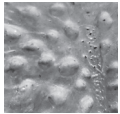# First remains of *Diplocynodon* cf. *ratelii* from the early Miocene sites of Ahníkov (Most Basin, Czech Republic)

Milan Chroust, Martin Mazuch, Martin Ivanov, Boris Ekrt & Àngel H. Luján

Fossil crocodylians from the early Miocene (Eggenburgian, MN3a) sites of Ahníkov (Most Basin, Czech Republic) are described in this paper. The new material presented here includes over 200 remains (bones, teeth and osteoderms), and therefore constitutes the largest crocodylian sample known from the fossil record of the Czech Republic. Assignment of the specimens to the fossil alligatoroid taxon *Diplocynodon* cf. *ratelii* Pomel, 1847 (family Diplocynodontidae) is justified by the presence of several cranial and postcranial features. In the Czech Republic, this species has been previously reported only from the Tušimice site (MN3, Most Basin, Ohře/Eger Graben). The majority of the material reported from Ahníkov is composed of disarticulated juvenile individuals. Both sites are most likely attributable to the specific environment of swampy areas, where crocodile hatchlings would hide from predators. The presence of the genus *Diplocynodon* supports the assumption of rather warm climatic conditions in Central Europe during the early to middle Miocene, as well as a swampy depositional environment previously inferred for Ahníkov. However, some squamate taxa suggest the existence of additional, surrounding palaeoenvironment characterised by a more open landscape with slightly drier conditions. • Key words: fossil crocodiles, alligatoroid, Ahníkov, Ohře/Eger Graben, Eggenburgian.

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Ahníkov (Most Basin, NW Czech Republic) is one of the most diverse and well-documented early Miocene sites in Central Europe. Apart from plant and invertebrate remains, to date, more than 150 species of fossil vertebrates have been reported (Dvořák *et al.* 2010). The fossil site is also known with the name of Merkur-North. Ahníkov is the name of a village destroyed due to the expansion of an opencast brown coal mine in the 1980s, which was called Merkur-North (Dvořák *et al.* 2010). According to Mach *et al.* (2017), both names (Ahníkov and Merkur-North) used for this palaeontological site are synonymous and the authors therefore referred to it as Ahníkov/Merkur Mine. However, we prefer to use just the name Ahníkov (for more details see Ekrt *et al.* 2016).

Ahníkov is located between the cities of Kadaň and Chomutov, more specifically 2 km SW from the Zelená village in the westernmost part of the Most Basin (Fig. 1). The site was discovered in the 1960s during drill cores prospection and the geological profile was exposed in the 1980s (Čtyroký *et al.* 1964a, b; Bůžek *et al.* 1988; Dvořák *et al.* 2010; Ekrt *et al.* 2016).

The Most Basin is the largest of the five Cenozoic freshwater basins along the Ohře/Eger Graben (Rajchl *et al.* 2009). The bedrock of the Most Basin consists of Proterozoic metamorphic rocks, covered by Carboniferous sediments and volcanic rocks; these are subsequently overlaid by Cretaceous marine sediments (Mach *et al.* 2014). At the site of Ahníkov, the bedrock is composed of deeply weathered biotitic paragneiss of pre-Variscan age. The Ohře/Eger Graben is the easternmost part of the European Cenozoic Rift System. The main volcanic activity and the beginning of sedimentation occurred

during the late Oligocene (see Rajchl *et al.* 2009 and references therein). As a result of subsidence, the Most Basin was infilled with fluvial sediments by the Central River (Pešek & Spudil 1986, Mach *et al.* 2017). This river flowed from Bohemia (Czech Republic) through the Most Basin (Fig. 1) into Saxony (Germany) and ended in the North Sea (Mach *et al.* 2014). The Central River formed a wide alluvial plain with large peat deposits and later on a lake developed. Then, lacustrine clays covered the peat accumulation. This was transformed into the lignite coal seam, which has been the main aim of the recent mining. The lake sediments have been dated magneto- and cyclostratigraphically approximately at 17.4 Ma (Matys Grygar *et al.* 2014), which corresponds to the onset of the Miocene Climatic Optimum. The upper parts of the lacustrine clays were eroded during the middle Miocene uplift of the basin (Ziegler & Dèzes 2007, Matys Grygar *et al.* 2014).

Most palaeontological findings were made in the 1980s and 1990s. In 1993, Ahníkov was declared a Natural Monument for the protection of eminent palaeontological location (Dvořák *et al.* 2010). At the beginning of the millennium, a series of landslides destroyed the original palaeontological site (hereinafter Ahníkov I) and consequently, the status of the Natural Monument was cancelled in 2009 (Ekrt *et al.* 2016). Not far from Ahníkov I, in the SE direction, there was a similar fossiliferous site that was named Ahníkov II (Ekrt *et al.* 2016). Unfortunately, this was covered and destroyed in 2018 as well.

According to Ekrt *et al.* (2016), three main lithological facies have provided fossils remains at Ahníkov: the mixture of clay and redeposited eroded bedrock; reworked, greenish volcanic ash rich in turtle shell fragments; and heterogeneous, irregularly rhythmic layers of claystones with a coal admixture, black or brown in colour, which are located just below the Main Coal Seam. All fossil remains are calcified and ranging in colour from grey to green, brown and black. The colour of the material depends on the rock origin. Additionally, sunlight and weathering processes changed the colour to substantially lighter. The preservation depends highly on the surface exposition time and the initial content of Fe-disulphides (mainly marcasite). Consequently, the Fe-disulphide degradation generates its products, gypsum and sulfuric acid. Especially, the material from coal rich facies is more affected. The fossilization process was influenced by mineral springs, which alkalized acidic swamps with calcium (Mach *et al.* 2017). Ahníkov II is formed by claystones with a coal admixture rich in fossil gastropods (Kadlecová *et al.* 2013).

From the sedimentological viewpoint, the Ahníkov fossil sites are located in the western margin of the Most Basin and the sediments therefore represent swamp and lacustrine environments. As for the age of Ahníkov, the locality belongs to the Holešice Member of the Most Formation, with micromammalian assemblages corresponding to the MN3a zone (Fejfar & Kvaček 1993, Fejfar *et al.* 2003, Matys Grygar *et al.* 2014, van den Hoek Ostende & Fejfar 2015).

The genus *Diplocynodon*

The extinct genus *Diplocynodon*, originally described by Pomel (1847), is a fossil alligatoroid considered endemic to Europe that was distributed widely from the Palaeocene to the Miocene (Hua 2004, Martin 2010, Delfino & Smith 2012, Martin *et al.* 2014). Up to nine different species are currently considered valid, the stratigraphically oldest of them being *Diplocynodon remensis* from the late Paleocene of France (Martin *et al.* 2014). During the Eocene epoch, *Diplocynodon* spread across Europe and diversified into five species: *D. tormis* from the middle Eocene of Spain (Buscalioni *et al.* 1992); *D. darwini* and *D. deponiae* from the middle Eocene of Germany (Ludwig 1877; Berg 1966, 1969; Frey *et al.* 1987; Rossmann & Blume 1999; Delfino & Smith 2012); and *D. elavericus* and *D. hantoniensis* from the late Eocene of France and England, respectively (Wood, 1846, Martin 2010, Rio *et al.* 2019). In the early Oligocene, *D. muelleri* from Spain is the only valid species (Kälin 1936, Piras & Buscalioni 2006). At the beginning of the Miocene, *D. ratelii* was the most widespread *Diplocynodon* species in Europe, having been reported from the present-day France, Spain and the Czech Republic (Pomel 1847, Vaillant 1872, Díaz Aráez *et al.* 2017, Luján *et al.* 2019, Macaluso *et al.* 2019). Finally, *D. ungeri* was recorded from the middle Miocene localities of Austria and France (Prangner 1845; Hofmann 1887a, b; Ginsburg & Bulot 1997; Martin & Gross 2011). In Central Europe, *Diplocynodon* is considered to have gone extinct during to a cooling event after the Miocene Climatic Optimum (Böhme 2003, Hua 2004, Delfino *et al.* 2007, Martin 2010, Delfino & Smith 2012, Martin *et al.* 2014). However, the records of cf. *Crocodylus* in the central Mediterranean at 9 Ma (Delfino & Rossi 2013, Delfino *et al.* 2021) together with the records of *Diplocynodon* sp. from several late Miocene European localities (Böhme & Ilg 2003) do not rule out a possibility of a short coexistence of both genera (see also Delfino & Rook 2008, Martin & Gross 2011).

