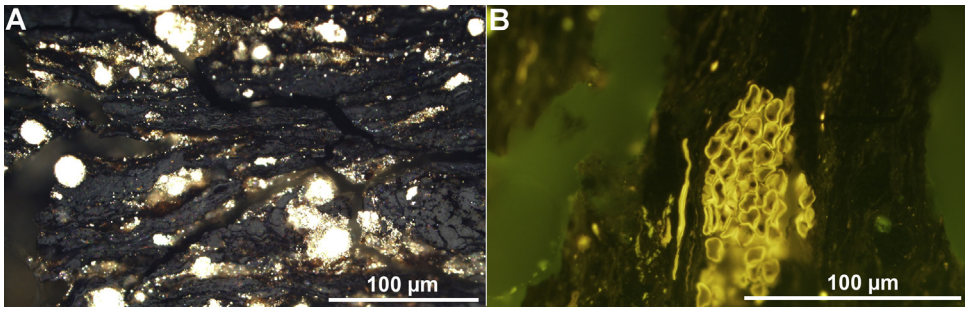

Fig. 2. Coal samples recovered (UW6526A1 and UW6526B1) respectively: oxyhumolite coal mass formed by huminite with crystalline and rhomboidal pyrite (**A**); coal fragments with dark huminite matter with yellow color of liptinite macerals (sporinite and resinite), in fluorescent mode (**B**).
Fig. 2. Échantillons de charbon récupérés (UW6526A1 et UW6526B1) respectivement : masse de charbon oxyhumolite formé d'huminite, ave pyrite cristalline et rhomboïdale (**A**) ; fragments de charbon avec une matière noire d'huminite et des macéraux de liptinite (sporinite et résinite) de couleur jaune, en mode fluorescent (**B**).

To confirm our evaluation of these sites, we further studied the coal matrix preserved in both skulls. Palynological analyses were not useful as all potential localities (Friedrich-Anna mine, Josef-Oswald mine, and Skyřice) have similar macroflora communities (pers. com. J. Dašková, 2018). Limited sediment samples from the skull are insufficient to run an isotopic analysis (pers. com. K. Mach, 2018). Moreover, data for some localities, in particular the exact levels at which fossils were found are currently not available or destroyed, further reinforcing our decision not to perform isotopic and palynological studies between localities. That matrix is mainly formed by clay minerals, bone splinters, and coal fragments. Around the bone fragments, organic materials (mainly coal) are dominant, whereas a red ferrous fill can be seen inside the lacunae. According to the International Classification ECE-UN (1998), coal is classified as a low-rank. It contains abundant pyrite crystals and organic fragments. Coal samples were identified as a partially weathered brown coal (oxyhumolite: Fig. 2A–B). Organic material is formed by gelled remains of plant tissue of lignin-cellulosic character (known as huminite macerals), and more specifically ulminite with clay minerals and crystalline and rhomboidal pyrites (Fig. 2A–B). Apart of huminite macerals, other liptinite components, such as sporinite, alginite, and rare inertinite macerals like funginite, were found (Table S1). Even though both rank and maceral composition of coal analysis perfectly fit with the age of the Tušimice site, this is not enough by itself to discount an alternative attribution to Friedrich-Anna mine and Skyřice sites.

5. Systematic paleontology

Order: CROCODYLIA Gmelin, 1789
Superfamily: ALLIGATOROIDEA Gray, 1844
Family: DIPLOCYNODONTIDAE Hua, 2004
Genus ***Diplocynodon*** Pomel, 1847
Diplocynodon ratelii Pomel, 1847
(Figs. 3–5)

5.1. Preservation of the specimens

We provide a brief explanation about the preservation state and conditions of both specimens. All descriptions, figures, and schematic drawings are provided in the next subsections.

UW6526A1-5: The specimen is a partial cranium (skull plus mandible) preserved in five portions: UW6526A1 (Fig. 3A–H), anterior and mid portion of the cranium; UW6526A2 (Fig. 3I–N), left fragment of the posterolateral part of skull table and three osteoderms; UW6526A3 (Fig. 3O–T), left fragment of the dentary with one dentary tooth; UW6526A4 (Fig. 3U–Z), right fragment of the angular with two dorsal osteoderms; UW6526A5 (Fig. 3A′–F′), and caudal vertebral body.

UW6526A1: The most complete specimen is dorsoventrally flattened and most of the posterior part of the braincase, posteriorly to the parietal, is missing (Fig. 3A–D). Main cranial cavities (the infratemporal fenestra and orbit) and some bones of the skull such as the basioccipital, basisphenoid, jugal, ectopterygoid, and surangular cannot be described in detail due to distortion or absence. The cranium is preserved in a slightly clockwise rotation relative to the correct anatomical position, which is clearly evident in the anterior tip of the snout. It is well prepared, but some small cracks are still filled with sediment. Nevertheless, the anterior portion of the palatal complex and some skull roof bones are preserved. In both lateral views, a convex shape is present, caused by postmortem compression (Fig. 3E–H). Both premaxillae are preserved, but the anterior margin of the left premaxilla is slightly eroded and therefore the first premaxillary teeth are not preserved (Fig. 3C–F). The left maxilla is almost complete, whereas the right one is somewhat compressed and lacks its posterior part. The central portion of the left nasal is broken. Similarly, both lacrimals are damaged and bear a couple of holes in dorsal view (Fig. 3A–D). The posterior portion of both prefrontals is slightly crushed. In any case, the preserved portion of the prefrontals is visible in dorsal view, although several microcracks are present. On the ventral side, the whole palatal area is quite crushed and

