

The new rare record of the late Oligocene lizards and amphisbaenians from Germany and its impact on our knowledge of the European terminal Palaeogene

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Abstract There have been only a few studies on squamates from the late Oligocene of Europe, resulting in significant gaps in our knowledge of the reptile faunas from the latest Paleogene. Here, we report on new late Oligocene fossil material from two German localities, Herrlingen 11 (MP 28) and Herrlingen 9 (MP 29). The material can be assigned to the following major clades: Iguanidae, Gekkota, Lacertidae, Amphisbaenia, and Anguimorpha. The iguanid material shows that this clade was much more widely distributed in the Oligocene of Europe than previously thought, and also represents the youngest known record of this clade for Eurasia and Africa, with the exception of Madagascar. Although very fragmentary, the gekkotan material appears to be more similar to early Miocene forms such as *Euleptes* or *Gerandogekko*, rather than to early Oligocene taxa like *Cadurcogekko*, as indicated by the small size and morphology. The resemblance of the gekkotan fossils to Miocene forms suggests potential faunal turnover prior to the Paleogene–Neogene transition. The amphisbaenian material is represented by several types; the first can be allocated to Blaniidae based on tooth count and the presence of a small 4th and an enlarged 3rd tooth, which is a derived feature. The second type is

attributed to *Palaeoblanus*. Other cranial material is assigned to Amphisbaenia indet. The lacertid material consists of several amblyodont forms such as *Dracaenosaurus*, *Pseudeumeces* and *Mediolacerta*, as typically seen in other Oligocene deposits from Europe, but also includes non-amblyodont taxa such as *Plesiolacerta* and an undetermined lacertid. Especially common among the material are anguimorphs, which are here represented by *Ophisaurus* and a form that appears identical to the French Oligocene taxon described as *Dopasia coderetensis*. Reinvestigation of the European Oligocene "*Dopasia*" (= *Ophisaurus*) shows that the taxa described as *D. frayssensis* and *D. coderetensis* are markedly different from the members of the clade *Ophisaurus* in the morphology of the posterior dentary region and that those taxa cannot be allocated to this genus. For this reason, we erected a new generic name: *Ophisauromimus* gen. nov. The composition of the Herrlingen fauna shows an interesting mix of ancient Paleogene and more modern Neogene faunal elements, while overall bearing many similarities to contemporaneous faunas from France.

Keywords Palaeogene · Squamata · Diversity · Anatomy · Europe

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Abbreviations

NMB Natural History Museum, Basel, Switzerland
SMNS Staatliches Museum für Naturkunde, Stuttgart, Germany

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Introduction

The Oligocene marks the end of the paratropical ‘greenhouse’ world of the Paleogene and the onset of the more modern-looking terrestrial ecosystems that dominated the Neogene

(see e.g. Rage 2013). Major changes during the Oligocene included a global expansion of grasslands and a regression of tropical broadleaf forests into lower latitudes as a result of global cooling (e.g. Jacobs et al. 1999; Zachos et al. 2001; Strömberg 2002, 2004). With respect to Europe, a terrestrial connection with Asia was established that opened a migration corridor for terrestrial biota (Haq et al. 1987). As a likely consequence of these major environmental and geographic changes, the early Oligocene fauna of Europe is thought to have experienced increased extinction and faunal turnover, also known as the “Grande Coupure” (Rage and Augé 1993; Rage 2013).

Unfortunately, our understanding of late Oligocene herpetofaunal dynamics is severely hampered by the paucity of suitable fossil studied localities, with only a handful of places known, such as Coderet in France (Augé 2005) and Rott and Oberleichtersbach in Germany (Mörs 1995; Böhme 2008). Because of the poor fossil record, the latest Oligocene, together with the early Miocene, has been referred to as the ‘Dark Period’ of European snake fossil history (Szyndlar and Rage 2003; Rage and Szyndlar 2005). In this respect, Čerňanský et al. (2015a) were recently able to show that squamate diversity was already high in the early Miocene (MN 2) of Germany, with many modern clades present, but overall the amount of herpetofaunal information from the Paleogene/Neogene transition remains poor for (central) Europe.

Here, we describe fossil lizard and amphisbaenian material from the upper Oligocene of southern Germany, i.e. Herrlingen 9 (MP 29) and Herrlingen 11 (MP 28). Since the 1960’s mining activities have revealed several fossiliferous fissure fillings from this area (Ziegler 2000). The rodents and the insectivores of Herrlingen 9 have been published in detail by Ziegler (1994, 1998), suggesting a correlation of Herrlingen 9 with the level of Rickenbach (MP 29) or slightly younger (Ziegler 2000). The avifauna from both localities was described by Manegold (2008), and the snakes of Herrlingen 11 have been described by Szyndlar and Rage (2003). Previously, lizards from this area have been described from Herrlingen 8 (MP 28) by Čerňanský and Augé (2012, 2013), documenting records of the lacertid taxa *Plesiolacerta erasthensesi* and *Pseudeumeces* cf. *cardurcensis* as well as indeterminate anguid material. The new lizard and amphisbaenian assemblage described in the present paper provides the opportunity to document further data about the herpetofaunal diversity in central Europe at the end of the Paleogene, which should prove useful for future analyses of past squamate diversity and faunal change.

Material and methods

This study is based on fossil material housed at the Staatliches Museum für Naturkunde (SMNS), Stuttgart, Germany. The photographs were taken with a Leica M125 binocular

microscope with axially mounted DFC500 camera; software: LAS (Leica Application Suite) v.4.1.0 (build 1264). Several specimens were photographed using a scanning electron microscope (SEM; FEI Inspect F50) at the Slovak Academy of Sciences (Banská Bystrica). The Herrlingen White Jurassic quarry, from which all the material was collected, is situated north of the Blau valley some 8 km west of Ulm (topographic map sheet 7525 Ulm NW, r 3566670/h 5365180). The fossils were collected by screen-washing or surface prospecting by R. Wannemacher in 1993 (Herrlingen 11) and by M. Rummel in 1991 (Herrlingen 9).

Relevant specimens were scanned using the micro-computed tomography (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-set was analysed using VG Studio Max v. 2.2 on a high-end computer workstation.

Systematic palaeontology

Squamata Oppel, 1811

Iguania Cope, 1864

Iguanidae Bell, 1825

Iguanidae indet.

(Fig. 1)

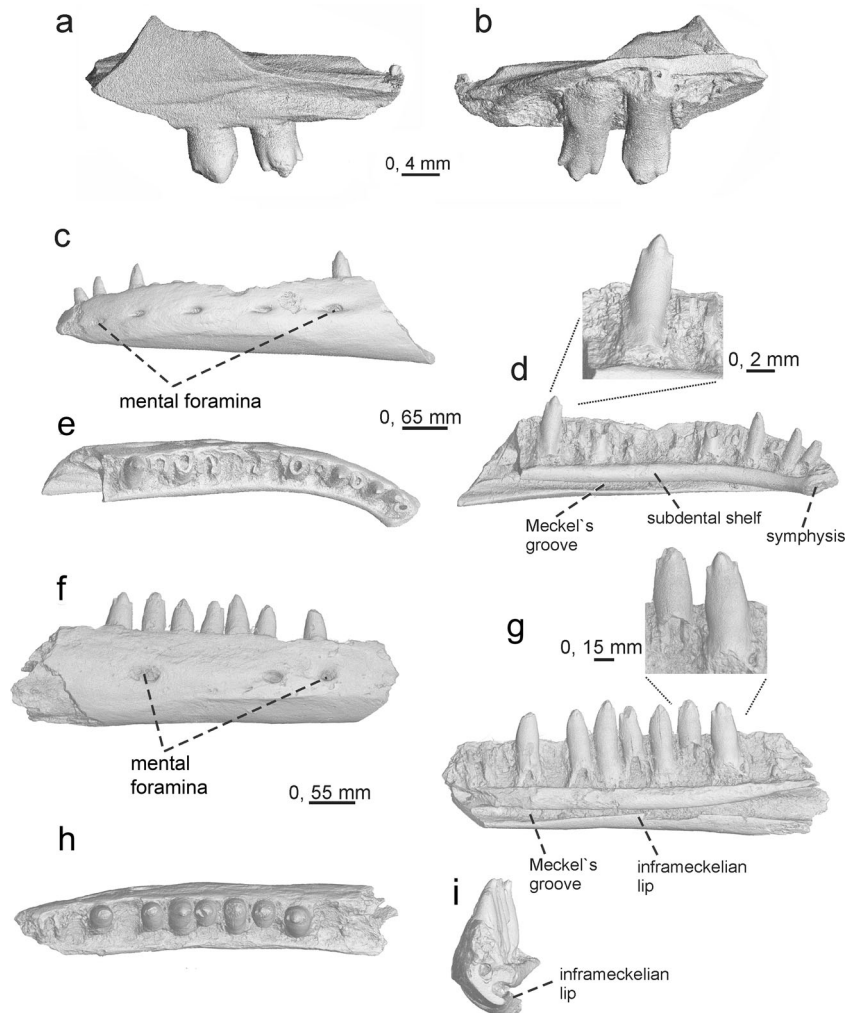
Locality, horizon and material: 1. Herrlingen 11; upper Oligocene (MP 28): maxilla SMNS 59446 b, two right dentaries SMNS 59459 e, f, one left dentary SMNS 59459 g. 2. Herrlingen 9; upper Oligocene (MP 29): maxilla SMNS 58233 c, SMNS 800040 g

Maxilla: All maxillae are only fragmentarily preserved. The alveolar crest is shallow, supporting 2 teeth. The supradental shelf is thin. Unfortunately, the nasal process is completely broken.

Dentary: The dentary is an anteroposteriorly elongated element. The anterior region is rounded in dorsal view, and strongly curved medially. Meckel’s groove is very narrow, but deep. In the mid-region, the ventral margin rises dorso-medially, forming a lamina, i.e. the so-called inframeckelian lip (sensu Smith 2009a). This septum is very close to the subdental shelf, so the opening of Meckel’s groove is very narrow. The thin subdental shelf is almost straight. In specimen SMNS 59459 e, the alveolar crest supports 12 tooth positions (seven teeth are still attached). The external surface of the preserved portion is smooth, and pierced by three mental foramina. In specimen SMNS 59459 g, 14 tooth positions are preserved (four teeth still attached). The labial surface is pierced by five foramina.

Dentition: The dentition is pleurodont, and teeth are closely spaced. The anterior teeth are pointed and slightly smaller than

Fig. 1 Iguanidae indet.: the maxilla SMNS 800040 g in **a** lateral and **b** medial aspect. The left dentary SMNS 59459 in **c** lateral, **d** medial (with tooth detail) and **e** dorsal aspect. The right dentary SMNS 59459 e in **f** lateral, **g** medial (with teeth detail), **h** dorsal, **i** anterior aspect



posterior ones. In the posterior region, teeth are strongly tricuspid, with a dominant central cusp and mesial and distal accessory cusps of equal size, which are well separated from the main one. The tooth necks become broader towards the base, but the tooth base itself is slightly compressed. The resorption pits are located at the bases of the teeth.

Remarks: All referred specimens, although fragmentarily preserved, show a high similarity to each other. Although Meckel's groove is open, it is also slightly restricted. The infra- and supra-Meckelian lips approach each other very closely, which is similar to *Geiseltaliellus* (Smith 2009b) and *Suzanniwana* (Smith 2009a, fig. 3 N), as well as some species of *Basiliscus*. Teeth are tricuspid (except for the anterior most ones), having symmetrically developed mesial and distal cusps around the central dominant cusp as it is typically seen in many iguanids (e.g. extinct *Geiseltaliellus* or extant *Basiliscus*). In contrast, tricuspid teeth in lacertids have usually a mesial cusp that is distinctly bigger than the distal one. According to Etheridge and de Queiroz (1988), tricuspid teeth represent a primitive condition for Iguanidae. The material described here is similar to that described by Augé and Pouit

(2012) from the locality of Pech-du-Fraysse (MP28, late Oligocene, France, Phosphorites du Quercy) and assigned to the genus *Geiseltaliellus*. However, because of its fragmentary character, we decided to assign the material from Herrlingen only to the family level.

Gekkota Camp, 1923

Gekkota indet.

(Figs. 2, 3)

Locality, horizon and material: 1.Herrlingen 11; upper Oligocene (MP 28): premaxilla SMNS 59459 a. 2.Herrlingen 9; upper Oligocene (MP 29): three fragments of the left dentaries, prefixed by SMNS 800040 a–c, two fragments of maxillae prefixed by SMNS 800040 d and f, isolated vertebra SMNS 80042.

Premaxilla: The bone is an unpaired, T-shaped element. It bears eight tooth positions, unfortunately all teeth are missing. The nasal process is wide, having a triangular posterodorsal end. Its external surface is flat. On the internal side, there is a ridge running along the entire length of the nasal process. It

