# The Early Miocene squamates of Amöneburg (Germany): The first stages of modern squamates in Europe

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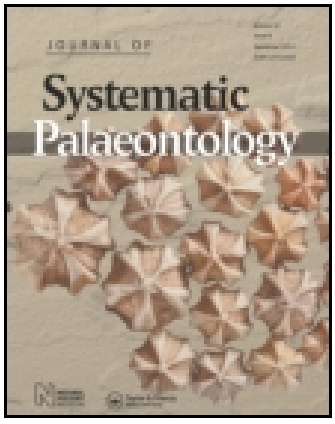



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# The Early Miocene squamates of Amöneburg (Germany): the first stages of modern squamates in Europe

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Squamate faunas from the MN 1–3 interval (earliest Miocene) are poorly known in Europe and worldwide. Our research brings the first report on a complete squamate fauna from the MN 2 zone in Europe. It comprises a relatively large number of specimens from Wiesbaden-Amöneburg in western Germany. MN 2 is part of a time interval (MP 29–MN 2) covering the latest Oligocene–earliest Miocene, which has been labelled the 'Dark Period' as far as snakes are concerned. Unexpectedly, a high diversity of squamates was discovered at Amöneburg. This fauna fills an important gap in our knowledge of herpetofaunas from this time interval in Europe, and it represents the first true beginnings of the modern fauna. The new finds are important for the two reasons. Firstly, the beginning of the Miocene heralds the temporary return to a paratropical humid climate after the relatively cool and dry Oligocene, and the Amöneburg material provides us with the opportunity to observe changes in herpetofaunas during this crucial interval. The fauna comprises some survivors from the Oligocene, and especially new forms which may have either originated locally, in Europe, or dispersed from the East. Secondly, the Early Miocene was marked by the collision of Eurasia with Africa, an event that potentially allowed immigration of African squamates into Europe. Since taxa with African affinities such as Chamaeleonidae and Cordylidae are missing from Wiesbaden-Amöneburg, this suggests that African taxa did not reach Europe in MN 2, but were able to enter it during MN 3. One new species, *Blanus thomaskelleri* sp. nov., is described.

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**Keywords**: palaeobiodiversity; palaeoclimate; African migration; Neogene; Europe



## Introduction

Squamates, such as lizards, snakes and amphisbaenians, are a highly successful group of terrestrial reptiles with an extended range of habitats and lifestyles, forming the largest Recent group of non-avian reptiles (e.g. Evans 2003). The transition between the Oligocene and Miocene is a turning point in the history of squamates in Europe. Following the comparatively cool and dry Oligocene, the return to a warm and humid climate by the earliest Miocene deeply influenced squamate fauna (Szyndlar & Rage 2003; Rage & Szyndlar 2005). Accepted history indicates that the main event occurred during the Early Burdigalian (Early Orleanian in terms of continental stratigraphy), and more precisely in zones MN 3 and MN 4, when a large wave of immigrants entered Europe (Ivanov 2001, 2002a; Szyndlar & Rage 2003; Čerňanský 2012). This coincided with the beginning of the Miocene Climatic Optimum (Böhme 2003). However, it is obvious that some changes occurred during MN 1 and MN 2, which together are roughly correlative with the Aquitanian or Agenian of continental stratigraphy (Steininger 1999). Their precise timing is uncertain because faunas from this time interval are almost unknown. In addition, the influence of the African–Eurasian terrestrial contact, which occurred during the Early Miocene, remains poorly understood.

Similarly to those of the latest Oligocene (MP 29 and MP 30), faunas from MN 1 and MN 2 were regarded as poor in diversity and somewhat peculiar; this interval has been labelled the 'Dark Period' for snakes by Szyndlar & Rage (2003) and Rage & Szyndlar (2005). In Europe, localities bearing squamates from MN 1 and MN 2 are known perhaps only from Germany and France. Aside from the German and French localities, only the Sardinian site of Oschiri has produced a squamate assemblage, although the age of this fauna is somewhat uncertain (MN 1 to MN 3 according to Venczel & Sanchiz 2006). Isolated taxa have been

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confirmed in other localities of MN 1 and MN 2 age but no complete fauna has been reported.

MN 3 contains a single rich and diverse fauna in Merkur-North in the Czech Republic (Ivanov, 2003; Klembara 2008, 2012; Čerňanský & Bauer 2010; Čerňanský & Venczel 2011; Čerňanský 2012). Several M4 faunal localities have been recognized, including Béon 1, France (Rage & Bailon 2005), Dolnice, Czech Republic (Roček 1984; Szyndlar 1987; Čerňanský 2010a, b), Petersbuch 2, Germany (Szyndlar & Schleich 1993; Čerňanský 2011) and also Vieux-Collonges, France (Ivanov 2000) which appears transitional between MN 4 and MN 5.

The present study is therefore the first report of a squamate fauna from the MN 1–MN 2 interval. More precisely, it deals with an assemblage of MN 2a age from Wiesbaden-Amöneburg in western Germany. The aims of this paper are to provide a detailed description of the new squamate material, to compare this fauna with other squamate assemblages of the Early Miocene, and to illustrate the main faunal changes that led to the colonization of Europe by the modern fauna.

## Geological setting

The Wiesbaden Formation extends widely in the Mainz Basin. Biostratigraphical studies during the past four decades have concentrated on the northern edge of the basin, in the localities of Mainz-Budenheim (Stapf & Hartmann 1981) and Wiesbaden-Amöneburg (Fig. 1). Previously known as the *Hydrobia* Beds, the lower boundary of the Wiesbaden Formation is defined by the first abundant occurrence of the foraminiferan *Lippsina demens*. The upper boundary is drawn at the base of a marine-brackish sequence yielding foraminifera, nannoplankton and otoliths of the fish genus *Gobius*. The Formation can be divided into three parts. The lower (brackish) and middle (lacustrine) parts are middle Aquitanian, containing the MN 2 mammal zone (Tobien 1988; Gürs & Mödden 1991; Reichenbacher 2000; Reichenbacher & Keller 2002). Reichenbacher (2000) assumed that the MN 2b and MN 3a mammal sub-zones of the Late Aquitanian–Early Burdigalian interval corresponded to the upper part of the Wiesbaden Formation, named the 'emerging facies'.


**Figure 1.** Location of the Wiesbaden-Amöneburg locality in Germany.

The squamate microvertebrate material described here was collected by Thomas Keller and colleagues from the lower brackish part of the Wiesbaden Formation where numerous freshwater and terrestrial gastropods, including *Gyraulus*, *Stagnicola* and *Planorbarius*, also occur. The skeletal remains are often fragmented *in situ*, suggesting that formation of the microvertebrate horizon most likely resulted from sporadic but massive freshwater inflows into the lagoonal area (T. Keller, pers. comm.). The studied material originated from Wiesbaden-Amöneburg (hereafter referred to as 'Amöneburg') and is dated as MN 2a. Schleich (1988a) previously reported from this site isolated osteoderms attributed to *Ophisaurus* sp. but without comment or illustration.

### Institutional abbreviations

**SGDB**: Geological collection of the Bilina opencast mine, Czech Republic; **SMF**: Senckenberg Research Institute, Germany; **PAL EV**: State Conservation Office Hessen, Germany.

## Material and methods

The fossils were recovered by screen washing and are housed in the SMF, prefixed by collection numbers of the PAL EV. The specimens were photographed using a scanning electron microscope (SEM) at the Slovak Academy of Sciences and a Leica (Wetzlar, Germany) stereomicroscope with digital camera using Automontage software at the SMF. The standard anatomical orientation system is used throughout this paper. The terminology used to describe the individual bone structures is based on Fejérváry-Láng (1923), Meszoely (1970), Klembara (1979, 1981, 2012), Klembara *et al.* (2010) and Rage & Augé (2010).

Specimens were compared with extant and extinct taxa housed in the SMF, American Museum of Natural History (New York, NY, USA), Bayerische Staatssammlung für Paläontologie (Munich, Germany), Carnegie Museum of Natural History (Pittsburg, PA, USA), Comenius University (Bratislava, Slovakia), Muséum National d'Histoire Naturelle (Paris, France), Natural History Museum (London, UK), and the University of Florida (Gainesville, FL, USA).

## Systematic palaeontology

**Squamata** Oppel, 1811
**Gekkota** Cuvier, 1817
**Gekkota indet.**
(Fig. 2)

**Material.** One left maxilla, PAL EV 2013/147.

**Description.** The maxilla is poorly preserved. It is rather elongated, and in medial view the supradental shelf is very well developed. It expands medially, particularly in its anterior portion, thus forming a table. The nasal process (*pars nasalis*) is broken, with only its base preserved. The alveolar crest (*crista dentalis*) is vertical and high. It bears at least 23 preserved tooth positions, with four teeth remaining visible. The posterior preserved portion is slender and straight and it tapers slightly distally. It bears an elongated jugal facet. The smooth lateral surface is pierced along its lower region by a series of five small supralabial foramina, with the line bearing the foramina forming a shallow groove posteriorly. A shorter series of two larger foramina is located dorsally, under the base of the nasal process.

The dentition is pleurodont. Unfortunately, only four teeth are preserved. However, the preserved tooth positions indicate the high number of closely packed teeth with narrow inter-dental gaps. These teeth are tall, cylindrical, straight and pointed. They lack striae and only small circular resorption pits are present lingually at the tooth bases.

**Remarks.** The high number of pleurodont cylindrical teeth is a typical feature of gekkotan lizards. One species of the extant 'Mediterranean' genus *Euleptes* (Sphaerodactylidae), *E. gallica* Müller, 2001, was described from the French locality of Montaigu (zone MN 2a; Müller 2001). The species is also known from Merkur-North (MN 3; Čerňanský & Bauer 2010). In addition, Müller & Mödden (2001) reported *Euleptes* sp. from Oppenheim/Nierstein (MN 2a, Germany). The specimen described here exhibits some similarities with *Euleptes*. Unfortunately, the missing nasal process makes precise attribution impossible, even at the genus level. Although another taxon, *Gerandogekko arambourgi*, was described by Hoffstetter (1946) from the earliest Miocene of Saint-Gérand, France (MN 1 and/or MN 2), the limited material here makes comparison with this taxon impossible.

**Lacertiformes** Estes *et al.*, 1988
**Lacertidae** Oppel, 1811
***Lacerta* s.l.** Linnaeus, 1758
***Lacerta poncenatensis*** Müller, 1996
(Fig. 3)

**Material.** Two fragments of right dentaries, PAL EV 2013/148–149; two fragments of left dentaries, PAL EV 2013/150–51; one right maxilla fragment, PAL EV 2013/152; one left maxilla fragment, PAL EV 2013/153; and one premaxilla, PAL EV 2013/154.

**Description.** The dentaries (Fig. 3A, B) are all incomplete. On the medial side, the deep Meckel's groove is fully open but narrow, especially in the anterior region (Fig. 3B). It is roofed by a well-developed subdental shelf which is slightly concave dorsally. It gradually becomes

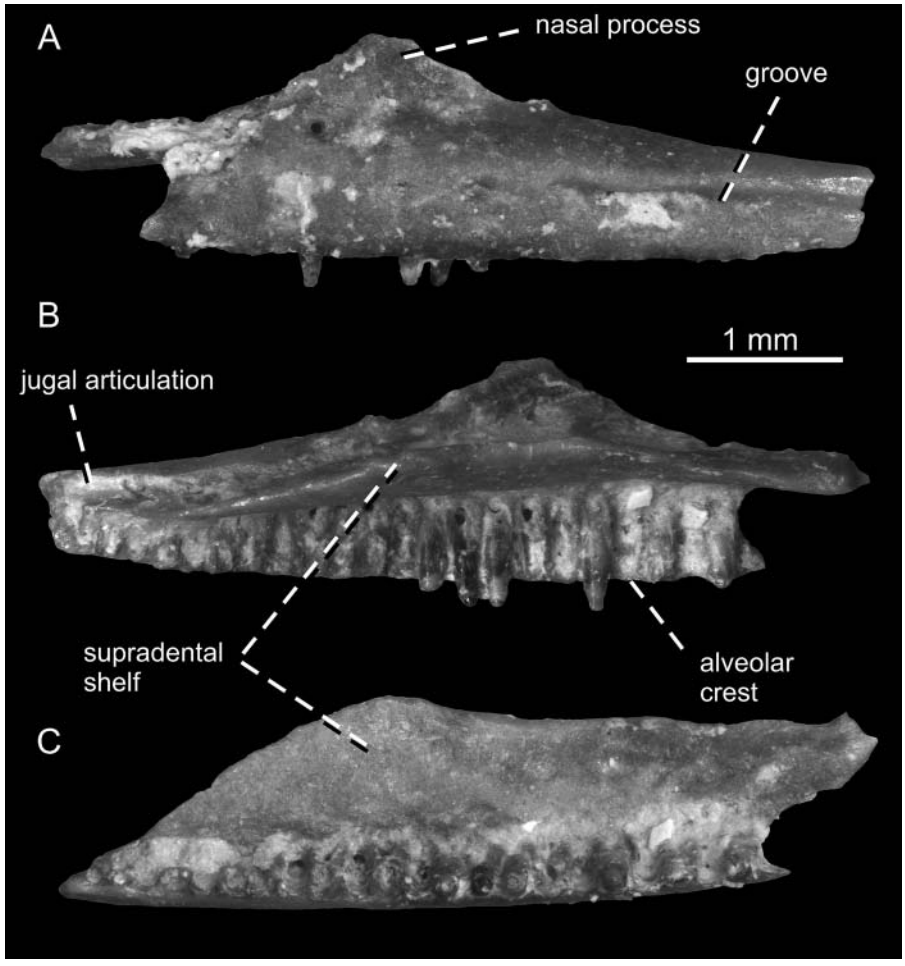


**Figure 2.** Gekkota indet., maxilla, PAL EV 2013/147 in **A,** lateral, **B,** medial and **C,** ventral views.



thinner posteriorly as a result of the presence of the facets for the splenial and coronoid on its ventromedial surface. The *sulcus dentalis* is only slightly developed, mainly in the anterior region of the dorsal surface of the shelf. Posteriorly, the rounded opening of the alveolar canal is visible behind the level of the anterior limit of the coronoid facet. Here, the intramandibular septum forms the ventromedial wall of this canal. In the best-preserved specimen (PAL EV 2013/148), the alveolar crest supports a row of 17 tooth positions, with six teeth preserved. However, since its anterior region and posterior ending are missing, the total number of teeth is unknown, but certainly would have been much higher. The ventral margin of the dentary is straight. The lateral surface bears a line of labial foramina along the middle region of the dentary (Fig. 3A), with the distance between them increasing anteriorly. At the level of the last posterior one, the coronoid process rises dorsally and teeth are also present in this region. On the dorsolateral surface of the posterior end, the articulation for the coronoid is preserved, showing that the coronoid overlapped the dentary dorsally.

All maxillae are fragmentary. In medial aspect (Fig. 3D), a large infraorbital foramen is present. It is elongated posteriorly, and a jugal articulation also occurs. The supradental shelf is well expanded medially, and ventrally it bears a *sulcus dentalis*. The lateral surface is pierced by a longitudinal line of several labial foramina (Fig. 3C). The nasal process is broken off in all specimens. A weak sculpture formed by numerous pits and grooves is present on the dorsal margin of PAL EV 2013/152.