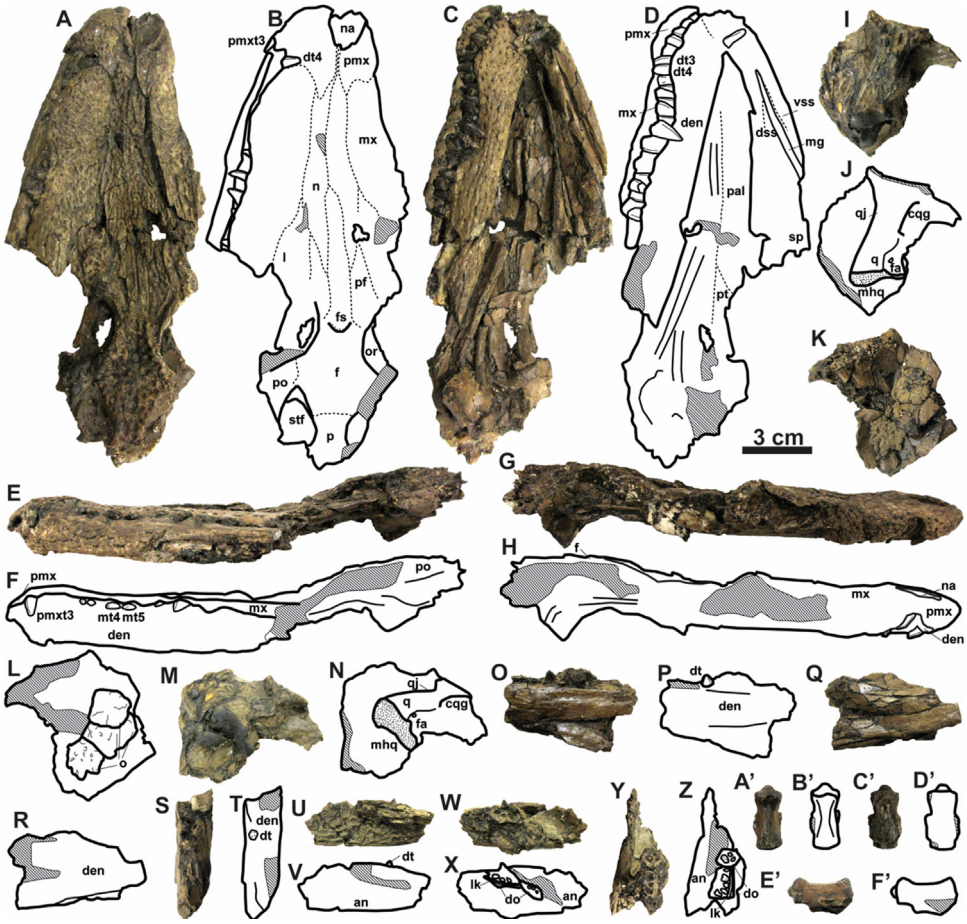

Fig. 3. Cranium and vertebra fossil remains, photos and drawings of *Diplocynodon ratelii* from Tušimice site. **A–H**. Anterior and mid portion of the cranium UW6526A1, in dorsal (**A–B**); ventral (**C–D**); left lateral (**E–F**); right views (**G–H**). **I–N**. Left fragment of the posterolateral part of skull table and three osteoderms UW6526A2, in posterior (**I–J**); anterior (**K–L**); dorsal views (**M–N**). **O–T**. Left fragment of dentary with one dentary tooth UW6526A3, in medial (**O–P**); lateral (**Q–R**); dorsal views (**S–T**). **U–Z**. Right fragment of the angular with two dorsal osteoderms UW6526A4, in lateral (**U–V**); medial (**W–X**); dorsal views (**Y–Z**). **A'–F'**. Caudal vertebral body UW6526A5, in dorsal (**A'–B'**); ventral (**C'–D'**); right lateral views (**E'–F'**). For abbreviations, see § *Material and methods*.

Fig. 3. Restes fossiles de crâne et vertèbre, photos et dessins de *Diplocynodon ratelii* du site de Tušimice. **A–H**. Partie antérieure et médiane du crâne UW6526A1, en vues dorsale (**A–B**) ; ventrale (**C–D**) ; latérale gauche (**E–F**) ; latérale droite (**G–H**). **I–N**. Fragment gauche de la partie postérolatérale de la plaque crânienne et trois ostéodermes UW6526A2, en vues postérieure (**I–J**) ; antérieure (**K–L**) ; dorsale (**M–N**). **O–T**. Fragment gauche de dentaire avec une dent de dentaire UW6526A3, en vues médiale (**O–P**) ; latérale (**Q–R**) ; dorsale (**S–T**). **U–Z**. Fragment droit de l'angulaire avec deux ostéodermes dorsales UW6526A4, en vues latérale (**U–V**) ; médiale (**W–X**) ; dorsale (**Y–Z**). **A'–F'**. Corps vertébral caudal UW6526A5, en vues dorsale (**A'–B'**) ; ventrale (**C'–D'**) ; latérale droite (**E'–F'**). Pour les abréviations, voir § *Matériel et méthodes*.

further some sutures of the bones are difficult to discern (Fig. 3C–D). The palatines are partially preserved, whereas the pterygoids are heavily damaged and the choanae are not preserved. Only both dentaries and the anterior portion of the splenials are preserved, but other bones, which form a mandible, are missing. Both dentaries and splenials are not in original anatomical position, they are rather rotated 90° to the right (Fig. 3C–D). Regarding dentition, some dentary and maxillary teeth are broken away, eroded or slightly compressed.

