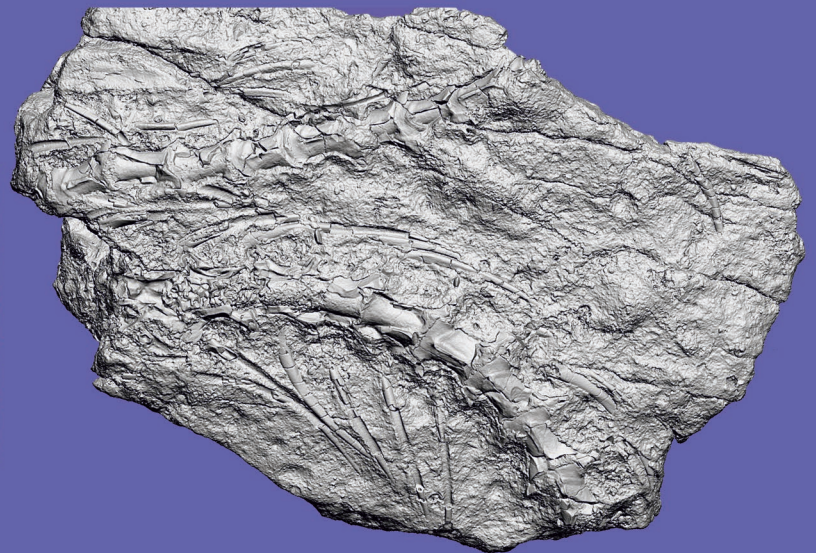


The first lacertid and partly articulated snake
from the Middle Miocene of the Devínska Kobyla Hill
in Slovakia, from the type locality
of the earliest known seal

Andrej ČERŇANSKÝ



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The first lacertid and partly articulated snake from the Middle Miocene of the Devínska Kobyla Hill in Slovakia, from the type locality of the earliest known seal

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ABSTRACT

I here describe lacertid and snake remains from the classic Middle Miocene (MN 6) locality Bonanza of the Devínska Kobyla Hill near Bratislava (Slovakia). The locality is famous for being a type locality of an early seal *Devinophoca* Koretsky & Holec, 2002. During the Middle Miocene, the area of Devínska Nová Ves was part of an archipelago in the western part of the Central Paratethys in the northern part of the Vienna basin. The fossils described here comprise an incomplete left maxilla of a lacertid lizard and an articulated portion of a vertebral column of a small colubrid snake with several ribs still attached. The maxilla is tentatively allocated here to *Lacerta* Linnaeus, 1758 and is a rare instance of the occurrence of the clade Lacertidae Opperl, 1811 in this environment during the Middle Miocene. Moreover, it represents the oldest known occurrence of this clade in Slovakia. Articulated snake specimens from the Cenozoic are rare and although only partly articulated, the specimen from Bonanza is therefore exceptional. On the basis of vertebrae alone, determination of fossil colubrids is very difficult. The morphology of the Bonanza specimen is most similar to the extant *Dolichophis* Gistel, 1868, as also to other small fossil snakes assigned to ‘*Coluber*’ Linnaeus, 1758 when that genus was a catch-all grade taxon recognised from both Europe and North America, notably ‘*Coluber*’ *dolnicensis* Szyndlar, 1987 and ‘*Coluber*’ *pouchetii* (Rochebrune, 1880). Because the potentially closest living relative of the European Miocene ‘*Coluber*’ is *Dolichophis*, I assigned tentatively the material from Bonanza to cf. *Dolichophis*, rather than to the wastebasket taxon ‘*Coluber*’.

KEY WORDS

Neogene,
Central Europe,
Squamata,
insular
paleoenvironment.

RÉSUMÉ

Le premier lacertide et serpent partiellement articulé du Miocène moyen de la colline Devínska Kobyla en Slovaquie, de la localité type du plus ancien phoque connu.

Je décris ici des restes de lacertidés et de serpents provenant de la localité classique Bonanza du Miocène moyen (MN 6) de la colline Devínska Kobyla près de Bratislava (Slovaquie). Cette localité est célèbre pour être le lieu type d'un phoque précoce, *Devinophoca* Koretsky & Holec, 2002. Au Miocène moyen, la région de Devínska Nová Ves faisait partie d'un archipel situé dans la partie occidentale de la Paratéthis centrale, dans la partie septentrionale du bassin de Vienne. Les fossiles décrits ici comprennent un maxillaire gauche incomplet d'un lézard lacertide et une partie articulée d'une colonne vertébrale d'un petit serpent colubride avec plusieurs côtes encore attachées. Le maxillaire est provisoirement attribué à *Lacerta* Linnaeus, 1758 et constitue un rare exemple de la présence du clade Lacertidae Oppel, 1811 dans cet environnement au cours du Miocène moyen. De plus, il s'agit de la plus ancienne occurrence connue de ce clade en Slovaquie. Les spécimens de serpents articulés du Cénozoïque sont rares et, bien que partiellement articulés, le spécimen de Bonanza est donc exceptionnel. La détermination des colubridés fossiles est très difficile sur la base des seules vertèbres. La morphologie du spécimen de Bonanza est très similaire à celle du *Dolichophis* Gistel, 1868 existant, ainsi qu'à celle d'autres petits serpents fossiles attribués à '*Coluber*' Linnaeus, 1758 lorsque ce genre était un taxon fourre-tout reconnu à la fois en Europe et en Amérique du Nord, notamment '*Coluber dolnicensis* Szyndlar, 1987 et '*Coluber pouchetii* (Rochebrune, 1880). Étant donné que le plus proche parent présumé actuel du '*Coluber*' du Miocène européen est *Dolichophis*, j'ai attribué provisoirement le matériel de Bonanza au cf. *Dolichophis*, plutôt qu'au taxon poubelle '*Coluber*'.

MOTS CLÉS
Néogène,
Europe centrale,
Squamata,
paléoenvironnement
insulaire.

INTRODUCTION

The early/middle Miocene transition initiated very important changes in Cenozoic climate evolution, which have deeply influenced Europe's squamate faunas. The beginning of the Miocene represents the temporary return to a warm and humid climate (the Miocene Climatic Optimum) after the relatively cool and dry Oligocene. The temperature reached a maximum at 18–16.5 Ma (Ottangian, Karpatian; see Böhme 2003; Rage 2013). Another important event is represented by the collision of Eurasia with Africa. This event allowed immigration of African squamates into Europe (Čerňanský 2010, 2012; Čerňanský *et al.* 2015; Georgalis *et al.* 2016, 2023). Later, during the early Badenian, probably unchanged temperature was present. *Python* sp., which is the most thermophilous reptile known from the European Neogene, is documented from Germany (15.0–14.9 Ma; Ivanov & Böhme 2011). However, this period is characterised by the strong increase of seasonality in precipitation (up to six dry months, in contrast to a period of high precipitation during the Ottangian and Karpatian; Böhme 2003). In the Central Europe, the squamate fauna remained rich, diverse and of tropical type during the middle Miocene (Rage 2013), including the last known chamaeleonids from MN 6 (Čerňanský 2011a).