In the Czech Republic, crocodylian fossil remains have been known since the 19th century. These early reports were based on isolated teeth and osteoderms (bony plates located under the skin) from the Vintířov village (close to Kadaň) and the Tušimice site (Josef-Oswald mine), both located in the Most Basin (Jokély 1858; Štúr 1873, 1879). Additional fragmentary finds of fossil crocodylians have been reported from the Most Basin during the 20th century, such as from the Tušimice site (a partial jaw,
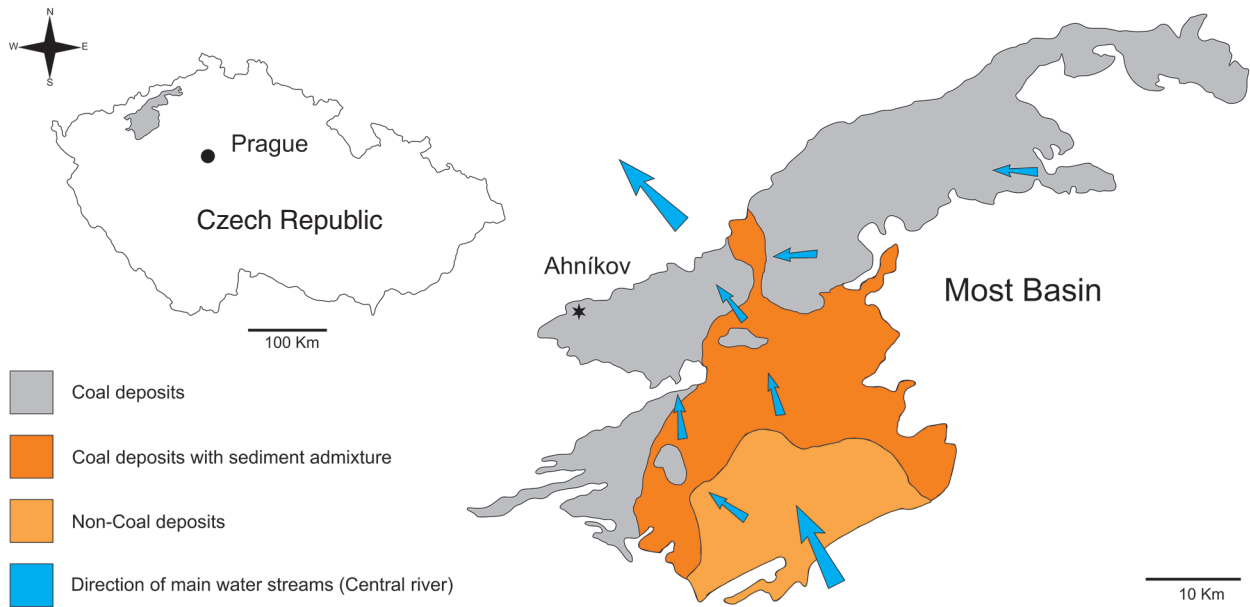
Figure 1. Geographic allocation of the Ahníkov fossil sites (early Miocene, Czech Republic) and a simplified geological map showing coal and non-coal deposits of the Holešice Member (Most Basin, MN3). Modified from Elznic *et al.* (2010).

an isolated tooth, osteoderms and postcranial bones: Laube 1901, 1910) and Břešťany (a natural mold of a mandible and two osteoderms; Frič 1903). In any case, the highest number of crocodylian fossil remains (skull fragments, postcranial bones and osteoderms) was collected during the 1990s at Ahníkov (Fejfar & Schleich 1994, Dvořák *et al.* 2010, Luján *et al.* 2019). In his Master thesis, Vejvalka (1997) preliminarily described the amphibian and squamate material, but also mentioned the crocodylian material referred to genus *Diplocynodon* sp. Lately, crocodylian material were figured and referred to *Diplocynodon* cf. *darwini* by Dvořák *et al.* (2010), but this taxonomic assignment has not been sufficiently justified. More recently, crocodylian remains from several Eocene and Oligocene sites in NW Czech Republic (Chroust *et al.* 2019) and the Tušimice site (early Miocene, Most Basin) have been described (Luján *et al.* 2019).

In this paper, we provide a comprehensive revision of the taxonomy and describe the most relevant specimens of the crocodylian remains available from Ahníkov. We discuss palaeoenvironmental conditions of the Ahníkov sites based on new data obtained not only from fossil crocodylians, but from a further analysis of squamate fauna.

Material and abbreviations

Crocodylian fossil remains were collected by Z. Dvořák, O. Janeček, P. Coufal and O. Fejfar between the 1990s

and 2016. Between 2013 and 2019, selected collections were transferred to the public collection of the National Museum in Prague, where they are currently housed. The material was collected from the surface, where it had naturally weathered. To date, over 200 fragments of crocodilian fossil remains have been recovered. The majority of them being isolated teeth and osteoderms. However, only about 60 specimens show taxonomically useful characters. Photographs were taken with a Nikon D60 camera.

Institutional abbreviations: NMP – National Museum, Prague, Czech Republic.

Systematic palaeontology

Order Crocodylia Gmelin, 1789
Superfamily Alligatoroidea Gray, 1844
Family Diplocynodontidae Hua, 2004

Genus *Diplocynodon* Pomel, 1847

Type species. – *Diplocynodon ratelii* Pomel, 1847.

Diplocynodon cf. *ratelii* Pomel, 1847
Figures 2–10

Material. – All specimens from Ahníkov consist of numerous disarticulated osteoderms and teeth, as well as postcranial and cranial bones, except for two skull (squa-

mosal and postorbital; NMP Pv 11611–12) and mandible bones (dentary and maxilla; NMP Pv 11632), which are preserved in the anatomical position (see more below). We provide all unpublished specimens of *Diplocynodon* cf. *ratelii* reported in this paper listed in Tab. 1.

Description. – All material is described separately in the anteroposterior direction, where the hindlimbs are the last.

P r e m a x i l l a : One partial left premaxilla (NMP Pv 11603; Fig. 2A) is preserved, being longer than wide. It is the anteriormost bone of the snout and contacts the maxilla posterolaterally and the nasal posteromedially.

The dorsal surface of NMP Pv 11603 is densely decorated by pits. Although two alveoli (the fourth and fifth) are discerned in the ventral view, teeth are missing (Fig. 2A). The fourth alveolus is the largest (Fig. 2A). Only the posteromedial margin of the incisive foramen is preserved and seems to be small.

M a x i l l a : Three fragments of the maxilla are available (NMP Pv 11604–05, 11632; Fig. 2B–F). They are longer than wide and the dorsal surface of bone is pitted. The lateral edge of the right maxilla is almost straight (Fig. 2B, D). In the ventral view, four alveoli without the teeth (roughly equal in size) are preserved (NMP Pv 11605; Fig. 2E). Specimen NMP Pv 11632

Table 1. List of fossil specimens of *Diplocynodon* cf. *ratelii* from the Ahníkov sites included in this study.