UW6526A2: This includes three disarticulated osteoderms and the left posterolateral portion of a skull formed by the quadratojugal, squamosal and quadrate (Fig. 3I–J). The quadratojugal is strongly damaged and only the central portion of the bone is present (Fig. 3I). Similarly, just a very small portion of the left squamosal is preserved. The quadrate is better preserved than the other bones (Fig. 3M–N). Three isolated osteoderms are attached as it can be ascertained in ventral view, but they are not in their original anatomical position (Fig. 3K–L).

UW6526A3: This is a fragment of the left dentary bearing one preserved tooth (Fig. 3O–P). In lateral view, this bone fragment is rather crushed, and posteriorly, another indeterminate fragment bone (most likely from a pterygoid) appears to be attached (Fig. 3Q–T).

UW6526A4: This corresponds to a partially preserved right angular (Fig. 3U–Z). Two dorsal osteoderms are attached, which are not in anatomical position (Fig. 3W–Z).

UW6526A5: This is an incomplete caudal vertebra comprising the vertebral centrum. The neural arch is entirely missing (Fig. 3A′–F′).

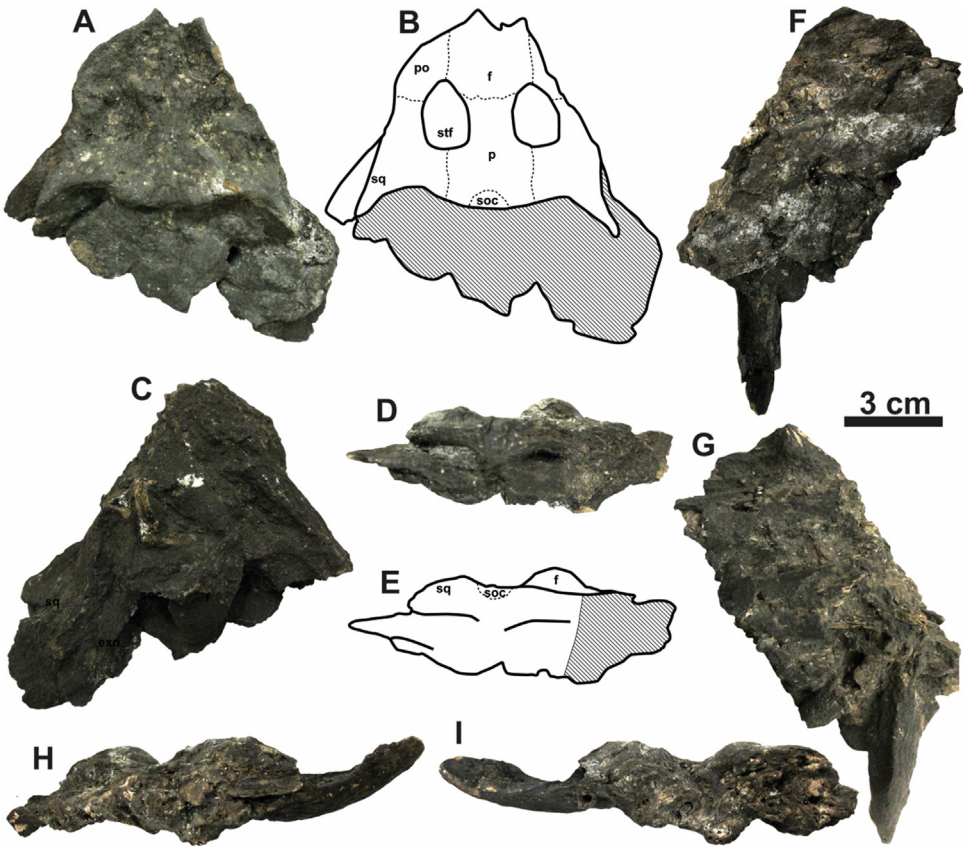

Fig. 4. Skull and mandible remains, photos and drawings of *Diplocynodon ratelii* from Tušimice site. **A–E**. Posterior portion of the skull UW6526B1, in dorsal (**A–E**); ventral (**C**); posterior views (**D–E**). **F–I**. Partial left angular UW6526B2, in dorsal (**F**); ventral (**G**); left (**H**); right lateral views (**I**). For abbreviations, see § *Material and methods*.

Fig. 4. Crâne et restes de la mandibule, photos et dessins de *Diplocynodon ratelii* du site de Tušimice. **A–E**. Partie postérieure du crâne UW6526B1, en vues dorsale (**A–E**) ; ventrale (**C**) ; postérieure (**D–E**). **F–I**. Angulaire gauche partiel UW6526B2, en vues dorsale (**F**) ; ventrale (**G**) ; latérale gauche (**H**) ; latérale droite (**I**). Pour les abréviations, voir § *Matériel et méthodes*.

UW6526B1: This is a posterior portion of the skull preserving the frontal, parietal, postorbital, squamosal, and supratemporal fenestra (Fig. 4A–B). The ventral and lateral sides are eroded and rather damaged. Bones such as the quadrate, quadratojugal, and squamosal are completely missing (Fig. 4C–E). The dorsal surface is well prepared, but the posterior surface is poorly prepared and most of the occipital bones are covered by a coal matrix.

