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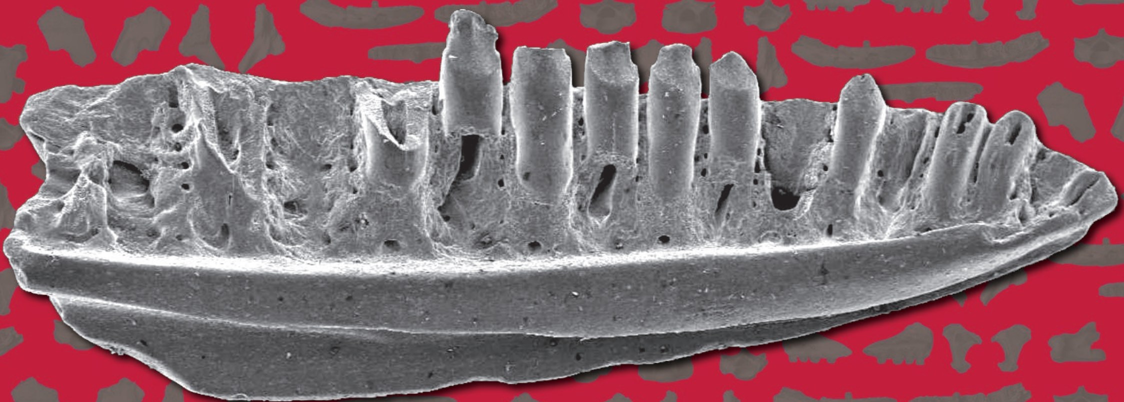

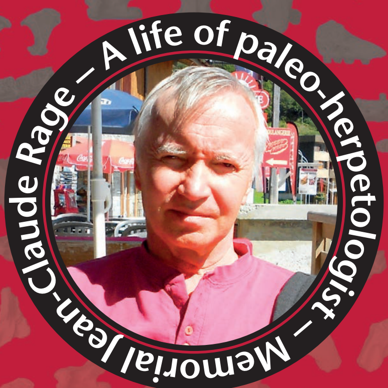

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ABSTRACT

Two fossiliferous karstic fissures from the Mokrá-Western Quarry, MWQ (1/2001 Turtle Joint; 2/2003 Reptile Joint) provided a diverse vertebrate fauna from the early Miocene (Burdigalian, MN 4) including squamates. The rather warm climatic conditions during the Miocene Thermal Maximum (17.8-17.7 Ma) enabled dispersal of thermophilic lizards and snakes throughout Central Europe. In total, ten major clades have been identified in MWQ localities, including: Lacertidae (Lacertidae indet., Lacertidae tooth morphotype 1 and 2); Amphisbaenia (Amphisbaenia indet.); ? Scincoidea (? Scincoidea indet.); Anguidae (*Pseudopus laurillardi* (Lartet, 1851), *Pseudopus* sp., *Ophisaurus* sp., and Anguinae indet.); Varanidae (*Varanus mokrensis* Ivanov, Klembara, Ruta & Böhme, 2018); Boidae (*Bavarioboa* cf. *hermi* Szyndlar & Schleich, 1993); Pythonidae (*Python* sp.); Colubridae (Colubridae gen. et sp. indet., *Coluber* [s.l.] sp., and "Colubrinae" indet., type 1), Natricidae (*Natrix* sp. and "Natricinae" indet.); Viperidae (Viperinae ['Oriental vipers' group], *Vipera* sp. ['European vipers' group]);

and Elapidae (Elapidae gen. et sp. indet.). *Python* sp. from the MWQ represents the first known occurrence of this most thermophilic Neogene squamate taxon within the area of Central Paratethys and we assume that MAT did not fall below 18-19 °C in the vicinity of this locality during the late Burdigalian stage. These humid subtropical to paratropical climatic conditions, also documented by several full-aquatic and semi-aquatic amphibians and reptiles, were suitable for the occurrence of other thermophilic lizard and snake taxa reported from MWQ, including *Varanus mokrensis*, *Pseudopus laurillardi*, *Bavarioboa*, large Elapidae and 'Oriental vipers'.

KEY WORDS
Squamata,
lizards,
snakes,
biogeography,
Neogene,
Moravia,
Central Europe.

RÉSUMÉ

Assemblage de squamates du Miocène inférieur de la carrière de Mokrá-Western (République tchèque) et ses implications paléobiogéographiques et paléoenvironnementales.

Deux remplissages karstiques fossilifères de la carrière Mokrá-Western, MWQ (1/2001 Turtle Joint; 2/2003 Reptile Joint) ont fourni une faune diversifiée de vertébrés du Miocène inférieur (Burdigalien, MN 4), y compris des squamates. Les conditions climatiques, plutôt chaudes, du Maximum Thermique Miocène (17,8-17,7 Ma) ont permis la dispersion des lézards et des serpents thermophiles dans toute l'Europe centrale. Au total, dix clades majeurs ont été identifiés dans les localités du MWQ, notamment: Lacertidae (Lacertidae indét., dents de Lacertidae morphotypes 1 et 2); Amphisbaenia (Amphisbaenia indet.); ? Scincoidea (? Scincoidea indet.); Anguidae (*Pseudopus laurillardi* (Lartet, 1851), *Pseudopus* sp., *Ophisaurus* sp., et Anguinae indet.); Varanidae (*Varanus mokrensis* Ivanov, Klembara, Ruta & Böhme, 2018): Boidae (*Bavarioboa* cf. *hermi* Szyndlar & Schleich, 1993); Pythonidae (*Python* sp.); Colubridae (Colubridae gen. et sp. indet., *Coluber* [s.l.] sp., et «Colubrinae» indet., type 1), Natricidae (*Natrix* sp. et «Natricinae» indet.); Viperidae (Viperinae [groupe des 'Vipères orientales'], et *Vipera* sp. [groupe des 'Vipères européennes']); Elapidae (Elapidae gen. et sp. indet.). *Python* sp. du MWQ représente la première occurrence connue de ce genre de squamate européen, et le plus thermophile, dans la région de la Central Paratethys; nous supposons ainsi que le MAT n'a pas chuté en dessous de 18-19°C dans cette localité au cours du Burdigalien tardif. Ces conditions climatiques humides, subtropicales à paratropicales, également documentées par plusieurs amphibiens et reptiles entièrement aquatiques et semi-aquatiques, étaient propices à la survenue d'autres taxons thermophiles de lézards et de serpents rapportés dans les localités du MWQ, notamment *Varanus mokrensis*, *Pseudopus laurillardi*, *Bavarioboa*, Elapidae et 'Vipères orientales'.

MOTS CLÉS
Squamata,
lézards,
serpents,
biogéographie,
Néogène,
Moravie,
Europe centrale.

INTRODUCTION

The early to early middle Miocene was the period of the last occurrences of highly thermophilic squamate taxa in Central Europe, e.g. Cordylidae, Chamaeleonidae, large Boidae including *Bavarioboa*, and Pythonidae (Ivanov 2001; Szyndlar & Rage 2003; Čerňanský 2010a, 2012; Ivanov & Böhme 2011). However, most of well-documented early and early middle Miocene squamate assemblages comes from the NAFB (North Alpine Foreland Basin), Germany. This is particularly the case for several localities such as Amöneburg and Ulm-Westtangende, both MN 2 (Čerňanský *et al.* 2015, 2016b; Klembara *et al.* 2017b), Petersbuch 2, MN 4a (Szyndlar & Schleich 1993; Szyndlar & Rage 2003; Klembara *et al.* 2010), Sandelzhausen, MN 5a (Szyndlar 2009) and Griesbeckerzell, MN 5 upper part − MN 6 base (Ivanov & Böhme 2011). In Central Europe, situated east of Germany, the early Miocene squamate assemblages are still poorly known. The only exceptions are Merkur-North, MN 3a (e.g., Ivanov 2002a; Klembara 2008, 2012, 2015; Klembara & Rummel 2018; Čerňanský 2012) and Dolnice, MN 4b (Klembara 1979, 1981; Roček 1984; Szyndlar 1987, 1991a, b; Čerňanský 2010a, b; Klembara & Rummel 2018) localities in Czech Republic and Oberdorf, MN 4a, in Austria (Szyndlar 1998; Čerňanský 2016).

The presence of diverse squamate assemblages with thermophilic taxa is closely related to the MCO (Miocene Climatic Optimum). The MCO was originally defined in the oceanic record (Flower & Kennett 1994); however, continental biota sensitively reflects increased early Miocene temperatures (Böhme 2003; Ivanov & Böhme 2011). Both the Miocene Thermal Maximum (17.8-17.7 Ma; Böhme & Winklhofer 2008) and subsequent MCO (from *c.* 17 Ma to *c.* 14 Ma) represent the warmest periods in the Neogene (Zachos *et al.* 2001). The occurrence of the last European pythons (*Python* sp.) in Griesbeckerzell 1a and 1b (Germany) indicates persistence of a rather warm subtropical or paratropical climate with MAT (Mean Annual Temperature) above 18.6 °C and 8.1 °C for the coldest month in this locality as late as the early middle Miocene, *c.* 15 Ma (Ivanov & Böhme 2011). This result is in accordance with a palaeobotanical record for the NAFB (Mosbrugger *et al.* 2005). However, little is known about the composition of the early Miocene squamate assemblages in the area of Central Paratethys and more specifically within the Carpathian Foredeep where the fossil record of early Miocene vertebrates is rather rare (Fejfar 1990). Therefore, early Miocene (MN 4, *sensu* Sabol

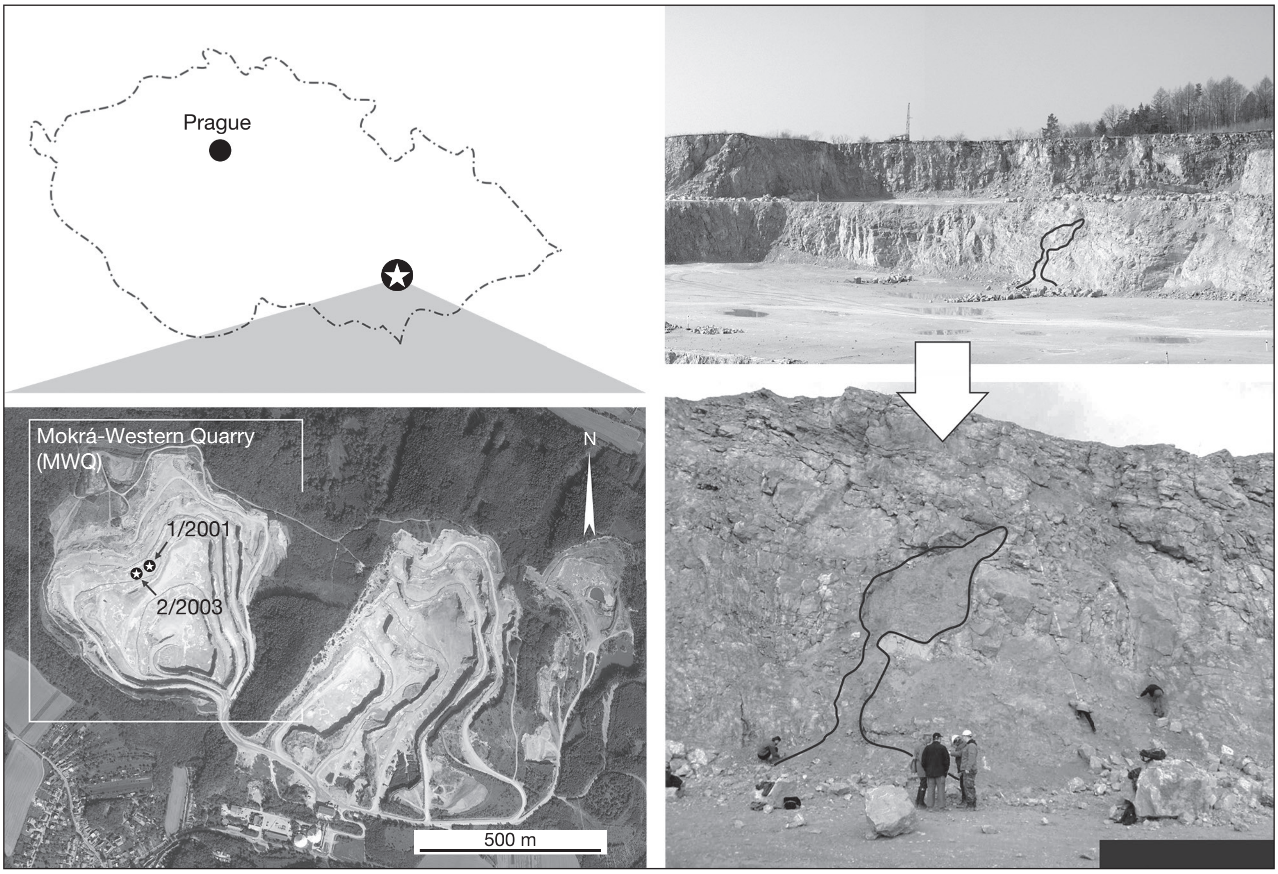

Fig. 1. — Topographic position of the Mokrá-Western Quarry with 1/2001 Turtle Joint and 2/2003 Reptile Joint (**A**). Position of the 1/2001 Turtle Joint at floor 380 m a.s.l. and field excavation of the fissure deposits in 2002 (**B**). The 2/2003 Reptile Joint has been discovered only few meters on the left from the 1/2001 Turtle Joint (modified after Ivanov *et al.* 2006).

et al. 2007) vertebrate assemblages from the Mokrá Quarry (Moravia, Czech Republic) are of a great importance.

The Mokrá open-cast limestone mine is located about 12 km ENE of the city of Brno on the Mokrá Plateau in the southern part of the Drahany Upland (Moravia, Czech Republic). The mine consists of three separate quarries: the western, the central and the eastern (Fig. 1); however, karst phenomena predominate in the Western Quarry (Ivanov *et al.* 2006). Fossiliferous karst fissures discovered in Mokrá-Western Quarry (MWQ) during the limestone mining, provided abundant osteological material of small and middle-sized vertebrates including the type material of *Varanus mokrensis* Ivanov, Klembara, Ruta & Böhme, 2018 (Ivanov 2008; Ivanov *et al.* 2006, 2018). Although new research on continental deposits of the Czech part of the Carpathian Foredeep uncovered Miocene vertebrate assemblages from several other localities (unpublished), karstic fissures in MWQ are among the most important early Miocene localities in Central Europe. The main aims of this paper are as follows: 1) description of squamate material (except of *Varanus* as recently published by Ivanov *et al.* 2018) which have never been studied in detail; and 2) contribution to the palaeo-biogeographical, palaeoclimatological and environmental interpretations based on the assemblage composition.

GEOLOGICAL SETTING

The Mokrá Plateau that is situated in the SE part of the Moravian Karst, lies in close proximity to the margin fault of the West Carpathian Foredeep. Devonian carbonates predominate in the Mokrá Plateau with lower Carboniferous flysh facies (Culm) occurring close to the eastern part of the plateau. The Devonian deposits represent the platform development of the Moravian Karst with basal clastics at the base and overlying massive and biodetritic limestones of the Vilémovice Limestone (Givetian-Frasnian). This limestone, which dominates in this part of the Mokrá Plateau, is represented by massive and biodetritic limestones. The overlying Líšeň Formation (Frasnian-Tournaisian) occurs only sporadically. It is made-up by the nodular Křtiny Limestone and dark grey biodetritic and well-bedded Hády-Říčka Limestone indicating the final stage of the carbonate sedimentation. The overlying Březina Formation (Tournaisian-Visean) represents the onset of tectonically strongly affected Culm facies overlain by the sandstones, shales and greywackes of the Rozstání Formation (Tournaisian) and the greywackes and conglomerates of the Myslejovice Formation (Tournaisian-Visean) (Ivanov *et al.* 2006). Carbonates of the Mokrá-Western Quarry tend to karstification as a result of their chemical character as well as mechanical deformations and processes of pressure dissolution (Hladil *et al.* 1987; Rez

2003). The whole southern part of the Moravian Karst lacks Mesozoic and Palaeogene sediments and this territory was most probably subject to intense weathering by that time. However, periodic ingressions from the Tethys Sea might have occurred during the Upper Jurassic and Upper Cretaceous (and/or Lower Cretaceous). In the Neogene, the Mokrá Plateau belonged to the Carpathian Foredeep and it was also situated in the northwestern foreland of this sedimentation area. Marine incursions penetrated into the Mokrá Plateau as a result of orogenic movements in the Flysch Belt of the Western Carpathians. However, Eggenburgian deposits are absent here. The Mokrá Plateau and its surroundings formed the elevated parts of the relief during the Ottnangian. It is possible that sedimentation occurred only in small, isolated freshwater basins that lacked marked communication with the oligohaline and/or brachyhaline foredeep environments developed more to the south. The marine sedimentation in the foredeep had moved far to the north-west since the Karpatian stage. The maximum Badenian transgression extended to the central and southern parts of the Moravian Karst (Procházka 1899). The marine transgression covered a majority of the Drahany Upland, as documented by palaeobathymetric analysis (Brzobohatý 1997). Remnants of Badenian sediments also occur in the Mokrá Quarry, e.g. on the third floor of the Western Quarry (Hladil *et al.* 1987). Badenian gravels and sands of the maximum thickness 30 m were reported from number of boreholes in the N-S valley situated between the Central and Western quarries (Brzobohatý *et al.* 2000). These clastic deposits are covered with green-grey clays (up to 4.6 m thick). Calcareous clays contain the rich lower Badenian microfauna (e.g. Foraminifera, Ostracoda, sponge spicules). The lower Badenian clays are usually covered by diluvia up to 15 m thick. A little thick loess completes the succession in places (Ivanov *et al.* 2006).

MATERIAL AND METHODS

Abundant early Miocene (MN 4) vertebrate material, including squamates, has been reported from two karst fissures in the Mokrá-Western Quarry (MWQ): 1/2001 Turtle Joint and 2/2003 Reptile Joint which no longer exist (Fig. 1). Both karst fissures filled with unstratified non-calcareous sandy-clays were developed within the strongly karstified Vilémovice Limestone at the floor 380 m a.s.l. Osteological material was freely dispersed in the sediment. Various skeletal elements were not preserved in their anatomical positions. The surface of mostly rather fragmentary bones is quite smooth and usually without traces of corrosion. We presuppose that bones were transported over a small distance as results not only from the absence of skeletal elements in anatomical positions but also from the preservation of the fine structures. Post-mortem disintegration apparently occurred before the material was swept into extended joints (Ivanov *et al.* 2006).

The sandy-clays from these two fissures (altogether 7.5 m^3, about 13 tons) were first treated by H_2O_2 in aqueous solution with optimum concentration corresponding approximately to a 1 (H_2O_2 30 %):100 (H_2O) ratio. After dissolving the clayey component, we washed sediments in sieves of 2 mm, 1 mm, and 0.5 mm mesh size. An electron environmental microscope JEOL JSM-6490LV, Leica MZ 16 microscopic system equipped with a Leica DFC 480 digital camera (5 mpx) as well as Leica M125 binocular microscope with axially mounted DFC500 camera [LAS software (Leica Application Suite) version 4.1.0 (build 1264)] were used for examination and photographs of the fossil material. The Leica IM-1000 and image processing program ImageJ (Schneider *et al.* 2012) were used for measurements. Abbreviations for measurements: cl, centrum length; naw, neural arch width; or, observed range.

TERMINOLOGY

The cranial terminology for Sauria clade follows Oelrich (1956), Klembara (1979, 1981) and Klembara *et al.* (2010). Dentition descriptions follow Edmund (1969) and Kosma (2004). Terminology for snake cranial osteology follows Szyndlar (1984). The axial terminology follows Hoffstetter & Gasc (1969) and Szyndlar (1984).

INSTITUTIONAL ABBREVIATIONS

SMM, Pal.	Ústav geologických věd Př.F. Masarykovy univerzity, Brno (Mendel Museum Collection).

REPOSITORY

Material has been deposited in the collections of the Department of Geological Sciences, Masaryk University, Brno, under registration numbers SMM/009-09-11/ 372009, Pal. 1400-2068.

SYSTEMATIC PALAEONTOLOGY

Order SQUAMATA Oppel, 1811
Superfamily LACERTOIDEA
Estes, de Queiroz & Gauthier, 1988
Family LACERTIDAE Oppel, 1811

LACERTIDAE indet.
(Fig. 2A, B)

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 2/2003 Reptile Joint: one left frontal (Pal. 1565).