Miocene squamates have only rarely been reported from Slovakia, and many aspects of the evolution of lizards and snakes in this area are still poorly understood. In the past, the Slovakian fossil herpetofauna has mainly been documented from the Middle Miocene (Early Astaracian, MN 6) locality known as the Devínska Kobyla Hill in the vicinity of Devínska Nová Ves (DNV) village (in former literature also known as Neudorf an dem March or Dévényújfalu), nowadays a suburban

part of Bratislava. This area is located at the base of the Malé Karpaty Mountains, at the junction of the Morava and Danube rivers. It is formed by several sites: DNV-Štokerauská vápenka, DNV-Bonanza, and DNV-Sandberg. The historically important ones are especially DNV-Štokerauská vápenka (Neudorf an dem March – die Spaltenfüllung or Zapfe's Fissures) and DNV-Sandberg (Theben Neudorf). The first represents a site with a terrestrial fossil record, whereas the vertebrates from the latter have been found in sands deposited in a marine environment. DNV-Bonanza was discovered in 1980s and connects both these sites by recording a gradual transition from terrestrial to marine conditions (Sabol *et al.* 2021). At DNV-Sandberg, only a few reptiles have been reported (crocodiles and turtles; Hoernes 1848; Holec & Schlögl 2000; Schlögl & Holec 2004; Holec 2006; Danilov *et al.* 2012), but no squamates. In contrast, several squamates have been documented from DNV-Štokerauská vápenka. Wettstein-Westerschheim (1955) described 21 isolated snake vertebrae from this locality. This author suggested, based of their length, their potential affinity with *Malpolon* (*Coelopeltis*) Fitzinger, 1826. However, according to Szyndlar (1984, 1991a), the determination of this material at genus level is impossible. Currently, the specimen is attributed to Colubrinae indet. (Szyndlar 1991a). Estes (1969) described gecko material from this locality as *Euleptes* (*Phyllodactylus*) sp. This material and some additional new gekkotan specimens have been studied by Čerňanský *et al.* (2018) and described as a new species *E. klembarai* Čerňanský, Daza & Bauer, 2018.

The “transitional” DNV site, Bonanza (48°12'13"N, 17°00'11"E), is a large karst fissure in the same non-active limestone quarry as DNV-Štokerauská vápenka. However, Bonanza is situated in the opposite wall of this quarry (Holec

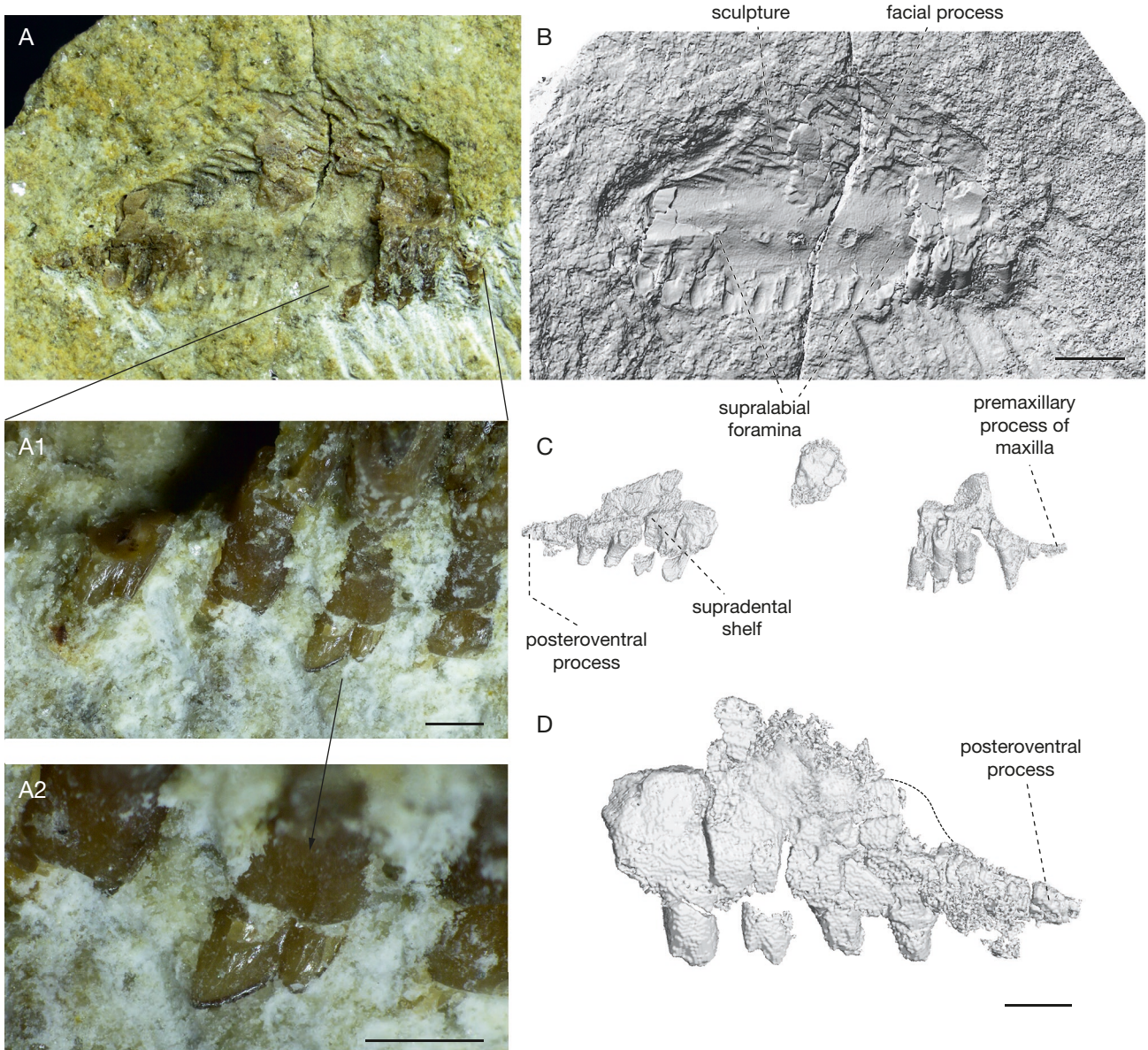


FIG. 1. — A left maxilla SNM Z 29221 of cf. *Lacerta* sp. from the Middle Miocene Bonanza locality: **A**, the prepared block of sediment, containing the specimen with details of the anterior teeth (the specimen is exposed in medial views whereas imprint shows the external surface); **B**, CT visualization of the whole specimen; **C**, virtual 3D model of the preserved bones in medial views; **D**, posterior region of the maxilla in lateral view. Scale bars: A-C, 1.5 mm; A1, A2, 200 μ m; D, 0.6 mm.

et al. 1987). The deposits of this locality contain fossils of terrestrial (incl. freshwater), semi-aquatic, and marine vertebrates (Sabol & Kováč 2006). It is famous for being a type locality of the seal genus *Devinophoca* Koretsky & Holec, 2002 (both *Devinophoca claytoni* Koretsky & Holec, 2002 and *Devinophoca emryi* Koretsky & Rahmat, 2015; Koretsky & Holec 2002; Koretsky & Rahmat 2015, 2016). The Bonanza site is the type locality of *Bufo priscus* Špinar, Klembara & Meszároš, 1993 (Špinar *et al.* 1993) and it has also yielded a partly articulated skeleton of *Ophisaurus* sp. (Čerňanský & Klembara 2017). In addition, the following snake taxa have been reported, all represented by disarticulated isolated vertebrae: Colubrinae B and D, Colubrinae indet., *Neonatrix* sp. and Elapidae C (Ivanov 1998).