| Catalogue no.	Anatomical description	Locality	Figure	Catalogue no.	Anatomical description	Locality	Figure
NMP Pv 11603	Premaxilla	Ahníkov I	2A	NMP Pv 11658	Tooth	Ahníkov I	6U
NMP Pv 11604	Maxilla	Ahníkov I	2B, C	NMP Pv 11659	Tooth	Ahníkov I	6V
NMP Pv 11605	Maxilla	Ahníkov I	2D, E	NMP Pv 11660	Tooth	Ahníkov I	6W
NMP Pv 11632	Partial maxilla and dentary	Ahníkov II	2F	NMP Pv 11661	Tooth	Ahníkov II	6X
NMP Pv 11607	Jugal	Ahníkov I	3A, B	NMP Pv 11662	Tooth	Ahníkov II	6Y
NMP Pv 11608	Jugal	Ahníkov I	3C, D	NMP Pv 11663	Osteoderm	Ahníkov I	7A
NMP Pv 11609	Jugal	Ahníkov I	3E, F	NMP Pv 11664	Osteoderm	Ahníkov I	7B
NMP Pv 11610	Jugal	Ahníkov I	3G, H	NMP Pv 11665	Osteoderm	Ahníkov I	7C
NMP Pv 11635	Frontal	Ahníkov II	4A	NMP Pv 11644	Osteoderm	Ahníkov II	7D
NMP Pv 11636	Frontal	Ahníkov II	4B	NMP Pv 11645	Osteoderm	Ahníkov II	7E
NMP Pv 11637	Frontal	Ahníkov II	4C	NMP Pv 11646	Osteoderm	Ahníkov II	7F
NMP Pv 11649	Frontal	Ahníkov II	4D	NMP Pv 11666	Osteoderm	Ahníkov II	7G
NMP Pv 11611	Postorbital	Ahníkov I	4E	NMP Pv 11667	Osteoderm	Ahníkov I	7H
NMP Pv 11639	Squamosal	Ahníkov II	4F	NMP Pv 11668	Osteoderm	Ahníkov I	7I
NMP Pv 11612	Squamosal	Ahníkov I	4G	NMP Pv 11627	Cervical vertebra	Ahníkov I	8A
NMP Pv 11613	Basioccipital	Ahníkov I	5A	NMP Pv 11621	Cervical vertebra	Ahníkov I	8B
NMP Pv 11619	Dentary	Ahníkov I	5B	NMP Pv 11647	Cervical vertebra	Ahníkov II	8C
NMP Pv 11614	Dentary	Ahníkov I	5C, E	NMP Pv 11648	Cervical vertebra	Ahníkov II	8D
NMP Pv 11615	Dentary	Ahníkov I	5F	NMP Pv 11625	Dorsal trunk vertebra	Ahníkov I	8E
NMP Pv 11640	Angular	Ahníkov II	5G	NMP Pv 11626	Dorsal trunk vertebra	Ahníkov I	8F
NMP Pv 11650	Tooth	Ahníkov I	6A–C	NMP Pv 11622	Dorsal trunk vertebra	Ahníkov I	8G
NMP Pv 11651	Tooth	Ahníkov I	6D–F	NMP Pv 11628	Dorsal trunk vertebra	Ahníkov II	8H, I
NMP Pv 11652	Tooth	Ahníkov I	6G–I	NMP Pv 11624	Dorsal trunk vertebra	Ahníkov I	8J
NMP Pv 11653	Tooth	Ahníkov I	6J–L	NMP Pv 11623	Caudal vertebra	Ahníkov I	8K
NMP Pv 11654	Tooth	Ahníkov I	6M–O	NMP Pv 11629	Partial humerus	Ahníkov I	9A–D
NMP Pv 11655	Tooth	Ahníkov I	6P–R	NMP Pv 11634	Partial femur	Ahníkov II	9E–H
NMP Pv 11656	Tooth	Ahníkov I	6S	NMP Pv 11630	Partial femur	Ahníkov I	9I–L
NMP Pv 11657	Tooth	Ahníkov I	6T	NMP Pv 11631	Partial metatarsal	Ahníkov I	9M–P
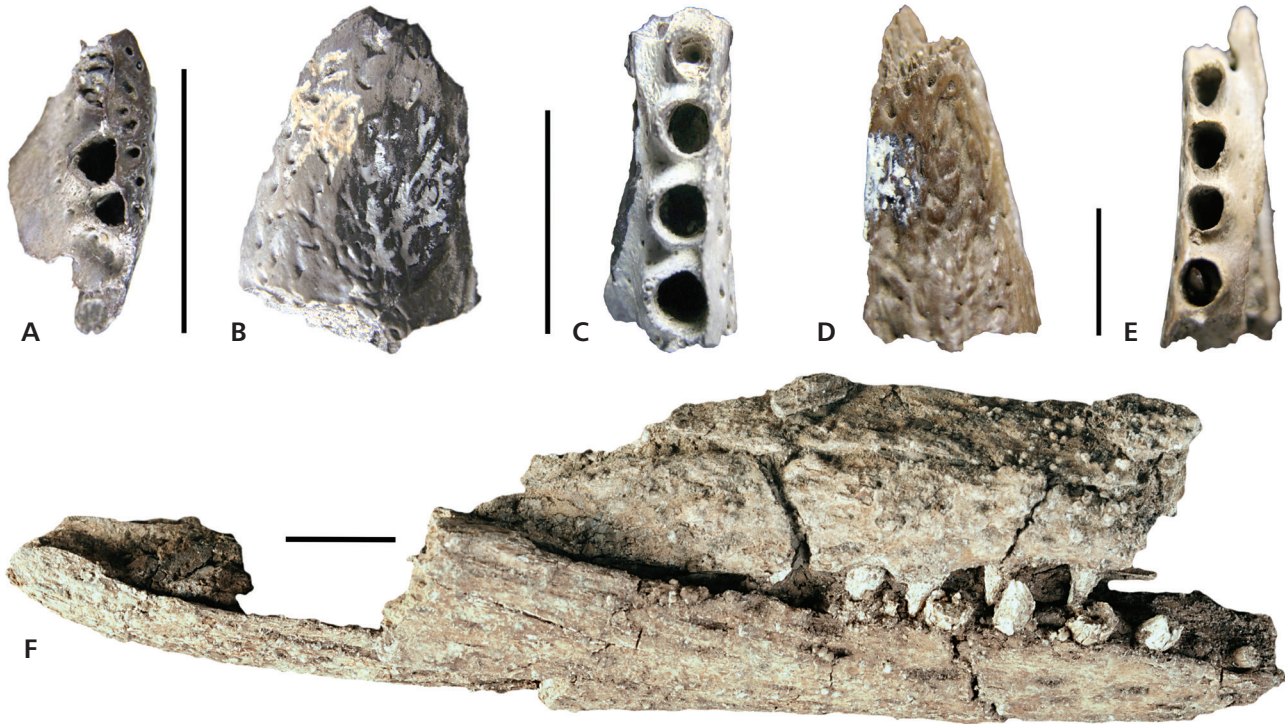
Figure 2. Cranial remains of the fossil alligatoroid taxon *Diplocynodon* cf. *ratelii* from the Ahníkov fossil sites (early Miocene, Czech Republic). A – NMP Pv 11603 left premaxilla in ventral view; B, C – NMP Pv 11604 left partial maxilla in dorsal (B) and ventral views (C); D, E – NMP Pv 11605 left partial maxilla in dorsal (D) and ventral views (E); F – NMP Pv 11632 right partial dentary and maxilla in right lateral view. Scale bar is 10 mm.

is a right fragment of the skull (Fig. 2F) preserving the maxilla and five incomplete teeth.

Jugal: Four jugals were recovered (NMP Pv 11607–10; Fig. 3A–H), which form the ventral margin of the orbits. They are longer than wide and posteriorly terminate in an acute process (Fig. 3A–H). Subcircular pits heavily ornamented their dorsolateral surface. All four preserved jugals display at least one large medial foramen (Fig. 3B, D, F, H). A very large medial jugal foramen is developed, just anteriorly to the postorbital bar in NMP Pv 11607 (Fig. 3B). The proximal part of the postorbital bar is preserved.

Frontal: Four posterior fragments of the frontals have been preserved (Fig. 4A–D). They are placed between the orbits and connect the snout with the skull table. The frontal is triangular, longer than wide and all of them show a pitted dorsal surface (Fig. 4A–D). They are markedly concave between the orbits, with elevated orbital margins. The posterior suture of the frontal is notably convex, not lineal, and discerned in three of the four bones (NMP Pv 11635–36, 11649; Fig. 4A, B, D). In NMP Pv 11637 (Fig. 4C), the posterior suture is not well preserved.

Postorbital: It is located on the anterolateral edge of the skull table, which is subtrapezoidal, slightly longer than wide (NMP Pv 11611; Fig. 4E, H). The postorbital contributes to the anterolateral margin of the supratemporal fenestra, the posterior orbital margin and the anterodorsal margin of the infratemporal fenestra. Only the proximal portion of the postorbital bar is preserved, which is slender and with sharp lateral edges.

Squamosal: Two squamosals are available (NMP Pv 11612, 11639; Fig. 4F, G), where one of them is almost complete (NMP Pv 11639; Fig. 4G,H). It is longer than wide and contributes to the posterolateral margin of the skull table. Its dorsal surface is rather flat and pitted. A short posterolateral process is developed in a posterolateral direction. Both dorsal and ventral rims of the squamosal groove are visible in the lateral view. The posteromedial margin of the squamosal is rather convex. The squamosal-parietal suture is straight. NMP Pv 11612 (squamosal; Fig. 4G) and NMP Pv 11611 (postorbital; Fig. 4E) belong to the same individual (Fig. 4H), as both bones fit well.

Basioccipital: The basioccipital (NMP Pv 11613; Fig. 5A) forms the ventral part of the occipital condyle and most of the basioccipital plate. The condyle has a semi-circular outline.