The almost completely preserved premaxilla is T-shaped (Fig. 3E–G). The alveolar crest is curved. The bone bears seven tooth positions, with three preserved, unicuspid, moderately pointed teeth. In medial view, the nasal process is narrow, rather elongated dorsally and pointed. It is inclined posteriorly. In its dorsal half, a strong median ridge forms a limit between two nasal articulation areas which are very narrow mediolaterally. The ethmoidal foramen is located close to the base of the nasal process. The supradental shelf is formed by two segments well expanded posteriorly that form the vomerine

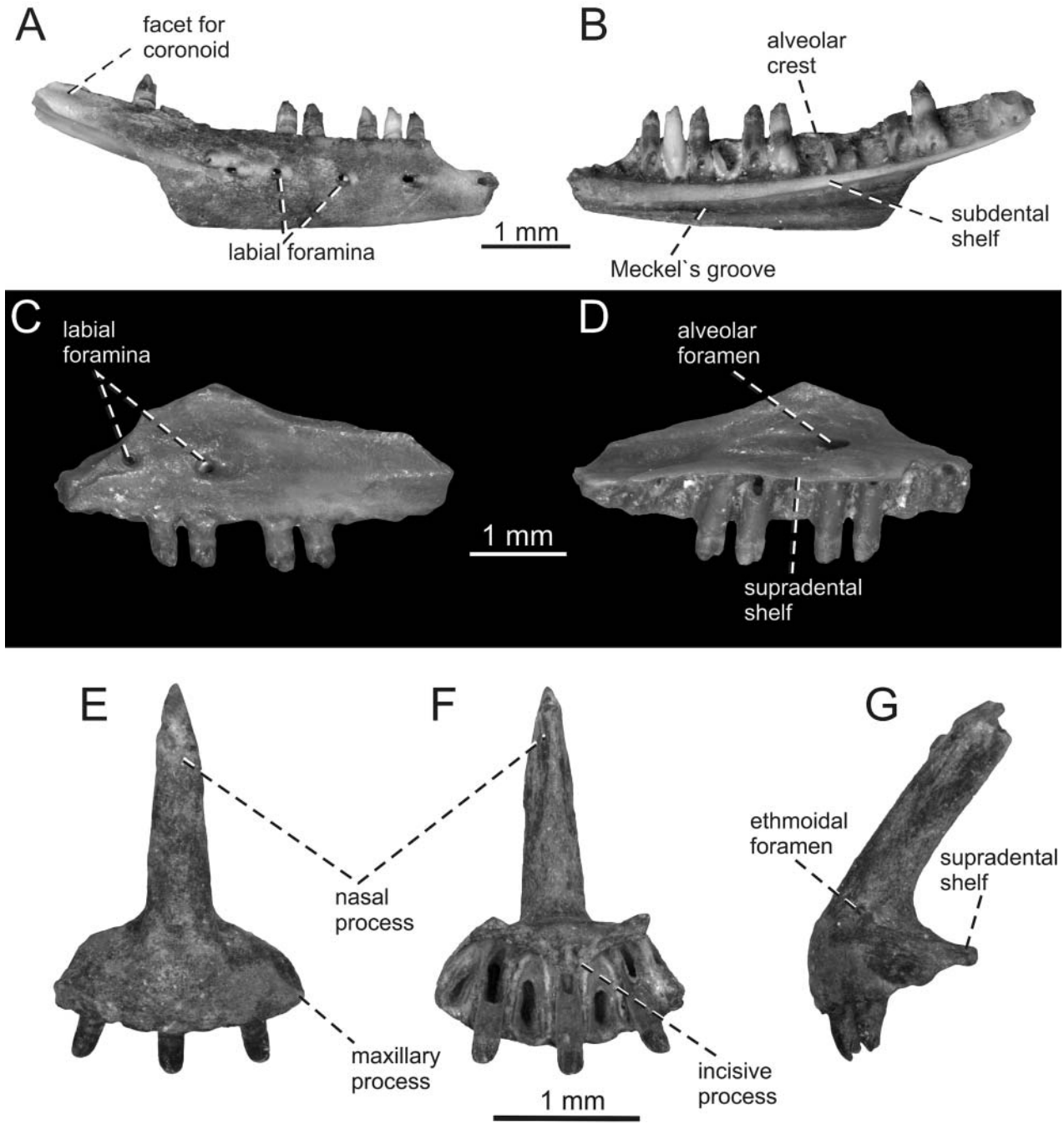


**Figure 3.** *Lacerta poncenatensis*. **A, B,** dentary, PAL EV 2013/148 in **A,** lateral and **B,** medial views. **C, D,** maxilla, PAL EV 2013/153 in **C,** lateral and **D,** medial views. **E–G,** premaxilla, PAL EV 2013/154, in **E,** anterior, **F,** posterior and **G,** lateral views.

processes. These segments have a contact in the centre of the shelf. The short, weakly bilobed median incisive process is located ventral to the supradental shelf. The *sulcus dentalis* is present. The external surfaces of the lateral ends of the horizontal maxillary process bear areas for articulation with the maxillae. The external surface of the premaxilla is smooth, except for the distal region of the nasal process, where weak sculpturing formed by small pits is still present.

The dentition is pleurodont. The teeth are tall, ranging from monocuspid in the anterior region of the dentary and on the premaxilla, to bicuspid with weak radial striations located on the labial side of the tooth crowns. Small circular resorption pits are present on the lingual aspects of the tooth

bases. The narrow inter-dental gaps at the preserved tooth bases indicate that the teeth were most likely closely spaced.

**Remarks.** *Lacerta poncenatensis* Müller, 1996 was previously described from the French locality of Poncenat (MN 2a). From the same locality, *L. filholi* was also reported (see Augé & Smith 2009). These two taxa are very similar. According to Müller (1996), the differences are as follows: (1) the number of teeth, with 21 in *L. filholi* and 23–25 in *L. poncenatesis*; (2) tricuspidity, where the posterior teeth are tricuspide in *L. filholi* but not in *L. poncenatensis*; and (3) size, with *L. poncenantensis* being smaller than *L. filholi* (at least based on the information available in 1996; J. Müller, pers. comm. 2013).

However, an incipient posterior cusp, rendering the teeth tricuspid, can also be present in *L. poncenatensis*, and although this cusp is more strongly developed in *L. filholi* (see Müller 1996), this lessens the distinction between the two species. In the Amöneburg material, there is no complete dentary to demonstrate the total number of teeth. All of the teeth are very close to each other, with only very small interdental gaps, which could indicate a high number of teeth. However, the number of teeth is often variable amongst lizards. Strong tricuspidity is not developed in any of our specimens, and the Amöneburg specimens are practically identical to those described by Müller (1996). There is a possibility that further research will demonstrate synonymy of these taxa, but based on present knowledge we refer to the lizard from Amöneburg as *L. poncenatensis*.

### Lacertidae indet.
(Fig. 4)

**Material.** One fragment of a right frontal, PAL EV 2013/155; two left jugals, PAL EV 2013/156–157; two right jugals, PAL EV 2013/158–159; one right pterygoid, PAL EV 2013/160; one basisphenoid, PAL EV 2013/161; two dorsal vertebrae, PAL EV 2013/162–163.

**Description.** The available specimen is a fragment of the posterior region of a right small frontal (Fig. 4A, B). Despite the fragmentary condition, it is possible to observe a feature typical for lacertids: the frontal expands laterally posterior to the *sulcus interfacialis*. The entire dorsal surface is well sculptured, containing pits and small curved grooves and ridges.

In ventral view, the most dominant structure in this region is a shallow but well-developed ridge (the *crista cranii frontalis*). The frontal lateral wall is inclined dorsolaterally and bears several foramina. The median contact with the other frontal has very slightly developed interdigitations. The posterior margin of the frontal bears a strong, triangular facet that overlapped the parietal tab. The entire posterior suture for parietal contact is strongly digitated and inclined posteroventrally.

The jugals are L-shaped in medial and lateral views (Fig. 4G, H). The dorsal third of the postorbital process is narrow and orientated posterodorsally. It bears a long lens-shaped articulation area for the postorbital. A medial ridge runs close to the anterior margin of the postorbital process; consequently, while the surface is narrow anterior to this ridge, the broad posterior area extends as a short posteroventral process. The medial ridge runs quite ventrally on the suborbital process, and the area dorsal to the ridge is relatively broad. Unfortunately, the anterior portion of the suborbital process is absent, but maxillary articulation is evident on the ventral aspect of the preserved portion. The lateral surface is pierced by several foramina.

The anterior ending of the pterygoid is divided into two small processes, but only the medial one is completely preserved (Fig. 4E, F). The palatine process is relatively short and broad, and pterygoid teeth are absent (Fig. 4F). The distinct ridge (*crista columellaris*) is present along the lateral margin of the pterygoid, and this rotates posteriorly to the medial margin of the quadrate process. The transverse process is short and robust, with its lateral portion curved much more anteriorly than the base of the process. Its anterior termination is pointed. The suborbital incisure is deep, but mediolaterally broad. Unfortunately, the basisphenoid process is not preserved. The *crista transversa dorsalis* forms a distinct and sharp crest on the dorsal surface of the pterygoid, and marks the lateral border of a distinctive fossa. The *fovea pterygoidea* is well rounded, but small and relatively shallow, while the quadrate process beyond the fovea is broken off.

PAL EV 2013/161 is a basisphenoid. Its dorsal surface is broadly concave (Fig. 4C). The basipterygoid processes are broad and laterally expanded, but they project rather weakly. The short and broad parasphenoid process is developed in the anterior sagittal region. It is formed by the two arms of the *cristae trabecularis* which are clearly visible in dorsal view. Therefore, the ending of the parasphenoid process is forked. Between these two arms, the narrow *facies trapezoideus* forms a shallow depression. A pair of anterior openings for the carotid canal lies at the internal sides of the bases of the *cristae trabecularis* in a relatively deep *retractor fossa*. The area more laterally located is pierced by two canals. The anterior opening of the Vidian canal is located between the base of the *crista trabecularis* and the lateral crest. Dorsally and above it, a pair of slightly smaller openings for the *abducens* canal is present. Posteriorly, beyond this area, a high basisphenoid crest (*crista sellaris*) is developed. This continues laterally up to the dorsally elevated alar processes (*processus alaris*). Posteriorly, beyond the basisphenoid crest, a broad depression is present. The common posterior opening for the Vidian and carotid canals is located close to the bases of the alar processes. However, only the left margin of the *isthmus basiocciput–sphenoidalis* is preserved at the

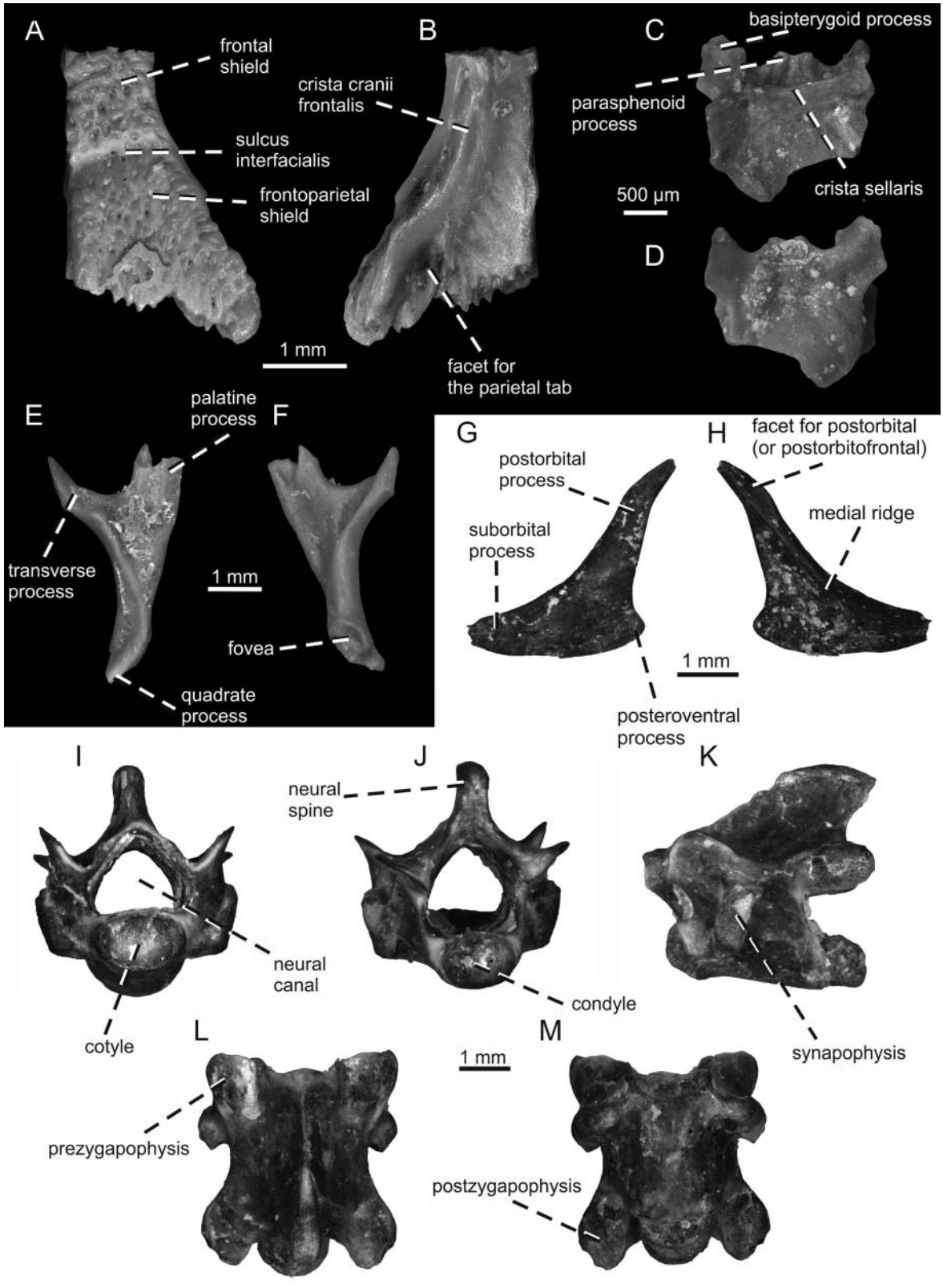


**Figure 4.** Lacertidae indet. **A, B,** frontal, PAL EV 2013/155 in **A,** dorsal and **B,** ventral views. **C, D,** basisphenoid, PAL EV 2013/161 in **C,** dorsal and **D,** ventral views. **E, F,** pterygoid, PAL EV 2013/160 in **E,** dorsal and **F,** ventral views. **G, H,** jugal, PAL EV 2013/156 in **G,** lateral and **H,** medial views. **I–M,** dorsal vertebra, PAL EV 2013/162 in **I,** anterior, **J,** posterior, **K,** lateral, **L,** dorsal and **M,** ventral views.

posterior end, with the right posterior portion absent. The ventral surface of the basispenoid is smooth (Fig. 4D).

The vertebrae are completely preserved (Fig. 4I–M). The neural spine is tall and distinctly inclined posteriorly. It originates on the anterior border of the neural arch and rises progressively posteriorly. Its top is slightly rounded. The neural canal is large and triangular in shape. Well-developed prezygapophyses are distinctly inclined dorsally; these have well-defined, roughly triangular articulation surfaces with rounded posterolateral margins. The postzygapophyses are oval and slightly elongated anteroposteriorly. The vertebrae are constricted between the pre- and postzygapophyses and consequently they are relatively broad in dorsal view. The centrum is quite long. The small condyle is elliptical and slightly depressed dorsolaterally, as is the cotyle. The condyle is well demarcated from the centrum by a constriction. The synapophyses are located anteriorly, and in lateral view they are kidney-shaped and slightly inclined anteroventrally. On the ventral side of the centrum, a pair of subcentral foramina is located, opening in the posterior region.

**Remarks.** Teeth are absent in the Amöneburg pterygoid. Pterygoid teeth can be either present or absent in lacertids and this character can even vary within a species. For example, while pterygoid teeth are absent in most *Podarcis muralis* specimens, SMF 49584 has one tooth on the right pterygoid, and SMF 50060 has three teeth, also on the right pterygoid. It is possible that at least some of the material described here as Lacertidae indet. is in fact *L. poncenatensis*, since the occurrence of this species at Amöneburg is recorded above. Unfortunately, the preservation, disarticulation and type of material does not allow precise determination, especially since only dentaries, maxillae and premaxillae are distinctly recognizable in *L. poncenatensis*. In addition, although other lacertids, such as *Pseudeumeces cadurcensis*, may have been present during the MP 30–MN 1 time interval in Gannat, France (see Augé & Hervet 2009), there is no evidence of this taxon in Amöneburg.

**Amphisbaenia** Gray, 1844
**Blanidae** Kearney, 2003
***Blanus*** Wagler, 1830
***Blanus thomaskelleri*** sp. nov.
(Fig. 5)

2011 *Blanus* sp. Čerňanský & Venczel: 75, fig. 2.

**Diagnosis.** Small species of *Blanus* distinguished from other species of this genus by its extremely short coronoid process which does not rise strongly dorsally.

**Derivation of name.** Named for Dr Thomas Keller, who discovered the material described in this article, and for his valuable contributions to vertebrate palaeontology.

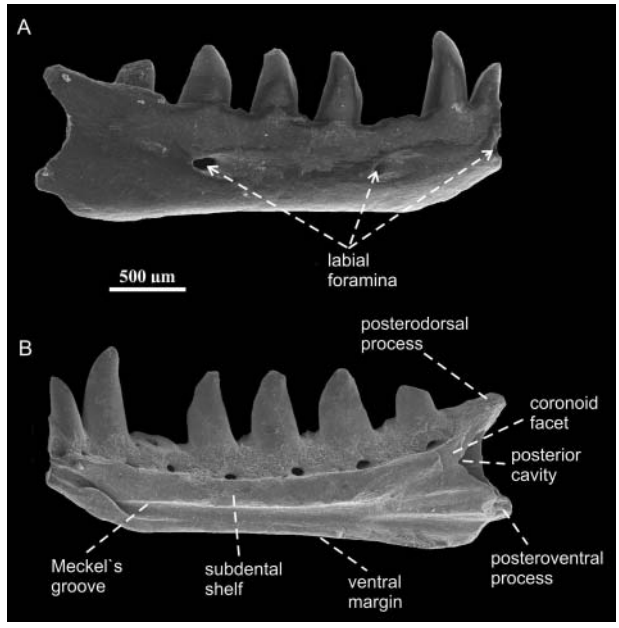


**Figure 5.** *Blanus thomaskelleri* sp. nov., holotype dentary, PAL EV 2013/271 in **A,** lateral and **B,** medial views.