UW6526B2: This is a partial left angular (Fig. 4F–I), which is not very well restored. The anterior part of the bone is embedded in a coal matrix and also most of the exposed bone is similarly covered with sediment (Fig. 4F–I).

5.2. Description

Premaxilla. This bone is completely preserved in UW6526A1, but slightly turned to the right and flattened (Fig. 3A–B). It is about 1.5 times longer than wide, with a rounded anterior margin. The premaxilla is at the anteriormost part of the snout and contacts the maxilla posterolaterally and the nasal posteromedially (Figs. 3A–B, 5B). Pits densely decorate all the dorsal surface of the bone, although it is less pronounced along the anterior edge. Sutures between the premaxilla, maxilla, and nasal are easily visible. An oval, ridge-like thickening surrounds the naris. This structure is continuous from the anterior margin to the posterior margin, where it becomes a shallow concavity (Fig. 3A–B, E–H). The external naris is almost completely surrounded by the premaxillae, with the anterior processes of the nasals forming the posterior most narial margin. The pointed posterior tip of the nasal penetrates into the maxilla at an acute angle (Figs. 3A–B, 5A). The premaxilla bears five teeth: the first four teeth in the left premaxilla and the second, fourth and fifth in the right one. The third and fourth teeth are the largest, and the fourth is largest (Figs. 3C–D, 5B). On both sides of this element, the posterior dorsal processes extent of the premaxillae reaches the level of the third maxillary tooth position (Figs. 3A–D, 5B). In ventral view, the incisive foramen cannot be confidently observed.

Maxilla. It is longer than wide and contacts the premaxilla anteriorly, the nasal medially, and the lacrimal, jugal, and palatine posteriorly (Fig. 3B and D). As in all diplocynodontids, the dorsal surface of the maxilla is pitted. The snout profile is slightly constricted at the level between the maxilla and premaxilla and the third and fourth dentary

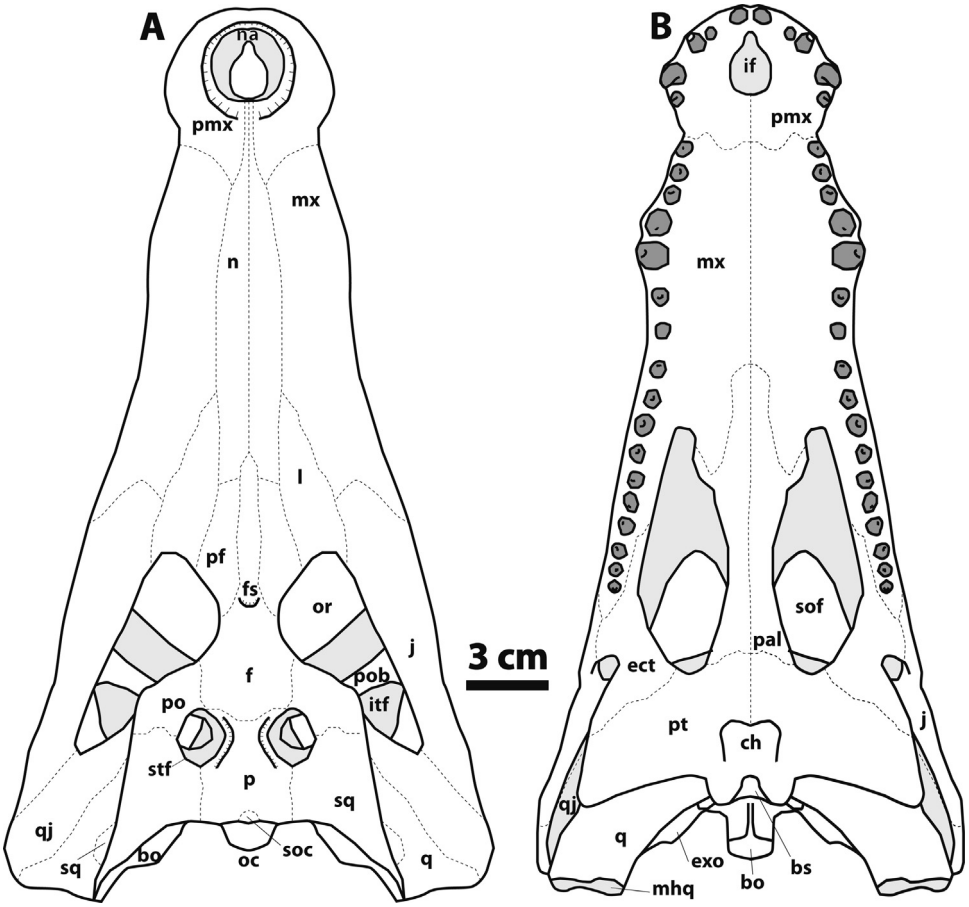

Fig. 5. *Diplocynodon ratelii* from Tušimice site. Reconstruction of the skull in: dorsal (**A**); ventral views (**B**). Dotted lines indicate bone sutures. For abbreviations, see § *Material and methods*.