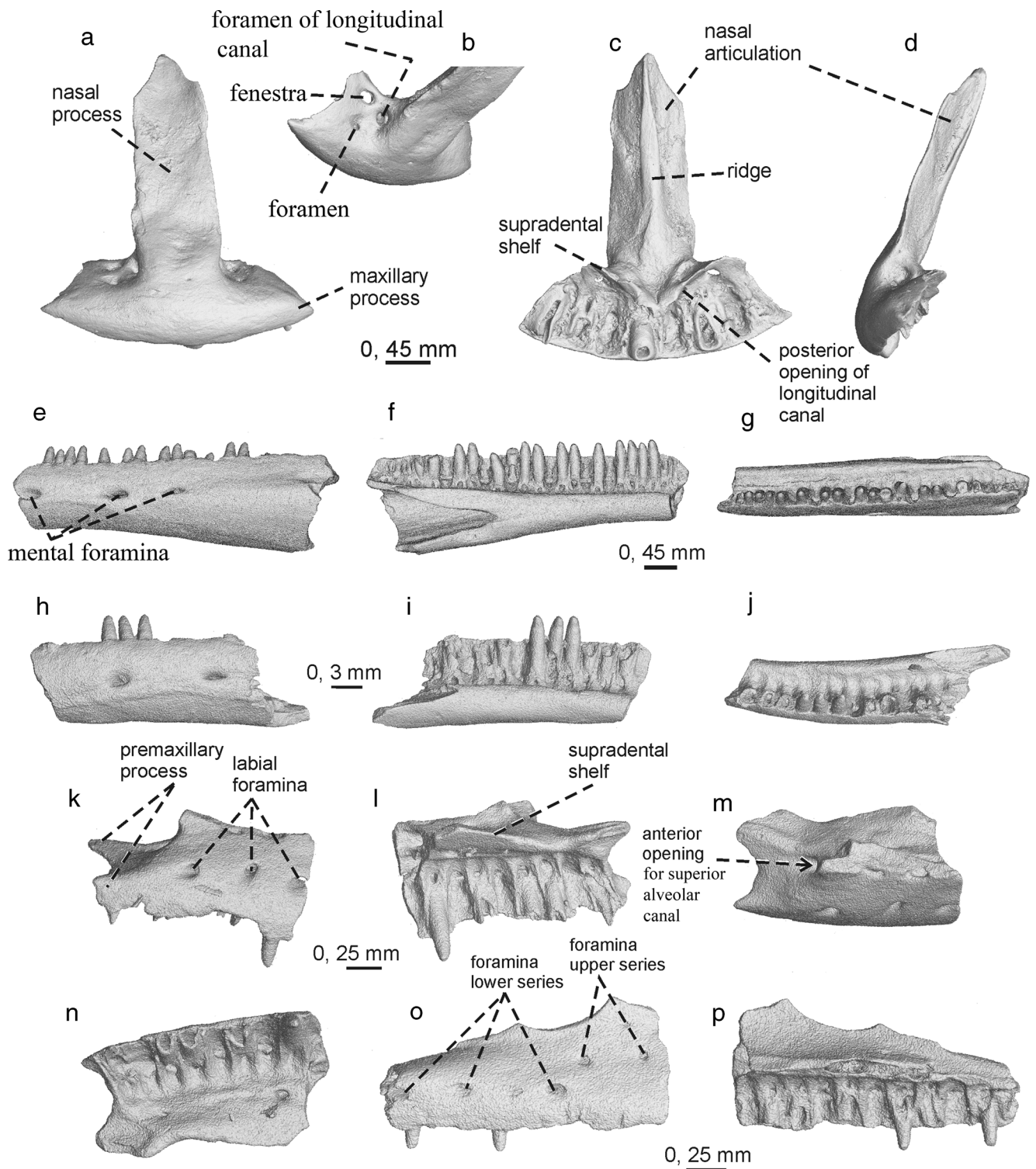


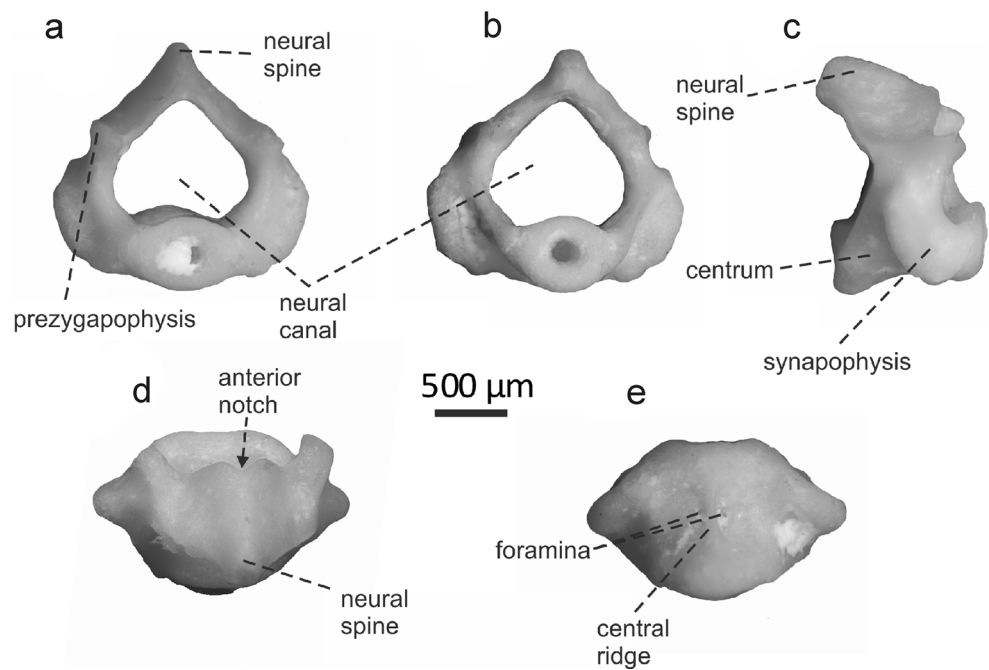
Fig. 2 Gekkota indet: premaxilla SMNS 59459 a in **a** anterior, **b** dorsoanterolateral, **c** posterior, **d** lateral aspects; left maxilla SMNS 800040 a in **e** lateral, **f** medial and **g** dorsal aspect. Left dentary 800040

b in **h** lateral, **i** medial and **j** dorsal view; left maxilla SMNS 800040 **d** in **k** lateral, **l** medial, **m** dorsal, and **n** ventral aspect; right maxilla SMNS 800040 **f** in **o** lateral and **p** medial aspect

lies in the sagittal region, separating the facet for the nasals on both sides. On the lateral side, close to the base of the nasal process, the foramen for the longitudinal canal is located. Its

posterior opening is located on the ventral side of the supraddental shelf (the foramen is developed only on the right side). CT images show that the canal is connected to the huge

Fig. 3 Gekkota indet.: isolated cervical vertebra SMNS 80042 in **a** anterior, **b** posterior, **c** lateral, **d** dorsal, **e** ventral aspect



central cavity inside the nasal process and forms a connection between left and right side. In addition, another smaller foramen is located more anterolaterally from the base of the nasal process, forming an opening for the canal running to the tooth bases (nutritive foramen). The supraddental shelf is V-shaped, and pierced by a fenestra on each side. The mid-region of the shelf forms the anterior edge of the medial foramen. The maxillary processes are well laterally expanded, forming a contact with the maxilla. The ventral margin of the premaxilla is rounded.

Maxilla: The description is based on a fragment of the anterior region of the left maxilla and a fragment of the posterior region of the right maxilla. The anterior region has a well-developed, medially expanded supraddental shelf. The anterior region of maxilla is divided, having short external ramus and broader more medially oriented internal ramus of the premaxillary process. The preserved portion bears 8 tooth positions, with 2 teeth still attached. The external surface is pierced by three labial foramina. The posterior portion bears 10 tooth positions, and 2 teeth are still attached. The supraddental shelf is narrow, and only slightly expanded medially.

Dentary: The description is based on a fragment of the left dentary. It bears 25 tooth positions, with 14 teeth still preserved. The entire preserved portion is narrow, becoming only slightly broader posteriorly. The anterior region (based on SMNS 800040 b) is curved medially. Meckel's groove is largely closed, and partly open only in the posterior region. The opening is triangular in shape, reaching to the level of the 10th preserved tooth position (in posterior aspect). The smooth lateral surface is pierced by three anteroposteriorly elongated mental foramina.

Dentition: There is a high number of pleurodont, closely packed cylindrical teeth with only small interdental gaps. The teeth are tall, cylindrical, straight and pointed. At the bases, they have oval resorption pits.

Vertebra: Only one isolated cervical vertebra is preserved. It is very small and lightly built. It is an anteroposteriorly short element, i.e. much higher than long. The neural canal is huge, nearly pentagonal in shape, and bordered by the neural arch. On the dorsal surface of the neural arch, a straight dorsal crest is gradually elevated posterodorsally. It forms a low neural spine that is slightly expanded posteriorly. In dorsal view, an anterior margin of the neural arch bears a shallow notch. The prezygapophysis is preserved only on the right side. It is small and square with rounded margins. It is inclined from the horizontal plane in an angle of 45°. The postzygapophyses are not preserved. The rodlike synapophyses are well developed, expanded laterally, and not as anteriorly located as is usual in dorsal vertebrae. They are orientated in anteroventral–posterodorsal direction. The centrum is amphicoelous and slightly depressed. In lateral view, it has a distinct constriction in its mid-region. In ventral view, it has a short keel in the central region. A pair of subcentral foramina is located close to this ridge.

Remarks: The Oligocene gekkotan lizard *Cadurcogekko piveteaui* was described by Hoffstetter (1946) from the Phosphorites du Quercy. However, besides the much larger body size of *Cadurcogekko*, there are also the other anatomical differences, such as 49 tooth positions and a much higher number of mental foramina. The Herrlingen material is very similar to *Euleptes* (Sphaerodactylidae) and *Gerandogekko* in the following features: (1) overall small size; (2) number of

teeth: although only 25 tooth positions are preserved, the anterior region is broken, so the real tooth number was higher (28 tooth number is observed in *E. gallica*, see Müller 2001; 29 for *Euleptes* sp., see Müller and Mödden 2001; and 31 for *E. europaea*, see Daza et al. 2014); (3) number of mental foramina: three are preserved, but the anterior region is broken making it likely that there were more; there are four mental foramina in *E. europaea* (Daza et al. 2014); and (4) opening for Meckel's groove reaching approximately to the same level anteriorly.

An anterior foramen located at the base of the nasal process of the premaxilla and a posterior foramen lying ventrally to it is present in many geckos (and other lizards), e.g. *Sphaerodactylus* (see Daza et al. 2008), representing the openings for the longitudinal canal, respectively. A huge central cavity is present inside of the nasal process, showing a similar condition to that of modern *Euleptes*. However, the third foramen of the Herrlingen premaxilla is not found in other modern geckos (Daza, personal communication 2015). As for the fenestra, a vaguely similar condition appears to be present in *Rhacodactylus auriculatus* (personal observation, see Digimorph 2002–2012). Another significant character is the shape of the nasal process, being very long and abruptly converging. In some modern geckos, e.g. *Cyrtodactylus*, the nasal process is very similar to that of the Herrlingen specimen, although not as long (Daza, personal communication 2015).

The Herrlingen material could represent the earliest known record of the clade *Euleptes*; however, more complete material is needed to support this claim. Schleich (1988a) reported the presence of a gekkotan lizard from the late Oligocene locality of Flörsheim (Mainz Basin, southern Germany), but this material requires a careful restudy.

Many gekkotan clades have amphicoelous vertebrae (e.g. most of Gekkonidae; see Hoffstetter and Gasc 1969). Amphicoelous vertebrae occur in nearly all sphaerodactylids (see e.g. Camp 1923; Hoffstetter and Gasc 1969; Kluge 1995), but the New World sphaerodactylids, in contrast, are mainly procoelous (Daza, personal communication 2014). All gekkotan material described here is very limited, therefore its precise allocation is impossible; although the material appears to have similarities with the clade Sphaerodactylidae, there is not enough support to exclude other clades.

Lacertiformes Estes et al., 1988

Lacertidae Oppel, 1811

Dracaenosaurus Pomel, 1846

Dracaenosaurus croizeti Gervais, 1848 – 1852

(Fig. 4 a–f, j–l)

Locality, horizon and material: 1. Herrlingen 11; upper Oligocene (MP 28): Three right dentaries SMNS 59461 a–c;

one left dentary SMNS 59461 d; one right maxilla SMNS 59461 e.

2. Herrlingen 9; upper Oligocene MP 29: Four fragments of right dentaries SMNS 58230 a–d; two fragments of left dentaries SMNS 58230 e, f; one right maxilla SMNS 58230 g.

Dentary: The dentaries are well preserved, although all are incomplete. They are robustly built and relatively short. In cross-section, they are C-shaped. On the medial side, the deep Meckel's groove is fully open and broad posteriorly, becoming distinctly narrower in the anterior region. This gives a nearly triangular, or wedge-shaped, to the whole dentary bone. In the posterior region, the rounded small alveolar foramen is located at the level of the largest posterior tooth. Anterior to this foramen, the intramandibular septum forms the ventromedial wall of the alveolar canal. Meckel's groove is roofed by a well-developed subdental shelf (sensu Rage and Augé 2010), which is slightly concave dorsally. It bears a facet for the splenial on the ventral side. On the dorsal side, the *sulcus dentalis* is well developed but shallow. The tooth number of the dentary with a complete dentition is 8. Posteriorly to the tooth row, the dentary rises to the posterodorsally slightly elevated coronoid process. This process is blunt, not markedly separated from the rest of the region. It bears a facet for the coronoid on its dorsomedial surface. The posterodorsal limit of the process is higher than the apices of the largest mandibular teeth. Additional processes cannot be identified. The lateral surface of the dentary is pierced by a series of on average 6 small mental foramina. They are located in the dorsal third of the dentary bone, close to the tooth row.

Maxilla: The maxillae are only incompletely preserved. The dentition is identical to that of the dentaries. The supradental shelf is well developed and the three most posterior teeth are preserved. The rounded superior alveolar foramen is located at the level of the largest posterior tooth. Here, the subdental shelf forms the palatine process. Posteriorly to it, the shelf becomes slightly wider, and bears a groove on its dorsal surface that serves for the articulation with the jugal. The nasal process is only partly preserved.

Dentition: The dentition is pleurodont and clearly heterodont. The amblyodont teeth are short, extremely blunt, with rounded, mediolaterally compressed, and antero-posteriorly slightly elongated apices, which becomes especially pronounced in the posterior region. The tooth size is increasing posteriorly and the largest tooth is usually the posteriormost one, although in some cases, a smaller tooth can be located in the posteriormost position. The largest tooth is distinctly bigger than the others and is mushroom-shaped (although it should be noted that the tooth is also compressed laterally). The tooth crowns bear very fine delicate vertical striations. In most cases, the tooth

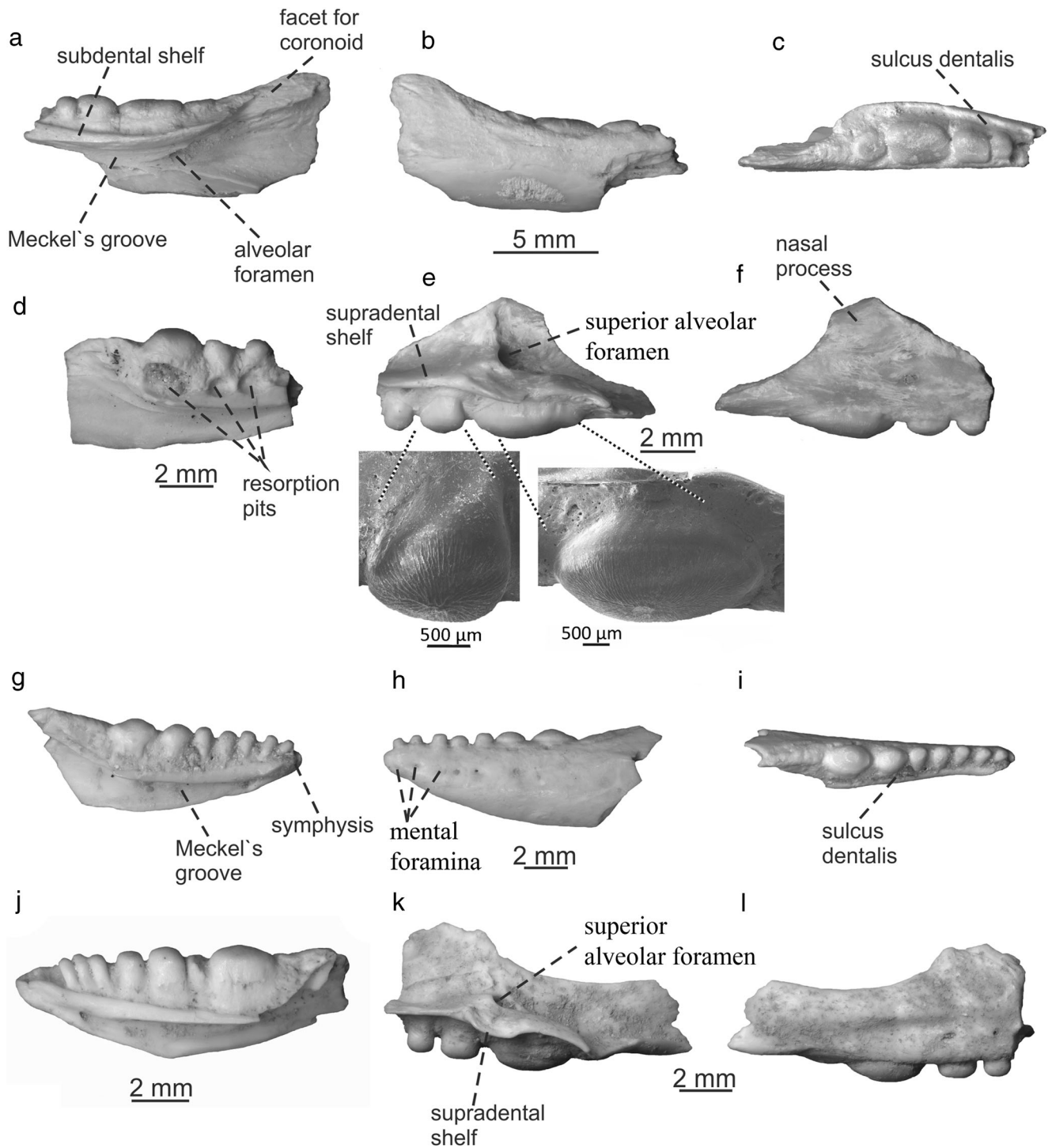


Fig. 4 *Dracaenosaurus croizeti*: right dentary SMNS 58230 a in a medial, b lateral, c dorsal aspect. Left dentary SMNS 58230 e in d medial aspect. Right maxilla SMNS 58230 g in e medial aspect with detail of teeth and f in lateral aspect. *Dracaenosaurus* sp.: the left

dentary SMNS 58230 h in g medial, h lateral, i dorsal aspect. *Dracaenosaurus croizeti*: right dentary SMNS 59461 a in j medial aspect. Right maxilla SMNS 59461 e in k medial and l lateral aspect

base is covered by cement, except for one dentary (SMNS 58230 e) in which huge, rounded resorption pits are exposed (Fig. 4d).