Dentary: Seven partially-preserved dentaries have been preserved (NMP Pv 11614–19, 11632; Fig. 5B–F). The dentary is the longest bone of the mandible and anteriorly converges with its counterpart side. Small pits
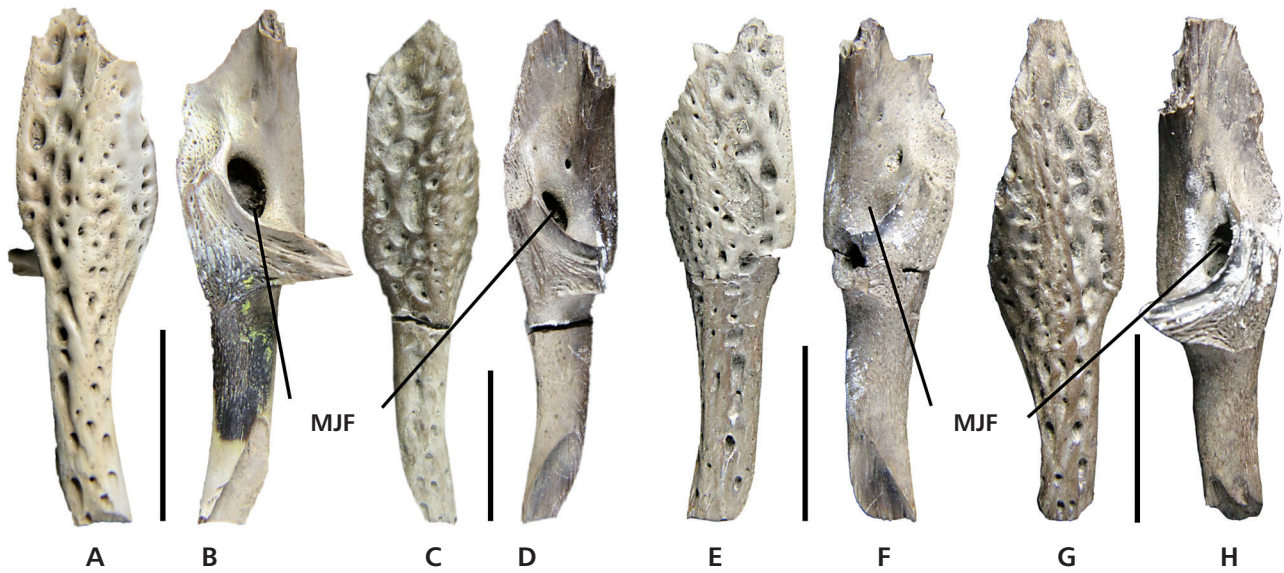
Figure 3. Jugal bones of the fossil alligatoroid taxon *Diplocynodon* cf. *ratelii* from the Ahníkov fossil sites (early Miocene, Czech Republic). A, B – NMP Pv 11607 in external (A) and internal views (B); C, D – NMP Pv 11608 in external (C) and internal views (D); E, F – NMP Pv 11609 in external (E) and internal views (F); G, H – NMP Pv 11610 in external (G) and internal views (H). Abbreviation: MJF – medial jugal foramen. Scale bar is 10 mm.
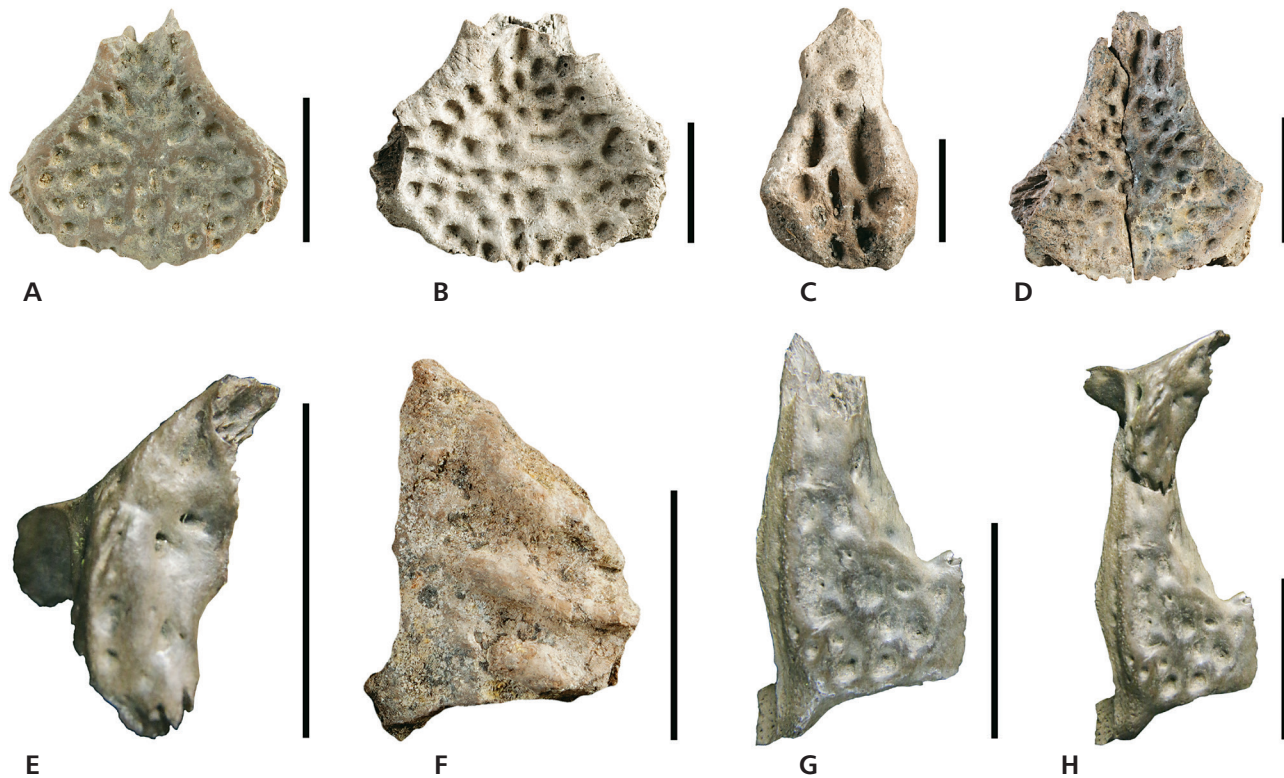

Figure 4. Cranial remains of the fossil alligatoroid taxon *Diplocynodon* cf. *ratelii* from the Ahníkov fossil sites (early Miocene, Czech Republic). A – NMP Pv 11635 partial frontal in dorsal view; B – NMP Pv 11636 partial frontal in dorsal view; C – NMP Pv 11637 partial frontal in dorsal view; D – NMP Pv 11649 partial frontal in dorsal view; E – NMP Pv 11611 postorbital in dorsolateral view; F – NMP Pv 11639 partial squamosal in dorsal view; G – NMP Pv 11612 partial squamosal in dorsal view; H – NMP Pv 11611–12 postorbital-squamosal in dorsal view. Scale bar is 10 mm.

Figure 5. Cranial and mandible remains of the fossil alligatoroid taxon *Diplocynodon* cf. *ratelii* from the Ahníkov fossil sites (early Miocene, Czech Republic). A – NMP Pv 11613 basioccipital in ventral view; B – NMP Pv 11619 partial dentaries in dorsal view; C–E – NMP Pv 11614 partial dentary in dorsal (C), left lateral (D) and internal (E) views; F – NMP Pv 11615 partial dentary in dorsal view; G – NMP Pv 11640 left partial angular in external view. Abbreviations: CNF – foramen for cranial nerve V; DSS – dorsal splenial suture; VSS – ventral splenial suture. Scale bar is 10 mm.

decorate the external surface of all preserved dentaries. The anterior part of all dentaries (*i.e.* just ahead of the second alveolus) is missing and therefore the tooth count and the symphyseal region cannot be evaluated. The best-preserved dentary (NMP Pv 11614; Fig. 5C–E) has eight alveoli. Only the second alveolus is partially preserved in NMP Pv 11619 (Fig. 5B). The third and fourth alveoli are confluent (Fig. 5B, C, F). The third alveolus is slightly larger than the fourth. The sixth alveolus preserves a whole tooth (Fig. 5C–E), whereas the fifth and seventh alveoli contain broken teeth. Both right dentaries (NMP Pv 11614–15; Fig. 5C, F) have eight alveoli. In the dorsal view, the dentary symphysis extends to the third or fourth alveolus (Fig. 5B, C, F) and therefore, the splenial is excluded from the symphysis, the ventral tip of which is longer than the dorsal one (Fig. 5E). The channel for cranial nerve V is also discernible in NMP Pv 11614 (Fig. 5E).

Angular: Five fragmentary angulars were recovered, whereas NMP Pv 11640 (Fig. 5G) is the best preserved among them. The angular is the posteroventral bone of the mandible. It is longer than wide and is U-shaped in anteroposterior view. The preserved portion of the external surface is heavily pitted. Only the ventral margin of the external mandibular fenestra is preserved (Fig. 5G). The medial margin of the angular bone forms the ventral border of the foramen intermandibularis caudalis.

