

The oldest known European Neogene girdled lizard fauna (Squamata, Cordylidae), with comments on Early Miocene immigration of African taxa

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ABSTRACT

This paper reports on the first record of cordylid lizards from the locality of Merkur-North. The fossil history of girdled lizards is very poorly known and this group was rare during the Lower Miocene in Europe. The fossils described herein come from grey calcareous marls at the base of the so-called “Main Brown Coal Seam”. These marls are interpreted as reworked volcanic ash and the sediments are considered as early Miocene in age and are precisely equated with the MN 3a zone. For this reason, the cordylid fauna from this locality is older than previously described Miocene material and it represents the oldest known Neogene cordylids in Europe. The material of the dentary is very similar to that of *Palaeocordylus bohemicus* Roček, 1984, described from the younger locality of Dolnice near Cheb. The intramandibular septum of the dentary described herein, lying ventromedially from the alveolar canal, has a free posterolateral portion. It represents the first report of this structure in cordylids. The maxilla is only fragmentarily preserved. The size difference between the maxillary and dentary elements, the number of teeth and, especially their morphology evokes the possibility of two different taxa. Unfortunately, it is impossible to decide on the basis of such limited material if both finds represent independent forms or only extreme forms of the same taxon.

KEY WORDS

Squamata,
Scincoidea,
Cordylidae,
Palaeocordylus,
Eggenburgian,
North-West Bohemia.

RÉSUMÉ

Les plus anciens « lézards » (Squamata, Cordylidae) du Néogène d'Europe. Remarques sur les immigrations de taxons africains au Miocène inférieur.

Les plus anciens lézards cordylidés du Néogène européen proviennent du Miocène inférieur de Merkur-Nord (République Tchèque). L'histoire des cordylidés fossiles est très mal connue et ce groupe est rare dans le Miocène inférieur d'Europe. Les fossiles décrits ici proviennent des marnes calcaires grises de la base de la « Main Brown Coal Seam ». Ces marnes sont interprétées comme des cendres volcaniques remaniées. Les sédiments sont datés du Miocène inférieur (zone MN 3a). Ainsi, la faune de ce gisement est plus ancienne que celles décrites précédemment du Miocène. Le dentaire de ce cordylidé est similaire à celui de *Palaeocordylus bohemicus* Roček, 1984, provenant du gisement plus récent de Dolnice, situé près de Cheb. La portion postérolatérale du septum intramandibulaire du dentaire, situé ventralement au canal alvéolaire, est libre. Le maxillaire est fragmentaire. La grande différence de taille entre maxillaire et dentaire, le nombre de dents et, surtout, leur morphologie suggèrent la possibilité de deux taxons différents. Malheureusement, sur la base du peu de matériel disponible, il est impossible d'établir si ces fossiles représentent des formes distinctes ou seulement des variations extrêmes du même taxon.

MOTS CLÉS

Squamata,
Scincoidea,
Cordylidae,
Palaeocordylus,
Eggenburgien,
Bohême nord-occidentale.

INTRODUCTION

This paper deals with the first occurrence of the family Cordylidae at the Lower Miocene (MN 3a) locality of Merkur-North. Girdled lizards (Cordylidae) are sub-Saharan Africa's only endemic squamate family. This family belongs to a clade of scincomorph lizards, the Cordyliformes. In addition to this family, this clade includes the Gerrhosauridae. The monophyly of cordyliformes based on morphological data suggested by Lang (1991) was confirmed by the cytogenetic study and analysis of mitochondrial DNA by Odierna *et al.* (2002). Relationships to other lizards remain problematic, but they appear to be close to the Scincidae (Estes *et al.* 1988; Lee 1998, 2002; Vicario *et al.* 2003; Whiting *et al.* 2003; Townsend *et al.* 2004).

Today, Cordylidae is the only lizard family restricted to Africa, and most species of the family occur in South Africa and adjacent countries (e.g., Estes 1983; Branch 1984); only *Cordylus angolensis* Bocage, 1895 and *C. rivaie* (Boulenger, 1896) can be found further north around Angola

or Ethiopia, respectively (Broadley & Branch 2002). Cordylidae contains 80 nominal taxa. This family has traditionally been divided into four genera: *Cordylus* Gronovius, 1763, *Pseudocordylus* Smith, 1838, *Chamaesaura* Schneider, 1801 and *Platysaurus* Smith, 1844 (Loveridge 1944; Lang 1991). A recent molecular study has produced a new view of the cordylids. Stanley *et al.* (2010) used three nuclear and three mitochondrial genes from 111 specimens, representing 51 of the 80 known taxa and recovered a comb-like tree with 10, well-supported, monophyletic lineages. Their taxonomic reassessment divides the family into 10 genera that correspond to the well-supported lineages. They recovered evidence that supports two subfamilies within the Cordylidae, the egg-laying Platysaurinae and the live-bearing Cordylinae.

The fossil record of cordylids is very poor. The oldest taxon is represented by a recently discovered fossilized lizard, *Konkasaurus mahalana* Krause, Evans & Gao, 2003. This specimen has been assigned to the Cordylidae, and it suggests that the family's range once extended to Madagascar (Krause *et al.* 2003). Assuming that the dating and taxonomy

of *K. mabalana* is correct, the Cordylidae family is at least 68 million years old. The taxon *Pseudolacerta mucronata* (Filhol, 1877) from the Eocene of France (Augé 2003), formed the basis of the record of the Cordylidae in Europe. However, Augé (2005) removed the species *P. lamandini* (Filhol, 1877) from *Pseudolacerta* De Stefano, 1903 and transferred it to the iguanid *Geiseltaliellus* Kuhn, 1944. He retained the species *P. mucronata* in *Pseudolacerta* (to which he added his new species *P. quercyini* Augé, 2005) and he assigned *Pseudolacerta* to the Iguanidae. The last occurrence of cordylids in Europe is regarded as early Oligocene (Augé 2005). However, Böhme & Lang (1991) demonstrated that “*Lacerta*” *rottensis* von Meyer, 1856 (latest Oligocene, MP30; Germany) should be referred to Cordyliformes, i.e. to the Cordylidae (Estes *et al.* 1988).