Remarks: The attribution of the material described here to *Dracaenosaurus croizeti* is based on the following characters: (1) dentary is a shorter, more massive and deep element; (2)

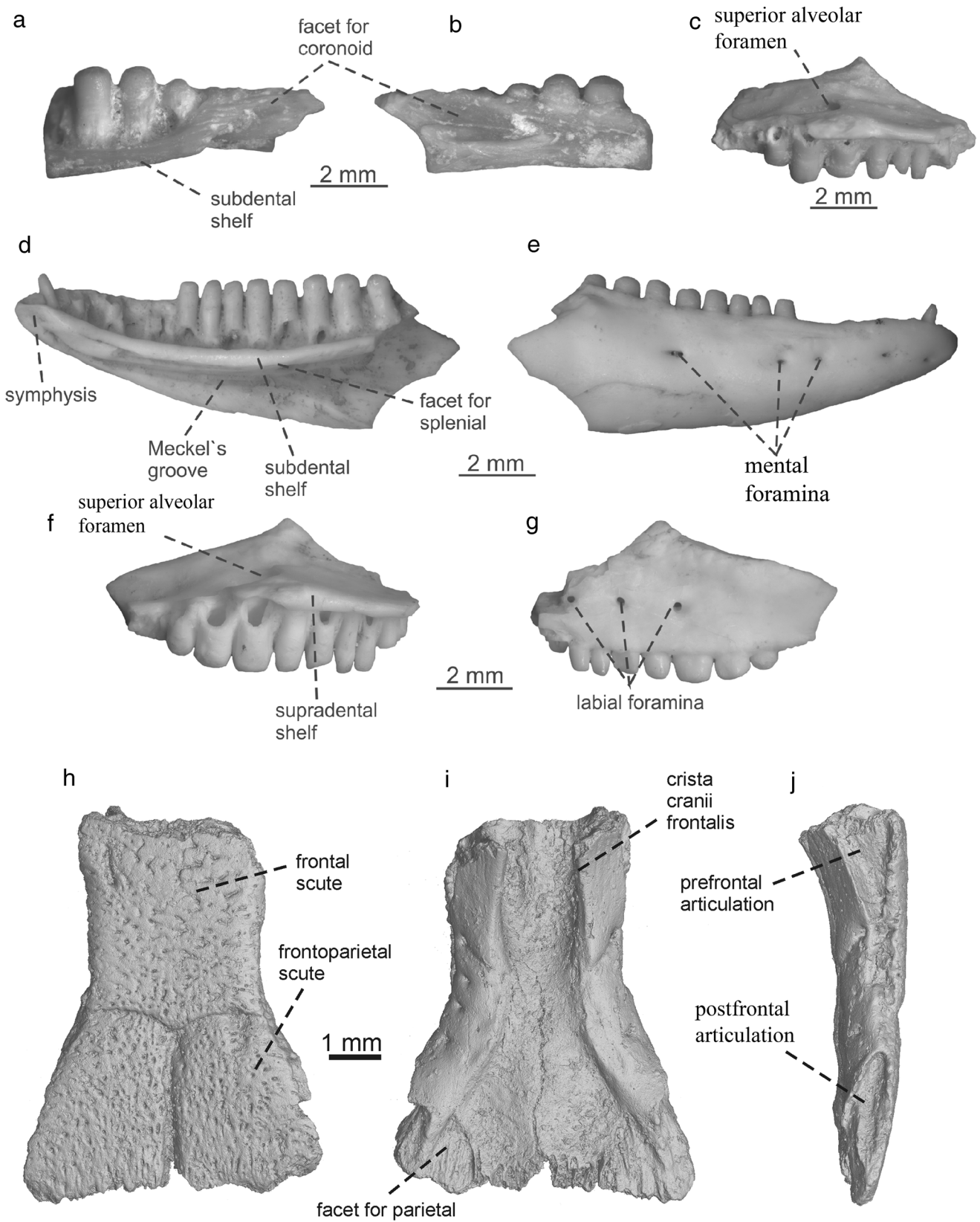


Fig. 5 *Pseudeumeces* cf. *cadurcensis*: right dentary SMNS 58232 a in a medial, b lateral aspect. Left maxilla SMNS 58232 b in c medial aspect. Right dentary SMNS 59461 f in d medial and e lateral aspect. Left

maxilla SMNS 59461 g in f medial and g lateral aspects. ? *Pseudeumeces* sp.: frontals SMNS 59458 a in h dorsal, i ventral and j lateral aspect

presence of strongly amblyodont dentition; and (3) low tooth number that is never higher than 8 (Müller 2004; Augé 2005).

Dracaenosaurus sp.
(Fig. 4 g–i)

Locality, horizon and material: Herrlingen 9; upper Oligocene MP 29: left dentary SMNS 58230 h.

Description and remarks: The description is based on one isolated left dentary. The general morphology is very similar to that of the dentaries described above. However, the posterior teeth are not as robust, as it is usually the case in *D. croizeti*. Unfortunately, it is impossible to decide on the basis of such limited material if both dentary types represent independent forms or only extreme forms of the same species.

Pseudeumeces Hoffstetter, 1944
Pseudeumeces cf. *cadurensis* (Filhol, 1877)
(Fig. 5)

Locality, horizon and material: 1. Herrlingen 11; upper Oligocene (MP 28): right dentary SMNS 59461 f and left maxilla SMNS 59461 g; 2. Herrlingen 9; upper Oligocene (MP 29): right dentary SMNS 58232 a and left maxilla SMNS 58232 b.

Maxilla: The elements are incomplete. The preserved portion of the Herrlingen 11 specimen bears nine tooth positions, and seven teeth are still in place. The supradental shelf is well developed, and well expanded medially. The superior alveolar foramen is located on the level of the 4th posterior tooth position. Posteriorly to this structure, the maxilla bears a facet for the jugal. The labial surface is pierced by three foramina in the Herrlingen 11 specimen and five in the Herrlingen 9 specimen. The foramina are slightly variable in size, but overall increase in size posteriorly. Unfortunately, the nasal process is broken in all specimens. However, the small preserved region of the process under the fracture is sculptured, formed by irregular straight grooves and very flat bulges.

Dentary: The description is based on a well-preserved specimen, unfortunately lacking its posterior region. It is a long, massive and ventrally arched bone, with a slight medial curvature at its anterior end. An alveolar crest supports a single row of 16 tooth positions, where 9 teeth and 7 empty tooth loci are preserved (since the tooth row is not completely preserved, the initial tooth number was most likely slightly higher). On the lingual side, Meckel's groove opens widely posteriorly and steadily narrows towards the anterior termination. The alveolar foramen is located at the level of the 4th posterior preserved tooth. Meckel's groove is roofed by the subdental shelf. The shelf is markedly arched ventrally. It gradually becomes thinner towards the posterior end, partly as a result of the presence of the facet for the splenial, situated on its ventral margin. However, the posterior portion is broken off and

missing. On its dorsal face, the *sulcus dentalis* is well developed. The labial surface is pierced by five mental foramina. On the dorsal region of the posterior end, the anterior beginning of the coronoid facet is preserved.

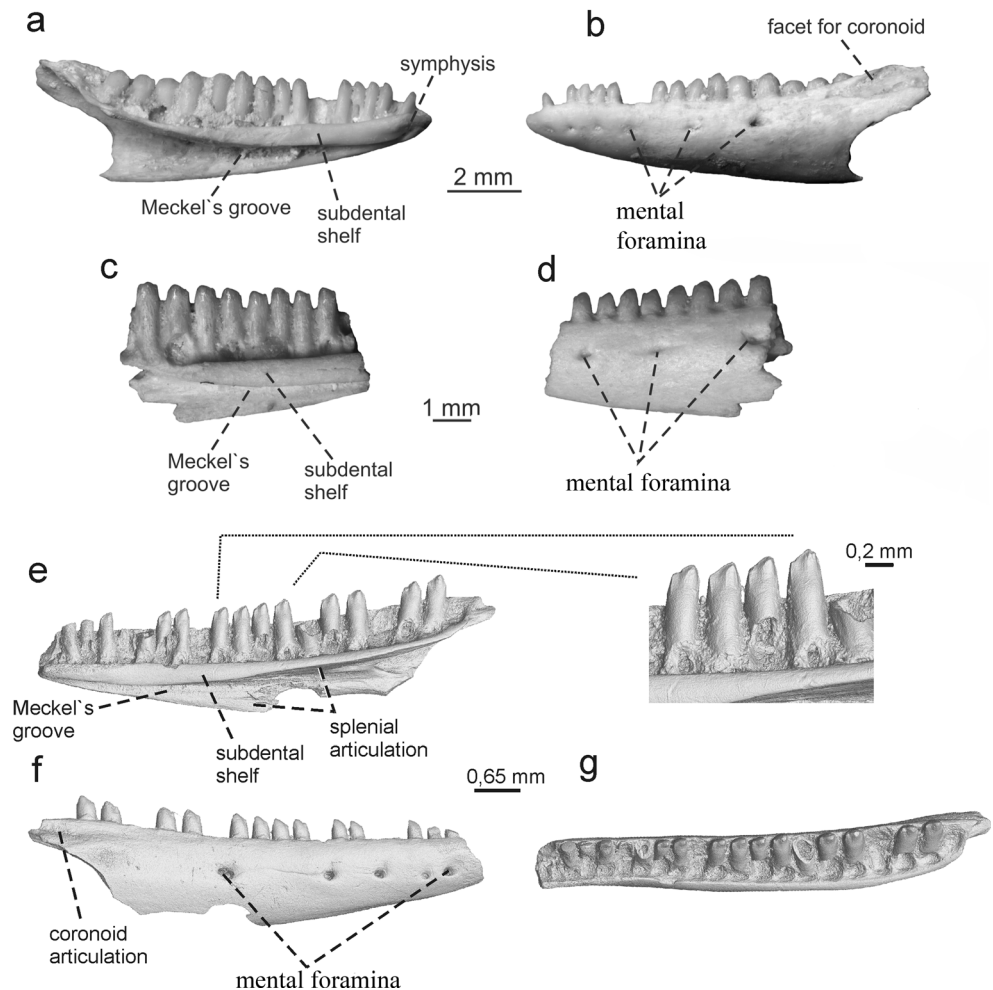
Dentition: The dentition is pleurodont and heterodont. The teeth are amblyodont, especially in the posterior region, forming robust cylinders. The teeth in the anterior region are slender and smaller. The largest tooth of the preserved portion of the dentary is the 2nd one from posterior, while the largest maxillary tooth is the 4th one. The more posteriorly located teeth are robust but distinctly lower. Lingually, some of the tooth crowns bear very fine and delicate vertical striations. The teeth are closely spaced with small inter-dental gaps. The tooth bases are more or less swollen lingually, with resorption pits sometimes preserved on the lingual side.

? *Pseudeumeces* sp.

Locality, horizon and material: Herrlingen 11; upper Oligocene (MP 28): frontals SMNS 59458 a.

Frontals: Frontals are fused and the traces of fusion are still possible to recognise in the mid-region of the ventral surface, mainly in the posterior portion of the frontals. The frontal bone is relatively short; however, the anterior portion of the frontals is broken and missing. The length of the preserved part, from the left anterior extremity to the level of the facet for the parietal, is 7.4 mm. In dorsal view, the bone is narrowest over the midorbital region, where a small constriction can be recognised. Here, the width is 3.5 mm. The element is only slightly broadened anteriorly (3.8 mm), but strongly posteriorly, i.e. the corners of the posterior region are expanded laterally, which forms the concave lateral edges of the element. Here, the width is 6.0 mm. The posterior region, which forms the contact with the parietal, is therefore much wider. The suture is almost straight, only slightly concave, and shows well-developed interdigitations. Osteoderms cover the dorsal surface of the frontal. The entire dorsal surface of these osteodermal scutes has a light ornamentation, which is more strongly expressed in the posterior portion of the bone. The ornamentation is formed by fine small, numerous foramina and grooves. The sulcus interfacialis, which makes the limit between the frontal scute and two posteriorly located frontoparietal scutes, is V-shaped, with rounded convex lateral branches. In lateral view, the frontal is slightly arched dorsally. Here, the margins of the bone bear facets for the prefrontal and the postfrontal bones. The facets are not in contact and the lateral margin of the frontal has therefore a free area around the mid-region, forming the dorsal part of the orbit. On the lateral surface, the lateral margins of the whole element are bordered by the *cristae cranii frontalis*. Anteriorly, these form the strong, but not deeply protruding, subolfactory processes. On the posterolateral corners of the internal surface, well-developed triangular facets for the parietal tabs are located. The whole surface continues into a depression anteriorly.

Fig. 6 *Mediolacerta cf. roceki*: left dentary SMNS 59446 a in **a** medial, **b** lateral aspect. Cf. *Plesiocacerta* sp.: left dentary SMNS 58233 b in **c** medial and **d** lateral aspect. Lacertidae indet. – tooth morphotype 5: right dentary SMNS 59459 b in **e** medial aspect with a detail of teeth, **f** lateral, **g** dorsal aspect



Remarks: The whole construction of the frontal is robust and the element is short. However, the anterior region in front of the subolfactory process is missing. In other lacertids, this region can form roughly one-quarter of the entire length of the element. If the length of the preserved part is 7.4 mm, it may be estimated that the whole element was between 9 and 10 mm long. The frontal is nearly identical to the frontal RH-B2–775 from Gannat, described as *Pseudeumeces cadurcensis* by Augé and Hervet (2009, fig. 4). However, since the frontal bones of *Mediolacerta* are unknown, the material here is only questionably attributed to *Pseudeumeces*.

Mediolacerta Augé, 2005

Mediolacerta cf. roceki Augé, 2005

(Fig. 6a, b)

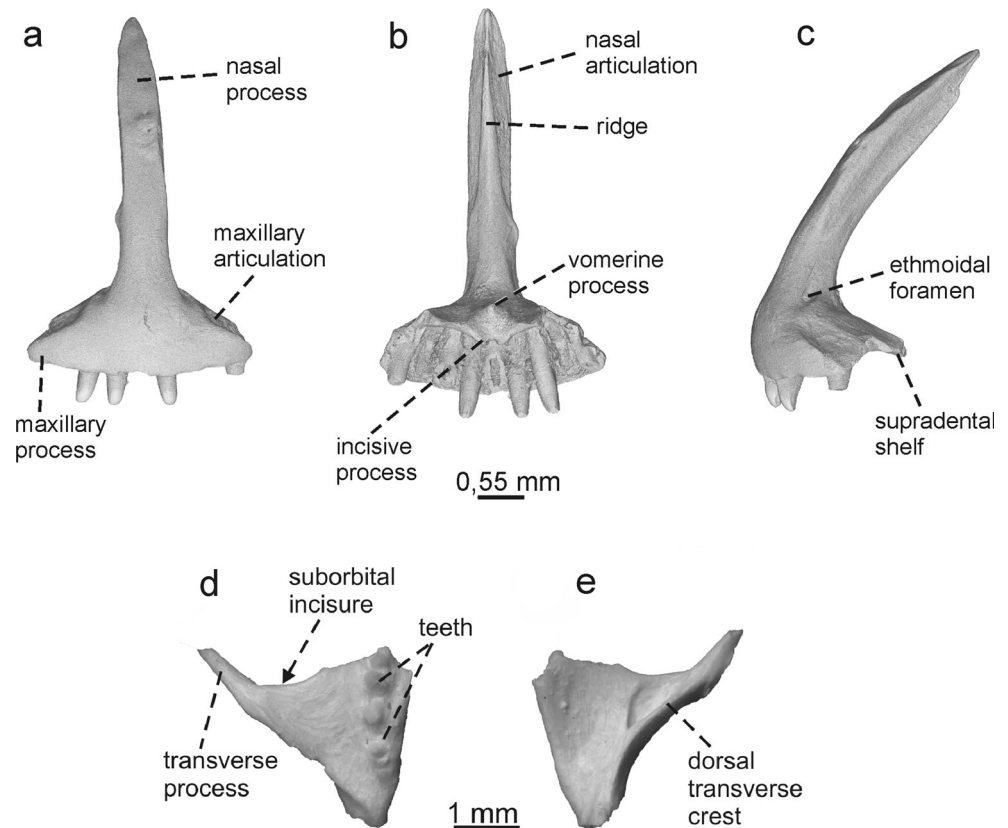
Locality, horizon and material: 1. Herrlingen 11 ; upper Oligocene (MP 28) : left dentary SMNS 59446 a 2. Herrlingen 9, upper Oligocene (MP 29): right dentary SMNS 58233 a.

