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DOI 10.1007/s12542-016-0329-1

RESEARCH PAPER

Another piece of the puzzle: the first report on the Early Miocene lizard fauna from Austria (Ottnangian, MN 4; Oberdorf locality)

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Received: 30 March 2016 / Accepted: 4 September 2016

Abstract The lizard fauna from the Early Miocene of Austria, namely from Oberdorf in the Styrian basin, is described here for the first time. The Oberdorf is a particularly interesting locality, because its paleoenvironment is slightly different from that of other Central European MN 4 localities, such as Dolnice in the Cheb basin. Oberdorf has rare forest and pond-like biotopes in a swampy environment near a river system. Although the fossil material is only fragmentarily preserved, it supplies important information about palaeobiodiversity and taxa spatial distribution in the Central Paratethys area during the Early Miocene. Six major lizard clades are present in Oberdorf: Gekkota, ? Chamaeleonidae, Lacertidae, ? Scincidae, Cordylidae and Anguidae. Many of these are first described from Austria. The Oberdorf lizard fauna composition is comparable to that in Lower Miocene localities including Petersbuch 2 in Germany and also Dolnice in the Czech Republic. The Oberdorf palaeobiodiversity is decidedly lower. The maxilla material designated Gekkota indet. resembles that in *Euleptes*; however, the limited preservation of the find precludes precise conclusions. Chamaeleonids are rare at Oberdorf, but the Scincoidea clade is abundantly represented. This includes the cordyloid material and the material tentatively assigned to Scincidae. Two types of lacertids are identified: *Lacerta* cf. *poncenatensis* and *Lacerta* sp. The first forms the youngest known record of this species. Among anguids, *Ophisaurus* cf. *spinari* occurs in this locality, indicating that this taxon habited a wider range of environmental conditions, for example, than *O. fejfari*.

Keywords Neogene · Squamata · Central Europe · Styrian basin · Central Paratethys

Kurzfassung Die Eidechsenfauna aus dem frühen Miozän von Österreich wird hier erstmalig beschrieben. Das fossile Material stammt aus Oberdorf im Steirischen Becken. Aufgrund seiner abweichenden Paläoumweltbedingungen im Vergleich mit anderen mitteleuropäischen MN 4-Lokalitäten, wie etwa Dolnice im Cheb-Becken, handelt es sich um eine äußerst interessante Fundstelle. Oberdorf ist geprägt von seltenem Waldbestand sowie teichähnlichen Biotopen, welche sich in einer sumpfigen Umgebung in der Nähe eines Flusssystems befinden. Obwohl das fossile Material nur fragmentarisch erhalten ist, liefert es wichtige Informationen zur Paläobiodiversität wie auch zur räumlichen Verteilung der Taxa innerhalb der zentralen Paratethys zur Zeit des frühen Miozäns. Sechs Eidechsen-Großgruppen konnten in Oberdorf identifiziert werden: Gekkota,? Chamaeleonidae, Lacertidae,? Scincidae, Cordylidae und Anguidae. Viele werden dabei erstmalig aus Österreich beschrieben. Die Zusammensetzung der dortigen Echsenfauna wird mit untermiozänen Lokalitäten verglichen, darunter beispielsweise Petersbuch 2 in Deutschland, sowie Dolnice in der Tschechischen Republik. Auffällig ist eine deutlich geringere Paläobiodiversität innerhalb der Oberdorfer Fundstelle. Das Maxillen-Material, als Gekkota indet. bestimmt, ähnelt deutlich demjenigen von *Euleptes*, jedoch erlaubt der schlechte Erhaltungszustand des Fundes keine eindeutige Zuordnung. Chamaeleoniden sind eher seltene Funde in Oberdorf, während Material der Scincoidea reichlich vertreten ist.

Communicated by Mike Reich.

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Dies beinhaltet Cordylidae-Material, wie auch welches, das vorläufig den Scincidae zugewiesen wird. Zwei Arten von Lacertiden können identifiziert werden: *Lacerta* cf. *poncenatensis* und *Lacerta* sp. Die erstgenannte Art repräsentiert hierbei das jüngste bisher bekannte Vorkommen dieser Spezies. Innerhalb der Anguiden ist *Ophisaurus* cf. *spinari* in dieser Lokalität vorhanden. Dies deutet darauf hin, dass dieses Taxon einen breiteren Bereich von Umweltbedingungen toleriert als beispielsweise *O. fejfari*.

Schlüsselwörter Neogen · Squamata · Zentraleuropa · Steirisches Becken · Zentrale Paratethys

Introduction

The lizard fauna from the Lower Miocene Oberdorf locality in Austria is described here. Fossil lizards from Austria have hitherto been documented only from the Middle Miocene (Böhme 2002; Tempfer 2003; Böhme and Vasilyan 2014) and the Upper Miocene (Tempfer 2005, 2009). Thus there was a significant knowledge gap in understanding the evolution of the squamate clade in this area in the Early Miocene. The Oberdorf fossil fauna is dated to the Mammal Neogene Zone MN 4 (17.6–17.2 Ma), correlated with the Ottnangian, Early Miocene (Daxner-Höck et al. 1998; Haas 1998). This zone belongs to the important time interval comprising the latest Oligocene (MP 29–30) and Early Miocene up to MN 4, documenting prominent faunal turnover which brought the modern squamate fauna to Europe (see Čerňanský et al. 2015). In this regard, the late Early Miocene (MN 3–4) provided marked change and an important wave of immigrants, including chamaeleonids and cordylids (Fejfar and Schleich 1994; Čerňanský 2010a, 2012; Georgalis et al. 2016). During the Ottnangian and Karpatian, the warm and humid Miocene Climatic Optimum peaked in Central Europe (i.e., at 18–16.5 Ma; see Böhme 2003), and squamate fauna increased markedly in both richness and diversity (Rage 2013). Lizards from this period are recognized from several localities in this area, such as Dolnice near Cheb in the Czech Republic (Klembara 1979; Roček 1984; Čerňanský 2010a, b) and Petersbuch 2 in Germany (MN 4a, ~18.5 Ma; Kosma 2004; Čerňanský 2011; Klembara et al. 2010).

However, the Oberdorf paleoenvironmental conditions are slightly different from those of Dolnice and Petersbuch 2, with its rare forest, pond-like biotopes and swampy environment close to a river system (see Daxner-Höck et al. 1998; Haas 1998; Kolcon and Sachsenhofer 1999; Kovar-Eder et al. 2001). The deposit at Oberdorf is located in the north-western part of the Styrian basin (Fig. 1), and forms part of the Köflach–Voitsberg lignite district. This formation with lignite was deposited in marginal facies in a fluvial environment (Haas 1998; Haas et al. 1998). This Neogene basin represents the most northwesterly sub-basin of the Pannonian Basin system, surrounded by Alpine fold belts (the Eastern Alps, Carpathians and Dinarides). The basin deposits are paleogeographically in the Central Paratethys province (Ebner and Stingl 1998).

Fig. 1 Location of the Oberdorf locality in Austria, with locations of Dolnice in the Czech Republic and Petersbuch 2 in Germany

The Oberdorf locality is formed by a lignite opencast mine. Fossils are concentrated in carbonaceous clay sediments and silts at the bottom of the O3 and O4 lignite-bearing layers (Daxner-Höck et al. 1998). These layers are treated as one unit, because almost identical faunal composition discovered there is at the same evolutionary stage and therefore coeval (Daxner-Höck 1998). A large multidisciplinary research report edited by Steininger was published in 1998. Concerning herpetofauna of this site, amphibian (Sanchiz 1998) and snake (Szyndlar 1998) remains have been described.

This paper is the first report on lizard fauna from this locality and the first report of an Early Miocene presence of this assemblage in Austria. Therefore, the aims of the paper are (1) to describe the preserved material in detail, (2) to resolve its taxonomic designation, and (3) to compare the faunal composition with that recorded for other Central European MN 4 localities.