In this article I describe an important new record of the family Lacertidae Opper, 1811, and a rare specimen of a colubrid snake based on articulated vertebrae and ribs. Articulated snake specimens from the Cenozoic are rare. They are usually known mostly from localities with exceptional fossilization conditions, such as the Eocene Messel locality in Germany (Smith *et al.* 2018; Scanferla & Smith 2020; Smith & Scanferla 2021; Chuliver *et al.* 2022) and the Eocene Bolca Fossil-Lagerstätte in Italy (Seghetti *et al.* 2022). The specimen from Bonanza is not the first one from Slovakia actually, as there is also a partly articulated skeleton of *Vipera berus* (Linnaeus, 1758) from the Late Pleistocene firm travertine at the famous Gánovce-Hrádok Neanderthal mound (Ivanov & Čerňanský 2017).

MATERIAL AND METHODS

The fossil material described here is deposited in the Slovak National Museum, Bratislava. Both specimens are embedded in limestone and were scanned using the micro-computed tomography (CT) facility at the Slovak Academy of Sciences in Banská Bystrica, using a phoenix v|tome|x L 240 micro-CT. The CT data sets were analysed using VG Studio Max 3.1. Specimens were photographed under a Leica M125 binocular microscope with axially mounted DFC500 camera [LAS software (Leica Application Suite) v.4.1.0 (build 1264)]. The standard anatomical orientation system is used throughout this paper. The image processing program ImageJ (Schneider *et al.* 2012) was used for measurements.

ABBREVIATIONS

Institutional abbreviation

SNM Z Slovak National Museum, Bratislava.

Other abbreviations

CT micro-computed tomography;
DNV Devínska Nová Ves;
MN Mammal Neogene zones.

SYSTEMATIC PALEONTOLOGY

SQUAMATA Opper, 1811

LACERTOIDEA Opper, 1811 (*sensu* Zheng & Wiens, 2016)

LACERTIDAE Opper, 1811

LACERTINI Opper, 1811

Lacerta Linnaeus, 1758

cf. Lacerta sp.

(Fig. 1)

MATERIAL EXAMINED. — Slovakia • Bratislava, Devínska Nová Ves, Bonanza site; Middle Miocene (MN 6b); SNM Z 29221, left maxilla.

LOCALITY AND HORIZON. — Slovakia, Bratislava, Devínska Nová Ves, Bonanza site; Middle Miocene (MN 6b).

DESCRIPTION

Maxilla

The left maxilla is fairly well preserved although incomplete – most of the specimen is an imprint of its lateral side in the sediment (Fig. 1). There is a subvertical crack running along the mid-portion of the element. The bone is partly preserved in the anterior and posterior region (some remains also occur in the central region of the facial process). The maximum anteroposterior length of the preserved portion is 10 mm and its maximum dorsoventral height is 5.6 mm. It bears 17 tooth positions (four and half teeth are still attached in the anterior section and remains of five teeth are partly preserved in the posterior section). The tooth row is almost complete and thus it can be estimated that the complete maxilla possessed around 18–19 teeth. The premaxillary process of the maxilla is damaged and covered by matrix.

The CT scan reveals that part of the external ramus of the premaxillary process is still preserved as a narrow expansion. The lateral face of the maxilla above the teeth is pierced by relatively large supralabial foramina arranged in a single line (five are preserved as imprints). The supradental shelf (*sensu* Rage & Augé 2010) is damaged, with small portions partly visible in the posterior and anterior sections. At the end of the anterior section, the anterior border of the cavum nasi can be recognized. It forms a slightly medially bulged ridge. Here, the anterior margin of the facial process rises upwards to form the posterior margin of the external naris. However, only the ventral portion of this region is preserved – the facial process is mostly preserved only as an imprint of its lateral surface. Based on this imprint, the facial process clearly possessed three attached osteodermal shields based on positive imprints of sulci. The sculpture (*sensu* Glynne *et al.* 2020) of these osteoderms is well developed and strong. It consists of densely spaced grooves and ridges (connected in some places). Most of these surface features are directed posterodorsally but there is an exception anteriorly where the orientation is rather irregular (roughly radial; this might indicate an ossification centre). The nasal process is roughly trapezoidal in shape. It is tall, forming an almost perpendicular wall. Its anteroposterior width is larger than its dorsoventral height. Its dorsal margin is probably not completely preserved, because this portion is usually slightly bent medially. In any case, a part of the frontal process can be recognized in the anterior region. The triangular prefrontal process is located in the dorsal region, posterior to the frontal process. Further posteriorly, the facial process gradually decreases ventrally and fluently continues into the posteroventral process of the maxilla. The latter gradually narrows posteriorly, having a concave dorsal margin. The posterior portion is poorly preserved, but its morphology indicates that it was stepped (Fig. 1D). The tooth row does not reach the posterior end of the bone, leaving a small posterior toothless portion.

DENTITION

The tooth implantation is pleurodont. The teeth are tall, rising above the dental crest by approximately one-third of the tooth length. In general, teeth are relatively robust and the tooth size appears to be slightly enlarged posteriorly. The tooth crowns are lingually slightly concave. All teeth which can be observed (including their imprints in the posterior section of the tooth row) are bicuspid (perhaps except for the first anterior preserved one which seems to be monocuspid). There is a dominant distal cusp which is large and pointed. A mesially located accessory cusp is well defined. It is separated from the dominant cusp by a notch, which further continues into a distinct groove. This groove gradually diminishes dorsally. The accessory cusp has a sharp appearance. It is relatively large, reaching a half of the mesiodistal width of the dominant cusp. Thus, the whole tooth crown seems to be almost bifurcated. The accessory cusp is more-or-less straight, whereas the dominant cusp is slightly curved posterolingually. For this reason, the mesial edge (the crista mesialis) of the