**Holotype.** PAL EV 2013/271, incomplete right dentary lacking the anterior portion.

**Referred material.** SGDB, Ah-771, left dentary from Merkur-North (MN 3a) in the Czech Republic.

**Type locality and horizon.** Amöneburg, near Frankfurt, Germany; Wiesbaden Formation, Early Miocene (MN2a), Agenian ( = Aquitanian).

**Range.** Germany and the Czech Republic, Early Miocene MN 2–MN 3.

**Description.** The dentary is very small (Fig. 5), with its anterior end broken off. The alveolar crest supports a row of seven tooth positions. Six typically monocuspid, shallowly pleurodont teeth are preserved. In medial view, Meckel's groove is fully open and narrow, forming a narrow groove that runs parallel to the ventral border of the bone, from the splenial tip to the narrow symphyseal articulation. Although the anterior region of the symphysis is missing, it is expanded ventrally, and there is a small symphyseal shelf formed by the ventral junction of the mandibles. Here, an angle at the symphysis of the dentary is present, as in most amphisbaenians (e.g. Gans 1974). Meckel's groove is roofed by a shallow, slightly curved subdental shelf (*sensu* Rage & Augé 2010), while its floor has an almost straight ventral margin which is slightly thickened anteriorly and quite curved dorsally. The *sulcus dentalis* is well developed, becoming shallower at the level of the posteriormost tooth. The posterior region of the ventromedial margin of the subdental shelf bears a triangular facet for the coronoid. This is therefore located

along the ventromedial region of the posterodorsal process and continues anteriorly to the level of the penultimate tooth. A facet for the splenial is located anteroventrally to the coronoid facet. The splenial in the Recent *Blanus cinereus* is a tiny splint of bone, covering Meckel's groove medially (e.g. Blain *et al.* 2007; Gans & Montero 2008). The posterior region of the dentary, behind the last tooth, is relatively short anteroposteriorly. There, the posterior cavity is well developed (*sensu* Gans & Montero 2008). The coronoid process (*sensu* Montero & Gans 1999) is rather short anteroposteriorly and its top is at a distinctly lower level than the preserved tooth apices. Only the posterior tip of the process is missing. In lateral view the otherwise smooth labial surface is pierced by three labial foramina. One is located at the level of the 7th tooth and another at the level of the interdental gap between the 4th and 5th teeth. The anterior foramen is only partly preserved, with its posterior portion at the level of the 2nd tooth.

The preserved teeth are shallowly pleurodont, and display the morphology typical of the genus *Blanus*. They are conical, robustly built and slightly recurved, with their apices orientated dorsally and the third one typically enlarged. In *Blanus*, the dentary bears seven, or usually even eight teeth, where the third one is enlarged (e.g. Gans & Montero 2008). In view of this observation and the damaged condition of the anterior region, the total number of teeth in this dentary is eight. Circular resorption pits are located at the bases of the teeth, and the interdental gaps are approximately half as large as the tooth bases.

**Remarks.** The coronoid process in both recent and extinct *Blanus* species is distinctly longer than that in *B. thomaskelleri* sp. nov., and it expands posterodorsally. In these species, the dorsoposterior limit of the coronoid process always lies at a higher level than the apices of the largest dentary teeth. The posterior portion behind the last tooth of the extant *B. cinereus*, for example, is much longer and more robustly built than in *B. thomaskelleri* sp. nov. The morphology of the posterior region of the dentary in this new species exhibits a peculiar condition, with the coronoid process being markedly low and short, not reaching a high level dorsally.

An amphisbaenian, *Palaeoblanus tobieni*, has already been reported from MN 1–MN 2 (Schleich 1988b). This genus does not clearly differ from *Blanus* (Augé 2005). It is present in MN 2 of Weisenau (Quarry Fp. 19) and Budenheim, Germany (Böhme & Ilg 2003). However, the generalized report in Schleich (1988b) from Weisenau means that it may have been present in MN 1, and may also occur in the Late Oligocene of Germany (MP 27 of Ehreinstein, and MP 27/28 of Gaimersheim; Schleich 1988b). Despite the weak distinction between *Blanus* and *Palaeoblanus*, *B. thomaskelleri* sp. nov. differs from the extinct genus in: (1) having the third tooth larger than the others, which is typical for *Blanus*, while the largest tooth in *Palaeoblanus* is the first one; and (2) lacking the dorsoventral slopes of the tooth crowns which occur in *Palaeoblanus*.

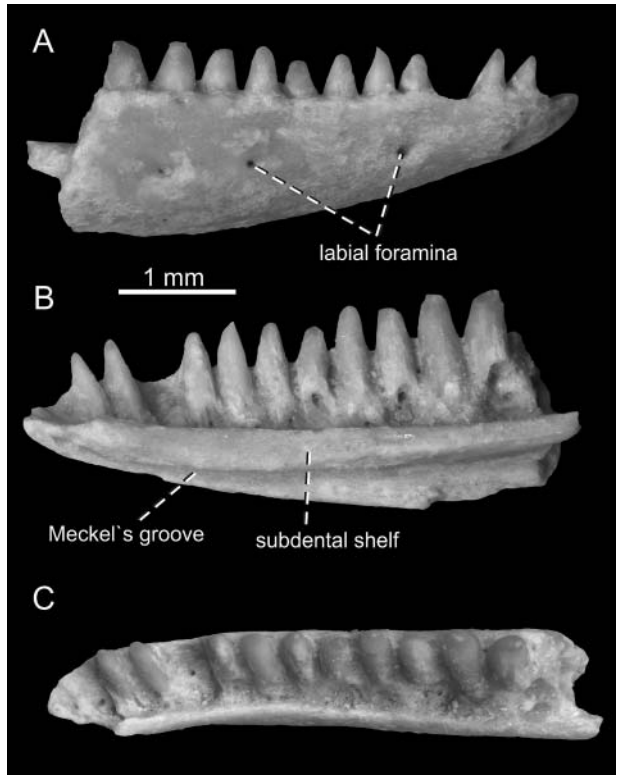


**Figure 6.** 'Scincomorphan' indet., dentary, PAL EV 2013/164 in **A,** lateral, **B,** medial and **C,** dorsal views.

**'Scincomorphan' indet.**
(Fig. 6)

**Material.** One right dentary, PAL EV 2013/164.

**Description.** Only a fragment of the anterior portion of a right dentary is preserved (Fig. 6). It has slight medial curvature at its anterior end but, unfortunately, the symphysial facet is missing. In medial aspect, Meckel's canal is fully open, but is narrow and orientated ventrally. It is roofed by the subdental shelf. The latter becomes gradually thinner posteriorly 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 subdental shelf and continues anteriorly up to the level of the 7th tooth. The alveolar crest is high. The *sulcus dentalis* is developed on the dorsal aspect of the subdental shelf, and the smooth lateral surface is pierced by a line of four labial foramina along its mid-region.

The dentition is pleurodont and 13 tooth positions are preserved (10 teeth are still visible). The teeth are very closely spaced. Resorption pits are present on the lingual

sides of some tooth bases. The teeth are relatively small in the anterior portion of the dentary, and here they are conical and pointed, becoming more blunt posteriorly. They are monocuspid and the last preserved tooth bears an incipient anterior cusp.

**Remarks.** Unfortunately, the poor preservation does not allow more precise determination of this specimen. In previous taxonomies, the specimen would have been attributed to the clade Scincomorpha. However, paraphyly of this group was suggested by some recent genetic-based phylogenetic analyses (e.g. Townsend *et al*. 2004; Vidal & Hedges 2009). Therefore we use the term 'scincomorphan' for the group to which we refer the specimen.

**Anguimorpha** Fürbringer, 1900
**Anguidae** Gray, 1825
**Anguinae** Gray, 1825
***Pseudopus*** Merrem, 1820
***Pseudopus* cf. *ahnikoviensis*** Klembara, 2012
(Fig. 7A–C)

**Material.** Right dentary, PAL EV 2013/165.

**Description.** The posterior portion of a right dentary is preserved (Fig. 7A–C). The alveolar surface supports a row of three preserved teeth. Meckel's groove is fully open medially and its roof is formed by the subdental shelf which bears splenial articulation. The posterior end of the dentary is incompletely preserved. The coronoid process is slender and its posterior tip is broken. Only the basal portion of the surangular process is preserved. The intramandibular septum is well developed and its posteroventral margin is fused indistinguishably with the root portion of the surangular spine which extends posteriorly. However, its end is broken. The angular process is perfectly preserved; it is short, pointed and orientated posteroventrally.

The lateral surface of the dentary is pierced by two mental foramina. The posterior mental foramen is located at the level of the second tooth from the posterior. A distinct wedge-shaped coronoid articulation is present on the lateral surface of the posterodorsal portion of the dentary, while the remainder of this surface is smooth.

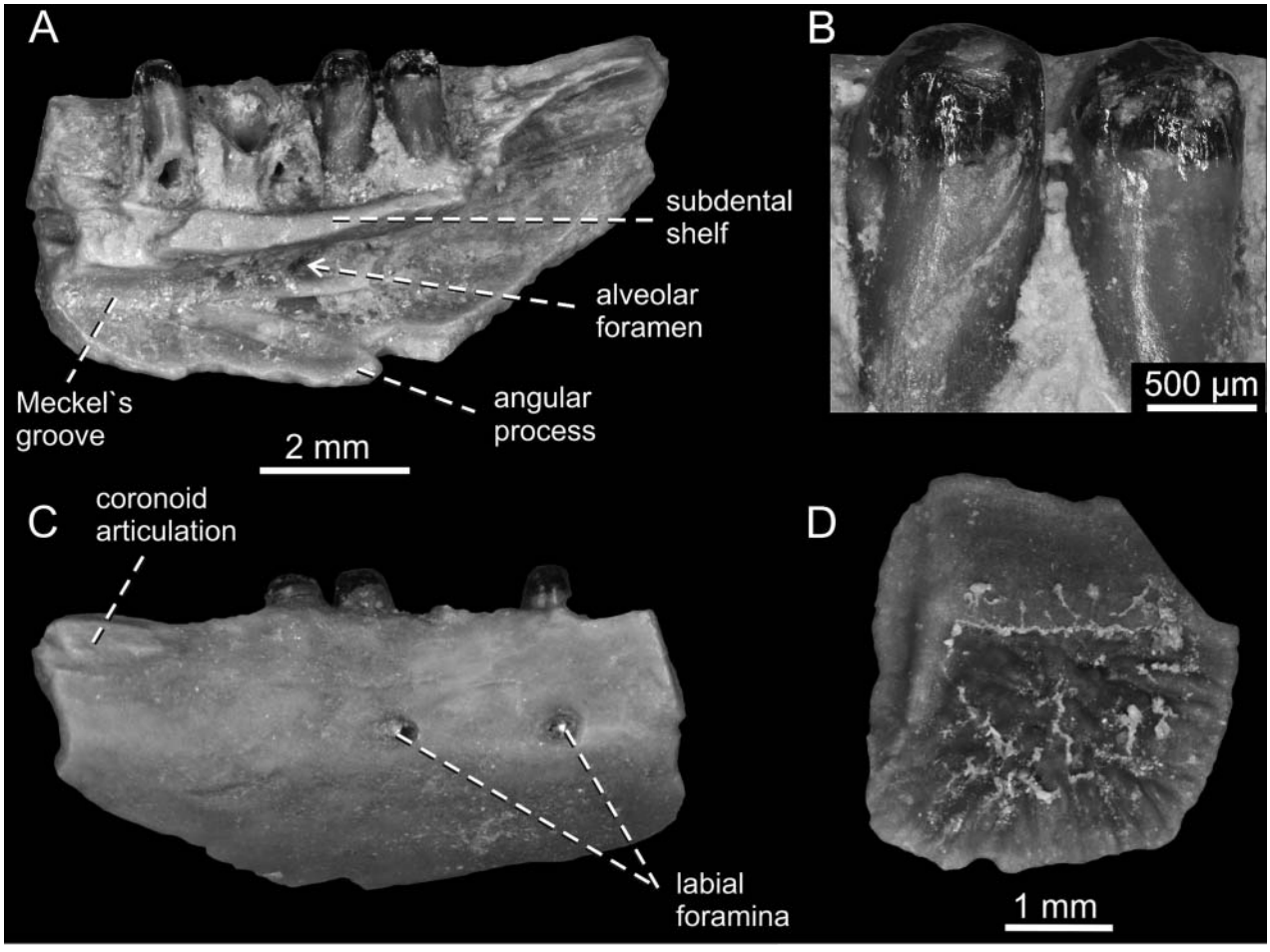


**Figure 7. A–C,** *Pseudopus* cf. *ahnikoviensis*, dentary, PAL EV 2013/165; **A,** medial view; **B,** detail of teeth; **C,** lateral view. **D,** *Pseudopus* sp., osteoderm, PAL EV 2013/166 in external views.

The dentition is pleurodont. The teeth are robust and blunt (Fig. 7B). Their apices are rounded and bear distinct mesiodistal cutting edges. The lingual surface of the apices is striated. The teeth are slightly compressed mesiodistally and, consequently, are slightly expanded labiolingually. Their bases bulge lingually.

**Remarks.** The dentary and teeth of PAL EV 2013/165 are massively built, similar to those of the Early Miocene anguine *Pseudopus ahnikoviensis* from Merkur-North (MN 3) in the Czech Republic (Klembara 2012). Unfortunately, the coronoid and surangular processes are not well preserved, thus rendering it impossible to estimate how far these processes extended posteriorly. The surangular spine, a structure present only in *P. ahnikoviensis* within the genus *Pseudopus* (Klembara 2012), is present. The morphology of the posterior teeth corresponds to that of the genus *Pseudopus*, and the teeth themselves are very similar to those of *P. laurillardi* (the oldest finds of which are from MN 4 in various European localities; Klembara *et al.* 2010) and *P. ahnikoviensis* (Klembara 2012). However, in contrast to the specimens from Amöneburg, teeth of *P. ahnikoviensis* specimens from the type locality lack apical striations (Klembara 2012). This may be due to intraspecific variability, similar to that seen in the extant *P. apodus* (Klembara *et al.* 2010). The typical feature of *P. laurillardi* is the presence of a lateromedially wide subdental shelf (Augé & Rage 2000; Rage & Bailon 2005; Klembara *et al.* 2010); this feature is absent in *P. ahnikoviensis* (Klembara 2012) and also in PAL EV 2013/165.

### ***Pseudopus* sp.**
(Fig. 7D)

**Material.** Five osteoderms, PAL EV 2013/166–170.

**Description.** All five osteoderms have a similar shape, being flattened and almost rectangular. They represent thoracal osteoderms from the dorsolateral portion of the armour. Their external surface bears a wide anterior gliding surface forming more than one-third of the entire anteroposterior length of the osteoderm. The lateral bevel is narrow. The ornamented surface is distinctly developed, with the central region of the ornamented portion consisting of tubercles and short ridges; from here, the ridges radiate to the periphery of the osteoderm. The anteroposterior keel is absent. The smooth internal surface of the osteoderms is pierced by a pair of small but well-defined foramina located in their central region.

**Remarks.** The morphology of the osteoderms corresponds to that of *Pseudopus* (Fejérváry-Lángh 1923; Klembara *et al.* 2010). There are no osteoderms that can be incontrovertibly attributed to *P. ahnikoviensis*, which is the smallest species of *Pseudopus* (Klembara 2012). It is also impossible to exclude that these Wiesbaden osteoderms belong to a small *P. laurillardi* specimen, although the fossils of this species are currently recorded in slightly younger horizons (Klembara *et al.* 2010). A further species of *Pseudopus* has recently been identified from Merkur-North (Klembara 2014). Since this has similar size to *P. ahnikoviensis*, it is impossible to determine whether the Wiesbaden osteoderms emanate from one of these species or from a currently unrecognized *Pseudopus* species.

### ***Ophisaurus*** Daudin, 1803
### ***Ophisaurus spinari*** Klembara, 1979
(Fig. 8A, B)

**Material.** Parietal, PAL EV 2013/171.

**Description.** Only one parietal is preserved. The parietal table has a quadrangular shape and an ornamented surface that is longer than wide (Fig. 8A). The ornamentation consists of tubercles, short anastomosing ridges and pits with basal foramina. Radiating ridges are present only at the periphery of the ornamented surface. The parietal foramen is located slightly posterior to the mid-length of the ornamented surface. The interparietal sulci are distinct, and they clearly delimit the positions of the unpaired interparietal and bilaterally located lateral shields. The anterior end of the interparietal sulcus reaches the anterolateral corner of the ornamented surface. The occipital sulcus delimits a small and triangular occipital shield. The interparietal and occipital sulci meet in a very short transverse sulcus. The lateral margins of the ornamented surface coincide with the lateral margins of the parietal table, while the anterolateral process (processus fronto-postfrontalis; Klembara 1979) of the parietal table is short and elongated anteroposteriorly. Short frontal tabs are visible in dorsal view. The smooth area (*area levis*) lying immediately posterior to the ornamented surface is approximately twice as long as the mid-length of the occipital ornamented shield. The arcuate edge (*carina arcuata*) forming the posterior margin of the parietal table gradually continues into the dorsal surface of the basal portion of the right supratemporal process, whose remaining portion is broken. Unfortunately, the left supratemporal process is completely absent.

