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ORIGINAL PAPER

Fossil squamate faunas from the Neogene of Hambach (northwestern Germany)

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Abstract Fossil squamate faunas from the Hambach lignite mine are described here for the first time. The material comes from two stratigraphic levels—the older, Hambach 6C (MN 5), is dated to the middle Miocene, whereas the younger sites Hambach 11 and 13 are dated to late Pliocene (MN 16). Although fragmentary, the Hambach 6C material reveals a diversity of squamates in a particularly interesting period—the beginning of the middle Miocene. The chamaeleonid material consists of a squamosal and the jaw fragments. The squamosal is a previously unknown element in European fossil chameleons and it is tentatively allocated here to *Chamaeleo* aff. *andrusovi*. This clade is very important as a climatic indicator at the beginning of the middle Miocene in central Europe because the lower mean annual temperature limit for chameleons is 17.4 °C. In addition to the chamaeleonid, two types of lacertid lizards are recognised based on the preserved morphology. The anguid material is allocated to *Pseudopus* cf. *ahnikoviensis*. This material forms the youngest record of this taxon. Additional anguid material is attributed to *Pseudopus* sp. and Anguidae indet. Snake fauna here consists of the following taxa: *Eoanilius*, *Bavarioboa*, cf. *Falseryx*, "*Coluber*", *Texasophis*, *Telescopus*, *Natrix*, cf. *Naja* and *Vipera*. Hambach 6C is the geologically youngest fossil site yielding remains of *Eoanilius*, possibly also youngest *Falseryx* (cf. *Falseryx*). Although the Hambach 11 and 13 upper Pliocene (MN 16) sites exhibit low palaeodiversity, there is a large assemblage of *Pseudopus* cf. *pannonicus. Natrix* and Colubrinae indet. are identified in the snake population.

Keywords Lizards · Snakes · Miocene · Pliocene · Lower Rhine Basin

Abbreviations

IPB-HaH	(Hambach Hauptflöz = Hambach 6C); Steinmann Institute Rheinische Friedrich-Wilhelms-Universität Bonn, Germany
IPB-HaR	(Hambach Reuverton = Hambach 11 and Hambach 13); Steinmann Institute Rheinische Friedrich-Wilhelms-Universität Bonn, Germany

Introduction

Lizards, snakes and amphisbaenians form the highly successful clade of terrestrial reptiles called Squamata (see, e.g. Gauthier et al. 2012; Wiens et al. 2012). These animals are particularly interesting because of their lizard to serpentiform body plan and size range, their locomotion and anti-predation strategies and especially because of their different feeding methods.

The squamate faunas described here come from two stratigraphic levels in the Hambach open pit mine. Remains from the older level come from the Miocene Hambach 6C (MN 5), whereas the younger Hambach 11 and 13 sites are dated to the late Pliocene (MN 16). Although there is a significant temporal difference, the herein described remains allow us to study

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faunal compositions and changes in two Neogene periods at the same locality.

The early/middle Miocene transition started very important changes in Cenozoic climate evolution. This time is also correspondent to the palaeogeographic reorganisation of the Central Paratethys realm (Zachos et al. 2001; Böhme 2003). In central Europe, the warm and humid Miocene episode (the Miocene Climatic Optimum) represents the temporary return of the paratropical humid climate (e.g. Böhme 2003), compared with the relatively cooler and drier Oligocene (Mosbrugger et al. 2005; for Oligocene squamate faunas, see e.g. Szyndlar and Rage 2003; Böhme 2008; Čerňanský and Augé 2012, 2013; Čerňanský et al. 2016). It peaked at 18–16.5 Ma (Ottnangian, Karpatian). Although probably unchanged temperature was present during the early Badenian, this period is characterised by the strong increase of seasonality in precipitation (up to six dry months, in contrast to a period of high precipitation during the Ottnangian and Karpatian; see Böhme 2003). It should be noted that *Python* sp., which is the most thermophilous reptile known from the European Neogene, was described from Grisbeckerzell 1b (15.0–14.9 Ma; see Ivanov and Böhme 2011). The early stage of this climatic transition (from approximately 16 to 14.8 Ma) was marked by major short-term variations in global climate, East Antarctic Ice Sheet volume, sea level and deep ocean circulation (Flower and Kennett 1994). The following major cooling between 14.8 and 14.1 Ma brought permanent change (Flower and Kennett 1994) and was most probably responsible for the extinction of many highly thermophilous squamate taxa in central Europe (see, e.g. Ivanov and Böhme 2011). The distribution, richness and diversity of squamates, as ectothermic animals, are highly dependent on temperature and climatic condition (see e.g. Haller-Probst 1997; Markwick 1998). For these reasons, these climate changes had marked impact on the squamate history (Rage 2013).

The Hambach 6C locality provides a unique vertebrate fauna from the European early middle Miocene (MN 5, 16.0–15.2 Ma; see Mörs et al. 2000). During the middle Miocene (MN 5), the squamate fauna remained rich, diverse and tropical in nature (see Rage 2013). Several other central European localities yielded squamate remains from MN 5 [Petersbuch 39-III (Klembara et al. 2010); Butenbach 1b and Unterempfenbach 1b (Böhme and Ilg 2003); Oggenhausen (Böttcher et al. 2009) and Wannenwaldtobel (Čerňanský 2011a; transitional period MN 5/6)]. Böhme (2010) reported a rich ectothermic vertebrate fauna from the slightly older German locality called Sandelzhausen (16.47 or 16.27 Ma, latest early Miocene, near the early/middle Miocene Boundary). In the following MN 6 zone, squamates are described from Litke in Hungary (15.2–14.8 Ma; Venczel and Hír 2015). Comparison of the Hambach 6C squamate fauna with slightly older and younger localities highlights changes in squamate faunas in central Europe in this particular period.

However, the temperature decrease in the late middle Miocene continued during the Pliocene and early Pleistocene (Böhme 2003). This caused faunal regionalization and decreased richness. Although thermophilic taxa remained present in western and southern Europe, they were absent from central Europe. Many taxa became extinct there during the late Pliocene and early Pleistocene (Rage 2013). It should be noted that many aspects of faunal existence at this time remain unknown because only the southern areas of western Europe are documented and the Pliocene of eastern Europe is practically unknown (see Rage 2013). It should be noted that several Pliocene faunas are known from Slovakia (Ivanovce MN 15b and Hajnáčka MN 16a; Klembara 1986; Čerňanský 2011b). Hambach 11 and 13 sites provide better understanding of faunal composition during this period.

The aims of this paper are (1) to describe the material recovered from Hambach in detail and (2) to compare taxa occurrence here with other localities in Europe, with the final goal of improving the knowledge of the Neogene squamate faunas of Europe. This should prove useful for future analyses of past squamate diversity and faunal change.

Material and methods

Dalsätt et al. (2006) report that the Hambach locality produced more than 4000 vertebrate remains which can be determined and classified. However, with the exception of anguid osteoderms, squamate remains are relatively rare because of squamate bone fragility and depositional environment. The fossils are recovered from channel fills and therefore consist of disarticulated, but mostly well preserved teeth, jaws and other elements. Squamate fossils are stained brown at both sites, similar to all other Hambach vertebrate remains. The material described herein was collected by two former Rheinbraun employees, Fritz von der Hocht and Bertram Wutzler, and co-author (TM) while screen-washing bulk samples. The specimens are housed in the palaeontological collections of the Steinmann Institute, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany, and catalogued under IPB-HaH (Hambach Hauprflöz = Hambach 6C) and IPB-HaR (Hambach Reuverton = Hambach 11 and Hambach 13).

Photographs were taken with a Leica M205 C binocular microscope with axially mounted DFC 290 HD camera, LAS software (Leica Application Suite) version 4.1.0. Several specimens were also photographed with scanning electron microscope (SEM—FEI Inspect F50) at the Slovak Academy of Sciences and at Museum für Naturkunde in Berlin.

The dentary of *Pseudopus* cf. *ahnikoviensis* was scanned using the micro-computed tomography (CT) facility at the Slovak Academy of Sciences in Banská Bystrica, using a Phoenix mikro-CTv|tome|x L240 with the following settings:

VxSize = 0.00300011; current = 140; voltage = 90; inttime = 6000; average = 1; steps = 1400; steps360 = 1400. The images were recorded over 360°. In addition, the *Pseudopus* cf. *pannonicus* maxilla was scanned using the CT facility at the Museum für Naturkunde Berlin, Germany, using a Phoenix GE Nanotom with the following settings: VxSize = 0.00199065; current = 150; voltage = 80; inttime = 1000; average = 2; steps = 1600; steps360 = 1600. The images were recorded over 360°. The CT data-sets were analysed by VG Studio Max v. 2.2 on a high-end computer workstation.

Geological setting and faunal content

The Hambach open pit mine, approximately 35 km west of Cologne (Fig. 1), is one of the world deepest open pit mines. It is situated in lignite-rich, relatively continuous Neogene deposits of the Lower Rhine Basin: a graben structure filled with debris from the rising Rhenish Massif following the Oligocene. The lignite seams interfinger with marine (beach) sands of the transgressing North Sea and with floodplain and fluvial sediments. Similar depositional environments reoccurred from the Oligocene to the early Pleistocene, over a time span of almost 20 Ma (Schäfer et al. 2004).

The late Orleanian (middle Miocene) Hambach 6C fauna was recovered from a huge channel fill in the Frimmers dorfseam of the Ville Formation (Schäfer et al. 2004). The Hambach 6C fauna contains the following: (1) marine and freshwater fish (sharks, rays, teleosts; Hierholzer and Mörs 2003), (2) amphibians (salamanders, anurans), (3) reptiles (turtles, alligators, squamates; Klein and Mörs 2003; Joyce et al. 2004), (4) birds (Dalsätt et al. 2006), (5) marine and semi-aquatic mammals (whales, dolphins, beavers, mustelids; Stefen and Mörs 2008; Mörs and Stefen 2010) and (6) terrestrial mammals (Ziegler and Mörs 2000; Rössner and Mörs 2001; Nemetschek and Mörs 2003; Mörs and Kalthoff 2004; Mörs 2006, 2008).

Fig. 1 Hambach location in Germany

These combined finds indicate estuarine settings in a large fluviatile system surrounded by extended coal swamps (Mörs et al. 2000; Mörs 2002). This palaeoecological reconstruction is supported by sedimentological and palaeobotanical evidence [see Schäfer et al. (2004) for further references]. The rich mammal association of more than 70 taxa at Hambach 6C is correlated with the late MN 5 of the European Land Mammal Zonation (Mörs et al. 2000; Mörs 2002). The high tetrapod diversity of tropical elements including chameleons, carettochelyine turtle and the primate *Pliopithecus* documents the “Mid-Miocene climate optimum”. This, in turn, supports the age of the fauna at approximately 15.5 Ma. A tropical-like climate at the time of Ville Formation deposition is also demonstrated by palaeoflora discovered in the Lower Rhine Basin (Utescher et al. 2000).

The late Pliocene (early Villanyian) Hambach 11/13 fauna is dominated by small vertebrates (Mörs 2002), with fossils collected from the two smaller contemporaneous Hambach 11 and 13 channel fills in the Reuver clay (Öbel beds; see Kemna 2005). The fauna comprises (1) freshwater fish (Hierholzer and Mörs 2003), (2) amphibians (salamanders, anurans), (3) reptiles (turtles, squamates), (4) birds (Dalsätt et al. 2006) and (5) both semi-aquatic and terrestrial mammals (Mörs et al. 1998; Lacombat and Mörs 2008). The depositional environment is interpreted as oxygenated water and currents in a river channel setting in close vicinity to lakes or oxbows (Mörs 2002). This reconstruction is supported by sedimentological and palaeobotanical evidence (e.g. Schwarz and Mörs 2000; Heumann and Litt 2002; Schäfer et al. 2004; Kemna 2005). The Hambach 11/13 fauna is correlated with MN 16a based on rodent association (Mörs et al. 1998; Mörs 2002). The late Pliocene age (approximate 2.5 Ma) is also documented by the depleted tetrapod diversity, although some “Tertiary” faunal elements remain present (e.g. *Andrias*, *Latonia*, *Chelydropsis* and *Pliopetaurista*). Palaeomagnetic and heavy mineral analyses by Kemna (2005) support this biostratigraphical dating.

Systematic palaeontology

Squamata Oppel, 1811
Iguania Cuvier, (1817)
Chamaeleonidae Gray, 1825
Chamaeleo Linnaeus, 1758–1759

Chamaeleo aff. andrusovi Čerňanský, 2010
(Fig. 2)

Material, horizon and locality: Right squamosal IPB-HaH 3900; middle Miocene (MN 5), Hambach 6C.

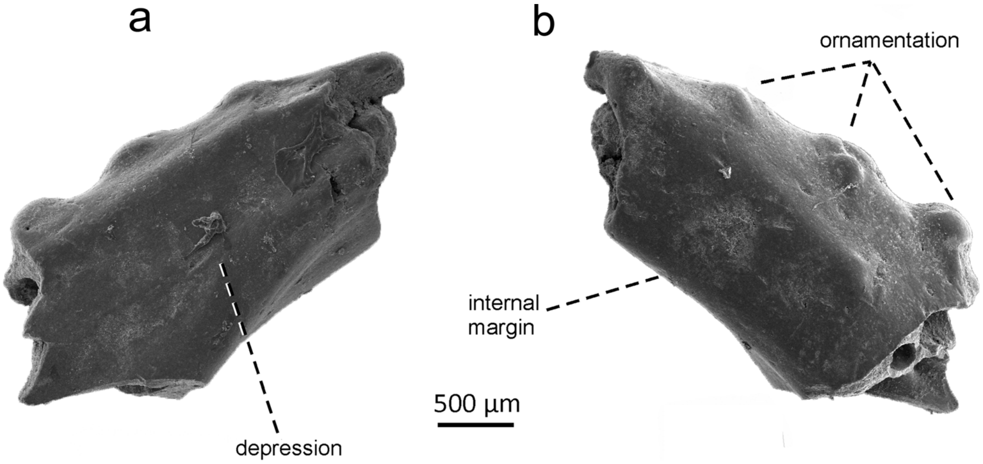


Fig. 2 *Chamaeleo* aff. *andrusovi*: squamosal (IPB-HaH 3900) in **a** internal aspect; **b** external aspect

Right squamosal: A small portion of a right squamosal is preserved. It is a rod-shaped bone, anterodorsally–posteroventrally depressed with sculpture on its latero-dorsal side. The sculpture consists of protuberances which decrease in size posteromedially. The posterior aspect of the bone is smooth, having only several foramina. The inner, anterior surface bears a shallow longitudinal depression which is centrally located and bordered by low ridges.