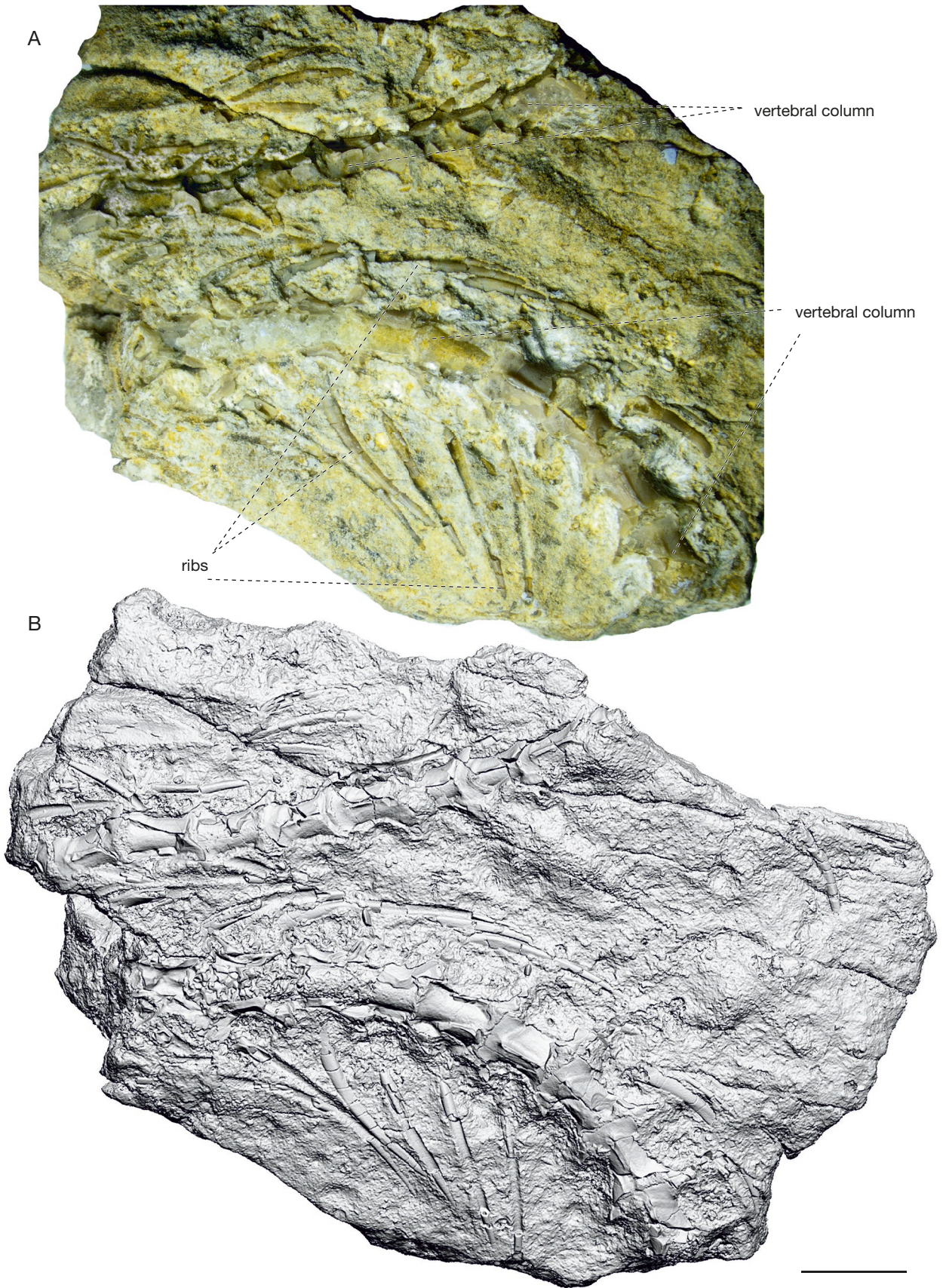


FIG. 2. — Cf. *Dolichophis* sp. SNM Z 29222 from the Middle Miocene Bonanza locality: **A**, the prepared block of sediment, containing the specimen exposed in dorsal view; **B**, CT visualization of the whole specimen. Scale bar: A, B, 4 mm.

dominant cusp is longer than its distal one. Weak striations can be recognized on the lingual side of the tooth crown. The tooth necks are slightly swollen lingually. Interdental gaps are present, the gap size in preserved anterior teeth forms approximately half of the mesiodistal length of the tooth shaft in the middle region.

COMMENTS

The DVN Bonanza lizard specimen SNM Z 29221 described here can be allocated to Lacertidae without doubts (see Discussion: Taxonomic allocation of the lizard). However, the material is limited, represented by an isolated and incomplete maxilla which is actually not the best elements for alpha taxonomy.

SERPENTES Linnaeus, 1758
 COLUBRIDAE Opperl, 1811
Dolichophis Gistel, 1868

cf. *Dolichophis* sp.
 (Figs 2-5)

MATERIAL EXAMINED. — Slovakia • Bratislava, Devínska Nová Ves, Bonanza site; Middle Miocene (MN 6b); SNM Z 29222, articulated portion of the vertebral column together with ribs in firm tabular limestone.

LOCALITY AND HORIZON. — Slovakia, Bratislava, Devínska Nová Ves, Bonanza site; Middle Miocene (MN 6b).

DESCRIPTION

Skeleton

The postcranial skeleton is mostly articulated (Fig. 2), although weathered. It represents a small snake, the maximum anteroposterior length of the best preserved vertebra being 4.4 mm. The whole specimen is embedded in limestone – unfortunately, the computed tomography reconstructions show that the rock density value is similar to that of the fossil. Even so, the exposed portions and CT revealed, at least partly, the morphology of these vertebrae. Eight and half vertebrae are preserved in the upper part of the slab, whereas nine and half are preserved in the lower part of the slab. The latter ones are larger, but only four have preserved the neural arch. The neural arch is moderately vaulted. The dorsal region of the neural arch is more-or-less flattened and bears the neural spine along its central section. The neural spine appears to be more-or-less trapezoidal in lateral view, but markedly low – in the fourth vertebra (counted from posterior) with fairly complete neural spine, its anteroposterior length (2.2 mm; Fig. 3) is approximately four times larger than its height. Its anterior and posterior margins are almost vertical, although note that the base of the anterior margin is slightly concave. Anteriorly, the neural spine starts to rise dorsally in the first quarter of its length and thus leaves a short, flat area of the neural arch anterior to the base of the neural spine. Here, at the anterior end, the zygosphenal

lip is well developed. It is slightly convex, having two small lateral lobes. In the vertebrae, in which it is preserved, there is no indication of the presence of a median notch. The zygosphenal articular facets are steep and markedly dorsally inclined to angle of around 50° from a horizontal plane (Fig. 3C, C1). In anterior view, the zygosphenon is distinctly wider than the cotyle. The neural canal is large, tunnel like, its width is more-or-less equal to its height (mostly observed in cross-section μ CT slices of this region). The zygantral area is poorly preserved in this section. A potential presence of a paracotylar foramen cannot be properly observed. The interzygapophyseal constriction is well developed as well as interzygapophyseal ridges. Prezygapophyses are anterolaterally oriented and the prezygapophyseal accessory processes are well-developed, narrow and pointed distally. Their length can be estimated to reach almost the length of the prezygapophyseal articulations. The prezygapophyseal articulations are almost horizontal, inclined in an angle of only 10° from the horizontal plane. Paradiapophyses are not well preserved. Note, however, that the parapophyses are damaged in most of the vertebrae and their shape is unknown. One exception is the third vertebra in the larger column (Fig. 4). They are moderately developed. A division into diapophyses and parapophyses can be recognized, being well developed (Fig. 4D). The ventral margin of the parapophyses extend ventrally, being located below the cotylar rim. The diapophysis in this vertebra appears to be located posteriorly relative to the parapophysis. The vertebral condyle and cotyle are moderately large, rounded. The condyle is connected to the centrum by a short “neck”. The centrum is anteroposteriorly elongated. The haemal keel is well developed, but ventrally short. It is narrow. The remaining vertebrae of this column located in the anterior section have damaged neural arches. Thus, the neural canal is exposed, being filled in by the calcite which forms an internal core of the canal. Here, prezygapophyses are well visible, having rounded articular surfaces. The postzygapophyses are distinctly expanded laterally. The cotyles and condyles are more-or-less rounded here as well.

The smaller vertebrae located in the second column are basically identical in morphology. They represent a distal portion of the vertebral column. The low neural spine can be observed in the posteriormost preserved complete vertebra (Fig. 5A, C-H). Here, the postzygapophyses are fairly complete, being posterolaterally oriented. Compared to the larger vertebrae, they have smaller articular areas relative to the prezygapophyses. Between the right and left postzygapophyses, a V-shaped notch is present (Fig. 5D). The zygantrum is well-developed.