Materials and methods

The studied material is housed in the Natural History Museum, Vienna (Austria), prefixed under individual NHMW numbers. These fossils come from the Oberdorf locality, where they are concentrated in carbonaceous clay sediments and silts at the bottom of the O3 and O4 lignite-bearing layers. Although both layers are treated as one unit (Daxner-Höck 1998), I used the exact information about layer location for each fossil (see the "Material and horizon" subsections). The specimens were photographed under a scanning electron microscope (SEM; FEI Inspect F50) at the Slovak Academy of Sciences in Banská Bystrica, and several photographs were taken using a Leica M125 binocular microscope with an axially mounted DFC500 camera [LAS software (Leica Application Suite) version 4.1.0 (build 1264)]. The standard anatomical orientation system is used throughout this paper, and terminology describing individual bone structures is based on Fejérváry-Lángh (1923), Meszoely (1970), Klembara (1979, 1981, 2012) and Rage and Augé (2010).

Systematic palaeontology

Squamata Oppel, 1811
Gekkota Cuvier, 1817

Gekkota indet.
Figure 2a, b

Material and horizon The right maxilla: NHMW 2016/0028/0001; Oberdorf 3.

Description

Maxilla Only the posterior portion of the right maxilla is preserved. Its dental crest is high, supporting 12 tooth positions (three teeth are still preserved). The nasal process is broken. The external surface of the preserved portion is pierced by two labial foramina, and a groove runs posteriorly from the second foramen. This character is often found in *Euleptes*.

Dentition The dentition is pleurodont, and the teeth are closely spaced, which is a character of geckos. Teeth are conical, slender, straight and well pointed, with a small foramen piercing each base.

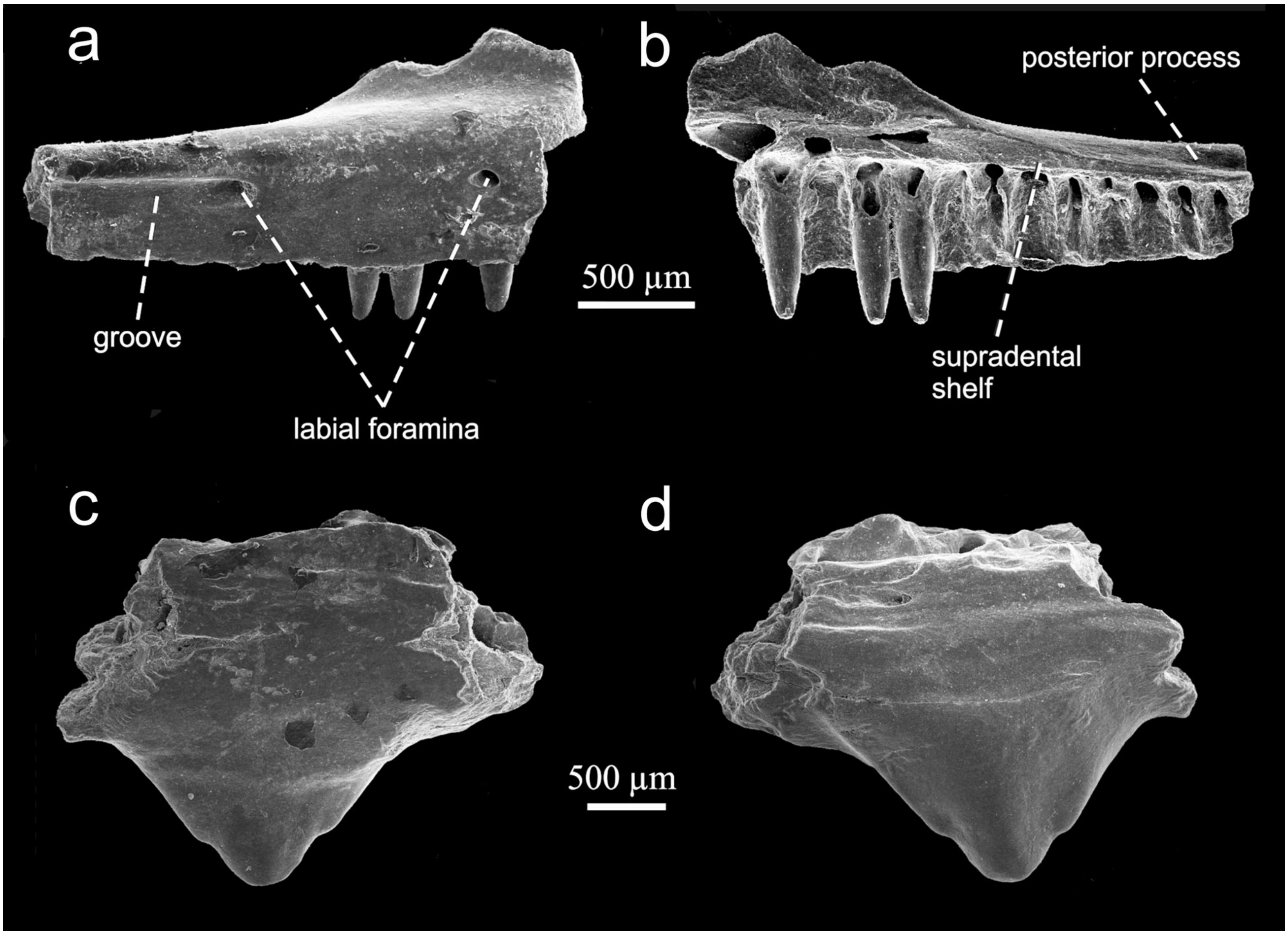

Fig. 2 Gekkota indet.; right maxilla NHMW 2016/0028/0001 in **a** lateral and **b** medial view. ? Chamaeleonidae indet. NHMW 2016/0028/0002 in **c** lateral and **d** medial view

Remarks

Although a similar groove running from the posteriormost labial maxillary foramen is frequently observed in members of the extant European taxon *Euleptes* (Daza et al. 2014), the fragmentary character of the Oberdorf find provides insufficient data for precise designation. The fossil record of the Gekkota clade is generally poor (Estes 1983; Müller and Mödden 2001; Augé 2005; Daza et al. 2014), thus reflecting the fragility of their usually small skeletal elements. Miocene gekkotans have been described from Germany and the Czech Republic [*Euleptes gallica* (Müller 2001; Čerňanský and Bauer 2010) and *Euleptes* sp. (Müller and Mödden 2001)] and also from Slovakia (Estes 1969). Extinct genera from the Miocene are represented by *Palaeogekko risgoviensis* from Germany (Schleich 1987) and *Gerandogekko* [to date, the latter taxon currently consists of two species: *G. arambourgi* and *G. gaillardi* (Hoffstetter 1946; Kluge 1967; Schleich 1985)]. In addition, there is indeterminate material from the Miocene of France (Augé and Rage 2000) and Germany (Čerňanský et al. 2015).

Iguania Cope, 1864
Acrodonta Cope, 1864
Chamaeleonidae Gray, 1825

? **Chamaeleonidae indet.**
Figure 2c, d

Material and horizon Jaw fragment NHMW 2016/0028/0002; Oberdorf 3.

Description and comment Only a small fragment of the jaw with one tooth is preserved. The dentition is acrodont, and the preserved tooth is triangular and tricuspid, with a dominant central cusp and smaller mesial and distal cusps. These latter are comparable in size, providing symmetry in lateral and medial view. There are no clear interdental grooves, thus suggesting the fragment is a portion of maxilla. Within the diapsids, acrodont tooth implantation occurs in trogonophiid amphisbaenids, Sphenodontia and acrodontan lizards (Estes et al. 1988; Gauthier et al. 2012). Due to the size of the preserved tooth and its tricuspidity, together with the geographical location and age of the locality, the allocation of the Oberdorf material to acrodontan lizard is beyond doubt. However, its allocation at the family level is questionable here, due to its fragmentary character, where the anterior region is not preserved. 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).

Scincomorpha Camp, 1923

Remarks It should be noted that molecular datasets often strongly support scincomorph paraphyly (e.g., Townsend et al. 2004; Vidal and Hedges 2009). There is, however, very little support for that in the morphological datasets (see Gauthier et al. 2012).