Remarks: The chamaeleonid fossil record is generally extremely poor, resulting in significant gaps in our knowledge of the evolution of this group. Apart from maxillae and dentaries, the only finds are the cranial bones from the Czech Republic (MN 4, Dolnice near Cheb) described as *Chamaeleo andrusovi* Čerňanský 2010 and a skull-bone fragment from Greece (MN 4, Aliveri; see Georgalis et al. 2016a). The Czech material consists only of parietal, jugals, prefrontal and the postorbital portion of postorbitofrontal. Therefore the squamosal described here is a new, additional bone. It was previously unknown in European fossil chameleons. Squamosal size indicates a small body size taxon, and it has pustular ornamentation resembling cranial elements in *Ch. andrusovi*. However, the material is only tentatively allocated to this taxon because the ornamentation is not strongly developed.

? Chamaeleonidae tooth morphotype 1.
(Fig. 3a–d)

Material, horizon and locality: Right maxilla IPB-HaH 3901, left maxilla IPB-HaH 3902; middle Miocene (MN 5), Hambach 6C.

Maxilla: All maxillae are only fragmentarily preserved, with the largest bearing four preserved teeth. The preserved portion of the labial surface is smooth.

Dentition: Dentition is acrodont; with the robust teeth increasing in size posteriorly. Teeth are not in contact to each other (for this state, see Čerňanský 2011a). Teeth are very slightly tricuspid (mesial and distal cusps are not distinctly stepped from the main central cusp). The teeth bear vertical (radial) striations.

Remarks: Chamaeleonids from this period were previously described from the Wannenwaldtobel 2 locality, middle Miocene (Čerňanský 2011a). The dentition in the material from the latter locality is similar to that described herein as ? Chamaeleonidae indet 1. (see Čerňanský 2011a, Fig. 6).

? Chamaeleonidae tooth morphotype 2
(Fig. 3e–f)

Material, horizon and locality: Right maxilla IPB-HaH 3903; middle Miocene (MN 5), Hambach 6C.

Maxilla: Only a fragment of the right maxilla with two teeth is preserved. In medial view, a small portion of the supradental shelf above the teeth is evident. The labial surface of the bone is smooth.

Dentition and comparison with ? Chamaeleonidae indet. 1.: The dentition is acrodont, with the teeth quite slender and more pointed in medial and lateral view than in the material described above as ? Chamaeleonidae indet 1. The striation is also present. However, the tricuspidity is more pronounced in the specimen IPB-HaH 3903 (mesial and distal cusps are markedly stepped from the central dominant cusp) compared to the above-described specimens (? Chamae leonidae indet. 1).

Remarks: All this maxillae material is only potentially attributed to chameleons because the anterior region is not preserved in either specimen. In contrast to chamaeleonids, agamids retain a trace of the primitive pleurodont condition in the anterior region (often in caniniform anterior teeth; Moody 1978; Moody and Roček 1980; "subpleurodont" of Averianov and Danilov 1996). Although differences present between two Hambach morphotypes allow to distinguish between them, a fragmentary nature of both records does not give enough support to fully exclude a matter of individual and/or onthogenetic variation.

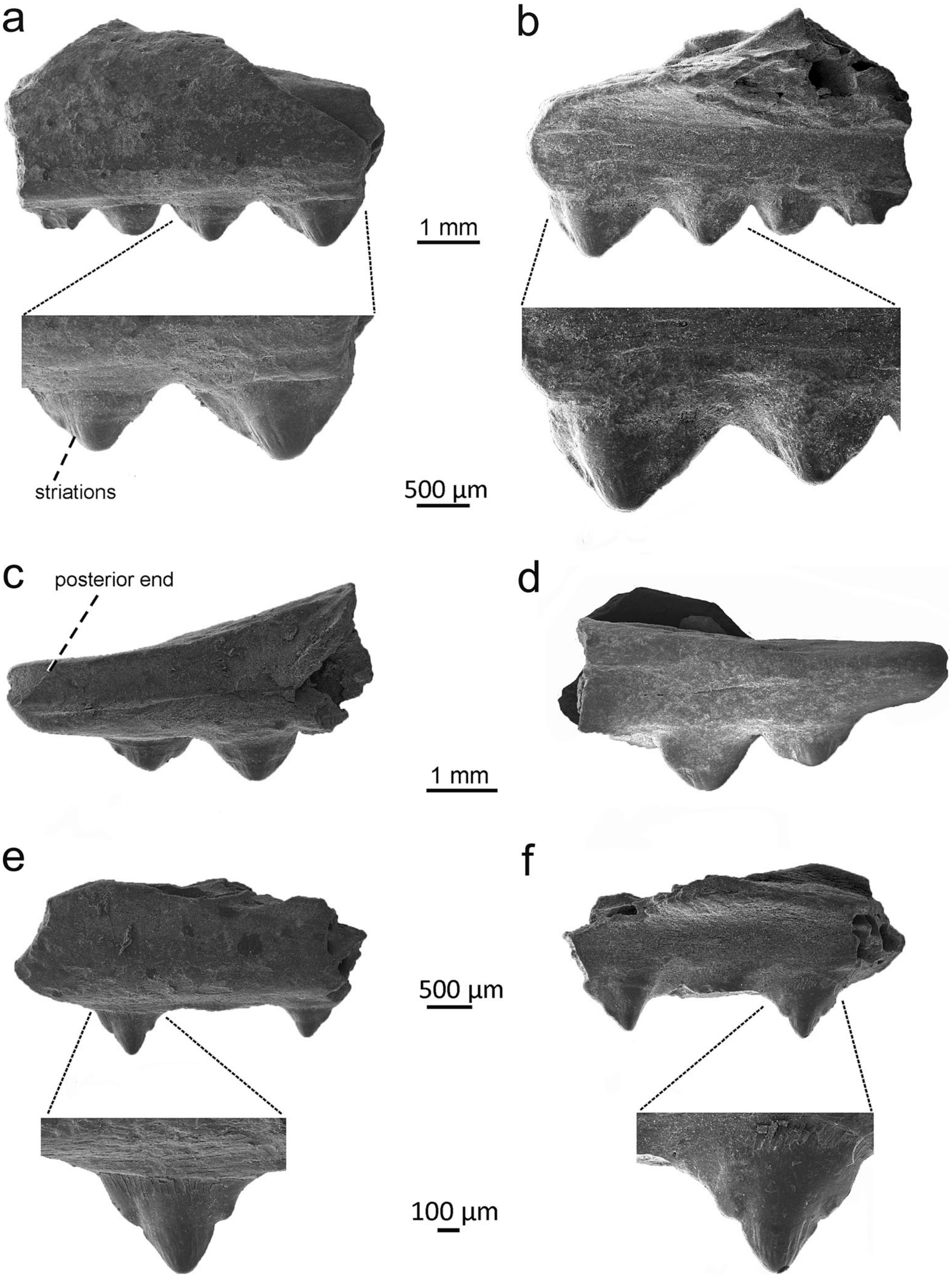


Fig. 3 ? Chamaeleonidae indet. 1: left maxilla (IPB-HaH 3902; **a**, **b**) and right maxilla (IPB-HaH 3902; **c**, **d**) and ? Chamaeleonidae indet. 2: right maxilla (IPB-HaH 3903; **e**, **f**); in lateral (**a**, **c**, **e**) and medial (**b**, **d**, **f**) aspects

Lacertiformes Estes et al., 1988
Lacertidae Oppel, 1811

Lacertidae indet. 1
(Fig. 4)

Material, horizon and locality: Left maxilla IPB-HaH 3701, two left dentaries IPB-HaH 3702–3703; middle Miocene (MN 5), Hambach 6C.

Maxilla: This fragment of a left maxilla with five teeth is very poorly preserved. The supradental shelf is dorsoventrally narrow, with a slightly convex course in this region. It gradually widens anteriorly.

Dentary: The preserved portion of the IPB-HaH 3702 left dentary has 11 tooth positions with 10 attached teeth, and the IPB-HaH 3703 dentary fragment bears eight tooth positions with five preserved teeth. The description is mainly based on the IPB-HaH 3702 specimen. Meckel's groove is fully open and deep. The ventral margin of the dentary is preserved only at its anterior end, with the remainder damaged. The robust subdental shelf (sensu Rage and Augé 2010) is rounded and slightly curved dorsally in its anterior

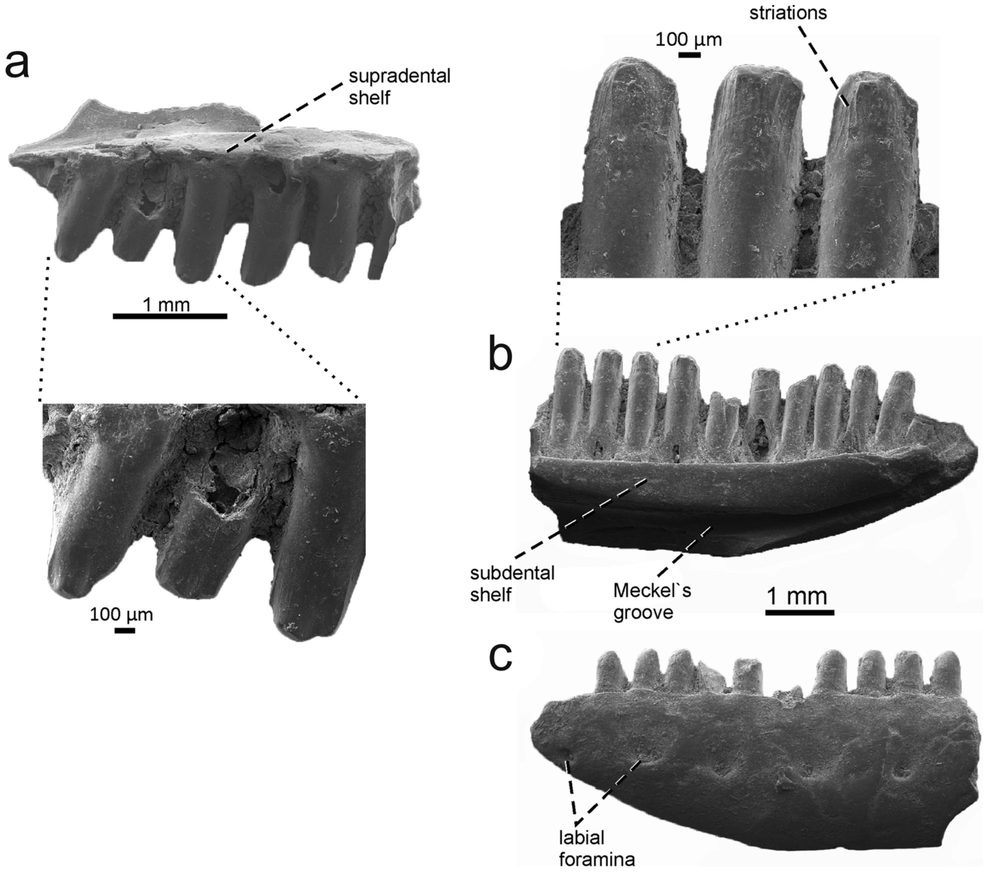


Fig. 4 Lacertidae indet. 1: maxilla (IPB-HaH 3701) in **a** medial aspect with detail of teeth; left dentary (IPB-HaH 3702) in **b** medial aspect with detail of teeth, **c** lateral aspect

region. Unfortunately, the symphyseal region is not preserved. The subdental shelf has a facet for the splenial on its ventral surface, reaching the level of the sixth preserved tooth from the anterior aspect. The sulcus dentalis on the subdental shelf dorsal surface traverses the entire preserved length. An oval alveolar canal is exposed in cross-section from the posterior aspect. The labial surface of IPB-HaH 3702 is pierced by a longitudinal series of five preserved foramina, whereas four of them are preserved in IPB-HaH 3703. The specimen IPB-HaH 3703 also has several irregular grooves, but this was most likely caused by postmortem and fossilisation processes and therefore taxonomically irrelevant.

Dentition: The dentition is pleurodont with robust teeth. Although most preserved teeth are bicuspid, they are monocuspid in the anterior region. There are small interdental gaps between the teeth, and the crowns have fine striation on their lingual aspects.

Lacertidae indet. 2
(Fig. 5)

Material, horizon and locality: Premaxilla IPB-HaH3704, left dentary IPB-HaH 3705; middle Miocene (MN 5), Hambach 6C.

Premaxilla: This is a small, slender element with five tooth positions and two teeth still attached. The nasal process is narrow and rectangular in shape. Unfortunately, its posterodorsal end is broken off. This process appears triangular in cross-section, and the maxillary processes are well developed and slightly expanded laterally in anterior view. In posterior view, the supradental shelf runs medially into a triangular ventrally pointed incisive process.

Dentary: The dentary is slender and almost straight. The preserved portion has 12 tooth positions, with four to six teeth partly preserved. Meckel's groove is fully open, but narrow. The subdental shelf is thin and almost straight. However, it gradually widens anteriorly and rises dorsally. The symphysial facet is unfortunately broken off and missing. In addition, the smooth labial surface is pierced by a longitudinal series of five preserved foramina.

Dentition: The dentition is pleurodont with fine teeth. The premaxillary and the anterior preserved dentary teeth are monocuspid, but the teeth in the posterior preserved region of the dentary are bicuspid with a small mesial cusp.

Remarks: The premaxilla is allocated to Lacertidae indet. 2 because of its similarity in size and tooth morphology to the dentary. It is possible that the material described here as Lacertidae indet. 2 can belong to the same taxon as material described above as Lacertidae indet. 1. The main differences are in size and robustness. Although it could be a younger ontogenetic stage, it is impossible to give enough support to this possibility because of the limitation of such fragmentary material.