Several ribs are still attached to the precaudal vertebrae and remain articulated with synapophyses. In some places, they are preserved only as imprints (Fig. 2).

COMMENTS

Note that computed tomography reconstructions show that the rock density value is very similar to that of the fossil. The rock block with its tiny bones is relatively thick, and unfortunately CT is unable to provide a usable 3D model with all features

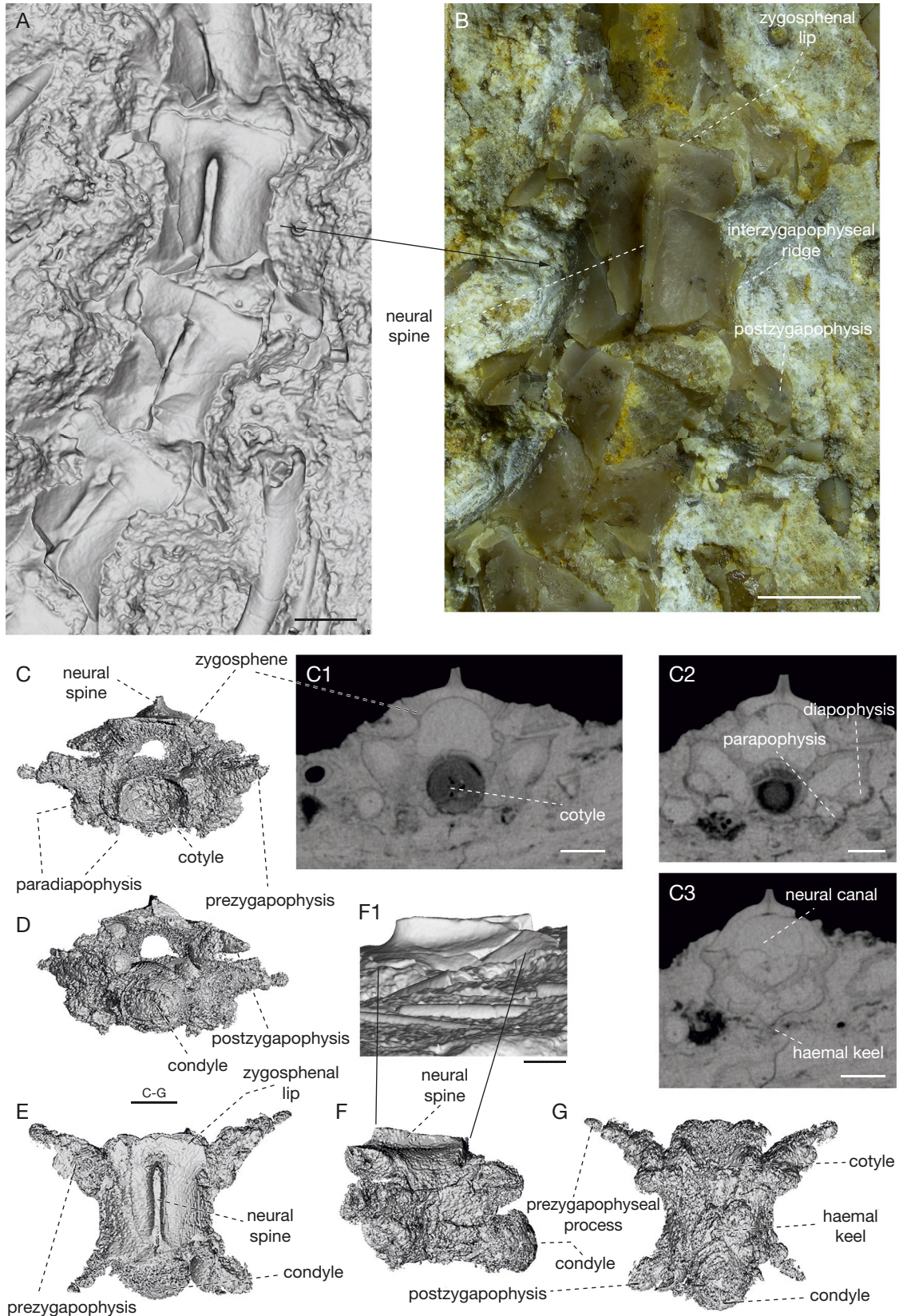


FIG. 3. — Cf. *Dolichophis* sp. SNM Z 29222 from the Middle Miocene Bonanza locality. The best preserved vertebra with fairly complete neural spine: **A**, virtual CT visualization of the posterior section of the vertebral column located in the lower portion of the block; **B**, photograph of the best preserved vertebra *in situ* (dorsal aspect); **C-G**, virtual 3D model of the vertebra: **C**, anterior view with coronal slice of: **C1**, anterior portion with the cotyle and zygosphene; **C2**, anterior portion with paradiapophyses; **C3**, mid-region of the vertebra with haemal keel; **D**, posterior; **E**, dorsal; **F**, lateral with detail of the neural spine *in situ*; **G**, ventral views. Scale bars: A, B, 1 mm; C-G, 0.95 mm; C1, C3, 0.85 mm; C2, 0.7 mm; F1, 0.6 mm.