Lacertiformes Estes et al., 1988
Lacertidae Oppel, 1811

***Lacerta* s.l.** Linnaeus, 1758
Type species Lacerta agilis Linnaeus, 1758

Lacerta* cf. *poncenatensis Müller, 1996
Figure 3a, b

Material and horizon Right dentary NHMW 2016/0028/0003; Oberdorf 3.

Description

Dentary This is an anteroposteriorly elongated, slightly dorsally concave, slender element. Meckel's groove is fully open and very narrow, but it becomes slightly wider posteriorly. The opening of the alveolar canal is located at the level between the fourth and fifth tooth (counted from the posterior), and the canal continues interiorly to the bone. It is separated from Meckel's groove by the ventrolaterally oriented intramandibular septum. There is a bony septum posterior to the opening, forming the lateral wall of Meckel's groove in this region and rising ventrally from the dental region (*pars dentalis*) at the level of the fourth posterior tooth. Further posteriorly, the entire region is slightly rising dorsally. It is posterodorsally oriented and retains dentition. The end is divided into two small and blunt processes. The thin, slightly concave subdental shelf runs anteriorly from this region and forms the roof of Meckel's groove dorsally. The shelf becomes gradually dorsoventrally broader and is very robust in the anterior preserved region. The facet for the splenial is located on the ventromedial aspect of the ventral bone margin. The dorsal portion of the splenial facet is observed on the ventral aspect of the posterior region of the shelf, projecting anteriorly at the level of the 13th tooth position. The sulcus dentalis is only slightly developed, mainly in the anterior region of the dorsal surface of the shelf. The dental crest supports 16 tooth positions (five teeth are still preserved). However, the anterior region is broken, so the number of teeth in the complete dentary was certainly higher.

The preserved portion of the smooth external surface is pierced by six mental foramina. The last posterior foramen, which is located at the level of the sixth tooth position, becomes more anteroposteriorly elongated. A sharp groove runs from this foramen to the level of the fourth posterior tooth. A facet for the coronoid is located in the posterodorsal region of the bone lateral aspect.

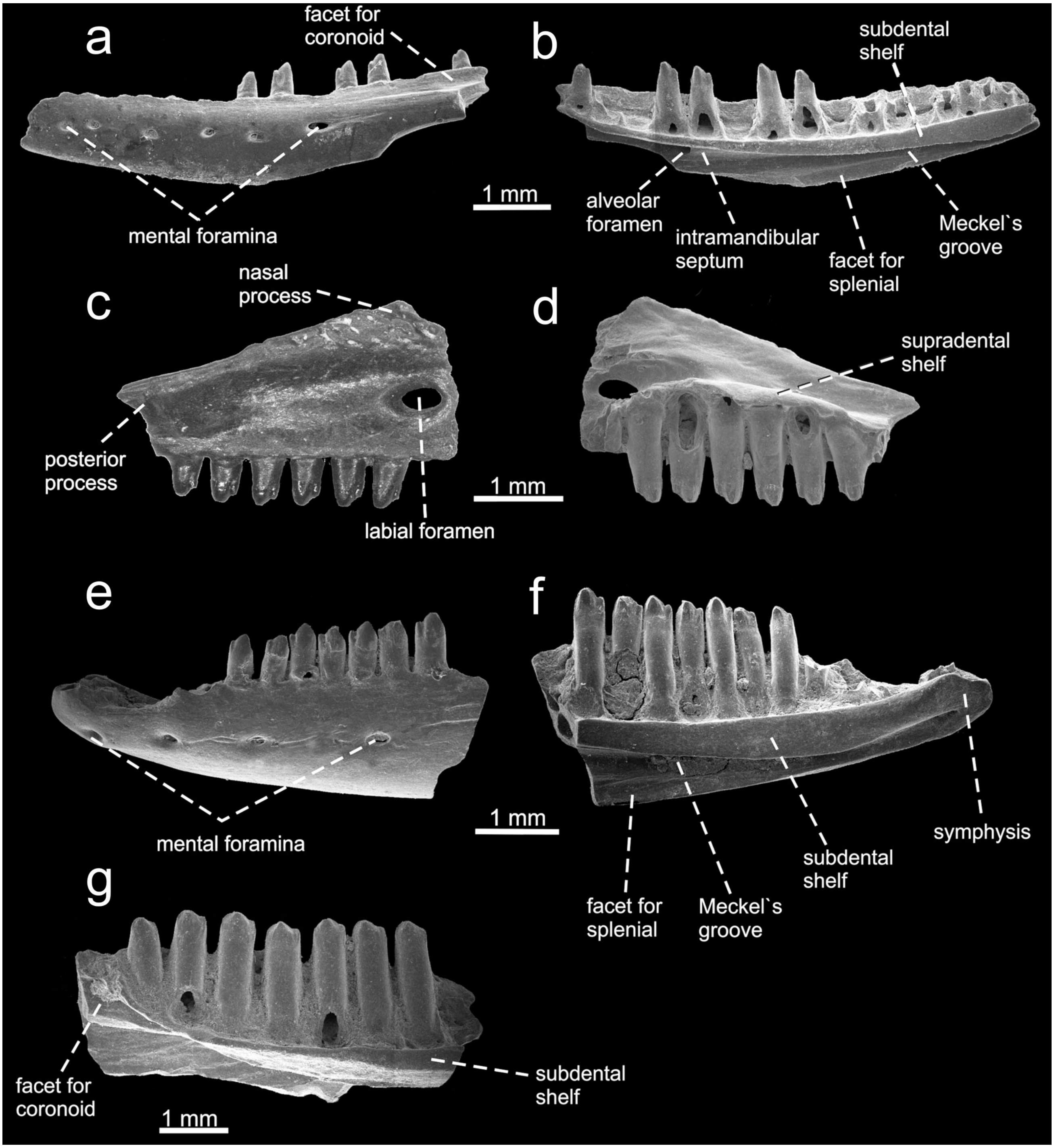

Fig. 3 *Lacerta* cf. *poncenatensis*; the left dentary NHMW 2016/0028/0003 in **a** lateral and **b** medial view. *Lacerta* sp.; right maxilla NHMW 2016/0028/0004 in **c** lateral and **d** medial view. Left dentary NHMW 2016/0028/0005 in **e** lateral and **f** medial view, left dentary NHMW 2016/0028/0006 in **g** medial view

Dentition The dentition is pleurodont. The teeth are robust and bicuspid, with a dominant distal cusp and smaller accessory mesial cusp. Large resorption pits are located at the tooth bases.

Remarks

The dentary morphology is identical to that of the material described by Müller (1996) from France and by Čerňanský et al. (2015) from Germany, in the following features: (1) the presence of robust bicuspid teeth, (2) wide interdental gaps, (3) dentary that is slender rather than broad, (4) a narrow Meckel's groove, (5) a dorsally elevated posterior dentary region, and (6) a ventral bony septum forming the lateral border of Meckel's groove behind the alveolar foramen which rises ventrally at the fourth tooth level. Both previously described finds are from MN 2. The fragmentary character of the Oberdorf finds allows only tentative classification at the species level; however, this material may be the youngest record of this species.

Lacerta sp.

Figure 3c–g

Material and horizon Right maxilla NHMW 2016/0028/0004, left dentary NHMW 2016/0028/0005; Oberdorf 3. Left dentary NHMW 2016/0028/0006; Oberdorf 4.

Description

Maxilla Only a fragment of the right maxilla is preserved. It bears seven tooth positions (six teeth are still attached). It has a thin supradental shelf. The groove running to the superior alveolar foramen posteriorly reaches the level of the fifth tooth. Unfortunately, the exact location of the superior alveolar foramen cannot be determined because the anterior portion is damaged. The medial aspect of the large elliptical labial foramen is exposed here. This foramen pierces the lateral surface of the bone. In this aspect, only the base of the nasal process is preserved, and ornamentation in this region is formed by pits, short grooves and ridges.