DESCRIPTION

Frontal

Only the anterior portion of the left frontal is preserved. The dorsal surface bears two osteodermal shields fused to the bone. The main region is occupied by the frontal shield, whereas the prefrontal shield is located in the anterolateral section. The dorsal regions of the shields are sculptured. The sculpture consists of irregularly distributed pits and several connected ridges. Both shields are separated one from another by a slightly rounded (medially convex) sulcus, which runs posterolaterally to the lateral margin of the bone. The anterior termination of the frontal is divided into larger lateral

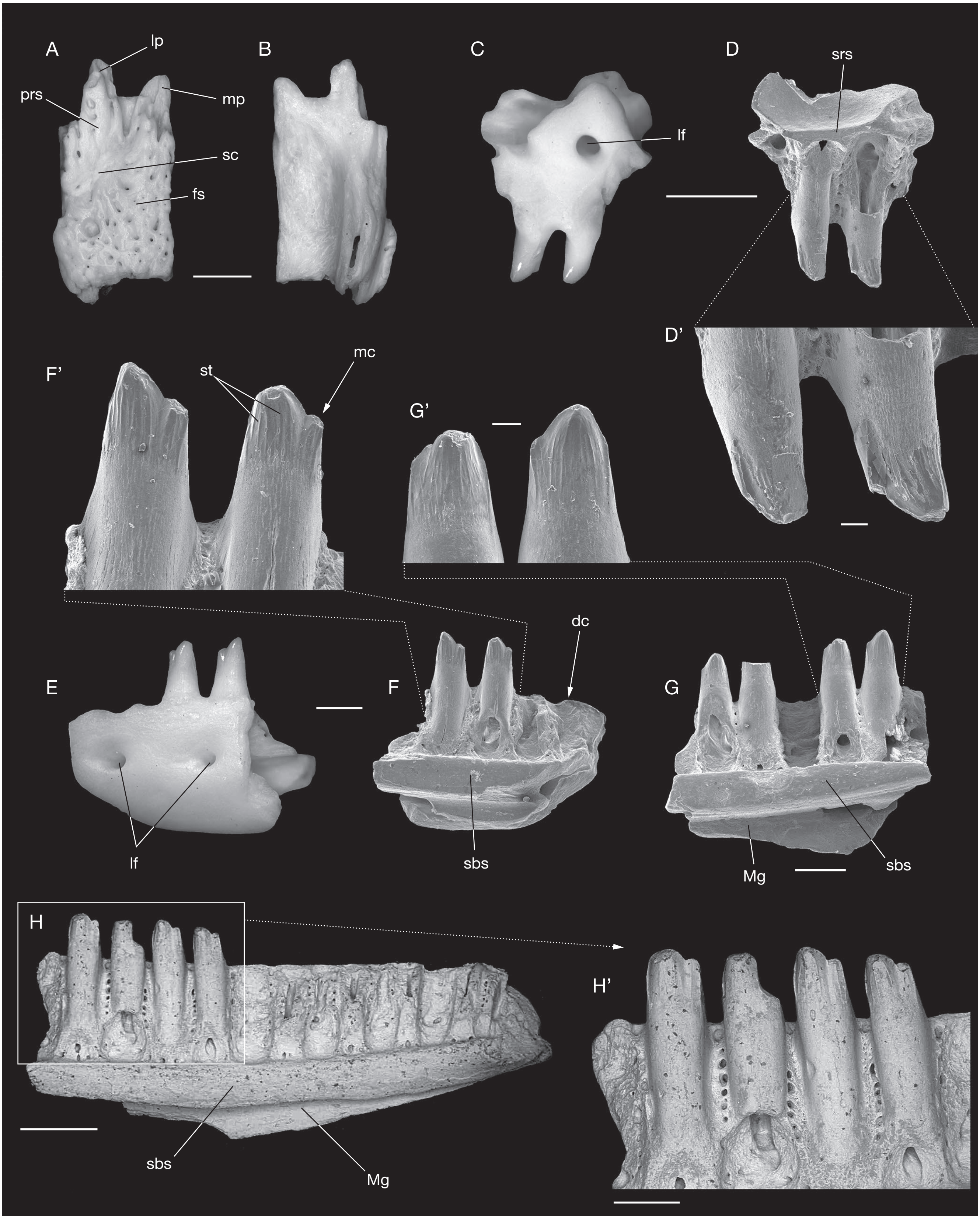

Fig. 2. — Lacertidae indet. from the early Miocene (MN 4) of MWQ. Left frontal Pal. 1565 (2/2003 Reptile Joint) in (**A**) dorsal and (**B**) ventral aspects. Lacertidae indet. tooth morphotype 1: right maxilla Pal. 1566 (2/2003 Reptile Joint) in (**C**) lateral and (**D**) medial aspects with detail of teeth. Left dentary Pal. 1567 (2/2003 Reptile Joint) in (**E**) lateral and (**F**) medial aspects with detail of teeth. Right dentary Pal. 1568 (2/2003 Reptile Joint) in (**G**) medial aspect with detail of teeth. Lacertidae indet. tooth morphotype 2: left dentary Pal. 1401 (1/2001 Turtle Joint) in (**H**) medial aspect with detail of teeth. Abbreviations: **dc**, dental crest; **fs**, frontal shield; **lf**, labial foramen (foramina); **lp**, lateral process; **mc**, mesial cusp; **Mg**, Meckel`s groove; **mp**, medial process; **prs**, prefrontal shield; **sbs**, subdental shelf; **sc**, sulcus; **srs**, supradental shelf; **st**, striations. Scale bars: A-D, H, 1 mm; D', G', 100 µm; E-G, H', 500 µm; F', 200 µm.

process and slightly smaller medial process. Between them, a wedge-shaped facet for the nasal is present, forming a bony septum. The facet for the posterodorsal termination of the maxillary nasal process is located lateral to the lateral process, however, this region is damaged. The medial margin, which forms a contact with the right frontal, is straight. On the internal surface, the frontal cranial ridge can be observed. This portion is unfortunately badly preserved – its section that would form an anteroventrally oriented subolfactory process is broken off.

LACERTIDAE indet. tooth morphotype 1
(Fig. 2C-G)

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: One left dentary (Pal. 1400). 2/2003 Reptile Joint: one right maxilla (Pal. 1566), 3 dentaries, 1 left + 2 right (Pal. 1567-1569).

DESCRIPTION
Maxilla
Only a small fragment of the right maxilla is preserved (Fig. 2C, D). This portion bears two teeth, which are bordered dorsally by the supradental shelf. The lateral surface is pierced by a large labial foramen.

Dentary
The description is based on two fragments – one represents a left dentary, whereas the second is a right dentary. The left dentary fragment (Fig. 2E, F) bears four tooth positions (two teeth are still attached). The right dentary (Fig. 2G) exhibits five and half tooth positions (four teeth are still attached, but the tooth crown of one tooth is broken off). The dental crest is low, and teeth exceed it by ½ of their height. The subdental shelf (*sensu* Rage & Augé 2010) is well developed, robust. However only its short portion is preserved. It gradually becomes thinner posteriorly (this can be observed mainly in the right dentary fragment), partly as a result of the presence of the facet for the splenial, situated on its ventral margin. The shelf forms the dorsal roof of the Meckel's groove, which is open but narrow. The lateral surface of the bone is smooth. In the preserved section, it is pierced by two labial foramina located slightly above the mid-section of the bone.

Dentition
The implantation is pleurodont. Teeth are high. The interdental gaps are large – the size of the gap forms approximately the ½ of the mesiodistal length of the tooth neck. The tooth crowns are bicuspid with a dominant distal (central) cusp and a smaller mesial cusp. The distal cusp is pointed in most cases and slightly directed posterolingually. The lingual portion of the crowns bears vertical striations. The striae are almost parallel, and their number is around ten. The tooth necks are slightly expanded lingually and they appear lightly more swollen if compared to the tooth crowns. The central part of the tooth base is pierced by a small resorption pit.

REMARKS
The maxilla and dentary have identical tooth morphology and thus can be attributed to the single taxon. Several features in the material from Mokrá described here resemble *Lacerta poncenatensis*: 1) the presence of robust bicuspid teeth; 2) the wide interdental gaps; and 3) the low dental crest. This taxon was originally described by Müller (1996) from the French locality of Poncenat (early Miocene, MN 2a). Later, it was also recognized in Germany (Čerňanský *et al.* 2015; early Miocene, MN 2) and Austria (Čerňanský 2016; early Miocene, MN 4). However, the fragmentary nature of the Mokrá material does not allow confident alpha taxonomy.

LACERTIDAE indet. tooth morphotype 2
(Fig. 2H)

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: One left dentary (Pal. 1401).

DESCRIPTION
Dentary
The description is based on the fragment of the anterior half of a left dentary. The element bears ten tooth positions (four teeth are still attached). The dental crest is high, and the teeth extend above it only in a quarter of their total height. The subdental shelf (*sensu* Rage & Augé, 2010) is robust, being only slightly concave in this section. Meckel's groove is open, narrow in the preserved section, but gradually widening posteriorly. The lateral surface of the bone is smooth, pierced by several labial foramina.

Dentition
The implantation is pleurodont. Teeth are tall and robust. The interdental gaps are small – the size of the gap forms approximately only a ¼ of the mesiodistal length of the tooth neck. The tooth crowns are bicuspid, with a dominant distal (central) cusp and a smaller mesial cusp. The lingual portion of the crowns bears vertical striations. The striae are almost parallel, and their number is around six. In medial aspect, the tooth necks are more or less as wide as the tooth crowns, in some cases gradually narrowing slightly ventrally. The necks appear slightly more swollen lingually if compared to the tooth crowns. The central part of the tooth base is pierced by a resorption pit.

REMARKS
Although the dentary described here possesses some similarities with the above described lacertid material, e.g. bicuspid teeth, several important differences can be observed: 1) large size; 2) the high dental crest; 3) small interdental gaps; 4) more robust teeth; and 5) low number of lingual striae on the tooth crowns. Because not all of those differences can be explained by ontogenetic changes, we suggest the presence of at least two lacertid taxa in MWQ.

Unranked clade AMPHISBAENIA Gray, 1844

AMPHISBAENIA indet.
(Fig. 3)

Blanus sp. – Ivanov *et al.* 2006: 229, table 2.

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 2/2003 Reptile Joint: One trunk vertebra (Pal. 1570).

DESCRIPTION

Trunk vertebra

A single trunk vertebra is preserved. It is small in size. A neural spine is absent, and the dorsal portion of the neural arch forms a median edge. In lateral view, the synapophysis is simple and large. The posterior portion of the neural arch is fused with the postzygapophyses, forming the dorsal roof (or lamina) between the left and right postzygapophyses. The neural canal is subtriangular with distinct lateral sinuses. The interzygapophyseal constriction is distinct and it occurs in the anterior half of the anteroposterior vertebral length. The dorsally tilted prezygapophyseal articular facets have an elliptical shape. A zygosphene is absent. The ventral side of the depressed centrum is flat, pierced by a pair of large subcentral foramina in the anterior ⅓ of the anteroposterior length. The lateral margins (subcentral ridges) are roughly parallel in ventral aspect. No constriction is developed at the base of the damaged condyle. The postzygapophyseal articular facets are oval and slightly enlarged posteriorly. The cotyle is distinctly laterally enlarged.

REMARKS

The vertebra described here can be attributed to Amphisbaenia based on the following combination of features (see Estes 1983): 1) the depressed centrum, having a flat ventral surface; 2) roughly parallel lateral margins in ventral aspect; 3) massive synapophyses; 4) the absence of a zygosphene (enabling distinction of amphisbaenians from scolecophidian snakes (Estes 1983; Rage 1984); and 5) the sinusoidal neural arch lacking a neural spine.

Family level allocation of an isolated vertebra is limited by a lack of clear diagnostic features for identification (Estes 1983; Augé 2005, 2012; Georgalis *et al.* 2016b). We can exclude rhineurids, which have a denticulate vertebral posterior margin. The same feature can be observed in trogonophiids as well (Kearney 2003; Augé 2012; Čerňanský *et al.* 2016a). Based on the geographical position of the locality and the age of the sediments, this vertebra most likely represents a blanid taxon. According to cranial elements, amphisbaenians reported from the Central European late Oligocene and Miocene localities are almost exclusively identified as belonging to the clade Blanidae (Roček 1984; Schleich 1988; Čerňanský & Venczel 2011; Čerňanský *et al.* 2016a). The morphology and dimensions of the vertebra described here are very similar to those of trunk vertebra of *Blanus gracilis* Roček, 1984 reported from the Czech early Miocene (MN 4b) Dolnice site (Roček 1984: 5, table 16).

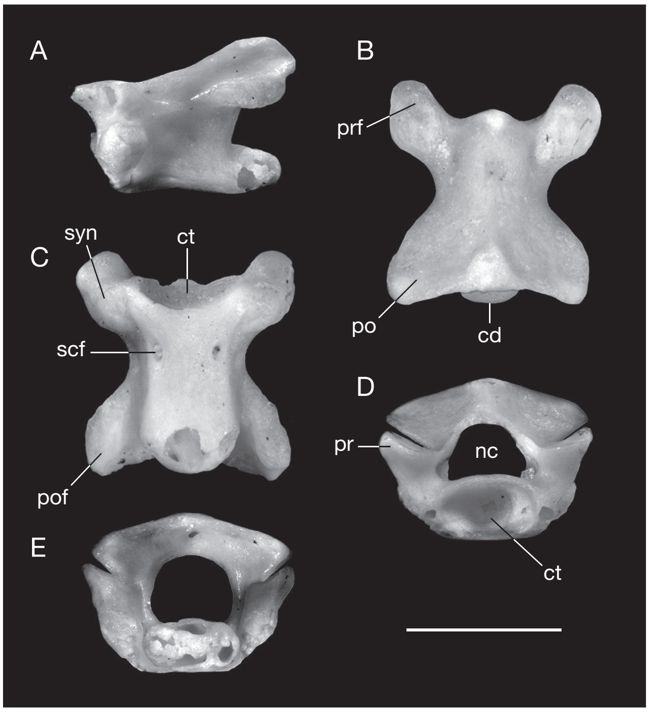

FIG. 3. — Amphisbaenia indet. from the early Miocene (MN 4) of MWQ. The trunk vertebra Pal. 1570 (2/2003 Reptile Joint) in (**A**) lateral, (**B**) dorsal, (**C**) ventral, (**D**) anterior and (**E**) posterior aspects. Abbreviations: **cd**, condyle; **ct**, cotyle; **nc**, neural canal; **po**, postzygapophysis; **pof**, postzygapophyseal articular facet; **pr**, prezygapophysis; **prf**, prezygapophyseal articular facet; **scf**, subcentral foramen; **syn**, synapophysis. Scale bar: 1 mm.

LACERTOIDEA indet.
(Fig. 4A, B)

Lacerta sp., small form – Ivanov *et al.* 2006: 229, table 2 (in part).

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 2/2003 Reptile Joint: two left dentaries (Pal. 1571, 1572).

DESCRIPTION

Dentary

The preserved fragments represent the anterior and mid-portion of the two left dentaries. Meckel's groove is fully open, although narrow in this region. It is roofed by a subdental shelf. The shelf gradually narrows posteriorly, caused by the presence of the facet for the splenial. This facet is situated on the ventral margin of the shelf. This facet reaches anteriorly to the level of the tenth tooth position (counted from anterior). The shelf is only slightly concave, so the small symphyseal region is only weakly elevated dorsally if compared to the posteriorly located shelf. A sulcus dentalis is present. The preserved portion of the dentary bears sixteen and half tooth positions (eight teeth are attached). The dental crest, which supports the teeth, is high (higher than the ventrally located Meckel's groove). Except for four labial foramina, which pierce the lateral side of the bone in its mid-line, the external surface is smooth.

Dentition

The implantation is pleurodont. Teeth are closely spaced with small interdental gaps. All teeth are badly preserved, with heavily weathered tooth crowns.

Remarks

Unfortunately, the poor preservation does not allow a more precise determination of this specimen. The heavily weathered tooth crown might be the result of predation and digestion, especially by birds of prey. This dentary very likely represents a lacertid, but this cannot be fully demonstrated. If such an allocation is correct, then it resembles the material described here as Lacertidae indet. tooth morphotype 2 rather than 1. The main similarity is that the interdental gaps of teeth here are small and the dental crest is high.

Superfamily SCINCOIDEA
Oppel, 1811

?SCINCOIDEA indet.
(Fig. 4C, D)

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 2/2003 Reptile Joint: one left maxilla (Pal. 1573).

Description

Maxilla

Only a fragment of the left maxilla is preserved. It bears five tooth positions (only one and half teeth are attached). The supradental shelf is thin and straight in the preserved portion. The nasal process is partly preserved. On the medial side of the nasal process, there is a fine ridge (carina maxillaris *sensu* Müller 1996) that runs posterodorsally. The ridge originates from the subdental shelf. This gives an estimation that this fragment represents the anterior region of a maxilla. In the lower region of the external surface, three irregularly spaced labial foramina are located. Besides this, the rest of the surface is smooth.

Dentition

The implantation is pleurodont. Only one tooth is more-or-less completely preserved. The lingual aspect of the crown is bordered by the culmen lateralis anterior and culmen lateralis posterior (terms after Richter 1994), between which the area is striated. This fine striation is formed by approximately six striae. The tooth crown termination is blunt. In medial aspect, it appears to be divided into rounded labial cusp, and a smaller, medially located lingual cusp. The tooth bases are pierced by small rounded resorption pits.

Remarks

The tooth morphology resembles that of Scincidae or Cordylidae (see Kosma 2004). Both groups have been previously described from several lower Miocene sites of Central Europe (e.g., Roček 1984; Čerňanský 2012; Čerňanský 2016). Unfortunately, the character of preservation of this maxillary fragment from Mokrá does not allow a more specific allocation.

Suborder ANGUIMORPHA Fürbringer, 1900
Family ANGUIDAE Gray, 1825
Subfamily ANGUINAE Gray, 1825

Genus *Pseudopus* Merrem, 1820

Pseudopus laurillardi (Lartet, 1851)
(Fig. 5A-D)

Pseudopus sp. – Ivanov *et al.* 2006: 229, table 2 (in part).

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: parietal (Pal. 1402). 2/2003 Reptile Joint: parietal (Pal. 1574).

Description

Parietal

Two parietals are partially preserved. The specimen Pal. 1574 represents the posterior region of the parietal table, together with the base of the right supratemporal process, whereas only the central portion of the right side of the parietal is preserved in the second specimen (Pal. 1402). The anterior region of the preserved portion of the parietal table is completely covered by osteodermal shields fused to the bone. These shields bear ornamentation which consists of pits, small ridges and short grooves. The small occipital shield, located in the posterior mid-region, is trapezoidal in shape. Its anteroposterior length is less than that of the posteriorly located smooth area (area levis) in both specimens. However, the smooth area is large only in specimen Pal. 1574. The interparietal shield, located anterior to the occipital shield, is only hardly distinguished from the large parietal shields located laterally. There is no parietal foramen within the preserved portion of the bone. The base of the supratemporal process is broad. Here, the arcuate edge (carina arcuata; *sensu* Klembara *et al.* 2017a) is developed. The supratemporal process gradually widens distally (this can be observed especially in specimen Pal. 1402). On the internal side, the process bears a robust ventrolateral ridge. In the larger specimen, Pal. 1574, a free ventrolateral surface is present lateral to the ridge. This is absent in the smaller Pal. 1402. In this specimen, a longitudinal facet for the supratemporal can be observed on the posterolateral side of the ridge. This facet reaches approximately to the level of the posterior margin of the parietal table. On the internal side of specimen Pal. 1574, a large oval parietal fossa is located in the posterior mid-region. It is bordered ventrally by the parietal lamina. Posterior to the parietal fossa, a postfoveal crest (crista postfovealis) is located. Between the postfoveal crests and the posterior margin of the parietal table, a shallow parietal notch is present. The cranial parietal ridges (cristae cranii parietalis) are partly preserved, the right one can be observed in the specimen Pal. 1402. Lateral to the cranial ridge, muscular facies are well developed, forming the lateral border of the parietal.