Cordylids were rare during the Neogene of Europe. Previously, Neogene cordylids from Europe were only known from Dolnice near Cheb (*Palaeocordylus bohemicus* Roček, 1984; Czech Republic, MN 4), Obergänserndorf (Cordylidae indet. Böhme 2002; Austria, MN5), Petersbuch 2 (*Bavaricordylus ornatus* Kosma, 2004; Germany, MN4a – however, this name was established in an unpublished work – thesis, therefore it should be a *nomen dubium*; Rage pers. comm.), Puttenhausen (Cordylidae indet. Abdul-Aziz *et al.* 2008; Germany, MN5 and the material described by Böhme (2010) as a new taxon of the genus *Bavaricordylus* – *B. mollasicus*; type locality is Puttenhausen B) and Sandelzhausen (MN 5; Böhme 2010).

The new material of cordylid lizards as described below from the Lower Miocene locality of Merkur-North (MN 3a) is much older than previously described European Neogene specimens and new information about the oldest known Neogene cordylids in Europe is given.

MATERIAL, LOCALITY AND GEOLOGICAL SETTING

This study presents the first record of a cordylid lizard from the Lower Miocene (Eggenburgian, MN3a) Merkur-North locality, Czech Republic (Fig. 1).



FIG. 1. — Location of the Merkur-North locality, Czech Republic.

All material was collected by screen-washing. The specimen is housed in the Geological collection of the Bilina opencast mine situated near Chomutov in the western part of the Czech Republic. The anatomical terminology of the individual skeletal elements used here is mostly that of Fějervary-Langh (1923) and Roček (1984). The nomenclature of the tooth crown follows Richter (1994) and Kosma (2004). The specimens were photographed using a scanning electron microscope (SEM).

The Merkur-North locality (Lower Miocene, MN 3a) is located in NW Bohemia and it was discovered in an opencast (lignite) mine near Chomutov. The specimens are preserved in grey calcareous marls at the base of the so-called “Main Brown Coal Seam”. The marls are interpreted as reworked volcanic ash. This locality has already yielded a rich material of various groups of fish, amphibians and reptiles, e.g., frogs (Kvaček *et al.* 2004), albanerptontids (Čerňanský 2010a), lacertids (Čerňanský & Joniak 2009), chameleonids (Fejfar & Schleich 1994; Čerňanský 2010b), choristoderans (Evans & Klembara 2005), amphisbaenids (Čerňanský & Venczel 2011), gekkonids (Čerňanský & Bauer 2010), anguimorph lizards (Klembara 2008) and snakes (Ivanov 2002). The sediments are also richly fossiliferous in remains of limnic and terrestrial molluscs, plants and mammals (Fejfar *et al.* 1997a, b, 1998; Kvaček *et al.* 2004).

ABBREVIATIONS OF REPOSITORIES

Ah-number SGDB Geological collection of the Bilina opencast mine, Czech Republic.

SYSTEMATIC PALAEOONTOLOGY

Order SQUAMATA Opper, 1811
 Infraorder SCINCOMORPHA Camp, 1923
 Superfamily SCINCOIDEA Opper, 1811
 Family CORDYLIDAE Gray, 1837

aff. *Palaeocordylus bohemicus* Roček, 1984
 (Figs 2-5)

LOCALITY AND HORIZON. — Merkur-North opencast mine; Lower Miocene (Eggenburgian), Lower Orleanium, zone MN 3a.

MATERIAL EXAMINED. — Right dentary (Ah-1088 SGDB).

DESCRIPTION

Dentary

This is a long, ventrally straight bone (Fig. 2), with a slight medial curvature at its anterior end. The symphyseal facet is small and square-shaped. In transverse section, the dentary is C-shaped with a smooth external surface. This surface is pierced by five labial foramina (*foramina pro rami nervorum alveolarium inferiorum*). The maximum width of the dentary occurs at the posterior end. There is a prominent coronoid process (*processus coronoideus*), which is distinctly elongate and slants posterodorsally with its dorsoposterior limit being higher than the apices of the largest mandibular teeth. This dentary bears up to 25 bicuspid teeth (three tooth sockets and 22 preserved teeth present in Ah-1088 SGDB). There is a relatively long non-toothed portion of the dentary posterior to the last tooth. The lingual surface of the bone shows a deep and open groove for Meckel's cartilage. However, its anterior portion is quite narrowed and it is shallower in this part. The horizontal lamina (*lamina horizontalis*) is straight and thick, especially in the anterior region, with a rounded medial margin. It gradually becomes thinner towards the posterior end as a result of the presence of the facet for the splenial on its ventromedial surface. The splenial facet turns on the ventral surface of the horizontal lamina and continues anteriorly up to the level of the 13rd tooth. At the level of the 10th tooth, the well-defined splenial facet on the medial surface of the ventral margin (*crista ventralis*) also begins.

Posteriorly behind the splenial facet, a distinctive coronoid facet is developed on the horizontal lamina and, anteriorly, it rises at the level of the 21th tooth position. The opening of the alveolar canal is small and it lies at the level of the 19th tooth. The intra-mandibular septum, lying ventromedially from the alveolar canal, has a free posteroventral portion (Figs 2; 3). A *sulcus dentalis* is present; it is narrow, but well developed along the tooth row, especially in the middle portion of the dentary.