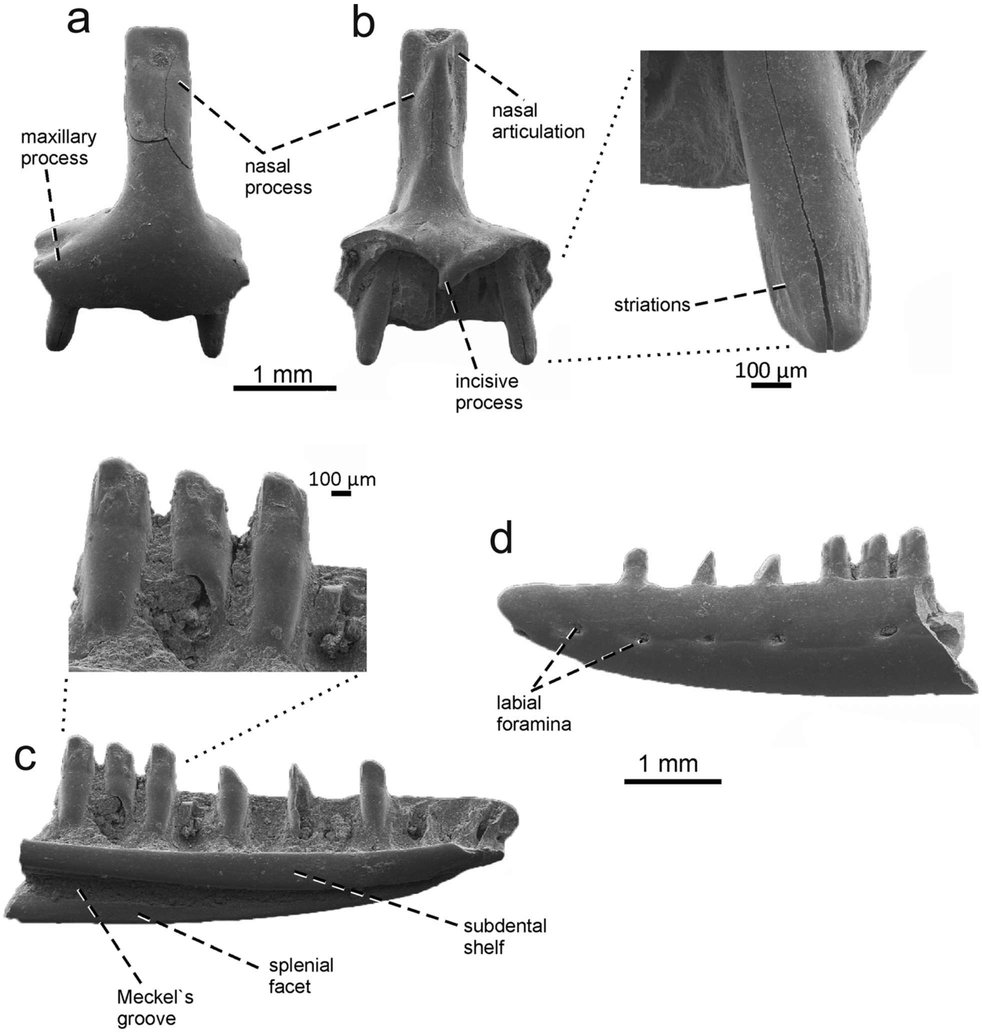


Fig. 5 Lacertidae indet. 2: premaxilla (IPB-HaH3704) in **a** external and **b** internal aspect with detail of tooth. Left dentary (IPB-HaH 3705) in **c** medial aspect with detail of teeth, **d** dentary in lateral aspect

Anguimorpha Fürbinger, 1900
Anguidae Gray, 1825
Anguinae Gray, 1825
Pseudopus Merrem, 1820

Pseudopus cf. *ahnikoviensis* Klembara 2012
(Fig. 6a–b)

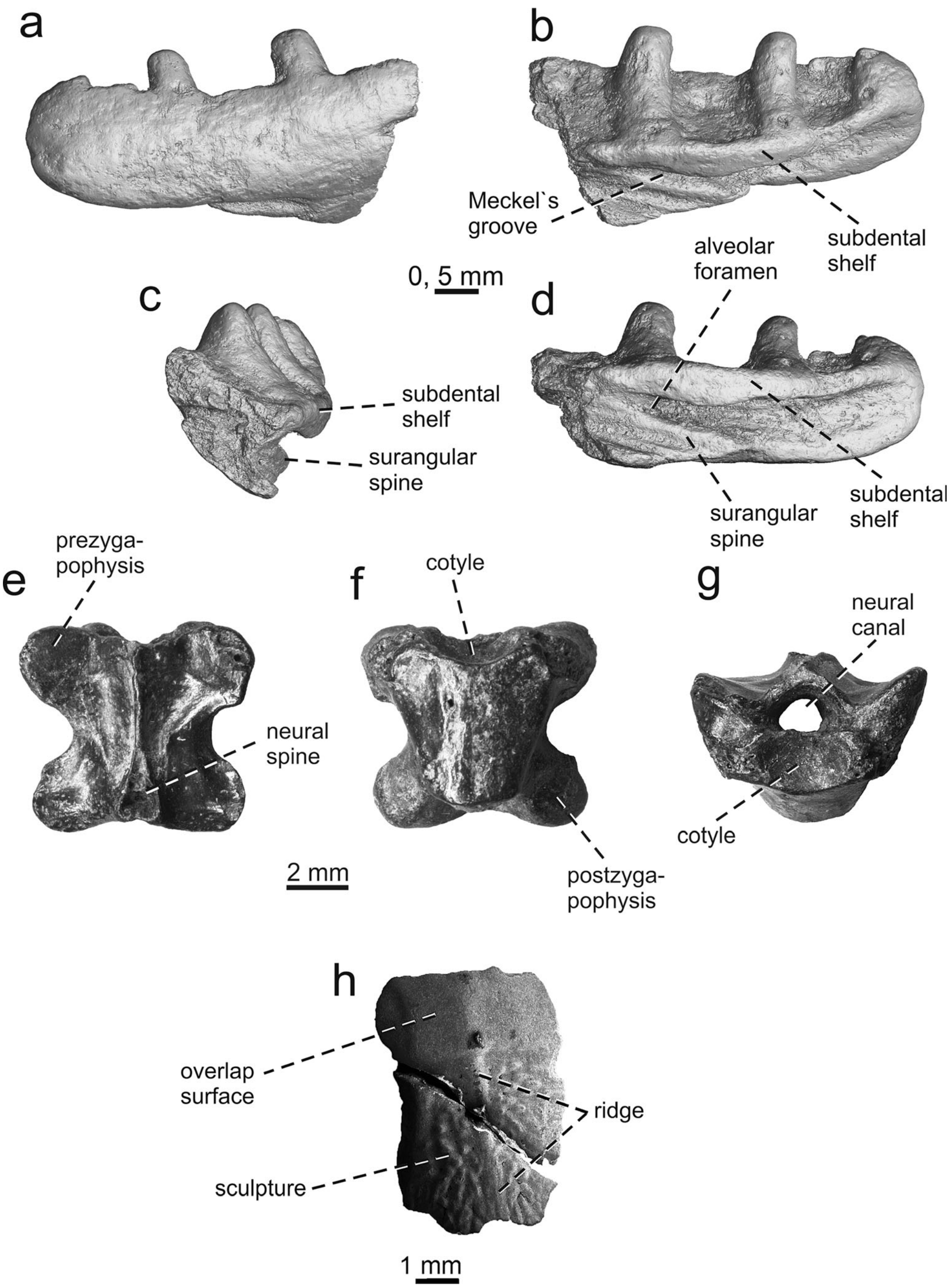
Material, horizon and locality: Right dentary IPB-HaH3706, left dentary IPB-HaH 3707; middle Miocene (MN 5), Hambach 6C.

Dentary: The dentaries are very poorly preserved, with only a fragment of the posterior region preserved in both specimens; IPB-HaH 3707 has five tooth positions with four teeth attached and IPB-HaH3706 has six tooth positions and two teeth present. This latter specimen is better preserved; therefore, the following description highlights its characters. The subdental shelf is thin, markedly concave with its posterior portion elevated dorsally. The sulcus dentalis is absent and Meckel's groove is fully open. The alveolar foramen is at the level of the fifth preserved tooth position from the posterior, and the surangular spine is preserved ventrally (see Klembara 2012; Klembara et al. 2014). Unfortunately, the angular process is broken off and missing. The coronoid and surangular processes are extremely weathered, short and blunt.

Dentition: The dentition is pleurodont, but shallow. The teeth are weakly conical with blunt tooth crowns. They are slightly curved posteriorly and their bases are pierced with small resorption pits. Some tooth apices in specimen IPB-HaH 3707 have fine striation, but both specimens are badly weathered.

Remarks: The presence of the surangular spine is an autapomorphic feature in *Pseudopus ahnikoviensis* (see Klembara 2012). In contrast to *Pseudopus laurillardi*, the subdental shelf is not medially expanded. Although the type material of *P. ahnikoviensis* exhibits absence of tooth striations, this may be due to preservation or individual variability (Klembara, personal communication 2015). For example, striation is present on tooth crowns from Amöneburg in Germany (MN 2) described by Čerňanský et al. (2015) as *P.* cf. *ahnikoviensis*. The material from Hambach is from a small-sized individual, most likely a juvenile.

Fig. 6 *Pseudopus* cf. *ahnikoviensis*: right dentary (IPB-HaH3706) in **a** lateral, **b** medial, **c** anteromedial and **d** ventromedial aspect. *Pseudopus* sp. 1: dorsal vertebra (IPB-HaH 3708) in **e** dorsal, **f** ventral and **g** anterior aspect. Anguidae indet.: osteoderm (IPB-HaH 3700) in **h** external aspect



Pseudopus sp 1.
(Fig. 6e–g)

Material, horizon and locality: dorsal vertebra IPB-HaH 3708; middle Miocene (MN 5), Hambach 6C.

Dorsal vertebra: The isolated vertebra is well preserved. The medial ridge runs almost the entire dorsal length of the neural arch, forming a neural spine posteriorly. Unfortunately, the dorsal portion of the neural spine is broken off, and the remainder narrows laterally and appears heart-shape in cross-section. The pre- and postzygapophyses are rounded, with a distinct interzygapophyseal rounded constriction separating them in dorsal aspect. The pentagonal neural canal is small, and the synapophyses form round structures on the lateral anterior portion of the vertebral centrum. The centrum is slightly elongated anteroposteriorly, gradually narrowing posteriorly. Its straight lateral margins give triangular centrum shape in ventral view. The cotyle is dorsoventrally depressed and only slightly taller than the dorsally located neural canal. The condyle is broken off.

Remarks: This vertebral type corresponds to *Pseudopus*. The following features enable this allocation: (1) the lateral margins of the centrum are straight rather than concave (Klembara 1981) and (2) the cotyle is taller than the neural canal (see Čerňanský et al. 2016).

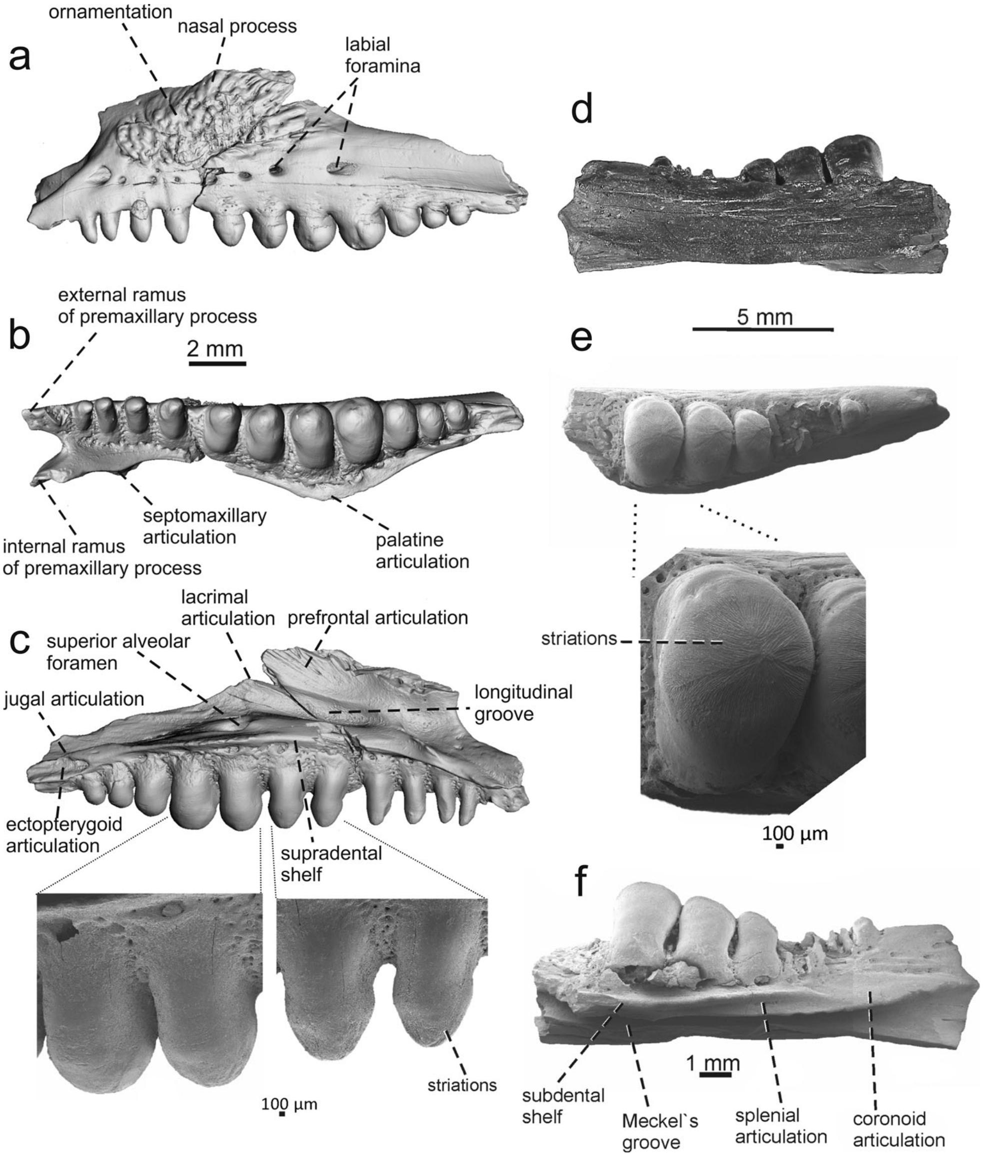


Fig. 7 *Pseudopus* cf. *pannonicus*: left maxilla (IPB-HaR 3002) in **a** lateral; **b** ventral; **c** medial aspects with details of teeth. Right dentary (IPB-HaR 3003) in **d** lateral, **e** dorsal with detail of tooth, **f** medial aspects

Anguidae indet 1.
(Fig. 6h)

Material, horizon and locality: Twenty osteoderms IPB-HaH 3700, caudal vertebra IPB-HaH 3709; middle Miocene (MN 5), Hambach 6C.