Dentition: More than 80 isolated teeth are available (Fig. 6A–Y). In general, all teeth are conical with smooth surfaces, medially curved and the lateral surface is more convex than the medial one. However, our examination reveals the presence of two morphotypes. The first

morphotype corresponds to the anterior part of the snout (*i.e.* premaxillary, dentary and anterior maxillary teeth). All of them are more curved lingually, with acute apical crowns and with faint longitudinal striations (Fig. 6A–R). Most large teeth have incremental lines with a different colour, which indicate the growth of the tooth (Fig 6A, I, M). Carinae occur on the anterior and posterior edges of all teeth. The second morphotype corresponds to the posterior part of the dentary and maxilla (Fig. 6S–Y), which contains shorter, globular and less lingually curved teeth. A small constriction that separates the tooth crown from the root is almost always present. They retain a modest carinae and relatively pointed tips (Fig. 6S–Y).

Osteoderms: More than 90 osteoderms are preserved (Fig. 7A–I). The dorsal osteoderms are subrectangular shaped. Their internal surface is pierced by foramina but not pitted (Fig. 7A–C). The dorsal surface presents a dense and more or less uniform network of subcircular pits. A longitudinal keel is developed along the central part of the element, which can be slightly curved. The anterior articular surface of the dorsal osteoderms is smooth (7A–C). The ventral osteoderms have two units (bipartite osteoderms), that are sutured together and always devoid of any keel. The anterior half of ventral osteoderm is generally wider than long (Fig. 7E), with a smooth and slightly thicker anterior articular surface (Fig. 7D–F). The posterior half of ventral osteoderm is subquadrate in shape and pitted (Fig. 7G–I).

Vertebrae: Ten isolated vertebrae were recovered from Ahníkov (Fig. 8A–K), including cervical, dorsal and caudal vertebrae. All vertebral centra are fully
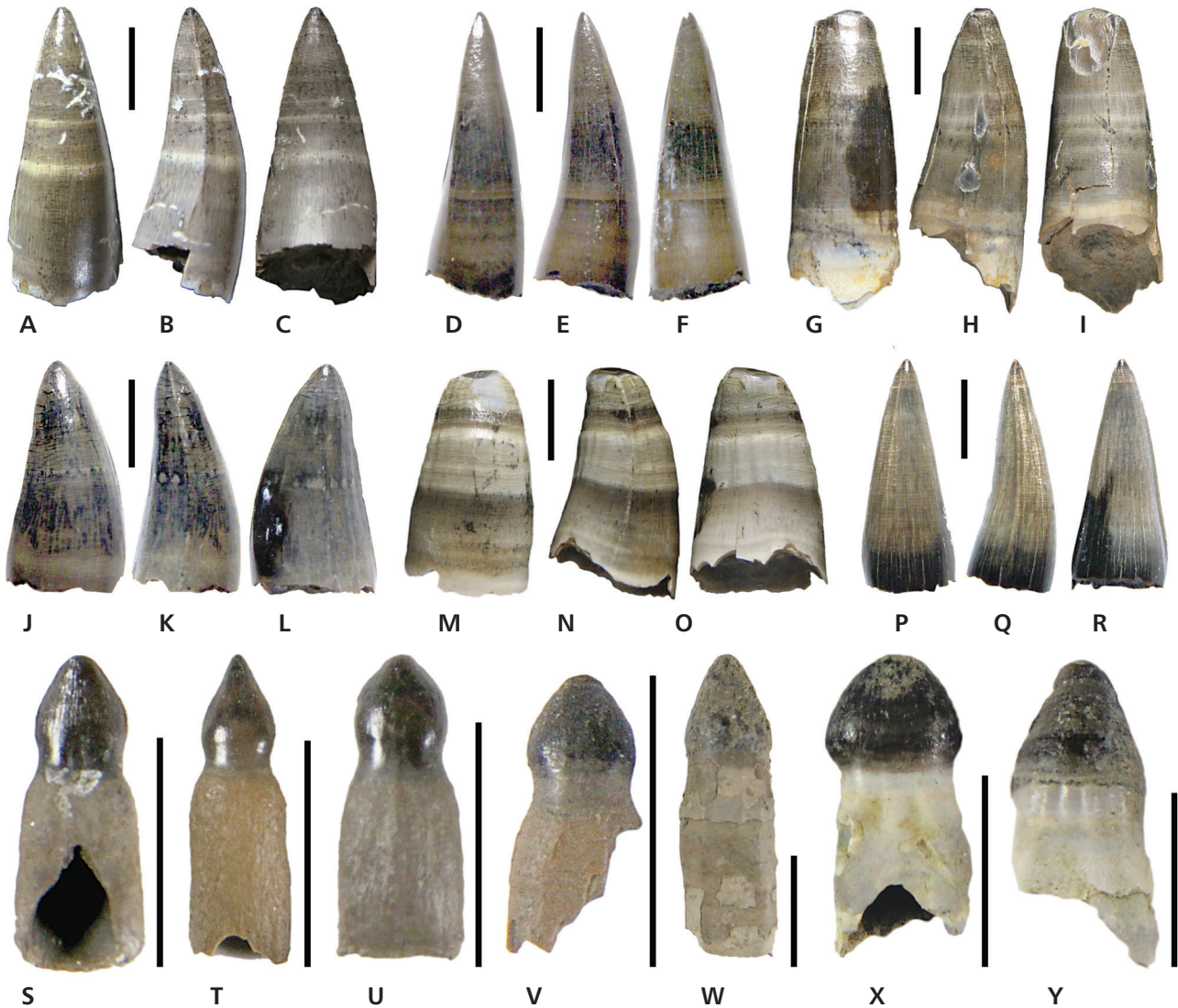
Figure 6. Teeth remains of the fossil alligatoroid taxon *Diplocynodon* cf. *ratelii* from the Ahníkov fossil sites (early Miocene, Czech Republic). A–C – NMP Pv 11650 in labial (A), anteroposterior (B), lingual views (C); D–F – NMP Pv 11651 in labial (D), anteroposterior view (E), lingual views (F); G–I – NMP Pv 11652 in lingual (G), anteroposterior (H), labial views (I); J–L – NMP Pv 11653 in labial view (J), anteroposterior view (K), lingual views (L); M–O – NMP Pv 11654 in labial (M), anteroposterior (N), lingual views (O); P–R – NMP Pv 11655 in labial (P), anteroposterior (Q), lingual views (R); S – NMP Pv 11656 in labial view; T – NMP Pv 11657 in labial view; U – NMP Pv 11658 in labial view; V – NMP Pv 11659 in labial view; W – NMP Pv 11660 in labial view; X – NMP Pv 11661 in labial view; Y – NMP Pv 11662 in labial view. Scale bar is 10 mm.

procoelous, are therefore concave anteriorly and convex posteriorly. Any cervical vertebrae preserve the neural arch (NMP Pv 11621, 11627, 11647–48; Fig. 8A–D). NMP Pv 11627 partially preserves the hypapophysis (Fig. 8A). The ventral surface of its cervical centrum lacks deep pits. The neural arch is not completely sutured to the vertebral centrum (NMP Pv 11621; Fig. 8B), which indicates that this is not an adult individual (Brochu 1996). Two lateral facets, the parapophyses, are discerned in the posterior part of the vertebral body. The size of the vertebral body of NMP Pv 11648 (Fig. 8D) suggests that it is most likely either the second, or third cervical. It has a fused isolated

osteoderm on its lateral surface. According to the general shape of the neural body (NMP Pv 11647; Fig. 8C), it seems this is the fifth cervical. The base of the left parapophysis is poorly preserved (Fig. 8C).

Unlike the cervical vertebrae, the dorsal vertebrae (NMP Pv 11622, 11624-26, 11628; Fig. 8E–J) have larger vertebral centra. Both ventral and lateral surfaces of the vertebral body are smooth, without remnants of the hypapophysis and the parapophyses. NMP Pv 11628 (Fig. 8H–I), has the neural arch poorly preserved, however, the preserved portion of the diapophysis extends laterally. The proximalmost part of the postzygapophysis is broken

off and fused with the neural arch. In the lateral view, the neural arch suture of NMP Pv 11624 is sinuous (Fig. 8J). Both NMP Pv 11625 and 11626, have a neural arch not fused to the vertebral body and these specimens, therefore, represent juvenile individuals (Fig. 8E, F).

The first caudal vertebra (NMP Pv 11623; Fig. 8K) is preserved without the neural arch. Although the vertebral centrum shares the same features as the dorsal vertebrae, however, the posterior condyle is very apical. The edge of the posterior condyle ends in a sharp ridge.