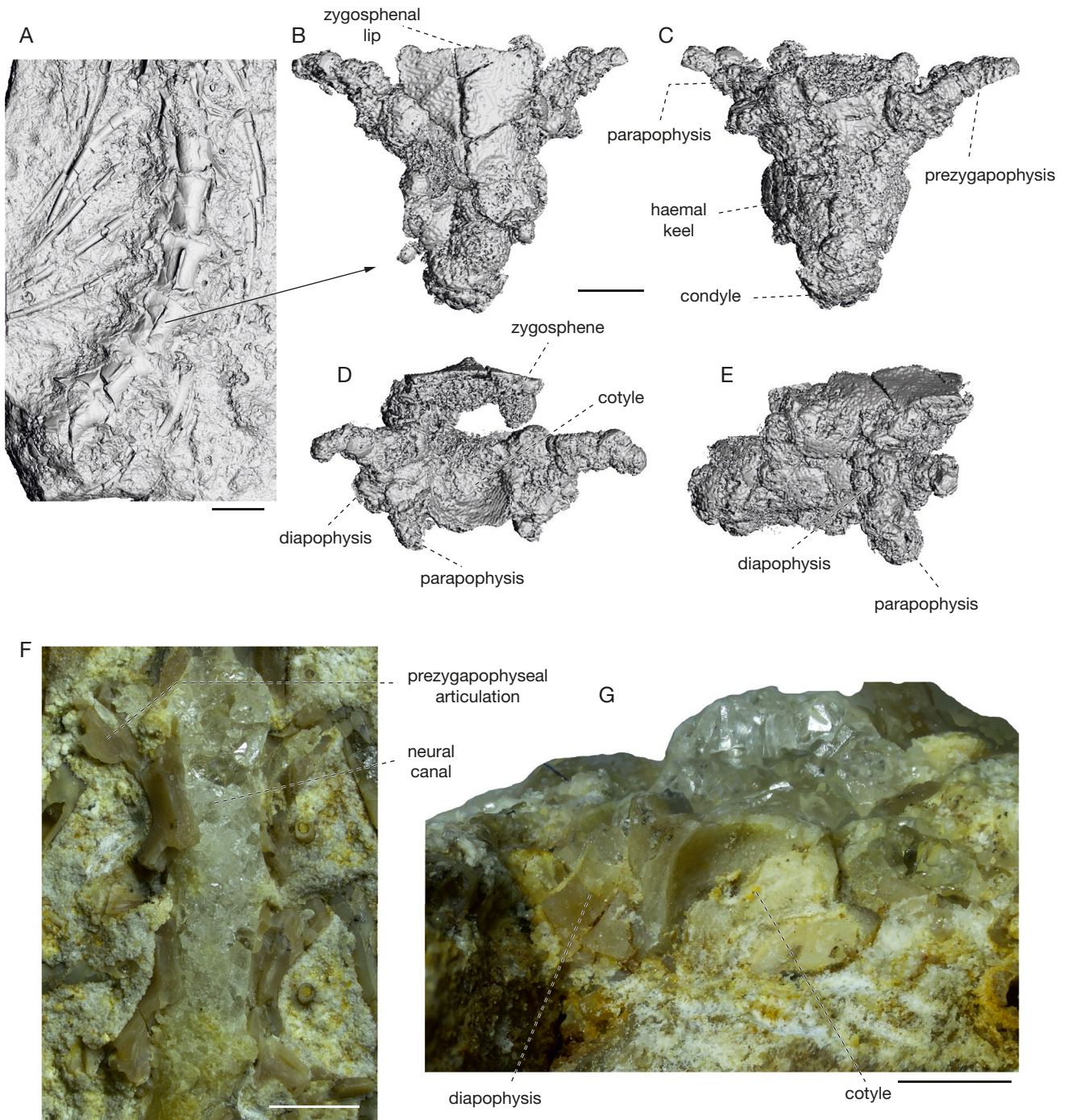


FIG. 4. — *Cf. Dolichophis* sp. SNM Z 29222 from the Middle Miocene Bonanza locality: **A**, virtual CT visualization of the posterior section of the vertebral column located in the lower portion of the block with indication of the segmented vertebrae; **B-E**, virtual 3D model of the vertebra in: **B**, dorsal; **C**, ventral; **D**, anterior; **E**, lateral views; **F, G**, the anterior section of the vertebral column in: **F**, dorsal; **G**, anterior views. Scale bars: A, 2.5 mm; B-F, 1 mm; G, 500 μ m.

clearly visible. On the basis of vertebrae alone (without cranial bones), determination of fossil colubrids is very difficult, even more so at the generic level. This specimen is provisionally allocated to Colubridae based on the combination of an elongated centrum, vaulted neural arch, short parapophyses with ventral border situated close below the cotylar rim and presence of a haemal keel. See Discussion below regarding areas of uncertainty.

DISCUSSION

TAXONOMIC ALLOCATION OF THE LIZARD

Specimen SNM Z 29221 is allocated to the Lacertidae on the basis of the following features (Estes *et al.* 1988; Kosma 2004; Čerňanský & Syromyatnikova 2019; Villa & Delfino 2019; Čerňanský 2024): 1) presence of well-separated and sculptured osteoderms fused to the lateral side of the ventral portion of

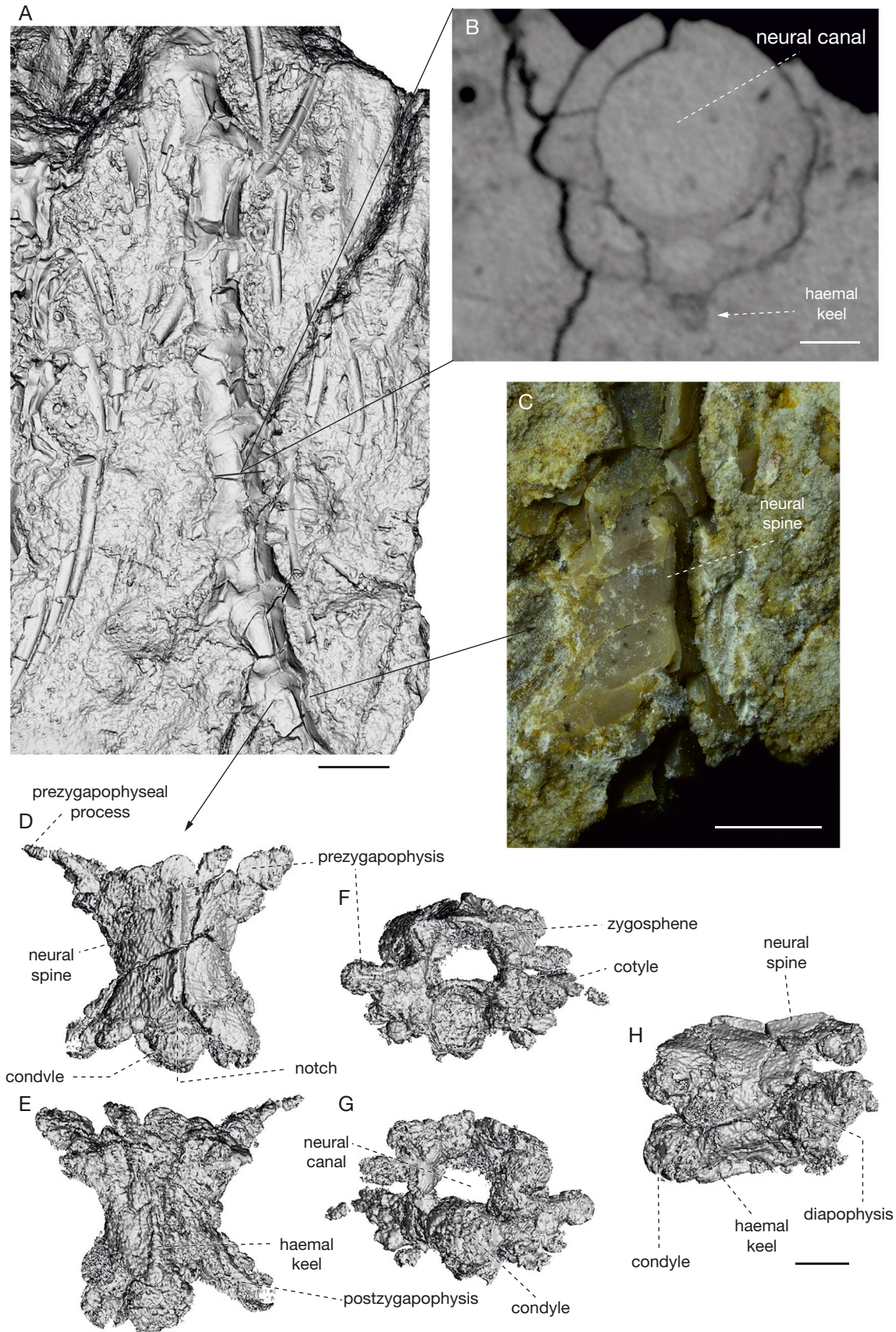


FIG. 5. — *Cf. Dolichophis* sp. SNM Z 29222 from the Middle Miocene Bonanza locality: **A-C**, the vertebral column from the upper part of the block in: **A**, dorsal view; **B**, coronal slice of the mid-section of the vertebra; **C**, the posterior and best preserved vertebra in this section *in situ*; **D-H**, virtual 3D model of the vertebra in: **D**, dorsal; **E**, ventral; **F**, anterior; **G**, posterior; **H**, lateral views. Scale bars: A, 2 mm; B, 0.4 mm; C, 1 mm; D-H, 0.8 mm.