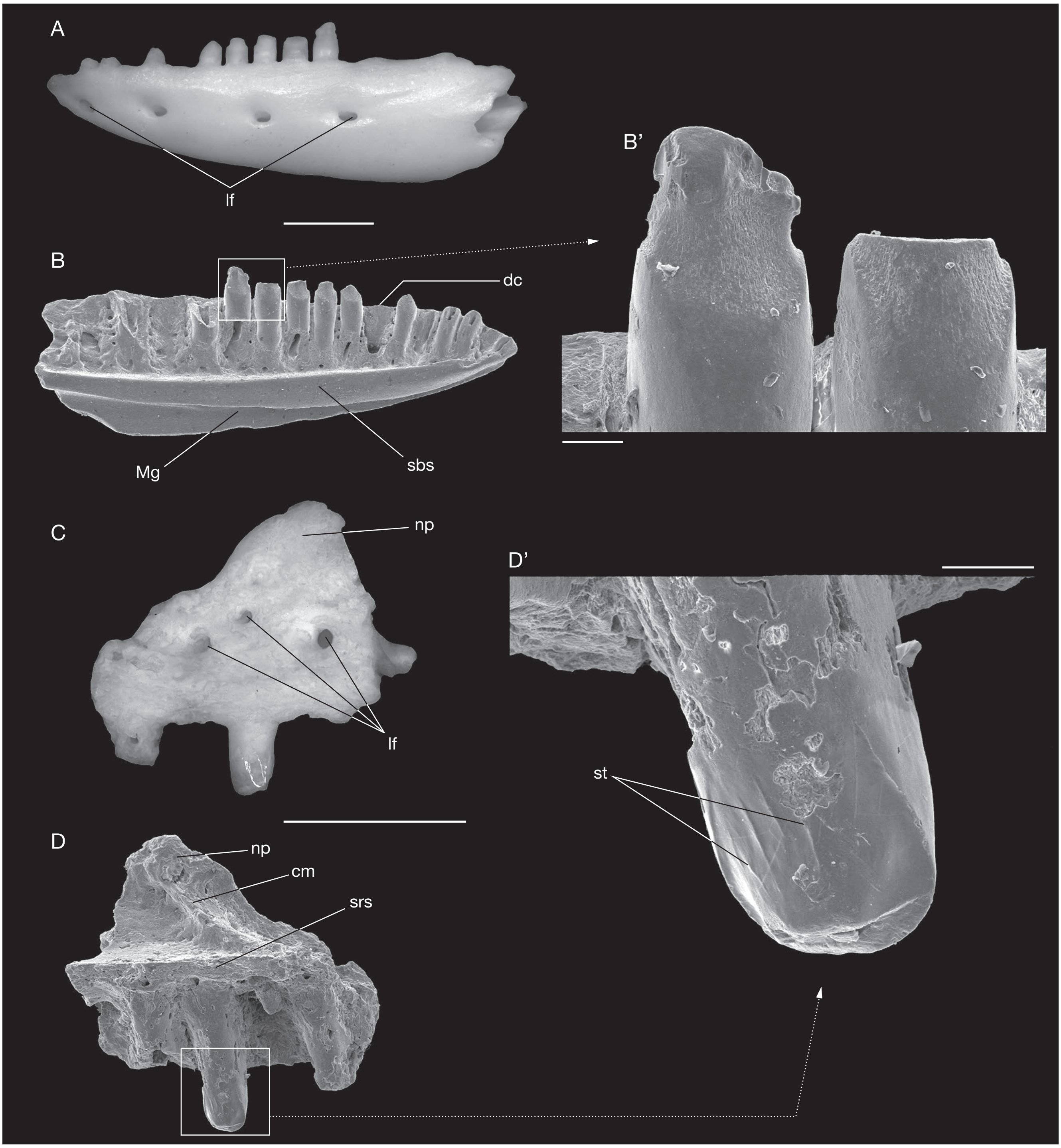

Fig. 4. — Lacertoidea indet. (**A**, **B**) and ? Scincoidea indet. (**C**, **D**) from the early Miocene (MN 4) of MWQ. Left dentary Pal. 1571 (2/2003 Reptile Joint) in (**A**) lateral and (**B**) medial aspects with detail of teeth. Left maxilla Pal. 1573 (2/2003 Reptile Joint) in (**C**) lateral and (**D**) medial aspects with detail of teeth. Abbreviations: **dc**, dental crest; **cm**, carina maxillaris; **lf**, labial foramina; **Mg**, Meckel`s groove; **np**, nasal process; **sbs**, subdental shelf; **srs**, supradental shelf; **st**, striations. Scale bars: A-D, 1 mm; B', D', 100 µm.

REMARKS

The presence of muscular facies (see Klembara *et al.* 2017a) on both parietals and the presence of the postfoveal crest allow the allocation of this material to *Pseudopus* (although it should be noted that short postfoveal crests are also present in *Ophisaurus holeci* [Klembara 2012; Čerňanský & Klembara 2017] and in some cases, narrow muscular facies can be observed in very large adult individuals of this taxon as well [see Klembara *et al.* 2017b]). Three species of *Pseudopus* are documented from early Miocene deposits of Europe: *P. laurillardi*, *P. ahnikoviensis* and *P. confertus* (see Klembara *et al.* 2010; Klembara 2012; Klembara 2015 – *P. rugosus* was later renamed to *P. confertus* by Klembara & Rummel 2018). The parietal Pal. 1574 clearly exhibits features present in *P. laurillardi*: 1) the presence of free ventrolateral surface (facies ventrolateralis *sensu* Klembara *et al.* 2010) of the supratemporal process, located lateral to the ventrolateral ridge (this feature is absent in *P. ahnikoviensis*, see Klembara 2012); and 2) the type of sculpture present on osteodermal shields fused to the bone, consisting of pits, small ridges and grooves rather than being vermicular as it is in *P. ahnikoviensis* (see Klembara 2012). Another feature is the absence of the parietal foramen in the preserved portion of the parietal – in *P. confertus*, this foramen is located closer to the posterior margin of the floor of the parietal fossa (see Klembara 2015). We can therefore estimate that the parietal foramen in Pal. 1574 was located more anteriorly than it is in *P. confertus*. The second parietal, specimen Pal. 1402, is problematic. The free ventrolateral surface of the supratemporal process appears to be absent. However, if size is considered, this specimen represents a small individual. In the small parietal described by Klembara *et al.* (2010: p. 166, fig. 5B), this feature is only incipiently developed and thus can be influenced by ontogeny. If our allocation is correct, then the parietal Pal. 1402 represents a juvenile individual of *P. laurillardi* (this can be supported by the presence of a similar type of ornamentation to that in Pal. 1574).

Pseudopus sp.
(Fig. 5E-Q)

Pseudopus sp. – Ivanov *et al.* 2006: 229, table 2 (in part).

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: maxilla, 1/2001 Turtle Joint: one right dentary (Pal. 1403), three trunk vertebrae (Pal. 1404-1406); 2/2003 Reptile Joint: left maxilla (Pal. 1575), left quadrate (Pal. 1576).

DESCRIPTION

Maxilla

Only the posterior region of a left maxilla is partly preserved. It bears four teeth still attached to the bone. An oval superior alveolar foramen is located at the level of the third tooth (counted from posterior). The whole preserved section of the maxilla gradually narrows posteriorly rather than being stepped, but the posterior termination is broken off. Here, a wedge-shaped facet for the jugal is present. It reaches almost to the level of the last preserved tooth. The lateral surface of the preserved portion is pierced by three labial foramina located dorsal to the teeth. The nasal process is only partly preserved, rising dorsally in this region.

Quadrate

The left quadrate is completely preserved, being robustly built. In lateral aspect, its dorsal portion is anteroposteriorly expanded. The dorsal margin of this portion is irregularly rounded. In dorsal aspect, this region is clearly divided by a central constriction into two large areas with roughened surfaces. The posteriorly located one is formed by a large cephalic condyle, having a face for the squamosal on the lateral side. The anterior portion is formed by a massive dorsal tuber (*sensu* Klembara *et al.* 2017a). Here, the quadrate reaches the highest level dorsally. From the posterior region of this anterior portion, a sharp tympanic crest (*sensu* Oelrich 1956) runs along the entire central region ventrally, being laterally expanded. In the dorsal region, a short anterolateral crest (*sensu* Klembara *et al.* 2017a) is located anterior to the tympanic crest. A small depression divides these two structures. The posterior region of quadrate is bordered by a markedly rounded (concave) posterior crest. In anterior view, the mandibular condyle is mediolaterally broad. Its ventral side is shallow, W-shaped with blunt peaks. On the medial surface of the quadrate, there is a prominent medial crest (*sensu* Oelrich 1956). Its ventral portion protrudes medially slightly more than the dorsal portion, as a result of bearing a distinct facet for the quadrate process of the pterygoid. A small, rounded quadrate foramen pierces the quadrate at approximately the mid-length of the posterior surface.

Dentary

The body of the right dentary (Pal. 1403) is slightly concave. However, this element is badly preserved, especially on the medial side. Here, the almost entire region of the subdental shelf (*sensu* Rage & Augé 2010) and the intramandibular septum are broken off and missing. For this reason, the alveolar canal is exposed. In the posterior region, only the splenial articulation and the coronoid articulation are partly preserved. They are separated from each other by a small gap formed by a bony ridge. As preserved, the dentary possesses twelve tooth positions, but only one tooth is still attached (the actual tooth number of the complete tooth row was probably slightly higher). The lateral surface of the bone is pierced by four labial foramina.

Dentition

A pleurodont tooth implantation is present. Teeth are amblyodont, being enlarged posteriorly to form blunt robust cylinders. No striations can be observed on the tooth crowns (this could be due to poor preservation or wearing of the occlusal surfaces). The penultimate maxillary tooth has a large tooth crown with a distinctly constricted neck. Thus, this tooth is mushroom-like shape. The tooth bases of maxillary teeth are ankylosed to their sockets and surrounded by a spongy (porous) bony tissue. The tooth crown of the dentary tooth is extremely weathered.

Trunk vertebrae

Several trunk vertebrae are present. They are robustly built. The neural spine starts to rise dorsally approximately at the

FIG. 5. — *Pseudopus* from the early Miocene (MN 4) of MWQ. *Pseudopus laurillardi*: parietal Pal. 1574 (2/2003 Reptile Joint) in (**A**) dorsal and (**B**) ventral aspects; parietal Pal. 1402 (1/2001 Turtle Joint) in (**C**) dorsal and (**D**) ventral aspects. *Pseudopus* sp.: left maxilla Pal. 1575 (2/2003 Reptile Joint) in (**E**) lateral and (**F**) medial aspects. Left quadrate Pal. 1576 (2/2003 Reptile Joint) in (**G**) lateral and (**H**) medial aspects. Right dentary Pal. 1403 (1/2001 Turtle Joint) in (**I**) lateral, (**J**) medial and (**K**) dorsal aspects. Trunk vertebra Pal. 1404 (1/2001 Turtle Joint) in (**L**) lateral, (**M**) dorsal, (**N**) ventral, (**O**) anterior and (**P**) posterior aspects. Trunk vertebra 1405 (1/2001 Turtle Joint) in (**Q**) anterior aspect. Abbreviations: **are**, arcuate edge; **cc**, cephalic condyle; **cd**, condyle; **cf**, facet for

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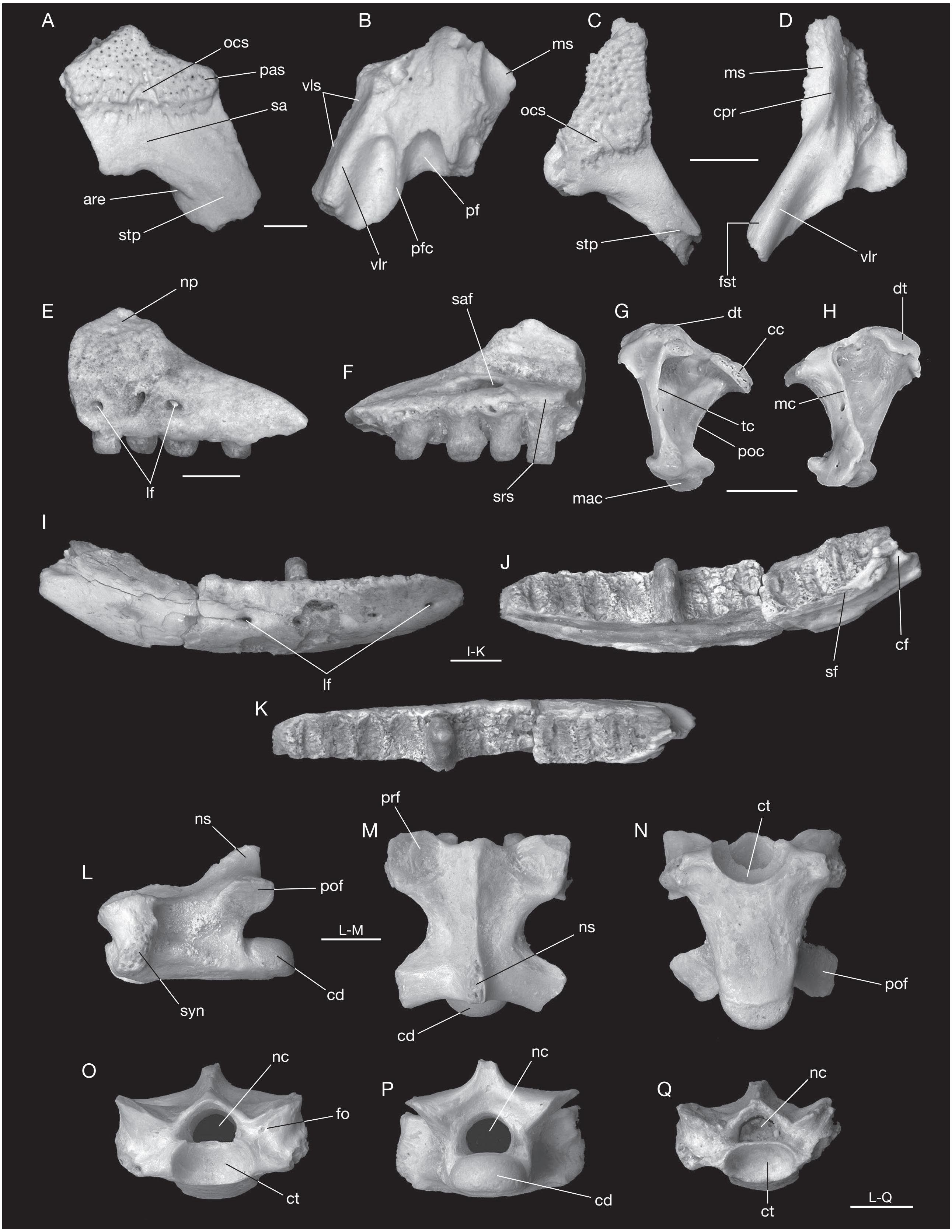

coronoid; **cpr**, cranial parietal ridge; **ct**, cotyle; **dt**, dorsal tuber; **fo**, foramen; **fst**, facet for supratemporal; **lf**, labial foramina; **mac**, mandibular condyle; **mc**, medial crest; **ms**, muscular surface; **nc**, neural canal; **ns**, neural spine; **np**, nasal process; **ocs**, occipital shield; **pas**, parietal shield; **pf**, parietal fossa; **pfc**, postfoveal crest; **prf**, prezygapophyseal articular facet; **poc**, posterior crest; **pof**, postzygapophyseal articular facet; **sa**, smooth area; **saf**, superior alveolar foramen; **sf**, facet for splenial; **srs**, supradental shelf; **stp**, supratemporal process; **syn**, synapophysis; **tc**, tympanic crest; **vlr**, ventrolateral ridge; **vls**, ventrolateral surface. Scale bars: 2 mm.

mid-length of the neural arch. However, this structure is damaged in all vertebrae, thus its exact shape is unknown. In dorsal view, the neural spine widens gradually slightly in a posterior direction and, based on the preserved portion, it probably did not exceed the condyle posteriorly. Anteriorly, a low medial ridge runs to the end of the neural arch, where it forms a small spike. The oval neural canal is small. Pre- and postzygapophyses are well expanded laterally. The interzygapophyseal constriction is well developed and deep. The prezygapophyses are dorsally inclined in an angle of around 30°. The articular surfaces are large, elliptical and oblong laterally. In anterior aspect, a pair of foramina is located ventral to the prezygapophyses, close to the neural canal (Fig. 5O). In lateral aspect, the postzygapophyses reach posteriorly approximately to the level of the mid-region of the condyle. Both condyle and cotyle are markedly depressed. The cotyle has an anteroventral orientation, whereas the condyle is posterodorsally oriented and they lack a precondylar constriction. The synapophyses are well-developed in the anterior region, being slightly posterolaterally oriented. The ventral region of the centrum is flat and the subcentral ridges are straight and gradually converge from anterior to posterior region.

Remarks

In the posterior region of the dentary (Pal. 1403), splenial articulations is present, located anterior to the coronoid articulation. In modern *P. apodus*, the coronoid extends further anteriorly and there is no facet for the splenial in this region (e.g., Klembara *et al.* 2010, 2014). However, the same dentary features seen in the dentary from Mokrá, can be observed in *P. ahnikoviensis* and *P. laurillardi*. Unfortunately, the medial side of the dentary is badly preserved and lacks most of the diagnostic features. *P. ahnikoviensis* is characterized by the presence of a surangular spine, whereas an autapomorphic feature of *P. laurillardi* is a medially expanded subdental shelf (Klembara *et al.* 2010; Klembara *et al.* 2014). Neither of those features can be demonstrated on the dentary from Mokrá and we decided to allocate it only to *Pseudopus* sp. The morphology of the quadrate strongly corresponds to that of *Pseudopus* (for *P. apodus* see Klembara *et al.* 2017a: fig. 27) and this specimen most likely belongs to this taxon. The trunk vertebrae described in this section possess two features characteristic for *Pseudopus* (Čerňanský *et al.* 2019): 1) the lateral margins of the centrum (subcentral ridges) are straight rather than concave (*Ophisaurus*) or parallel with their anterior-most sections being expanded laterally (*Anguis*); and 2) the height of the neural canal is distinctly less than the height of the cotyle.

Genus *Ophisaurus* Daudin, 1803

Ophisaurus sp.
(Fig. 6A-E)

Material. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: one trunk vertebra (Pal. 1407).

Description

Trunk vertebra

The vertebra is robustly built. The neural spine starts to rise dorsally from the area of anterior region of the neural arch. However, the dorsal portion of the neural spine is damaged. In lateral aspect, the neural spine reaches posteriorly only to the level of the anterior end of the condyle. The oval, tunnel-like neural canal is medium-sized. Pre- and postzygapophyses are well expanded laterally, but the interzygapophyseal constriction is relatively shallow, not as deep as it is in the *Pseudopus* vertebrae described above. This gives Pal. 1407 a broad appearance in dorsal aspect. The prezygapophyses are dorsally inclined at an angle of around 33°. The articular surfaces are large, elliptical and oblong laterally. In anterior aspect, a pair of foramina is located ventral to the prezygapophyses, approximately at the level of the dorsal margin of the cotyle. In lateral aspect, the postzygapophyses reach posteriorly approximately to the level of the mid-region of the condyle. Both condyle and cotyle are depressed. The synapophyses are well-developed, large, and located close to the anterior edge of the neural arch pedicel. They are slightly posterolaterally oriented. The ventral region of the centrum is flat, although it has two visible edges which run from the level of the cotyle and gradually weaken posteriorly. A pair of subcentral foramina is located close to the cotyle. The subcentral ridges are concave.

Remarks

The trunk vertebra described here can be allocated to *Ophisaurus* based on the following features (Čerňanský *et al.* 2019): 1) the lateral margins of the centrum (subcentral ridges) are concave; and 2) the height of the neural canal is greater than the height of the cotyle.

Anguinae indet.
(Fig. 6F-K)

Material. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: one right and one left coronoid (Pal. 1408-1409), 38 osteoderms (Pal. 1410-1447); 2/2003 Reptile Joint: 374 osteoderms (Pal. 1577-1950).