H u m e r u s : One almost complete left humerus is preserved (NMP Pv 11629; Fig. 9A–D). The proximal epiphysis lacks the deltopectoral crest (Fig. 9C), whereas the humeral shaft is slightly damaged (Fig. 9A). In dorsal view, both the proximal and distal epiphyses are posteriorly offset (Fig. 9A) and consequently, the posterior margin of the humeral shaft is strongly concave. The major trochanter is much longer than the minor, extending below of the maximum height of the humeral head, whereas the minor ends at the beginning of the humeral
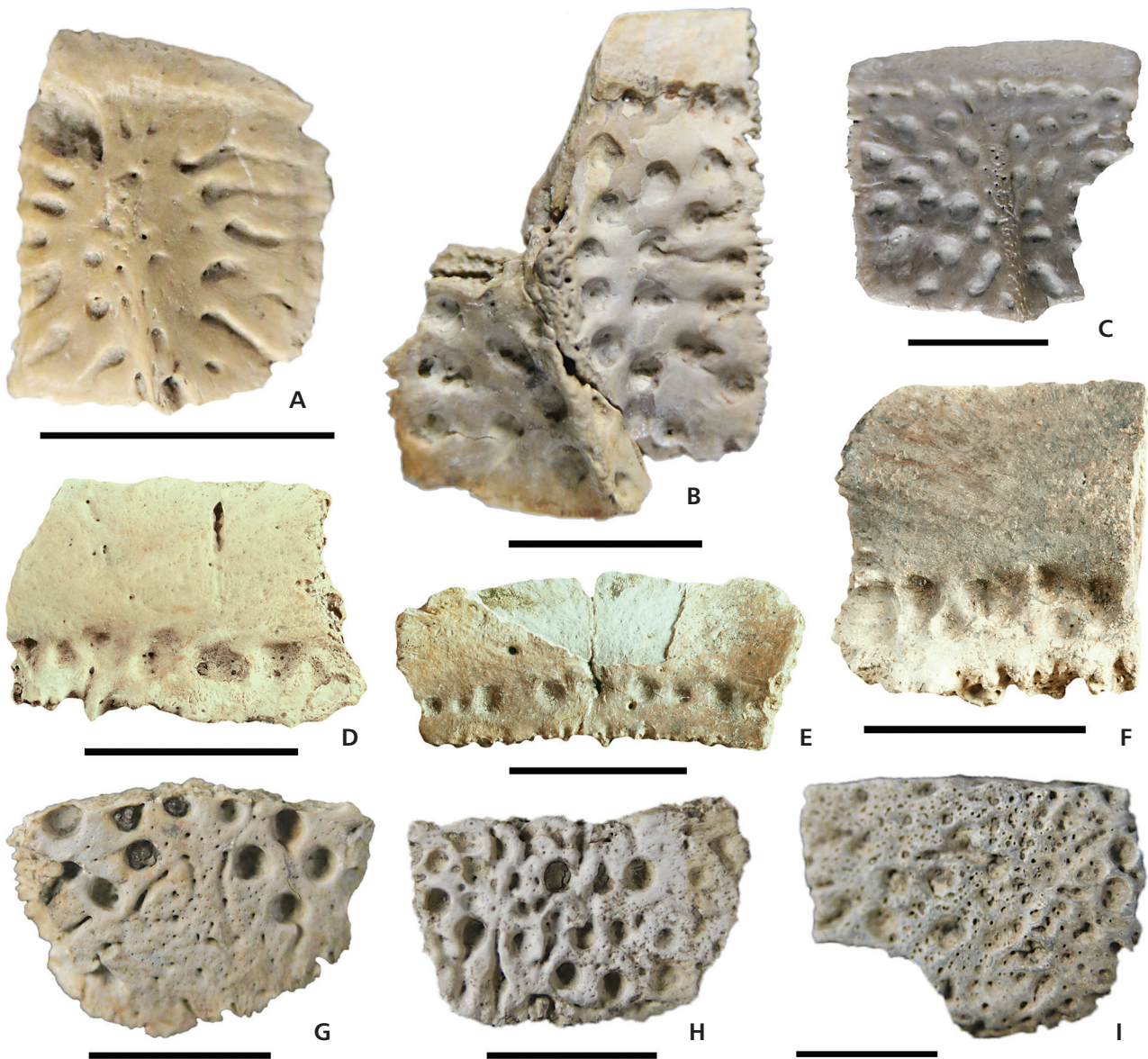

Figure 7. Osteoderms of the fossil alligatoroid taxon *Diplocynodon* cf. *ratelii* from the Ahníkov fossil sites (early Miocene, Czech Republic). A – NMP Pv 11663 dorsal osteoderms in external view; B – NMP Pv 11664 dorsal osteoderm in external view; C – NMP Pv 11665 dorsal osteoderm in external view; D – NMP Pv 11644 anterior ventral osteoderm in ventral view; E – NMP Pv 11645 anterior ventral osteoderm in ventral view; F – NMP Pv 11646 anterior ventral osteoderm in ventral view; G – NMP Pv 11666 posterior ventral osteoderm in ventral view; H – NMP Pv 11667 posterior ventral osteoderm in ventral view; I – NMP Pv 11668 posterior ventral osteoderm in ventral view. Scale bar is 10 mm.

head. The humeral head is elliptical-shaped (Fig. 9A). On the lateral margin of the humeral shaft, a single scar for the insertion of Musculus teres major and M. latissimus dorsi is preserved. The medial and lateral hemicondyles of the distal extremity are not equidimensional, being the medial one the largest and rounded (Fig. 9A, C). A prominent trochlea divides the lateral and medial hemicondyles of the humerus (Fig. 9C).

F e m u r : Two femora are preserved: a complete proximal left epiphysis (NMP Pv 11634; Fig. 9E–H) and a partial right proximal epiphysis (NMP Pv 11630; Fig. 9I–L). The proximal epiphysis of the femur is medio-laterally compressed (Fig. 9E–H). Both the insertion of the M. pubo-ischio-femoralis internus and externus are preserved (Fig. 9H), the latter being quite large in NMP Pv 11630 (Fig. 9K). The M. iliofemoralis crest is well developed in the dorsal direction (Fig. 9E, F). Although it is slightly eroded, the scarf after the 4th trochanter is also preserved (Fig. 9I).

M e t a t a r s a l : An undetermined partial right metatarsal is available (NMP Pv 11631; Fig. 9M–P). The distal epiphysis of the metatarsal is missing, whereas the proximal one is quadrangular, with perpendicular lateral margins. The diaphysis is subrectangular in cross-section. The proximal facet is slightly concave.

Discussion

Taxonomic status of the studied material

The specimens reported from Ahníkov are referred to the alligatoroid genus *Diplocynodon* in having: (1) two subequal and confluent alveoli in both the maxilla (fourth and fifth alveoli) and dentary (third and fourth alveoli); (2) keeled dorsal osteoderms; (3) bipartite ventral osteoderms; (4) and hypapophysis located toward the centrum (*e.g.* Brochu 1999, Martin *et al*. 2014). Despite the fact that it is not diagnostic at the genus level, the material from Ahníkov displays a very large medial jugal foramen, which is typical for all diplocynodontid crocodylians (see Brochu 1997).