Dentition

The dentition is pleurodont. The teeth are middle sized and blunt, typically bicuspid with *cusps labialis* and *cusps lingualis* (Fig. 4). Teeth are labially attached to the dental parapet almost over their entire length, with only the tooth crowns rising above the parapet. The teeth are closely distributed. The sizes of the inter-dental gaps are very small. The tooth necks are more or less swollen lingually (Fig. 5). Resorption pits are present on the lingual sides of some tooth bases. In the anterior portion of the dentary, the teeth are relatively smaller. The labial surface of the teeth is smooth. A pattern of striations has developed on the lingual surface of the tooth crown between the *culmen lateralis anterior* and *culmen lateralis posterior* (terms after Richter 1994). They begin below the tip of the tooth on the antero- and posterolabial portions of the tooth surface and run down, becoming less distinctive on the lowermost region of the tooth crown without joining each another. There are about six striae on the lingual side and these converge apically. The morphology of the tooth crowns is similar to that of the recent species *Cordylus cataphractus* Boie, 1828 (see Kosma 2004: pl. I., figs 4-6; however this taxon has a lot of other differences).

REMARKS

The Cordylidae, Scincidae Gray, 1825 and Paramacellodidae Estes, 1983 are highly related groups (Evans & Chure 1998). The attribution to the family Cordylidae is beyond doubt, based on the combination of the following features: 1) the Meckelian canal is narrow to its anterior termination, but fully opened. The tendency toward closure of the Meckelian canal could be a characteristic of

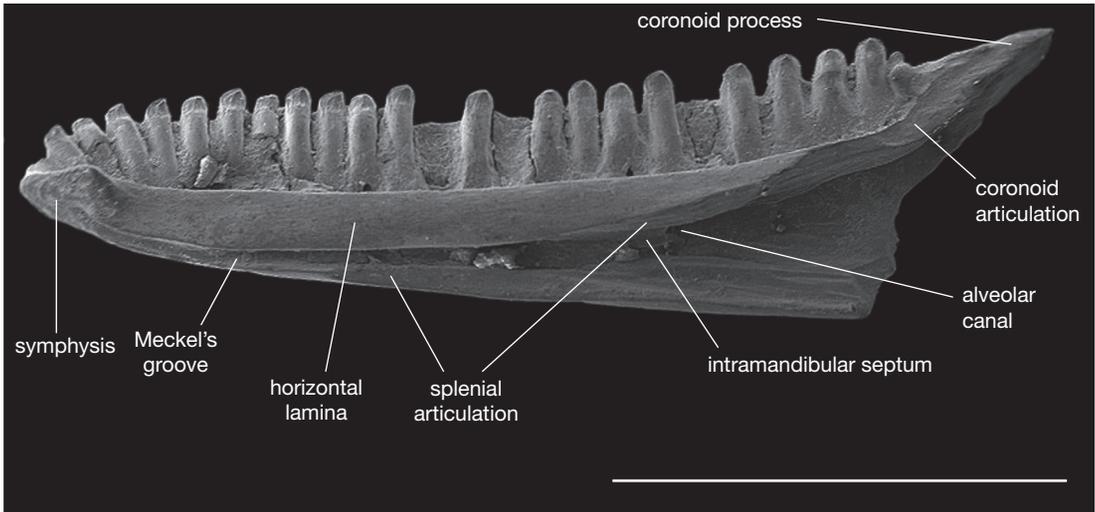


FIG. 2. — aff. *Palaeocordylus bohemicus* Roček, 1984 from the locality Merkur-North; right dentary (Ah-1088 SGDB) in lingual view. Scale bar: 5 mm.

Scincidae as many scincid lizards show a closed Meckelian canal, in contrast to cordylids, which all have an open Meckelian canal (Augé & Smith 2009); 2) the *crista ventralis* is straight in lateral view (after Lang 1991). However, some scincids also have a straight ventral border of the dentary (Augé & Smith 2009); 3) the *sulcus dentalis* is well developed; and 4) the high number of blunt and conical anteroposteriorly compressed teeth with well developed lingual cusps and the presence of lingual striae on the crowns. The presence of the lingual cusp is more common among the cordylids than the scincids (Folie *et al.* 2005).

The dentary is basically identical with the species described by Roček (1984) as *Palaeocordylus bohemicus* from the younger deposits of the Dolnice locality near Cheb (MN 4). However, there are also some differences: 1) in the holotypic dentary DP FN 97, the splenial facet on the horizontal lamina and also on the ventral margin reaches anteriorly to the level of the 9th tooth position. On the dentary described herein, the splenial facet reaches the level of the 13rd tooth on the horizontal lamina and the 10th tooth level on the ventral margin of the dentary; 2) the external surface of the dentary from Merkur-North is pierced by five

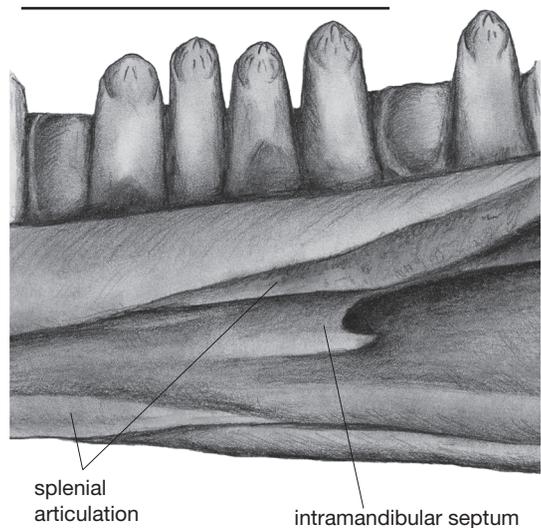


FIG. 3. — aff. *Palaeocordylus bohemicus* Roček, 1984; detail of the region with intramandibular septum. Scale bar: 2 mm.

mental foramina, which is in contrast to holotypic dentary, where the row of foramina reaches seven. Given typical intraspecific variation in this characteristic among lizards (Klembara pers. comm.), I consider this characteristic to be insignificant;