Description

Coronoid

Both left and right coronoids are preserved, but the right one is in better condition. The element is a chevron shaped bone, with several major processes. The dorsal process, which is located in the mid-region, is shortest. However, it is a robust structure, slightly curved posteriorly. On the lateral side, the central region bears a ridge (or keel) for muscle attachment. The posterior process is broad. On its medial side, a strong muscular crest forms the anterior border of the adductor (mandibular) fossa. The whole posterior process is bent posteromedially and, in lateral aspect, the internal side has a wrinkled appearance (it is slightly sculpted by grooves). The anteromedial and anterolateral processes are incomplete. They are separated one from another by a well-developed notch. It shows that the coronoid process of the dentary overlapped this region. A wider base is present on the anteromedial process.

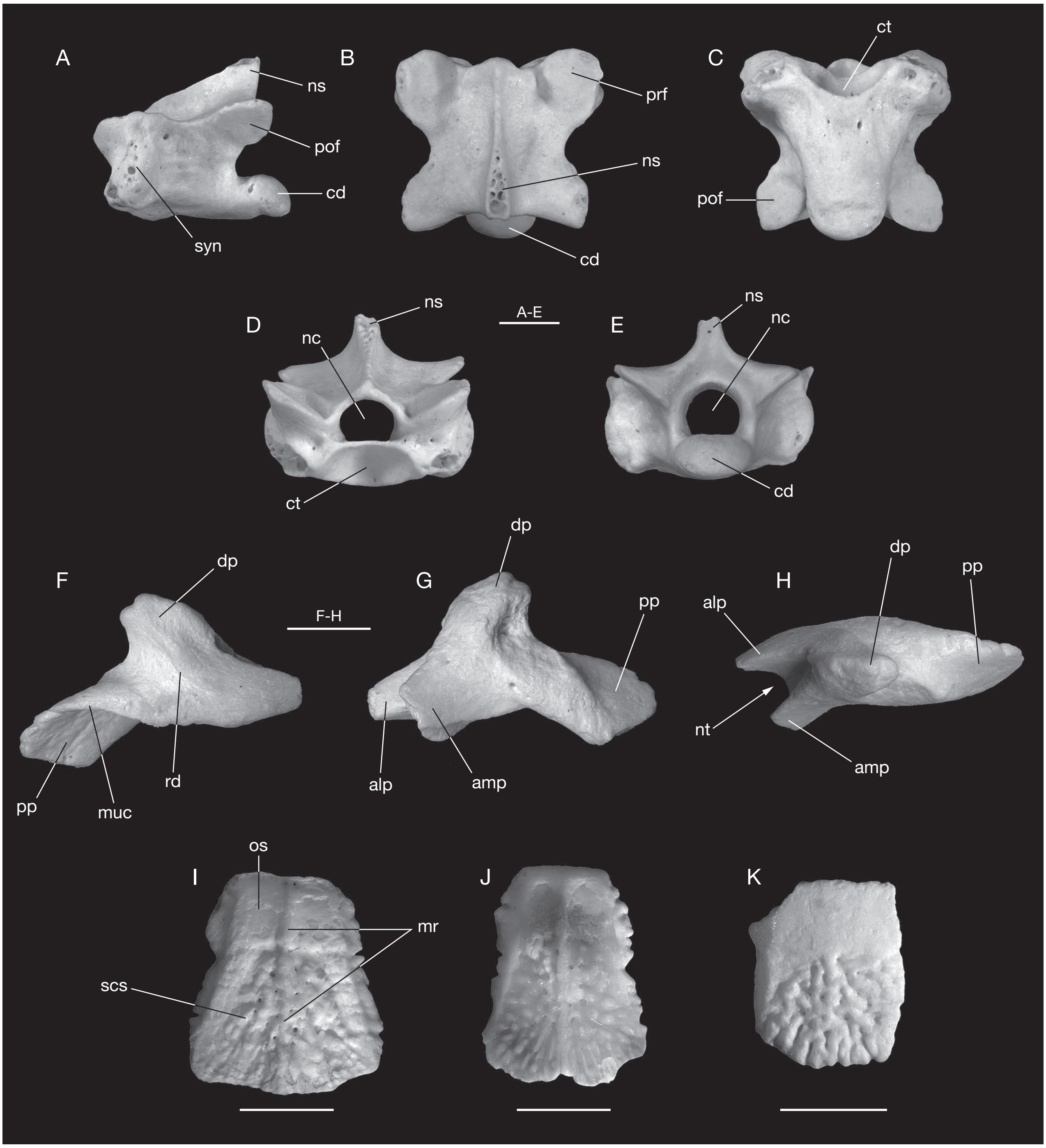

Fig. 6. — *Ophisaurus* and Anguinae indet. from the early Miocene (MN 4) of MWQ. Trunk vertebra Pal. 1407 (1/2001 Turtle Joint) of *Ophisaurus* sp. in (**A**) lateral, (**B**) dorsal, (**C**) ventral, (**D**) anterior and (**E**) posterior aspects. Anguinae indet.: right coronoid Pal. 1408 (1/2001 Turtle Joint) in (**F**) lateral, (**G**) medial and (**H**) dorsal aspects. Osteoderms Pal. 1577-1579 (2/2003 Reptile Joint) in (**I-K**) external aspects. Abbreviations: **alp**, anterolateral process; **amp**, anteromedial process; **cd**, condyle; **ct**, cotyle; **dp**, dorsal process; **mr**, medial ridge; **muc**, muscular crest; **nc**, neural canal; **ns**, neural spine; **nt**, notch; **os**, overlap surface; **pof**, postzygapophyseal articular facet; **pp**, posterior process; **prf**, prezygapophyseal articular facet; **rd**, ridge; **scs**, scupltured surface; **syn**, synapophysis. Scale bars: 2 mm.

Osteoderms

The osteoderms are of two morphotypes. The first morphotype (Fig. 6I, J) is represented by a slender, flat, trapezoidal osteoderm. This type possesses a low medial ridge running along its entire central region, including both sculptured region and smooth overlap surface. The ornamentation is formed by short ridges, tubercles and pits diverging from the central region. The sculptured region forms approximately ⅔ of the entire length of the osteoderm. The rest is formed by a smooth anterior overlap surface. The lateral bevel is highest close to the overlap surface. The central part of the internal surface is pierced by three foramina.

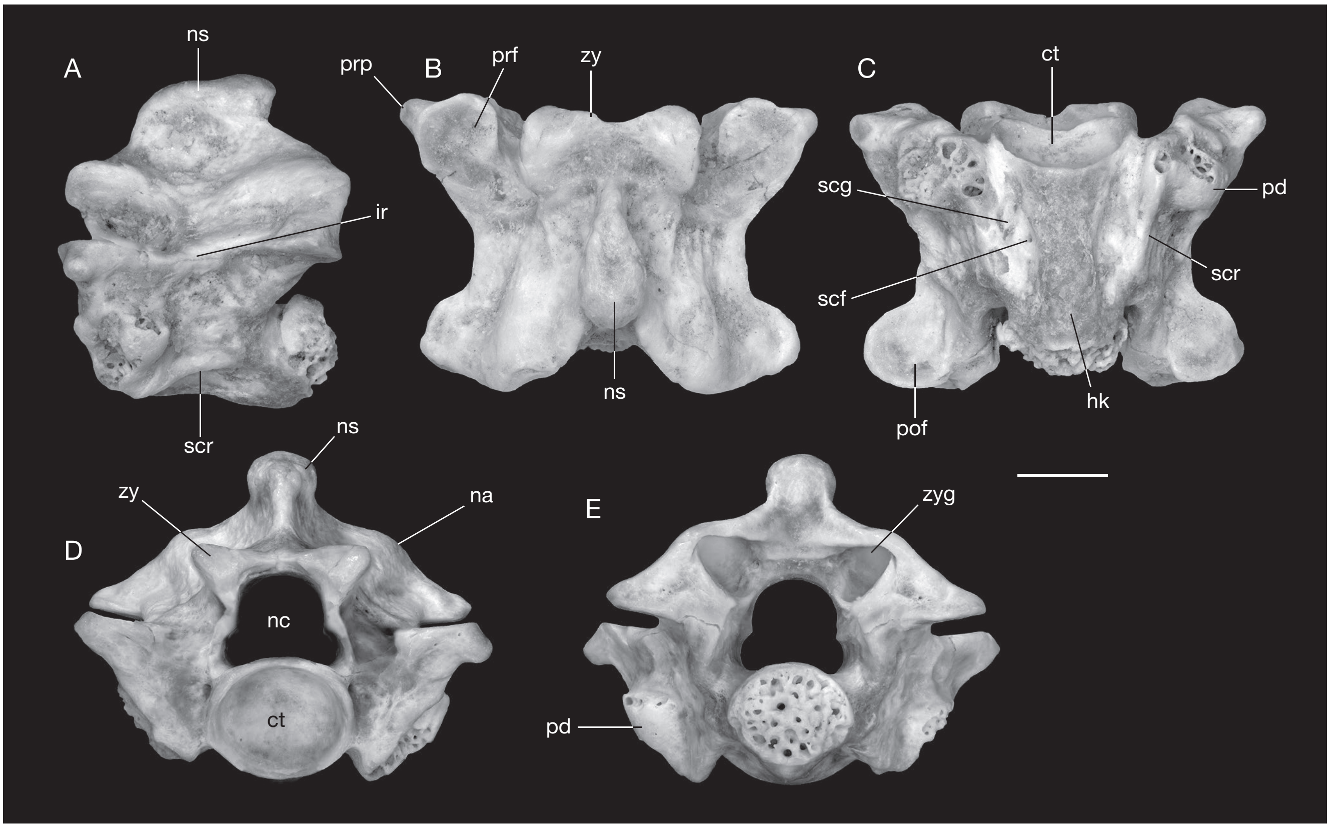

FIG. 7. — *Bavarioboa* cf. *hermi* from the early Miocene (MN 4) of MWQ. Posterior trunk vertebra Pal. 1448 (1/2001 Turtle Joint) in left lateral (**A**), dorsal (**B**), ventral (**C**), cranial (**D**) and caudal (**E**) views. Abbreviations: **ct**, cotyle; **hk**, haemal keel; **ir**, interzygapophyseal ridge; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **pd**, paradiapophysis; **pof**, postzygapophyseal articular facet; **prf**, prezygapophyseal articular facet; **prp**, prezygapophyseal process; **scf**, subcentral foramen; **scg**, subcentral groove; **scr**, subcentral ridge; **zy**, zygosphene; **zyg**, zygantrum. Scale bar: 2 mm.

Osteoderms of the second morphotype (Fig. 6K) are roughly rectangular in shape. This morphotype almost lacks the medial ridge – ornamentation is arranged only in the centre to form an indistinct ridge. This osteoderm type also differs from the first morphotype by its sculpture. It is denser because the ridges are broad, with narrow grooves between them. The smooth overlap surface is large. The internal surface is pierced by three foramina.

Suborder SERPENTES
Linnaeus, 1758
Infraorder ALETHINOPHIDIA
Nopcsa, 1923
Booid grade snakes
Family BOIDAE Gray, 1825
Genus *Bavarioboa* Szyndlar & Schleich, 1993

Bavarioboa* cf. *hermi Szyndlar & Schleich, 1993
(Fig. 7)

Bavarioboa cf. *hermi* – Ivanov & Musil 2004: 228, 229, fig. 3C, D. — Ivanov *et al.* 2006: 229, table 2.

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: One posterior trunk vertebra (Pal. 1448).

DESCRIPTION

Trunk vertebra

The only preserved trunk vertebra is almost complete with partial damage to the large paradiapophyses, the cranial margin of the zygosphene and the caudal margin of the condyle. In lateral view, the neural spine rises at about the level of the zygosphenal base. The cranial margin of the neural spine is inclined caudally with a rounded anterodorsal margin. The articular surfaces of the zygosphene are widely oval. The short interzygapophyseal ridges are rather sharp. The small lateral foramina, situated close below the interzygapophyseal ridges, do not sit within depressions. The short and dorsally bent subcentral ridges are well-developed, especially in the anterior half of the centrum. In dorsal view, the partially damaged prezygapophyseal articular facets were originally broadly subtriangular to oval in outline. The prezygapophyseal processes are rather short (about a quarter of the prezygapophyseal facets length). The zygosphene was almost straight with small lateral lobes; however, the medial part of the zygosphenal lip is rather damaged in the preserved specimen. The dorsal margin of the neural spine becomes thick towards its caudal margin. The caudal margin of the neural arch forms a relatively shallow notch. In ventral view, the haemal keel is laterally wide with a rounded ventral surface. The subcentral foramina are rather small and developed on either side of the haemal keel base. The

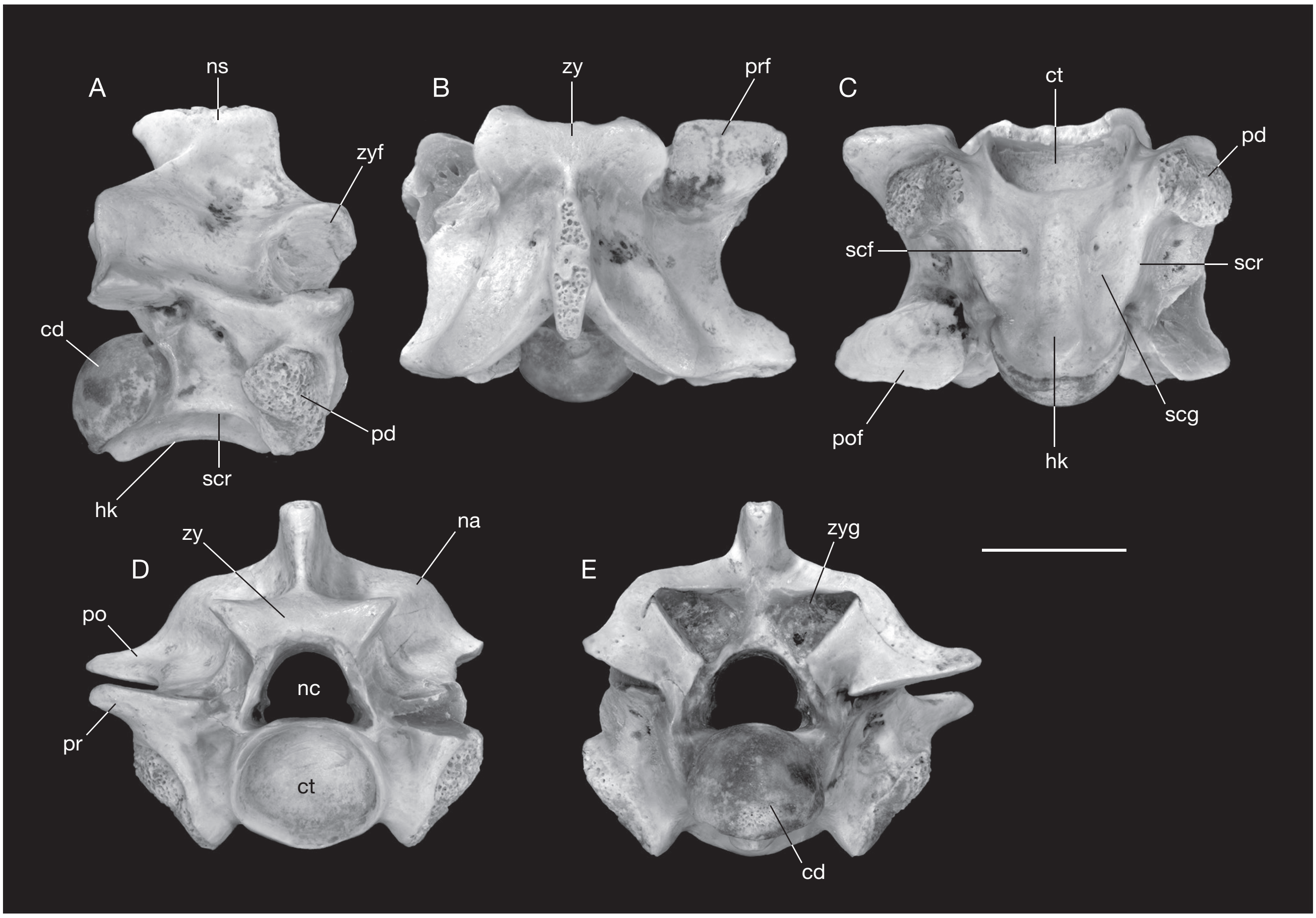

Fig. 8. — *Python* sp. from the early Miocene (MN 4) of MWQ. Posterior trunk vertebra Pal. 1449 (1/2001 Turtle Joint) in right lateral (**A**), dorsal (**B**), ventral (**C**), cranial (**D**) and caudal (**E**) views. Abbreviations: **cd**, condyle; **ct**, cotyle; **hk**, haemal keel; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **pd**, paradiapophysis; **po**, postzygapophysis; **pof**, post zygapophyseal articular facet; **pr**, prezygapophysis; **prf**, prezygapophyseal articular facet; **scf**, subcentral foramen; **scg**, subcentral groove; **scr**, subcentral ridge; **zy**, zygosphene; **zyf**, zygosphenal facet; **zyg**, zygantrum. Scale bar: 5 mm.

subcentral grooves are wide and deep. The postzygapophyseal articular facets are subrectangular in shape. In cranial view, the prezygapophyses are tilted slightly dorsally. Prezygapophyseal articular facets are situated high above the neural canal base roughly at the level of the dorsal margin of the lateral sinuses. The cranial margin of the zygosphene is slightly concave with strongly build lateral sinuses and a rather thin central part. The neural arch is vaulted. The neural canal is rounded with rather wide and shallow lateral sinuses. Depressions are developed on either side of the slightly dorsoventrally depressed cotyle. The paracotylar foramina are absent. In caudal view, the zygantrum is wide. The condyle is slightly depressed dorsoventrally. The vertebral dimensions are as follows (Pal. 1448): cl: = 5.19 mm; naw = 6.73 mm; cl/naw = 0.77.

Remarks

The massive structure of vertebra, the cl/naw ratio < 1, the relatively large dimensions, and the absence of paracotylar foramina as well as the relatively slender structure of the zygosphenal rim support the assignment to the subfamily Boinae. The single preserved vertebra resembles that of the genus *Bavarioboa* by the almost straight cranial margin of the zygosphenal lip in dorsal view, as well as the dorsally thickened neural spine that is typical for the posterior trunk vertebrae of *Bavarioboa hermi* (see Szyndlar & Rage 2003). *B. ultima* Szyndlar & Rage, 2003 from the German late early Miocene Rothenstein 13 locality (late Burdigalian, MN 5), originally assigned to *B. hermi* by Szyndlar & Schleich (1993), differs mainly by the lower neural spine as well as longer prezygapophyseal processes (Szyndlar & Rage 2003).

Family Pythonidae Fitzinger, 1826
Genus *Python* Daudin, 1803

Python sp.
(Fig. 8)

Boidae gen. et sp. indet. (large form) – Ivanov & Musil 2004: 228, 229, fig. 3A, B.

Boidae gen. et sp. indet – Ivanov *et al.* 2006: 229, table 2.

Material. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: two trunk vertebrae (Pal. 1449, 1450).

Description

Trunk vertebrae

The more complete middle trunk vertebra (Pal. 1449) has lost the left prezygapophyseal facet as well as the lateral extension of the left postzygapophysis. In lateral view, the vertebra is anteroposteriorly shorter than high. The strongly vaulted neural arch is caudally upswept above the zygantrum. The neural spine has a gently eroded dorsal margin and is slightly longer than high. Its cranial margin is vertical and rises in the middle of the zygosphene length. The caudal margin of the neural spine is inclined posteriorly behind the neural arch. The interzypapophyseal ridges are rather sharp. The zygosphenal surfaces are wide and irregularly oval. They are characterised by conspicuously large dimensions. The lateral foramina are large, and they sit in shallow depressions. The haemal keel is arched upwards. In dorsal view, the wide zygosphene possesses distinct lateral lobes; the damaged medial lobe was rather small. The neural spine is thick. The right prezygapophyseal articular facet is subtriangular. The prezygapophyseal process is rather short and it is hardly visible from the dorsal aspect. The interzygapophyseal constriction is shallow. The neural arch widens triangularly in a caudal direction. The median notch, developed at the caudal margin of the neural arch, reaches anteriorly as far as the cranial margin of the postzygapophysis. In ventral view, the paradiapophyses are massively developed. The large right postzygapophyseal articular facet has a subtriangular outline and is laterally elongated. In this view, the haemal keel is relatively wide with subcentral foramina situated at both sides of its base. In cranial view, the relatively thin prezygapophyses are tilted slightly dorsally with their base situated just above the floor of the neural canal. The lateral extension of the preserved right postzygapophysis is conspicuously thin. The neural arch is strongly vaulted, and the neural canal is rounded with short lateral sinuses. The straight cranial margin of the zygosphene is thick along its entire width. Deep depressions occur on either side of a large cotyle of almost circular outline. Paracotylar foramina are absent. In caudal view, the zygantrum is large and laterally wide. The postzygapophyses are tilted dorsally like the prezygapophyses. Several very small foramina are arranged in a line on caudal side of both postzygapophyses. The condyle is almost circular with a depressed ventral margin. The vertebral dimensions are as follows: larger specimen (Pal. 1449): cl = 7.32 mm; naw = 10.39 mm; cl /naw = 0.70. Smaller specimen (Pal. 1450): cl = 5.45 mm; naw = 8.15 mm; cl/naw = 0.67.