The frontal articulation areas on the ventral surface of the parietal are distinct, and ovoid in shape (Fig. 8B). The anterior margin interposed between these ovoid frontal articulations is digitate. The most dominant structure of the ventral surface is the parietal cranial crest (*crista cranii parietalis*), which reaches the lateral margin of the parietal table, and thus no muscular surface (*facies muscularis*) is present. The posterior end of the parietal cranial crest reaches the medial margin of the basal portion of the supratemporal process where it joins the posterior end of the juxtaotic crest. Thus, the postfoveal crest is absent.

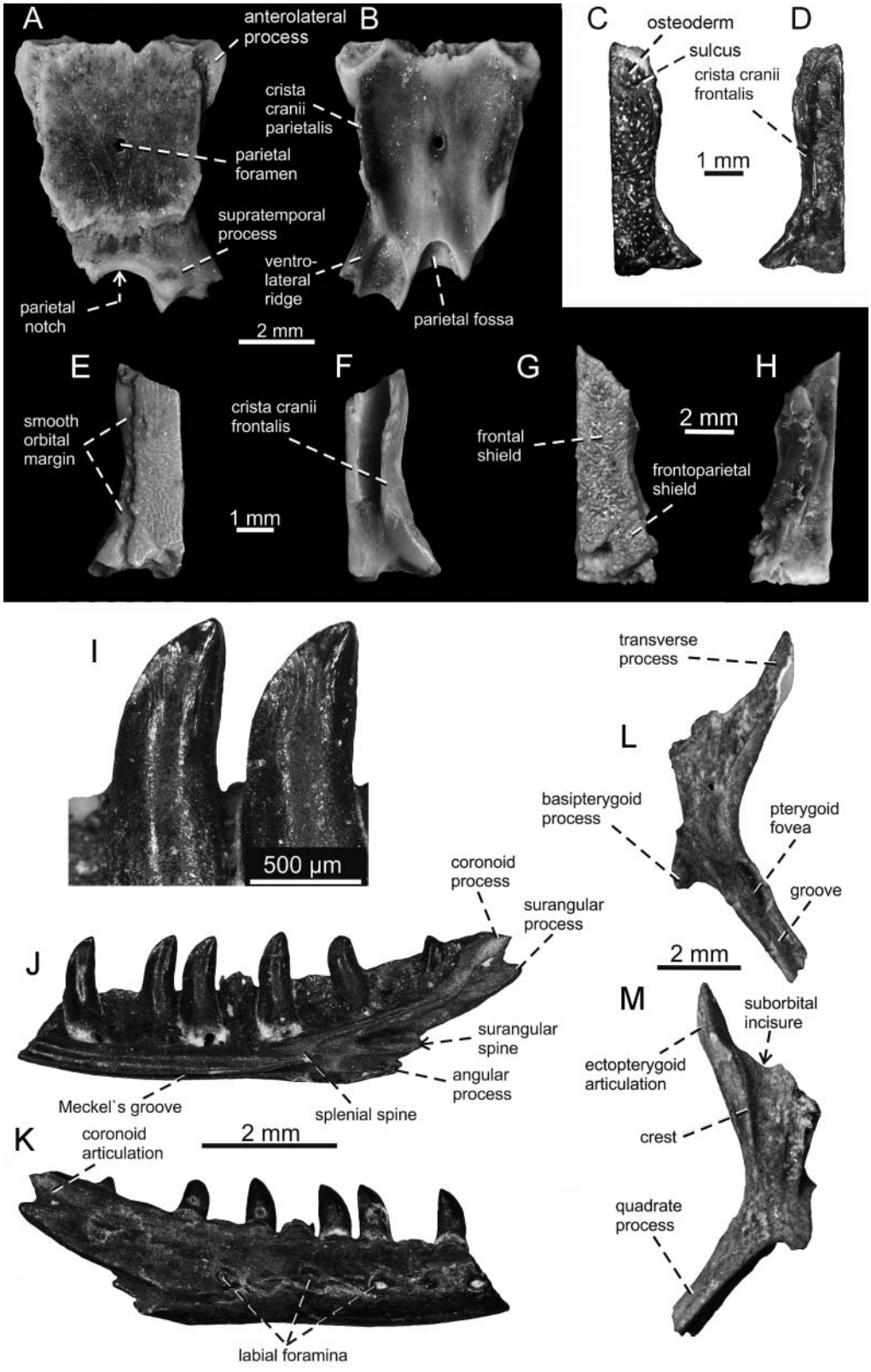


**Figure 8.** *Ophisaurus spinari* **A, B** and *Ophisaurus* sp. **C-M.** Parietal PAL EV 2013/171 in **A,** dorsal and **B,** ventral views. Frontals (from smallest to largest one) PAL EV 2013/172–174 in **C, E, G** dorsal and **D, F, H** ventral views. Dentary PAL EV 2013/276 in **I,** detail of teeth; **J,** medial and **K,** laterial view on the dentary. Pterygoid PAL EV 2013/175 in **L,** dorsal and **M,** ventral views.

The parietal fossa has a semicircular anterior margin. The posterior portion of the parietal lamina bears a tiny pit. The arcuate edge lies anterior to the level of the posterior tips of the parietal cranial crests, and the parietal notch is distinct. The ventrolateral ridge of the supratemporal process is well developed, coinciding with the lateral margin of the supratemporal process anterior to the articulation of the latter.

**Remarks.** The morphology of the parietal PAL EV 2013/171 is very similar to that of *Ophisaurus spinari* described from the Early Miocene (MN 4) of Dolnice in the Czech Republic (Klembara 1979, pl. 1, fig. 2, pl. 2, fig. 2; Klembara 1981, fig. 1, pl. 2, fig. 1). The only difference is the anteroposterior length of the occipital ornamented shield, which is shorter in the parietal described here. However, the size and also sometimes the shape of the occipital shield vary within the anguine genera *Ophisaurus*, *Anguis* and *Pseudopus*. This depends on the size of the osteoderm lying immediately posterior to the occipital shield of the parietal. This osteoderm can expand anteriorly at the expanse of the occipital shield (e.g. Klembara *et al.* 2010). The parietal PAL EV 2013/171 represents the oldest record of *Ophisaurus spinari* and its first occurrence outside the Czech Republic.

### *Ophisaurus* sp.

(Fig. 8C–M)

**Material.** Left frontal PAL EV 2013/172; right frontals PAL EV 2013/173–174; right pterygoid PAL EV 2013/175; right dentary PAL EV 2013/276.

**Description.** Three frontal bones are available, with two of these being smaller (PAL EV 2013/172 and PAL EV 2013/173) and one larger (PAL EV 2013/174). PAL EV 2013/173 is completely preserved (Fig. 8C, D), and this is long and slender, with more or less distinct mediolateral constriction slightly posterior to its mid-length. The ornamentation covers most of the dorsal surface of the frontal and forms three shields of different sizes. The largest is the frontal shield which is partly separated from the rounded osteoderm covering the anteriormost surface of the frontal (Fig. 8C). The frontal shield is posteriorly separated by sulci from the mediolaterally elongated interfrontal shield and subquadrangular frontoparietal shield. The sulcus between the frontal and interfrontal shields is shorter than that between the frontal and frontoparietal shields. The frontal shield is slightly constricted in two of these frontals (Fig. 8C, G). The ornamentation is best developed in the largest specimen (Fig. 8G). It consists of tubercles, short anastomosing ridges and grooves and pits. At the lateral margin of the frontal shield, the ridges are orientated anterolaterally, whereas they are orientated anteromedially at the medial margin. The posterolateral process of the frontal is well developed and its dorsal surface is smooth. Its anterior margin bears a distinct groove for articulation with the postfrontal. The long orbital margin of the frontal is smooth, and the nasal articulation is slightly roughened.

On the ventral surface, the frontal cranial crest forms a deep wall along the lateral margin of the bone (Fig. 8D, F, H). This crest is deepest and sharpest in the anterior two-thirds of its course, with its anterior section extending into a small, but distinct process (Fig. 8G). Posteriorly, the crest becomes gradually shallower, mediolaterally wider and rounded. The anterolateral margin of the frontal is distinctly grooved, indicating a strong prefrontal articulation, which extends slightly posterior to the mid-length of the frontal. A small triangular parietal tab is present on the posterior margin of the frontal.

The pterygoid is a triradiate element (Fig. 8L, M). The palatine process is broken. The basal portion is broad. Here, the tooth row is present and continues posteriorly on the body of the pterygoid, extending to its narrowest part. One of the teeth is well preserved. This is conical, with a blunt tip. A distinct ventral transverse crest is present along the posterior margin of the transverse process, with a deep pterygoid sulcus between the crest and the tooth row. The transverse process is short and robust, with a pointed anterior termination. The suborbital incisure is deep and mediolaterally narrow. The obtuse process (for this term see Klembara, 2014) is short and blunt and forms a distinct flange. The quadrate process is long and mediolaterally compressed, but unfortunately its posterior portion is broken. The dorsal transverse crest is distinct and sharp. The pterygoid fovea is large and deep, and is keyhole in shape.

The right dentary is almost completely preserved (Fig. 8J, K). The coronoid process is partly broken. It is estimated that its posterior end here reached the level of the posterior end of the surangular process, or slightly more posteriorly. The surangular process is well preserved, with a slightly rounded posterior ending. The surangular spine is present, but its posterior tip is broken. The root portion of the angular process is preserved. The alveolar foramen lies at the level of the 4th tooth (2nd preserved tooth), from the posterior aspect. The splenial spine forming the anteroventral margin of the anterior inferior alveolar foramen lies at level of the distal wall of the 6th tooth (3rd preserved tooth) from the posterior. The dental crest is distinct and its section anterior to the splenial spine forms a dorsoventral wall for articulation with the splenial. The portion of the dental crest lying posterior to the anterior inferior alveolar foramen bears a distinct groove marking the posterior section of the splenial articulation. Further posteriorly, the dental crest has a smooth surface and is dorsoventrally widened. It represents the anteromedial process of the coronoid articulation. Meckel's canal opens ventrally. The posterior portion of the intramandibular septum is indistinguishably fused to the internal wall of the dentary.

The lateral wall of the dentary is somewhat roughened, mostly near the mental foramina. Seven mental foramina of varying size are preserved. Anterior to the coronoid incisure there is a slightly roughened surface, which indicates articulation with the anterolateral process of the coronoid.

The dentition is pleurodont. The alveolar portion bears 11 tooth positions, with four teeth completely preserved. These teeth are conical, slightly curved posteriorly and have pointed tips. The mesial and distal cutting edges are well developed. The medial surface of the apices is striated (Fig. 8I), and striae extend onto the surface of the cutting edges.

**Remarks.** The general morphology of the frontals described above corresponds to that of fossil and extant species of the genus *Ophisaurus*. The pattern and intensity of the ornamentation correspond to those of the large adult specimens of the extant *Ophisaurus* and are somewhat similar to those of *Pseudopus ahnikoviensis* (Klembara 2012). However, in *P. ahnikoviensis* the anterolateral corner of the frontal ornamented shield reaches the lateral margin of the frontal. This condition is absent in the frontals described herein, and also in the frontals of the extant species of *Ophisaurus*.

The frontal described here has a rounded osteoderm covering the anteriormost portion of the frontal and this is partly fused with the anterior margin of the frontal shield. This feature is unusual in both fossil and Recent *Ophisaurus*. There is no additional shield situated anterior to the frontal shield in *Ophisaurus*, *Anguis* and *Pseudopus*, and this rounded element is most likely an osteoderm secondarily fused with the anterodorsal portion of the frontal (see also Klembara, 2014).

The morphology of the pterygoid corresponds to that of the extant species of *Ophisaurus* and *Anguis*. However, the pterygoid of *Anguis* lacks teeth. In *Pseudopus*, the basal portion of the transverse process typically runs an almost transverse course (Klembara *et al.* 2010). The pterygoid from the Early Miocene (MN 4) of Dolnice, referred to as *Ophisaurus* sp., is very similar to PAL EV 2013/175, but it has a well-developed denticulate field with an elliptical shape (Klembara 1981, pl. 2, fig. 2). The keyhole shape of the pterygoid fovea in PAL EV 2013/175 is quite exceptional for *Ophisaurus*.

The general morphology of the dentary corresponds to that of *Ophisaurus*. The teeth are similar to those of other Miocene anguines such as *Ophisaurus acuminatus* (Jörg 1965) or Anguine morphotype 1 from the Merkur locality (Klembara 2014). Although the teeth of these anguines are also of conical shape and have well-developed cutting edges, they lack the striations on the medial surface of their apices. The shape of teeth and the striation pattern of the tooth apices of *Ophisaurus* sp. described here are very similar to those of the Recent *O. harti* (Klembara 2014) from South-East Asia.

### Anguinae indet.
(Fig. 9A–G)

**Material.** Right quadrate PAL EV 2013/176; dorsal vertebrae PAL EV 2013/177–179; caudal vertebrae PAL EV 2013/180–181; osteoderms PAL EV 2013/182–267.

**Description.** The right quadrate is preserved (Fig. 9A, B). Its dorsal region is anteroposteriorly expanded. The dorsal surface of the cephalic condyle is slightly convex and protrudes posteriorly. The anterior surface of the quadrate is laterally expanded and bordered there by a columnar portion forming a sharp ridge. In anterior view, the mandibular condyle is W-shaped with slightly blunt peaks. On the medial surface of the quadrate, there is a prominent tympanic crest bearing a small tubercle on its ventral aspect. A small, rounded foramen pierces the quadrate at approximately mid-length.

Several isolated dorsal vertebrae are available. These are quite robust (Fig. 9C, D). On the dorsal aspect, the neural spine is very low and its posterior end is broken. The neural canal is tall. The prezygapophyses have well-defined oval articular surfaces. The postzygapophyses are relatively smaller than the prezygapophyses and have elliptical articulation surfaces. The interzygapophyseal constriction is marked. The cotyle is deep, similar to the condyle, and dorsoventrally depressed. The boundary between the centrum and condyle is not clearly marked ventrally. The centrum is triangular in ventral view, with slightly concave lateral walls. The ridges are slightly developed at the ventral side and run an almost parallel course. A pair of anteroposteriorly elongated subcentral foramina is located in the anterior quarter of the centrum. The zygosphene and zygantrum are absent.

The caudal vertebrae are narrower and more elongated than those of the trunk region (Fig. 9E, F). The pre- and postzygapophyses are small but well developed. The condyle and cotyle are markedly depressed. Unfortunately, the haemapophyses fused to the posterior portion of the centrum, anterior to the condyle, are broken in all specimens. The anterolaterally orientated transverse processes are long and massive. The medial dorsal ridge has two processes: (1) the triangular pseudospine, located in the anterior region; and (2) the tall, anteroposteriorly short neural spine in the posterior region.