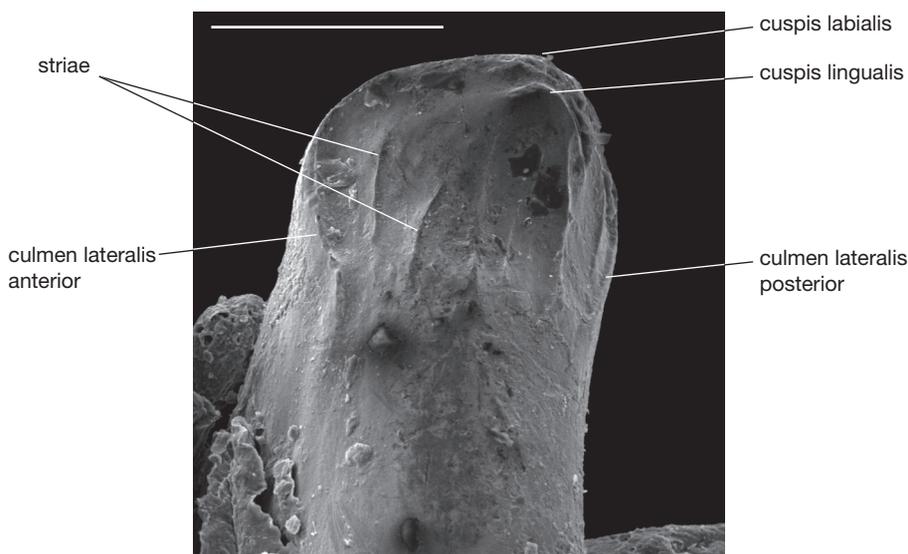


FIG. 4. — aff. *Palaeocordylus bohemicus* Roček, 1984; detail of the tooth from the medial region of the dentary tooth row in lingual view (terms after Richter 1994). Scale bar: 200 μ m.

and 3) the striations are not so distinctly developed, with less striae than in the material from Dolnice (see Roček 1984: pl. I., figs 2-5; pl. II., fig. 1; where-in the number of striae in the dentary teeth is around 8 instead of 6). However, this is variable feature and therefore conveys only informative value. The number of striae in e.g., *Cordylus cataphractus* varies between individuals (Kosma 2004). The number and arrangement of the striae also vary within the tooth row of a single individual in the material described by Kosma (2004) as in *Bavaricordylus ornatus*. Although the labial surface of the teeth is smooth in the dentary described herein, this feature can also vary. Although the striation can be well-developed in the Dolnice material, it can also exist to a lesser degree on the labial surface (Roček 1984).

All these quoted differences could be caused by ontogenic changes and intraspecies variability. The total antero-posterior length of the dentary described here is 10 mm which is much less than the dentary described by Roček from Dolnice (the holotype DP FN5P 97 – section of the left dentary with a 19 tooth position is 14,8 mm, even with the most posterior portion broken

away). For this reason, the dentary from the Merkur – North locality could represent a juvenile ontogenetic stage of development. Because of a lack of knowledge of variations during ontogeny in the Lower Miocene cordylids due to such limited material, it is better to attribute this material to aff. *Palaeocordylus bohemicus*, because of its similarity.

COMPARISON

Although the taxonomical validity of the genus *Bavaricordylus* remains problematic, I have compared the material described here with the material attributed by Kosma (2004) and Böhme (2010) to this taxon.

The material of cordylids described herein differs from the Petersbuch 2 material described by Kosma (2004) as a new taxon – *Bavaricordylus ornatus* (MN4a) in the following features: 1) the tooth crowns of the Petersbuch 2 material possess a more striking pattern of striations with 20 distinct striations on the lingual surfaces of the tooth crowns and weak striations on their labial surfaces; Kosma 2004); 2) the *culmines lateres* of the Petersbuch 2 material are prominent and

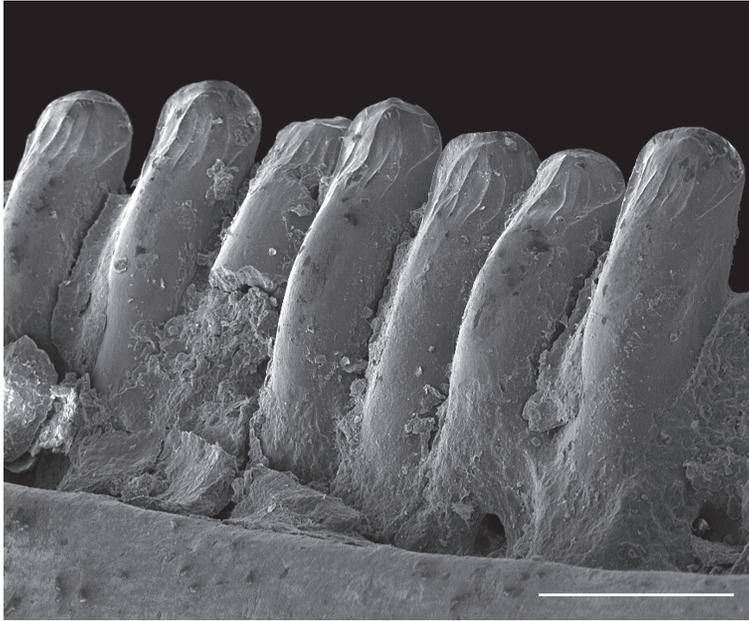


FIG. 5. — aff. *Palaeocordylus bohemicus* Roček, 1984; detail of the 6th-12th tooth in posterolingual view. Scale bar: 500 μ m.

their ventral portion reaches the tooth shafts; and 3) the labial surface of the Petersbuch 2 dentary shows rough facets for the attachment of osteoderms.