Remarks

The following combination of features indicate assignment of the better preserved vertebra to the extant genus *Python* (see Szyndlar & Rage 2003): 1) the large vertebra is massively built with cl/naw ratio < 1; 2) the absence of paracotylar foramina; 3) the caudal section of the strongly vaulted neural arch is upswept above the zygantrum; and 4) the zygosphenal roof is thick in anterior aspect. The markedly developed sharp subcentral ridges indicate that this vertebra was situated close/or within the posterior section of the trunk region. *Python* sp. from MWQ particularly resembles the only known extinct *Python* species, *Python europaeus* Szyndlar & Rage, 2003, reported from French early Miocene Béon 1 (MN 4) and Vieux-Collonges (MN 5) localities (Szyndlar & Rage 2003; Rage & Bailon 2005), and from the middle Miocene (MN 6, base) of Griesbeckerzell 1a, Germany (Ivanov & Böhme 2011). However, *Python* sp. from MWQ differs from *P. europaeus* by the following features: 1) the zygosphene of *Python* sp. is not straight – conspicuous lateral lobes are present; 2) in cranial view, the zygosphenal lip is slightly less massive compared to that of *P. europaeus*; and 3) lateral extensions of postzygapophyses are more slender than the same structures in *P. europaeus*. The trunk vertebrae of *Python* sp. from MWQ are smaller than middle trunk vertebrae of *P. europaeus* (Szyndlar & Rage 2003). As the morphology and build of the zygosphene strongly depends on the ontogenetic stage, it is possible that vertebrae of *Python* sp. belonged to subadult specimens.

‘Booidea’ indet.

Material. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: three trunk vertebrae (Pal. 1451-1453); 2/2003 Reptile Joint: five trunk vertebrae (Pal. 1951-1955).

Description

Trunk vertebrae

The preserved trunk vertebrae are too fragmentary. Their massive structure, combined with the wide haemal keel as well as the absence of paracotylar foramina enables assignment only to the indeterminate ‘Booidea’.

Unranked clade COLUBROIDES Zaher, Grazziotin, Cadle, Murphy, Moura-Leite & Bonatto, 2009
Superfamily Colubroidea Oppel, 1811
Family Colubridae Oppel, 1811
Subfamily “Colubrinae” (*sensu* Szyndlar 2012)
Genus *Coluber* (s.l.) Linnaeus, 1758

Coluber (s.l.) sp.
(Fig. 9)

Coluber sp. 1 – Ivanov & Musil 2004: 229 (in part).

Coluber sp., type I – Ivanov *et al.* 2006: 229, table 2 (in part).

Material. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: Two anterior trunk vertebrae (Pal. 1454-1455), 6 middle trunk vertebrae (Pal. 1456-1461), 2 caudal vertebrae (Pal. 1462, 1463). 2/2003 Reptile Joint: Two trunk vertebrae (Pal. 1956-1957), 2 caudal vertebrae (Pal. 1958-1959).

Description

Anterior and middle trunk vertebrae

The only two preserved anterior trunk vertebrae differ from those from the middle trunk portion by the presence of hypapophysis instead of haemal keel and higher neural spine (Pal. 1454; Fig. 9A-E). All preserved middle trunk vertebrae are at least partially fragmentary with neural spines mostly

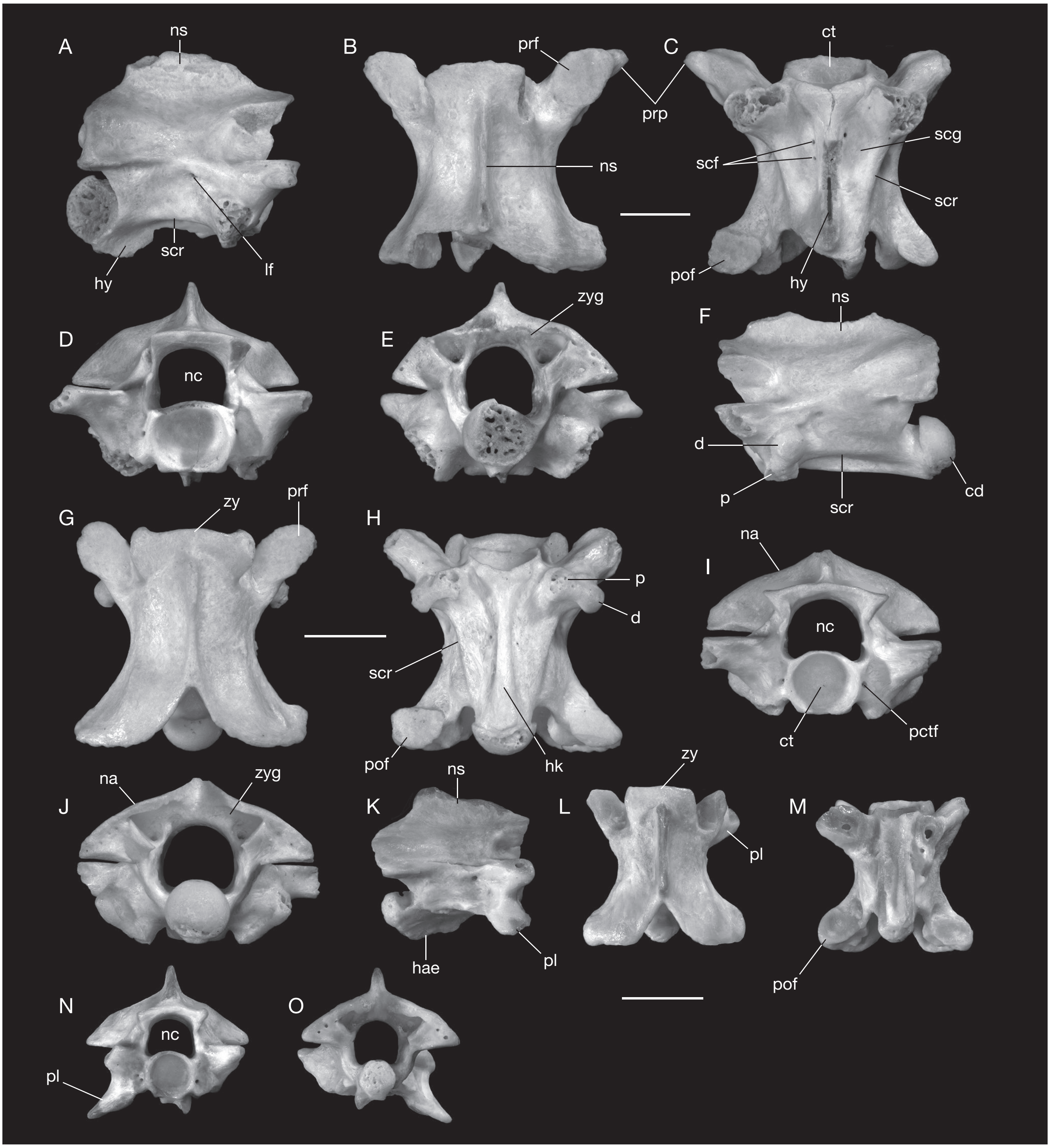

Fig. 9. — *Coluber* (s.l.) sp., from the early Miocene (MN 4) of MWQ. Anterior trunk vertebra Pal. 1454 (1/2001 Turtle Joint) in right lateral (**A**), dorsal (**B**), ventral (**C**), cranial (**D**) and caudal (**E**) views. Middle trunk vertebra Pal. 1456 (1/2001 Turtle Joint) in left lateral (**F**), dorsal (**G**), ventral (**H**), cranial (**I**) and caudal (**J**) views. Anterior caudal vertebra Pal. 1462 (1/2001 Turtle Joint) in right lateral (**K**), dorsal (**L**), ventral (**M**), cranial (**N**) and caudal (**O**) views. Abbreviations: **cd**, condyle; **ct**, cotyle; **d**, diapophysis; **hae**, haemapophysis; **hk**, haemal keel; **hy**, hypapophysis; **lf**, lateral foramen; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **p**, parapophysis; **pctf**, paracotylar foramen; **pl**, pleurapophysis; **pof**, postzygapophyseal articular facet; **prf**, prezygapophyseal articular facet; **prp**, prezygapophyseal process; **scf**, subcentral foramen; **scg**, subcentral groove; **scr**, subcentral ridge; **zy**, zygosphene; **zyg**, zygantrum. Scale bars: 2 mm.

broken-off close to their bases. In lateral view, the preserved neural spine base of the most complete specimen (Pal. 1456; Fig. 9F-J) indicates that the neural spine was probably at least twice longer than high. The caudal margin of the neural spine was inclined posteriorly as documented by specimen Pal. 1956. The well-developed interzygapophyseal ridges are short. The lateral foramina occur just below these ridges. The prominent subcentral ridges are moderately dorsally arched.

The large diapophyses are well-separated from somewhat smaller parapophyses. Although parapophyses are incomplete in all specimens, their ventral margin apparently extended below the cotylar rim. In dorsal view, the wide zygosphene has developed lateral lobes. The medial lobe is rather wide. The prezygapophyseal articular facets are oval with long axis directed antero-laterally. The prezygapophyseal processes are broken-off close to their bases. The epizygapophyseal spines are moderately developed. A deep notch occurs at the caudal margin of the neural arch. In ventral view, the straight subcentral ridges form the lateral margins of a cranio-caudally elongated centrum of narrowly triangular shape. The subcentral grooves are wide and shallow. The subcentral foramina are rather small. The haemal keel is narrow and reaches posteriorly almost to the cranial margin of the small rounded condyle. Small subcotylar tubercles occur at the ventral margin of the cotylar rim. The postzygapophyseal articular facets are subrectangular and slightly laterally elongated. In cranial view, the neural arch is vaulted, and the neural canal is wide and rounded with wide and shallow lateral sinuses. The cranial margin of the zygosphenal lip arches dorsally. The small paracotylar foramina occur within depressions on either side of the rounded cotyle. In caudal view, the zygantrum is wide. The vertebral dimensions of the largest specimen (Pal. 1456) are as follows: cl = 4.52 mm; naw = 3.21 mm; cl/naw = 1.41.

Caudal vertebrae
The rarely preserved caudal vertebrae are relatively short. In lateral view, the neural spine of the better-preserved specimen was twice as long as high. Its cranial margin rises in the middle of the zygosphene length. The zygosphenal facets are oval. The preserved base of the right pleurapophysis is directed antero-ventrally. Haemapophyses are broken-off close to their bases. In dorsal view, the zygosphene is almost straight. The prezygapophyseal articular facets are oval in outline. The preserved base of the right pleurapophysis in specimen Pal. 1462 (Fig. 9K-O) is anterolaterally directed indicating anterior caudal position within the vertebral column. In cranial view, the zygosphene is arched dorsally. The small paracotylar foramina occur on either side of the circular cotylar rim.

REMARKS

The gracile structure of vertebrae with cl/naw ratio > 1, the presence of paracotylar foramina, as well as well-developed neural spine, the presence of prezygapophyseal processes, and the haemal keel developed in trunk vertebrae enable assignment to "Colubrinae". The middle trunk vertebrae resemble those of the genus "*Coluber*" on the basis of the following combination of characters: 1) strongly cranio-caudally elongated centrum of trunk vertebrae; 2) the vaulted neural arch; 3) the well-developed and narrow haemal keel; and 4) the prezygapophyseal processes which were probably long, based on the well-developed prezygapophyseal processes in anterior trunk vertebrae. "Colubrines" referred to the genus "*Coluber*" have frequently been reported from the European Neogene (e.g., Szyndlar 1991a, 2005, 2009, 2012; Szyndlar & Schleich 1993; Ivanov 2002a, b; Ivanov & Böhme 2011; Rage & Bailon 2005; Venczel 1994, 1998, 2001). There are four large "colubrine" species in the European Miocene: *Coluber dolnicensis* Szyndlar, 1987 (MN 3a-MN 4), *C. caspioides* Szyndlar & Schleich, 1993 (MN 3a-?MN 6), *C. suevicus* (Fraas, 1870) (MN 3a-MN 7+8) and *C. pouchetii* (de Rochebrune, 1880) (MN 4-MN 9). *Coluber* (s.l.) sp. differs from *C. dolnicensis* in the absence of a prominent step in the anterior part of the haemal keel (Szyndlar 1987; Ivanov 2002a). It differs from *C. caspioides* in the smaller dimensions and the wider zygosphene (Szyndlar & Schleich 1993; Ivanov 2002a). *Coluber* (s.l.) sp. differs from *C. suevicus* in the more vaulted neural arch and clearly smaller diameter of the prezygapophyseal articular facets (Szyndlar & Böhme 1993; Ivanov 2002a). It differs from *C. pouchetii* in the apparently much lower neural spine and a cervical hypapophysis inclined posteroventrally rather than ventrally (Augé & Rage 2000; Szyndlar 2009). *Coluber* (s.l.) sp., type 1 resembles *C. hungaricus* (Bolkay, 1913) reported from the early middle Miocene (MN 6) of Germany (Ivanov & Böhme 2011), the middle Miocene to early Pliocene (?MN 6-MN 9; MN 13-MN 14) of Hungary (Venczel 1994, 1998, 2001), and the middle Miocene of Kazakhstan (Ivanov *et al.* 2019) in: 1) the same dimensions; 2) most probably in the same height of the neural spine; 3) a similarly wide medial lobe of the zygosphene; and 4) a parapophysis of the same length as the diapophysis (Venczel 1994; Szyndlar 2005). *C. hungaricus* displays a high intraspecific variability and the largest specimens have a dorsally thickened neural spine, parapophyses larger than diapophyses, as well as well-developed subcotylar tubercles (Venczel 1998). Despite this variability, *Coluber* (s.l.) sp. cannot be attributed to *C. hungaricus* because of the presence of much more distinct, sharp, and straight subcentral ridges, a deeper notch in the caudal margin of the neural arch, as well as the smaller condyle. Because of the incomplete preservation of the rather scarce material we avoid a species level identification.

"COLUBRINAE" indet., type 1
(Fig. 10)

Coluber sp. 2 – Ivanov & Musil 2004: 229 (in part).

Coluber sp., type II – Ivanov *et al.* 2006: 229, table 2 (in part).

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: 15 trunk vertebrae (Pal. 1464-1478), 2 caudal vertebrae (Pal. 1479, 1480); 2/2003 Reptile Joint: Six trunk vertebrae (Pal. 1960-1965), 2 caudal vertebrae (Pal. 1966, 1967).

DESCRIPTION

Trunk vertebrae
Preserved fragmentary vertebrae (Fig. 10A-L) are rather small with a maximum length of 4.16 mm for the largest vertebra and a width of 2.55 mm. In lateral view, the cranial

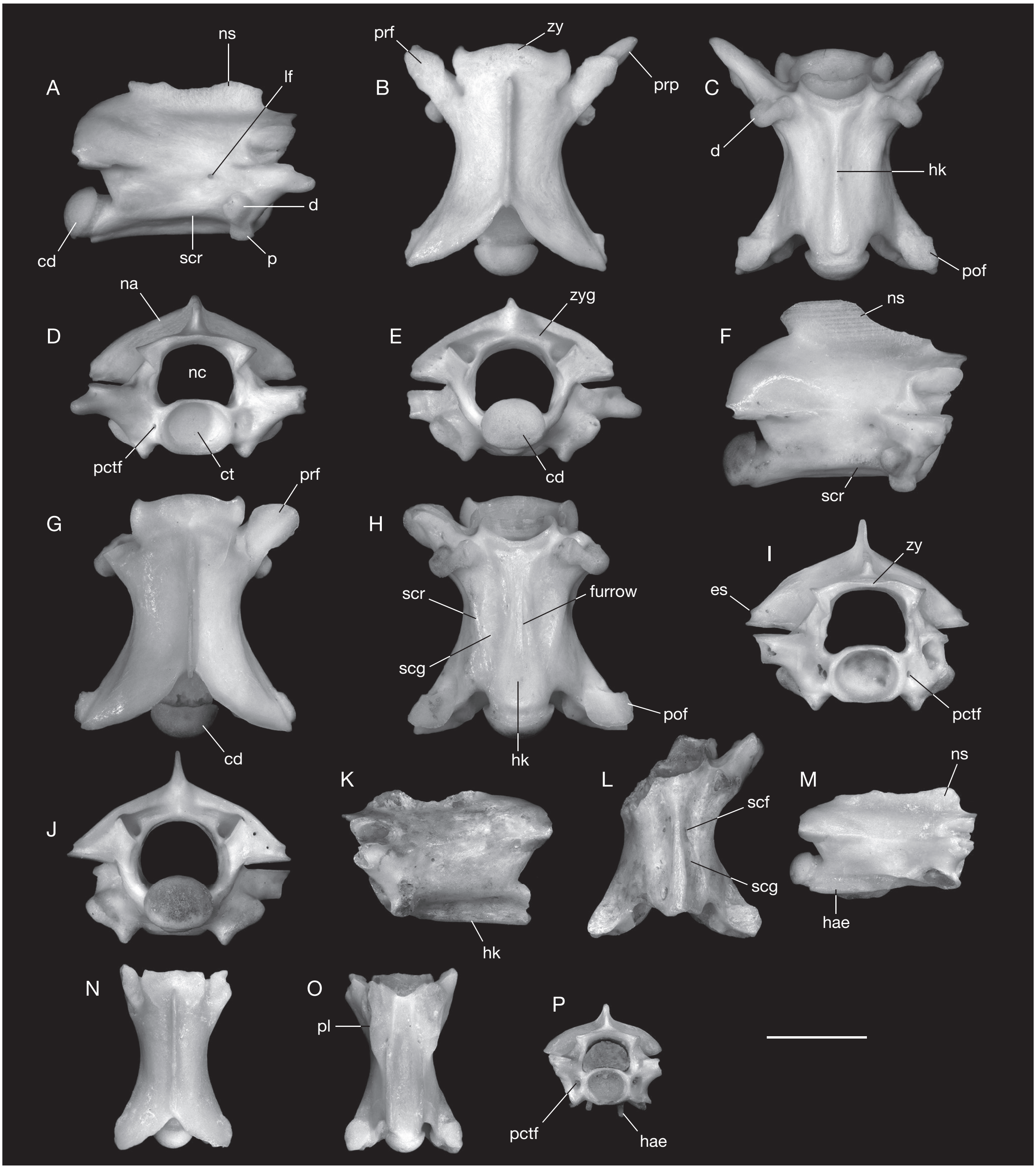

Fig. 10. — "Colubrinae" indet., type 1 from the early Miocene (MN 4) of MWQ. Middle trunk vertebra Pal. 1464 (1/2001 Turtle Joint) in right lateral (**A**), dorsal (**B**), ventral (**C**), cranial (**D**) and caudal (**E**) views. Middle trunk vertebra Pal. 1465 (1/2001 Turtle Joint) in right lateral (**F**), dorsal (**G**), ventral (**H**), cranial (**I**) and caudal (**J**) views. Posterior trunk vertebra Pal. 1466 (1/2001 Turtle Joint) in left lateral (**K**) and ventral (**L**) views. Caudal vertebra Pal. 1966 (2/2003 Reptile Joint) in right lateral (**M**), dorsal (**N**), ventral (**O**) and cranial (**P**) views. Abbreviations: **cd**, condyle; **ct**, cotyle; **d**, diapophysis; **es**, epizypapophyseal spine; **hae**, haemapophysis; **hk**, haemal keel; **lf**, lateral foramen; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **p**, parapophysis; **pctf**, paracotylar foramen; **pl**, pleurapophysis; **pof**, postzygapophyseal articular facet; **prf**, prezygapophyseal articular facet; **prp**, prezygapophyseal process; **scf**, subcentral foramen; **scg**, subcentral groove; **scr**, subcentral ridge; **zy**, zygosphene; **zyg**, zygantrum. Scale bar: 2 mm.

margin of the neural spine is inclined anteriorly whereas caudal margin is inclined posteriorly. The neural spine is about twice to three times longer than high (Fig. 10A, F). The interzygapophyseal ridges are absent or indistinctly developed. The lateral foramina sit in shallow depressions. The paradiapophyses are markedly small with parapophysis somewhat smaller than the diapophysis. The subcentral ridges are almost straight but on the anteriormost trunk vertebrae they are dorsally slightly arched (Fig. 10A). In dorsal view, the zygosphene is wide with small and pointed lateral lobes and a rather wide and blunt medial lobe; thus, the cranial margin of the zygosphene appears to be convex. The prezygapophyseal articular facets are rather small with an oval outline and their long axis extended anterolaterally. The only preserved right prezygapophyseal process is slender and almost as long as the prezygapophyseal facet. It is anterolaterally directed with a pointed distal termination. In ventral view, the vertebral centrum is elongated craniocaudally. The morphology of the haemal keel strongly depends on its position within the vertebral column. On anterior trunk vertebrae, the haemal keel is narrow and sometimes has a sharp ventral margin. In the middle trunk vertebrae, the haemal keel extends slightly towards the caudal margin of the centrum, and rather indistinct furrows sometimes occur along the haemal keel's axis. In the posterior trunk vertebrae, the ventral margin of the haemal keel is rather flat and may laterally overhang its narrow base slightly (Fig. 10K, L). The subcotylar tubercles are absent, the subcentral grooves are shallow, and the subcentral foramina are very small. The subcentral ridges are usually rather blunt. The parapophyses are rather short. The postzygapophyseal articular facets are subrectangular and slightly laterally elongated. In cranial view, the neural arch is vaulted, and the neural canal is wide and rounded with small lateral sinuses. The cranial margin of the zygosphenal lip is arched dorsally but the medial lobe can be bent slightly ventrally. The prezygapophyseal processes are also bent slightly ventrally. The paracotylar foramina occur within deep depressions on either side of the slightly dorsoventrally depressed cotyle. In caudal view, the zygantral area is wide. The base of the condyle is flattened. The vertebral dimensions of the largest vertebrae from 1/2001 Turtle Joint are as follows (n = 7): cl: or = 3.65-4.16 mm; naw: or = 2.19-2.55 mm; cl/naw: or = 1.56-1.71, mean 1.65 ± 0.05.