Many flat oblong osteoderms are preserved (Fig. 9G). An ornamented surface of well-developed ridges, grooves and pits covers most of the external surface; with the ridges forming an anastomosing pattern in the central ornamented area. A strong midline keel dominates here, and this continues on the gliding surface immediately anterior to the ornamentation. The lateral bevel is narrow. Several

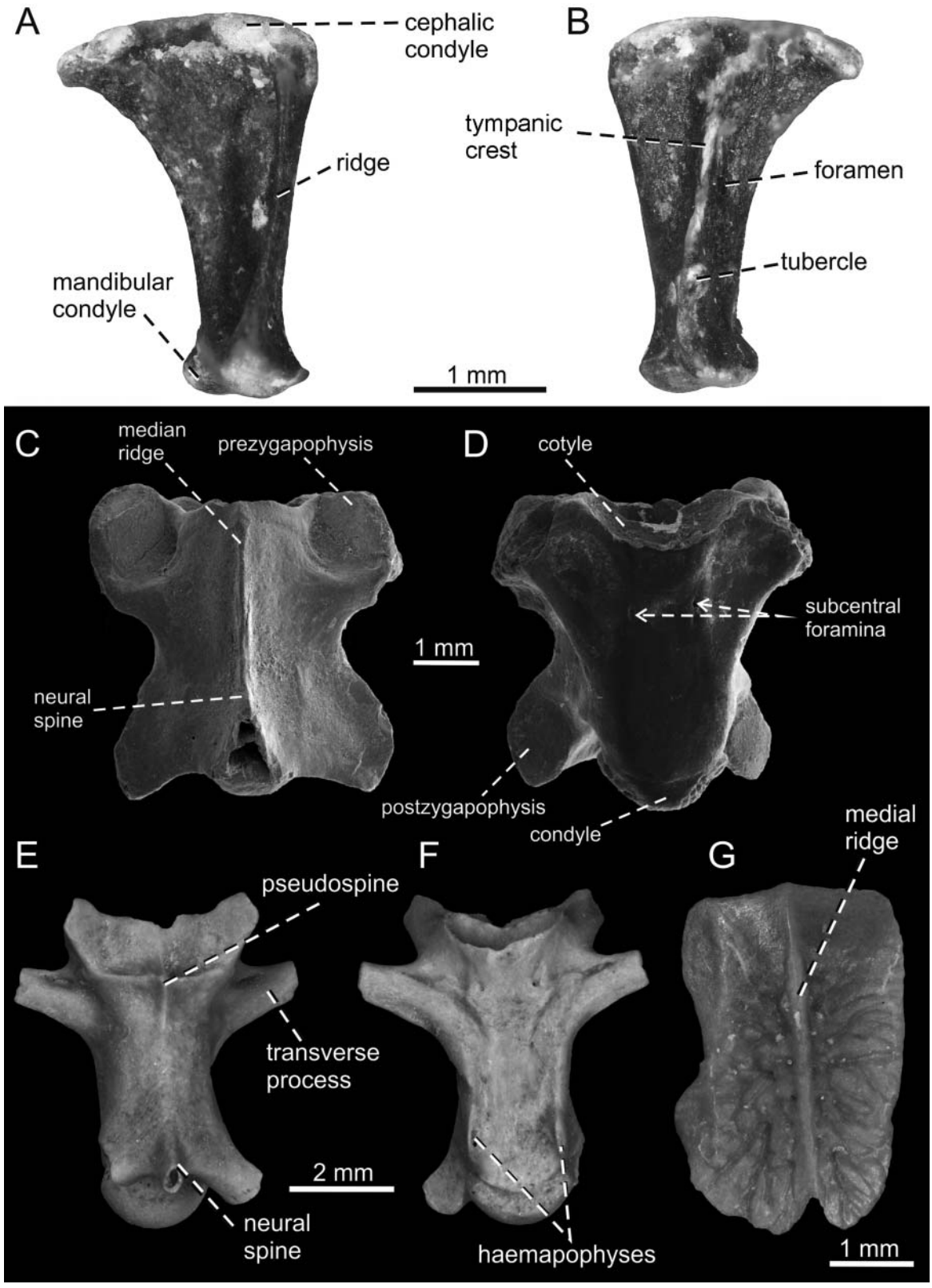


**Figure 9.** Anguidae indet. **A, B,** quadrate, PAL EV 2013/176, in **A,** lateral and **B,** medial views; **C, D,** dorsal vertebra, PAL EV 2013/177 in **C,** dorsal and **D,** ventral views; **E, F,** caudal vertebra, PAL EV 2013/180, in **E,** dorsal and **F,** ventral views; **G,** osteoderms, PAL EV 2013/182, external view.

osteoderms have a rather distinct notch in their posterior margin, immediately posterior to the midline keel.

**Remarks.** The quadrate corresponds in size and morphology to those of the juvenile specimens of *Ophisaurus* and *Pseudopus*, but it has no features to allow more precise determination.

For dorsal vertebrae, the concave lateral walls of the centrum are a typical feature of *Ophisaurus*, in contrast to the straight lateral walls in *Pseudopus* adults (Klembara 1981, fig. 3). The Amöneburg vertebrae are very similar to those of the genus *Ophisaurus*. In *Anguis*, the lateral walls are almost parallel in ventral view, with a slight constriction immediately posterior to the subcentral foramina (Klembara 1981, fig. 3). The vertebrae described herein are very similar to those of cf. *Ophisaurus* sp. (morphotype I) described from the Early Miocene (MN 4) of Dolnice (Roček 1984) and also to those of the Anguine morphotype B from the Late Eocene–Early Oligocene deposits of the Hampshire Basin in southern England (Klembara & Green 2010, fig. 6F, G). However, for definitive attribution, we are not sufficiently conversant with the vertebrae of the similarly sized Early Miocene *P. ahnikoviensis*, which is considered similar to *Ophisaurus* in some respects (Klembara 2012).

The osteoderms described here are very common in many Early Miocene European localities (e.g. Klembara 1981, 1986; Estes 1983). Since both *Ophisaurus* and *Pseudopus* exist in this time interval (Rage & Bailon 2005; Klembara *et al.* 2010; Klembara 2012), it is impossible to determine to which of these genera the osteoderms belong. In addition, very similar osteoderms have been described from the Late Eocene–Early Oligocene deposits of the Hampshire Basin in southern England (Meszoely & Ford 1976; Klembara & Green 2010), and also from several other European Eocene and Oligocene localities (Augé 1992, 2005).

**Platynota** Baur, 1890
**Shinisauria** Conrad, 2008
Genus ***Merkurosaurus*** Klembara, 2008
***Merkurosaurus ornatus*** Klembara, 2008
(Fig. 10A, B)

**Material.** Jugal PAL EV 2013/268.

**Description.** One left jugal is preserved (Fig. 10A, B), and this is L-shaped in medial and lateral views. It has two long processes, the postorbital and suborbital processes forming the posteroventral margin of the orbit. From their junction, a third, short but distinct process extends posteroventrally. The orbital lamina is sharp and slightly curved. The jugal is triangular in cross section, with a flat external wall, while its medial wall bears a ridge running along the entire bone. Its lateral surface bears weakly developed ornamentation, consisting of short ridges and grooves radiating from the central region. A shallow depression extends dorsally along the lateral surface of the postorbital process, and the anterior end of the suborbital process is pointed. Its dorsomedial surface bears a short roughened articular facet for the lacrimal. This articulation surface extends somewhat posterolaterally, but does not reach the anteromedial jugal margin. The ventral wall of the suborbital process bears a distinct articulation area for the maxilla. This articulation area is long and there is also a deep and ovoid articulation area for the ectopterygoid immediately posterior to it. On the medial surface of the postorbital process, two foramina are located in front of the strong medial ridge. The triangular articular facet for the postorbital (or postorbitofrontal) is located on the medial surface of the dorsal region of the postorbital process. Unfortunately, the dorsal end of the latter process is broken.

**Remarks.** The morphology of the jugal described here is almost identical to that of the jugal of *Merkurosaurus ornatus* described by Klembara (2008) from Merkur-North in the Czech Republic. However, it differs in some details, such as the intensity of ornamentation, which is much less developed in our specimen, although the extent of ornamentation is considered individual variation.

**cf. *Merkurosaurus ornatus*** Klembara, 2008
(Fig. 10C)

**Material.** Osteoderm PAL EV 2013/277.

**Description.** An approximately ovoid osteoderm is preserved (Fig. 10C). Its dorsal surface is distinctly ornamented, and it bears a tall, thin keel running through the entire length of the osteoderm. Ridges and grooves radiate from the keel and it bears more or less distinct notches. The remaining surface of the osteoderm has distinct pits of variable size. The osteoderm is unimbricated with an irregular margin. The ventral surface of the osteoderm has variously sized deep pits.

**Remarks.** The morphology of the osteoderm is very similar to that of the extant *Shinisaurus* and extinct *Merkurosaurus* (Klembara 2008) and also to *Bahndwivici*, a shinisaurid from the Early Eocene of North America (Conrad 2006). A similar osteoderm was recovered from the latest Oligocene (MP 30 of Oberleichtersbach, Germany). This was referred to as *Merkurosaurus* sp. by Böhme (2008), and is the earliest reported occurrence of the genus.

**Shinisauria indet.**
(Fig. 10D, E)

**Material.** Fragment of parietal PAL EV 2013/269.

**Description.** Only the right portion of the anterior region of the parietal is preserved (Fig. 10D, E). The

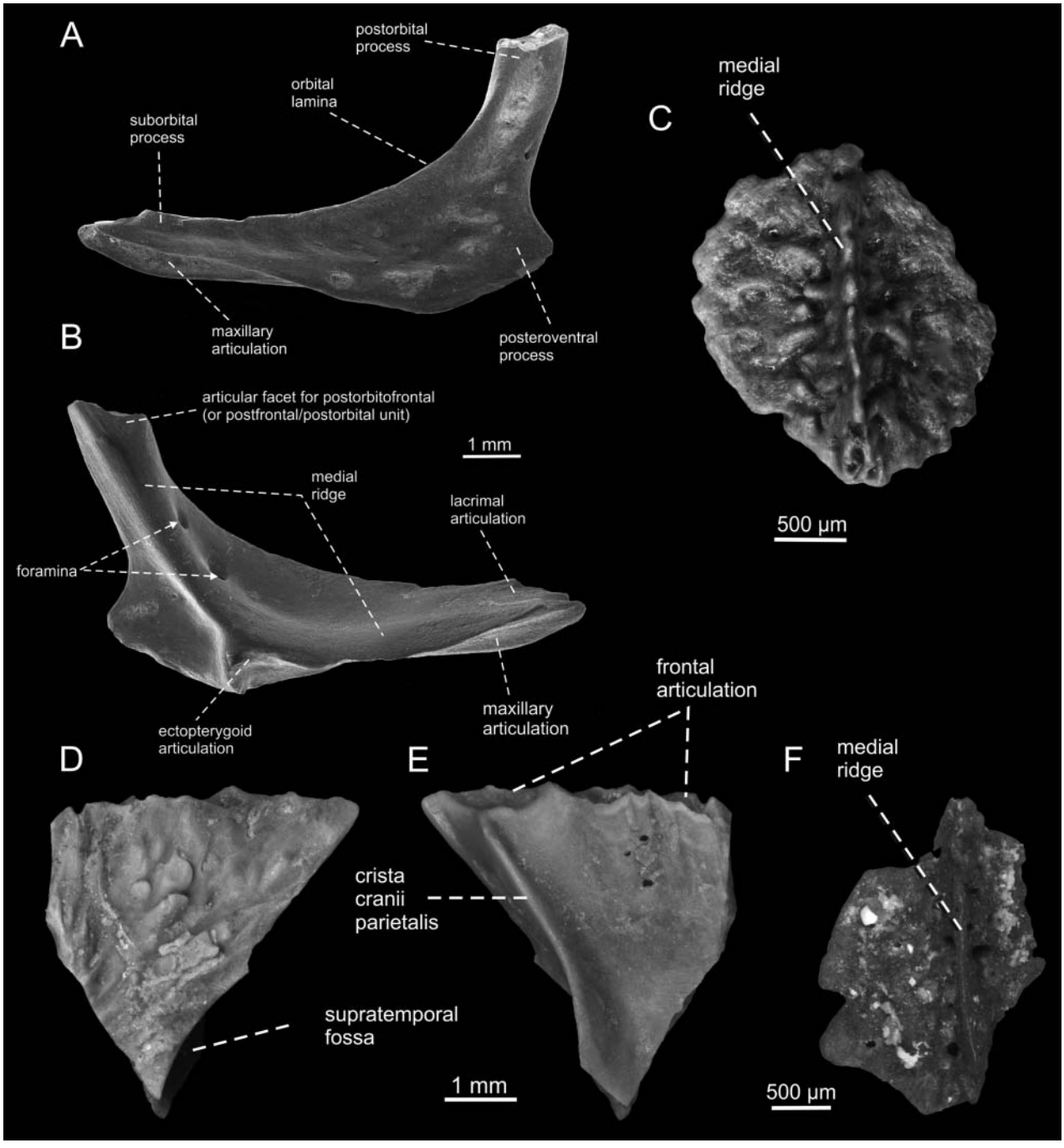


**Figure 10. A, B,** *Merkurosaurus ornatus*, jugal, PAL EV 2013/268, in **A,** lateral and **B,** medial views. **C,** cf. *Merkurosaurus ornatus*, osteoderm, PAL EV 2013/277, in dorsal view. **D, E,** Shinisauria indet. parietal, PAL EV 2013/269, in **D,** dorsal and **E,** ventral views. **F,** Platynota indet., osteoderm, PAL EV 2013/270, in external view.

ornamentation on the dorsal surface consists of grooves, ridges and flat pustules or tubercles grouped together and radiating from the central region. A sharp parietal cranial crest is present on the ventral aspect close to the lateral margin, running a curved, slightly laterally concave course. The anterior margin is distinctly interdigitated.

**Remarks.** The ornamentation of the preserved portion of the parietal is almost identical to that of the parietal of *Merkurosaurus ornatus* from Merkur-North (Klembara 2008, fig. 4). However, the ornamentation is not so pronounced in the Amöneburg osteoderm. Although this specimen shows some similarity with *Merkurosaurus*, it

lacks diagnostic features to support its assignment to this genus.

**Platynota indet.**
(Fig. 10F)

**Material.** Osteoderm PAL EV 2013/270.

**Description.** The osteoderm is composed of a broad plate and a tall and strongly developed medial ridge that runs the entire length of the plate (Fig. 10F). The ornamentation, if any, is weak, with rare, poorly marked ridges and depressions restricted to a small area near the keel. Pits of various sizes are scattered along the remaining surface of the plate, and several deep pits are also present on the internal surface.

**Remarks.** This isolated osteoderm resembles PAL EV 2013/277 referred to cf. M*erkurosaurus ornatus* (see above). However, the weak ornamentation restricted to a small area close to the keel is reminiscent of Necrosauridae, a platynotan taxon which may be related to shinisaurs. Although necrosaurid osteoderms have a tall keel similar to that in shinisaurids, in cross section the keel appears as a lamina perpendicular to the plate as in shinisaurs, while the necrosaurid keel arises progressively from the plate with a cross sectional triangular shape. On the basis of such limited material, we cannot exclude attribution to Necrosauridae reported from the Late Palaeocene to Early Oligocene in Europe (Augé & Smith 2009; Rage 2012), but still unrecognized in the Miocene. However, the abrupt rise of the keel is more consistent with shinisaurs and the differences between this osteoderm and PAL EV 2013/277 could result from regional variation in the body. Since this relationship cannot be confirmed on the basis of only two osteoderms, the one described here is attributed only to an indeterminate platynotan.

**Serpentes** Linnaeus, 1758
**Booid grade snakes**
**?'Tropidophiids'**
**?Tropidophiinae** Brongersma, 1951
**?*Falseryx*** Szyndlar & Rage, 2003
**?*Falseryx* sp.**
(Fig. 11)

**Material.** Four trunk vertebrae PAL EV 2013/2–5.

**Description.** The vertebrae are small (Fig. 11) and slightly wider than long; in the largest well-preserved vertebra, centrum length is 2.4 mm. Their neural arch is depressed and indented by a moderately deep posterior median notch. The interzygapophyseal constriction is well marked. The neural spine is low and anteroposteriorly short, occupying approximately one-third of the neural arch length. The dorsal border of the neural spine is well defined, horizontal and does not appear thickened.

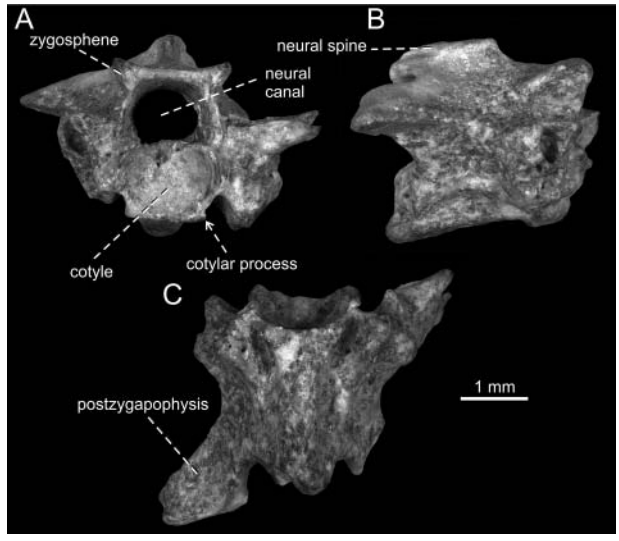


**Figure 11.** ?*Falseryx* sp., trunk vertebra, PAL EV 2013/2, in **A,** anterior, **B,** lateral and **C,** ventral views.

The anterior border is either vertical or anteriorly slanted. The zygosphene is gracile and as wide, or slightly wider, than the cotyle. Its roof is flat to slightly concave in anterior view, while its anterior border is straight or slightly concave in dorsal view. The cotyle is somewhat depressed. On the largest vertebra, the ventral part of the cotylar rim forms small ventrolateral cotylar processes (*sensu* LaDuke 1991). These processes are incipient on the second vertebra but absent on the other two specimens. The vertebrae lack paracotylar foramina. The prezygapophyseal facets lie above the level of the floor of the neural canal, with their major axis oblique in dorsal view. Prezygapophyseal processes are present, but short. The paradiapophyses are massive, anteroposteriorly higher than long and indistinctly divided into dia- and parapophyseal areas. Ventrally, they reach the level of the cotylar rim and they may project slightly ventral to it. The centrum is comparatively narrow, bearing a clearly distinct haemal keel.