Dentary: The dentary from Herrlingen 11 is nearly completely preserved, only the posteroventral part is missing. It is a

long, massive and ventrally only slightly arched bone, with a slight medial curvature at its anterior end. The tooth row is completely preserved and the alveolar crest supports a single row of 18 tooth positions, in which 14 teeth are preserved. Meckel's groove is narrow and shallow in the anterior region, but more open posteriorly. The alveolar foramen is located at the level of the 4th posterior tooth. Meckel's groove is roofed by an only slightly arched subdental shelf. The shelf gradually becomes thinner towards the posterior end, partly as a result of the presence of the facet for the splenial, situated on its ventral margin. The *sulcus dentalis* is present on the dorsal face of the shelf. The posterior end of the shelf bears a facet for the coronoid. It shows that the coronoid overlapped the dentary. The articulation surface is much more exposed in the posterodorsal region of the labial side. Here, a strong facet for the coronoid reaches the level of the penultimate tooth. The rest of the labial surface is pierced by six mental foramina, located in the dorsal third of the bone.

Dentition: The dentition is pleurodont and heterodont. The teeth in the anterior region are slender and smaller, while the posterior teeth are more robust and blunt. The robustness of the teeth increases posteriorly, although the highest tooth is

Fig. 7 Lacertidae indet.: premaxilla SMNS 59459 in **a** anterior, **b** posterior, **c** lateral aspect; right pterygoid SMNS 96570 a in **d** ventral and **e** dorsal aspect



located approximately in the middle of the tooth row, i.e. the 13th tooth (counting from anterior). The last three teeth are still robust, but much lower. The teeth are bicuspid, having mesial accessory cusp and the crowns bear striations, mainly on their lingual sides.

Remarks: The material described here is identical to that from the Phosphorites du Quercy (stratigraphic occurrence MP23-MP30). The only difference is that the subdental shelf and the symphysis of the Herrlingen specimen are slightly more robust. Otherwise, it conforms well to the diagnosis given in Augé (2005), i.e. the first anterior teeth pointed and the posterior teeth enlarged and striated with some of them bearing at least one cusp. These features are different from *Pseudeumeces* and *Dracaenosaurus*.

Plesiolacerta Hoffstetter, 1942
cf. *Plesiolacerta* sp.
(Fig. 6c,d)

Locality, horizon and material: Herrlingen 9, upper Oligocene (MP 29): left dentary SMNS 58233 b.

Dentary: The description is based on a fragment of the left dentary. In transverse section, the dentary is C-shaped. The fragment bears nine tooth positions, with eight teeth still in place. In lingual aspect, Meckel's groove is fully open, although narrow in comparison to, e.g. *Lacerta*

agilis. The subdental shelf is robust and becomes thinner posteriorly. Its dorsal face possesses a well-developed sulcus dentalis. The subdental shelf is rounded in cross-section. The labial surface is smooth and pierced by three mental foramina.

Dentition: The dentition is pleurodont. Teeth are high, with small interdental gaps. Their crowns are bicuspid, having a central dominant cusp and accessory anterior one. The posterior most tooth shows an additional posterior cusp.

Remarks: The attribution to *Plesiolacerta* is based mainly on the dentition and rounded subdental shelf of the dentary in cross-section (see Čeřmanský and Augé 2013). Unfortunately, the material is very fragmentary, so our interpretation needs to be met with caution.

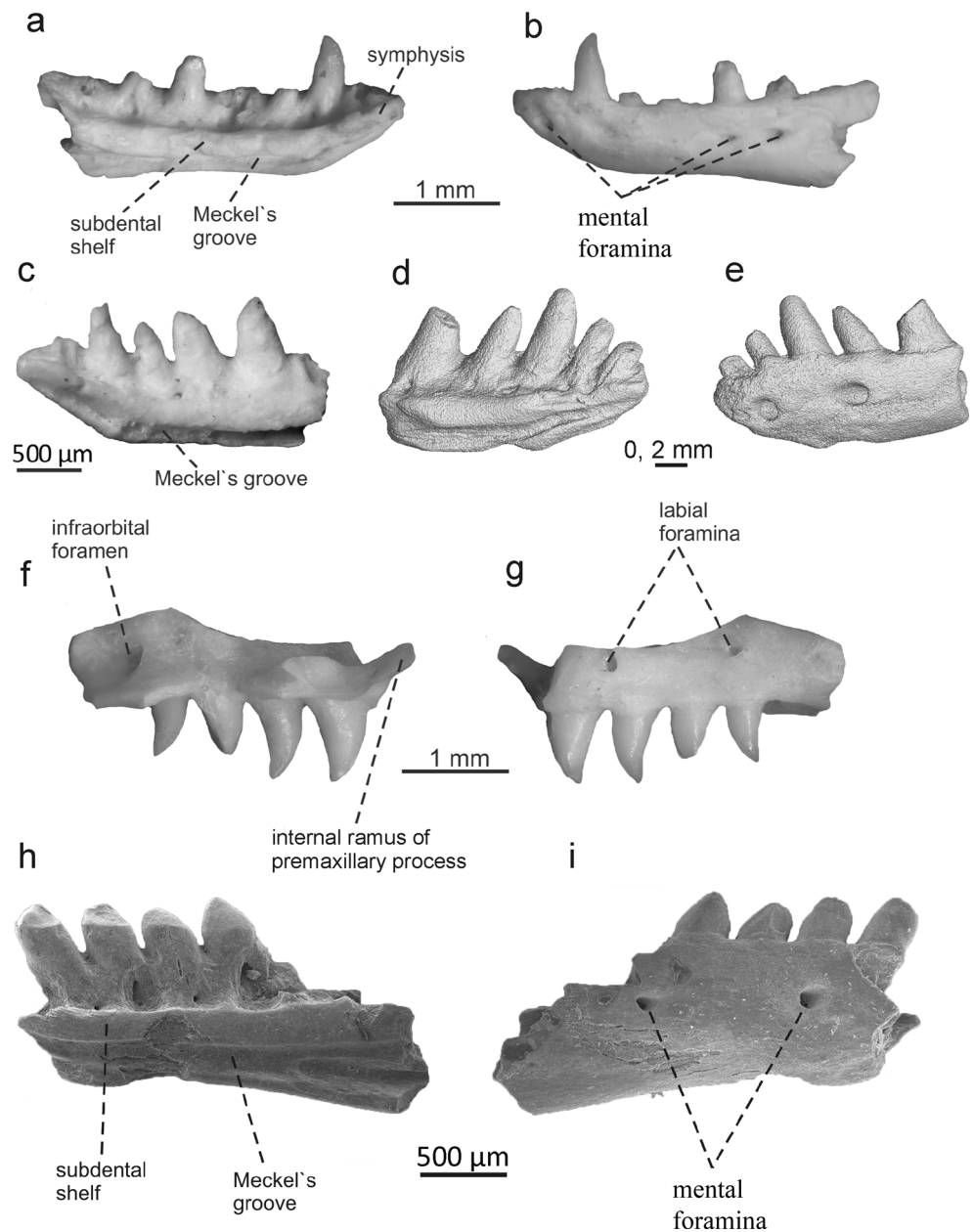
Lacertidae indet. – 5th tooth morphotype.
(Fig. 6e–g)

There is additional lacertid material that can be distinguished from the above specimens by its tooth morphology. It shows that there were at least five different lacertid taxa in Herrlingen.

Locality, horizon and material: Herrlingen 11, upper Oligocene (MP 29): three right dentaries SMNS 59459 b–d.

Dentary: The element is slender. Meckel's groove is fully open and narrow in the anterior region, becoming slightly

Fig. 8 Blanidae indet.: left dentary SMNS 59448 a in **a** medial, **b** lateral aspect; right dentary SMNS 59448 b in **c** medial aspect; left dentary SMNS 800040 h in **d** medial and **e** lateral aspect; left maxilla SMNS 59448 c in **f** medial, **g** lateral aspect. *Palaeoblanus* cf. *tobieni*: right dentary SMNS 59446 c in **h** medial and **i** lateral aspect



wider posteriorly. The subdental shelf is thin, having an articulation with the splenial on its ventromedial side. The sulcus dentalis is located on the dorsal region of the subdental shelf. All dentaries are incompletely preserved, whereas the best-preserved one bears 19 tooth positions with 13 teeth still attached. The external side is smooth and pierced by five mental foramina. The posterodorsal-most portion has a triangular depression, representing the articulation with coronoid.

Dentition: The dentition is pleurodont. Teeth are bicuspid, with a posterior dominant cusp and an anterior smaller one. Tooth size increases posteriorly. The tooth bases bear resorption pits.

Remarks: The dentary material is very slender and small in comparison to the other lacertid taxa described here. The

dentition shows no tendency towards amblyodonty. The bicuspid teeth might recall the above described material of cf. *Plesiolacerta* sp. However, they are not so densely spaced here.

Lacertidae indet.

(Fig. 7)

Locality, horizon and material: Herrlingen 11, upper Oligocene (MP 28): premaxilla SMNS 59459 h; right pterygoid SMNS 96570 a,

Premaxilla: The premaxilla is a T-shaped, delicately built element. It is almost completely preserved. The nasal process is very long and narrow, having a pointed posterodorsal end. In cross-section, the process is triangular in shape. On its internal side, a

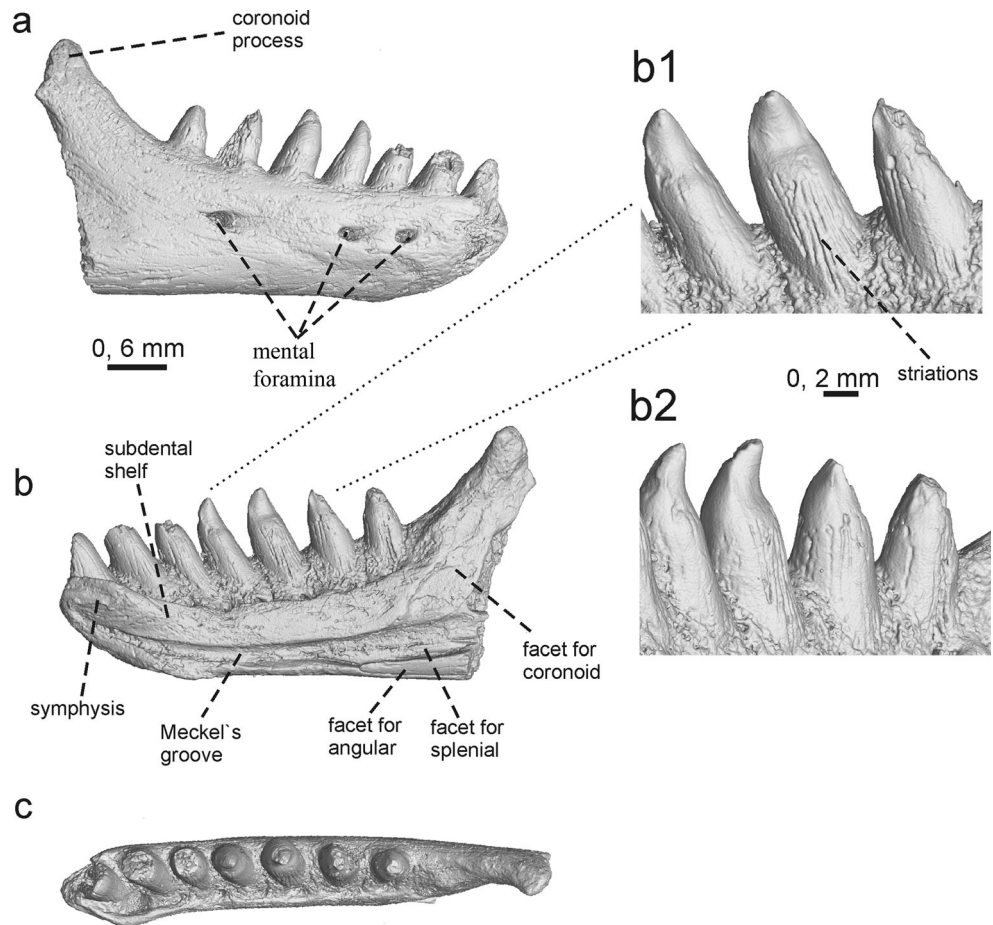
ridge is located along its mid-region. It forms a limit between nasal articulations. The alveolar crest is curved. The bone bears nine tooth positions, with four preserved, unicuspid, moderately pointed teeth. The supradental shelf is formed by two segments, which are well expanded posteriorly. The dorsal side bears a small bulge, i.e. the vomerine process. The short, weakly bilobed median incisive process is located ventral to the supradental shelf. The maxillary processes are well expanded posterolaterally, bearing a facet for the maxilla in the dorsal region. On the lateral side, the ethmoidal foramen is located close to the base of the nasal process.

Pterygoid: The pterygoid is only fragmentarily preserved. The transverse process is well developed and thin. Between this process and the palatine process, there is a broad area. On the dorsal side, this area possesses a wedge-shaped facet that is bordered laterally by a sharp transverse crest. The palatine process bears teeth on its ventral side.

Remarks: The premaxilla and the pterygoid show a typical lacertid morphology. However, it is not possible to associate these elements more precisely to the lacertid material described above.

Amphisbaenia Gray, 1844
Blanidae Kearney, 2003

Fig. 9 *Amphisbaenia* indet. 1: right dentary SMNS 800040 i in **a** external, **b** internal aspect with detail of teeth (b1 medial, b2 anteromedial aspect) and **c** dorsal aspect



Blanidae indet.
(Fig. 8a–g)

Locality, horizon and material: 1. Herrlingen 11, upper Oligocene (MP 28): left dentary SMNS 59448 a, right dentary SMNS 59448 b; one left maxilla SMNS 59448 c. 2. Herrlingen 9, upper Oligocene (MP 29): left dentary SMNS 800040 h.

Maxilla: A nearly complete left maxilla is preserved, only the nasal process is broken and missing. It is a relatively short element. The small alveolar crest supports four pointed teeth, which are slightly recurved posteriorly. The premaxillary process is short. The medial surface of the palatal shelf bears a large hemispherical cavity, which houses Jacobson’s organ (Montero and Gans 1999). The supradental shelf is thin, but unfortunately broken. The alveolar foramen is located in the posterior region. The labial surface is pierced by two foramina.

Dentary: The description is based on 3 fragmentary dentaries, which all are small, anteroposteriorly elongated elements. Meckel’s groove is fully open and narrow. The alveolar crest supports a row of eight tooth positions. In the anterior region, there is a small symphyseal shelf formed by the ventral junction of the mandibles. Here, the anteroventral angle at

the symphysis of the dentary is present, as in most modern amphisbaenians (e.g. Gans 1974). Meckel's groove is roofed by a shallow, slightly curved subdental shelf, whereas its floor has a ventral margin that is slightly thickened anteriorly and slightly concave in the mid-region. The labial surface is pierced by four mental foramina.

Dentition: The dentition is pleurodont. At the tooth bases, there are small oval resorption pits. The largest maxillary tooth is the first anterior one, and overall tooth size is decreasing posteriorly. The dentary teeth are well pointed, and only slightly recurved posteriorly. The 4th anterior dentary tooth is smaller than the others. Unfortunately, almost all dentary teeth are more or less eroded.

Remarks: Previously, the modern genus *Blanus* was allocated to Amphisbaenidae, but by now it is considered that it branched prior to the common ancestor of Amphisbaenidae and Trogonophidae, and the clade Blanidae is supported by both morphological (Kearney 2003) and molecular (Pyron et al. 2013) evidence. The attribution of the dentaries from Herrlingen to the clade Blanidae is based on the combination of the following characters: (1) in

Blanus, the 4th tooth in the tooth row is smaller than 3rd and 5th tooth (the 3rd one usually being largest), which is a character present also in the Herrlingen material; (2) the tooth count of *Blanus* is variably eight or seven [e.g. 10 dentaries of fossil *Blanus* from the late Pliocene (MN 16) of Iles Medas, Spain, possessed eight teeth and only one had seven teeth (Bailon 1991)]. Although tooth count is not an unambiguous synapomorphy of *Blanus*, allocation to this clade is very likely given the additional presence of (3) the number of mental foramina in extant *Blanus* being usually four (although this can slightly vary), with the biggest one being the first one (see Gans and Montero 2008; p. 643, fig. 3.9), which is similar to the material described here.