the facial process of maxilla; 2) the tooth morphology (the presence of bicuspid teeth and weak striations on the crowns is common among members of Lacertidae, including *Lacerta*); and 3) the maxillary tooth row does not reach the posterior end of the bone but leaves a small posterior toothless portion. The specimen SNM Z 29221 represents a typical insectivorous lacertid similar to extant members of the genus *Lacerta*. This can be supported by the presence of the following features:

1) the posteroventral process of the maxilla appears to be stepped (the maxillary-jugal suture is distinctly stepped, so its course is sinuous, see Arnold *et al.* 2007: fig. 8) as it is in *Lacerta*, *Iberolacerta* Arribas, 1999, *Podarcis* Wagler, 1830 and *Darevskia brauneri* (Méhely, 1909) (see Barahona 1996: fig. 10.4. Lmm; Barahona & Barbadillo 1998: fig. 5b; Arnold *et al.* 2007; Čerňanský & Syromyatnikova 2019: figs 36C; 37C; Villa & Delfino 2019). A step is absent in most taxa (Arnold *et al.* 2007), e.g. extant *Timon* Tschudi, 1836, *Zootoca* Wagler, 1830, *Gallotia* Boulenger, 1916 and extinct *Janosikia* Čerňanský, Klembara & Smith, 2016 (Barahona 1996; Müller 2002; Khosravani *et al.* 2011; Čerňanský *et al.* 2016; Dubke *et al.* 2018; Tschopp *et al.* 2018; Čerňanský & Syromyatnikova 2019; Villa & Delfino 2019; Čerňanský 2024);

2) a well-developed dermal sculpture is present on the lateral surface of the facial process (see Dubke *et al.* 2018; Čerňanský & Syromyatnikova 2019; Villa & Delfino 2019). The sculpture consists of distinct grooves and ridges (the pattern clearly consists of densely spaced ridges and grooves that are typical for the genus *Lacerta*; see Čerňanský 2024);

3) the teeth of the material from Bonanza are robust and closely spaced, with small interdental gaps. Teeth are less robust in *Podarcis* (see Čerňanský 2024: fig. 6). The gaps are much larger in *Zootoca vivipara* (Lichtenstein, 1823) (teeth of this species are slender, see Kosma 2004: fig. 51; Čerňanský & Syromyatnikova 2019: fig. 37O).

However, due to the limited data, allocation of the DVN Bonanza maxilla at the genus level is doubtful and has to be met with caution. In any case, the stratigraphically similarly aged *Eddartetia sansaniensis* Augé & Rage, 2000 known from the type locality Sansan in France (the Middle Miocene, MN 6) can be excluded, because *Eddartetia* Augé & Rage, 2000 is characterized by a unique feature among lacertids – a constriction below the tooth crown (Augé & Rage 2000). Neogene lacertids with amblyodont dentition such as *Janosikia* and *Ligerosaurus* Augé, Bailon & Malfay, 2003 from the Miocene, and *Maiorialacerta* Bailon, Boistel, Bover & Alcover, 2014 from the Pliocene (Augé *et al.* 2003; Bailon *et al.* 2014; Čerňanský *et al.* 2016), can be excluded as well. Although the dermal sculpture in the Bonanza specimen is strongly developed, note that the size, enlarged foramina on the lateral surface of the maxilla and tooth count might indicate a possible sign of juvenile/subadult condition (e.g. Barahona & Barbadillo 1997, 1998; Evans 2008; Čerňanský & Syromyatnikova 2019; Villa & Delfino 2019).

TAXONOMIC ALLOCATION OF A SNAKE

The specimen from Bonanza represents a small snake (this raises the possibility of a juvenile). This specimen can be allocated to

Colubridae based on the combination of the following features (Rage 1984; Szyndlar 1984, 1991a, 1991b; Georgalis *et al.* 2017): 1) lightly built morphology; 2) elongated centrum; 3) vaulted neural arch; 4) synapophyses clearly divided into diapophyses and parapophyses; 5) parapophyses with ventral border situated close below the cotylar rim; and 6) presence of haemal keel. Unfortunately, another feature typical for this group – a presence of paracotylar foramina – cannot be observed without doubts. The presence of the haemal keel instead of a hypapophysis on the mid-trunk vertebrae has been used for a long time to distinguish fossil “colubrine” from natricines within the colubridean clade (Szyndlar 1984; Ivanov 2000, 2002a; Georgalis *et al.* 2019). However, it is usually advised to use quotation marks when referring to Neogene vertebrae of “colubrine” snakes (‘Colubrinae’), because the absence of hypapophysis in mid- and posterior trunk vertebrae is also documented, beyond Colubridae, in the more distantly related Dipsadidae Bonaparte, 1838 and Psammophiidae Bourgeois, 1968 (Szyndlar 2012; Georgalis & Scheyer 2022; Georgalis & Szyndlar 2022). On the basis of vertebrae alone (without cranial bones), however, determination of fossil colubrids is very difficult, even at the generic level. In any case, the absence of the hypapophyses on relatively long and slender vertebrae and the relatively low neural spines indicate allocation of this material to the grade genus ‘*Coluber*’. Fossil representatives of this genus are relatively common in the European Neogene (Bachmayer & Szyndlar 1985, 1987; Szyndlar & Böhme 1993; Szyndlar & Schleich 1993; Venczel 1994, 1998; Ivanov 2002a). Note that the potentially closest living relative of the European Miocene ‘*Coluber*’ is *Dolichophis* (formerly *Coluber*) *caspius* (Gmelin, 1789) (see below), widely distributed today in the southeastern parts of the European continent (Szyndlar 2009), including the Balkans, Turkey, and regions around the Caspian and the Black Sea (Schcherbak & Böhme 1993; Nagy *et al.* 2010; Sahlean *et al.* 2019).

The shape of the neural canal resembles previously described vertebrae by Ivanov (1998) as ‘Colubrinae D’. Based on its morphology, the Bonanza specimen SNM Z 29222 might represent a small form similar to the extant *Dolichophis*, as also one of the three, morphologically similar (Szyndlar 2005), fossil species that were assigned to the genus ‘*Coluber*’ when that genus was a catch-all grade taxon recognised from both Europe and North America (for American *Coluber constrictor*, see Parmley 1988: fig. 3f, g): ‘*Coluber dolnicensis*’ Szyndlar, 1987 [reported originally from the Early Miocene (MN 4) type locality at Dolnice (Czech Republic; Szyndlar 1987), later also from MN 3 of Merkur-North (Czech Republic; Ivanov 2002a)], ‘*Coluber pouchetii*’ (Rochebrune, 1880) [MN 6 of Sansan, France (Augé & Rage 2000), Late Miocene MN 9; Rudabánya (Hungary; Szyndlar 2005)] and ‘*Coluber caspioides*’ Szyndlar & Schleich, 1993 [the Early Miocene (MN 4) type locality Petersbuch 2 (Germany; Szyndlar & Schleich 1993), later also Oberdorf in Austria (as *Coluber* cf. *C. caspioides*; Szyndlar 1998), Merkur-North (MN 3; Czech Republic; Ivanov 2002a), also from the middle Miocene (MN 7 + 8) of La Grive M (as *Coluber* cf. *dolnicensis*; Ivanov 2002b), Griesbeckerzell (as ‘*Coluber*’ cf. *caspioides*; Langhian, Early

Badenian, Ivanov & Böhme 2011) and Litke, Hungary (MN 6; Venczel & Hír 2015)]. According to Augé & Rage (2000: 297), '*C. pouchetii* and '*C. dolnicensis* are morphologically very similar and Szyndlar (1998) suggested that these species may represent actually a single species. Later, this was, however, not supported by Ivanov (2002a), who based his statement on some cranial bones referred to both '*C. pouchetii* and '*C. dolnicensis*.