Fig. 5. *Diplocynodon ratelii* du site de Tušimice. Reconstruction du crâne en vues : dorsale (**A**) ; ventrale (**B**). Les lignes en pointillés indiquent les sutures osseuses. Pour les abréviations, voir § *Matériel et méthodes*.

teeth (Figs. 3A–B, 5A–B). This notch can be discerned behind the last premaxillary–maxillary tooth in lateral view, which is divided by the premaxillary–maxillary suture (Figs. 3A–D, 5A–B). The suture with the nasal and lacrimal is almost straight. Because both maxillae are not fully preserved, the complete tooth count cannot be estimated. The anteriormost eleven teeth are preserved in the left maxilla, whereas the right element bears only eight teeth (Figs. 3A–D, 5B). With regard to the tooth size, the first maxillary tooth is the smallest, and from the second to the fifth, they gradually increase. However, the fourth and fifth teeth are instead confluent (Figs. 3C–D, 5B).

Nasal. It is elongated and located along the midline of the snout. The nasals form most of the snout length. The anterolateral margin of the nasal contacts the premaxilla and the maxilla, and the posterior margin contacts the frontal and lacrimal (Fig. 3B). As with most bones on the dorsal surface, rounded pits densely ornament the nasals. The anterior end of the bone is narrow and clearly extends to the external naris, preventing the premaxilla from meeting posterior to the naris (Fig. 3A–B). Posteriorly, the nasals reach their maximum width in the area of contact with the lacrimal and frontal. The nasals are bifurcated posteriorly and separated by an anterior frontal projection. Each bifurcation tapers to a point between the prefrontal and frontal. The left nasal displays a wide contact with the lacrimal (UW6526A1: Fig. 3A–B).

Prefrontal. The preserved portion of each bone in UW6526A1 is triangular in shape, and each contact at least the nasal anteriorly, the lacrimal anterolaterally, and the frontal medially (Fig. 3A–B). Its anterior tip inserts between the nasal and the lacrimal. The suture between the lacrimal and the prefrontal, only seen on the right prefrontal, reaches the anteromedial margin of the orbit, and therefore the prefrontal participates in the anterior margin of the orbital rim (Figs. 3B and 5A).

Lacrimal: It is roughly triangular in shape and narrows medially. The lacrimal contacts the maxilla anterolaterally, the nasal anteromedially and the prefrontal medially (Figs. 3A–B, 5A). The lacrimal extends further anteriorly than the prefrontal, and although both lacrimals are partially preserved in UW6526A1, it can be estimated that the lacrimal is anteroposteriorly longer than the prefrontal.

Frontal. The frontal is complete in UW6526A1 and contacts the nasal and prefrontal anterolaterally, the postorbital laterally, and the parietal posteriorly. It has a

subtriangular shape, is posteriorly wide, and narrows anteriorly (Fig. 3A–B). The frontal and maxillary external surfaces are much heavily pitted than other bones. A marked dorsoventral step is recognizable at the middle of the frontal, further delimitating this bone into two parts (Figs. 3A–B, 5A): the main body, which is markedly concave at the level of the orbits and shows an elevated orbital margin, and the anterior process, which is approximately 1.5 times longer than the body. The interorbital region is rather wide, approximately equal in width, to the supratemporal fenestra. The posterior portion of the frontal in UW6526A1 and UW6526B1 is slightly concave between the orbits (Fig. 4A–B).

Postorbital. The left postorbital is preserved in UW6526A1 (Fig. 3A–B) and both are preserved in UW6526B1 (Fig. 4A–B). The postorbital is subrectangular and wider than long. It meets the frontal anteromedially, the supratemporal fenestra medially, and the squamosal posteriorly. The postorbital contributes to the posterior orbital margin, the anterolateral margin of the supratemporal fenestra and the anterodorsal margin of the infratemporal fenestra (Figs. 3A–B, 4A–B, 5A). However, in both postorbitals preserved in UW6526B1, sediment covers and obscures the ornamentation and sutures with the squamosal and frontal. The dorsal surface of the bone is rather flat in both individuals.

Squamosal. This is preserved only in UW6526B1. It contacts the postorbital anteriorly, the parietal medially, and the quadrate ventrolaterally (Figs. 4A–B, 5A). The squamosal is longer than wide. There is a pronounced crest on the posterolateral margin of this bone. The posteromedial margin is concave anteriorly and contacts the postorbital and supraoccipital medially. The postorbital–squamosal suture is slightly anterior to the center of the supratemporal fenestra (Fig. 4A–B). Connection to the quadrate and paroccipital process is preserved only on the right squamosal.

Parietal. Its shape is roughly rectangular, it is longer than wide, with a distinct constriction developed between the supratemporal fenestrae (Figs. 3A–B, 4A–B, 5A). It contacts the frontal anteriorly, the squamosal posterolaterally, and the supraoccipital posteriorly. The parietal is completely preserved in UW6526B1 and forms part of the supratemporal fenestral margins (Fig. 4A–B). The fronto-parietal suture is clearly visible and is slightly concave posteriorly. As with the frontal, the dorsal surface of the parietal is heavily pitted, although matrix fills most of the pits. The parietal-squamosal suture is parasagittal direction, and further it is approximately equal in length to that of the fronto-parietal suture. However, the parietal does not reach the posterior margin of the skull and supraoccipitals are in contact (Figs. 4A–B, 5A).

Supraoccipital. This small bone is preserved on the posterior mid-region to the skull table (UW6526B1: Fig. 4A–B). It meets at least the parietal anteriorly and squamosal laterally. In dorsal view, the supraoccipital has a subsemicircular shape, with a rounded posterior margin (Figs. 4A–B, 5A).