As for the species level, the ventral anterior tip of the splenial (preserved in two dentaries: NMP Pv 11614–15, Fig. 5C–F) is longer than the dorsal one and is excluded from the dentary symphysis. This splenial condition displayed by the material from Ahníkov is also seen in *D. deponiae*, *D. elavericus*, *D. tormis*, *D. hantoniensis*, *D. darwini*, *D. ungeri*, and *D. ratelii* (Martin 2010, Brochu *et al*. 2012, Delfino & Smith 2012, Martin *et al*. 2014, Díaz Aráez *et al*. 2017, Luján *et al*. 2019). Three of the four preserved frontals (NMP Pv 11635, NMP Pv
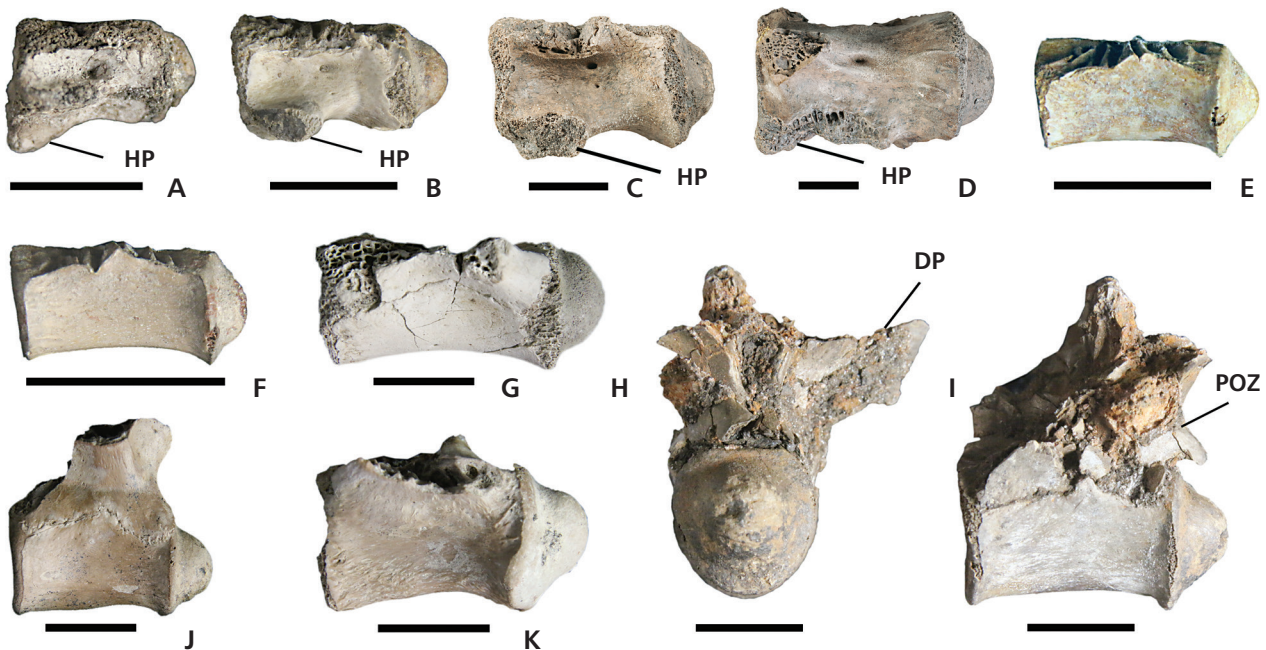

Figure 8. Vertebrae remains of the fossil alligatoroid taxon *Diplocynodon* cf. *ratelii* from the Ahníkov fossil sites (early Miocene, Czech Republic). A – NMP Pv 11627 cervical vertebra in left lateral view; B – NMP Pv 11621 cervical vertebra in left lateral view; C – NMP Pv 11647 cervical vertebra in left lateral view; D – NMP Pv 11648 cervical vertebra in left lateral view; E – NMP Pv 11625 dorsal vertebra in left lateral view; F – NMP Pv 11626 dorsal vertebra in left lateral view; G – NMP Pv 11622 dorsal vertebra in left lateral view; H – NMP Pv 11628 dorsal vertebra in caudal view; I – NMP Pv 11628 dorsal vertebra in left lateral view; J – NMP Pv 11624 dorsal vertebra in left lateral view; K – NMP Pv 11623 caudal vertebra in left lateral view. Abbreviations: DP – diapophysis; HP – hypapophysis; PA – parapophysis; POZ – postzygapophysis. Scale bar is 10 mm.
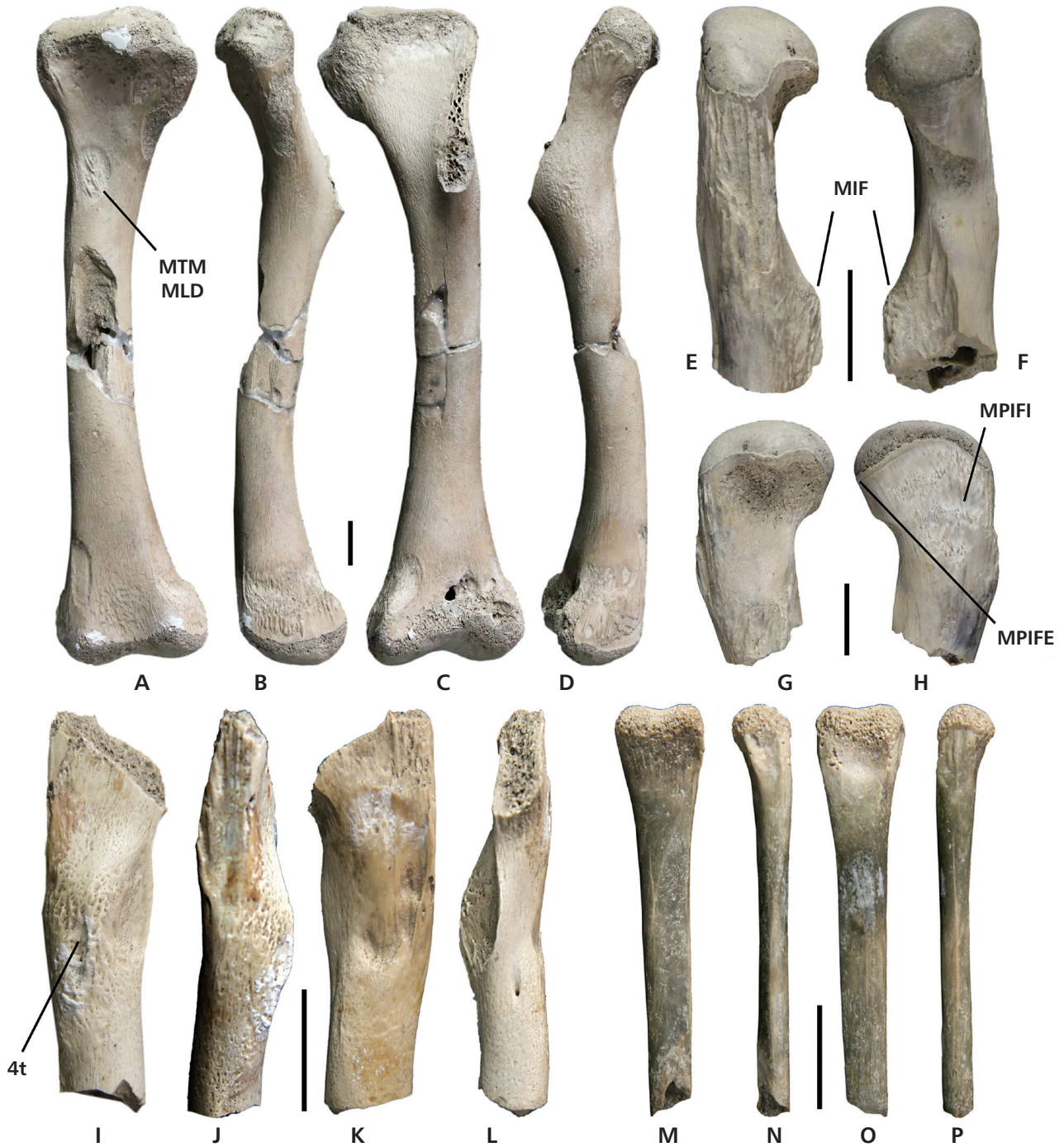
Figure 9. Postcranial remains of the fossil alligatoroid taxon *Diplocynodon* cf. *ratelii* from the Ahníkov fossil sites (early Miocene, Czech Republic). A–D – NMP Pv 11629 partial left humerus in ventral (A), lateral (B), dorsal (C), medial views (D); E–H – NMP Pv 11634 partial left femur in medial (E), lateral (F), ventral (G) and dorsal (H) view; I–L – NMP Pv11630 partial right femur in ventral (I), medial (J), dorsal (K) and lateral views (L); M–P – NMP Pv 11631 right metatarsal in ventral (M), medial (N), dorsal (O), lateral views (P). Abbreviations: MIF – Musculus iliofemoralis; MLD – M. latissimus dorsi; MPIFE – M. pubo-ischio-femoralis externus; MPIFI – M. pubo-ischio-femoralis internus; MTM – M. teres major; 4t – 4ᵗʰ trochanter. Scale bar is 10 mm.