The maxilla described here is identical to that of extant European *Blanus* in (1) having four pointed, slightly posteriorly recurved teeth, although according to Bolet et al. (2014), there is some variation in the maxillary tooth count (i.e. in one specimen of *B. strauchi*, four teeth are present on the right maxilla and only three on the left); (2) tooth size decreases posteriorly; and (3) two labial foramina pierce the external surface (see e.g. Gans and Montero 2008; p. 636, fig. 3.7). Whereas more complete material would be needed for a well-

Fig. 10 Comparison of internal dentary regions around the connection of dentary to other mandibular bones in extant taxa: **a** *Blanus strauchi* with cross-section (a1) of the region with angular, and cross-section (a2) of the further anterior region with splenial attached to the ventral area of Meckel's groove; **b** *Cadea blanoides*; **c** *Bipes canaliculatus*; and **d** *Amphisbaena alba*

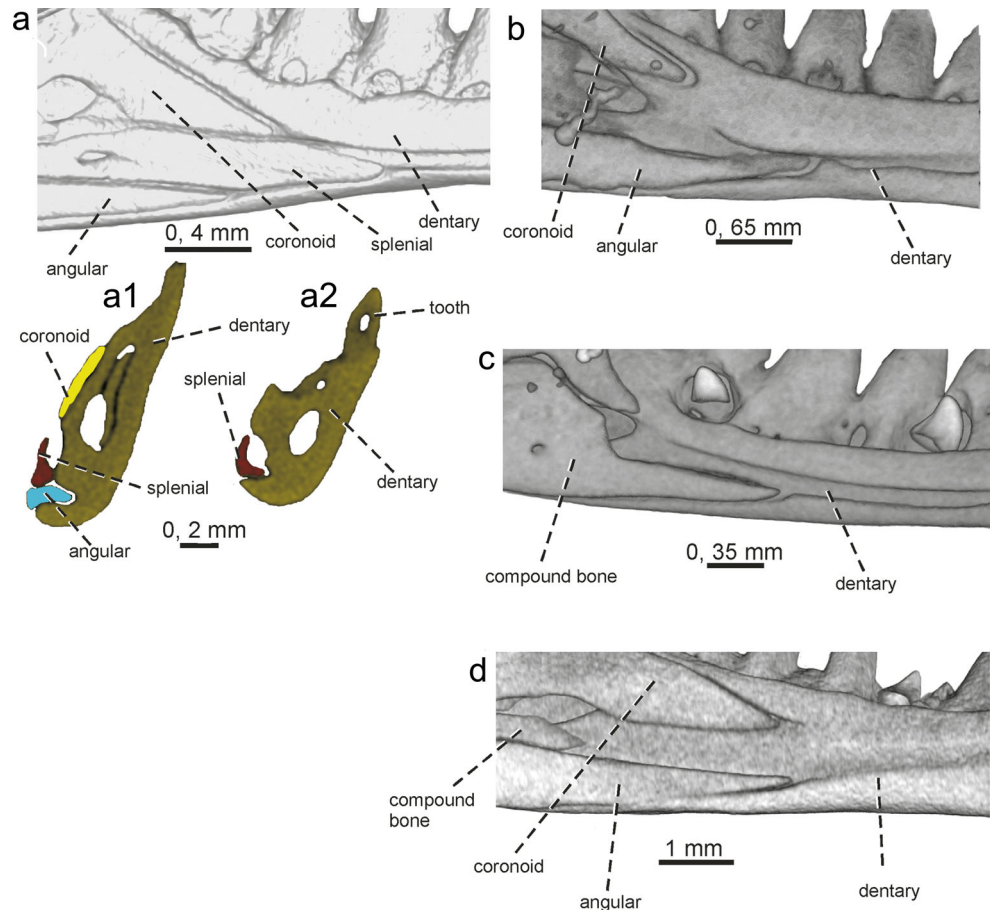
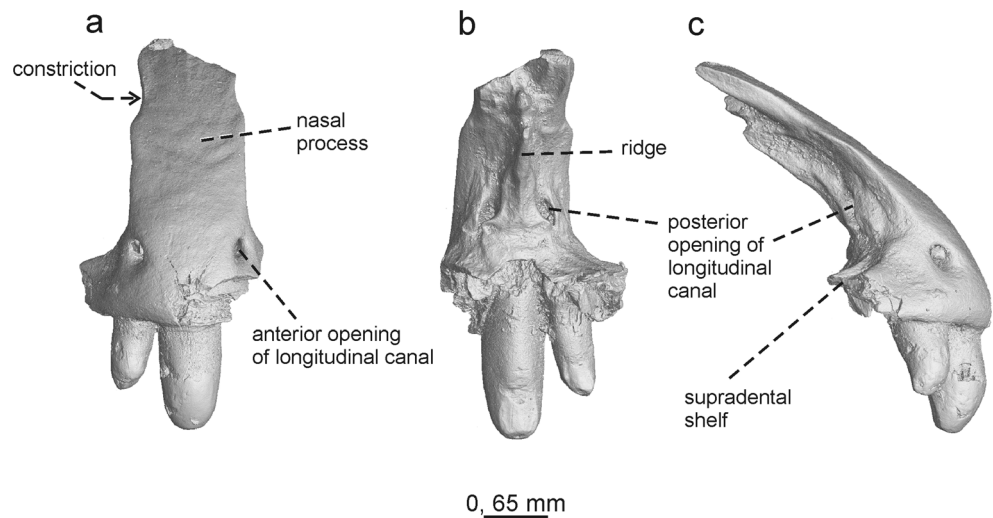


Fig. 11 *Amphisbaenia* indet. 2: premaxilla SMNS 59459 i in **a** anterior, **b** posterior, and **c** lateral aspect



justified generic allocation, we consider it reasonable to assign the material to *Blanidae*.

Palaeoblanus Schleich, 1988b

Palaeoblanus cf. *tobieni* Schleich, 1988b

(Fig. 8h, i)

Locality, horizon and material: Herrlingen 11, upper Oligocene (MP 29): One fragment of the right dentary prefixed by SMNS 59446 c.

Dentary: Only a fragment of the right dentary with four teeth is preserved. The element is shallow, Meckel's groove is fully open. In its posterior region, an opening for the alveolar canal is located. Meckel's groove is roofed by a straight subdental shelf. Two mental foramina are preserved on the external surface of the bone.

Dentition: The dentition is pleurodont. The teeth are conical and bluntly tipped. They are markedly inclined anteriorly.

Remarks: The type locality of *Blanus tobieni* is Weisenau, which is in a MN 1 terrestrial horizon in Germany (Schleich 1988b). Subsequently, this taxon has been reported from a series of upper Oligocene–upper Miocene (MP 27–MN 13/14) localities from Germany, France, Italy and Spain (Böhme and Ilg 2003). Although we here allocate this dentary to *Paleoblanus* (the material has a marked tooth slope and conical and labiolingually compressed teeth as typically seen in *Palaeoblanus*), the features that define this taxon are plesiomorphic within *Amphisbaenia* (Augé 2012). This taxon clearly requires revision.

Amphisbaenia indet. 1

(Fig. 9)

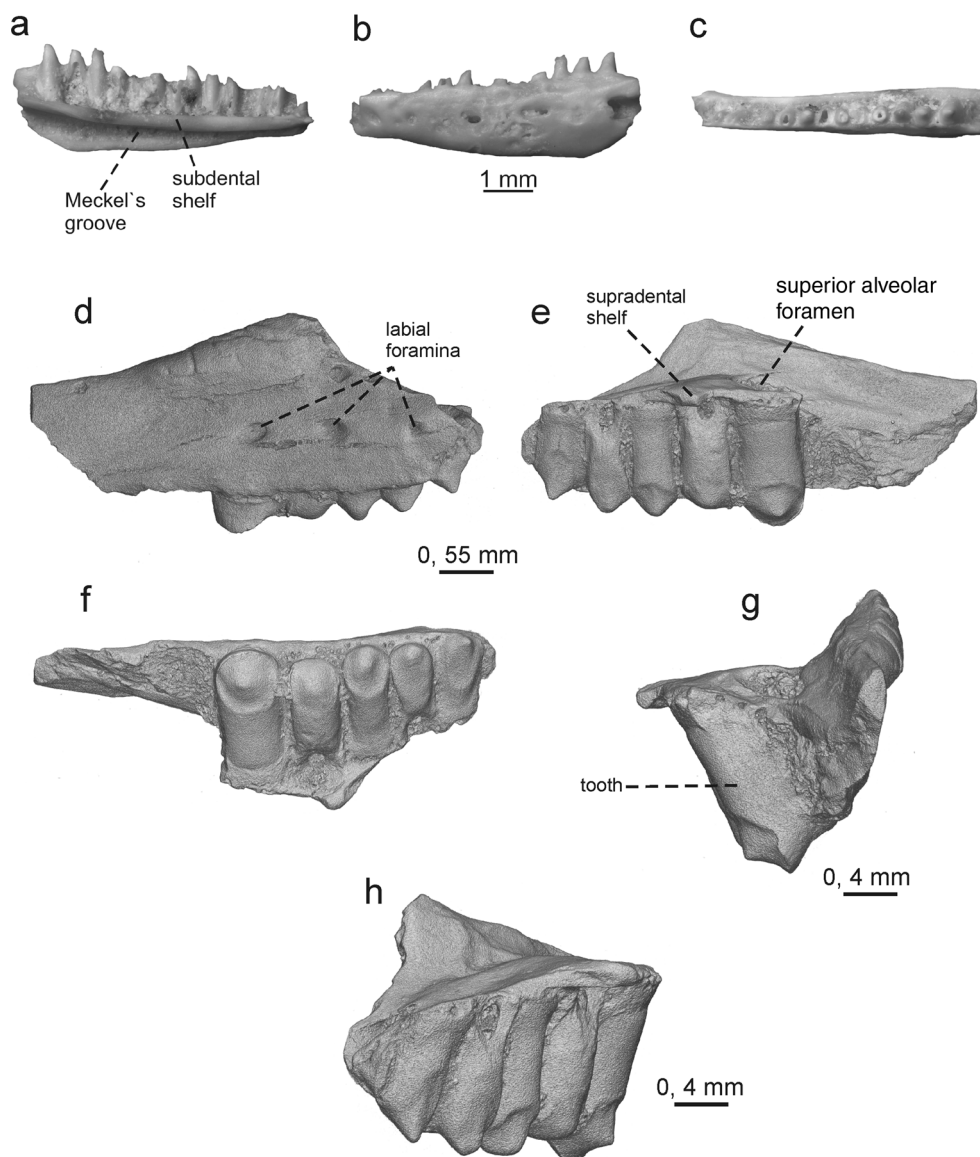
Locality, horizon and material: Herrlingen 9, upper Oligocene (MP 29): right dentary SMNS 800040 i.

Dentary: The right dentary is almost completely preserved. It is slightly concave, small and robust. The alveolar shelf bears

7 teeth. Meckel's groove is fully open, becoming gradually narrower anteriorly. At the level of the second anterior tooth, the dentary is weakly angled, i.e. the anterior region with the symphysis rises dorsally (see Gans 1974). The ventral margin of the dentary is slightly dorsally convex. A narrow facet is developed on the posterior region of the ventral margin which reaches the level of the second tooth (counting from posterior) and probably represents a facet for the angular. Dorsal to it, there is another, very tiny facet. It is located in the ventral region of Meckel's groove, reaching further anteriorly than the facet for the angular. It most likely represents a contact with the splenial. Meckel's groove is roofed by a broad subdental shelf. Posterior to it, the coronoid facet is developed, reaching to the level of the posteriormost tooth. The coronoid process of the dentary is very tall, taller than the apices of the tallest teeth. Its dorsal end is slightly bent medially and the whole process is anteroposteriorly short. Ventrally, an alveolar foramen is developed, which is bordered by the intramandibular septum. The otherwise smooth lateral region is pierced by three mental foramina located out of midline, i.e. closer to the tooth row. The anterior region is damaged, so it is possible that the total number of mental foramina might have been four. Posteriorly, a small triangular depression is visible. However, the posterior end is broken.

Dentition: The dentary teeth are subpleurodont, pointed, inclined slightly anteriorly (except for the two last posterior teeth, which are less inclined than the others), while their apices are recurved. The shaft of the teeth is noticeably swollen compared to the apices. The largest tooth is the 5th, counting from anterior (unfortunately, the anterior teeth have all broken apices, so it is impossible to estimate their true size). All dentary teeth have vertical striations. The striation is weakly developed on the labial side, but more pronounced on the lingual side. They are going up from the base, reaching the level where the teeth are swollen medially. However, it cannot be fully excluded that these striations appeared only due to postmortal and diagenetic processes.

Fig. 12 "Scincomorphan" indet. 1: left dentary SMNS 58233 d in **a** medial, **b** lateral, **c** dorsal aspect. "Scincomorphan" indet. 2: right maxilla SMNS 59446 d in **d** lateral, **e** medial, **f** ventral, **g** posterior, **h** anteromedial aspect



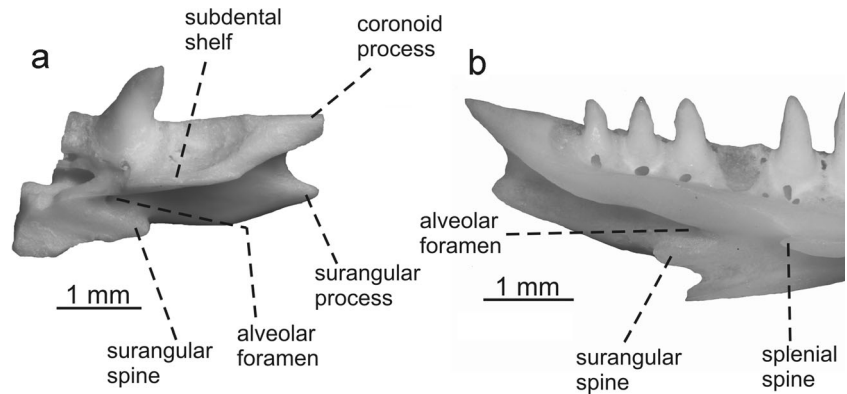
Until now, striations have been reported only at the base of the teeth in *Campinosaurus* (Augé 2005). In modern *Amphisbaenia*, striations have never been reported. The tooth bases are pierced by small resorption pits, and covered by cement.

Remarks: The allocation to the clade *Amphisbaenia* is unambiguous. The dentary might represent a member of *Blanidae* based on overall similarity with modern *blanids*; however, the characters are largely plesiomorphic, including: (1) Meckel's groove is fully open, well developed; (2) pleurodont dentition (in members of the clade *Trogonophiidae*, an acrodont dentition is present); and (3) the presence of the splenial (this element is fully absent in *Amphisbaenidae* or *Bipedidae*), indicated by a tiny facet above the facet for the angular. This tiny facet continues further anteriorly than the facet for the angular, from which it is separated. This is similar to the situation seen in *Blanus cinereus*, where the splenial is attached in the

same region (Gans and Montero 2008). We exclude the possibility that this facet reflects the presence of a compound bone instead of a separate splenial, because if a true compound bone is present (e.g. in *Bipes biporus*, *Leposternon scutigerum* or *Monopeltis anchietae*; see Gans and Montero 2008), it never reaches as far anteriorly as the facet described here (see Fig. 10).

The dorsal end of the coronoid process is slightly bent medially. This condition was also observed in the material from Dolnice described by Roček (1984) and is also variably present in Recent *Blanus* (Venczel and Ştiucă 2008). Recently, Rage and Augé (2015) described dentary fragments and vertebrae from the lower Oligocene of Valbro in France. These authors allocated the material to the clade *Amphisbaenidae*, although more comparative studies of recent taxa would be desirable to give more support to

Fig. 13 *Ophisaurus* sp.: right dentary SMNS 59448 d in **a** medial aspect; **b** comparison to *Ophisaurus koellikeri* (NMB 18668)



such an interpretation. The dentary described by Rage and Augé (2015) differs in many characters from those described here; for example, the Meckelian groove is markedly constricted anteriorly, as it appears to be among at least some members of Amphisbaenidae (Smith 2009a).

Amphisbaenia indet. 2
(Fig. 11)

Locality, horizon and material: Herrlingen 11, upper Oligocene (MP 29): premaxilla SMNS 59459 i.