The cordylid material described herein differs from that of Puttenhamen B described by Böhme (2010) as *Bavaricordylus molassicus* in the following features: 1) the dentary from Puttenhamen B is more robust; 2) the *crista ventralis* of the dentary from Merkur-North is straight whereas it is curved in that from Puttenhamen B; 3) the number of striae is up to 12 in the material from Puttenhamen B (Böhme 2010); and 4) Puttenhamen B material has more anteriorly attached splenial; at the level of the 7th tooth position (Böhme 2010).

The material of indeterminate cordylids from the Korneuburg Basin located in Obergänserndorf, Austria is fragmentary, and this makes comparison with other specimens extremely difficult. The horizontal lamina is more robust in the dentary described herein compared to the dentary material described from this locality by Böhme (2002).

Superfamily SCINCOIDEA Oppel, 1811

? Cordylidae indet.
(Fig. 6)

LOCALITY AND HORIZON. — Merkur-North opencast mine; Lower Miocene (Eggenburgian), Lower Orléanum, zone MN 3a.

MATERIAL EXAMINED. — Left maxilla (Ah-939 SGDB).

DESCRIPTION

Maxilla

The maxilla is robust and subtriangular in shape (Fig. 6). Unfortunately, it is not completely preserved. Its posterior end is broken and the majority of the anterior portion is also missing. The external surface of the nasal process, above the row of seven labial foramina (*foramina pro rami nervorum alveolarium superiorum*), is ornamented by pits and very short irregular grooves. Unfortunately, the dorsal-most portion of the nasal process and the whole premaxillary process is broken. The dorsal section of the posterior portion behind the nasal process is short,

well bounded from the dental portion (*pars dentalis*) of the maxilla – the distal end of the nasal process is stepped, forming a posteriorly oriented triangular tip. The region below the labial foramina is smooth. The inner surface bears a prominent well-developed straight supradental shelf which supports the tooth bases along the entire tooth row. There are 12 preserved teeth. The shelf distinctly widens medially approximately between the second and last third of its length. Here, a large infraorbital foramen is situated at the level of the 3rd posterior tooth counted from the back. A deep and broad depression extends from this foramen to the posterior end of the maxilla and forms the articulation for the jugal. Although the *sulcus dentalis* is well-developed, unfortunately it is impossible to demonstrate its continuation since this part is mostly unpreserved on the material.

Dentition

The dentition is pleurodont. The teeth are high, robust and slightly curved lingually. The tooth shafts are tall with their bases slightly expanded lingually and oval in cross-section. Huge circular resorption pits are present on the lingual sides of some maxillary tooth bases. The teeth are closely distributed with inter-dental gap sizes very small or even absent between some maxillary teeth. The apical parts of the teeth are variable exhibiting heterodont dentition. The anteriorly situated teeth are larger and considerably more pointed. They are slightly posteriorly oriented with the crowns bent posteromedially. The teeth of the posterior section of the tooth row are lower and blunter, being close to each other, and of irregular size. They are slightly bicuspid with a main cusp and an anteriorly situated lateral cusp. The labial surfaces of the tooth crowns are slightly convex with weak radial striations. A pronounced pattern of striations has developed on the lingual surface of the tooth crown between the *culmen lateralis anterior* and *culmen lateralis posterior* (terms after Richter 1994). The number of striae on the lingual side is variable, but mostly around 10-11 and (14 in the last tooth). The angle between the *crista mesialis* and the *crista distalis* of the posterior teeth measures around 110 degrees. As a result of this apical angle, the occlusal cutting edges are generally relatively sharp.

REMARKS

The attribution of the maxilla to Scincoidea is beyond doubt. However within the superfamily Scincoidea, Scincidae and Cordylidae are often difficult to distinguish (Gao & Fox 1996). The exact identity of the maxilla Ah-939 SGDB from Merkur-North is also rather uncertain. The tooth morphology present here and the combination of the distinctive *sulcus dentalis*, wide posterior portion, the robust shape and the presence of dermal sculpturing are more common among the cordylids than the scincids. Unfortunately, the isolated maxilla lacks enough diagnostic features to support this, thus enabling determination to the family level somewhat questionable.

The number of striae on the lingual surface of the crowns is similar to that of the material described from Puttenhausen B by Böhme (2010), where the number reaches 12. It also possesses similar characteristics to heterodont dentition. However, the morphology of the tooth crowns is different – all teeth are unicuspid and distinctly blunter in the material from Puttenhausen B (after Böhme 2010), where the striae are mostly indistinct. In the material from the locality of Petersbuch 2, described by Kosma (2004) as *Bavaricordylus ornatus*, the cristae form the blunt apical portion with an apical angle of about 150 degrees. There, approximately 20 striae are present. The morphology of the tooth crowns in the maxilla described herein is certainly closer to that of *Palaeocordylus* Roček, 1984, especially in the anteriorly situated teeth which are very similar to that on the premaxilla of *P. bohemicus* from Dolnice (DP FNSP 114; in Roček 1984: pl. III, figs 3; 5). In *P. bohemicus*, the infraorbital foramen is situated at the level of the 5th tooth position from the back, while it lays at the level of the 3rd one in the material described here.

DISCUSSION AND CONCLUSION

All previously described specimens of Neogene cordylids come from deposits younger than the material described herein. The dentary of the cordylid from Merkur-North is very similar to that of the younger Dolnice fossil, described as *Palaeo-*

cordylus bohemicus by Roček (1984). The difference in the size of the maxillary and dentary elements described here, the number of teeth and especially their morphology, evokes the possibility of two different taxa. Unfortunately, it is impossible to decide on the basis of such limited material if both finds represent independent forms or only extreme forms of the same taxon. The material of *Palaeocordylus bohemicus* from the Dolnice locality also presents variability in features.