11636 and NMP Pv 11649: Fig. 4A, B, D) indicate that the shape of the frontoparietal suture is concavoconvex (instead of linear). Therefore, material from Ahníkov only resembles the condition of *D. ratelii* and *D. ungeri*, which distinguishes the described material from the remaining species of *Diplocynodon* with the only exception of *D. elavericus* (in which it is not preserved). The previous species (*i.e. Diplocynodon elavericus* and *D. ungeri*)
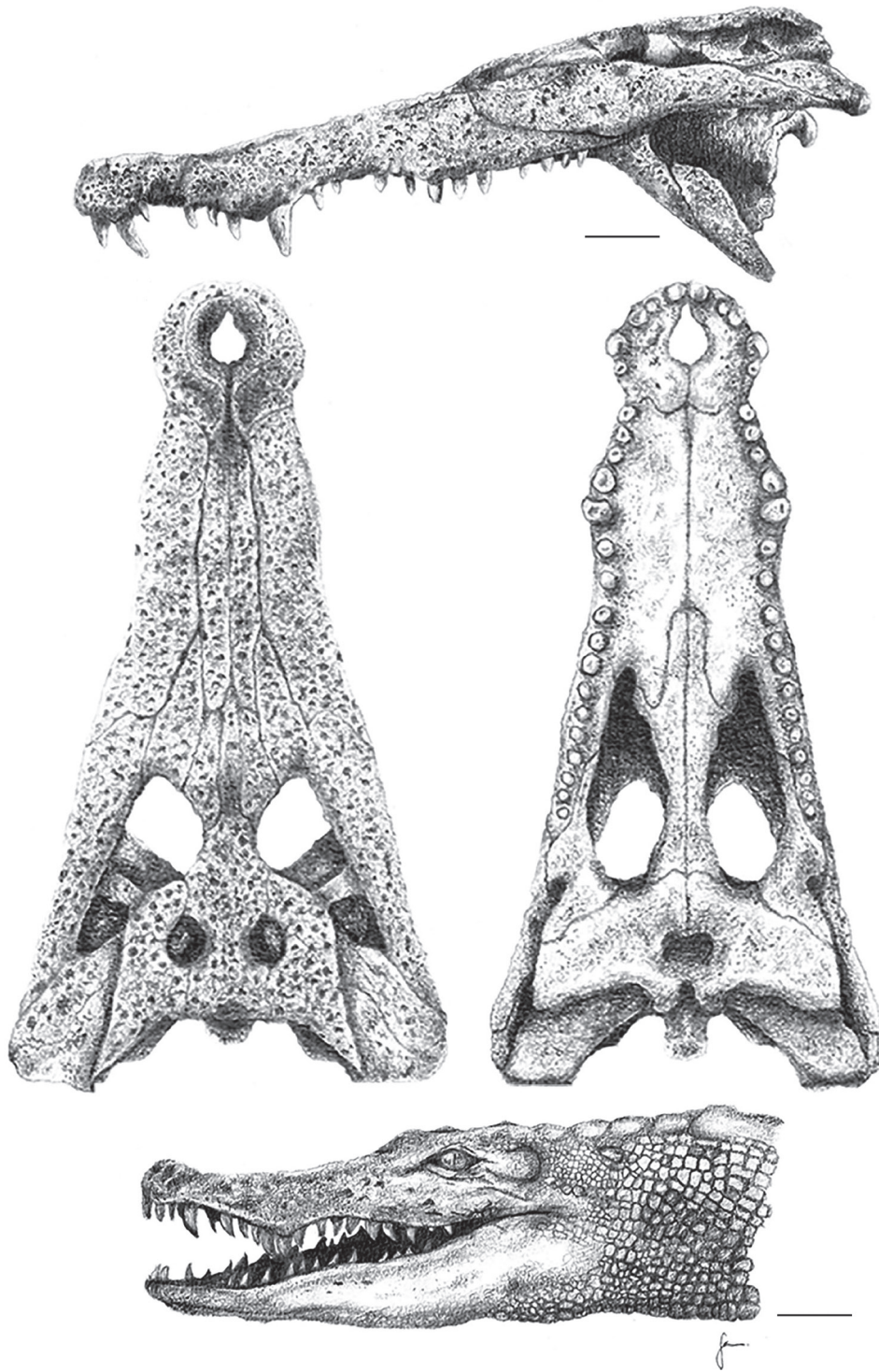
Figure 10. Hypothetical reconstruction of an adult of *Diplocynodon* cf. *ratelii* from Ahníkov (early Miocene, Czech Republic). Scale bar is 30 mm. Original artwork by S. Barbachano.

can be discounted based on symphyseal extension of the dentary as well. Particularly, the symphysis is longer in *D. ungeri* and *D. elavericus* than in *D. ratelii* and Ahníkov specimens, in which is reaching either the posterior margin of the fourth or fifth dentary alveoli (Brochu *et al.* 2012, Delfino & Smith 2012, Martin *et al.* 2014, Díaz Aráez *et al.* 2017, Luján *et al.* 2019). Given the absence of the anteriormost part of the snout in the reported material, which avoids us to evaluate the relationship between the naris and the nasals, we cannot unequivocally ascribe the Ahníkov material at the species level (*i.e. Diplocynodon ratelii*). According to the above-mentioned

combination of features, we herein refer the material to *Diplocynodon* cf. *ratelii*. A hypothetical reconstruction of an adult individual of *D.* cf. *ratelii*, which is inspired by the Spanish material from Els Casots, is illustrated in Fig. 10.

Comparison of the Ahníkov material and palaeoenvironmental implications

The material from the Ahníkov fossil sites resembles *Diplocynodon ratelii* from the early Miocene sites of France (type locality: Saint-Gérand-le-Puy, MN2), Spain (Els Casots, MN4) and the Czech Republic (Tušimice, MN3) in many patterns (see above the taxonomic section). However, the specimens from Ahníkov are notably smaller than the French, Spanish and Czech specimens of *D. ratelii* from other localities, which is assumed to reflect an earlier ontogenetic stage (*i.e.* juveniles). This assumption is not only based on the small size of the remains, but further on the morphology of the vertebrae (*i.e.* the neural arch is not sutured to the vertebral centrum: see Brochu 1996). Because of the high number of crocodylian specimens recovered from Ahníkov, we dismiss the possibility that taphonomic factors could have played any important role. In fact, the number of crocodylian remains is relatively high (over 100 bones, teeth and osteoderms). Thus, the only plausible and most likely hypothesis explaining the high abundance of juveniles is the palaeoenvironment – a swampy area, rich in flooding rivers and shallow lakes (Kvaček *et al.* 2004, Mach *et al.* 2014, Ekrt *et al.* 2016, Mach *et al.* 2017). For the genus *Diplocynodon*, we tentatively assume an ecological behavior similar to that in extant alligators and caimans. In the latter, the juveniles prefer wetlands covered by vegetation and near-shore areas or rivers over open waters (Stevenson 2019). In extant populations of the American alligator (*Alligator mississippiensis*), the juveniles are much more abundant than adult individuals (Altrichter & Sherman 1999, Lutterschmidt & Wasko 2006). Besides, the mortality of juveniles is higher than that of adults mainly due to predation pressure and this would consequently significantly increase the number of recovered fossils (Somaweera *et al.* 2013). Therefore, the high number of juveniles seems attributable to specific palaeoecological conditions at Ahníkov, *i.e.* suitable local habitat (near-shore wetlands), which permitted the care for the hatchlings. Similar conditions were described from Silveirinha, Portugal (Antunes 2003). Indeed, the presence of many amphibians (frogs and salamanders), reptiles (crocodylians, turtles and "natricine" snakes) and plant remains clearly supports this interpretation (Fejfar & Kvaček 1993, Hurník & Kvaček 1999, Ivanov 2002, Kvaček *et al.* 2004). However, some squamates, such as viperid snakes (*Vipera* sp., '*V. aspis*' complex:

Ivanov 2002), lizards (*Lacerta* sp. and *Palaeocordylus bohemicus*: Čerňanský & Joniak 2009, Čerňanský 2012), geckos (*Euleptes gallica*: Čerňanský & Bauer 2010), glass lizards (*Pseudopus ahnikovensis*, *P. confertus*, *Ophiosaurus holeci*: Klembara 2012, 2015; Klembara & Rummel 2018) and amphisbaenians (*Blanus thomaskelleri*: Čerňanský & Venczel 2011, Čerňanský *et al.* 2015) were associated with a more open environment, with a lower density of trees and slightly drier conditions. Thus, the swampy environment of Ahníkov, a suitable habitat for alligatoroids, was surrounded by one or even several other environments.

Conclusions

Crocodylian remains from the early Miocene (MN3) sites of Ahníkov (Most Basin, Czech Republic) are herein described and referred to *Diplocynodon* cf. *ratelii*.

Therefore, this material represents the second confirmed record of this taxon in the Most Basin, where only the species *Diplocynodon ratelii* had been previously reported from the site of Tušimice (MN3). The presence of this freshwater alligatoroid is consistent with the palaeoenvironmental reconstruction of the site as a shallow swampy environment. In addition, the high abundance of crocodylian juveniles supports this palaeoenvironmental reconstruction, where crocodile hatchlings could hide from predators. However, some squamate taxa recovered from Ahníkov were associated with a more open environment and drier conditions and consequently suggest diverse surrounding palaeoenvironments.

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