**Remarks.** The overall morphology of these vertebrae is clearly reminiscent of the erycine boid *Bransateryx* and of the tropidophiine 'tropidophiid' *Falseryx*. The similarity between the trunk vertebrae of these two booid genera is astonishing (Szyndlar & Rage 2003), and only caudal vertebrae unrecognized in Amöneburg specimens enable definitive distinction. *Bransateryx* is a typical Erycinae (Boidae), possessing strongly shortened posterior caudal vertebrae with additional processes (Hoffstetter & Rage 1972; Szyndlar 1987, 1994). *Bransateryx* is recognized from MP 22 (Early Oligocene) to MN 2 (Early Miocene) (Szyndlar & Rage 2003). In *Falseryx*, although the succession of caudal vertebrae is characteristic of the tropidophiines, each caudal vertebra lacks peculiar characteristics permitting identification, while a single caudal enables

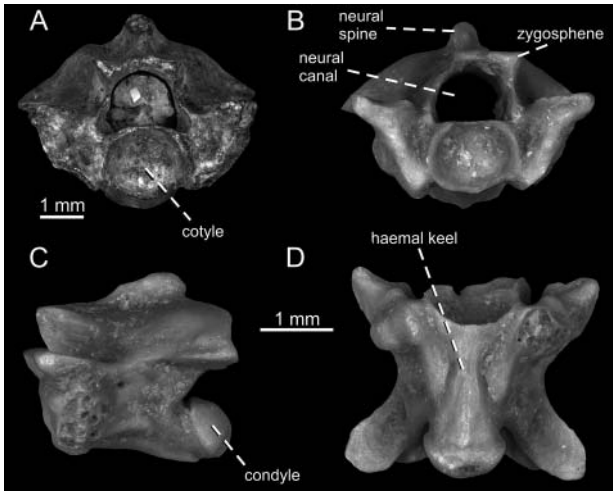


**Figure 12.** Booid indet., trunk vertebrae, PAL EV 2013/6–7, in **A, B,** anterior, **C,** lateral and **D,** ventral views.

identification in erycines. *Falseryx* was reported from MP 21 (Earliest Oligocene) of Belgium (*F. neervelpensis*; Szyndlar *et al*. 2008) and MN 4 (Early Miocene) of Germany and the Czech Republic (*F. petersbuchi*; Szyndlar & Rage 2003). The genus may also be present in MN 3 or 4 (Early Miocene) in Spain and MN 7+8 (late Middle Miocene) in Germany (Szyndlar & Rage 2003). This discontinuous stratigraphical range most likely results from palaeogeographical events (Szyndlar & Rage 2003). However, the temporary absence of *Falseryx* between MP 22 and MN 2 or 3 may be partly artefact since the caudal vertebrae of non-erycines were not thoroughly surveyed in the collections.

The snake from Amöneburg is tentatively referred to as *Falseryx*, simply because erycine caudals are lacking from this locality. Although this is a very uncertain basis for identification, it must be noted that, if this snake is really *Falseryx*, then it represents the earliest representative of this genus in the Miocene.

### Booid indet.
(Fig. 12)

**Material.** Two trunk vertebrae PAL EV 2013/6–7.

**Description.** The largest vertebra has a centrum length of 3 mm, being slightly larger than the largest one assigned to ?*Falseryx*, whose largest vertebra cannot be measured. However, this booid is small. The overall morphology of these two vertebrae differs from that of ?*Falseryx*, being slightly shorter and wider, and having a deeper posterior median notch (Fig. 12). In addition, the neural arch is depressed, but less so than in ?*Falseryx*. The articular facets of the zygapophyses are larger and the paradiapophyses clearly project ventrally below the cotylar rim. The neural spine appears to be slightly longer anteroposteriorly. The two vertebrae lack ventrolateral cotylar processes. In the larger of the two available vertebrae, that likely emanates from the posterior trunk region, the haemal keel is wide and poorly demarcated from the centrum.

**Remarks.** Small booids are typical components of European fauna from the latest Oligocene (MP 29–MP 30) and earliest Miocene (MN 1–MN 2). Non-booid snakes were also small during this interval, labelled the 'Dark Period' for booids (Szyndlar 2012; Rage & Szyndlar 2005). During the Oligocene portion of this interval, three booids were identified in Europe: the erycine Boidae *Bransateryx* and the 'tropidophiids' *Platyspondylia* and *Rottophis* (Szyndlar & Böhme 1996; Szyndlar & Rage 2003). Apart from the possible *Falseryx* described above, only the erycine *Bransateryx* has been reported from the earliest Miocene. However, many such reports may contain errors. Only one caudal vertebra from MN 1 in Paulhiac, France (Hoffstetter & Rage 1972) and some skull bones from MN 2a in Poncenat, France (Müller 1998) demonstrate the presence of the genus in MN 1–MN 2. All trunk vertebrae of booids from this interval are small and they have a depressed neural arch, thus exhibiting morphology recognized in erycine trunk vertebrae. These vertebrae from the earliest Miocene of Europe were indeed referred to as the Erycinae (Hoffstetter & Rage 1972). Similar snakes from the Cenozoic (Early Palaeocene–Middle or Late Miocene) of North America were also assigned to the Erycinae (Holman 2000). However, Szyndlar & Böhme (1996) claimed that non-erycine booid snakes may have such trunk vertebrae. Therefore, assignment of small booids possessing trunk vertebrae with depressed neural arches to Erycinae cannot be confirmed when erycine caudals are absent. As a result, the affinity of these small snakes within booids remains uncertain.

The vertebral morphology of the booids from MN 1–MN 2 appears rather homogenous, but there is more than one taxon. For example, the two vertebrae from Amöneburg differ from those from the rich St-Gérand complex (MN 1 and MN 2) in France. However, such comparisons are beyond the scope of this present study.

### **Colubridae** Oppel, 1811
### Natricine colubrids

**Remarks.** 'Natricines' is a subdivision of colubrids traditionally used by palaeontologists. The natricine morphology of vertebrae is homogenous, with the presence of hypapophyses throughout the trunk region being a significant feature. However, this does not mean that this assemblage is monophyletic.

### ***Natrix*** Laurenti, 1768
### cf. *Natrix* sp.

**Material.** Three trunk vertebrae PAL EV 2013/8–10.

**Description.** Although all three vertebrae are incomplete, they possess combined characteristics typical of natricines. Here, the ventral aspect of the centrum is almost flat and well-limited laterally by marked subcentral ridges; well-developed and laterally compressed hypapophyses are present; the parapophyseal processes are developed and project anteroventral to the cotylar rim. The neural arch is vaulted. The centrum of the largest vertebra is 3.8 mm long. Some individual features distinctive within natricines are noted. The neural spine is high and its anterior and posterior borders overhang, thus making it hatchet shaped. The neural arch is clearly vaulted. The ventral face of the centrum is narrow. The zygosphenal facets form clearly elongate ellipses whose major axis is sub-horizontal. The cotylar rim produces ventrolateral cotylar processes, whose small size is unusual in natricines.

**Remarks.** The length and lateral compression of the hypapophysis, the hatchet-shaped neural spine and the vaulted neural arch are characteristics consistent with the extant genus *Natrix*. The Amöneburg specimens do not form part of the Oligocene or Early Miocene species of the genus. They differ from all of these in having anteroposteriorly elongate, almost horizontal zygosphenal facets and markedly smaller ventrolateral cotylar processes. They further differ from the only Oligocene species, *N. mlynarskii*, in being less massive and in possessing a narrower centrum. The high neural spine and narrow centrum are reminiscent of *N. merkurensis* and *N. sansaniensis*. However, apart from the morphology of the zygosphenal facets and ventrolateral cotylar processes, *N. merkurensis* known from MN 3 (Ivanov 2002a) and perhaps MN 4 (Rage & Bailon 2005) is easily distinguished from the Amöneburg natricine by its clearly less vaulted neural arch, whereas *N. sansaniensis*, which ranges from MN 3a (Ivanov 2002a) to MN 6 (Augé & Rage 2000) or perhaps MN 7 + 8 (Ivanov 2002b), has a more vaulted neural arch. *N. longivertebrata*, present in the Early Miocene of Europe (MN 4; Rage & Bailon 2005), clearly differs from the Amöneburg natricine in its more elongate and more massive vertebrae, in addition to its stronger ventrolateral cotylar processes (the shape of the zygosphenal facets is variable in *N. longivertebrata*, although they are never close to horizontal). Finally, although the natricine from Amöneburg most likely represents a new species, available material here does not permit erection of a new taxon.

Natricine colubrids are rare before MN 4 (Szyndlar 2012). The earliest representative of the group (*N. mlynarskii*) is recognized from the European Oligocene, but its precise age (?MP 22) cannot be confirmed (Rage 1988). In Europe, natricines were especially infrequent during the Dark Period; they are absent from the Oligocene part of this interval and the only possible previous report of a natricine from the Miocene part (from Oschiri, Sardinia) is doubtful because the age of the locality is not precisely known (MN 1 to MN 3; Venczel & Sanchiz 2006). Therefore, the natricine from Amöneburg is both the only confirmed member of the group from the Dark Period and also the earliest confirmed representative from the European Neogene.

### *Neonatrix* Holman, 1973
### cf. *Neonatrix* sp.
(Fig. 13A–C)

**Material.** One anterior (PAL EV 2013/11) and one posterior (PAL EV 2013/12) trunk vertebrae.

**Description.** These two small vertebrae (the longest centrum being 2.6 mm) share common features indicating that they belong to the same taxon (Fig. 13A–C). These features are: neural canal broad; zygosphene thin and wide; articular facets of zygosphene small; neural spine rather low and anteroposteriorly long; cotyles and condyles circular and small; paracotylar foramina present; ventral face of the centrum flat to concave and well limited by sub-central ridges and the hypapophysis is blade-like and anteroposteriorly elongate. In addition, the two vertebrae are short by colubrid standards and their paradiapophyses are distant from the centrum; however, these two features result from the position of the vertebrae in the trunk region and are likely not characteristic of the taxon. Some differences between the two specimens reflect these different positions, but have no taxonomic significance. In PAL EV 2013/11, the zygosphene is more convex dorsally and its articular facets face more ventrally than in PAL EV 2013/12, which is typical for anterior trunk vertebrae. The neural canal and the neural spine of PAL EV 2013/11 are higher than those of PAL EV 2013/12; this difference is usual between anterior trunk and more posterior vertebrae. While the centrum of the posterior trunk vertebra is ventrally hollowed by shallow subcentral grooves, the ventral aspect of the anterior vertebra is almost flat.

The posterior part of the neural arch is preserved only in the posterior trunk vertebra. It is moderately vaulted and indented by a shallow and obtuse median notch. Foramina are present lateral to the zygantrum; as frequently observed in natricine snakes.

**Remarks.** The absence of mid-trunk vertebrae prevents reliable comparisons, since vertebrae from this portion of the vertebral column are generally used as reference material. The morphology of the hypapophysis in the two specimens from Amöneburg is quite striking, possessing the appearance of a deep haemal keel. This is a blade originating below the cotylar rim, becoming deeper posteriorly and approaching the cotyle; its ventral border is curved. Such morphology is recognized only in *Neonatrix*

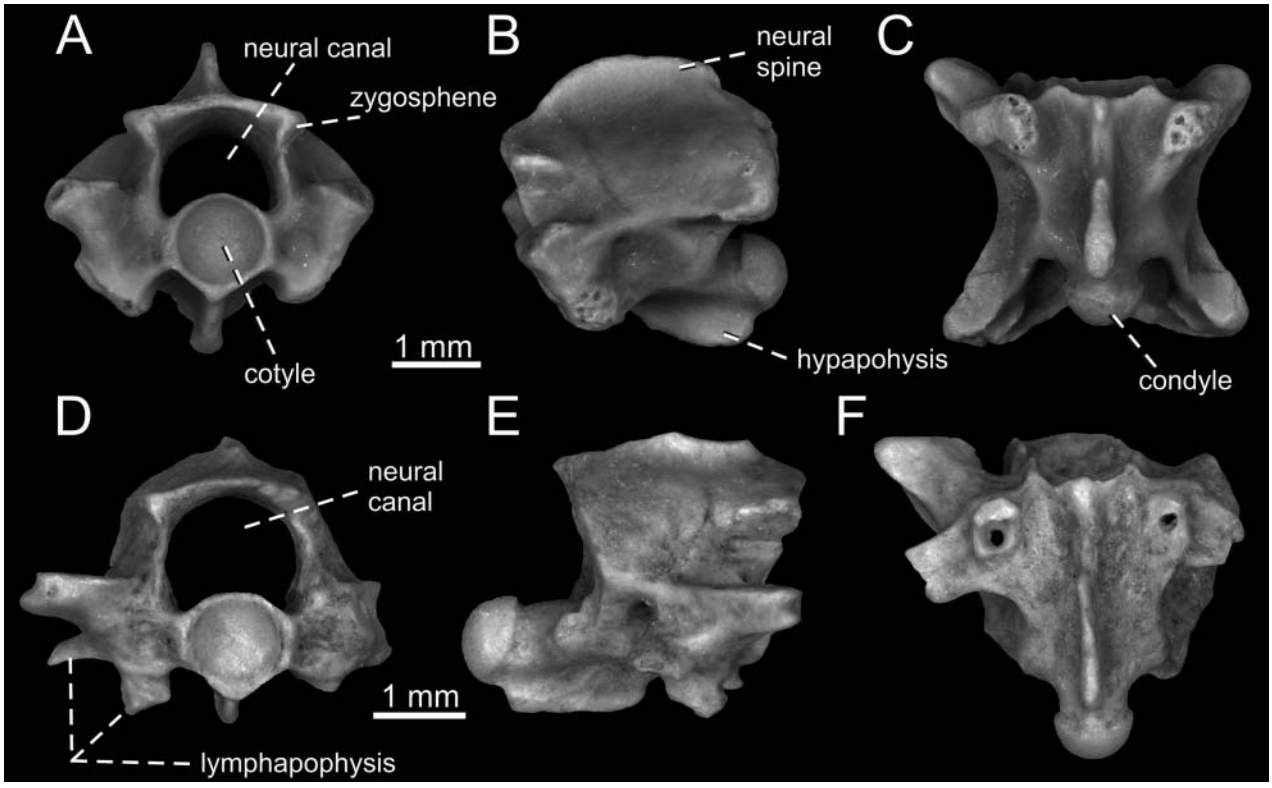


**Figure 13. A–C,** cf. *Neonatrix* sp., posterior trunk vertebra, PAL EV 2013/12, in **A** anterior, **B,** lateral and **C,** ventral views. **D–F,** ?*Neonatrix* sp., cloacal vertebra, PAL EV 2013/110, in **D,** anterior, **E,** lateral and **F,** ventral views.



*natricoides* from the Middle Miocene (MN 6) of Sansan, south-western France (Augé & Rage 2000). However the Amöneburg specimens differ from *N. natricoides* in having a clearly lower neural spine, a broader neural canal and a wider zygosphene.

The genus *Neonatrix* was erected by Holman (1973) for the species *N. elongata* from the Middle Miocene of the USA. It was characterized by its short hypapophysis, which in some species can be regarded as a deep haemal keel. Several species were subsequently referred to *Neonatrix*, although the genus is based on a single characteristic that is a priori liable to convergence. It may be suspected that *Neonatrix* is a polyphyletic assemblage, but this cannot be clearly demonstrated and therefore the genus is retained. Based only on the individual morphology of the hypapophysis and its similarity to that of *Neonatrix natricoides*, the Amöneburg fossil is tentatively referred to this genus.

Although *Neonatrix* is recognized from MN 4 to MN 7 + 8 in Europe, it has also doubtfully been reported from younger levels, up to MN 14 (Early Pliocene) (Szyndlar 2012). In North America, *Neonatrix* ranges from the early Hemingfordian to the middle Hemphillian. It is therefore known from the Miocene, except in its earliest (late Arikareean) and latest (late Hemphillian) periods (Holman 2000). Consequently, if the snake from Amöneburg actually belongs to *Neonatrix*, then it represents the earliest member of this taxon.

### ?*Neonatrix* sp.
(Fig. 13D–F)

**Material.** One cloacal vertebra PAL EV 2013/110.

**Description.** Since the vertebra is provided with lymphapophyses (Fig. 13D–F), it therefore emanates from the cloacal region (Szyndlar & Rage 2003). Only the proximal parts of all processes of the lymphapophyses are preserved. Apart from the lymphapophyses, which replace the paradiapophyses, the specimen closely resembles the trunk vertebrae referred to cf. *Neonatrix*. More specifically, the neural canal is broad, the zygosphene is wide and thin and has small articular facets and the cotyle and condyle are small. Although the neural spine is broken away, it was long anteroposteriorly. One paracotylar foramen opens on either side of the cotyle. Unfortunately, the posterior part of the neural arch is missing and it is impossible to state if it was vaulted. The ventral face of the centrum is flat and it bears a blade-like hypapophysis or haemal keel. The latter is rectangular, moderately deep and elongate anteroposteriorly, with vertical anterior and posterior borders. This blade occupies half the length of

the centrum and it is prolonged anteriorly in a ridge which reaches the cotylar rim.

**Remarks.** The presence of a hypapophysis on the cloacal vertebrae is a characteristic of 'tropidophiids' (Szyndlar & Rage 2003; Szyndlar *et al.* 2008). Although this may suggest assignment of this vertebra to the possible 'tropidophiid' (?*Falseryx*) from the locality, this vertebra is not consistent with those tentatively referred to *Falseryx*. Its zygosphene is markedly wider, its neural canal larger, and its cotyle and condyle clearly smaller. In addition, its neural spine is not restricted to the posterior part of the neural arch.