Caudal vertebrae

The more complete vertebra (Fig. 10M-P) is fragmentary with loss of the distal tips of the pleurapophyses and haemapophyses as well as damaged prezygapophyses. In lateral view, the neural spine height is about a quarter of its length. In dorsal view, the vertebra is strongly elongated craniocaudally. The neural arch is cylindrical. Prezygypophyses with strongly elongated prezygapophyseal articular facets are directed anteriorly rather than anterolaterally. Therefore, we conclude that these caudal vertebrae belong to the same taxon as above described trunk vertebrae.

REMARKS

The trunk vertebrae of this tiny snake are characterized by: 1) small dimensions; 2) interzygapophyseal ridges absent or moderately developed; 3) medial lobe of the zygosphene sometimes bent ventrally; 4) slender anterolaterally directed prezygapophyseal processes with pointed distal terminations; 5) markedly small paradiapophyses with a short parapophysis that is somewhat smaller than the diapophysis; and 6) the rather blunt subcentral ridges. The vertebrae differ from those of extinct Eurasian small "colubrine" genera including Oligocene (MP 22, MP 30) and early to late Miocene (MN 4-MN 9) *Texasophis* (Rage & Holman 1984; Augé & Rage 2000; Szyndlar 1987, 1991a, 1994; Ivanov & Böhme 2011; Ivanov *et al.* 2019), late Miocene (MN 13) *Hispanophis* (Szyndlar 1985), middle Miocene (MN 6, MN 7+8) *Paleohetorodon* (Rage & Holman 1984; Holman 2000), and two new genera of late Miocene or early Pliocene (MN 13/MN 14) colubrid snakes (Georgalis *et al.* 2019) by the presence of blunt subcentral ridges and markedly small paradiapophyses. Such small paradiapophyses with rather short parapophyses do not occur in any known Eurasian fossil "colubrines" nor in studied extant representatives. Although similarly small paradiapophyses as well as blunt subcentral ridges occur in the Asiatic and North American genus *Opheodrys* Fitzinger, 1843, the epizygapophyseal spines are underdeveloped, the prezygapophyseal articular facets are widely oval to almost circular in outline, and the prezygapophyseal processes are much shorter in this extant genus (Parmley 1990; Holman 2000). Although "Colubrinae" indet., type 1 possibly represents a new taxon, the vertebral morphology of most Asiatic small "colubrines" is unknown and a more precise comparison will be necessary.

COLUBRIDAE gen. et sp. indet.
(Fig. 11)

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: One trunk vertebra (Pal. 1484).

DESCRIPTION

Trunk vertebra

This vertebra is strongly damaged. In lateral view, the cranial margin of the neural spine is inclined anteriorly, and the caudal margin was probably inclined posteriorly. The neural spine was 1.5 times longer than high. The zygosphenal facets are widely oval in outline. In dorsal view, the prezygapophyseal articular facets are oval with the long axis directed anterolaterally. In ventral view, the subrectangular postzygapophyseal articular facets are slightly laterally elongated. In cranial view, the neural arch is vaulted. The neural canal is rounded with markedly developed lateral sinuses. The zygosphenal roof is moderately arched dorsally. Small paracotylar foramina occur on both sides of the rounded cotyle.

REMARKS

This fragmentary vertebra represents the largest colubrid specimen reported from MWQ. The vaulted neural arch, the high neural spine, the presence of parapophyseal processes (broken-off at the base) as well as paracotylar foramina on either side of the cotyle undoubtedly indicate assignment to Colubridae. However, we cannot observe the ventral part

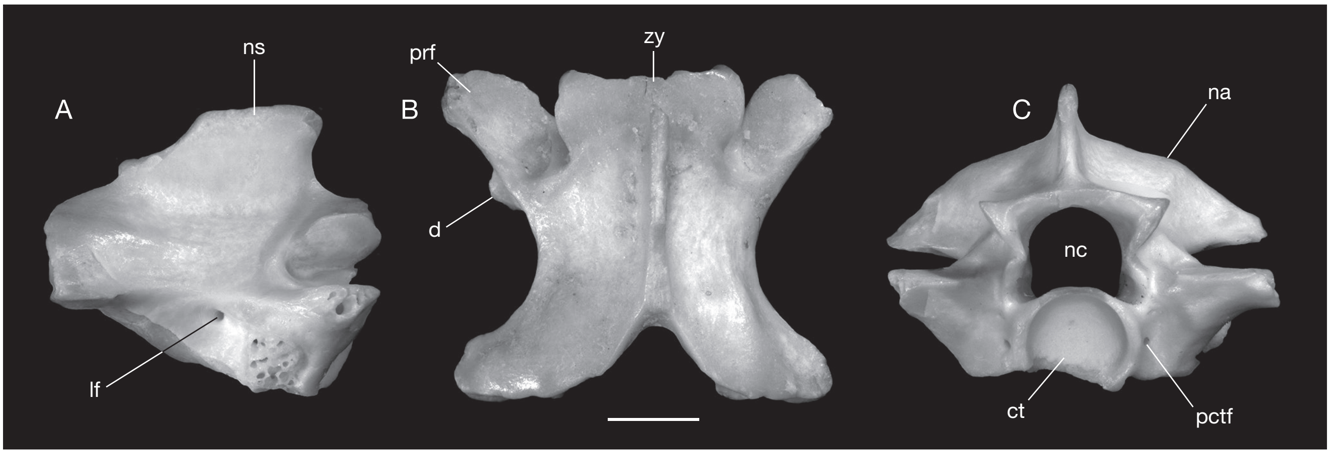

Fig. 11. — Colubridae gen. et sp. indet. from the early Miocene (MN 4) of MWQ. Trunk vertebra Pal. 1484 (1/2001 Turtle Joint) in right lateral (**A**), dorsal (**B**) and cranial (**C**) views. Abbreviations: **ct**, cotyle; **d**, diapophysis; **lf**, lateral foramen; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **pctf**, paracotylar foramen; **prf**, prezygapophyseal articular facet; **zy**, zygosphene. Scale bar: 2 mm.

of the vertebra to check the presence/absence of a haemal keel or hypapophysis. The vertebra lacks the strong elongation and cylindrical shape of the neural arch frequently occurring in European "natricines". Therefore, we conclude that the vertebra most probably belonged to a large-sized "Colubrinae".

COLUBRIDAE indet.

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: 11 trunk vertebrae (Pal. 1485-1495), 4 caudal vertebrae (Pal. 1496-1499). 2/2003 Reptile Joint: Ten trunk vertebrae (Pal. 1974-1983), 10 caudal vertebrae (Pal. 1984-1993).

REMARKS

All preserved vertebrae are rather fragmentary and a more precise identification other than at the family level is not possible.

Family NATRICIDAE Bonaparte, 1838
Subfamily "NATRICINAE" (*sensu* Szyndlar 2012)
Genus *Natrix* Laurenti, 1768

Natrix sp.
(Fig. 12A-E)

Natrix sp. – Ivanov & Musil 2004: 229.

Natrix sp., type I – Ivanov *et al.* 2006: 229, table 2 (in part).

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: Two trunk vertebrae (Pal. 1481-1482); 2/2003 Reptile Joint: Two trunk vertebrae (Pal. 1968-1969).

DESCRIPTION

Trunk vertebrae

The most complete specimen, Pal. 1968, is fragmentary with the hypapophysis and right prezygapophyseal process broken off, and strongly damaged paradiapophyses (Fig. 12A-E). The vertebral centrum is cylindrical. In lateral view, the interzygapophyseal ridges are moderately developed. The completely preserved neural spine is about twice as long as high. Its cranial margin is inclined anteriorly whereas the caudal margin is inclined posteriorly. The small lateral foramina are situated in shallow depressions. The well-developed subcentral ridges are arched dorsally. In dorsal view, the prezygapophyseal articular facets are almost oval. The prezygapophyseal processes are about two thirds of the prezygapophyseal facets length. The cranial margin of the mostly damaged zygosphene has developed a wide medial lobe and small lateral lobes. The epizygapophyseal spines are absent. In ventral view, the hypapophysis expands laterally in a cranial direction to form a triangular anterior keel. The very small subcentral foramina are situated on both sides of the hypapophysis. In cranial view, the neural arch is slightly vaulted, and the neural canal is rounded with short lateral sinuses. The parapophyseal processes are separated from the rounded cotyle by deep furrows. The paracotylar foramina are situated on both sides of the cotyle. The left paracotylar foramen is doubled in Pal. 1968. The small paracotylar tubercles occur at the ventral margin of the cotyle. The vertebral dimensions of the figured specimen (Pal. 1968) are as follows: cl = 4.60 mm; naw = 2.72 mm; cl/naw = 1.69. The largest specimen (Pal. 1481) measures as follows: cl = 4.93 mm; naw = 2.85 mm; cl/naw = 1.73.

REMARKS

Assignment to the "natricine" snakes is based on the presence of hypapophyses in precloacal vertebrae, the vaulted neural arch, the high neural spine, and the presence of paracotylar foramina on either side of the cotyle. The most complete vertebra with laterally directed prezygapophyses, an elongated centrum with a triangular anterior keel on the hypapophysis, and a neural spine inclined both anteriorly and posteriorly permit identification of the preserved vertebrae to the genus *Natrix* whose fossil remains are abundant in Central Europe as early as the early Miocene (Ivanov 2002a; Čerňanský *et al.* 2015). *Natrix* sp. differs from early Miocene *N. merkurensis*

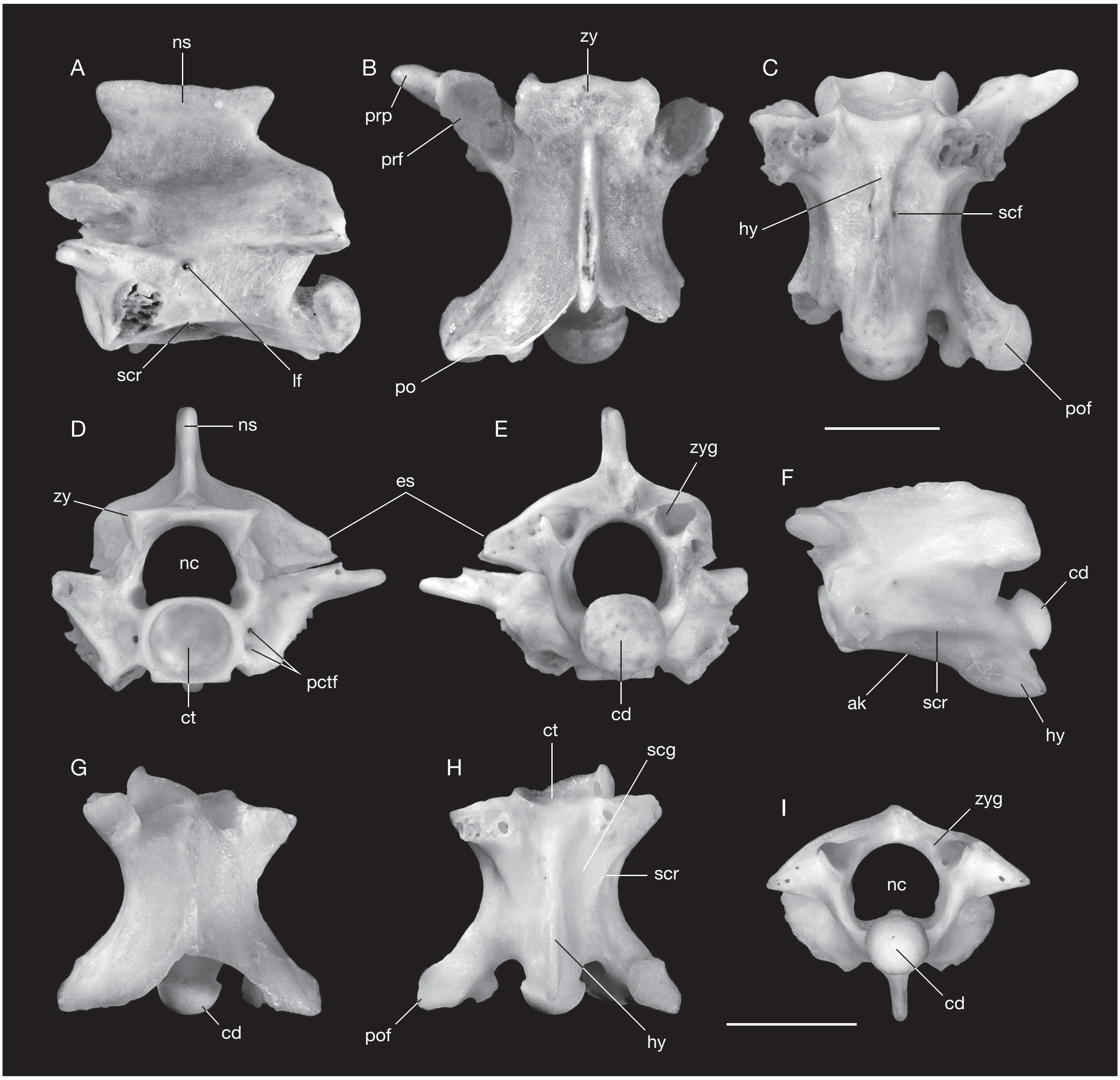

Fig. 12. — *Natrix* sp. and "Natricinae" indet. from the early Miocene (MN 4) of MWQ. *Natrix* sp.: trunk vertebra Pal. 1968 (2/2003 Reptile Joint) in left lateral (**A**), dorsal (**B**), ventral (**C**), cranial (**D**) and caudal (**E**) views. "Natricinae" indet.: trunk vertebra Pal. 1483 (1/2001 Turtle Joint) with preserved hypapophysis in left lateral (**F**), dorsal (**G**), ventral (**H**) and caudal (**I**) views. Abbreviations: **ak**, anterior keel; **cd**, condyle; **ct**, cotyle; **es**, epizypapophyseal spine; **hy**, hypapophysis; **lf**, lateral foramen; **nc**, neural canal; **ns**, neural spine; **pctf**, paracotylar foramen; **po**, postzygapophysis; **pof**, postzygapophyseal articular facet; **prf**, prezygapophyseal articular facet; **prp**, prezygapophyseal process; **scf**, subcentral foramen; **scg**, subcentral groove; **scr**, subcentral ridge; **zy**, zygosphene; **zyg**, zygantrum. Scale bars: 2 mm.

Ivanov, 2002 (MN 3a-?MN 4; Ivanov 2002a; Rage & Bailon 2005) in its smaller dimensions, elongated prezygapophyseal facets, shorter prezygapophyseal processes, and more distinct lateral lobes of the zygosphene. It differs from *N. sansaniensis* (Lartet, 1851), reported from the early and middle Miocene (MN 3-?MN 7+8; Augé & Rage 2000; Ivanov 2000, 2002a, b), in the less vaulted neural arch and flattened prezygapophyseal processes (Szyndlar 2005). *N. longivertebrata* Szyndlar, 1984 reported from the late Miocene (MN 9, MN 10/11; Ivanov 1997; Tempfer 2005) and Pliocene (MN 14-MN 16; Szyndlar 1984, 1991b; Venczel 2001), and doubtfully as early as the middle Miocene (?MN 6-?MN 7+8; Rage & Szyndlar 1986; Szyndlar 1991c), has more elongated vertebrae and a much lower neural spine. *Natrix* sp. closely resembles the extinct *N. rudabanyaensis* Szyndlar, 2005 reported from the early late Miocene of Rudabánya, Hungary (MN 9a; Szyndlar 2005) and perhaps the middle Miocene of Tauţ, Romania (MN 7+8; Venczel & Ştiucă 2008) in: 1) the same height and shape of the neural spine; 2) moderately developed subcentral ridges; 3) elongated prezygapophyseal facets; and 4) flattened prezygapophyseal processes (Szyndlar 2005). However, the absence of the hypapophysis and paradiapophyses prevents alpha taxonomy.

"NATRICINAE" indet.
(Fig. 12F-I)

cf. *Neonatrix* sp. – Ivanov *et al.* 2006: 229, table 2.

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: One trunk vertebra (Pal. 1483). 2/2003 Reptile Joint: Four trunk vertebrae (Pal. 1970-1973).

DESCRIPTION
Trunk vertebrae

The most complete vertebra (Pal. 1483) has strongly damaged prezygapophyses and the zygosphene, and the neural spine is broken-off close to its base. In lateral view, the interzygapophyseal ridges are moderately developed and lateral foramina are situated within deep depressions. The subcentral ridges are nearly straight. The distal termination of sigmoid hypapophysis does not reach posterior to the caudal border of condyle. In dorsal view, the vertebra is cylindrical, the damaged zygosphene was wide relative to the neural arch width. Epizygapophyseal ridges are absent. In ventral view, the subcentral grooves are very shallow and short and the subcentral foramina are rather small and situated just posterior to the base of the hypapophysis. The subcotylar tubercles are missing. The damaged postzygapophyseal articular facets have a subrectangular outline and are not elongated laterally. In cranial view, the neural arch is slightly vaulted, and the large neural canal has developed conspicuously large and wide lateral sinuses. The cranial margin of the zygosphene was arched dorsally. The small paracotylar foramina are situated within wide depressions on either side of the rounded cotyle. The vertebral dimensions of the best-preserved specimen (Pal. 1483) are: cl = 3.51 mm; naw = 2.24 mm; cl/naw = 1.57.