Dentary The anterior region of the left dentary NHMW 2016/0028/0005 bears 13 tooth positions (seven teeth are still attached), while the posterior preserved element NHMW 2016/0028/0006 bears seven teeth. Meckel's groove is narrow but fully open, with the straight ventral margin of the dentary coursing posteroventrally. The subdental shelf becomes dorsoventrally broader anteriorly, but narrows close to the symphysis, where the shelf rises slightly dorsally. This forms its concave course. The symphysis is rectangular and small. The splenial facet reaches the level of the eighth tooth (counted from the anterior). The dental crest is tall. The lateral surface of the anterior portion of the dentary is pierced by four mental foramina. Specimen NHMW 2016/0028/0006 has a distinct, slightly wrinkled wedge-shaped facet for the coronoid process (Fig. 3g). This facet reaches the level of the sixth tooth (counted from the posterior). It becomes broader posteriorly as it runs in the dorsomedial region behind the tooth row.

Dentition The dentition is pleurodont with teeth high and bicuspid, although the mesial cusps in the first two preserved teeth are not so markedly developed. The lingual aspect of the tooth crowns has very fine vertical striations, and the tooth necks bulge slightly medially, with small interdental gaps.

Remarks

The morphology of the posterior dentary area and dentition differ from the above-described *Lacerta* cf. *poncenatensis* as follows: (1) the teeth are taller and more slender rather than low, (2) there are only small interdental gaps, and (3) the posterior region of the dentary is robust, with a posterior portion behind the tooth row. The morphology here more strongly resembles *Lacerta* sp. described from the Czech locality Dolnice (see Roček 1984: pl. IV, figs. 1–3). In addition, the teeth in specimen NHMW 2016/0028/0005 are clearly more slender and bicuspid than in specimen 0006, with the mesial cusp distinctly developed, well-separated from the dominant cusp by a small notch, and the main cusps more pointed rather than blunt. However, these differences can also be present in a single dentary, e.g., in *Lacerta viridis* (see, e.g., Kosma 2004: p. 36, fig. 39; Čerňanský et al. 2016a: fig. 8). These two specimens therefore most likely belong to the same taxon.

Lacertidae indet.

Figure 4a–e

Material and horizon Right frontal NHMW 2016/0028/0007; Oberdorf 4. Anterior portion of the right frontal NHMW 2016/0028/0008, parietal NHMW 2016/0028/0009; Oberdorf 3.

Description

Frontal The anterior portion and almost half the posterior portion of the right frontal bones are preserved as two distinct specimens. The anterior end of the frontal NHMW 2016/0028/0008 bears two elongated, unornamented oval surfaces that are separated by an anteroposteriorly elongated short central spur. The unornamented surfaces are the sutural facet for the nasal and facet for maxilla located laterally. The rest of the dorsal surface of the specimen is covered by the frontal osteodermal shield and small prefrontal shield. The specimen NHMW 2016/0028/0007, representing the posterior region, is long and slightly expanded posteroventrally. The preserved dorsal part is entirely covered by a partly preserved frontal shield and a posterior frontoparietal one. These are separated by the convex *sulcus interfacialis*, and are ornamented by densely spaced pits and small ridges. The frontoparietal suture interdigitation is well-developed and the entire contact is posterolaterally inclined. The internal region has a wide

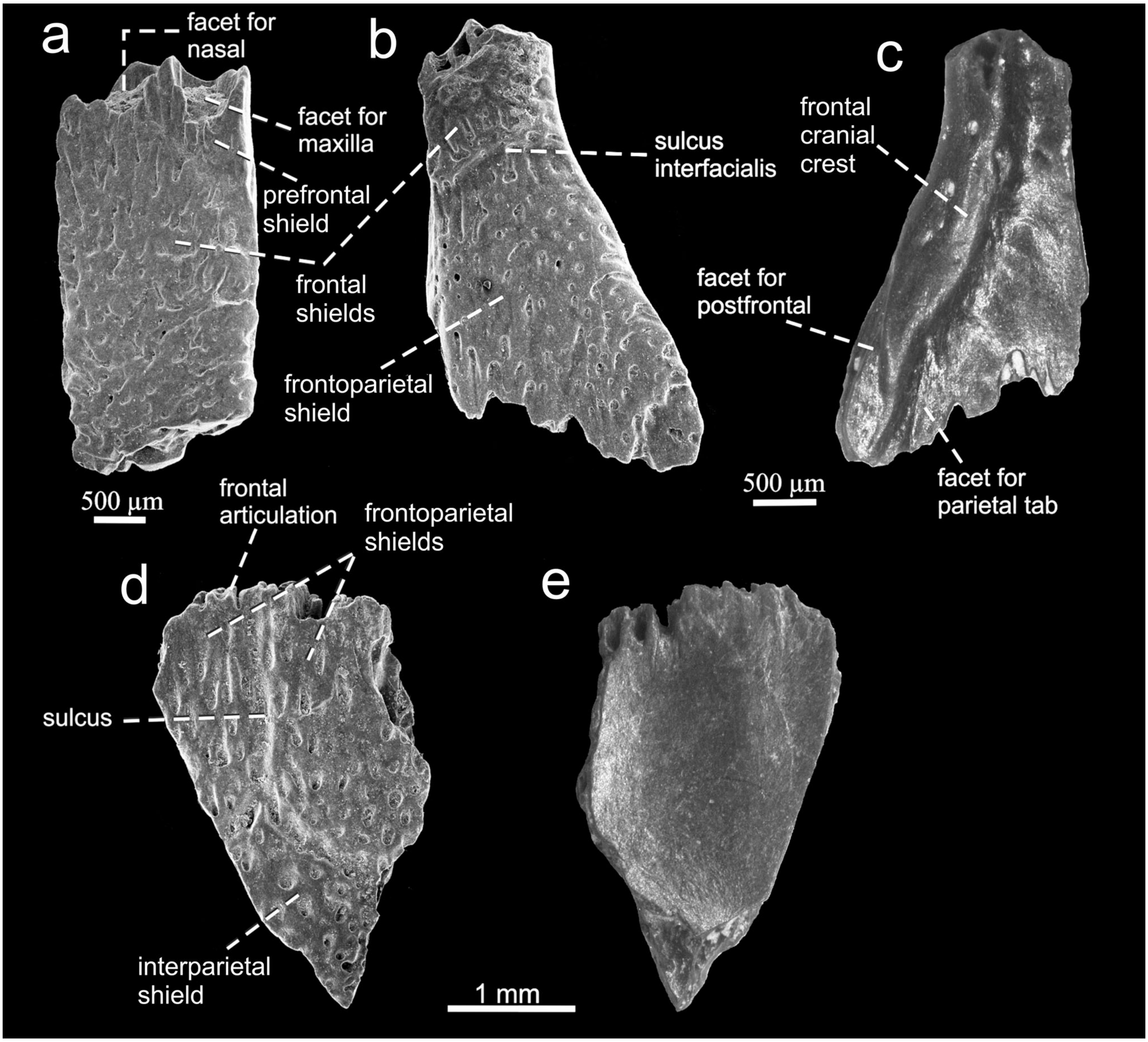

Fig. 4 Lacertidae indet.; right frontal NHMW 2016/0028/0008 in **a** external view. Right frontal NHMW 2016/0028/0007 in **b** external and **c** internal view; parietal NHMW 2016/0028/0009 in **d** external and (**e**) internal view

ridge on its lateral aspect (frontal cranial crest). The lateral surface of the ridge is pierced by two large rounded foramina located anteriorly and two smaller foramina located posteriorly. The posterior end of the ridge is thinner because the postfrontal facet is present here. A wedge-shaped facet for the parietal tab lies medial to the ridge.

Parietal An anterior fragment of the right portion of the parietal bone is preserved. Its dorsal surface has three osteodermal shields separated by a groove, which is shaped like an 'upside-down letter Y'. The interparietal shield is clearly restricted here, does not reach the frontal bone, and the ornamentation is almost identical to that of the frontal bone. However, the pits here differ by being more elongated on the periphery, so that the transition from pits to grooves is more visible. The internal surface is smooth.