Apart from the presence of lymphapophyses, the morphology of this vertebra is consistent with those of cf. *Neonatrix*. However, the presence of a hypapophysis (or deep haemal keel) on the cloacal vertebrae is quite unusual in Colubridae. Since cloacal and caudal vertebrae have not been described for *Neonatrix*, comparisons are impossible. On the basis of overall similarity, this specimen is regarded as possibly being a *Neonatrix* cloacal vertebra.

### Colubrine colubrids

**Remarks.** The 'colubrines' are an artificial assemblage used for palaeontological purposes. In contrast to trunk vertebral hypapophyses in natricines, these occur only in the cervical vertebrae of colubrines.

### ***Coluber* s.l.** Linnaeus, 1758

### ***Coluber* s.l. 1**

(Fig. 14A–C)

**Material.** Seventy-two trunk vertebrae PAL EV 2013/13–84.

**Description.** The largest vertebra with a 5.5 mm centrum length corresponds to a mid-sized colubrid. The vertebral morphology is clearly of the '*Coluber*' type (Szyndlar 1987, 1991). The vertebrae are relatively elongate, with a well-marked interzygapophyseal constriction (Fig. 14A–C). In dorsal aspect, the anterior border of the zygosphene is straight to slightly convex between the weakly salient lateral lobes. The zygosphene is wider than the circular cotyle. The relatively small articular facets of the prezygapophyses are oblique in dorsal view. The prezygapophyseal processes are elongate and they project anterolaterally. The paradiapophyses comprise a laterally salient diapophysis and an almost flat parapophysis. The neural arch is somewhat depressed and its posterior borders are weakly convex to almost straight in posterior view. The neural spine is entirely preserved in only one vertebra, and here it is moderately high with weakly overhanging anterior and posterior borders. The centrum is narrow and well limited laterally by straight subcentral ridges. The haemal keel is clearly distinct and thin; its shape varies from gladiate to spatulate (*sensu* Auffenberg 1963). In a few vertebrae, the haemal keel forms a slight step in the anterior portion of the centrum.

**Remarks.** Colubrines with vertebrae of the *Coluber* type first occurred in the European earliest Oligocene. The earliest species referred to *Coluber* s.l. is '*Coluber*' *cadurci*, whose assignment to *Coluber*, as defined today, is most likely erroneous but cannot be definitively rejected. *C. cadurci* is known from MP 21 to MP 30 (Rage 2006); the species may also have been present in MN 1 and MN 2 in Germany and France (Rage 1988; Szyndlar & Schleich 1993). Four other species referred to *Coluber* have been reported from the Early Miocene of Europe: *Coluber dolnicensis* (MN 3a–MN 4; Ivanov 2002a; Szyndlar 1987), *C. caspioides* (MN 3a–MN 4; Ivanov 2002a; Szyndlar & Schleich 1993), *C. suevicus* (MN 3a–MN 7 + 8; Ivanov 2002a; Szyndlar & Böhme 1993) and *C. pouchetii* (MN 4–MN 6, ?MN 9; Rage & Bailon 2005; Augé & Rage 2000; Szyndlar 2005).

The Amöneburg fossil clearly differs from *C. cadurcensis* in having a higher neural spine, larger cotyles and condyles, a non-trilobate zygosphene, and stronger subcentral ridges. The moderately depressed neural arch and the presence of a step in the anterior part of the haemal keel of some vertebrae indicate *C. pouchetii* and *C. dolnicensis*. However, these two species show a peculiar feature lacking in the Amöneburg specimens: their diapophysis is clearly shifted posteriorly with respect to the parapophysis. The Amöneburg colubrine differs from *C. caspioides* in having paradiapophyses facing more ventrally in anterior view, smaller prezygapophyseal facets, slightly more gracile prezygapophyseal processes and posterior trunk vertebrae possessing a slightly convex zygosphenal border as seen in dorsal view. It is distinguished from *C. suevicus* by its dia- and parapophysis which are distinct from each other and, regardless of the size of the vertebrae, by the smaller prezygapophyseal facets and longer prezygapophyseal processes.

Finally, although this Amöneburg colubrine is most likely a new species of *Coluber* s.l., morphological differences are often subtle within colubrines and definitive comparisons require well-preserved specimens. Since none of the Amöneburg vertebrae is complete, this precludes erection of a new species.

### ***Coluber* s.l. 2**

(Fig. 14D–F)

**Material.** Twenty trunk vertebrae PAL EV 2013/85–104.

**Remarks.** These vertebrae closely resemble those of *Coluber* s.l. 1 (Fig. 14D–F). However, their cotyles and condyles appear slightly smaller. In addition, the rare preserved prezygapophyseal processes are somewhat less

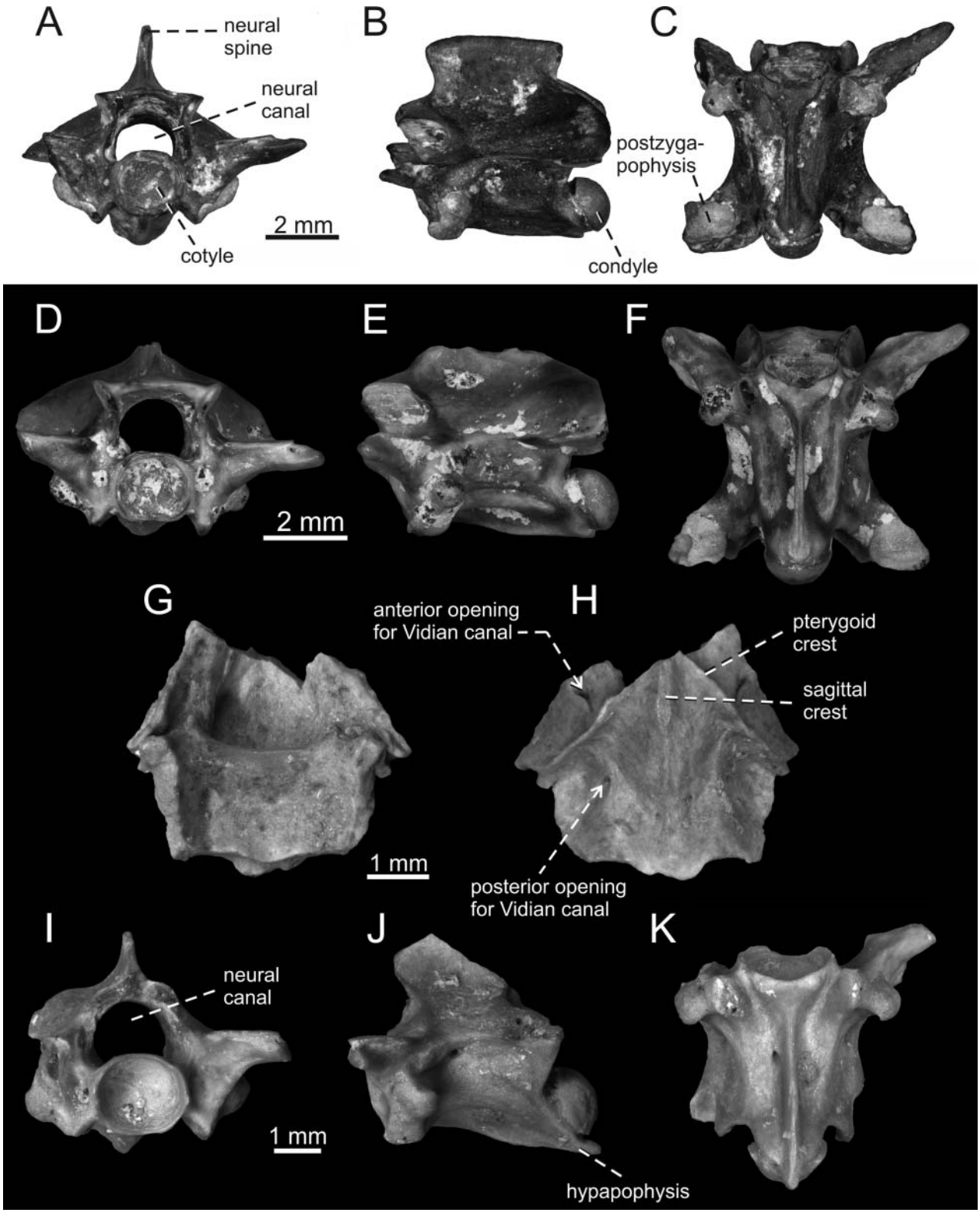


**Figure 14. A–C,** *Coluber* s.l. 1, trunk vertebra, PAL EV 2013/13, in **A,** anterior, **B,** lateral and **C,** ventral views. **D–F,** *Coluber* s.l. 2, trunk vertebra, PAL EV 2013/86, in **D,** anterior, **E,** lateral and **F,** ventral views. **G, H,** *Coluber* s.l. indet., parabasisphenoid, PAL EV 2013/105, in **G,** dorsal and **H,** ventral views. **I–K,** Colubroid indet., trunk vertebra, PAL EV 2013/106, in **I,** anterior, **J,** lateral and **K,** ventral views.

gracile and the only preserved neural spine appears lower than that in *Coluber* s.l. 1. This vertebral sample may represent a species distinct from, but closely allied to *Coluber* s.l. 1, this cannot be definitively confirmed.

### *Coluber* s.l. indet.
(Fig. 14G, H)

**Material.** One incomplete parabasisphenoid PAL EV 2013/105.

**Description.** This parabasisphenoid specimen lacks its parasphenoid portion (Fig. 14G, H). The preserved part is characterized by the presence of two lamellar, salient and oblique pterygoid crests (*sensu* Szyndlar 1984), which are distant from the bone's posterior margin. A sagittal crest is present. The position of the anterior opening of the Vidian canal presents an identifying feature. The opening on either side is clearly anterior to the pterygoid crest and not hidden by it. In addition, the opening is prolonged medially by a narrow slit, with a low crest running along the posterior border of the slit and slightly overhanging it. The posterior openings of the Vidian canals ('common' foramina) are distant from the posterior and lateral margins of the bone. These are strongly asymmetric, with the right foramen larger than the left. In addition, the right foramen is prolonged by a groove directed posterolaterally, while the left foramen is tiny, partly concealed by a small amount of matrix and lacks a groove on that side.

The anterior foramen for the *abducens* nerve is not visible on either side of the inner dorsal aspect. This foramen most likely opens in the notch for the sympathetic nerve located dorsal to the basipterygoid process (*sensu* Szyndlar 1984), together with the foramen for this nerve. The posterior foramina for the *abducens* nerve are markedly asymmetric, with the left one being much smaller.

**Remarks.** The lack of thickenings forming articular facets on the pterygoid crests or basipterygoid processes precludes assignment to snakes of the henophidian grade, namely booids, in this locality. On the other hand, the presence of lamellar and salient pterygoid crests demonstrates that this parabasisphenoid is not from an Elapidae or Viperidae. Judging from all snake vertebral types identified in this locality, this parabasisphenoid is consistent only with Colubridae. Within Colubridae, the position of the pterygoid crests and posterior openings of Vidian canals distant from the posterior border of the bone shows that this specimen cannot be assigned to Natricinae. Its overall morphology and, more specifically, the morphology of its pterygoid crests are clearly consistent with *Coluber* s.l., but it is impossible to assign it definitively to either *Coluber* s.l. 1 or 2 (even assuming that these two are distinct species). The peculiar morphology of the anterior orifices of the Vidian canals and asymmetry of the posterior openings of these canals and of the posterior foramina for the *abducens* nerve, are certainly significant at the species level. These combined characteristics have not previously been observed in living or extinct species.

### **Colubridae** Oppel, 1811 **or Elapidae** Boie, 1827
### Colubroid indet.
(Fig. 14I–K)

**Material.** One trunk vertebra (PAL EV 2013/106).

**Description.** Although this single vertebra is quite incomplete, the preserved features are significant (Fig. 14I–K). The vertebra is lightly built, with a large neural canal. The cotyle is comparatively large and slightly depressed, with a paracotylar foramen present on either side. The prezygapophyseal facets are located markedly above the floor of the neural canal. The prezygapophyseal processes were well developed, as demonstrated by the remaining base of the left one, but their length cannot be estimated. The dia- and parapophyseal areas are quite distinct. Well-marked subcentral ridges clearly delimit the ventral aspect of the centrum, and its posterior half is almost flat. Narrow subcentral grooves are present in the anterior half. A thin, strongly laterally compressed hypapophysis is present, with its ventral margin sigmoid in lateral aspect. The hypapophysis ends in a point, extending almost horizontally below the condyle and reaching or perhaps even projecting beyond its posterior level.

**Remarks.** This vertebra demonstrates it is a colubroid by its light build, broad neural canal, well-developed prezygapophyseal processes, distinct dia- and parapophyseal areas and by the presence of paracotylar foramina. On the other hand, the morphology of the hypapophysis, and more specifically its posteroventral ending, is unusual. The centrum, well delimited by marked subcentral ridges, is reminiscent of Elapidae and natricine Colubridae, and this is consistent with the lateral compression of the hypapophysis. In contrast to the hypapophysis of most snakes, which is directed more or less posteroventrally, the hypapophysis of PAL EV 2013/106 projects almost posteriorly. This orientation is close to that of 'Natricinae D' from MN4/5 in Vieux-Collonges, France (Ivanov 2000), and *Micronatrix* from the Clarendonian (Middle/Late Miocene) of the USA (Parmley & Hunter 2010), but it remains more ventral. A more similar orientation occurs in small elapids and assignment to this family appears possible. However, the poor preservation of this single specimen precludes unequivocal referral.

Although natricines are recognized from the Early Oligocene (see above), no elapid is confirmed before MN 4 in Europe (Szyndlar & Rage 1990). However, Kuch *et al.* (2006) assigned an isolated fang from Oppenheim/Nierstein Quarry in Germany to elapids. Since this locality is considered MN 2a, this record would be the earliest elapid

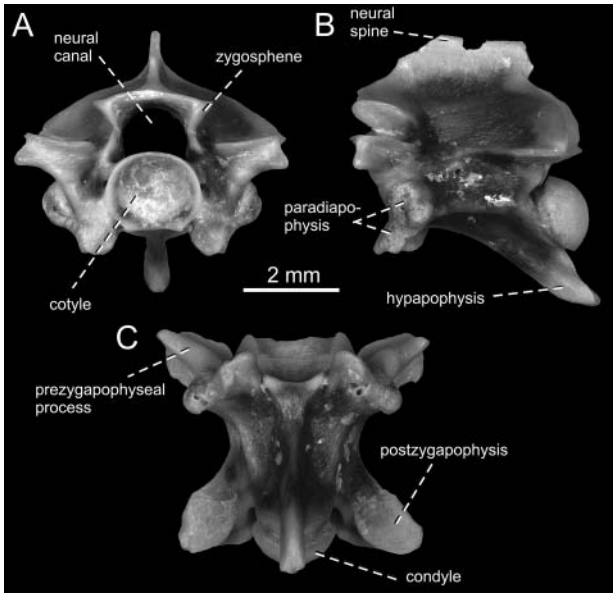


**Figure 15.** *Vipera* cf. '*aspis* complex', trunk vertebra, PAL EV 2013/107 in **A,** anterior, **B,** lateral and **C,** ventral views.

from Europe. The fang is relatively curved and its canal is not fully closed anteriorly. Although these characteristics are more or less similar to those of elapids, but also to those of replacement fangs of vipers are not definitive, and therefore, assignment of this fang to elapids cannot be accepted without reservation.

Finally, although both the Amöneburg incomplete vertebra and the fang from Oppenheim/Nierstein may signify elapids, such referrals cannot be confirmed, and consequently the earliest currently accepted European elapids are in MN4.

**Viperidae** Laurenti, 1768
***Vipera*** Laurenti, 1768
***Vipera* cf. '*aspis* complex'**
(Fig. 15)

**Material.** Three trunk vertebrae PAL EV 2013/107–109.

**Description.** The vertebrae display characteristics that clearly signify Viperidae (Fig. 15). Although the vertebrae as a whole are somewhat depressed in form, the neural arch is quite strongly depressed. The cotyle and condyle are large. A straight hypapophysis is present on all vertebrae. The ventral portion of the condyle lies against the posterior margin of the hypapophysis. The prezygapophyseal facets are inclined towards the horizontal and the prezygapophyseal processes are short. The paradiapophyses are narrow and tall, and relatively elongate parapophyseal processes prolong them anteroventrally. The subcentral ridges are weakly marked.

In addition, it should be added that these vertebrae are generally medium-sized, with the largest centrum length being 4.6 mm. The cotylar rim forms ventrolateral cotylar processes, and the paracotylar notches are very narrow. Since the neural spine is damaged on all specimens, the height cannot be estimated.

**Remarks.** Szyndlar & Rage (1999, 2002) recognized three distinct assemblages within *Vipera*: the '*V. berus* complex', '*V. aspis* complex' and 'oriental vipers'. The Amöneburg viper markedly differs from those of the oriental complex. The vertebrae of the latter are clearly larger, shorter and their neural arch is more strongly flattened. Distinction between the *aspis* and *berus* complexes is more difficult, especially when only mid-trunk vertebrae are available, as in these Amöneburg specimens. The vertebrae of the *V. berus* complex appear to be smaller and slightly more elongate than those from Amöneburg. Moreover, the preserved part of the neural spine on PAL EV 2013/107 suggests that it was higher than that in the *V. berus* complex. On the other hand, the vertebrae from Amöneburg are consistent with those of the *V. aspis* complex. Therefore, with all things considered and also due reservation, these fossils are assigned to the *V. aspis* complex.