Exoccipital. This bone is partly preserved only on UW6526B1, and it forms the posterooccipital end of the skull as preserved. It borders the dorsolateral margin of the foramen magnum (Fig. 4D–E).

Quadrate. It is partially preserved as an isolated fragment of UW6526A2 (Fig. 3I–L). The left portion of the quadrate meets the squamosal medially and the quadratojugal laterally. Contact with the exoccipital cannot be evaluated in dorsolateral view (Fig. 3I–L). The cranio-quadrate groove and foramen aereum can be ascertained only in UW6526A2. In particular, the foramen aereum is placed very far from their medial margin (Fig. 3I–J). Both hemicondyles are visible in posterior view, and the lateral one appears to be slightly larger than the medial one. The dorsal surface of the lateral hemicondyle appears to be dorsal to its medial counterpart.

Quadratojugal. A small portion of the left quadratojugal is partially preserved in UW6526A2 (Fig. 3I–L). The anterior portion is missing, but the quadratojugal contacts the quadrate posteromedially. No additional descriptive details can be provided.

Palatine. Only the posterior portion of this bone is preserved in UW6526A1. It is located posteromedial to the maxilla and anterior to the pterygoid (Figs. 3C–D, 5B). The anterior preserved portion is covered by bone fragments most likely derived from the lower jaw. A fissure between the palatines is roughly preserved.

Pterygoid. The pterygoids are poorly preserved, crushed and damaged in UW6526A1 (Fig. 3C–D). The posterior margins of the suborbital fenestra are formed by the paired pterygoids, and the medial margins are formed by the palatines (Figs. 3C–D, 5B).

Dentary. The dentaries converge anteriorly to each other. This bone contacts the splenial medially. Contacts with the surangular and angular cannot be restored. In UW6526A1, the mandibles are displaced. For this reason, the tooth count as well as the symphyseal region cannot be entirely observed (Fig. 3C–H). Nine teeth are visible in the right dentary. The third and fourth teeth are close to each other and equally large (Fig. 3C–D). Moreover, the tooth row is concavoconvex in lateral view, not linear, and also the most pronounced concavity occurs behind the fourth dentary tooth (Fig. 3C–D). Small pits decorate the external surface of both dentaries. UW6526A3 represents a left dentary fragment with one completely preserved tooth (Fig. 3O–P) and a sediment-filled alveolus (Fig. 3S–T).

Splenial. The splenial is completely preserved on the left mandible UW6526A1 (Fig. 3C–D). It lies on the medial surface of the dentary posterior to the dentary symphysis. It medially covers the Meckelian groove. Both dorsal and ventral splenial tips can be seen on the medial surface in UW6526A1. They neither contact each other nor reach the dentary symphysis. The ventral end of the splenial is anteriorly longer than the dorsal end, and it reaches the level of the fourth dentary tooth (Fig. 3C–D).

Angular. The angular forms the entire posteroventral portion of the mandible. In lateral view, the concave shape of the angular forms an obtuse posterior process visible in both UW6526A4 (Fig. 3U–V) and UW6526B2 (Fig. 4H). The ventral margin of the external mandibular fenestra can be observed only in UW6526B2 (Fig. 4H–I). Despite of the presence of some overlapping sediment, the external surface of the angular (Figs. 3U, 4H) preserves ornamentation formed by large irregular to subcircular pits.

Dentition. All teeth in both mandibles are attached to bone in a normal anatomical connection: UW6526A1 (Fig. 3A–H) and UW6526A3 (Fig. 3O–T). However, no additional isolated teeth are available. Our examination reveals the presence of five premaxillary teeth (Fig. 3C–D), more than eleven maxillary teeth (Fig. 3A–D), and at least nine dentary teeth (Fig. 3C–D). The total number of maxillary and dentary teeth is probably higher. In general, all teeth (premaxillary, maxillary, and dentary) are similarly conical, medially curved and with the slender and acute apical crowns. Furthermore, they are characterized by the conspicuous cutting edges and a lateral surface that is more convex than the medial one. The enamel is smooth, but some teeth have basal striations. Based on the state of preservation of UW6526A1, with the mandible completely attached to base of the skull, we cannot identify occlusal pits.

Vertebra. One partially procœlous vertebra is preserved. It corresponds to a neural centrum without arch (UW6526A5: Fig. 3A′–F′). The absence of the parapophysis indicates that it is not a cervical vertebra. This fragment represents most likely a caudal vertebra. In posterior view, the neural centrum is square-shaped.

Osteoderms. Five osteoderms are preserved: three in internal position (UW6526A2: Fig. 3K–L); and two dorsal in external position (UW6526A4: Fig. 3Y–Z). None are in anatomical position. They are subrectangular in shape, having an internal surface pierced by foramina, but not pitted. A dense, uniform network of subcircular pits is found on the dorsal osteoderms preserved in UW6526A4. A longitudinal keel is developed along the midline of the pitted regions. Because the anterior margins of the dorsal osteoderms are not preserved, we cannot ascertain if the anterior articular surface is smooth.