REMARKS
The sigmoid shape of the hypapophysis, with an anterior keel sloping towards the cotylar rim is reminiscent of precaudal vertebrae of the genus *Palaeonatrix* Szyndlar, 1982 (see Młynarski *et al.* 1982) reported from the early Miocene (MN 4) of Dolnice, Czech Republic (Rage & Roček 1983; Szyndlar 1987), Petersbuch 2 and Langenau, Germany (Szyndlar & Schleich 1993), Oberdorf, Austria (Szyndlar 1998) and the middle Miocene of Sansan, France (MN 6; Augé & Rage 2000) and Opole, Poland (MN 7+8; Młynarski *et al.* 1982). However, a generic allocation is impossible because the relatively low neural spine which characterizes the genus *Palaeonatrix* (Szyndlar 1987, 1991b) is not preserved in studied specimens from MWQ. Although the very strongly developed subcentral ridges are typical for the genus *Palaeonatrix* (Szyndlar 1987) we cannot exclude the possibility that the subcentral ridges were shorter and less distinct in vertebrae situated anterior to the preserved vertebra. Because of the limited fossil material and lack of information on intracolumnar variability, a more precise assignment is not possible.

Family VIPERIDAE Oppel, 1811
Subfamily VIPERINAE Oppel, 1811
Genus *Vipera* Laurenti, 1768

Vipera sp. ('European vipers' group)
(Fig. 13A-H)

Vipera sp. 2 ('European vipers') – Ivanov & Musil 2004: 230.

Vipera sp. ('European vipers' group) – Ivanov *et al.* 2006: 229, table 2.

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 2/2003 Reptile Joint: three trunk vertebrae (Pal. 2022-2024).

DESCRIPTION
Trunk vertebrae

The vertebrae are rather fragmentary with the neural spines broken-off close to their bases, and loss of the paradiapophyses and hypapophysis. In lateral view, the interzygapophyseal ridge of the best-preserved vertebra (Pal. 2022) is short. The lateral foramina are situated just below the interzygapophyseal ridges. The subcentral ridges are clearly bent dorsally. In dorsal view, the cranial margin of the zygosphene has developed small lateral lobes and a wide medial lobe. The right prezygapophyseal articular facet is subtriangular to oval in outline. The prezygapophyseal process is rather short. The epizygapophyseal spines are moderately developed. In ventral view, the subcentral grooves are deep, possibly indicating a more posterior position of the vertebra within the precloacal region. The hypapophysis is strongly built, extending anteriorly into a short triangular anterior keel. In cranial view, the neural arch is depressed dorsoventrally, and the neural canal is rounded with prominent lateral sinuses. The cranial margin of the zygosphene is vaulted dorsally. Large paracotylar foramina occur on either side of the rounded cotyle. The vertebral dimensions of the largest vertebra (Pal. 2023) are as follows: cl = 3.75 mm; naw = 2.85 mm; cl/naw = 1.32.

REMARKS
The vertebrae are typically viperine with a dorsoventrally depressed neural arch and prezygapophyses tilted up dorsally. The vertebrae are assigned to the 'European vipers'. Because of their small dimensions we conclude that the vertebrae could probably belong to the '*Vipera aspis*' complex. A more precise identification is not possible because of poor preservation.

VIPERINAE ('Oriental vipers' group)
(Fig. 14A-N; Fig. 15A-J)

Vipera sp. 1 ('Oriental vipers') – Ivanov & Musil 2004: 230.

Vipera sp. ('Oriental vipers' group) – Ivanov *et al.* 2006: 229, table 2.

MATERIAL. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: one left maxilla (Pal. 1501), isolated fang (Pal. 1502), 30 trunk vertebrae (Pal. 1503-1532). 2/2003 Reptile Joint: 28 trunk vertebrae (Pal. 1994-2021).

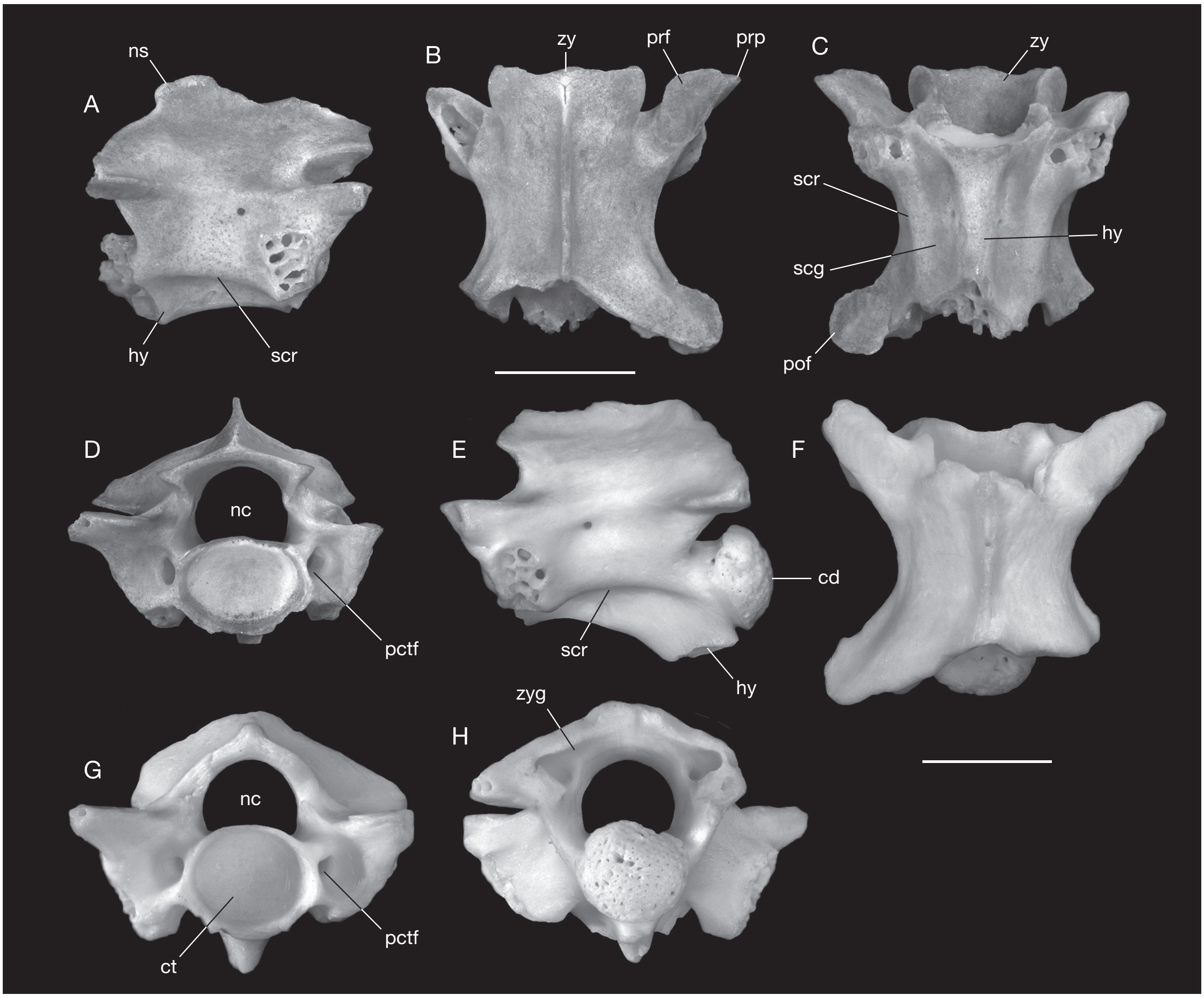

Fig. 13. — *Vipera* sp. ('European vipers' group) from the early Miocene (MN 4) of MWQ. Trunk vertebra Pal. 2022 (2/2003 Reptile Joint) in right lateral (**A**), dorsal (**B**), ventral (**C**) and cranial (**D**) views. Trunk vertebra Pal. 2023 (2/2003 Reptile Joint) in left lateral (**E**), dorsal (**F**), cranial (**G**) and caudal (**H**) views. Abbreviations: **cd**, condyle; **ct**, cotyle; **hy**, hypapophysis; **nc**, neural canal; **ns**, neural spine; **pctf**, paracotylar foramen; **pof**, postzygapophyseal articular facet; **prf**, prezygapophyseal articular facet; **prp**, prezygapophyseal process; **scg**, subcentral groove; **scr**, subcentral ridge; **zy**, zygosphene; **zyg**, zygantrum. Scale bars: 2 mm.

Description

Maxilla

Only a left maxilla is preserved (Fig. 14A, B). In rostral view, the body of the bone is high, especially along its medial margin. The ascending process is long, and it is inclined medially. A small process for the prefrontal connection occurs medially at its distal termination. A ridge extends from the base of the ascending process as far as its distal termination. A large, slightly oval, foramen occurs opposite to the medially directed maxillary-prefrontal process. In caudal view, a wide groove for connection with the ectopterygoid occurs above the base of the fangs. This groove is deep, and it is restricted dorsally by a transverse ridge. This ridge extends from the medial margin of the bone (where it forms two small processes) as far as the middle of the ascending process width. In medial view an oval foramen occurs within the deep, wide orifice. This orifice is restricted dorsally by a ridge.

Dentition

A single fang of about 1 cm length is preserved (Fig. 14C). It is long and slender, and is curved slightly caudally. A canal extends within the tooth and has a strongly elongated/slit-like orifice situated mesially, close to the pointed tip of the fang. The slightly widened basal portion of the fang is damaged and does not preserve the orifice of the venom canal.

Trunk vertebrae

Numerous fragmentary trunk vertebrae (Fig. 14D-N; Fig. 15A-J) are preserved, mostly with broken-off neural spines and hypapophyses. In lateral view, the neural spine was about as high as long in anterior precaudal vertebrae.

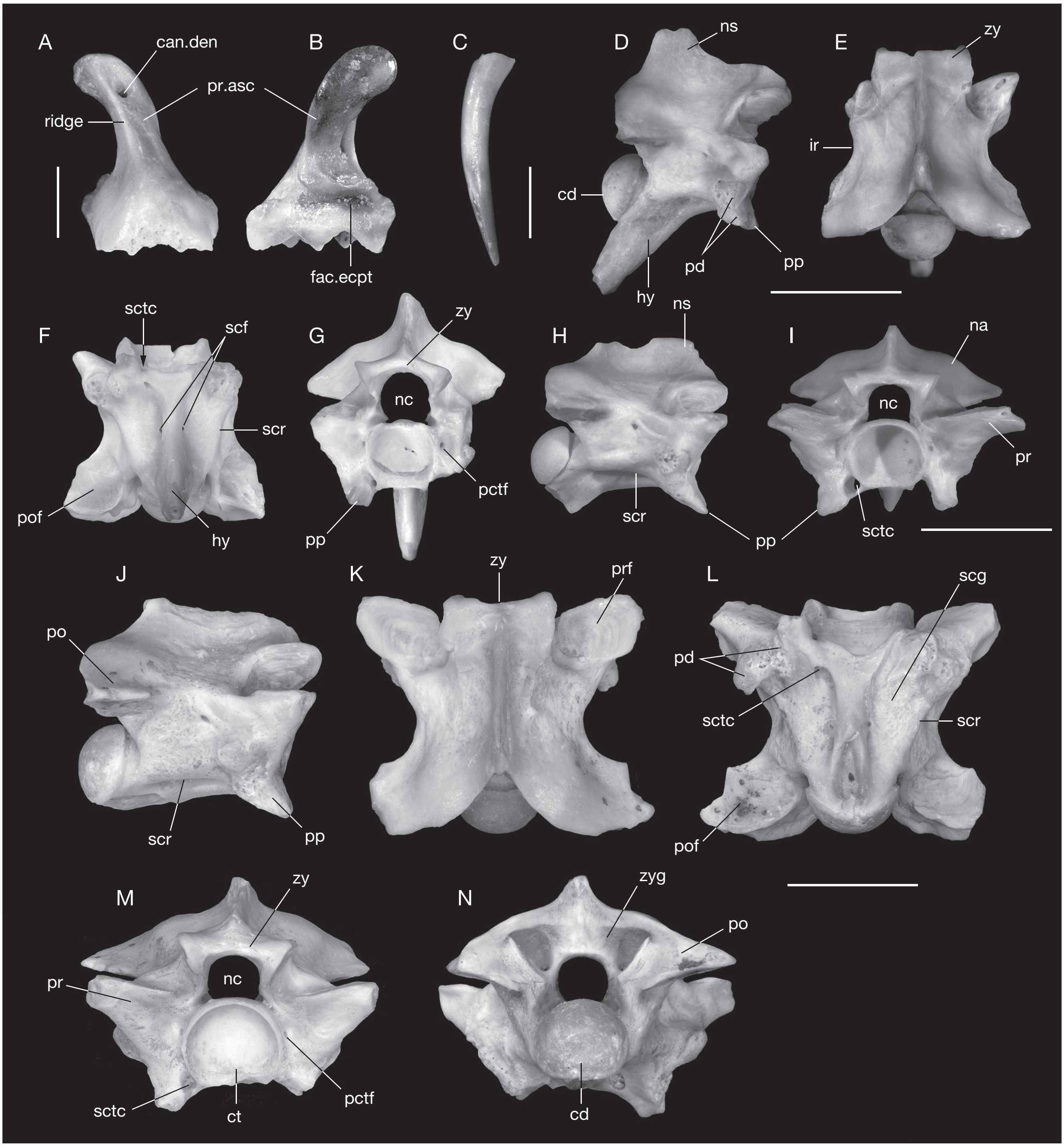

Fig. 14. — Viperinae ('Oriental vipers' group) from the early Miocene (MN 4) of MWQ. Left maxilla Pal. 1501 (1/2001 Turtle Joint) in rostral (**A**) and caudal (**B**) views. Fang Pal. 1502 (1/2001 Turtle Joint) in anterolateral (**C**) view. Anterior trunk vertebra Pal. 1503 (1/2001 Turtle Joint) in right lateral (**D**), dorsal (**E**), ventral (**F**) and cranial (**G**) views. Trunk vertebra Pal. 1504 (1/2001 Turtle Joint) in right lateral (**H**) and cranial (**I**) views. Vertebra from the middle part of the trunk section Pal. 1505 (1/2001 Turtle Joint) in right lateral (**J**), dorsal (**K**), ventral (**L**), cranial (**M**) and caudal (**N**) views. Abbreviations: **can.den**, dental canal; **cd**, condyle; **ct**, cotyle; **fac. ecpt**, facet for contact with ectopterygoid; **hy**, hypapophysis; **ir**, interzygapophyseal ridge; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **pctf**, paracotylar foramen; **pd**, paradiapophysis; **po**, postzygapophysis; **pof**, postzygapophyseal articular facet; **pp**, parapophyseal process; **pr**, prezygapophysis; **pr.asc**, ascending process; **prf**, prezygapophyseal articular facet; **r**, ridge; **scf**, subcentral foramen; **scg**, subcentral groove; **scr**, subcentral ridge; **sctc**, subcotylar canal; **zy**, zygosphene; **zyg**, zygantrum. Scale bars: A-C, 2 mm; D-N, 5 mm.

The most complete neural spine lacks its cranial margin, but it seems possible that it was vertical or slightly anteriorly inclined. The interzygapophyseal ridges are well-developed and sometimes rather sharp. Lateral foramina are large and are situated in shallow depressions. The parapophyses are well-separated from the diapophyses and the parapophyseal processes are strongly built and directed antero-ventrally. The subcentral ridges are conspicuous. The

FIG. 15. — Viperinae ('Oriental vipers' group) from the early Miocene (MN 4) of MWQ. Middle trunk vertebra Pal. 1994 (2/2003 Reptile Joint) in right lateral (**A**), dorsal (**B**), ventral (**C**), cranial (**D**) and caudal (**E**) views. Posterior trunk vertebra Pal. 1506 (1/2001 Turtle Joint) with an indication of bifurcation in the distal tip of the hypapophysis in left lateral (**F**), dorsal (**G**), ventral (**H**), cranial (**I**) and caudal (**J**) views. Abbreviations: **cd**, condyle; **ct**, cotyle; **d**, diapophysis; **hy**, hypapophysis; **na**, neural arch; **nc**, neural canal; **pctf**, paracotylar foramen; **pof**, postzygapophyseal articular facet; **pp**, parapophyseal process; **pr**, prezygapophysis; **prf**, prezygapophyseal articular facet; **prp**, prezygapophyseal process; **scf**, subcentral foramen; **scr**, subcentral ridge; **sctt**, subcotylar tubercle; **zy**, zygosphene; **zyg**, zygantrum. Scale bars: 5 mm.

condyle is developed on a very short neck. The rarely preserved hypapophyses of anterior trunk vertebrae are long, straight, and directed posteroventrally. The pointed distal termination of the hypapophysis of middle and posterior trunk vertebrae is directed caudally. The hypapophysis of the posteriormost trunk vertebrae have indication of bifurcation on its distal tip. In dorsal view, the vertebrae are markedly short and wide. The cranial margin of the zygosphenal lip is concave, straight, or with a small medial lobe. The medial lobe is better developed in posterior trunk vertebrae. The prezygapophyseal articular facets are widely oval to subtriangular (although partial damage cannot be excluded). The prezygapophyseal processes are broken-off close to their bases. Epizygapophyseal spines are absent. In ventral view, the subcentral grooves are shallow, and the large subcentral foramina are situated on both sides of the base of the wide hypapophysis. The ventromedial margin of parapophyseal processes is always medially enlarged and it is usually fused with the ventrolateral extensions of the cotylar rim (subcotylar tubercles). The blood vessels of the circulatory system passed through the canals on both sides of the hypapophyseal base. The postzygapophyseal articular facets have an irregularly triangular outline. In cranial view, the neural arch is strongly flattened dorsoventrally. The cranial margin of the zygosphene is straight. The prezygapophyses are tilted up dorsally. The paracotylar foramina are situated on both sides of the rounded cotyle. The subcotylar tubercles are usually fused with bases of parapophyseal processes. The vertebral dimensions of the largest vertebrae from 1/2001 Turtle Joint are as follows (n = 7): cl: or = 6.98-7.76 mm; naw: or = 6.31-7.03 mm; cl/naw: or = 1.02-1.15, mean 1.09 ± 0.05.

Remarks

The maxilla partially resembles that of the '*xanthina*' clade of *Montivipera* in the shape of the medial margin of the body of maxilla. The maxilla of Viperinae ('Oriental vipers' group) differs from that of extinct *Macrovipera gedulyi* (Bolkay, 1913) (for current generic allocation see Cordea *et al.* 2017) in the medially strongly inclined ascending process. However, the presence of a sharp ridge situated on the rostromedial margin of the process, as well as the single orifice of the dental canal being located close to the distal termination of the process typically occur in this extinct species (Szyndlar & Rage 2002; Cordea *et al.* 2017). A study at the late Miocene (MN 13) Polgárdi site in Hungary shows that maxilla morphology is highly variable in *M. gedulyi* (Szyndlar & Rage 2002: 421, fig. 4). Findings of venomous fangs are rarely discussed in palaeoherpetological literature because isolated teeth do not allow identification even at the subfamily level (Szyndlar & Rage 2002). However, the venom fang is typified by its large dimensions, and the maxilla as well as almost all the viperid vertebrae at MWQ belonged to 'Oriental vipers'. Therefore, it is almost certain that the isolated venom fang belonged to a large 'Oriental viper'.

The large massive vertebrae with a low cl/naw ratio as well as long, straight hypapophyses and strongly dorsoventrally depressed neural arches enable identification of vertebrae as belonging to 'Oriental vipers'. Distinct subcotylar tubercles are not usually observed in recent 'Oriental vipers' (Szyndlar & Rage 1999; pers. observation) but in fossil representatives, at least small subcotylar tubercles frequently occur (Szyndlar 1988; Zerova 1992; Szyndlar & Rage 1999). However, the fusion of the ventromedial margin of the parapophyseal processes with strongly developed subcotylar tubercles has not been observed in either extant or extinct 'Oriental vipers'. A medial elongation of the medial margin of the parapophyseal processes was reported in posteriormost trunk vertebrae just anterior to the cloacal region, e.g. in *Macrovipera ukrainica* (Zerova, 1992) (Zerova 1992: fig. 10). The strange development of the parapophyseal region in trunk vertebrae of 'Oriental vipers' from MWQ is probably not due to intraspecific variation or abnormal (pathological) development because the same vertebrae have been reported from the coeval (MN 4), still unpublished, locality 3/2005 in Mokrá-Central Quarry. Although 'Oriental viper' from MWQ is not identified below the subfamily level, it is probable that this true viper could represent the genus *Macrovipera*. If it is true, the first occurrence of the genus *Macrovipera* could be placed to the late early Miocene.

Viperidae indet.