Premaxilla: The bone is an unpaired, T-shaped, and robust element. The nasal process is markedly broad. Posterodorsally, there is very fine step on both sides of the lateral margins. This step makes the posterodorsal region slightly narrower. Unfortunately, the end of the process is broken. The internal side of the nasal process bears a longitudinal sharp ridge along its mid-region. The ridge becomes wider in its anteroventral region. Here, a pair of foramina is located laterally to the ridge. These foramina represent the posterior opening for the longitudinal canal. The supraddental shelf is thin, but unfortunately broken. The external surface is smooth. A pair of foramina is located under the nasal process, representing the anterior opening for the longitudinal canal. Only the right maxillary process is partly preserved, the left one is broken.

Dentition: The dentition of premaxilla is pleurodont. Only two teeth are preserved, but, assuming symmetry, we can estimate that there were at least 5 tooth positions. The central tooth is distinctly enlarged, and the tooth apices are blunt.

"Scincomorphan" indeterminate 1.
(Fig. 12a–c)

Locality, horizon and material: Herrlingen 9, upper Oligocene (MP 29): dentary SMNS 58233 d

Dentary: The dentary is poorly preserved. It is a slender, anteroposteriorly long bone. Meckel's canal is fully open but narrow, especially in the anterior region. The dentary gradually becomes narrower anteriorly, but only up to the level of

the 4th preserved tooth position. The subdental shelf is thin, bearing a facet for the anteromedial process of the coronoid. The facet reaches to the level of the penultimate tooth. Further anteriorly, the facet for the splenial turns completely ventrally, reaching the level of the 6th preserved tooth position. The sulcus dentalis is only weakly developed. The dentary possesses 14 tooth positions, and four teeth are still preserved. The lateral surface is pierced by six mental foramina.

Dentition: The dentition is pleurodont. Teeth are pointed, having the tips slightly recurved posteriorly. No additional cusps are observed. Tooth size appears to increase posteriorly.

Remarks: The fully open Meckel's groove, the pleurodont dentition and the presence of a sulcus dentalis (although only weakly developed) appear "scincomorphan" in the traditional morphological sense. However, there are major discrepancies regarding the monophyly or the paraphyly of this clade, between morphology-based (see e.g. Gauthier et al. 2012) and molecule-based analyses (e.g. Townsend et al. 2004; Vidal and Hedges 2009). We therefore decided to use the term "scincomorphan" only in a descriptive, but not phylogenetic, sense.

"Scincomorphan" indeterminate 2.
(Fig. 12d–h)

Locality, horizon and material: Herrlingen 11; upper Oligocene (MP 28): right maxilla SMNS 59446 d.

Maxilla: Only a fragment of the right maxilla with five teeth and one tooth locus is preserved. The maxilla is relatively small. Most of the thin supraddental shelf is broken. At the level of the largest preserved posterior tooth (i.e. second posterior tooth), the huge oval superior alveolar foramen is preserved. The maxilla terminates in a straight posterior process and forms a step contact with the jugal. From the level close to the last posterior tooth position, the dorsal edge of the maxilla rises gradually anterodorsally and forms the nasal process. However, the anterior portion of the process is broken and missing. The labial surface of the maxilla is pierced by three foramina. One isolated small foramen is located on the dorsal region of the posterior maxillary process.

Dentition: The dentition is pleurodont. Tooth size markedly increases posteriorly and the posterior most tooth is very robust. In lingual view, tooth crowns are separated from the tooth necks by rounded horizontal lingual gooves; the conical, slightly pointed crown is slightly smaller than the rest of the tooth. The neck is cylindrical and slightly anteroposteriorly depressed. The largest preserved tooth is slightly different from the remainder of the teeth; in posterior view, its apex is slightly divided, having a labial edge and a more ventromedially oriented lingual cusp, which forms a blunt bulge. A shallow U-shaped transverse saddle connects them. All teeth are without striations. The tooth bases are slightly expanded lingually, especially in the posterior most tooth.

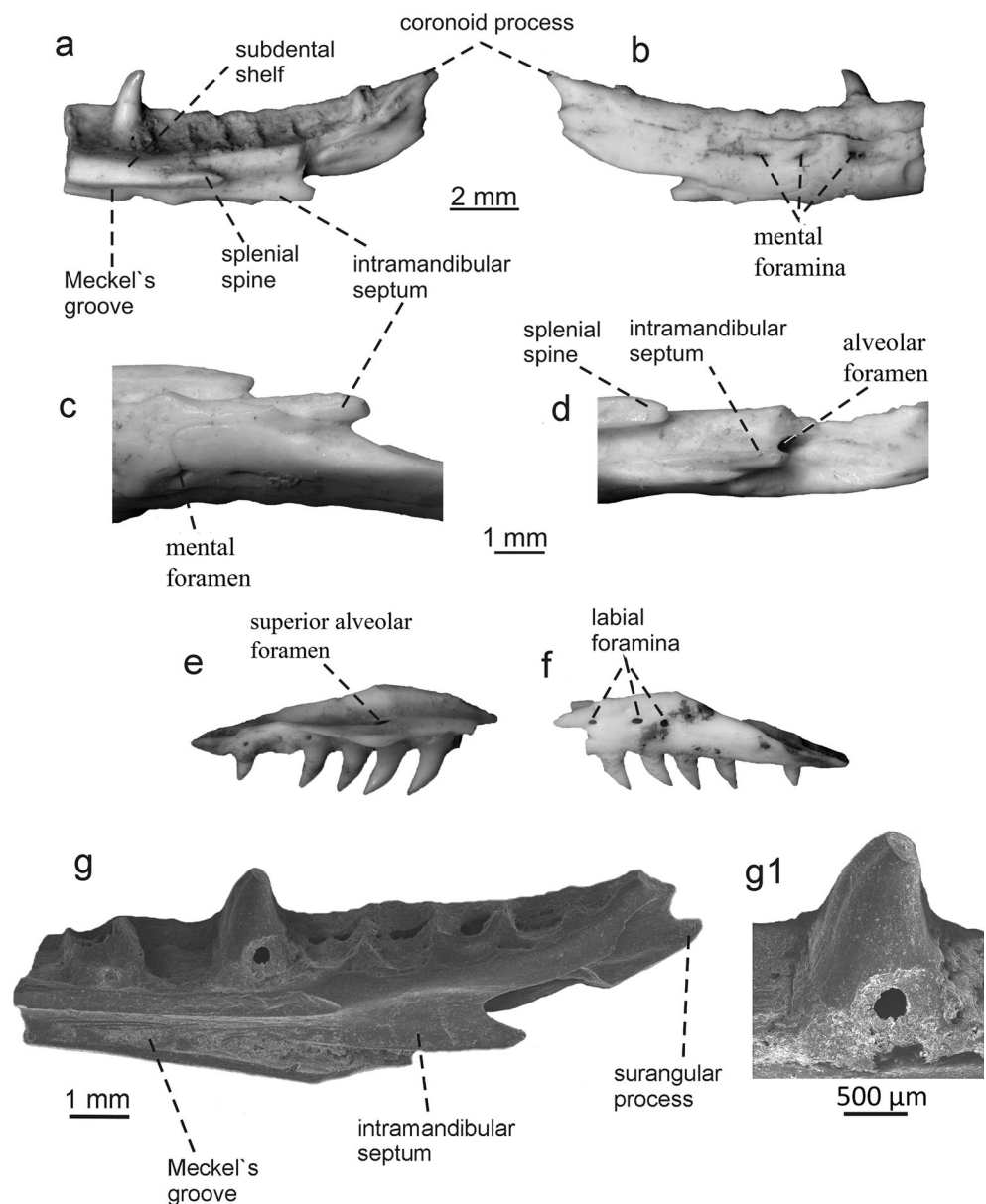
Remarks: The general tooth morphology corresponds to that of Scincoidea (see Kosma 2004). However, a similar morphology of transversely bicuspid teeth is also present in members of the Mesozoic teioid clade Polyglyphanodontinae (see Estes 1983; Nydam et al. 2007). Also, the recent taxon *Teius teyou* appears to have a similar condition (A.Č., personal observation). Additional and better preserved material is needed for a better systematic assignment.

Anguimorpha Fürbringer, 1900

Anguidae Gray, 1825

Ophisaurus Daudin, 1803

Fig. 14 *Ophisauromimus coderetensis* comb. nov., right dentary SMNS 59448 e in **a** medial, **b** lateral aspect. Detail of the region with intramandibular septum in **c** ventrolateral, **d** ventral aspect. Left maxilla SMNS 59448 f in **e** medial, **f** lateral aspect. Right dentary SMNS 58231 a in **g** medial aspect and **g1** detail of tooth



Ophisaurus sp.
(Fig. 13a)

Locality, horizon and material: Herrlingen 11; upper Oligocene (MP 28); posterior portion of right dentary, SNMS 59448 d.

Dentary: Only the posterior portion of the dentary with one tooth is preserved. Although the tip of the coronoid process is broken, it is possible to infer that the coronoid process extended further posteriorly than the surangular process. The surangular process is pointed. The alveolar foramen lies at the level of the second tooth (counted from posterior). Immediately ventral to the alveolar foramen, a short and blunt surangular spine is present. The angular process is broken. The preserved portion of the subdental shelf is mediolaterally narrow and Meckel's canal opens ventromedially. The ventromedial margin of the intramandibular septum is indistinguishably fused with the internal wall of the dentary.

Dentition: The preserved tooth is pleurodont and has a small resorption pit at its base. The tooth crown is conical and slightly inclined posteriorly. The apex of the tooth is pointed, the mesial and distal cutting edges are well developed. The lingual surface of the apex is not striated. The base of the crown is mediolaterally broadened and not distinctly bulged lingually.

Remarks: The morphology of this portion of the dentary corresponds to that of *Ophisaurus* (cf. Klembara et al. 2014). This is indicated by the typical *Ophisaurus* features like the presence of the surangular spine separated from the intramandibular septum (Klembara 2012; Klembara et al. 2014). The surangular spine is also present in the so far oldest and smallest species of *Pseudopus*, *P. ahnikoviensis*, from the Early Miocene of Merkur (Czech Republic); however, its posterior dentition is typically amblyodont and thus completely different from that of *Ophisaurus* (see Klembara 2012).

The dentary of *Ophisaurus* sp. is most similar to that of North African and Asian species of *Ophisaurus* (Fig. 13b; Klembara et al. 2014): (1) a blunt tip of the surangular spine is present in large specimens of *O. koellikeri* (Fig. 13b; Klembara et al. 2014, fig. 10H); (2) the posteroventral margin of the intramandibular septum is fused with the internal wall of the dentary (present in *O. koellikeri* and *O. gracilis*); (3) the alveolar foramen lies at the level of the penultimate tooth [present in *O. koellikeri*; this is also similar to the condition in *Ophisaurus* (= *Dopasia*) *roqueprunensis* (Augé 1992)]; and (4) bases of the teeth do not bulge lingually (present in all species of *Ophisaurus* from North Africa and South-east Asia).

However, contrary to *Ophisaurus* from North Africa and South-east Asia, the posterior-most portion of the dentary of *Ophisaurus* sp., from which the surangular process extends posteriorly, is dorsoventrally broader (best visible in medial view; Fig. 13). In this aspect, the condition in SNMS 59448 d is much more similar to that of *Ophisaurus* (= *Dopasia*)

roqueprunensis from the early to late Oligocene of France and Belgium (Augé 1992; Augé and Smith 2009). In addition to this, the tooth of SNMS 59448 d is much more robust relative to the penultimate tooth of similarly sized specimens of extant *Ophisaurus* (Fig. 13; Klembara et al. 2014). Contrary to extant *Ophisaurus*, the lingual surface of the apex of the tooth of SNMS 59448 d is not striated, similar to that of fossil Miocene anguines like *Anguine* morphotype 1 in Klembara (2015, fig. 5).

Ophisauromimus gen. nov.

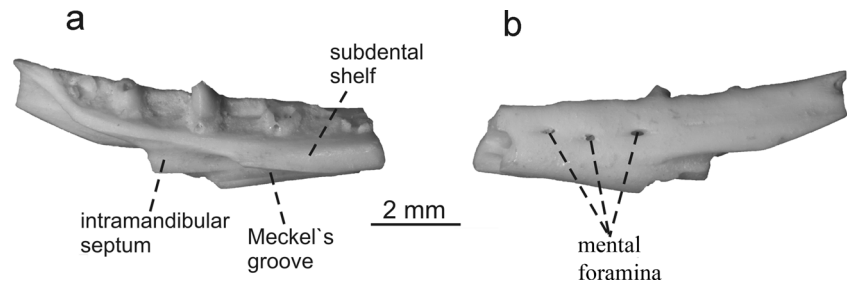
Type species: *Ophisauromimus coderetensis* (Augé, 2005)

Derivation of generic name: *Ophisaurus* plus the Greek *mimos* meaning “imitator” – lizard mimicking *Ophisaurus*.

Diagnosis: Long and slender dentary exhibits the following features: (1) the intramandibular septum forms dorsoventrally broad plate from which a distinct and pointed process extends posteriorly and the posteroventral margin of the intramandibular septum is free; (2) the Meckelian groove is completely open ventrally; and (3) the apices of teeth are curved posteriorly, the medial and distal cutting edges are present, the lingual surface of apices is not striated and bases are mesiodistally broadened.

Remarks: Three species of *Anguinae* have been described from the Oligocene of Europe (France and Belgium; for review, see Augé 2005): *Dopasia roqueprunensis* (Augé 1992; Augé and Smith 2009), *D. frayssensis* Augé 2005 and *D. coderetensis* Augé 2005. Augé (2005) started to use the generic name *Dopasia* (originally used by Gray 1853 for the living species *D. gracilis* from South-east Asia), for all extinct and extant species from South-east Asia and North Africa instead of the previously used name *Ophisaurus* (Boulenger 1899) for all species living in North America, South-east Asia and North Africa. As recently argued, it is more prudent to use the name *Ophisaurus* for all living species from North America, South-east Asia and North Africa (Klembara et al. 2014). The anatomy of the dentary of *Ophisaurus* is very uniform (Klembara et al. 2014), and the dentary of the Oligocene *Ophisaurus roqueprunensis* (species formerly assigned to *Dopasia*) also displays the distinguishing features of *Ophisaurus*. However, the other two late Oligocene species, *D. coderetensis* and *D. frayssensis*, differ in one principal feature from *Ophisaurus*: the intramandibular septum is a dorsoventrally broad plate extending into a process reaching posteriorly to the alveolar foramen (Fig. 14a–d, g). Instead, in *Ophisaurus* the intramandibular septum is a dorsoventrally narrow wall and its posterior margin ends at the level of the alveolar foramen. In addition to this, a process called the surangular spine (Klembara 2012) extends posteriorly from the posterior portion of the dentary (Klembara et al. 2014). Thus, the posterior end of the intramandibular septum and the surangular spine are two different features in *Ophisaurus*. The

Fig. 15 Cf. *Ophisauromimus*, SMNS 59448 g, left dentary in **a** medial, **b** lateral aspect



morphology of the intramandibular septum as present in *D. coderetensis* and *D. frayssensis* is absent not only in *Ophisaurus*, but also in *Pseudopus* and *Anguis*. Thus, we create a new generic name, *Ophisauromimus* gen. nov., for these two Oligocene species, only one of them (*Ophisauromimus coderetensis*) being present at Herrlingen. Otherwise, the morphology of the preserved dentaries of the species corresponds to that of Anguinae.

Ophisauromimus coderetensis comb. nov. (Augé, 2005) (Fig. 14)

1986 *Ophisaurus* B – Augé, p. 127, fig. 52.

2005 *Dopasia coderetensis* – Augé, p. 237, fig. 156 – 157.

2015 *Dopasia* s.l. sp. – Rage and Augé, p. 33.

Diagnosis: A species of *Ophisauromimus* that differs from *O. frayssensis* (the only other species of the genus; Augé 2005) by the following features: (1) dentary relatively longer and slender; (2) splenial spine lies at level of the anterior half of the 5th tooth from posterior (contrary to the anterior half of the 3rd tooth from posterior of *O. frayssensis*); and (3) number of teeth is up to 16 (contrary to 9 in *O. frayssensis*).

Locality, Horizon and Material: 1. Herrlingen 11; upper Oligocene (MP 28): left maxilla SMNS 59448 f. right dentary SMNS 59448 e. 2. Herrlingen 9; upper Oligocene (MP 29): right maxilla SMNS 58231 b, right dentary SMNS 58231 a.