Scincoidea Oppel, 1811
Scincidae Gray, 1825

? **Scincidae indet.**
Figure 5

Material and horizon Right frontal NHMW 2016/0028/00010; Oberdorf 3. Right postfrontal NHMW 2016/0028/0011, left postfrontal NHMW 2016/0028/0012, parietal NHMW 2016/0028/0013; Oberdorf 4.

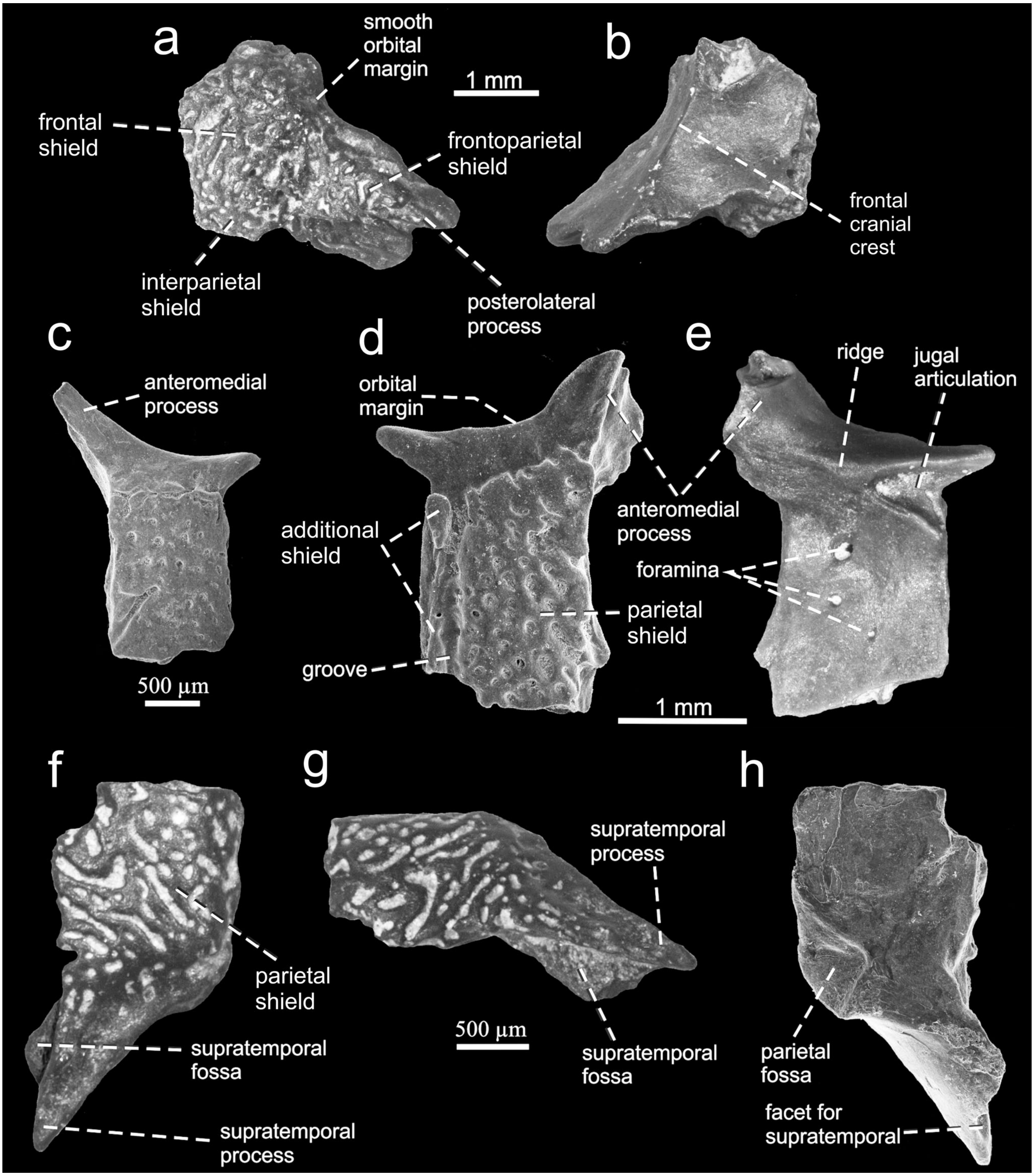

Fig. 5 ? Scincidae indet.; right frontal NHMW 2016/0028/00010 in **a** external and **b** internal view. Right postfrontal NHMW 2016/0028/0011 in **c** external view. Left prefrontal NHMW 2016/0028/0012 in **d** external and **e** internal views. Parietal NHMW 2016/0028/0013 in **f** external, **g** lateral and **h** internal view

Description

Frontal Only the posterior part of the right frontal bone is preserved. The long triangular posterolateral process, with its frontoparietal osteodermal shield, is distinctly laterally expanded. The anteromedial region is covered by the frontal shield, and the dorsal surface of both osteodermal shields is ornamented by irregular grooves and ridges. An interparietal shield with pit-ornamented dorsal surface is present in the posteromedial region, but its border with the frontal shield is faint. The osteodermal shields do not fully cover the frontal table, which is exposed laterally as a narrow area. The internal surface of the frontal has a ridge close to the lateral border, formed by the frontal cranial crest (the *crista cranii frontalis*). Its preserved lateral wall is distinctly sloped, pierced by three foramina.

Postfrontal Two postfrontal bones are preserved. They have different ontogenetic developmental stages, and the left is larger than the right. The description is based mainly on the larger left postfrontal. It is sub-rectangular and anteroposteriorly short, with anteroventral and anterodorsal expansions formed by the narrow, pointed jugal process and a broad and blunt anteromedial process. The latter process is long and narrower in the smaller specimen. The facet for the frontal bone is bordered laterally by a ridge. Further posteriorly, a long narrow facet for the parietal bone is present on the dorsomedial margin. The anterior margin of the bone is slightly concave, forming the posterodorsal border of the orbit. While a short area behind the orbit is exposed, the rest of the external surface is covered by two osteodermal shields, separated by a well-developed longitudinal groove. A large, dominant medial shield coincides with the parietal shield and occupies most of this region. Below this is a noodle-like element, dorsoventrally narrowed and anteroposteriorly elongated. The osteodermal shields are ornamented with pits of varied size, which form grooves on the periphery. The ornamentation is much less developed in the smaller specimen. The ornamentation has a form identical to the parietal described above.

The internal aspect is more robust anteriorly, where a ridge forms the slightly concave orbit border. This ridge is the dorsal continuation of the jugal medial ridge (sensu Čerňanský et al. 2014), and it has a triangular, wedge-shaped articulation for the jugal bone in its posteroventral section. The posteriorly located surface is flat, smooth and pierced by the following three foramina, which decrease in size posteriorly: (1) the anterior-most is largest and lies at the level of the upper third of the bone (postfrontal foramen sensu Gelnaw 2011), (2) the next is posterior to the first anterior foramen, and (3) the smallest lies outside the line of the others, on the mid-level bone area. While the posterior end of the larger specimen is broken off in its ventral section, the smaller specimen has its posterior portion divided into two parts by a shallow broad notch on the ventrolateral aspect of the bone.

Parietal The parietal consists of the parietal plate with ornamented surface and two posterolaterally divergent supratemporal processes. Unfortunately, only the left posterior region is preserved. The parietal table is completely covered by an osteodermal shield, most likely representing a parietal shield, and the occipital shield appears to be absent. Its ornamentation is different-sized pits and relatively anterolaterally oriented grooves. The supratemporal process is incompletely preserved, and the lateral view reveals ~140° posteroventral inclined contact with the parietal table. The process has a shallow depression on its posterodorsal surface. On the ventrolateral aspect is located the supratemporal fossa for parietal-temporal muscle attachment (see Gauthier 1982; Gauthier et al. 2012). The fossa reaches only the base of the supratemporal process and is not exposed anteriorly on the parietal table. The internal surface has a partly preserved parietal fossa and mirror symmetry suggesting that the complete fossa was most likely rhomboidal. A sharp ventrolateral ridge runs from the posterior of the fossa to the ventrolateral region of the supratemporal process, and the ventral aspect of this ridge has a small, partially preserved facet for the supratemporal.