Material. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: 32 trunk vertebrae (Pal. 1533-1564). 2/2003 Reptile Joint: 46 trunk vertebrae (Pal. 2025-2070).

Remarks

All preserved vertebrae are rather fragmentary and a more precise identification other than at the family level is not possible.

Superfamily Elapoidea Boie, 1827
Family Elapidae Boie, 1827

Elapidae gen. et sp. indet.
(Fig. 16)

Elapidae gen. et sp. indet. – Ivanov & Musil 2004: 230.

Material. — MWQ, early Miocene, Burdigalian, Orleanian, MN 4: 1/2001 Turtle Joint: One trunk vertebra (Pal. 1500).

Description

Trunk vertebra

The only preserved vertebra is fragmentary with loss of the left prezygapophysis and the right prezygapophyseal process. In lateral view, the neural spine is broken-off close to its base, but the caudal part of the neural spine indicates that it was originally rather low. The interzygapophyseal ridges are moderately developed. The epizygapophyseal ridges are missing. The subcentral ridges are arched slightly dorsally. The hypapophysis is straight and its base rises at one quarter of the centrum length. The distal termination of the hypapophysis is absent but apparently it was short and did not reach behind the caudal margin of the condyle. In ventral view, the subcentral grooves are shallow and subcentral foramina are rather small. The postzygapophyseal articular facets are subcircular to irregularly shaped. In cranial view, the neural arch is slightly vaulted, and the neural canal is rounded with a wide diameter and short lateral sinuses. The damaged cranial margin of the zygosphenal lip was arched dorsally with raised zygosphenal facets. The paracotylar foramina occur on either side of the rounded cotyle. The small laterally directed subcotylar tubercles occur at the ventral margin of the rounded cotylar rim. The vertebral dimensions are as follows: cl = 5.40 mm; naw = 3.57 mm; cl/naw = 1.51.

Remarks

The single preserved vertebra was assigned to the family Elapidae on the basis of the presence of a short and straight hypapophysis that begins far from the ventral margin of the cotylar rim, the absence of epizygapophyseal ridges and the likely presence of a low neural spine. The morphology of Elapidae gen. et sp. indet. is identical with that of a vertebra of Elapidae indet. reported from the late Miocene (MN 9) of Rudabánya, Hungary (Szyndlar 2005). According to Szyndlar (2005), the only preserved Rudabánya specimen is similar to numerous small-sized elapids known from the European Miocene including *Micrurus* (*M. gallicus* Rage & Holman, 1984). However, the Mokrá specimen is larger. Both the morphology and dimensions of the largest vertebra resemble those of vertebral morphotype Elapidae B reported from the French early Miocene (MN 5) Vieux-Collonges site, with the exception of the rather short condylar neck in French specimens (Ivanov 2000: fig. 14). In accordance with Ivanov (2000), on the basis of relatively high cl/naw ratio, we conclude that this middle trunk vertebra of an indeterminate Elapidae from 1/2001 Turtle Joint can be attributed to large-sized elapids of possibly Asiatic origin (perhaps *Naja*).

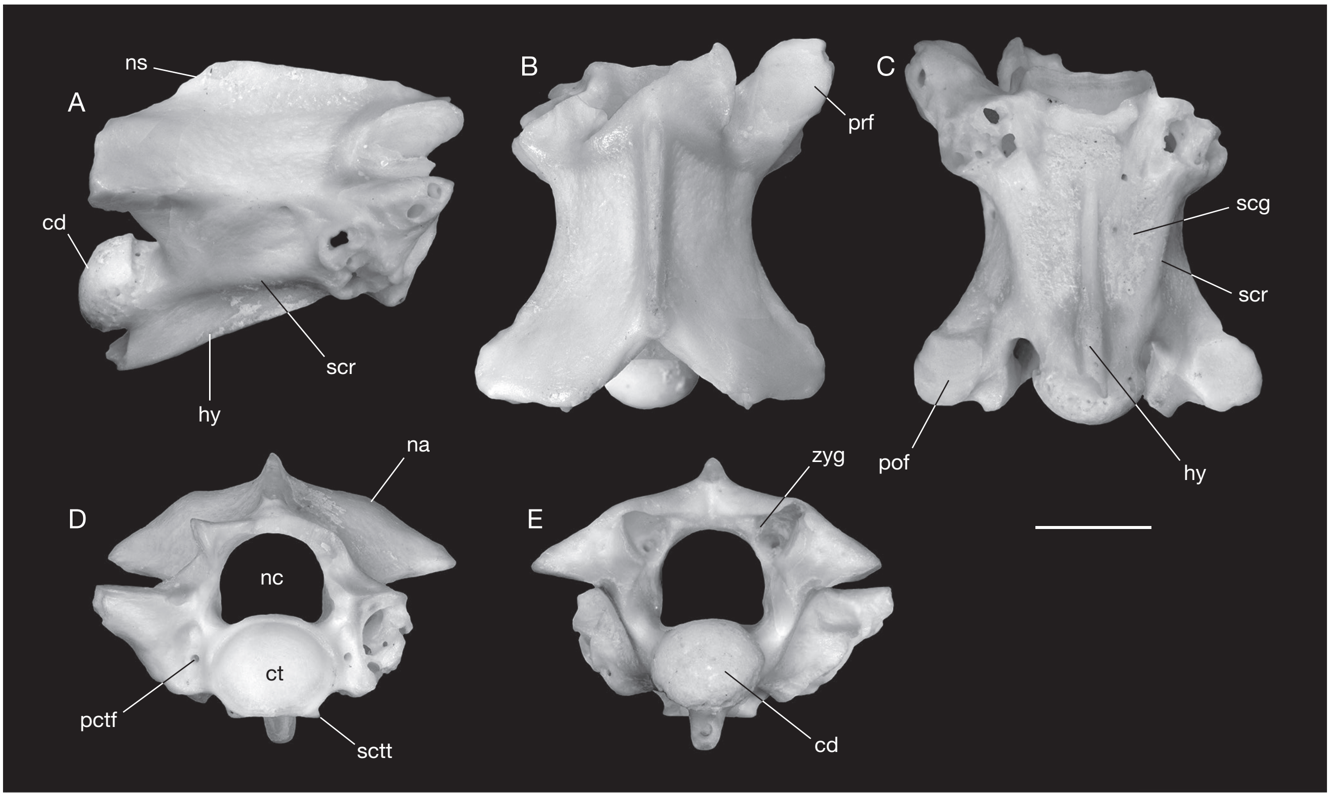

FIG. 16. — Elapidae gen. et sp. indet. from the early Miocene (MN 4) of MWQ. Trunk vertebra Pal. 1500 (1/2001 Turtle Joint) in right lateral (**A**), dorsal (**B**), ventral (**C**), cranial (**D**) and caudal (**E**) views. Abbreviations: **cd**, condyle; **ct**, cotyle; **hy**, hypapophysis; **na**, neural arch; **nc**, neural canal; **ns**, neural spine; **pctf**, paracotylar foramen; **pof**, postzygapophyseal articular facet; **prf**, prezygapophyseal articular facet; **scg**, subcentral groove; **scr**, subcentral ridge; **sctt**, subcotylar tubercle; **zyg**, zygantrum. Scale bar: 2 mm.

DISCUSSION

Mokrá-Western Quarry karstic fissures (1/2001 Turtle Joint; 2/2003 Reptile Joint) have yielded abundant assemblages of small- and medium-sized vertebrates (Ivanov *et al.* 2006; Sabol *et al.* 2007). Although early Miocene squamates are well-known from Central Europe, most MN 4 Zone localities are situated in Germany in the North Alpine Foreland Basin, NAFB (e.g. Szyndlar & Schleich 1993; Szyndlar & Böhme 1993; Szyndlar & Rage 2003). The only exceptions east of Germany are the localities of Dolnice, Czech Republic (e.g. Klembara 1979, 1981, 2015; Moody & Roček 1980; Roček 1984; Szyndlar 1987, 1991a, b) and Oberdorf, Austria (Szyndlar 1998; Čerňanský 2016). Together with Oberdorf (lignite open-mine), MWQ is the only known squamate locality of the MN 4 Zone in the Central Paratethys realm.

Although specimens are fragmentary, eleven major clades of squamates can be identified in MWQ: Lacertidae, Amphisbaenia, ? Scincoidea, Anguidae, Varanidae (for this clade, see Ivanov *et al.* 2018), Boidae, Pythonidae, Colubridae, Natricidae, Viperidae and Elapidae (Table 1). Besides varanids, alpha taxonomy is possible only for the anguine parietals that can be assigned to *Pseudopus laurillardi*. The MWQ lizard and snake fauna shows a typical composition of these squamates reported from Central Europe during the early Miocene.

Squamate assemblages of Oberdorf and MWQ are closely similar, especially as regards lizards. However, snakes reported from MWQ indicate a warmer condition. Large Boidae (*Bavarioba*) are present at both localities but the MWQ assemblage yielded a rare occurrence of Pythonidae. *Python* sp. from MWQ represents one of the first appearances of this taxon in Europe together with *Python europaeus* reported from the French early Miocene localities of Béon 1, MN 4b (Rage & Bailon 2005) and Vieux-Collonges, MN 5 (*Python* sp. – *sensu* Ivanov 2000; Szyndlar & Rage 2003). Although phylogenetic analyses based on molecular or combined morphological/molecular data indicate either an Asiatic (Wiens *et al.* 2012; Pyron *et al.* 2013; Reeder *et al.* 2015) or African (Reynolds *et al.* 2014; Figueroa *et al.* 2016) origin of the genus *Python*, the oldest known possible *Python* (cf. *Python* sp.) was reported from the early Miocene (MN 3) of Sperrgebiet, Namibia (Rage 2008). Therefore, it seems probable that Miocene representatives of *Python* penetrated into Europe from Africa via the '*Gomphotherium* land bridge' whose emergence resulted from the collision of the Afro-Arabian plate with Eurasia during the early Miocene (MN 4; e.g., Gheerbrant & Rage 2006). The genus *Python* represents the most thermophilic reptile in the European Neogene (Ivanov & Böhme 2011). As the extant representatives of the genus *Python* appear in areas where the mean annual temperature (MAT) varies between 18.6 °C and 21.4 °C (Guo *et al.* 2009; Müller &

TABLE 1. — List of squamate reptiles from the middle Miocene Mokrá-Western Quarry localities MWQ (1/2001 Turtle Joint; 2/2003 Reptile Joint), indicating the habitat and behavior.

Higher taxa	**Family**	**Identified taxa**	**Habitat/Behaviour**	**MWQ, 1/2001**	**MWQ, 2/2003**
Lacertoidea + Scincoidea	Lacertidae	Lacertidae indet.	terrestrial, heliophile	–	•
		Lacertidae indet. tooth morphotype 1	terrestrial, heliophile	•	•
		Lacertidae indet. tooth morphotype 2	terrestrial, heliophile	•	–
	Amphisbaenidae	Amphisbaenia indet.	fossorial	–	•
		? Scincoidea indet.	?	–	•
Anguiomorpha	Anguidae	*Pseudopus laurillardi* (Lartet, 1851)	terrestrial, woodland, heliophile, humid	•	•
		Pseudopus sp.	terrestrial, heliophile	•	•
		Ophisaurus sp.	terrestrial, heliophile, grassland, open woodland	•	–
		Anguinae indet.	terrestrial, heliophile	•	•
	Varanidae	*Varanus mokrensis*	terrestrial, heliophile	•	•
Serpentes	Boidae	*Bavarioboa* cf. *hermi*	terrestrial, heliophile	•	–
	Pythonidae	*Python* sp.	terrestrial or peri-aquatic, heliophile	•	–
		‘Booidea’ indet.	?	•	•
	Colubridae	*Coluber* (s.l.) sp.	terrestrial, heliophile, open areas	•	•
		“Colubrinae” indet. 1	peri-aquatic, heliophile, grassland or bushes	•	•
	Natricidae	*Natrix* sp.	semi-aquatic, heliophile, open woodland	•	•
		“Natricinae” indet.	heliophile, open woodland	•	•
		Colubridae gen. et sp. indet.	heliophile	•	–
		Colubridae indet.	?	•	•
	Viperidae	*Vipera* sp. (‘European vipers’ group)	heliophile, open woodland	–	•
		Viperinae (‘Oriental vipers’ group)	terrestrial, heliophile, humid to arid environment, grassland	•	•
		Viperidae indet.	?	•	•
	Elapidae	Elapidae gen. et sp. indet.	terrestrial, heliophile, woodland to grassland	•	–

Hennings 2009) we can conclude that MAT in MWQ did not fall below 18-19 °C. These high temperatures and humid conditions within the Miocene Climatic Optimum were suitable for dispersal of other thermophilic lizard and snake taxa in Central Europe including *Varanus*, *Pseudopus laurillardi*, *Bavarioboa*, ‘Oriental vipers’ and large Elapidae also reported from MWQ (Table 1).

At least two different colubrine taxa are present in MWQ. Fragmentary vertebrae of *Coluber* (s.l.) sp. partially resemble those of *C. hungaricus*. Although *C. hungaricus* shows a high intraspecific variability (see Venczel 1994, 1998), *Coluber* (s.l.) sp. from MWQ is a different species. Therefore, *C. hungaricus* („*Coluber*” *hungaricus*; *sensu* Ivanov & Böhme 2011) from the early middle Miocene of Griesbeckerzell 1a (Germany) remains the first known occurrence of this species. The early Miocene is characterised by the appearance of several colubroid snake taxa in which an Asiatic or even North American origin was hypothesized (Rage & Holman 1984; Szyndlar & Schleich 1993; Ivanov 2001; Ivanov *et al.* 2000; Szyndlar 2012). However, adequate data elucidating the Miocene evolution of the snake fauna in Asia are still lacking. Rage & Danilov (2008) hypothesized that Eurasian snake communities were largely homogenous during the Miocene but the snake fauna reported from the middle Miocene (MN 7+8) of Kazakhstan did not support this homogeneity because several taxa, e.g., *Gloydius*, *Elaphe* aff. *dione*, most probably never occurred in Central Europe (Ivanov *et al.* 2019). It is still impossible to say whether most of the squamate newcomers penetrated into Central Europe around the northern border of the Paratethys realm or from the south-east via the Balkan Peninsula. However, it seems rather probable that migration from the south-east was more important during the late early Miocene. This is documented by diverse amphibian and reptile assemblages from the early Miocene (MN 4) Greek localities of Karydia and Aliveri which indicate that at least several Central European taxa, e.g., *Chamaeleo andrusovi* Čerňanský, 2010, dispersed into the Balkan Peninsula after the emergence of the ‘*Gomphotherium* land bridge’ (Georgalis *et al.* 2016a, 2017).

‘Oriental vipers’, which became widespread in Europe during MN 4 (Szyndlar & Schleich 1993; Szyndlar & Rage 1999, 2002), belong to the most abundant snake taxon in MWQ. The first occurrence of ‘Oriental vipers’ in Central Europe antedated the first appearance of large elapids (related to *Naja*) as documented by their first appearance in the early Miocene (MN 3) of Germany (MI, unpublished).

PALAEOENVIRONMENT

Both karst fillings from MWQ (1/2001 Turtle Joint; 2/2003 Reptile Joint) are approximately coeval corresponding to the MN 4 Zone (Ivanov *et al.* 2006; Sabol *et al.* 2007; Sabol, pers. comm.). Based on the amphibian and reptile assemblage, the analysis given by Ivanov *et al.* (2018) indicated open steppe to open forest environments with damp and marshy habitats surrounding MWQ during MN 4 Zone.

The newly revised squamate assemblage (Table 1) supports previous analyses. There is a predominance of heliophilic taxa inhabiting various terrestrial environments in both fissures including Lacertidae, Anguidae (*Pseudopus laurillardi*, *Pseudopus* sp.), Varanidae (*Varanus mokrensis*), Colubridae (*Coluber* (s.l.) sp.) and Viperidae (Viperinae 'Oriental vipers' group). *P. laurillardi* probably had a greater ecological plasticity than the extant *P. apodus*, which inhabits open to poorly vegetated environments of arid and sub-arid territories in South-East Europe and West and Central Asia (Obst 2004). Based on fossil distribution, the extinct *P. laurillardi* preferred forested habitats with sub-humid to humid climate during the Miocene Climatic Optimum (subtropical semi-deciduous limestone forest, subtropical oak–laurel forest; see Böhme 2003; Böhme *et al.* 2007; Klembara *et al.* 2010). This fits well with the interpretation of MWQ as corresponding to the warm humid phase of the Miocene Climatic Optimum. Among Colubridae, peri- and semi-aquatic taxa have also been reported including 'natricines' (*Natrix* sp., "Natricinae" indet. and "Colubrinae" indet. type 1 (similar to *Opheodrys*). The genus *Opheodrys* preferably inhabits biotopes with dense vegetation and bushes in close proximity to permanent water reservoirs (Harding 1997).

Despite the similar age of both fissures, the 1/2001 Turtle Joint amphibian assemblage revealed drier conditions compared to that of 2/2003 Reptile Joint. This was documented by the scarcity of *Triturus* Rafinesque, 1815 and absence of certain aquatic or heliophobic forms such as *Chioglossa* Bocage, 1825 and *Mertensiella* Wolterstorff, 1925 (Ivanov 2008; Ivanov *et al.* 2018). This finding is partially supported by a composition of squamate assemblages. The 1/2001 Turtle Joint assemblage lacks fossorial forms unlike the 2/2003 Reptile Joint assemblage where Amphisbaenia indet. and a potential scincoid (possibly related to Scincidae or Cordylidae) are present although majority of scincoids do not represent strictly fossorial forms (Table 1).

The small mammal material appropriately supplements results obtained by the study of the MWQ herpetofauna. Preliminary results for the small mammals were published by Sabol *et al.* (2007). This material, together with that of large mammals, is again under study, but remains unpublished. Based on the fossil record, the cricetid rodents *Megacricetodon* and *Democricetodon* were ground-dwelling genera, indicating open forest conditions and warm weather. *Palaeosciurus* was a burrowing diurnal sciurid living in an open environment (Brujin 1999). The appearance of the cricetid genus *Melissiodon* indicates the presence of wooden areas and somewhat more humid conditions (Jovells-Vaqué & Casanovas-Vilar 2018), where it could find small invertebrates to feed on (Wessels *et al.* 2018). The large mammal association consists mainly of cervids and one species of suid. Although these taxa required forest biotopes (Rössner 2004), they may also have lived close to a swampy environment.

Essentially, the mammal assemblages from 1/2001 and 2/2003 indicate warm weather conditions with patches of open-forest and open steppe, and the presence of marshy areas, typical of karst landscapes. Moreover, the wetter conditions of 2/2003 in comparison with 1/2001 are consistent with the presence, although scarce, of eomydid *Ligerimys* sp. (Daams & Freudenthal 1988; Van der Meulen & Daams 1992), and the more abundant record of the extinct erinaceid *Galerix* (Ziegler 1999), as well as other erinaceids. Taken together, this is in agreement with palaeoecological conclusions based on the herpetofauna.

CONCLUSIONS

Two fossiliferous karstic fissures from the Mokrá-Western Quarry (1/2001 Turtle Joint; 2/2003 Reptile joint) have yielded a diverse fauna of early Miocene (Orleanian, MN 4) vertebrates including squamates. The rather warm climatic conditions during the Miocene Thermal Maximum (17.8-17.7. Ma) enabled dispersal of thermophilic lizard and snake taxa through the whole of Central Europe. In total, eleven major clades have been identified in MWQ i.e., Lacertidae, Amphisbaenia, possible Scincoidea, Anguidae, Varanidae, Boidae, Pythonidae, Colubridae, Natricidae, Viperidae and Elapidae. The presence of *Python* sp. in the MWQ documents the first known occurrence of this most thermophilic European squamate taxon within the area of Central Paratethys. As the extant representatives of the genus *Python* appear in areas with MAT between 18.6 and 21.4 °C we conclude that MAT in MWQ did not fall below 18-19 °C. These high temperatures, together with a presence of full aquatic or semi-aquatic amphibians and reptiles (*Ptychogaster* – Luján *et al.* in press, *Natrix*, possibly also Colubrinae indet. 1), indicate humid subtropical to paratropical climatic conditions at this locality during the late Burdigalian stage (MN 4). The presence *Pseudopus laurillardi* indicates deciduous forest in the close vicinity of the locality. This conclusion is also supported by the composition of the amphibian and mammal fauna.

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