Maxilla: Posterior and partially the middle portions of the maxillae are preserved in both localities. They are associated with the dentaries on the basis of the similar tooth morphology. The alveolar surface supports eight tooth positions in the Herrlingen 9 specimen and five well-preserved teeth are present in the Herrlingen 11 specimen SMNS 59448 f (Fig. 14e, f). The supradental shelf is thin and slightly expanded medially at the level of the oval superior alveolar foramen. The superior alveolar foramen is located at the level of the 5th tooth counted from posterior. A facet for the jugal articulation is preserved on the dorsal surface of the posterior portion of the maxilla. The lateral surface of the preserved portion of the maxilla is pierced by several foramina of various size (Fig. 14f).

Dentary: Both dentaries represent posterior portions (Fig. 14a–d, g, h). The dentary is long and slender. The subdental shelf is thin and transversely narrow anteriorly,

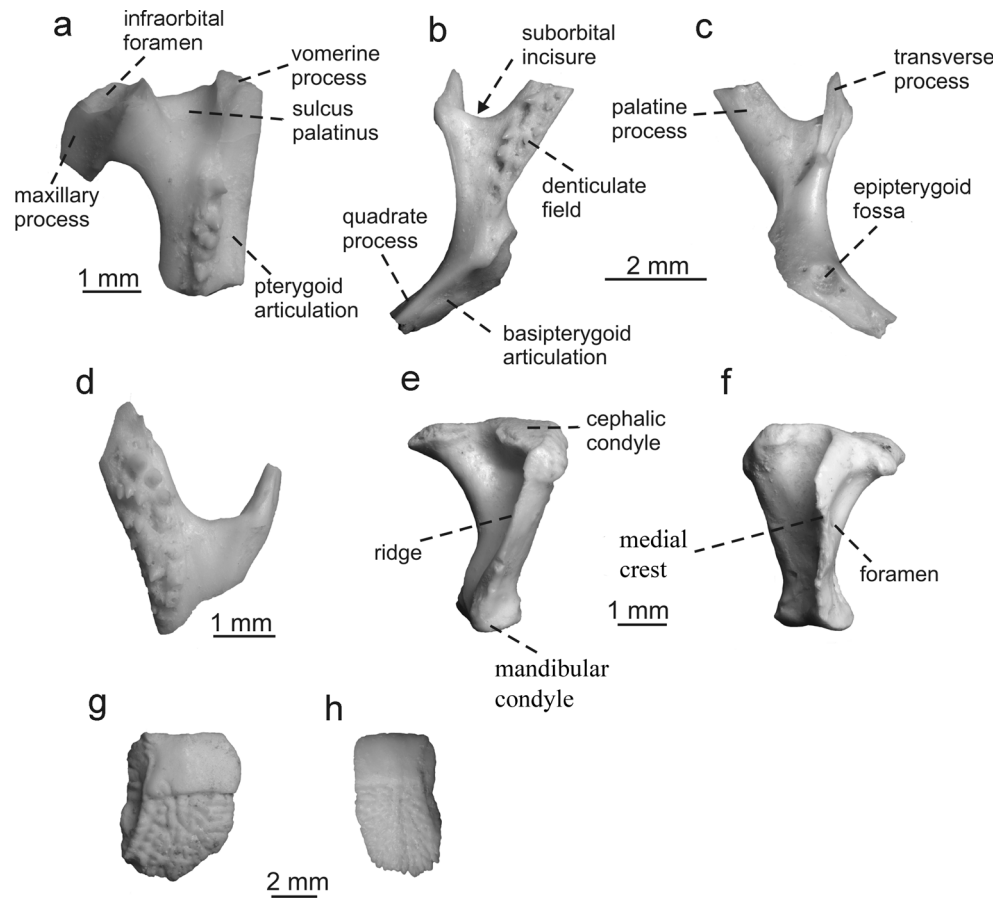
roofing over Meckel's groove, which is narrow and opens ventrally and posteriorly. The alveolar surface of the Herrlingen 11 specimen (SMNS 59448 e) supports nine tooth positions; one complete tooth and the basal portion of another tooth are present (Fig. 14g, h). At the level of the 6th tooth counted from posterior (and at the level of the 5th tooth counted from posterior in the Herrlingen 9 specimen SMNS 58231 a), a pointed splenial spine is located. Posterior to this area, the subdental shelf is slightly curved dorsally and becomes less distinct. The subdental shelf has a smooth surface in its posterior section, which represents the facet for the coronoid articulation. The coronoid process is pointed and reaches posteriorly the level of the posterior end of the surangular process located ventral to it. The angular process is broken. The intramandibular septum forms a dorsoventrally broad plate and posteriorly extends into a distinct and pointed process. The tip of the process reaches posterior to the alveolar foramen. The posteroventral margin of the intramandibular septum is free. The alveolar foramen lies at the level of the 3rd tooth counted from posterior.

The lateral wall of the dentary is somewhat roughened, mostly around the mental foramina. The mental foramina pierce the dentary in its mid-region. Anterior to the coronoid incisure, there is a slightly roughened surface indicating the articulation with the anterolateral process of the coronoid.

Dentition: The dentition is pleurodont; the tooth bases have small resorption pits. The teeth are conical, slightly curved posteriorly and have pointed tips. The mesial and distal cutting edges are well developed. The lingual surfaces of the apices are not striated.

Remarks: *Ophisauromimus coderetensis* was described on the basis of the dentaries from the late Oligocene of France by Augé (2005). The material described here from Germany is the first record of this species outside of France. Recently, Rage and Augé (2015) described the dentary of an anguine from the early Oligocene (MP 22) of Valbro, France (Quercy). The authors write: “A large intramandibular septum divides the Meckelian groove posterior to the splenial spine. The ventral edge of the septum remains free. Posteriorly, the septum is notched and it ends posteroventrally as a rather long spine.” Although they give no figure of the specimen, the description of the dentary indicates that it could represent *Ophisauromimus coderetensis*, as such a morphology of the intramandibular septum cannot represent *Ophisaurus*

Fig. 16 Anguinae indet.: right palatine SMNS 96570 b in **a** ventral aspect. Right pterygoid SMNS 96570 c in **b** ventral, **c** dorsal aspect. Left pterygoid SMNS 96570 d in **d** ventral aspect. Right quadrate SMNS 59447 in **e** lateral and **f** medial aspects. Osteoderms SMNS 59444 in **g**, **h** external aspect

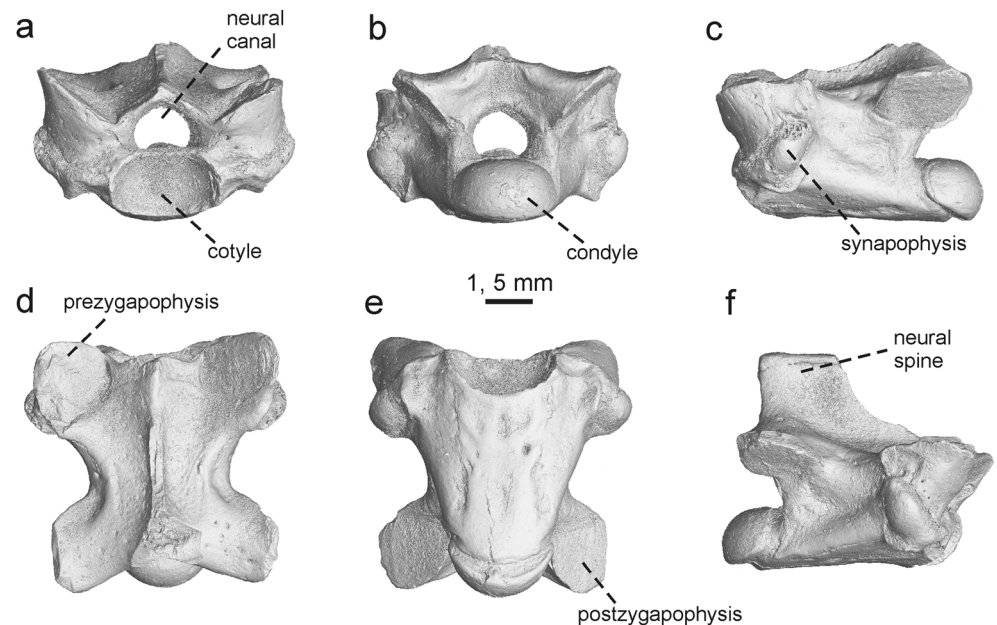


(=*Dopasia*). As for the dentition, the authors write: “Valbro shows a tooth morphology that appears to be more consistent with *D. coderetensis* than with the other species“ (Rage and Augé 2015, p. 34). Thus, we consider the dentary of Valbro

described as *Dopasia* s.l. sp. provisionally as conspecific with *O. coderetensis*.

Bailon and Augé (2012) described a new member of Anguinae, *Ragesaurus medasensis* (aff. *Ophisaurus* Bailon

Fig. 17 Anguinae indet.: dorsal vertebra SMNS 80038 a in **a** anterior, **b** posterior, **c** lateral, **d** dorsal, and **e** ventral aspect. Dorsal vertebra SMNS 80038 b with well-preserved neural spine in **f** lateral aspect



1991), from the Early Pleistocene of Spain. The only specimen representing this species is a small right dentary. Although the authors see the potential affinity of this species to *Ophisaurus*, the dentary of *R. medasensis* exhibits an apomorphic feature that is also distinctive for *Ophisauromimus*, i.e. a large, perpendicular intramandibular septum drawn out posteriorly into a small process and the ventrolateral margin of the septum is free. Such a morphology of the intramandibular septum is absent in *Ophisaurus*. The distinctive features of *Ragesaurus* and of the only species *R. medasensis*, in contrast to *Ophisaurus*, *Anguis*, *Ophisauriscus*, *Helvetisaurus* and *Pseudopus*, are as follows (Bailon and Augé 2012): (1) the anterior inferior alveolar foramen is medially bordered by a small perpendicular septum; (2) in ventral view, the Meckelian groove is very narrow in the mid-length of the dentary; and (3) teeth are conical, their bases are not mesiodistally expanded, their apices are not striated and their mesial and distal cutting edges are absent. Although the anatomy of the intramandibular septum is similar in *Ragesaurus* and *Ophisauromimus*, the above three features distinguish both genera.

The morphology of the intramandibular septum as exhibited by *Ophisauromimus* and *Ragesaurus* is very similar to that of exclusively North American members of Gerrhonotinae, like *Barisia*, *Abronia* and *Mesaspis* (see also Gauthier 1982, fig. 31). However, the morphology of the teeth of gerrhonotines is completely different from that of *Ophisauromimus*. Further, a morphology of the intramandibular septum similar to that of *Ophisauromimus* is also present in the North American fossil lizard *Odaxosaurus piger* (Mesozoely 1970, fig. 10c). Given the early occurrence of *O. piger* (Cretaceous and Palaeocene of North America), it might be that such a morphology of the intramandibular septum is a symplesiomorphy (suggested by Gauthier 1982 as well as the primitive anguid condition).

cf. *Ophisauromimus*
(Fig. 15)

Locality, Horizon and Material: Herrlingen 11; upper Oligocene (MP 28): SMNS 59448 g, posterior portion of left dentary.

Dentary: The posterior portion of the dentary is slender and gradually rises posterodorsally. The splenial spine is present at the level of the 5th tooth counted from posterior. The alveolar foramen is at the level of the 4th tooth counted from posterior. The intramandibular septum forms a distinct dorsoventral wall. The coronoid process is short and pointed. The surangular process is broken; however, it is estimated that its posterior portion extended further posteriorly than the coronoid process. The more or less smooth lateral surface is pierced by several mental foramina located slightly dorsally to the mid-height of the dentary. All teeth are broken.

Remarks: This fragmentary dentary corresponds to *Ophisauromimus* in one feature, i.e. the intramandibular septum is a tall perpendicularly oriented wall. However, its posteriormost portion is broken, so that it is not known whether or not the septum extended into a process. However, the morphology of the posteriormost portion of the dentary, the position of the splenial spine and the position of the alveolar foramen correspond to conditions of *Ophisauromimus*. We tentatively conclude that the dentary fragment SMNS 59448 g belongs to this taxon.

Anguinae indet.
(Figs. 16, 17)

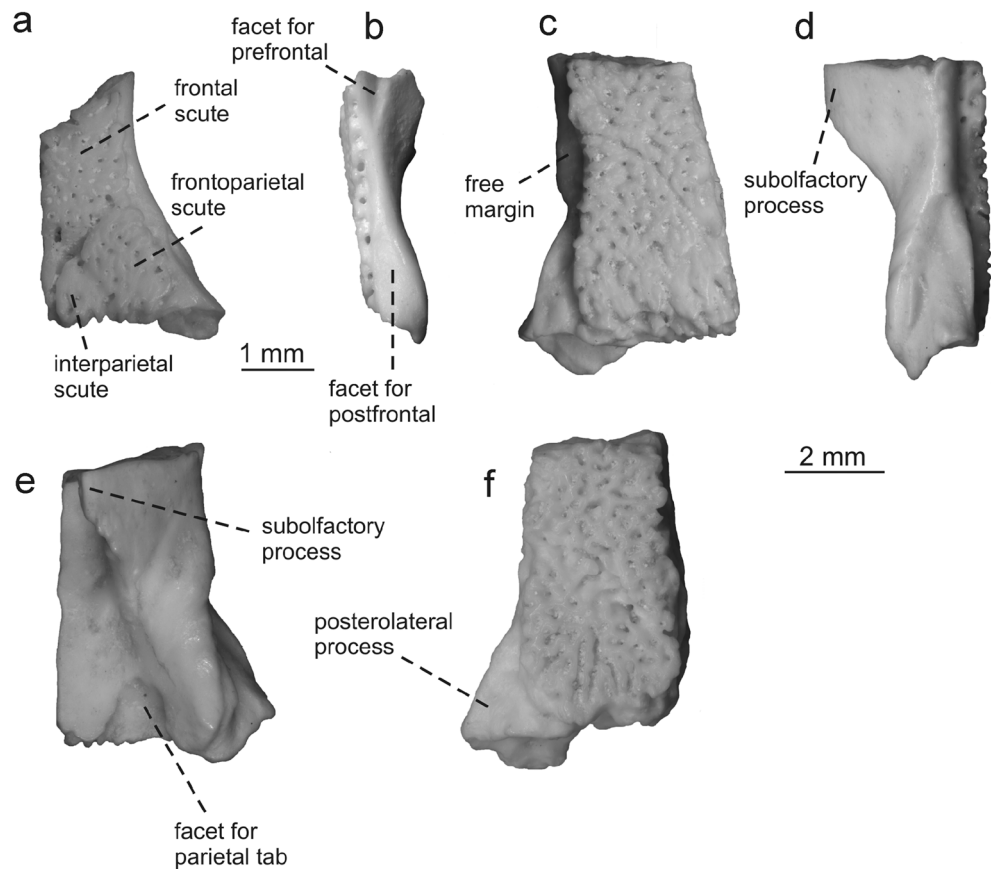
Locality, horizon and material: 1. Herrlingen 11, upper Oligocene (MP 28): quadrate SMNS 59447, osteoderms SMNS 59444, palatine SMNS 96570 b; pterygoids SMNS 96570 c, d. 2. Herrlingen 9, upper Oligocene (MP 29): osteoderms SMNS 80039, 22 dorsal vertebrae SMNS 80038 a, 10 caudal vertebrae SMNS 80038 b.

Quadrate: The right quadrate is preserved (Fig. 16e, f). Its dorsal portion is anteroposteriorly expanded. The dorsal surface of the cephalic condyle is almost straight and its surface is roughened. The anterior surface of the quadrate is laterally expanded and bordered by a columnar portion forming a sharp ridge. In anterior view, the mandibular condyle is shallow, W-shaped with blunt peaks. On the medial surface of the quadrate, there is a prominent medial crest. Unfortunately, its central region is broken. A small, rounded foramen pierces the quadrate at approximately mid-length of the posterior surface. Such a morphology strongly corresponds to *Ophisaurus* and partially to *Anguis*. However, we do not know the quadrate of *Ophisauromimus*.