6. Discussion

6.1. Comparison of Tušimice material

Specimens from the Tušimice site (MN3, Czech Republic), Els Casots (MN4, Spain) and Saint-Gérand-le-Puy (MN2, France) are similar in many general patterns, such as the decoration and general outline of the skull, size of the orbits, and supratemporal and suborbital fenestrae. The material from Tušimice is roughly equal in size to Spanish material, but they are notably smaller than French specimens of *D. ratelii.* The smaller size of both individuals at Tušimice site is most surely reflecting an earlier ontogenetic stage. In terms of intraspecific variability, UW6526A1 shows a slightly broader preorbital area (clearly discernible from dorsal outline) unlike the specimens from Els Casots (IPS951 and IPS14721). However, our inspection of *D. ratelii* from Saint-Gérand-le-Puy suggests that this taxon can display both nose morphologies, as in Els Casots site (MNHN SG539), or alternatively as in the Tušimice site (MNHN SG13729a). The naris tends to be elliptical, slightly longer than wide, in IPS951 from Els Casots (not evaluable in Tušimice material: UW6526A1). Similarly, both variations are present in the naris from the type locality, being rather subcircular in MNHN SG652 or even slightly heart shaped as in MNHN SG13729a or MNHN SG652. All these above-mentioned distinctions may be due to different ontogenetic stages of the individuals, and therefore are inside the intraspecific variation of the species. Given that molecular data have revealed several modern crocodile species to be cryptic species complexes (Eaton et al., 2009; Hekkala et al., 2011; McAliley et al., 2006; Shirley et al., 2014), it is necessary to take into account all these morphological differences. More detailed comparisons of type material *D. ratelii* (not studied in detail yet) together with other poorly studied (Brinkman and Rauhe, 1998; Ginsburg and Bulot, 1997) or unpublished *Diplocynodon* remains (Montaigu: Delfino and Rossi, 2013), would be required to evaluate the ranges of the intraspecific variation of *D. ratelii* from the early Miocene of Europe.

6.2. Taxonomic attribution of the remains

As shown in the palynological and petrological results section, the crocodylian fossil remains stored at IGUW (Vienna, Austria) were most likely recovered from the Tušimice site (Bohemia, Czech Republic). These specimens can be referred to Alligatoroidea based on a dorsomedially located foramen aereum and a small, ventrally reflected medial hemicondyle of the quadrate (Brochu, 1999, 2003; Díaz Aráez et al., 2017; Martin, 2010; Martin and Gross, 2011; Martin et al., 2014). The combination of enlarged, subequal and confluent alveoli in both maxillary (fourth and fifth) and the dentary (third and fourth), together with the anterior extension of the lacrimal (which is longer than the prefrontals) allows us to refer them to *Diplocynodon* (Brochu, 1999; Díaz Aráez et al., 2017; Martin, 2010; Martin and Gross, 2011; Martin et al., 2014). At the species level, the material described here, in turn, displays the same combination of features as in the type species *D. ratelii*: the shape of the fronto-parietal suture (concavoconvex, not linear); the contour of the naris (a crest-like thickening on the margin of the external naris); the extension of the dentary symphysis (it reaches the posterior margin of the fourth alveolus); the relative position of the splenial, Meckelian groove and dentary symphysis (the splenial is excluded from the dentary symphysis and the ventral end of the splenial is anteriorly longer than the dorsal end); and the relationship between the nasals and external naris (the anterior tip of the nasals reach externally the posterior rim of the external naris). In fact, *D. ratelii* differs uniquely from the other species of *Diplocynodon* in having the nasals that do reach externally (but do not bisect) the posterior rim of the external naris (Díaz Aráez et al., 2017).

These diagnostic features were taken from Brochu et al. (2012), although codings for the above-mentioned characters were provided for five of the nine valid current species only: *D. darwini* (Ludwig, 1877), *D. hantoniensis* (Wood, 1846), *D. muelleri* (Kälin, 1936), *D. ratelii* Pomel, 1847 and *D. tormis* Buscalioni et al., 1992. Two recent additional added two species: *D. deponiae* (Frey et al., 1987) by Delfino and Smith (2012); and *D. elavericus* Martin, 2010, *D. ungeri* (Prangner, 1845), and *D. remensis* Martin et al., 2014 by Martin et al. (2014).

Diplocynodon represents a group of European endemic fossil alligatoroids that were rather abundant and widely distributed in the Late Paleogene to the Middle Neogene

deposits of Europe (Delfino and Smith, 2012; Díaz Aráez et al., 2017; Hua, 2004; Martin, 2010; Martin et al., 2014). According to Martin et al. (2014), up to nine species are taxonomically valid. In any case, *Diplocynodon* most probably arose during the Paleocene, as some of its most diagnostic features (e.g., the presence of two subequal and confluent alveoli in both the maxilla and dentary) are already present in its basal-most known members (Martin et al., 2014). During the late Miocene, *Diplocynodon* was restricted to South European refuges until became extinct due to a cooling event. For this reason, a short coexistence interval with *Crocodylus* cannot be excluded (Böhme, 2003; Delfino and Rossi, 2013; Delfino et al., 2007).

Cranial remains from Tušimice correspond to *Diplocynodon ratelii* recovered from the lower Miocene of France (Vaillant, 1872) and Spain (Díaz Aráez et al., 2017). This is based on two mandibular and three skull features. Based on the left medial surface of the dentary of UW6526A1 (Fig. 3C–D; see character #54 of Brochu et al., 2012), the ventral anterior tip of the splenial is longer than the dorsal one and there is no splenial symphysis. This is true for in seven of the nine *Diplocynodon* species: *D. darwini*, *D. deponiae*, *D. elavericus*, *D. hantoniensis*, *D. ratelii, D. tormis* and *D. ungeri* (Brochu et al., 2012; Delfino and Smith, 2012; Díaz Aráez et al., 2017; Hofmann, 1887; Martin et al., 2014). Although in *D. muelleri* the splenial is also excluded from the symphysis, its dorsal tip is longer than the ventral one. That means an inverse condition for the dorsal tip of the splenial, if compared to all the above-mentioned species (Brochu et al., 2012). According to Martin et al. (2014), the splenial participates in the mandibular symphysis in *D. remensis*. For this reason, the Tušimice remains cannot be allocated to *D. muelleri* or to *D. remensis*.