One of the features that Augé & Rage (2000) have defined as a vertebral character of '*Coluber pouchetii*', is the presence of a small median notch of zygosphenes in numerous vertebrae. This feature (as far as a preservation of the specimen allows) seems to be absent in the Bonanza specimen. However, the notch also occurs in some vertebrae of '*C. caspioides*'. According to Ivanov & Böhme (2011), the two features which allow to safely distinguish the trunk vertebrae of '*C. pouchetii* from '*C. caspioides* are only as follows: 1) the almost vertical anterior and posterior margins of the high neural spine; and 2) the diapophysis, which is as large as the parapophysis or somewhat larger. Trunk vertebrae of '*C. dolnicensis* can be recognized by a slightly convex zygosphenal roof, the prominent step in anterior part of the haemal keel and by the diapophyses, which are shifted far behind the parapophyses (Szyndlar 1987). The zygosphenal roof of the Bonanza specimen is slightly convex. The haemal keel is mostly damaged and although a step appears to be present in vertebra on Figure 4E, one cannot exclude that this could be actually only an artifact due to the bad preservation. Parapophyses are, however, mostly damaged in the Bonanza specimen. In this situation, it is very difficult (rather impossible) to distinguish the species '*C. pouchetii* and '*C. dolnicensis* (in lateral view, they have diapophyses located behind the parapophyses) from the species '*C. caspioides* (its diapophyses are located dorsal the parapophyses). In any case, the remains of this area in some vertebrae appear to indicate rather posteriorly located diapophyses (this would exclude the latter species). The differentiation of '*C. pouchetii* from '*C. dolnicensis* is possible only on the basis of a greater number of vertebrae including both middle and posterior trunk vertebrae (note that '*C. dolnicensis*, is slightly smaller than '*C. pouchetii*). The ideal would be the anterior trunk vertebrae (previously referred to as cervical), in which it is assumed that the species '*C. pouchetii* had the hypapophysis directed anteroventrally (see Szyndlar 1987; Szyndlar & Schleich 1993; Ivanov 2002a). This feature is usually observed only in some egg eating colubrids (e.g. *Dasyplectis* Wagler, 1830 and *Elaphe* Fitzinger, 1833), but not in modern members of *Coluber* (Szyndlar 2005). But these vertebrae are not preserved in the Bonanza specimen and thus their morphology is unknown. For this reason I decided to allocate the specimen SNM Z 29222 tentatively only at the genus level.

Although the traditional name '*Coluber*' is widely used in the European paleontological literature, it should be noted that Szyndlar (2012) suggested that '*Coluber caspioides* should be probably referred, together with '*C. suevicus* (Fraas, 1870), '*C. dolnicensis* and '*C. pouchetii*, to the extant genus *Dolichophis* rather than to the wastebasket taxon '*Coluber*'. However, Szyndlar (2012) did not formally establish new

generic combinations for his proposal. This option was later followed by Georgalis *et al.* (2017) who tentatively assigned their colubrid material from the latest Miocene Anó Metochi locality to cf. *Dolichophis*. I decided to follow this statement and assigned tentatively the material from Bonanza to cf. *Dolichophis*, rather than to the wastebasket taxon '*Coluber*'.

PALEOECOLOGY – LIFE ON A PREHISTORIC ISLAND IN CENTRAL EUROPE

During the Middle Miocene, the area of Devínska Nová Ves was part of an archipelago in the western part of the Central Paratethys in the northern part of the Vienna basin (Kvaček *et al.* 2006). At that time, the sea and sea-shore of Devínska Kobyla Hill was inhabited by sharks, seals, sirens together with whales and dolphins (Sabol & Holec 2002; Sabol *et al.* 2021). Zapfe's fissure and Bonanza represent an area, that was an island during, at least, a certain time, isolated from the nearest land by a shallow strait (Sabol & Kováč 2006). The fossil record from this area yielded several faunal elements (e.g. *Pliopithecus vindobonensis* (Zapfe & Hürzeler, 1957), *Keramidomys carpathicus* (Schaub & Zapfe, 1953) and *Democricetodon vindobonensis* Schaub & Zapfe, 1953) which indicate an isolated character of the assemblage over a critical time period (necessary for the evolution of such endemic forms; see Fejfar & Sabol 2009). The isolation of this territory might have facilitated allopatric speciation for forms such as *Euleptes klempari* (Čerňanský *et al.* 2018). The palaeoenvironment of this area is interpreted as a forest area close to water bodies (Sabol 2005a). Moreover, the presence of several marine taxa such as fish, sharks, seals, and marine bivalves, indicates a mixed insular or peninsular area, with subtropical forests close to freshwater bodies and in the vicinity of a saltwater sea (Sabol 2005a, b; Sabol *et al.* 2021). Except of *Devinophoca*, this environment was also occupied by, e.g. a mammutid proboscidean *Zygodon turicensis* (Schintz, 1824) (Holec 2002). Although no record is reported directly from Bonanza, *Griphopithecus suessi* Abel, 1902 was discovered at Sandberg, so hominids occurred in this area as well (Abel 1902; Holec & Emry 2003). The specimen SNM Z 29221 clearly shows that lacertids were present in this environment, together with other lizards such as *Ophisaurus* Daudin, 1803 (Anguimorpha; Čerňanský & Klempara 2017) and *Euleptes* (Gekkota; Čerňanský *et al.*, 2018). Moreover, the DNV Bonanza lacertid represents stratigraphically so far the oldest known member of the Lacertidae clade in Slovakia. Previously, the Miocene record of this group was documented only from the Upper Miocene (MN 9) locality of Borský Svätý Jur (Čerňanský 2011b). Overall, squamates are relatively diverse at the localities of Devínska Kobyla Hill, containing several clades. Besides lizards, the Bonanza was also occupied by several snake taxa, e.g. *Neonatrix*, elapid (see Introduction) and cf. *Dolichophis*. The Mediterranean taxon *Dolichophis caspius* represents a large-bodied colubrid species growing up to 2 m in length (Schcherbak & Böhme 1993). It occupies primarily open steppe grasslands and forest steppe habitats (Schcherbak & Böhme 1993; Sahlean *et al.* 2014). Its habitat also includes rocky riverbanks and swampy areas

(Covaciuc-Marcov & David 2010). This is not inconsistent actually with the suggested environment of the Devínska Kobyla Hill during the Middle Miocene.

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Availability of materials and data

All specimens are catalogued and accessible in the fossil collection of Slovak National Museum in Bratislava. Digital surface models of the figured fossil specimens are available on Morphosource and Virtual Collections:
SNM Z 29221: <https://www.morphosource.org/concern/media/000620091?locale=en>
SNM Z 29222: <https://www.morphosource.org/concern/media/000620097?locale=en>

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