Palatine: The anterior half of the right palatine is preserved (Fig. 16a), representing an anteroposteriorly elongated plate. The maxillary process is robust and posterolaterally expanded. Its anterior portion is bordered by the infraorbital foramen. The palatine sulcus is mediolaterally broad. The ventral surface of the palatine bears an anteroposteriorly elongated field of ellipsoidal shape with small teeth. The teeth are conical, with broad bases. The tips of the teeth are pointed and curved posteriorly. The morphology of the palatine and teeth is most similar to that of *Ophisaurus*.

Pterygoid: The transverse process is completely preserved in SMNS 96570 c (Fig. 16b, c). It is short, but massively built. A distinct dorsal transverse crest is located on its dorsal surface. Between the transverse and the palatine processes, a broad suborbital incisure is present. The proximal portion of the quadrate process is well preserved. The basiptyergoid articulation is deep. The epiptyergoid crest is distinct, although slightly broken. Only the root of the obtuse process (for this term, see Klembara 2015) is preserved. The epiptyergoid fossa is rounded and located on

Fig. 18 Squamata indet. 1: right frontal SMNS 59458 b in **a** dorsal, **b** lateral aspect. Left frontal SMNS 59458 c in **c** dorsal, **d** lateral and e ventral aspect. Left frontal SMNS 59458 d in **f** dorsal aspect



the dorsal surface of the root of the quadrate process, at the level of the posterior end of the epipterygoid crest. The ventral surface of the pterygoid bears a large area with teeth (Fig. 16b, d). The teeth located at the lateral margin of the denticulate area are robust and arranged in a row. The remaining teeth are smaller and rather scattered. The teeth have a morphology similar to those of the palatine. Overall, the morphology of pterygoid and teeth is most similar to *Ophisaurus* and clearly different from, e.g.

Anguis, in which both palatine and pterygoid lack dentition. The elements described here probably represent the same species because of the very similar morphology of the dentition.

Dorsal vertebrae: The isolated vertebrae are well preserved (Fig. 17). The vertebral centrum is slightly anteroposteriorly elongated, gradually becoming narrower posteriorly. In ventral aspect, the lateral margins of the centrum (subcentral ridges) are straight, giving the centrum a

Fig. 19 Squamata indet. 2: left dentary SMNS 800040 j in **a** lateral, **b** medial, **c** dorsal aspect

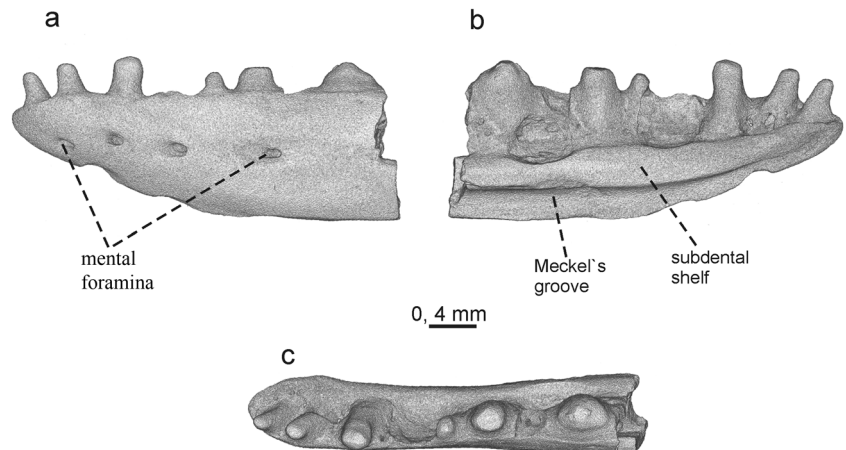


Table 1 List of taxa examined from Herrlingen localities and comparison to the locality Oberleichtersbach

	MP 28 (Herrlingen 8 and 11)	MP 29 (Herrlingen 9)	MP 30 (Oberleichtersbach; after Böhme 2008, modified)
Iguanidae	Iguanidae indet.	Iguanidae indet.	-
Gekkota	Gekkota indet.	Gekkota indet.	-
Lacertiformes + Scincoidea	<i>Dracaenosaurus croizeti</i>	<i>Dracaenosaurus croizeti</i> <i>Dracaenosaurus</i> sp.	-
	<i>Pseudeumeces</i> cf. <i>cadurcensis</i>	<i>Pseudeumeces</i> cf. <i>cadurcensis</i>	?
	<i>Mediolacerta</i> cf. <i>roceki</i>	<i>Mediolacerta</i> cf. <i>roceki</i>	-
	cf. <i>Plesiolacerta</i> sp.	cf. <i>Plesiolacerta</i> sp.	-
	-	-	? <i>Miolacerta</i> sp.
	Lacertidae indet.		<i>Lacerta</i> sensu lato (1–4)
Amphisbaenia	Blanidae indet.	Blanidae indet.	-
	<i>Palaeoblanus</i> cf. <i>tobieni</i>		-
	Amphisbaenia indet. 2	Amphisbaenia indet. 1	Amphisbaenia indet. (vertebra)
	"Scincomorphan" indet. 2	"Scincomorphan" indet. 1	-
Anguinae	<i>Ophisaurus</i> sp.	-	<i>Ophisaurus</i> sp.
	-	-	cf. <i>Anguis</i> sp.
	<i>Ophisauromimus coderetensis</i>	<i>Ophisauromimus coderetensis</i>	-
Shinisauria	-	-	? <i>Merkurosaurus</i> sp.
Squamata indet.	Squamata indet. 1	Squamata indet. 2	-

triangular shape. The deep cotyle is dorsoventrally depressed, as is the condyle. The height of the cotyle is slightly taller than the height of the dorsally lying neural canal. The condyle is separated from the body of the centrum by a slight narrowing, although a precondylar constriction is absent. The ventral surface of the centrum has a very shallow, longitudinal groove in the central region. The lateral margins of this groove form low, weak and parallel ridges, and only in a few vertebrae there are two subcentral foramina. The pre- and postzygapophyses are rounded and a distinct interzygapophyseal constriction separates them in dorsal aspect. The synapophyses represent rounded articulation surfaces, located on the lateral side of the anterior portion of the centrum. The small neural canal is pentagonal in cross-section. The neural spine is extended dorsally, forming a posterodorsally elevated process. Anteriorly, it continues almost along the entire dorsal side of the neural arch as a median ridge.

Remarks: This type of vertebrae corresponds to that of *Pseudopus*. There are two features which allow for this assignment: (1) the lateral margins of the centrum are straight; and (2) the cotyle height is taller than the height of the neural canal. Similar to the osteoderms (see below), these vertebrae might represent the oldest skeletal record of *Pseudopus*. However, because we do not know the morphology of the vertebrae of *Ophisauromimus*, we prefer the preliminary designation as Anguinae indet.

Caudal vertebrae: The caudal vertebrae are narrower, more elongate and less depressed than the dorsal vertebrae, and also

the pre- and postzygapophyses are relatively smaller. Cotyle and condyle are dorsoventrally depressed. The hemal arches are fused to the centrum and lie in the posterior portion of the centrum. Unfortunately, their ends are broken. The anteroventrally oriented transverse processes are well developed and originate from the anterior portion of the centrum. The neural spine is posterodorsally oriented and pointed.

Osteoderms: Two types of osteoderms are preserved. The first type is represented by massive osteoderms, nearly square in shape, with an absence of the medial ridge (Fig. 16g). The gliding surface is large and occupies almost half of the size of the dorsal surface. The ornamented surface consists of strongly developed tubercles. The lateral bevel is distinctly developed. Such osteoderms are partially similar to the dorsal osteoderms of *Pseudopus*, i.e. the shape of the tubercles on the osteoderms is apomorphic (convergent in Glyptosaurinae). If so, these osteoderms are the first evidence (possibly along with the above-described vertebrae) of *Pseudopus* in the Oligocene and the oldest record of this genus. However, as in the case of other bones described above as Anguinae indet., we do not know the osteoderms of *Ophisauromimus* and therefore refrain from making such an inference. The second type is slender, rectangular, and bearing a low medial ridge (Fig. 16h). The gliding surface occupies almost half of the size of the dorsal surface. The ornamented surface consists of short grooves diverging from the highest section of the median ridge. The lateral bevel is highest close to the

gliding surface. This type of morphology corresponds to that of *Ophisaurus*.

Squamata indet. 1
(Fig. 18)

Locality, horizon and material: Herrlingen 11, upper Oligocene (MP 28): Three frontals SMNS 59458 b-d.

Frontal: Three paired frontals are preserved. Based on the size, robustness and the intensity of the ornamentation of the attached osteoderm, they appear to represent different ontogenetic stages (most likely one late juvenile stage and two adult). The description is mainly based on the two adult specimens. The frontal is heavily built, very robust and short. Unfortunately, the anterior region in front of the subolfactory process is broken and missing in all preserved specimens. For this reason, the exact length of the element can be only estimated. The preserved element is rectangular in shape with a slightly expanded posterolateral corner. The smallest specimen has a well-rounded, concave lateral margin. The dorsal surface is covered by osteodermal scutes; however, the lateral and mainly posterolateral regions of the frontal table are exposed. The sulcus interfacialis, which makes the border between the frontal scute and the two frontoparietal scutes, is curved and turned posteriorly. The frontoparietal scute is axe-shaped. In the posterior mid-region, a small triangular portion of the interparietal scute is preserved. The dermal scutes are strongly ornamented. The ornamentation consists of foramina, distinct grooves and ridges. The contact with the parietal is straight and interdigitated. In lateral view, the margin of the bone bears facets for the prefrontal and the postfrontal bones. The facets are not in contact and therefore the frontal has a free lateral margin (partly forming the dorsal border of the orbit). The ventral side bears extremely robust crista cranii, forming the subolfactory process anteriorly. It is very broad, slightly curved and expanded medially almost to the contact with the other frontal. The end is broken in all studied specimens, therefore it is not clear if the subolfactory processes of the two frontals were in contact. In the posterior region, the huge rounded facet for the parietal tab is located, bordered by the crista cranii laterally. In ventral view, the lateral portion of the facet undercuts the crista cranii, so the connection with the parietal tab was extremely strong.

Remarks: The frontals described here are very unusual. They are very robust and short (although the anterior region is broken, the relative proportions can be estimated based on the distance between the cristae cranii and position of the prefrontal facet). A noteworthy character is the heavily developed subolfactory process. The interparietal scute reaches the frontal, which is a condition present in e.g. *Anguimorpha* or *Iguania* (plesiomorphic condition). In the Palearctic clade of lacertids, the interparietal scute is isolated from the frontal, located approximately in the

central region of the parietal. However, in many members of the African radiation, the interparietal scute does reach the frontal.

Squamata indet. 2
(Fig. 19)

Locality, horizon and material: Herrlingen 9, upper Oligocene (MP 29): left dentary SMNS 800040 j.

Dentary: The anterior half of the left dentary is preserved. Meckel's groove is fully open, but very narrow and positioned ventromedially. The subdental shelf is thin, straight, rising only very slightly dorsally. The preserved portion bears seven tooth positions with six teeth still attached. The lateral surface is pierced by four mental foramina, located in the mid-line.

Dentition: the dentition is pleurodont. The first anterior teeth are conical and thin, whereas further posteriorly the teeth become broader. The last preserved tooth shows a wide base. It is very blunt, tending weakly to develop mesial and distal accessory cusps. Its implantation is more or less subpleurodont. The penultimate preserved tooth is small.

Remarks: The material bears some resemblances to that described by Augé (2005, fig. 206a-b) as *Lacertilia* indet. from the locality Malpérié, Phosphorites du Quercy (Eocene, MP 17), i.e. both dentition and the shape of Meckel's groove are similar in the respective specimens. However, poor preservation renders any further interpretation difficult.

Discussion

Both faunas (Herrlingen 11 and Herrlingen 9) are very similar (see Table 1), revealing a so far unknown combination of lizard taxa, with several being firstly described from Central Europe. For a long time, iguanids from Europe were known only from the paratropical Eocene. More recently, Augé and Pouit (2012) described several specimens from the locality of Pech-du-Fraysse (MP 28, late Oligocene, France, Phosphorites du Quercy) and assigned them to the iguanid genus *Geiseltaliellus*. These authors suggest that the re-occurrence of this clade in the late Oligocene after an absence in the earlier Oligocene might indicate that a refugium was present somewhere. According to several other authors (Schmidt-Kittler and Vianey-Liaud 1975; Szyndlar and Rage 2003), there was a geographical barrier (i.e. a seaway, the Rhine graben) between western and central Europe in the Oligocene, and Augé and Pouit (2012) mentioned differences between terrestrial vertebrate faunas inhabiting France and Germany at that time. However, similarity of the Herrlingen lizard faunas to that of the late Oligocene French faunas (Phosphorites du Quercy) shows that migration ways between France and Germany were open at least during MP 28.

Moreover, the material from Herrlingen 9 (MP 29) represents the youngest known record of Iguanidae in the entire Euroasia and Africa except Madagascar (see Pough et al. 2004). As such, iguanids were certainly more common and broadly distributed in Europe during the late Oligocene than previously thought. The iguanid material described here is similar to that of the material from France assigned by Augé and Pouit (2012) to the taxon *Geiseltaliellus*, which is on the stem of Corytophaninae (Smith 2009b), occurring today in the wet tropical areas of Mexico, Central America, and northwestern South America. However, the fragmentary nature of both records does not give enough support for such a precise determination.

Some of the amphisbaenian material can be allocated to Blanidae with sufficient certainty. There is already evidence for the presence of this lineage from the middle Eocene (*Cuvieribaena* described by Čerňanský et al. 2015b), and potentially even older, i.e. *Blanosaurus* from the earliest Eocene (Folie et al. 2013). The latter material, however, can only be tentatively attributed to the family Blanidae and so far lacks true phylogenetic support. The Herrlingen material represents the oldest known record of blanids possessing characters of the modern members of the clade.

Several anguimorph lizards are present in Herrlingen. The revision of the European Oligocene "*Dopasia*" shows that the taxa *D. frayssensis* and *D. coderetensis* are markedly different from the members of the clade *Ophisaurus*. For this reason, we erected a new generic name. This taxon has not (yet?) been found in the slightly younger German locality Oberleichtersbach (MP 30). There, in contrast, a shinisaurid has been reported (Böhme 2008). In spite of the abundant fauna, lizards from Oberleichtersbach appear to be less diverse than Herrlingen, being already more similar to early Neogene faunas (although it should be noted that local environments can have a huge impact on the preserved fossils, which may cause a bias). The Herrlingen localities support previous observations that amblyodont lacertids were very common during the Oligocene (Augé 2005). In Oberleichtersbach (Table 1), the non-amblyodont types of lacertids appear to be very diverse (according to Böhme 2008, *Miolacerta* and four morphotypes of *Lacerta* are present; the allocation at the genus level might be questionable, due to the fragmentary character of preserved elements, and only one isolated lizard tooth of uncertain identity represents amblyodonty). Although more systematic studies are needed, this change in lacertid composition and diet might reflect palaeoecological changes in the terminal Oligocene. At the beginning of the Miocene, in MN 2 of Germany, a highly diverse fauna of modern-looking European squamates is already present (Čerňanský et al. 2015a). The amblyodont forms are represented by lacertids, e.g. *Janosikia ulmensis* (Čerňanský et al. 2016) and the anguimorph *Pseudopus* (the oldest known member of this clade comes from Amöneburg; Čerňanský et al. 2015a),

which later became, in MN 3, the most commonly found durophagous form in Europe. However, caution is needed when making inferences on the diet of fossil amblyodont forms. Whereas the presence of amblyodont dentitions suggests a preference for hard-shelled prey, this does not mean that the respective lizard species is restricted to such a diet (see, e.g. Vanhooydonck et al. 2007). For example, Rifai et al. (2005) reported that the stomach of modern *Pseudopus apodus* contained both arthropods (88,7 %) and mollusks (5, 3 %), and Çiçek et al. (2014) showed that insects are the predominant food (86.1 %), with gastropods forming only 8.3 % of the prey. In fact, there are only a few durophagous specialists in the world today. Among Tupinambinae, for example, only *Dracaena* is a truly durophagous form, whereas other teiids with amblyodont teeth are omnivorous (Meccolli and Yanosky 1994; Kiefer and Sazima 2002). Similar patterns have been observed for the amblyodont bluetongued skinks (*Tiliqua*) from Australia, the diet of which also includes plant matter such as seeds (Christian et al. 2003; Shea 2006).

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