Osteoderms: The osteoderms are rectangular, slender and flat elements. They have a smooth anterior surface and a longer sculptured posterior one. A low medial ridge runs along their entire central regions, although it is less visible on the smooth portion. The sculpture in the posterior section is formed by short grooves, bulges and ridges diverging from the central region.

Caudal vertebra: The vertebra is narrow and anteroposteriorly elongated. The neural spine is broken off. The pre- and postzygapophyses are rounded, with the prezygaopohyses being slightly larger than postzygapophyses. Only the bases of the laterally expanded transverse processes are preserved. These originate from the anterior portion of the centrum. The cotyle and condyle are dorsoventrally depressed. The haemapophyses are fused to the posterior portion of the centrum, but their ends are broken off.

Pseudopus cf. *pannonicus* (Kormos, 1911)
(Figs. 7, 8)

Comment: The location of the material described in the following part (below Anguidae indet. 1) reflects its stratigraphic position. The lizard material described here was discovered at the Hambach 11 and 13 upper Pliocene sites.

Material, horizon and locality: Left maxilla IPB-HaR 3002 (Hambach 11), right dentary IPB-HaR 3003 (Hambach 11), two left nasals IPB-HaR 3004–3005 (Hambach 13); upper Pliocene (MN 16), Hambach 11 and 13.

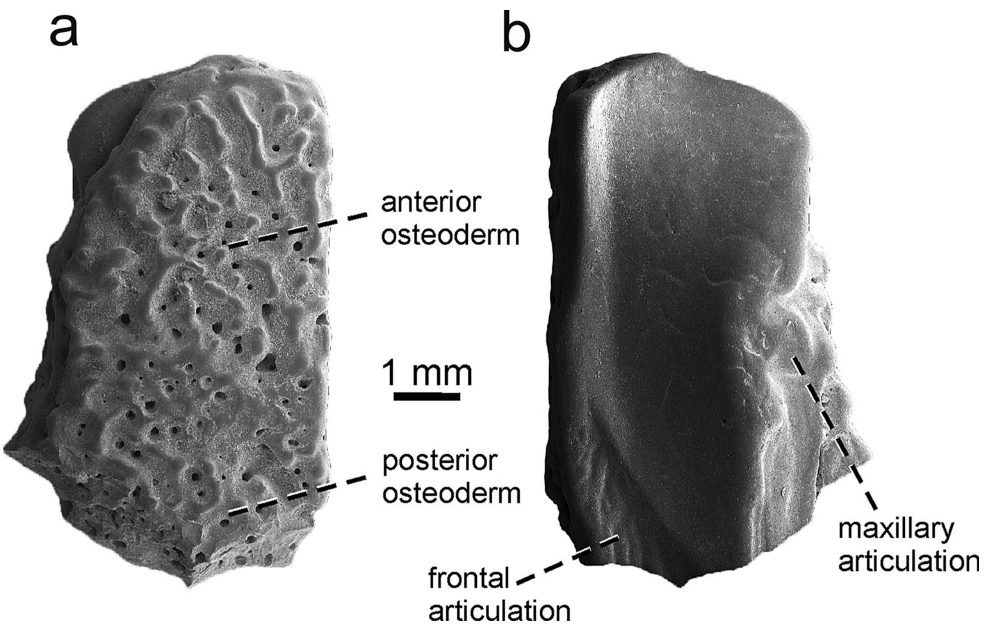


Fig. 8 *Pseudopus* cf. *pannonicus*: left nasal (IPB-HaR 3004) in **a** external and **b** internal aspects

Maxilla: The robust anteroposteriorly elongated left maxilla is almost completely preserved. Whereas 11 of the 12 tooth positions have teeth, a short area posterior to the last tooth lacks dentition. The dorsal aspect of the thin slightly convex supradental shelf has a superior alveolar foramen at the level of the fifth posterior tooth. The adjacent supradental shelf is expanded medially in this area, forming a palatine articulation. A groove indicating jugal articulation is preserved on the posterior dorsal surface of the maxilla. On the more ventral level, there is a distinct ectopterygoid articulation facet on the medial aspect of the posterior part of the maxilla. It reaches the last tooth level. The anterior extremity of the maxilla is divided into a short external ramus of the premaxillary process and a broader, more medially oriented and slightly more dorsally developed internal ramus. An oval premaxillary fenestra is present between these rami. The lacrimal was located where the nasal process rises dorsally between the fourth and fifth posterior tooth. The internal surface of the nasal process has a posterodorsally trending ridge which contacts the supradental shelf at the level between the fourth and fifth anterior teeth. This ridge forms the border of a distinct anterodorsal longitudinal groove. Dorsally, the nasal process has a massive rugosity for prefrontal articulation.

The external region of maxilla has eight labial foramina of varying size. The nasal process is covered with several fused ornamented osteoderms. This ornamentation consists of several irregular ridges, grooves and foramina. Unfortunately, the dorsal portion of the nasal process is broken off.

Left nasal: Description is based on the well preserved, almost complete specimen IPB-HaR 3004. It is trapezoidal, with its dorsal surface covered by ornamented osteoderms. The ornamentation comprises several irregular wormy ridges and foramina. Whereas the two osteoderms in *Peudopus apodus* are well separated by a groove, the division here is not so distinct. The anterolateral process is short, broad and blunt, but the premaxillary process is broken. The anteroposteriorly elongated depression on the ventral nasal aspect narrows posteriorly for frontal articulation. The margins of the depression are formed by shallow ridges, but again, this region is mostly broken. Maxilla articulation is present on the lateral nasal aspect.

Dentary: The description is based on the posterior fragment of the right dentary, where four teeth are present in the seven preserved tooth positions. The subdental shelf is thin in this region, and the facet for the coronoid reaches the level between the third and fourth posterior tooth position. Further anteroventrally, the facet for the splenial forms a sharp ridge which continues anteriorly below the subdental shelf. Meckel's groove is fully open. The external dentary surface is almost smooth, with only several longitudinal shallow grooves below the teeth. The coronoid process is broken off.

Dentition: The dentition is pleurodont and heterodont. The anterior teeth are small and pointed but others enlarge posteriorly to form blunt robust cylinders—amblyodont dentition. The fourth posterior maxillary tooth is the largest. The tooth crowns have delicate striations on their labial and lingual surfaces, and several teeth have small oval resorption pits at their bases.

Remarks: This material is from a relatively large fossil anguine lizard, with the following main characters: (1) a splenial facet is anterior to the coronoid facet. In modern *P. apodus*, the coronoid extends further anteriorly and there is no facet for the splenial in this region (see e.g. Klembara et al. 2010, 2014) and (2) the absence of a medially expanded subdental shelf (its presence is an autapomorphic feature of *P. laurillardi*). Although very limited, this dentary material appears identical to that of *P. pannonicus* frequently described from the same stratigraphic level. The fossil

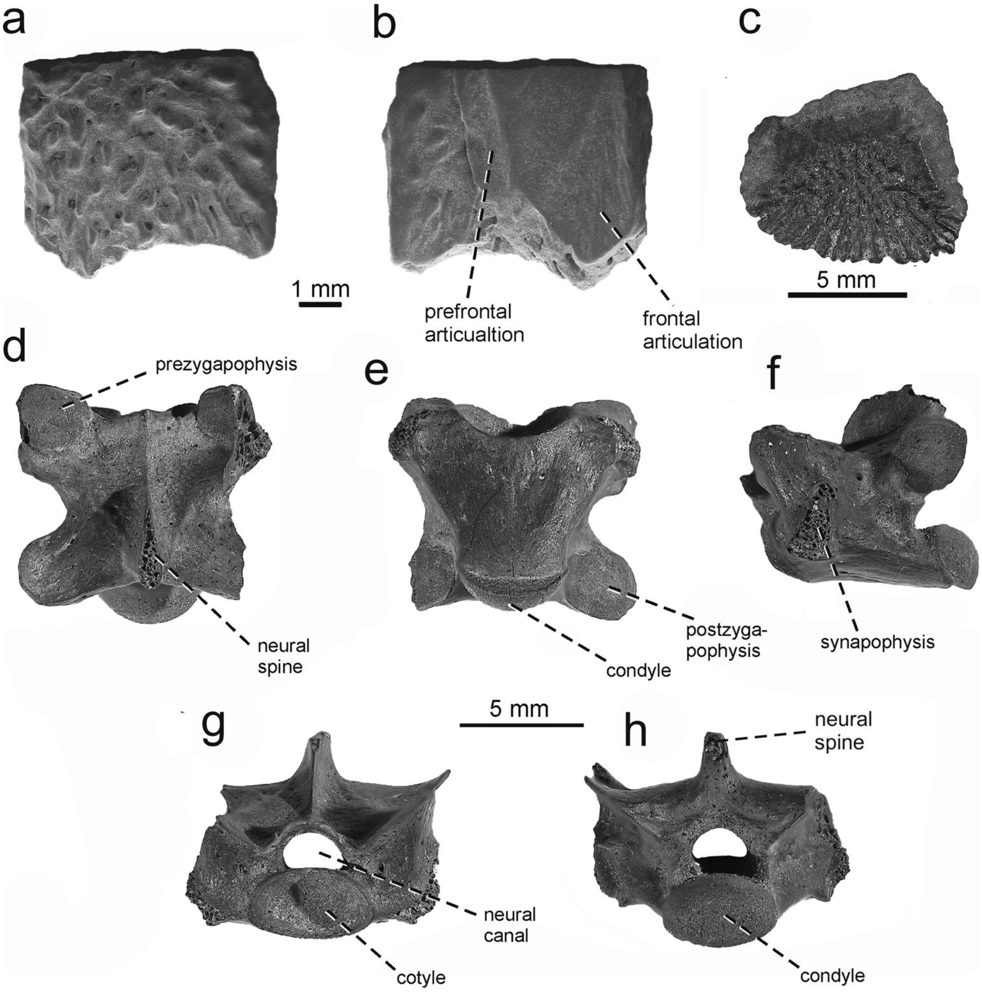


Fig. 9 *Pseudopus* sp. 2: right nasal (IPB-HaR 3006) in **a** external and **b** internal aspects. Osteoderm (IPB-HaR 3007) in **c** external aspect. Dorsal vertebra (IPB-HaR 3006) in **d** dorsal; **e** ventral; **f** lateral; **g** anterior; **h** posterior aspects

record of *P. pannonicus* is first known from MN 9 and the youngest finds are from the Pleistocene (see Klembara et al. 2010). The maxilla is associated with the dentary bone because of their identical size and dentition, and nasal association is based on the same type of ornamentation present in the nasal process of the maxilla.

Pseudopus sp. 2
(Fig. 9)

Material, horizon and locality: Right nasal IPB-HaR 3006 (Hambach 11), four dorsal vertebrae IPB-HaR 3007 (Hambach 11), twenty osteoderms IPB-HaR 3008 (Hambach 11 and 13); upper Pliocene (MN 16), Hambach 11 and 13.

Right nasal: Although this element consists only of the mid-posterior portion of the nasal bone, it is relatively large (with 6.1 mm width). Its dorsal surface is covered by ornamented osteoderm, with ornamentation of relatively straight, short ridges, bulges and pits. On the ventral surface, a depression is located. On its medial side, the articulation with frontal is present. It has a triangular shape in the preserved portion. The lateral margin of this depression is formed by a low ridge, and the nasal lateral border has an anteroposteriorly elongated narrow surface for prefrontal articulation. More laterally, there is an area ornamented by several obscure bulges.

Dorsal vertebrae: The dorsal vertebrae are isolated, robust and vary in size, thus reflecting ontogenetic and individual variation. The largest one also has the longest anteroposterior length at 12.6 and 14.5 mm width. The centrum has almost straight lateral margins in ventral view. The ventral surface of the centrum is very flat and smooth, with small subcentral foramina in its posterior region. The condyle and cotyle are markedly depressed. The neural canal is small and heptagonal. The neural arch is robust, especially in the dorsal region where a median ridge is present. This ridge is weakly developed in the anterior half of the neural arch, but it rises dorsally to form the neural spine in posterior region. The synapophyses, which are located on the anterior portion of the centrum, are dorsoventrally elongated. The prezygapophyseal facets are large and relatively square with blunt margins, whereas the

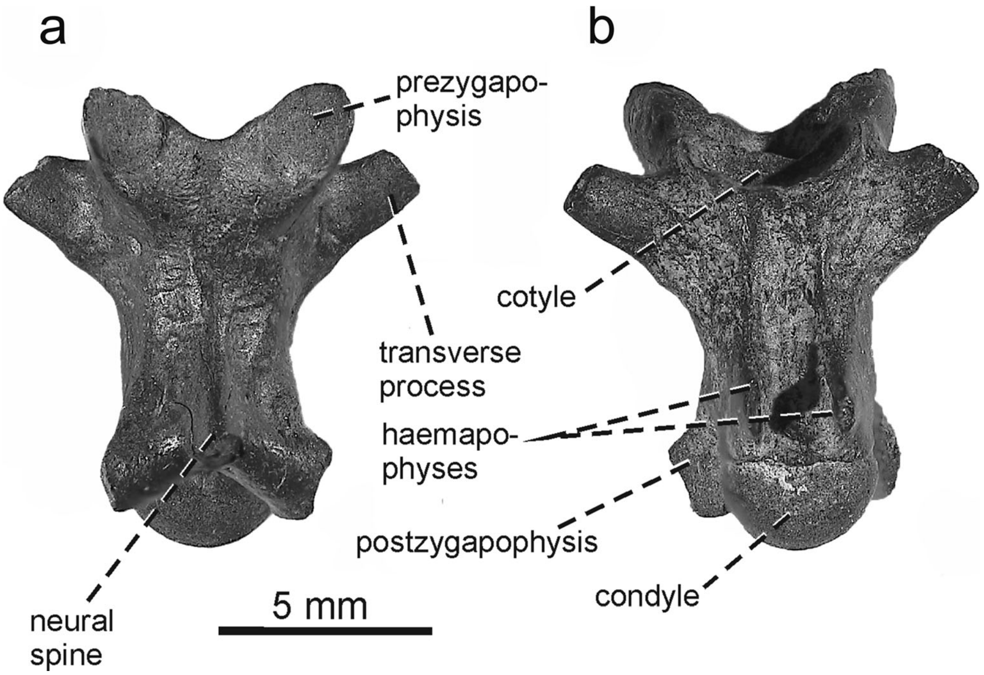


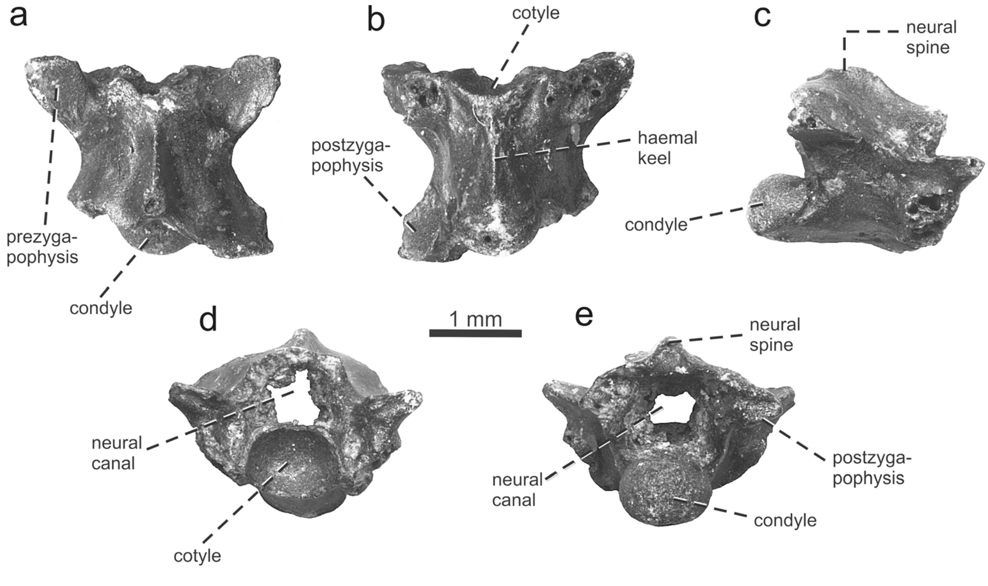
Fig. 10 Anguidae indet.: caudal vertebra (IPB-HaR 3009) in **a** dorsal and **b** ventral aspects

postzygapophyses are slightly smaller with oval articulation surfaces in ventrolateral aspects.