Remarks

All cranial elements here are allocated to the same taxon, based on identical osteodermal shield ornamentation. Based on the preserved portion of the parietal, the occipital shield appears to be absent. Such a character state is almost the rule in non-lacertid scincomorphans (Borsuk-Białynicka et al. 1999). Moreover, the type of fossa formation for parietal-temporal muscle attachment, as present here, is observed in some members of the Scincidae clade, e.g., in *Brachymeles gracilis* + *Amphiglossus splendidus* + *Acontias percivali* + *Feylinia polylepis*, but absent in, e.g., *Cordylus*, *Zonosaurus*, *Lacerta* and *Pseudopus* (see Gauthier et al. 2012).

The frontal bone has no obvious facet for the parietal tab, which is uniformly present in lacertiforms and xantusiids. Although some cordylids and scincids may also have this facet, it is usually absent (see Estes et al. 1988). The interparietal shield appears to reach the frontal bone in its posteromedial region.

The postfrontal described here has an ornamented osteodermal shield attached to the external surface. The narrow, anteroposteriorly elongated additional shield indicates possible fusion of the postorbital and postfrontal. In addition, the osteodermal shield attached to the postfrontal is absent in Anguinae but present in Scincoidea, and also seen in Lacertidae (as for lacertiforms, not in teiids). The postfrontal is anteroposteriorly shorter than in lacertids, where it closes the supratemporal fenestra, and Estes et al. (1988) classify this feature as lacertid synapomorphy. The Oberdorf taxon supratemporal fenestra was most likely restricted only by the postfrontal. This condition is present in many scincids, where a temporal arch is present. In cordylids, the supratemporal fenestra is limited primarily

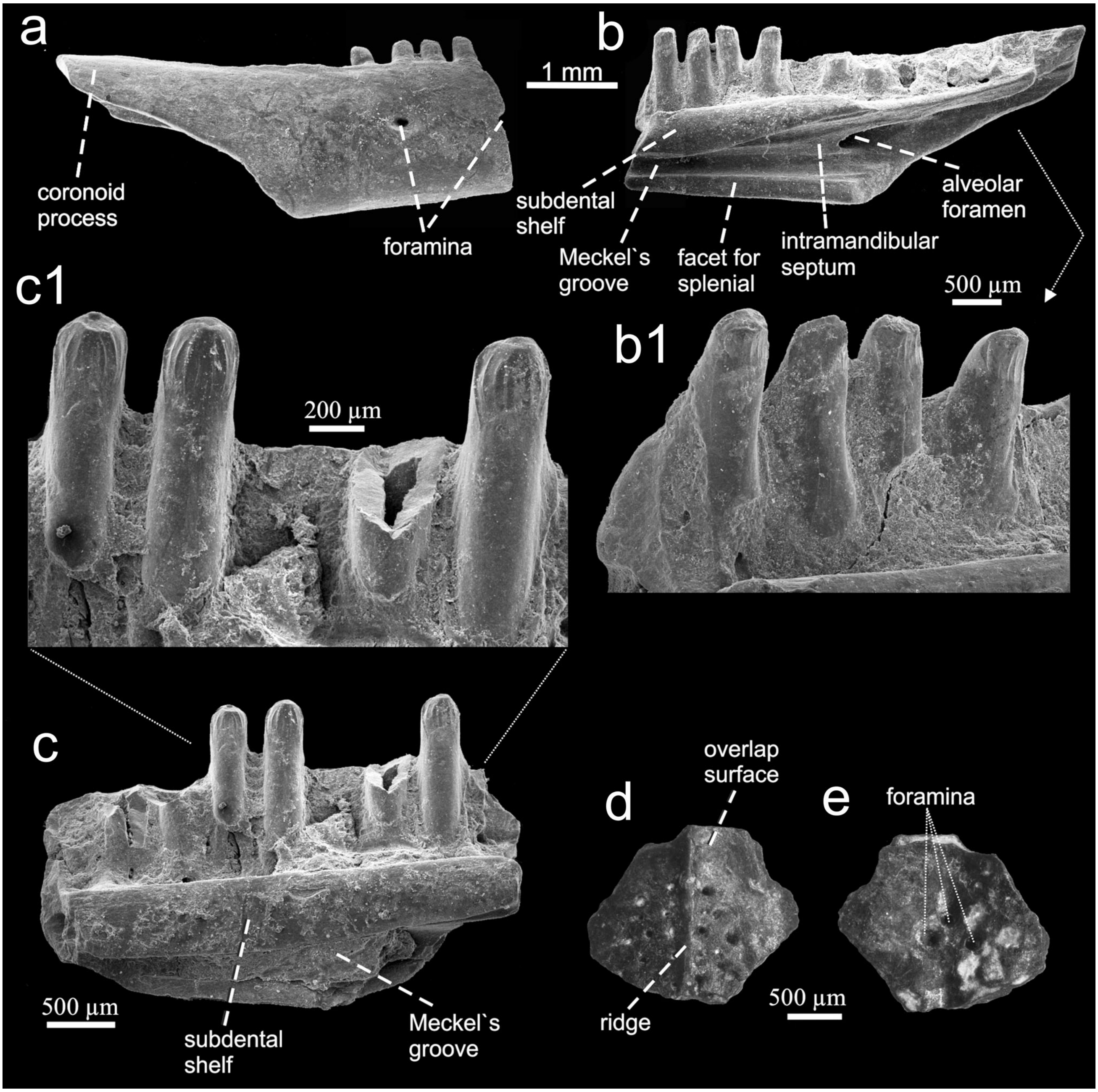

Fig. 6 Cordylidae indet.; right dentary NHMW 2016/0028/0014 in **a** lateral and **b** medial view, with **b1** detail of teeth in anteromedial view. Right dentary NHMW 2016/0028/0015 in **c** medial view with detail of teeth **c1**. ? Cordyliformes indet.; body osteoderm NHMW 2016/0028/0016 in **d** external and **e** internal view

by the postorbital (see Estes et al. 1988). In conclusion, all these characters indicate Scincidae affinity.

Cordyliformes Fitzinger, 1826
Cordylidae Mertens, 1937

Cordylidae indet.
Figure 6a–c

Material and horizon Posterior portion of the right dentary NHMW 2016/0028/0014; Oberdorf 4. Right dentary NHMW 2016/0028/0015; Oberdorf 03.

Description

Dentary The dentary is a slender, anteroposteriorly elongated bone with the ventral crest running a straight course. Meckel's groove is open but narrow. The opening of the alveolar canal is located at the level between the seventh and sixth tooth positions (counted from the posterior). It is separated from Meckel's groove medioventrally by the intramandibular septum. The subdental shelf is robust and dorsoventrally thick, but it is markedly less distinctive at the level of the alveolar canal opening. It has a dental sulcus on its dorsal aspect and a facet for splenial in the medial section of the ventral margin of the bone. The ventral ending of the bone is broken. Specimen NHMW 2016/0028/0014 has 12 tooth positions (four teeth present in the anterior section), and specimen NHMW 2016/0028/0015 has nine tooth positions, with three attached teeth. The dental crest supports teeth laterally to approximately half their height. The posterior end of the dentary runs to a slightly dorsally raised coronoid process.

One mental foramen and half of another are preserved in the mid-region of the bone, and these pierce the smooth surface of the lateral aspect. The posterior one lies between the ninth and tenth tooth positions, and the anterior is between the 12th and 13th positions.

Dentition The dentition is pleurodont. In the medial aspect, the tooth crowns have a larger, labial blunt edge, forming a labial cusp, and a smaller, medially located sharper, more pointed lingual cusp. The lingual aspect of the crown is bordered by the *culmen lateralis anterior* and *culmen lateralis posterior* (terms after Richter 1994). This region has six diverged striae which incline mesially and distally in the ventral direction. The tooth necks appear relatively swollen on the lingual aspect.