The intramandibular septum of the dentary described herein, lying ventromedially from the alveolar canal, has a free posterolateral portion. It represents the first report of this structure in cordylids. The free posteroventral margin of the intramandibular septum is characteristic of nonglyptosaurine Anguinae (see Conrad 2004), however the ventral margin completely fuses with the body of the dentary in many other anguimorphs (see e.g., Meszoely 1970; Sullivan 1979; Gauthier 1982). The intramandibular septum of the dentary bone has been a much-discussed character in squamate phylogeny (e.g., Estes 1964; Gauthier 1982; Estes *et al.* 1988). The intramandibular septum of Meckel's canal was first identified by Estes (1964) in anguids. A posteriorly placed subdivision of Meckel's canal, with a well developed intramandibular septum separating Meckel's cartilage from the lateral blood vessels and nerves, occurs in all xenosaurids, anguids, *Heloderma*, *Lanthanotus* and *Varanus* (Estes *et al.* 1988). A poorly developed septum was considered characteristic of most lizards (also Lacertidae, see e.g., Lee & Scanlon 2001; Augé & Hervet 2009), whereas a well-developed septum was a synapomorphy of Anguimorpha (Gauthier 1982). Pregill (1981) identified an intramandibular septum in some iguanids. Some chamaeleonids have a similar situation which is convergent on the basis of other characteristics (Estes *et al.* 1988), and it has been extensively discussed in snakes (e.g., Lee & Scanlon 2001). However, it is questionable how significant it is within the cordylids.

The beginning of the Miocene was marked by the return of tropical climatic conditions and the collision of Eurasia with Africa. These events allowed migration of a new squamate fauna into Europe, including a new migration of squamate

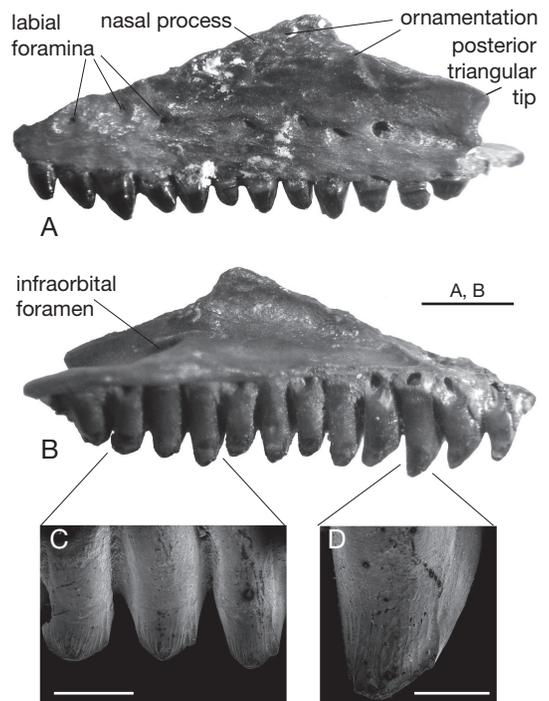


FIG. 6. — ? Cordylidae indet.; the left maxilla Ah-939 SGDB: **A**, labial view; **B**, **C**, **D**, lingual views with the details of the tooth crowns. Scale bars: **A**, **B**, 2.5 mm; **C**, 1 mm; **D**, 500 µm.

lineages which were extinct in Europe during the cooler and drier Oligocene, but which had survived in Africa. Among these lineages were Varanidae, Chamaeleonidae, Scoleophidia, and most likely Scincidae (Rage & Augé 1993). There are two possibilities concerning cordylid lizards:

1) the earliest known occurrence (MN 3a) of Neogene cordylids in Europe is described above. The cordylids and chamaeleonids are missing in slightly older localities such as Ulm (MN 2 zone) located in S-E Germany not far from the Czech boundary. We can therefore suggest that cordylids arrived by the transition between zones MN 2 and MN 3. This also corresponds to the migration of chamaeleons, the earliest appearance of which is also recognized in the same locality (Fejfar & Schleich 1994; Čerňanský 2010b);

and 2) on the other hand, if "*Lacerta*" *rottensis* (latest Oligocene of Germany) is a cordylid lizard, then there is the possibility that these lizards enjoyed

uninterrupted occurrence during the Oligocene/Miocene boundary in Europe. The cooler and drier Oligocene may have been an ideal environment for the cold-adapted, rock-dwelling cordylids. According to the recent taxa, cordylids are terrestrial, predominantly arid-land species of the scrub forest to grasslands and they often occur in boulder fields and rocky outcrops. Cordylids hide in rock crevices or burrows which some species dig for themselves (e.g., *Cordylus giganteus* Smith, 1844) (see Bauer 1998).

The life-style of the extant taxa is in contrast with the locality character of the Merkur deposits, which indicates a freshwater molasse (see Kvaček *et al.* 2004). Similar conditions occur in the Bavarian Freshwater Molasse, from where the cordylids were described (Kosma 2004). Cordylids could be an allochthonous component in these environments, post-mortally transported from close, more arid areas, perhaps situated higher in mountain regions. Another possibility is that they were habituated to more humid climatic conditions during the Lower Miocene in Central Europe.