Osteoderms: The osteoderms are flat and almost square. Their external surface presents an anterior short smooth area and a posterior ornamented region. The ornamentation consists of irregular grooves, ridges and foramina. Each osteoderm has a smooth margin for contact with the next osteoderm. The longitudinal keel is absent. The internal surface is almost smooth, but pierced by a pair of foramina in its anterior third.

Remarks: The dorsal vertebrae have the typical morphology of *Pseudopus* (see remarks above in *Pseudopus* sp. 1). The independent allocations of the vertebrae described herein to *Pseudopus* sp. 1 and 2 are due to the following two reasons: (1) overall smaller size of the vertebra from Hambach 6C if compared to the vertebrae from Hambach 11; (2) the older stratigraphic level (MN 5) of Hambach 6C. The nasal bone and some dorsal vertebrae and osteoderms are very large. This could suggest that all the material may be allocated to *P.* cf. *pannonicus*. It should be noted that the nasal ornamentation is slightly different to the wormy ridges on the smaller left nasal described above. This difference, however, may just result from larger size or individual variability.

Fig. 11 *Eoanilius* sp.: trunk vertebra (IPB-HaH 3801) in **a** dorsal, **b** ventral, **c** lateral, **d** anterior, **e** posterior aspects



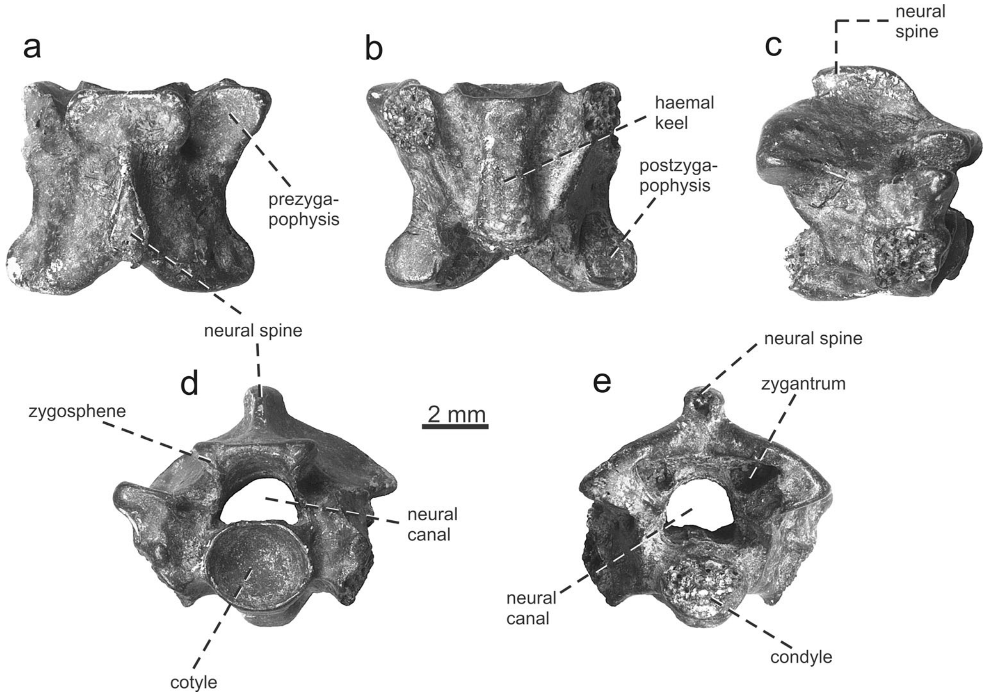


Fig. 12 *Bavarioboa* sp.: trunk vertebra (IPB-HaH 3825) in **a** dorsal; **b** ventral; **c** lateral; **d** anterior; **e** posterior aspects

Anguidae indet. 2
(Fig. 10)

Material, horizon and locality: Two caudal vertebrae IPB-HaR 3009, upper Pliocene (MN 16), Hambach 11.

Caudal vertebrae: The caudal vertebrae are elongate and narrow, less depressed than the dorsal vertebra described above. The cotyle and condyle here are dorsoventrally depressed. The pre- and postzygapophyses are both small. The haemapophyses are fused to the posterior portion of the centrum, but unfortunately their ends are broken off and missing. The anteroventrally oriented transverse processes are also broken, with only their bases preserved. The neural spine is posterodorsally oriented and pointed.

Remarks: Despite similar morphology, the independent allocations of the caudal vertebrae to Anguidae indet. 1 and 2 are due to the different age of the fossils (middle Miocene vs. late Pliocene).

Serpentes Linnaeus, 1758
Aniliidae Fitzinger, 1826
Eoanilius Rage 1974

Eoanilius sp.
(Fig. 11)

Material, horizon and locality: Five trunk vertebrae (1. IPB-HaH 3801; 3802; the remainder prefixed by IPB-HaH 3824); middle Miocene (MN 5), Hambach 6C.

Vertebrae: The vertebrae are characterised by very small dimensions and relatively simple morphology. The centrum of all vertebrae is cylindrical and approximately equally wide and long. The centrum in the best preserved vertebra (IPB-HaH 3801) is 1.9 mm long and 1.7 mm wide. The haemal keel is broad, but indistinct, laterally accompanied by shallow subcentral grooves. The neural arch is strongly depressed. The neural spine is extremely low and restricted to the posterior portion of the neural arch. The pre- and postzygapophyseal articular facets are relatively large, oval-shaped and slightly elongated. The preserved prezygapophyseal processes are very short and barely visible in dorsal view. The zygosphenal roof is damaged in all vertebrae and the paradiapophyses are strongly eroded. The cotyle and condyle are flattened dorsoventrally. The paracotylar foramina are absent.

Remarks: While current distribution of the Aniliidae is in the tropical Americas, these fossil vertebrae are clearly referrable to the extinct genus *Eoanilius*, which belongs to this family. The oldest remains of this genus, type-species *Eoanilius europae* come from the late Eocene of France (Rage 1974) and also some other West European countries. *Eoanilius* is considered the only ophidian genus which survived the “Grande Coupure” event at the European Eocene/Oligocene boundary. Geologically younger remains of this snake, usually referred to another species, *Eoanilius oligocenicus* Szyndlar 1994, have been reported from several German, French and Italian localities dated from the early Oligocene to early Miocene (see Szyndlar 2009; Rage and Augé 2014; and references

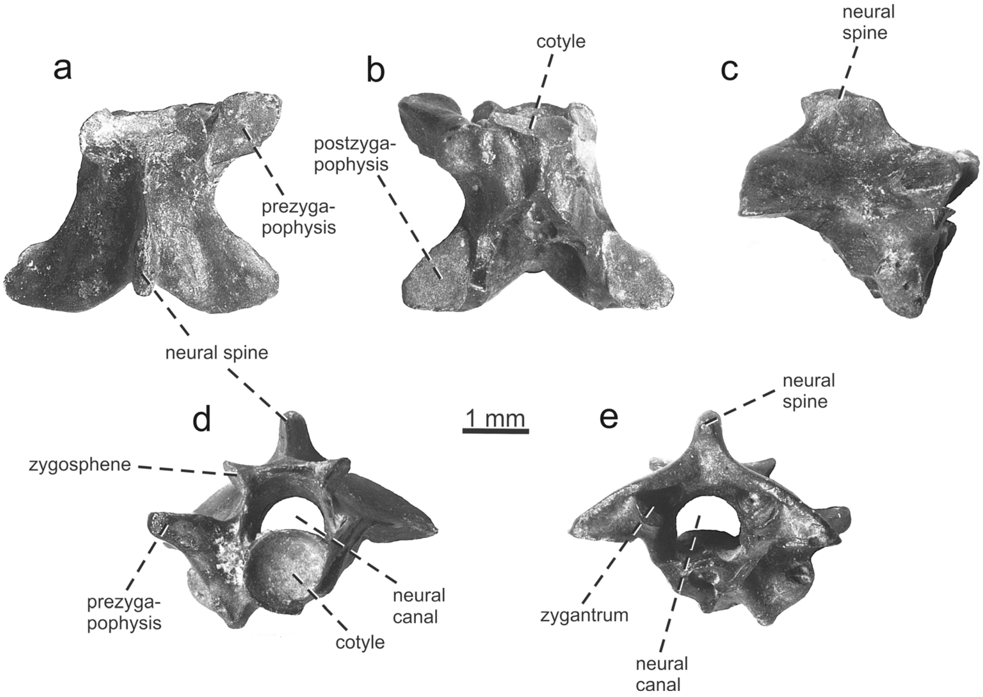


Fig. 13 cf. *Falseryx* sp.: trunk vertebra (IPB-HaH 3830) in **a** dorsal; **b** ventral; **c** lateral; **d** anterior; **e** posterior aspects

therein). Interestingly, *Eoanilius* was a dominant element in the middle early Miocene (MN 2 and 3) snake assemblages of southern Germany (Szyndlar and Rage 2003). The Hambach *Eoanilius* remains are most likely *E. oligocenicus* species, but this cannot be precisely demonstrated because available material is scarce. In any case, Hambach and the German Sandelzhausen locality (Szyndlar 2009) are the geologically youngest fossil sites yielding remains of *Eoanilius*.

Boidae Gray, 1825
Bavarioboa Szyndlar and Schleich, 1993

Bavarioboa sp.
(Fig. 12)

Material, horizon and locality: Five trunk vertebrae (IPB-HaH 3825; 3807; 3013; 3814; 3818); middle Miocene (MN 5), Hambach 6C.

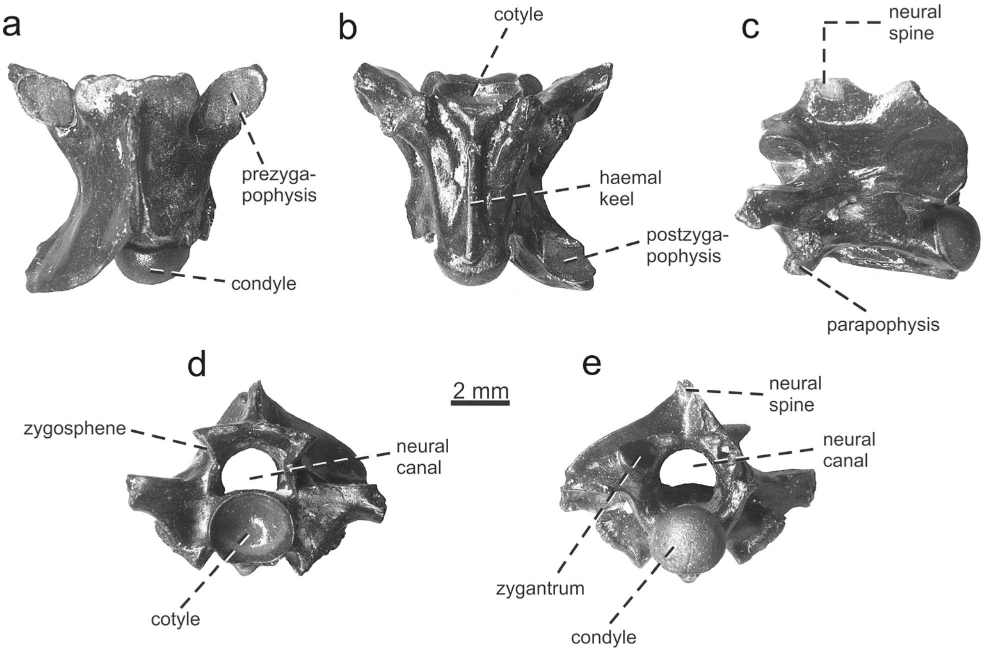


Fig. 14 "*Coluber*" sp.: trunk vertebra (IPB-HaH 3808) in **a** dorsal; **b** ventral; **c** lateral; **d** anterior; **e** posterior aspects

Vertebrae: These come from the middle trunk of the vertebral column. The vertebrae are preserved in relatively good condition, perhaps because of their robust morphology. While they are equally high and long in lateral view, they are distinctly wider than long from the dorsal aspect. The largest and best preserved vertebra has 4.7 mm centrum length and 5.8 mm width. The vertebral interzygapophyseal constriction is moderately expressed. The centrum is triangular in shape. The haemal keel is prominent, relatively broad and uniform in width throughout its length; it is rounded in cross-section. The subcentral grooves and subcentral ridges are prominent. The neural arch is depressed. The neural spine is very low, approximately three times longer than high. It is thick and widens posteriorly to occupy half the length of the neural arch and begins immediately behind the zygosphenal articular facets. In anterior view, the zygosphenal roof is straight; in dorsal view, it is slightly convex or roughly straight and provided with 2 minute lateral lobes. While the prezygapophyseal articular facets are oval, the postzygapophyseal articular facets appear subsquare. The prezygapophyseal processes are short and barely visible from above. The paradiapophyses are subsquare in shape, slightly higher than long, with indistinct subdivision into para- and diapophyseal portions. The latter portion, however, is eroded in most vertebrae. The cotyle and condyle are slightly flattened. The subcentral and lateral foramina are large. The paracotylar foramina are absent except in specimen HaH–3801–3 with one orifice asymmetrically located on the right aspect of the cotyle.