Remarks

The tooth morphology as it is present here, the straight ventral margin and open Meckel's groove, are characters considered suggestive of cordylid affinity (see, e.g., Lang 1991; Folie et al. 2005; Augé and Smith 2009). The preserved portion of the dentary resembles the Merkur-North material (MN 3) described by Čerňanský (2012) from the Czech Republic as aff. *Palaeocordylus bohemicus*. Unfortunately, the tooth crowns of this specimen are poorly preserved. While the Merkur material is the oldest occurrence of this clade from the Neogene of Europe, several other cordyloids have been described there from the Miocene. In addition, *Palaeocordylus bohemicus* from Dolnice in the Czech Republic (MN 4; Roček 1984) is similar in age to the Oberdorf specimen. There is also material from Petersbuch 2 described by Kosma (2004) as a new taxon, *Bavaricordylus*. Since this name was used only in an unpublished thesis, it is not valid (Čerňanský 2012). Petersbuch 2 material differs from material described here in (1) having a much higher number of tooth crown striae, with 20 present on the lingual aspect, and (2) the prominent *culmen lateralis anterior* and *posterior* (terms after Richter 1994) that reach much more ventrally.

Böhme (2010) also described material from Puttenhausen B which differs from Oberdorf material in also having more striae—the crown lingual aspects have up to 12 striations—and Böhme (2002) further interpreted fragments from the Korneuburg Basin (middle Miocene of Austria) as Cordylidae; however, detailed revision is required before accepting this assignment.

? **Cordyliformes indet.**

Figure 6d, e

Material and horizon Osteoderm NHMW 2016/0028/0016; Oberdorf 4.

Description

Osteoderm The incompletely preserved osteoderm is flat but thicker than anguid osteoderms (see below). A low medial ridge runs along the entire external portion. The anterior gliding surface is short and has no distinct border with the posterior ornamented section. The ornamentation consists of regularly distributed pits. The relatively smooth internal surface is pierced by three large foramina in the central region, and this region also bears a shallow groove which is more pronounced posteriorly.

Scincoidea indet.

Figure 7

Material and horizon Right maxilla NHMW 2016/0028/0017, anterior region of the left dentary NHMW 2016/0028/0018; Oberdorf 4. Left dentary NHMW 2016/0028/0019; Oberdorf 03.

Description

Maxilla Only a fragment of the right maxilla is preserved. It has six teeth attached. The external surface is pierced by two labial foramina.

Dentary Description is based on two dentary fragments, which are very poorly preserved. The dental crest of the largest specimen NHMW 2016/0028/0018 has eight teeth. Meckel's groove is narrow, but fully open even in the anterior end, and it mainly runs ventrally. It is roofed by a robust subdental shelf that is slightly elevated dorsally near the symphysis. The external surface of the fragment is pierced by large mental foramina.

Dentition The dentition is pleurodont. Teeth are closely distributed. The crowns have typically blunt labial and lingual cusps, and lingual aspects have striation restricted between the *culmen lateralis anterior* and *posterior*. The maxillary portion has five crown striae in all teeth except the last. The last tooth has seven striae, and dentary crowns have 7–8. These differences can indicate specimens from different-aged individuals. Meanwhile, the mesial and distal borders have no ventral contact; the crowns are slightly curved lingually and the tooth necks are slightly swollen.

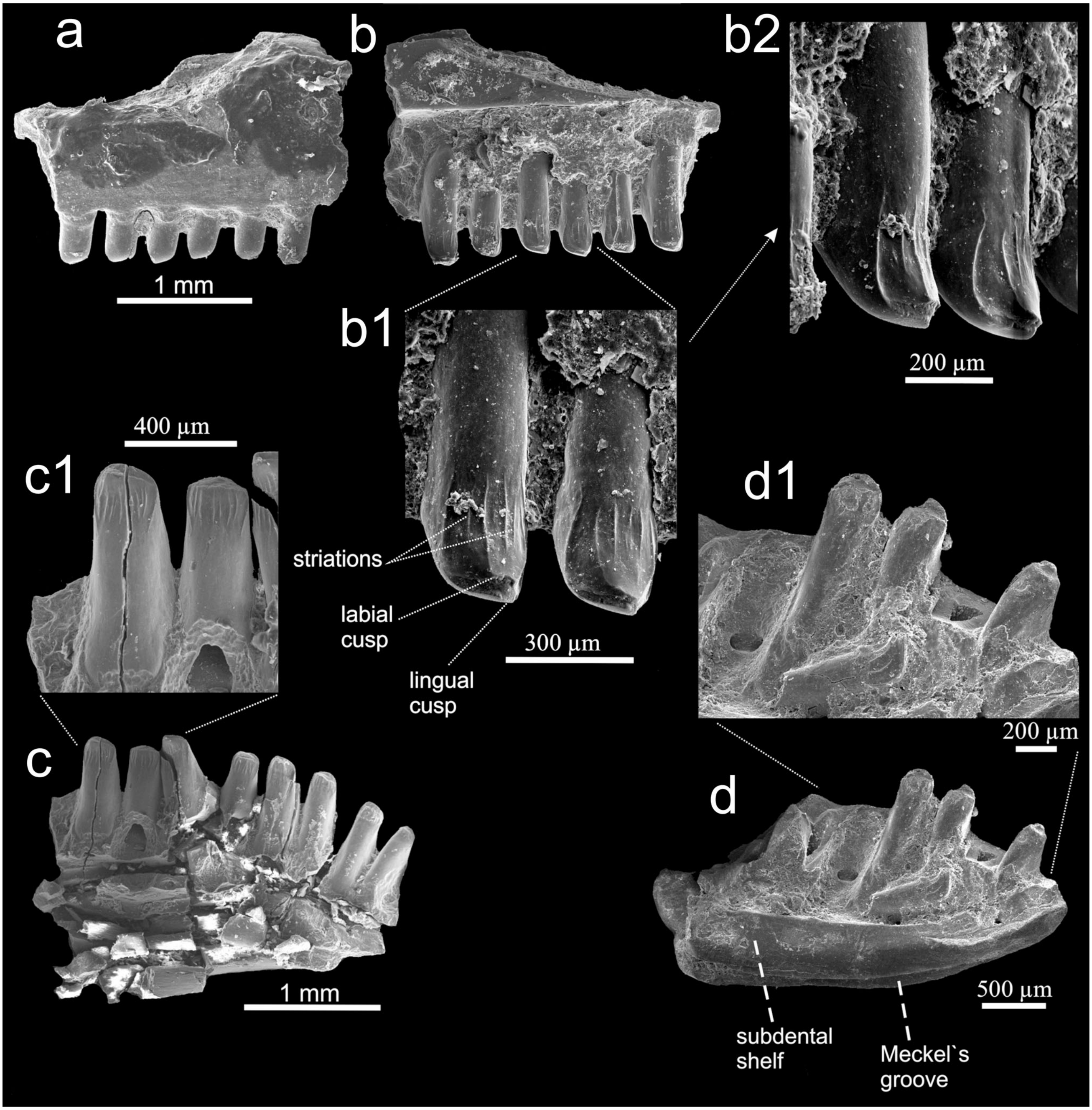

Fig. 7 Scincoidea indet.; right maxilla NHMW 2016/0028/0017 in **a** lateral and **b** medial view, with detail of teeth in **b1** medial and **b2** anteromedial view. Left dentary NHMW 2016/0028/0019 in **c** medial view with detail of teeth in **c1** medial view. Left dentary NHMW 2016/0028/0018 in **d** medial view with detail of teeth **d1**

Remarks

While allocation of the described material to the Scincoidea clade is indisputable, family level interpretation is questionable because of the fragmentary nature of the preserved elements. The tooth crown striations of the specimen are considered scincid rather than cordylid, because striations are less complex, and the lingual striae are almost parallel as in scincids. Precise determination is not possible, because some extant cordylids also have similar patterns in their tooth crown morphology (Kosma; pers. comm. 2016). Moreover, the importance of ontogenetic and individual variability in this case remains unknown. Meckel's groove is narrow, but fully open even in the anterior region of the dentary, while closure is a general tendency in many Scincidae, including *Acontias*, *Egernia* and *Mabuya* (see Kosma 2004), as well as in *Eutropis* (pers. observ. 2016). Although this is different from cordylids, which all have an open Meckel's groove (Augé and Smith 2009), nothing is certain, because the scincids *Eumeces schneideri* (pers. observ. 2016) and *Chalcides* have a fully open Meckel's groove, and it is partly closed in *C. ocellatus* and *C. mionecton* (see Caputo 2004). Therefore, this material is attributed to Scincoidea without family specification.