Szyndlar & Rage (1997) reported the *V. berus* complex from the earliest Miocene (MN 1 and MN 2) of France, but they later corrected this (1999), stating that the identification based on material from France and Germany was erroneous. According to Szyndlar & Rage (2002), the *V. berus* complex first occurred later in Europe: during the Late Miocene (MN 9) in Eastern Europe and only during the latest Pliocene (MN 17) in Western Europe. It should be noted that, since MN 17 is now accepted as Early Pleistocene, this indicates that the *V. berus* complex was absent in Western Europe prior to this defined Pleistocene.

Böhme (2008) reported a possible viperid (as '?Viperidae indet.') from the latest Oligocene (MP 30) of Oberleichtersbach, Germany. However, this is based on only two 'badly preserved' vertebrae. Moreover, the best-preserved specimen is an anteriormost trunk ('cervical') vertebra, and this is insufficient for identification (Rage 1984, p. 56). This snake from Oberleichtersbach is more likely a colubrid. The earliest known confirmed vipers come from the MN 1–MN 2 interval and they form part of the *V. aspis* complex (Szyndlar & Rage 1999, 2002); and the Amöneburg viper fulfils these prerequisites. Szyndlar & Rage (2002, p. 423) reported vipers from MN 1 at Hessler and Weisenau, in Germany, although according to Böhme & Ilg (2003) the Hessler site (now known as Wiesbaden-Biebrich) and also the Weisenau site, which has yielded vipers, are MN 2a in age. However, vipers may have been present in MN 1 as Weisenau includes beds of MN 1 age and reports of viperids from Weisenau, with less precision, may be from such an MN 1 bed. In addition, viperids are present in Saint-Gérand, France; the Saint-Gérand label is reserved for a mixed-fossil collection from several localities of MN 1 and MN 2, close

to Saint-Gérand in central France. It is impossible to determine whether viper ages in this collection are MN 1, MN 2, or both. Regardless of the precise age of the earliest known vipers, MN 1 or MN 2, the Amöneburg *Vipera* is amongst the oldest.

### Indeterminate snake material

**Material.** One incomplete compound bone PAL EV 2013/111; 35 trunk and caudal vertebrae PAL EV 2013/112–146.

**Remarks.** The interest of this material is that most specimens apparently belong to colubrids (but this cannot be unequivocally demonstrated because they are caudal vertebrae and this is based on the overall morphology of incomplete specimens only), adding to the number of colubrids in the locality and thus to their dominance.

### Squamata indet.
(Fig. 16)

**Material.** One incomplete left portion of an atlas PAL EV 2013/272; fragments of humeri (two proximal and one distal part) PAL EV 2013/273–274; one left pelvis PAL EV 2013/275.

**Description.** A complete squamate atlas consists of three loosely united parts – the two halves of the neural arch and the ventrally located first intercentrum – but only a fragment of the left portion is preserved in this specimen (Fig. 16A). In lateral view, the pedicle is wider dorsally. The lamina is preserved above, forming the dorsal part of the neural arch. It is broad in lateral view, but pointed and almost triangular in shape. The posterodorsal process is not completely preserved. Its projection, where the zygapophyseal articulation area is located, is broken away. The ventral region, located below the pedicle, possesses a triangular transverse process that is well developed, pointed and orientated posterolaterally. This specimen does not possess any characteristics to allow its precise placement amongst lizards.

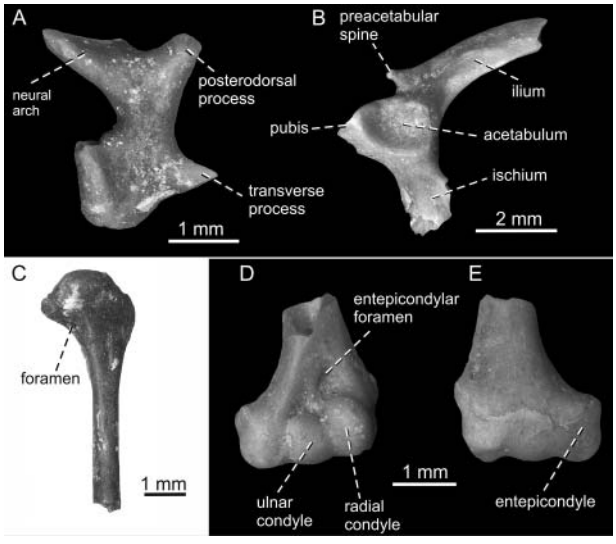


**Figure 16.** Squamata indet. **A,** atlas, PAL EV 2013/272, in lateral view. **B,** pelvis, PAL EV 2013/275, in lateral view. **C,** proximal region of humerus, PAL EV 2013/273, in ventral view. **D,** distal region of humerus, PAL EV 2013/274 in **D,** ventral and **E,** dorsal views.

The pelvis is partly preserved. The ilium is an elongated bone. Its anterodorsal margin forms a sharp crest, while the posteroventral one is more rounded. Unfortunately, the end of the ilium is broken, with parts missing. On the proximal aspect, the preacetabular spine forms an anterodorsally orientated short and blunt process. A small foramen is located on the lateral side, close to this region. The elliptical acetabulum is large (Fig. 16B). The ischium is only partly preserved, becoming broader ventrally and having a very shallow depression on its lateral wall. Here a small foramen is located. Only the base of the pubis, which forms a part of the anterior region of the acetabulum, is preserved. Unfortunately, the rest of the pelvis is broken and missing.

The humerus is elongate, with the proximal and distal epiphyses fused. The proximal extremity is broad and elliptically rounded. It forms the upper surface of the head of the bone. The elliptical foramen for the brachial nerve (Lécuru 1968) is located on the medial surface, directly below the head (Fig. 16C). The bone becomes narrow distally, forming a slim diaphysis. The distal part bears a well-developed, larger elliptical radial condyle (capitellum *sensu* Romer 1956) with a smaller ulnar condyle on its ventral aspect (Fig. 16D). The large entepicondylar foramen, forming the orifice of the brachial nerve, is located above the capitellum. The entepicondyle (attachment for *flexor muscules*) is robust and broad. The opposite side, forming the supinator process, is distinctly smaller and the ectepicondylar foramen is located here. The dorsal surface forms the attachment for the *extensor muscules* of the forearm (Fig. 16E).

**Remarks.** The fused epiphyses and the presence of proximal and distal openings for the brachial nerve are typical of lizards (Lécuru 1968; Estes *et al.* 1988).

## Discussion

Faunas of hitherto accepted MN 2 age are poor in number and have remained largely unstudied. The study of the squamate assemblage from Amöneburg in western Germany is the first report of this magnitude on a fauna of this age, which is very rich and diverse by earliest Miocene standards. The extent of this diversity was unexpected; with the assemblage comprising at least 14 taxa

**Table 1.** List of taxa examined from Wiesbaden-Amöneburg.

| Gekkota | Lacertiformes + 'Scincomorphan' | Anguimorpha | Amphisbaenia | Serpentes |
|---|---|---|---|---|
| Gekkota indet. | *Lacerta poncenatensis*<br>Lacertidae indet.<br>Scincomorpha indet. | *Pseudopus* cf. *ahnikoviensis*<br>*Ophisaurus spinari*<br>*Ophisaurus* sp.<br>Anguidae indet.<br>*Merkurosaurus ornatus*<br>cf. *M. ornatus*<br>Shinisauria indet.<br>Platynota indet. | *Blanus thomaskelleri* sp. nov. | ?*Falseryx* sp.<br>Booid indet.<br>cf. *Natrix* sp.<br>cf. *Neonatrix* sp.<br>?*Neonatrix* sp.<br>*Coluber* s.l. 1<br>*Coluber* s.l. 2<br>Natricinae or Elapidae indet.<br>*Vipera* cf. '*aspis* complex' |

which cannot all be definitively assigned at species- or genus-level (Table 1).

At least three taxa assigned to a genus or species in other MN 2 localities are absent at Amöneburg. Anilioid snakes have been reported from two localities of MN 2 age: Ulm-Westtangente (Germany) and Montaigu-le-Blin (France). In both localities, the group apparently includes *Eoanilius* (Szyndlar & Böhme 1993; Szyndlar & Rage 2003). *Eoanilius* is recognized from the Middle Eocene (MP 16; Rage 2012) to the late Early Miocene (MN 5; Szyndlar 2009). Although present in the MN 2–MN 5 interval in Germany, neither *Eoanilius* nor any other anilid is present in the Amöneburg specimens. *Lacerta filholi* is first known from the Early Oligocene (MP 22; Augé 2005) and occurs frequently in the Oligocene. It survived the Oligocene–Miocene transition, and Augé (2005) reported its last occurrence from Poncenat, MN 2 in France. It was not identified at Amöneburg, unless synonymy with *Lacerta poncenatensis* is demonstrated (see above). *Bransateryx* is an erycine snake common in the Oligocene, but after this epoch it has been confidently reported only from Paulhiac (MN 1) in France (Rage & Szyndlar 2005). However, Müller (1998) also reported it from Poncenat, a locality of MN 2 age in France. Identification from the latter locality was based on some skull bones that compare closely with those of *Bransateryx vireti* from Coderet (MP 30, France). However, there are no caudal vertebrae of erycines at Poncenat, which renders the presence of *Bransateryx* in this locality extremely doubtful. Regardless of these assertions, no erycine is amongst the Amöneburg specimens. From these three taxa, the two anilioid and the erycine snakes were more or less fossorial. Therefore, this local absence may be environmentally determined.

The fauna from Amöneburg includes only two confirmed survivors from the Oligocene, *Merkurosaurus* (reported from the latest Oligocene; Böhme 2008) and *Ophisaurus* (known since the Late Eocene; see Klembara & Green 2010, with the oldest evidence of *O. spinari* presented herein). Apart from this latter find, only two snakes from Amöneburg may be holdovers. The small indeterminate booid from Amöneburg is reminiscent of Oligocene and MN 1–MN 2 forms. In Europe, such booids disappeared after MN 2, and small booids at younger levels belong only to erycine Boidae. Unfortunately, neither Oligocene nor earliest Miocene booids were studied and it is impossible to determine whether the snake from Amöneburg is related to an Oligocene or a Miocene form. *Falseryx*, assuming that this snake is actually present at Amöneburg, may be either a survivor of Early Oligocene representatives of the genus, or a forerunner of the late Early Miocene members of the genus.

Various taxa that are common in the Oligocene and occur in MN1 (and possibly in MN 2) are absent amongst the Amöneburg collections. Amongst these are the amblyodont lacertid lizards and the snakes *Platyspondylia* and *Bransateryx*. Amblyodont Lacertidae had somewhat enlarged (amblyodont) teeth and were represented by several genera and species (Augé 2005). The presence of amblyodont teeth in lacertids is a feature known to be acquired repeatedly and independently at different times in the European Tertiary (Augé 2005). However, while amblyodont lacertids were common during the Oligocene, amblyodont taxa became rare following this epoch (Roček 1984; Augé *et al.* 2003) and the amblyodont condition was clearly weaker than in the Late Oligocene forms *Pseudeumeces* and *Dracaenosaurus*. Apart from *Pseudeumeces*, which may have been present in MN 1 (Augé & Hervet 2009), it is not possible to state whether amblyodont forms from the Miocene are closely related to those of the Oligocene or if they evolved independently. Regardless of this, the Oligocene–Miocene transition profoundly affected amblyodont lacertids. *Platyspondylia* was a small 'tropidophiid' snake, which was common in the Oligocene but did not survive the end of the epoch (MP 30). The erycine *Bransateryx* reached MN 1, but its presence in MN 2 is doubtful, as discussed (see above). Regardless, it is lacking in the Amöneburg assemblage. The absence of these taxa at Amöneburg indicates a clear change from earlier faunas. This change is magnified by the presence of newcomers that enriched the fauna:

*Lacerta poncenatensis*, *Pseudopus* cf. *ahnikoviensis*, cf. *Neonatrix*, *Coluber* s.l. 1 and 2 (which appear to be closely related to a younger Miocene complex of *Coluber*), ?elapids and *Vipera* of the '*aspis* complex'. The presence of several colubrid taxa highlights a distinct change from the earlier faunas. Previously, colubrids were considered to dominate snake populations only after the Dark Period, i.e. after MN 2 (Szyndlar 2012), but the Amöneburg fauna indicates that this dominance began earlier, during MN 2.

The presence of new taxa in MN 2 may have resulted from local originations, but at least some of these newcomers (the platynotan, cf. *Neonatrix*, ?elapids, and the *Vipera* if not already present in MN 1) were immigrants because no potential ancestors existed in Europe. Based on the fact that none of the taxa exhibit African affinities, it is presumed that these immigrants emanated from Eastern European and/or Asian sources.

Although the Amöneburg fauna reflects a change with regards to the Oligocene, it does not include taxa that entered Europe with the great wave of dispersals initiated during MN 3 and spread throughout Europe mainly during MN 4.

In the single locality of MN 3 age, Merkur-North, newcomers include cordylid lizards (aff. *Palaeocordylus bohemicus*; Čerňanský 2012), chamaeleonids (Fejfar & Schleich 1994; Čerňanský 2010a), boine snakes of the Miocene complex of *Bavarioboa* (*Bavarioboa* sp., small size; Ivanov 2002a; Szyndlar & Rage 2003) and, if not already present in MN 2, elapid snakes. Here, cordylids deserve comment. The presence of cordyliforms (?Cordylidae) in the Eocene was confirmed (Bolet & Evans 2013) and they were perhaps present in the latest Oligocene (MP 30) in Germany (Böhme & Lang 1991). The report from the latest Oligocene is problematic because the only specimen (a postcranial skeleton) is lost and recognized only from a drawing. Its interpretation therefore remains questionable. In addition, it should be noted that Böhme & Ilg (2003) referred *Ophisaurus ulmensis* from Obere Eselsberg (MN 2, Germany) to the genus *Palaeocordylus*. Thus, cordylids would be present in MN 2. However, as originally recognized by Gerhard (1903), *O. ulmensis* (currently under revision by AČ and JK) cannot be assigned to cordylid. Finally, aff. *Palaeocordylus bohemicus* from MN 3 is the earliest confirmed member of the second cordylid record in Europe, the first one being clearly older and most likely restricted to the Eocene. Therefore, during MN 3, two taxa with African affinities, the chamaeleonids and the cordylids, reached Europe (assuming that there was no cordylid there in the latest Oligocene).

Newcomers are more numerous in MN 4 localities: the varanid *Varanus*, large boids (*Python*, large *Bavarioboa*), various colubrids, the elapid *Naja* and large viperids of the 'oriental complex' of *Vipera* (Szyndlar & Schleich 1993; Ivanov 2001; Rage & Bailon 2005). As for MN 2, most newcomers appear to be immigrants from the east. These mainly involve snakes (Ivanov 2001; Szyndlar 2012), amongst which are *Naja* (represented by *N. romani*; Szyndlar & Rage 1990) and the *Vipera aspis* complex which is a typically Eurasian assemblage. Although the indeterminate species of *Varanus* and *Python europaeus* from MN 4 may be of African origin, this cannot be demonstrated unequivocally (Szyndlar & Rage 2003; see also Vidal *et al.* 2012).

It should be noted that the material from localities of this time interval was collected by several palaeontologists and that we do not know how all collections were made; therefore, it is not possible to undertake more rigorous analyses or statistical tests. However, on the basis of the available material, we may conclude that the time interval comprising the latest Oligocene (MP 29–30) and Early Miocene up to MN 4 resulted in a prominent faunal turnover which brought modern squamate fauna to Europe. This conclusion should be bolstered by new collections from the localities in question. Nevertheless, we are convinced our portrait will not be significantly altered. This turnover was not abrupt, so that MN 2 illustrated by Amöneburg fauna appears to represent the intermediate of three stages. The first stage followed the extinction of the terminal Oligocene (and ?MN 1). The second stage, represented by Amöneburg, of MN 2 age (?MN 1), followed the arrival of immigrants from the east, while the third and final stages corresponded to the wave of dispersals into Europe during MN 3 and MN 4, including immigrants of eastern and African origin.

These three stages are clearly related to climate change. During the comparatively dry and cool Oligocene, several forms developed via adaptation to this environment. The temporary return of a warm and humid climate (e.g. Mosbrugger *et al.* 2005) abruptly eliminated some forms such as *Platyspondylia*, while others, including the Oligocene assemblage of amblyodont lacertids and *Bransateryx*, disappeared more gradually during the Oligocene–Miocene transition. Moreover, the climate change brought new taxa to Europe. A subsequent rise in temperature during MN 3 (Miocene Climatic Optimum; Böhme 2003) brought a second, large wave of immigrants. Coupled with the possibility of African taxa arriving in Europe, these immigrants led to colonization of the continent by the richest squamate fauna in European prehistory.

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