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REFERENCES

- ABDUL-AZIZ H., BÖHME M., ROCHOLL A., ZWING A., PRIETO J., WIJBRANS J., HEISSIG K. & BACHTADSE V. 2008. — Integrated stratigraphy of the Early to Middle Miocene Upper Freshwater Molasse in Lower Bavaria (Germany, Bavaria). *International Journal of Earth Sciences (Geologische Rundschau)* 97: 115-134.
- AUGÉ M. 2003. — La faune de Lacertilia (Reptilia, Squamata) de l'Éocène inférieur de Prémontré (Bassin de Paris, France). *Geodiversitas* 25: 539-574.
- AUGÉ M. 2005. — Évolution des lézards du Paléogène en Europe. *Memoires du Muséum national d'Histoire naturelle* 19. *Publications Scientifiques du Muséum Paris*, 369 p.
- AUGÉ M. & HERVET S. 2009. — Fossil lizards from the locality of Gannat (late Oligocene-early Miocene, France) and a revision of the genus *Pseudeumeces* (Squamata, Lacertidae). *Palaeobiodiversity and Palaeoenvironments* 89: 191-201.
- AUGÉ M. & SMITH R. 2009. — An assemblage of early Oligocene lizards (Squamata) from the locality of Boutersem (Belgium), with comments on the Eocene-Oligocene transition. *Zoological Journal of the Linnean Society* 155: 14-170.
- BAUER A. M. 1998. — Lizards, in COGGER H. G. & ZWEIFEL R. G. (eds), *Encyclopedia of Reptiles and Amphibians*. San Diego, Academic Press: 126-173.
- BÖHME M. 2002. — Lower vertebrates (Teleostei, Amphibia, Sauria) from the Karpatian of the Korneuburg Basin-Palaeoecological, environmental and palaeoclimatic implications. *Beiträge zur Paläontologie* 27: 339-353.
- BÖHME M. 2010. — Ectothermic vertebrates (Actinopterygii, Allocaudata, Urodela, Anura, Crocodylia, Squamata) from the Miocene of Sandelzhausen (Germany, Bavaria) and their implications for environment reconstruction and palaeoclimate. *Paläontologische Zeitschrift* 84: 3-41.
- BÖHME W. & LANG M. 1991. — The reptilian fauna of the Late Oligocene locality Rott near Bonn (Germany) with special reference to the taxonomic assignment of "*Lacerta rottensis*" Von Meyer, 1856. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* H.9: 515-525.
- BRANCH W. R. 1984. — Cape lizards. 7. Plated and girdled lizards. *Naturalist (Port Elizabeth)* 28: 21-27.
- BROADLEY D. G. & BRANCH W. R. 2002. — A review of the small east African *Cordylus* (Sauria: Cordylidae), with the description of a new species. *African Journal of Herpetology* 51: 9-34.
- ČERNÁNSKÝ A. 2010a. — Albanerpetontid amphibian (Lissamphibia: Albanerpetontidae) from the Early Miocene of the locality Merkur-North (north-west Bohemia): data and a description of new material. *Acta Geologica Slovaca* 2: 113-116.
- ČERNÁNSKÝ A. 2010b. — A revision of chamaeleonids from the Lower Miocene of the Czech Republic with description of a new species of *Chamaeleo* (Squamata, Chamaeleonidae). *Geobios* 43: 605-613.
- ČERNÁNSKÝ A. & JONIAK P. 2009. — New finds of lacertids (Sauria, Lacertidae) from the Neogene of Slovakia