Remarks: *Bavarioboa* is an extinct representative of the boid subfamily Boinae, whose present distribution is restricted to the Americas, Madagascar and some West Pacific islands. *Bavarioboa* has several species which were the commonest European snakes in the second half of the Oligocene, with late Oligocene or early Miocene remains of this snake, also discovered in eastern Turkey (Szyndlar and Hoşgör 2012). *Bavarioboa* reappeared in Europe at the end of the early Miocene (Szyndlar and Rage 2003), and the geologically youngest remains of *Bavarioboa* come from the middle Miocene (MN 6) of Griesbeckerzell in Germany (Ivanov and Böhme 2011).

With its very low neural spine, convex zygosphene with 2 minute lateral lobes and a paracotylar foramen, the Hambach snake most resembles *Bavarioboa ultima*. This species was described from the Rothenstein 13 site in southern Germany, which is coeval with Hambach 6C (Szyndlar and Rage 2003). However, it does not exhibit the key diagnostic trait of *B. ultima* of a dorsally thickened neural spine. The presence of paracotylar foramina is an important diagnostic feature of the subfamily Boinae, although it is not certain whether this trait is apomorphic. Within the genus *Bavarioboa*, the presence of paracotylar foramina is restricted to two species (and one unnamed form) only; besides, the foramina occur only in a part of the vertebrae belonging to these snakes.

Tropidophiidae (Brongersma, 1951)
Falseryx Szyndlar and Rage 2003

cf. *Falseryx* sp.
(Fig. 13)

Material, horizon and locality: One trunk vertebra (HaH–3830); middle Miocene (MN 5), Hambach 6C.

Vertebra: This sole vertebra is badly preserved, especially lacking a left prezygapophysis, condyle and a considerable posterior part of the centrum. The vertebra is very small, with centrum width 2.1 mm. Its striking feature is a very deep interzygapophyseal constriction when viewed from dorsal and ventral aspects. The neural arch is strongly depressed. The neural spine is relatively low. This latter begins immediately behind the posterior border of the zygosphenal articular facets, occupying one third the length of the neural arch. The postzygapophyseal articular facets have teardrop shape. The (right) prezygapophyseal articular facet is rhomboid-shaped. The prezygapohyseal process is very short but clearly visible from above. The zygosphenal roof is concave in anterior view and wider than the circular cotyle. The paracotylar foramina are absent.

Remarks: The overall morphology of this vertebra closely resembles the extinct species of boid erycine *Bransateryx* and tropidophiid *Falseryx*, in which caudal vertebrae show the most genera-distinguishing features. These are very complex in the former and quite simple in the latter. Unfortunately, the ophidian material from Hambach does not contain any non-colubroid caudals. The only trunk vertebra available is temporarily identified as cf. *Falseryx*, based on the supposition that the last representatives of the genus *Bransateryx* became extinct in Europe in the early Miocene (Szyndlar and Rage 2003). Remains of *Falseryx* were reported from the early Oligocene of Belgium (Szyndlar et al. 2008) as well as from several late early to middle Miocene European sites (Szyndlar and Rage 2003; Čerňanský et al. 2015).

Colubridae (*s.l.*) Oppel, 1811

In this paper, we employ the subdivision of the family Colubridae (*s.l.*) into two informal subfamilies "Colubrinae" (or "colubrines") and "Natricinae" (or "natricines"). Although this classification is inconsistent with current modern colubrid systematics, it is commonly utilised in ophidian palaeontology. The criterion for subdivision of colubrids into these groups is the presence or absence of vertebral hypapophyses. In "colubrines", the hypapophyses are restricted to the

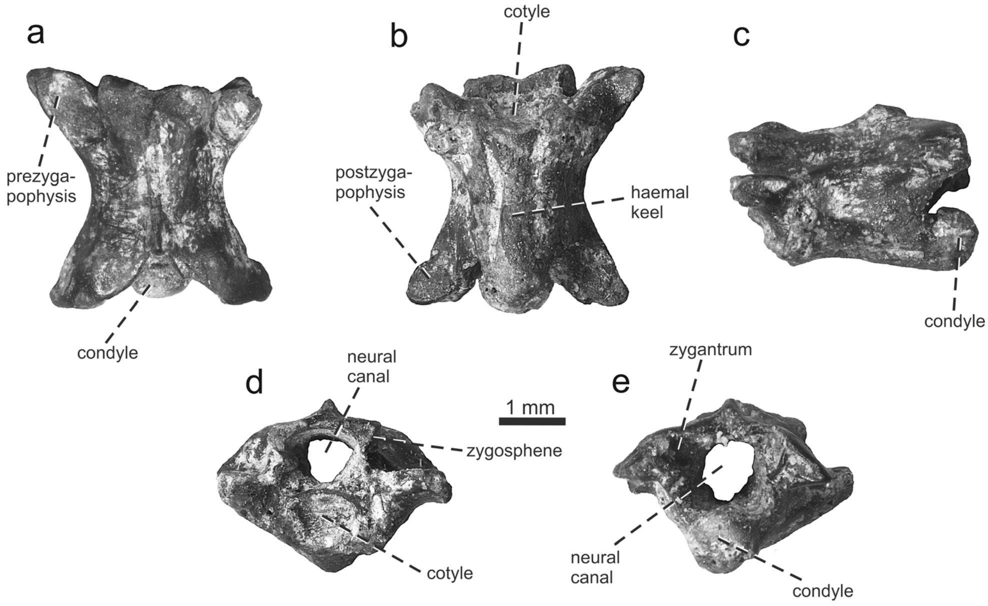


Fig. 15 *Texasophis* sp.: trunk vertebra (IPB-HaH 3841) in **a** dorsal; **b** ventral; **c** lateral; **d** anterior; **e** posterior aspects

anterior trunk portion of the vertebral column, whereas in "natricines" they occur throughout the trunk portion of the column.

"Colubrinae"
Coluber (s.l.) Linnaeus, 1758

"*Coluber*" sp.
(Fig. 14)

Material, horizon and locality: Forty-two trunk vertebrae (IPB-HaH 3800; 3826; 3831; 3803; 3804; 3852; 3808; 3857; 3815; 3816; 3817; 3820; 3822; 3823); middle Miocene (MN 5), Hambach 6C.

Vertebrae: The vertebrae are all preserved in relatively fragmentary state and come from the middle trunk of the vertebral column. Some of them belonged to extremely large snakes: the measurements of centrum length and width in the three largest vertebrae (IPB-HaH 3815; 3816 and 3823) are 11.4 and 9.5 mm, 13.0 and 11.7 mm, and 13.7 and 10.0 mm, respectively. These bones undoubtedly come from oversized individuals, because the overwhelming majority of available vertebrae are from distinctly smaller (although adult) snakes. For example, the best preserved "average size" vertebra (IPB-HaH 3808, Fig. 14) has 7.4 mm centrum length and 4.5 mm width.

The centrum is triangular in ventral view and always distinctly longer than wide, regardless of absolute

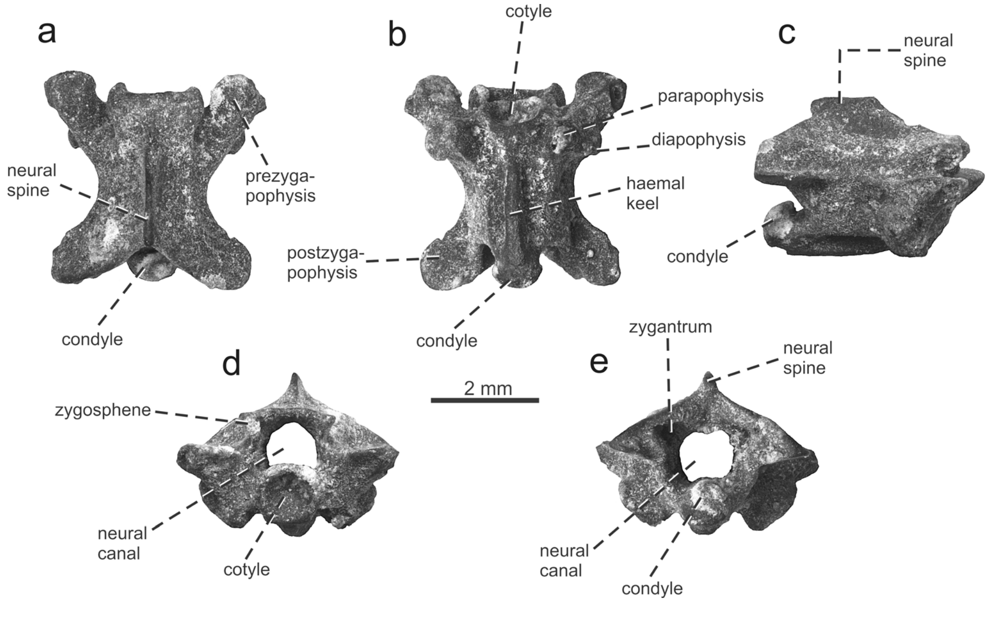


Fig. 16 *Telescopus* sp.: trunk vertebra (IPB-HaH 3853) in **a** dorsal; **b** ventral; **c** lateral; **d** anterior; **e** posterior aspects

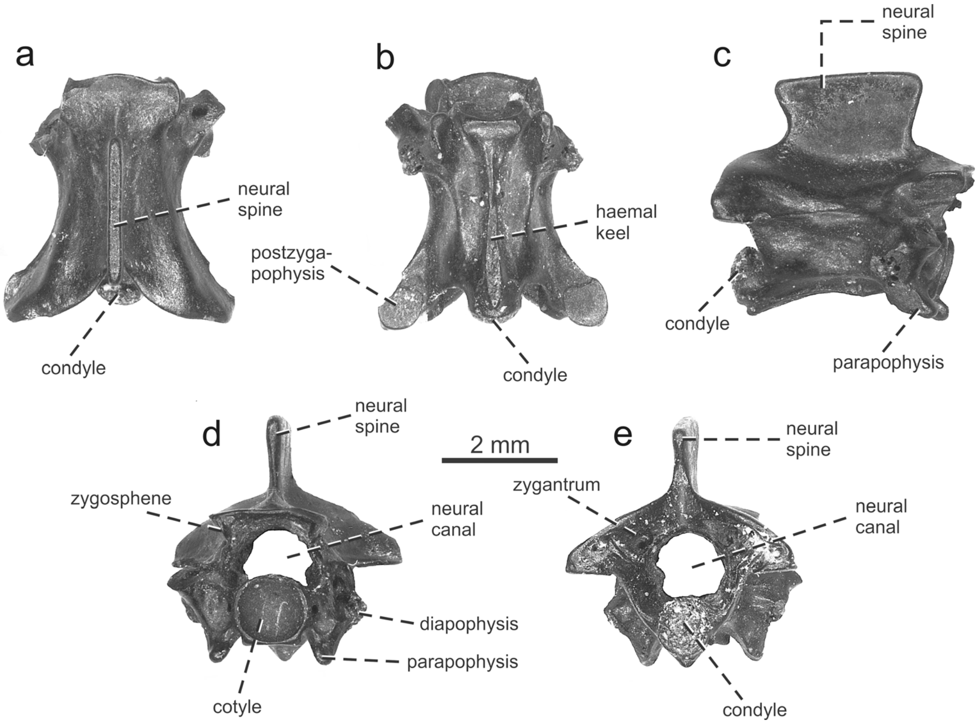


Fig. 17 *Natrix* sp.: trunk vertebra (IPB-HaH 3842) in **a** dorsal; **b** ventral; **c** lateral; **d** anterior; **e** posterior aspects

dimensions. The subcentral ridges are well developed. The haemal keel is distinct and cuneate-shaped, forming a sharply cut step anteriorly before it reaches the cotyle lip. The neural arch is moderately vaulted and accompanied by minute epizygapophyseal spines in some vertebrae. The neural spine, which is partly preserved only in a few vertebrae, is relatively longer than high. The zygosphenal roof is also preserved in few vertebrae, and it is roughly straight or "crenate" with three indistinct lobes. While the prezygapophyseal articular facets are oval, the postzygapophyseal facets are mostly subsquare. The prezygapophyseal processes are damaged or the tips (if partly preserved) are missing. The paradiapophyses are moderately developed, with the dia- and parapophyseal portions of roughly equal length. The cotyle and condyle are slightly depressed dorsoventrally. The lateral, subcentral and paracotylar foramina are quite distinct.

Remarks: Large snakes, traditionally classified as members of the genus *Coluber* (*s.l.*), have been very common members of many ophidian assemblages since their European appearance at the end of the early Miocene. The Hambach colubrid most closely resembles conditions observed in the vertebrae of the four large-sized fossil species (and perhaps related): *Coluber dolnicensis*, *C. caspioides*, *C. suevicus* and *C. pouchetii*. All these species are more or less similar to the living European snake, *Dolichophis* (formerly *Coluber*) *caspius*. However, the informal generic name "*Coluber*" is preferred here when referring to the extinct species for two reasons: (1) because of accepted relationships between the living *Dolichophis caspius* and alleged fossil relatives and (2) relationships among particular extinct species generally remain unclear. The taxonomic status of these colubrids has been discussed in detail in several papers (e.g. Augé and Rage 2000; Rage and Bailon 2005; Szyndlar 2005, 2012; Ivanov and Böhme 2011).

*Texas*ophis Holman 1977

Texasophis sp.
(Fig. 15)

Material, horizon and locality: Two trunk vertebrae (IPB-HaH 3832; 3841); middle Miocene (MN 5), Hambach 6C.