Concerning the symphyseal extension of the dentary (character #54 #49 of Brochu et al., 2012), UW6526A1 possesses a shorter symphysis and reaching the fourth or fifth dentary alveoli (Fig. 3C–D), as in *D. ratelii*, *D. muelleri,* and *D. remensis* (Brochu et al., 2012; Díaz Aráez et al., 2017; Martin et al., 2014). In contrast, a larger dentary symphysis at the level of the sixth to eighth alveoli can be observed in *D. elavericus*, *D. ungeri*, *D. hantonensis*, and *D. darwini* (Brochu et al., 2012; Hofmann, 1887; Martin and Gross, 2011; Martin et al., 2014). Even though the symphyseal extension of the dentary is not preserved in *D. tormis* or *D. deponiae*, this feature confirms that the Tušimice material is much consistent with *D. ratelii* (Brochu et al., 2012; Díaz Aráez et al., 2017; Martin et al., 2014).

Only one specimen from Tušimice (UW6526A1: Fig. 3A–B) preserves the snout, which preserves a crest-like thickening on the margin of the external naris (character #85, Brochu et al., 2012). Just two species within *Diplocynodon* included in previous analyses, *D. ratelii* and *D. muelleri*, display this trait (Díaz Aráez et al., 2017; Piras and Buscalioni, 2006). The margin of the external naris cannot be evaluated in *D. elavericus*, *D. tormis*, and *D. ungeri*. In any case, this feature supports an attribution to *D. ratelii*.

Both UW6526A1 and UW6526B1 from Tušimice (Figs. 3A–B, 4A–B) preserve a modestly posteriorly convex frontoparietal suture between the supratemporal fenestrae as in *D. ratelii* and *D. ungeri* (Brochu et al., 2012; Díaz Aráez et al., 2017; Martin et al., 2014). Conversely, an extremely concavoconvex suture is observed in other *Diplocynodon* species except for *D. elavericus*, in which the posterior skull table is damaged and therefore not preserved (Martin, 2010). Hence, this combination of features also reinforces an attribution to *D. ratelii*.

The relationships between the nasals and the external naris (character #82, Brochu et al., 2012) were studied in Tušimice material. UW6526A1 (Figs. 3A–B, 5A) clearly shows that the anteromedial projection of the nasals extends to the external naris. According to Díaz Aráez et al. (2017), this condition is present exclusively in all specimens of *D. ratelii*. This feature cannot be evaluated for *D. elavericus* and *D. deponiae* (Delfino and Smith, 2012; Martin, 2010). The extension of the nasal into the external naris is also consistent with referring the Tušimice material to *D. ratelii* rather than to any other named *Diplocynodon* species.

Finally, the described specimens from Tušimice site (MN3) possess the same diagnostic features as *D. ratelii*, and further display a set of features that discard confidently all other recognized species of *Diplocynodon*. The new material reported here from a latter locality represents the first report of *Diplocynodon* from the Most Basin (Eger Graben, Czech Republic). Therefore, this occurrence extends the geographic distribution of *D. ratelii* in central Europe, which was previously limited to western Europe (MN2 of France and MN4 of Spain). As stated above, the cranial differences reported at Tušimice, Els Casots, and Saint-Gérand-le-Puy may be due to younger ontogenetic stages or intraspecific variation. Based on sedimentological evidence and the abundant remains of anurans and freshwater snails, Tušimice represents a fluvio-lacustrine depositional system surrounded by bottomland swamp forest environments (Grygar et al., 2017a, 2017b; Kvaček et al., 2004). This paleoenvironmental reconstruction is reinforced by a micromammal assemblage associated with forested and humid environments (Fejfar, 1989; Fejfar and Kvaček, 1993). During the Miocene Climatic Optimum, central Europe presented high humidity and temperatures, which are optimal conditions for large ectothermic reptiles such as alligatoroids (Böhme, 2003; Delfino and Rossi, 2013). The presence of alligatorid *Diplocynodon* further supports the fluvio-lacustrine depositional system surrounded by bottomland swamp forest environments inferred for the Tušimice site. In particular, *Diplocynodon* needed permanent water bodies to live and a relatively high mean temperature (not less than 14.2 °C) to thermoregulate (Böhme, 2003; Delfino and Rossi, 2013; Markwick, 1998).

7. Conclusions

Diplocynodon ratelii was previously known only from the early Miocene (MN2) of France (Saint-Gérand-le-Puy, MN2; type locality) and Spain (Els Casots, MN4). The new material reported here from the Czech site of Tušimice extends the geographic distribution of *D. ratelii* in central Europe and represents the first report of *D. ratelii* from the Eger Graben, and more specifically from the Most Basin (Czech Republic). The presence of this freshwater crocodylian at Tušimice site fits well with a relatively high-temperature climate (mean annual temperature not less

than 14.2 °C), as well as a fluvio-lacustrine depositional system surrounded by bottomland swamp forest environments.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.crpv.2019.04.002.

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