- and Czech Republic. *Acta Geologica Slovaca* 1: 57-64. (in Slovak with an English summary).
- ČERNÁNSKÝ A. & BAUER A. M. 2010. — *Euleptes gallica* Müller (Squamata: Gekkota: Sphaerodactylidae) from the Lower Miocene of North-West Bohemia, Czech Republic. *Folia Zoologica* 59: 323-328.
- ČERNÁNSKÝ A. & VENCZEL M. 2011. — An amphisbaenid reptile (Squamata, Amphisbaenidae) from the Lower Miocene of Northwest Bohemia (MN 3, Czech Republic). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 260: 73-77.
- CONRAD J. L. 2004. — Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). *Zoological Journal of the Linnean Society* 141: 399-434.
- ESTES R. 1964. — Fossil vertebrates from the late Cretaceous Lance formation, eastern Wyoming. *Univ. Calif. Publ. Geol. Sci.* 49:1-180.
- ESTES R. 1983. — *Encyclopedia of Paleoherpétology. Part 10 A. Sauria terrestria, Amphisbaenia*. New York: Gustav Fischer Verlag, 248 p.
- ESTES R., DE QUEIROZ K. & GAUTHIER J. 1988. — Phylogenetic relationships within Squamata, in ESTES R. & PREGILL G. (eds), *Phylogenetic relationships of the lizard Families*. Stanfors, CA: Stanford University Press, 119-281.
- EVANS S.E. & CHURE D.C. 1998. — Paramacellodid lizard skull from the Jurassic Morrison Formation at Dinosaur National Monument, Utah. *Journal of Vertebrate Paleontology* 18: 99-114.
- EVANS S. & KLEMBARA J. 2005. — A choristoderan reptile (Reptilia, Diapsida), from the Lower Miocene of Northwest Bohemia (Czech Republic). *Journal of Vertebrate Paleontology* 25: 171-184.
- FEJFÁR O., LANGH A. M. 1923. — Beiträge zu einer Monographie der fossilen Ophisurier. *Palaeontologia Hungarica* 1: 123-220.
- FEJFÁR O. & SCHLEICH H. H. 1994. — Ein Chamäleonfund aus dem unteren Orleanium des Braunkohlentagebaus Merkur-Nord (Nordböhmen). *Courier Forschungsinstitut Senckenberg* 173: 167-173.
- FEJFÁR O., ENGESSEB B. & TOMIDA Y. 1997a. — New eomyid genus and species of *Apeomys* Falbusch (Eomyidae [?], Rodentia, Mammalia). Affinity from the early Miocene (MN zones 3 and 4) of Europe and Japan, in AGUILAR J.-P., LEGENDRE S. & MICHAUX J. (eds), Actes du Congrès Biochrom '97, *Mémoires et travaux de l'Institut de Montpellier, Ecole Pratique des Hautes Études* 21: 705-706.
- FEJFÁR O., HEIZMANN E. P. J. & MAJOR P. 1997b. — *Metaschizotherium* cf. *wetzleri* (Kowalewsky) from the early Miocene of the Czech Republic and South Germany, in AGUILAR J.-P., LEGENDRE S. & MICHAUX J. (eds), Actes du Congrès Biochrom '97, *Mémoires et travaux de l'Institut de Montpellier, École Pratique des Hautes Études* 21: 707-709.
- FEJFÁR O., RUMMEL M. & TOMIDA Y. 1998. — New eomyid genus and species from the early Miocene (MN zones 3-4) of Europe and Japan related to *Apeomys* (Eomyidae, Rodentia, Mammalia), in TOMIDA I., FLYNN L. J. & JACOBS L. L. (eds), Advances in Vertebrate Paleontology and Geochronology. *National Science Museum Monographs* 14: 123-143.
- FOLIE A., SIGÉ B. & SMITH T. 2005. — A new scincormorph lizard from the Palaeocene of Belgium and the origin of Scincoidea in Europe. *Naturwissenschaften* 92: 542-546
- GAO K. & FOX R. C. 1996. — Taxonomy and evolution of late cretaceous lizards (Reptilia: Squamata) from western Canada. *Bulletin of Carnegie Museum of Natural History* 3: 1-107.
- GAUTHIER J. A. 1982. — Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming, and a revision of the Anguioidea. *Contributions to Geology, University of Wyoming* 21: 7-54.
- IVANOV M. 2002. — The oldest known Miocene fauna from Central Europe: Merkur-North locality, Czech Republic. *Acta Paleontologica Polonica* 47: 513-534.
- KLEMBARA J. 2008. — A new anguimorph lizard from the Lower Miocene of North-West Bohemia, Czech Republic. *Paleontology* 51: 81-94.
- KOSMA R. 2004. — *The Dentition of Recent and Fossil Scincomorph Lizards (Lacertilia, Squamata) – Systematics, Functional Morphology, Paleology*. Unpublished Ph. D. thesis, University of Hannover.
- KRAUSE D. W., EVANS S. E. & GAO K. Q. 2003. — First definitive record of Mesozoic lizards from Madagascar. *Journal of Vertebrate Paleontology* 23: 842-856.
- KVAČEK Z., BÖHME M., DVOŘÁK Z., KONZALOVÁ M., MACH K., PROKOP J. & RAJCHL M. 2004. — Early Miocene freshwater and swamp ecosystems of the Most Basin (northern Bohemia) with particular reference to the Bílina Mine section. *Journal of Czech Geological Society* 49: 1-40.
- LANG M. 1991. — Generic relationships within Cordyliformes (Reptilia: Squamata). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Biologie* 61: 121-188.
- LEE M. S. Y. 1998. — Convergent evolution and character correlation in burrowing reptiles: Towards a resolution of squamate relationships. *Biological Journal of the Linnean Society* 65: 369-453.
- LEE M. S. Y. 2002. — Soft anatomy, diffuse homoplasy, and the relationships of lizards and snakes. *Zoologica Scripta* 29: 101-130.
- LEE M. S. Y. & SCANLON J. D. 2001. — On the lower jaw and intramandibular septum in snakes and anguimorph lizards. *Copeia* 2001: 531-535.
- LOVERIDGE A. 1944. — Revision of the African lizards of the family Cordylidae. *Bulletin of the Museum of Comparative Zoology at Harvard College* 95: 1-118.
- MESZOELY C. A. M. 1970. — North American fossil anguid lizards. *Bulletin of the Museum of Comparative Zoology* 139: 87-150.

- ODIERNA G., CANAPA A., ANDREONE F., APREA G., BARUCCA M., CAPRIGLIONE T. & OLMO E. 2002. — A Phylogenetic Analysis of Cordyliformes (Reptilia: Squamata): Comparison of Molecular and Karyological Data. *Molecular Phylogenetics and Evolution* 23: 37-42.
- PREGILL G. 1981. — Late Pleistocene herpetofaunas from Puerto Rico. *University of Kansas Museum of Natural History, Miscellaneous Publications* 71: 1-72.
- RAGE J. C. & AUGÉ M. 1993. — Squamates from the Cenozoic of the western part of Europe. A review. *Revue de Paléobiologie* 7: 199-216.
- RICHTER A. 1994. — Lacertilia aus der Unteren Kreide von Una und Galve (Spanien) und Anoual (Marokko). *Berliner geowissenschaftliche Abhandlungen E* 14: 1-147.
- ROČEK Z. 1984. — Lizards (Reptilia: Sauria) from the Lower Miocene locality Dolnice (Bohemia, Czechoslovakia). *The Papers of the Czechoslovak Academy of Sciences* 94: 1-69.
- STANLEY E. L., BAUER A. M., JACKMAN T. R., BRANCH W. R., LE FRAS P. & MOUTON N. 2010. — Between a rock and a hard polytomy: Rapid radiation in the rupicolous girdled lizards (Squamata: Cordylidae). *Molecular Phylogenetics and Evolution* 58: 53-70.
- SULLIVAN R. M. 1979. — Revision of the Paleogene genus *Glyptosaurus* (Reptilia, Anguillidae). *Bulletin of the American Museum of Natural History* 163: 1-72.
- TOWNSEND T. M., LARSON A., LOUIS E. & MACEY J. R. 2004. — Molecular phylogenetics of squamata: The position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Systematic Biology* 53: 735-757.
- VICARIO S., CACCONE A. & GAUTHIER J. 2003. — Xantusiid “night” lizards: A puzzling phylogenetic problem revisited using likelihood-based Bayesian methods on mtDNA sequences. *Journal of Molecular Phylogenetics and Evolution* 26: 243-261.
- WHITING A.S., BAUER A.M. & SITES J.W. Jr. 2003. — Phylogenetic relationships and limb loss in sub-Saharan African scincine lizards (Squamata: Scincidae). *Journal of Molecular Phylogenetics and Evolution* 29: 582-598.

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