Vertebrae: The two fragmentary vertebrae from the vertebral column mid-trunk come from one or more small individuals. The centrum is elongate and the larger specimen, IPB-HaH 3841, has 2.6 mm centrum length and 2 mm width. The haemal keel is robust, wide and flattened, broadening posteriorly. The subcentral ridges are distinct. The neural arch is depressed. The neural spine is missing in both vertebrae, but its remnants indicate it was extremely low in stature. The zygosphenal roof is slightly convex in anterior view, with its anterior border partly missing in both vertebrae. The pre- and postzygapophyseal articular facets are ovaloid. The prezygapophyseal processes are short and obtuse. The paradiapophyses are moderate in size, but eroded. The cotyle and condyle are orbicular. All vertebral foramina are small but distinct.

Remarks: The extinct *Texasophis* genus was originally described from the Miocene of North America (Holman 1977), and it has unclear relationship with recent "colubrines". Several species were later described from the European Oligocene and early to middle Miocene. For the up-to-date record of the European *Texasophis*, see Ivanov and Böhme (2011), Szyndlar (2012) and Venczel and Hír (2015).

The Hambach vertebrae clearly display characteristic features of the *Texasophis* genus, including elongated form, a low neural spine, strongly built haemal keel and distinct subcentral ridges. The presence of a relatively broad haemal keel makes them most similar to *Texasophis meini*, originally described from the French Miocene (Rage and Holman 1984).

Telescopus Wagler, 1830

Telescopus sp.
(Fig. 16)

Material, horizon and locality: One trunk vertebra (IPB-HaH 3853); middle Miocene (MN 5), Hambach 6C.

Vertebra: This sole vertebra of a relatively small snake is quite well preserved and comes from the middle trunk of the vertebral column. The only missing elements are the anterodorsal portion of the neural spine and tips of the prezygapophyseal processes. The centrum is elongate, with 2.9 mm length and 2.1 mm width. The haemal keel is strongly built, wide and flattened. While the keel distinctly broadens posteriorly, the anterior portion is separated from the prominent subcotylar lip by a deep constriction. The subcentral grooves are narrow and deep, and the subcentral ridges are strong, extending from the posterior margin of the parapophyses to the condyle. The neural arch is depressed and devoid of epizygapophyseal spines. The neural spine is very low and slightly overhanging posteriorly. When complete, the spine may have been four times longer than high. The zygosphenal roof is slightly convex in anterior view, and its anterior border is roughly straight. In dorsal view, it has two small lateral lobes. The pre- and postzygapophyseal articular facets are ovoid-shaped. Although the prezygapophyseal processes are damaged distally, they are strongly built. The parapophyses are relatively long and distinctly longer than the diapophyses in lateral view. The cotyle and condyle are orbicular. All vertebral foramina are distinct.

Remarks: This vertebra has a number of peculiarities characteristic of the living genus *Telescopus*. These include a distinctly longer parapophyses than diapophyses, an extremely low neural spine and a flattened robust haemal keel.

The extant *Telescopus* is widely distributed throughout Eurasia and Africa and *Telescopus fallax* is currently present in southeastern Europe. *Telescopus* fossil remains have also been reported from several localities in eastern and central Europe, ranging in age from the early Miocene to Pleistocene (see: Szyndlar 2005, 2012, for the up-to-date lists of the fossil record).

"Colubrinae" indet. 1

Material, horizon and locality: Fifty-seven trunk vertebrae (IPB-HaH 3828; 3835; 3838; 3844; 3805; 3806; 3855); middle Miocene (MN 5), Hambach 6C.

Remarks: Although these vertebral fragments (rather than fragmentary vertebrae) may have represented the "colubrine" genera described above, we cannot exclude the possibility that some fragments, especially those from small or very small snakes, may have belonged to other "colubrine" taxa.

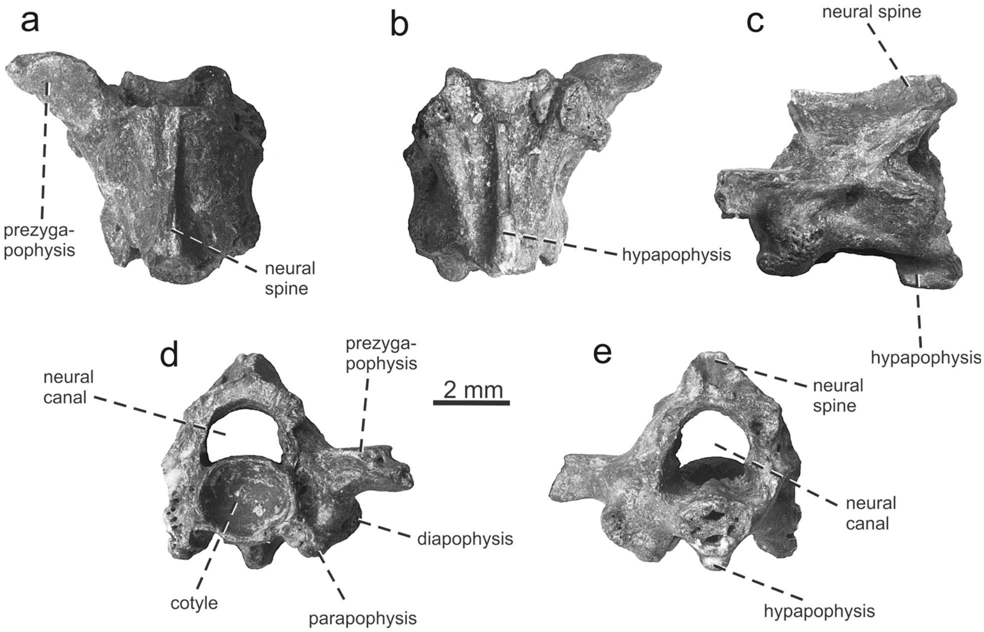


Fig. 18 cf. *Naja* sp.: trunk vertebra (IPB-HaH 3833) in **a** dorsal; **b** ventral; **c** lateral; **d** anterior; **e** posterior aspects

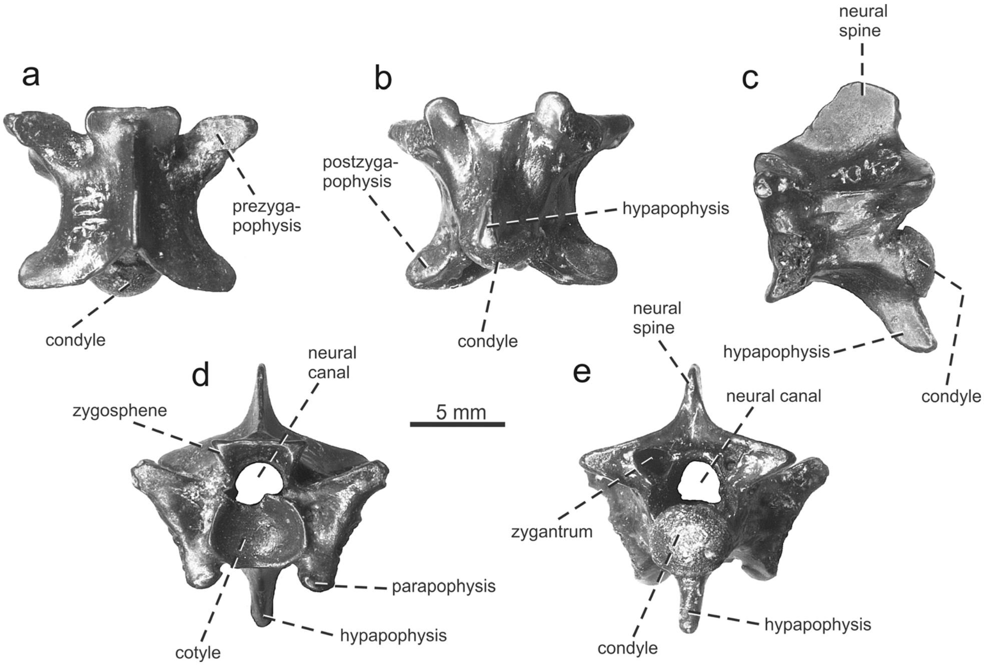


Fig. 19 *Vipera* sp. ("Oriental viper"): trunk vertebra (IPB-HaH 3811) in **a** dorsal; **b** ventral; **c** lateral; **d** anterior; **e** posterior aspects

"Colubrinae" indet. 2

Material, horizon and locality: One trunk vertebra (IPB-HaR 3001); upper Pliocene (MN 16), Hambach 11.

Remarks: The vertebra is badly damaged and its allocation at the generic level is impossible. The independent allocations of the vertebrae to "Colubrinae" indet. 1 and 2 are due to the different age of the fossils (middle Miocene vs. late Pliocene).

"Natricinae"
Natrix Laurenti, 1768

Natrix sp. 1
(Fig. 17)

Material, horizon and locality: Two trunk vertebrae (IPB-HaH 3842; 3843); middle Miocene (MN 5), Hambach 6C.

Vertebrae: The two fragmentary vertebrae are from the vertebral column mid-trunk. Their centra are considerably elongated, with a flat ventral surface laterally delimited by moderately developed subcentral ridges. Vertebra IPB-HaH 3842 (Fig. 17) has 3.5 mm centrum length and 2.1 mm width. The hypapophysis is lacking in both vertebrae. The neural arch is depressed. The neural spine is relatively lower than long, with weakly expressed anterior and posterior overhangs. The diapophyses are generally as long as the parapophyses. The parapophyseal processes are prominent, obtuse in shape and directed anteriorly. The zygosphenal roof is slightly convex in dorsal view. The prezygapophyseal articular facets are oval-shaped and elongate. The postzygapophyseal articular facets are small and subsquare. The prezygapophyseal processes are missing in both vertebrae. The cotyle and condyle are orbicular in shape. The subcentral, lateral and paracotylar foramina are distinct.

Remarks: The vertebral anatomical characteristics are typical of the living genus *Natrix*. Unfortunately, the shape of the hypapophysis, which is one of the most significant diagnostic features in this snake, remains unknown. Interestingly, the vertebrae scarcely resemble those of several extinct *Natrix* species described from the late early/early middle Miocene. Instead, by their morphology as well as relatively small size, the vertebrae are most similar to another fossil species, namely *Natrix rudabanyaensis*, reported from several late middle Miocene to late Miocene sites of Hungary and Romania (Szyndlar 2005; Venczel and Ştiucă 2008; Venczel and Hír 2013). Unfortunately, the scarcity and poor preservation of this fossil material make precise identification to specific level impossible.

The oldest record of *Natrix* in Europe comes from the early Oligocene (Rage 1988), and remains of this genus seldom occurred in fossil sites until the end of the early Miocene. The great boom of *Natrix* (represented by as many as six extinct species), along with other (exclusively fossil extint) genera of "natricines", took place in the European continent in the period between the late early and early late Miocene (MN 4 to 9) (Szyndlar 2012, and references therein).

"Natricinae" indet.

Material, horizon and locality: Nine trunk vertebrae (HaH–3827; 3834; 3837; 3849; 3854; 3821); middle Miocene (MN 5), Hambach 6C.

Remarks: Although these vertebrae are badly damaged, some of them may have formed part of the above mentioned *Natrix*. Most vertebrae, however, based on their relatively small dimensions, may have belonged to other genera. Regarding small-sized "natricines", in some cases their vertebrae may be practically undifferentiable from those of tiny members of the family Elapidae. This is also the case of one minute vertebra from Hambach (IPB-HaH 3821).

Natrix sp. 2

Comment: The location of the material described here as *Natrix* sp. 2 (below "Natricinae" indet.) reflects its stratigraphic position (upper Pliocene).

Material, horizon and locality: Four trunk vertebrae (IPB-HaR 3010; 3401); upper Pliocene (MN 16), Hambach.

Remarks: These vertebrae have several characteristic traits of the *Natrix* genus, but poor preservation precludes their identification at the species level. The independent allocations of the vertebrae to *Natrix* sp. 1 and 2 are mainly due to the different age of the fossils (middle Miocene vs. late Pliocene).

Elapidae Boie, 1827
Naja Laurenti, 1768

cf. *Naja* sp.
(Fig. 18)

Material, horizon and locality: Six trunk vertebrae (IPB-HaH 3833; 3845; 3850; 3859); middle Miocene (MN 5), Hambach 6C.

Vertebrae: The vertebrae are referred to the genus *Naja*, with reservation. Most of them come from the middle portion of the column of one or more subadult rather than adult individuals, as indicated by the relatively broad neural canals. The bones are poorly preserved with the most protruding parts lacking. Only IPB-HaH 3833 clearly displays *Naja* characteristics. Although it too is badly damaged for certainty, it appears to be one of the posteriormost vertebrae in the vertebral trunk.

The centrum width of the largest IPB-HaH 3833 specimen is 3.2 mm and its length is estimated at ±5.5 mm, but precise measurement is impossible because of the missing condyle. The centrum is triangular in ventral view, with almost flat ventral surface and well-developed subcentral ridges. The neural arch is vaulted. Remnants of the neural spine in one vertebra indicate that this structure was low. The paradiapophyses are well developed. The solely preserved parapophyseal process is strongly built, projected anteriorly and obtuse. The shape of the zygosphenal roof is unknown. The prezygapophysis is completely preserved in one vertebra, and this has a relatively short but strongly built and obtuse-shaped process. The prezygapophyseal facet is relatively large and elongated. The cotyle and condyle are suborbicular. The subcentral, lateral and paracotylar foramina are distinct.

The hypapophysis is preserved only in vertebra IPB-HaH 3833. It is restricted to the posterior portion of the centrum and appears square-shaped in lateral view. However, the remaining vertebrae have only hypapophyseal remnants, so definitive shape remains uncertain.

Remarks: Cobras do not currently live on the European continent. European cobra fossils, originally described as members of the extinct genus *Palaeonaja* (Hoffstetter 1939), are exclusively classified under the extant *Naja* genus (Szyndlar and Rage 1990). This taxon first appeared in Europe at the end of the early Miocene and dominated many ophidian assemblages in the remaining phases of the Neogene (for reviews of the fossil record, see Szyndlar and Rage 1990; Szyndlar 2005).

Cobra vertebrae found at European fossil sites are quite easily differentiated from other snakes. They closely resemble large-sized "colubrine" vertebrae, but contrary to the latter, they are provided with hypapophyses throughout the precloacal region of the column; moreover, they are characterised by relatively low neural spines. The vertebrae of cf. *Naja* from Hambach display some of these characteristics. Although the vertebrae are relatively small by cobra standard, this may be due to the presumed juvenile forms.

The peculiar shape of the hypapophysis in specimen IPB-HaH 3845 is a highly characteristic feature in the posteriormost trunk vertebrae of living Asiatic *Naja* species. These snakes are considered the closest relatives of cobras which inhabited Europe in the past (Szyndlar 2005).

Viperidae Oppel, 1811
Vipera (s.l.) Laurenti, 1768

Vipera sp. ("Oriental viper")
(Fig. 19)

Material, horizon and locality: Eight trunk vertebrae (IPB-HaH 3846; 3809; 3811; 3812; 3819; 3860); middle Miocene (MN 5), Hambach 6C.

Vertebrae: Compared with most Hambach ophidian remains, these vertebrae referred to the "Oriental vipers" are relatively well preserved. Most come from the mid-trunk portion of the vertebral column, but one almost completely preserved IPB-HaH 3811 vertebra (Fig. 19) is from the posterior portion of the column.

All vertebrae are apparently from oversized individuals with large dimensions. The largest IPB-HaH 3809 specimen has 8.6 mm centrum length and 8.3 mm width. In the posterior

Table 1 List of squamate taxa examined from Hambach 6C and comparison with other localities

	Sandelzhausen (16.47–16.27; Szyndlar 2009; Böhme 2010)	Hambach 6C (16.0–15.2)	Litke 1, 2 (15.2–14.8 Ma; Venczel and Hír 2015)	Griesbeckerzell 1b (15–14.9 Ma; Ivanov and Böhme 2011)	Griesbeckerzell 1a (14.77 Ma; Ivanov and Böhme 2011)
Chamaeleonidae	Two morphotypes	Two morphotypes	–	Chamaeleonidae	–
Agamidae	–	–	*Agama*	–	–
Lacertidae	*Miolacerta*	?	*Miolacerta*	–	–
	Lacertidae indet. 1 and 2	Lacertidae indet. 1 and 2	?	*Lacerta* s.l.	*Lacerta* s.l.
Blanidae	*Palaeoblanus*	–	–	–	–
Scincidae	*Trophidophorus*	–	–	–	–
	Scincidae indet. 1 and 2	–	–	–	Scincidae indet.
Cordylidae	"*Bavaricordylus*"	–	–	–	–
		–	–	–	? Cordylidae indet.
Anguidae	*Ophisaurus*	?	*Ophisaurus*	–	*Ophisaurus*
	Pseudopus laurillardi	*Pseudopus* cf. *ahnikoviensis*	–	*Pseudopus laurillardi*	*Pseudopus laurillardi*
Varanidae	–	–	*Varanus*	–	–
Aniliidae	*Eoanilius*	*Eoanilius*	–	–	–
Boidae	*Bavarioboa*	*Bavarioboa*	–	–	*Bavarioboa*
	–	–	*Eryx*	–	–
Pythonidae	–	–	–	*Python*	*Python*
Tropidophiidae	–	cf. *Falseryx*	–	–	–
Colubridae s.l.	*Coluber* s.l.	*Coluber* s.l.	*Coluber* s.l.	*Coluber*	*Coluber*
	–	*Texasophis*	*Texasophis*	–	*Texasophis*
	Telescopus	*Telescopus*	–	–	–
	Natrix	*Natrix*	–	–	*Natrix*
	Neonatrix	–	*Neonatrix*	–	–
Elapidae	*Naja*	cf. *Naja*	–	–	?
	–	–	–	–	*Micrurus*
Viperidae	*Vipera*	*Vipera*	–	*Vipera*	*Vipera*

trunk vertebra (IPB-HaH 3811), the centrum is 7.7 mm long and 7.0 mm wide. The centrum is triangular in ventral view. The subcentral ridges and subcentral grooves are distinct, especially in the anterior portion of the centrum. The distal parts of the hypapophyses are missing in most vertebrae, but their posteroventrally directed remnants demonstrate that they were long and straight. The neural arch is strongly depressed and devoid of epizygapophyseal spines. Although the neural spine is missing in most vertebrae, the preserved remnants suggest it was very high. The almost complete spine in the posterior trunk vertebra is distinctly longer than high. The zygosphene is very thick in anterior view and approximately straight in dorsal view. The prezygapophyseal articular facets are oval-shaped and laterally elongated. Prezygapophyseal processes are relatively short and obtuse. The paradiapophyses are slender, dorsoventrally elongated. They have long, flattened parapophyseal processes noticeable in anterior and ventral view. The cotyle and condyle are distinctly dorsoventrally depressed. All vertebral foramina are clearly visible.

Remarks: The vertebral centra are almost as wide as long. Their large dimensions and other characteristics enable the vertebrae to be confidently referred to "Oriental vipers". Extant species are currently classified in *Macrovipera* and *Montivipera* genera. Differentiation of these taxa solely on vertebral morphology is unrealistic, so it is preferable to use the term »*Vipera* ("Oriental viper")« for the fossil snakes. Similarly, although several fossil species of "Oriental vipers" have been described from European Neogene localities (see Szyndlar and Rage 2002, for review), it is almost impossible to differentiate them on vertebral characteristics.

The relatively low neural spine preserved in the IPB-HaH 3811 posterior trunk vertebra indicates that the remains did not belong to *Daboia*. *Daboia* is a different large viper inhabiting Spain in the Pliocene, with recent distribution in southern

Asia. In contrast to all members of the *Vipera* (*s.l.*) complex, the *Daboia* neural spine in posterior trunk vertebrae has equal length and height (Szyndlar 1988).

Current "Oriental vipers" are distributed in Asia and northern Africa, and their European range is restricted to a few localities in the southeastern outskirts of the continent. Together with fossil cobras, "Oriental vipers" first appeared in Europe at the end of the early Miocene and dominated many ophidian assemblages in the Neogene (for up-to-date review of the fossil record, see Georgalis et al. 2016b).

Vipera sp. ("*aspis* complex")

Material, horizon and locality: Three trunk vertebrae (IPB-HaH 3839; 3847); middle Miocene (MN 5), Hambach 6C.
Remarks: Compared to the "Oriental vipers", these vertebral fragments are from snakes with distinctly smaller dimensions. The centrum in the best preserved vertebra is 3.9 mm long and 2.8 mm wide. The absolute dimensions, centrum length/width ratio and other characteristics indicate that the fossils belong to the "*aspis* complex" of the genus *Vipera* (s.l.). These snakes appeared in Europe in the beginning of the Miocene; for the current opinions on the oldest vipers of the "*aspis* complex", see Čerňanský et al. (2015). At the end of the early Miocene, these snakes became common in the European continent (Szyndlar and Rage 2002); today, they inhabit a vast area of southern Europe.

Colubroidea indet.

Material, horizon and locality: Thirty-six caudal vertebrae (IPB-HaH 3829; 3836; 3840; 3848; 3851; 3856); middle Miocene (MN 5), Hambach 6C.
Remarks: These vertebrae are most likely from the caudal portion of the column in the above mentioned members of the Colubridae, Elapidae and Viperidae clades. Poor preservation and little taxonomic significance of colubroid caudals preclude identification even at the family level.

Discussion

Hambach 6C (middle Miocene, MN 5)

The squamate material from Hambach 6 C can be assigned to the following major clades: Chamaeleonidae, Lacertidae, Anguidae, Aniliidae, Boidae, Tropidophiidae, Colubridae, Elapidae and Viperidae. The snake remains are exclusively vertebrae, and of these, 149 come from the middle trunk of the column, with a further 36 from the caudal area. All vertebrae are preserved in fragmentary state and most are badly damaged, making precise identification difficult.

The squamosal of a European Miocene chameleon is described here for the first time. Its markedly developed sculpture is more typical of taxa with a low casque, as in *Furcifer* or *Calumma*, but it is more or less absent in the high casque-headed extant taxon *Chamaeleo calyptratus* (see Čerňanský et al. 2014, fig. 13). This supports previous observations based on the parietal (see Čerňanský 2010) that the Miocene *Ch. andrusovi* lacks a highly elevated dorsal casque. In addition, the two types of maxillary dentition found in the locality might indicate the presence of at least two chamaeleonid taxa at Hambach. The presence of this clade in Hambach MN 5 also provides an information on temperature because the lower mean annual temperature limit for chameleons is 17.4 °C (see Haller-Probst 1997).

The lacertid material also consists of two morphotypes, although ontogenetic variation cannot be fully excluded in this case. Anguid material is attributed to *Pseudopus* cf. *ahnikoviensis*, *Pseudopus* sp. and Anguidae indet. The first-mentioned taxon was previously known only from the lower Miocene zones MN 2–4 (see Klembara 2012; Čerňanský et al. 2015). Its presence in Hambach 6C enables further understanding of the *Pseudopus* clade history. It demonstrates this taxon, which represents the smallest species of the genus *Pseudopus* (see Klembara 2012) most likely survived at least until the beginning of the middle Miocene (zone MN 5). However, more complete material is required for stronger support for this statement. The presence of this taxon in Hambach 6C fits well with the palaeoenvironmental conditions of this locality (estuarine settings in a large fluviatile system surrounded by extended coal swamps; see Mörs et al. 2000; Mörs 2002). *P. ahnikoviensis* was described from the Merkur-North locality (MN 3; the Czech Republic)—this locality is interpreted as area flooded by rivers, with run-off spreading into flatlands and creating swamps and shallow lakes (Kvaček et al. 2004). However, *P. ahnikoviensis* occurred in wider environmental conditions. This taxon is documented in Dolnice (MN 4) as well (see Klembara 2012), where only 374 mm mean annual precipitation is estimated (Vida 2015). Chamaeleonids are documented from both Czech localities (Moody and Roček 1980; Fejfar and Schleich 1994; Čerňanský 2010; for snake faunas, see Szyndlar 1987; Ivanov 2002).

As for snakes, the material from Hambach contains at least one taxon indicative of warm (although not extremely warm) climate, namely the "Oriental viper". Unfortunately, the identity of another possibly useful element indicating higher temperatures, namely the cobra, is not certain (cf. *Naja*). The assemblage lacks super-thermophilous elements, like *Python*. The entire snake assemblage is typical for the European middle Miocene. Moreover, Hambach 6C is the geologically youngest fossil site yielding remains of *Eoanilius*, possibly also youngest *Falseryx* (cf. *Falseryx*).

Comparison with other Miocene localities

The slightly older Sandelzhausen squamate fauna exhibits higher diversity [Szyndlar (2009); Böhme (2010), see Table 1 here]. Two types of chamaeleonids are also present in Sandelzhausen. Besides clades occurring in Hambach, some other clades are recorded there (amphisbaenian, ? cordylid and *Neonatrix*). This may be explained by continual Sandelzhausen excavation for 44 years and the 150 tons of sediment screen-washed (see Böhme 2010). Besides Sandelzhausen, the snake assemblage from Hambach closely resembles coeval or similar age ophidian faunas from other German sites. These especially include slightly younger Griesbeckerzell (Ivanov and Böhme 2011; lizards are dominated here by *P. laurillardi*; see Klembara et al. 2010), and to a lesser extent the early Miocene Amöneburg locality (Čerňanský et al. 2015).

The slightly younger Litke localities in Hungary (early Badenian MN 6, see Venczel and Hír 2015) have a different taxa composition compared to Hambach 6 C (see Table 1). Thermophilous taxa are represented at Litke by agamid and monitor lizards. The anguid record includes *Ophisaurus* material, while the Lacertidae clade is represented by *Miolacerta* there. Venczel and Hír (2015) have suggested that chameleons are absent in Litke 1 and 2 most likely because of the different palaeoclimatic and palaeoenvironmental conditions generated by ongoing geodynamic processes in the eastern Central Paratethys. Ivanov and Böhme (2011) mentioned a presence of this clade in Griesbeckerzell 1b (15.0-14.9 Ma).

Finally, *Falseryx* is present only in Hambach, neither in Sandelzhausen nor Litke. Conversely, *Neonatrix* (a likely aquatic snake) is absent at Hambach but is present at Sandelzhausen and Litke. *Eryx* is present only in Litke, but the overall Litke snake fauna diversity is distinctly lower (see Table 1)

Hambach 11 and 13 (late Pliocene, MN 16)

Although these late Pliocene localities have very low taxonomic palaeodiversity, large *Pseudopus* members are abundant. Some elements can be allocated to *P.* cf. *pannonicus. P. pannonicus* has been described from the following central European sites, dated from the upper Miocene to Pleistocene; (1) the Austrian Vienna Basin [Harzhauser and Tempfer (2004); loc. Atzelsdorf, MN 9; Tempfer (2009)]; (2) Hungary [loc. Polgárdi, MN 13, Venczel (2006)] and (3) Slovakia [loc. Ivanovce, MN 15, Klembara (1986); for additional taxa described there, see Čerňanský (2011b)].

Several taxa became extinct in central Europe during the MN 16 zone, due to climatic aridization (see e.g. Ivanov 2007). However, *Pseudopus pannonicus* survived until MN 17 and Klembara et al. (2010) report that this species had very broad ecological plasticity in various environments. The fossil material of *P. pannonicus* is frequently found in localities with sub-humid to humid climate, indicating that forested environments are preferential habitats for this species. Much higher palaeobiodiversity is recorded from the similarly aged Polish Weze II locality (although it should be noted that local environments can have a huge impact on the preserved fossils). The lizard fauna there is documented by *P. pannonicus*, *Anguis* cf. *fragilis*, *Lacerta* cf. *viridis* and *Lacerta* sp., whereas snake material includes "*Elaphe paralongissima*" (the specific distinction is doubtful here. Most likely, the remains belonged to the extant *Zamenis longissimus*; see Szyndlar 2012) and *Natrix* cf. *longivertebrata* (after Młynarski et al. 1984). Snake material in the late Pliocene of Hambach consists of *Natrix* sp. and Colubrinae indet., with the first-mentioned taxon present in the late Pliocene of Hajnáčka (Slovakia; see Čerňanský 2011b: here, only *Natrix natrix* has been identified for Squamata).

In conclusion, in contrast to the beginning of the middle Miocene (MN 5), the Pliocene part of the Hambach localities demonstrate absence of "Mediterranean" taxa, including the chamaleonids in the late Pliocene (MN 16) of Germany. Our study supports previous observations that decrease in the diversity of European herpetofauna ranged from the end of the Miocene climatic optimum to the Pleistocene and Holocene. As Szyndlar (1991a, b) and Rage and Roček (2003) state, this period marked rapid climate change due to Quaternary glacial cycles which had such strong influence on ectothermic animals.

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Compliance with ethical standards

Conflict of interest Authors proclaim no conflict of interest.

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