The dentition of the specimens from Oberdorf is similar to material described from the Bavarian Freshwater-molasse. Kosma (2004) described this as "*Bavariascincus mabuyaformis*", tentatively allocated to Scincidae, and he correctly recognized that this tooth morphology strongly resembles that in many extant skink, including *Emoia* and *Mabuya*. Kosma (2004) considers that this indicates ecotype more than taxonomic value.

Anguimorpha Fürbringer, 1900
Anguidae Gray, 1825
Anguinae Gray, 1825
Ophisaurus Daudin, 1803

Type species Ophisaurus ventralis (Linnaeus, 1766)

Ophisaurus* cf. *spinari Klembara, 1979
Figure 8

Material and horizon Two parietal fragments NHMW 2016/0028/0020-21; Oberdorf 4.

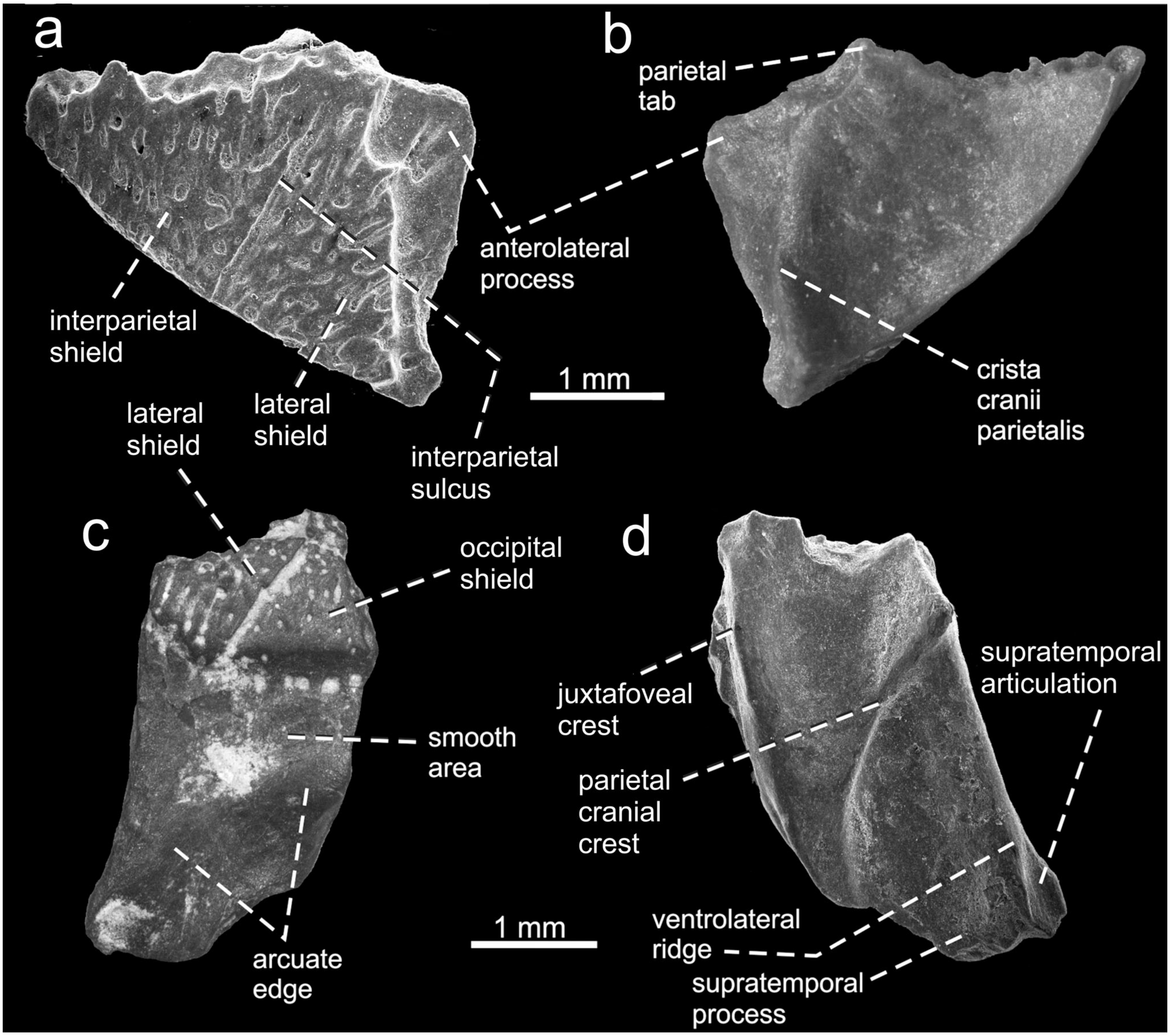

Fig. 8 *Ophisaurus* cf. *spinari*; the anterolateral right corner of the parietal NHMW 2016/0028/0020 in **a** external and **b** internal view, posterolateral left portion of the parietal NHMW 2016/0028/0021 in **c** external and **d** internal view

Description

Parietal Description is based on two fragments. The first is a right portion of the anterior region where the parietal table is covered by interparietal and lateral osteodermal shields. These are separated by a straight groove (the *sulcus interparietalis*) which runs anterolaterally to the end of the ornamented section of the parietal fragment. The ornamentation consists of pits, ridges and grooves. The anterolateral corner of the parietal table is exposed and forms a short anterolateral process (sensu Klembara 2015). The parietal internal surface is smooth, with the anterior section of the parietal cranial crest rising and then becoming ventrally deeper in the posterior direction.

The second fragment is a left parietal posterior portion, with a clear trapezoidal occipital shield. The posterior end of the interparietal shield is anterior to the occipital shield, and the lateral shield (sensu Klembara 2015) is partially preserved on the left aspect. The osteodermal shields are ornamented with pits of varied size and short grooves. A smooth area of the parietal table with a fine arcuate border is exposed posteriorly, and it is slightly anteroposteriorly longer than the anteroposterior length of the occipital shield. Only the anterior broad base of the supratemporal process is preserved. In the internal aspect, the lateral margin of the process is bordered by a ventrolateral ridge bearing the supratemporal facet. A slightly rounded, posteromedially curved portion of the parietal cranial crest is recognizable on the internal aspect. A triangular depression medial to this crest is bordered medially by the low juxtafoveal crest.

Remarks

Both fragments are allocated to the same taxon based on morphology and ornamentation. The preserved parietal portion is identical to that of *Ophisaurus spinari* from Dolnice (Klembara 1979; Roček 1984) in the following features: (1) the *sulcus interparietalis* runs to the anterolateral corner of the ornamented region, rather than ending medially to the corner, and (2) the course of the posterior section of the parietal cranial crest is not straight, but curves posteromedially. However, because of the fragmentary nature of the Oberdorf material, its precise allocation at species level must be met with caution.

Ophisaurus sp.
Figure 9a–i

Material and horizon Frontal NHMW 2016/0028/0022, dentary 2016/0028/0023; six dorsal vertebrae 2016/0028/0024-29, Oberdorf 4.

Description

Frontal The left frontal is largely preserved, with only the anterior portion broken off. It is anteroposteriorly elongated, with a concave lateral margin and a laterally expanded posterolateral corner forming a well-defined posterolateral process. The rectangular-shaped frontal osteodermal shield has irregular borders, and covers most of the dorsal region but not the most lateral area, thus leaving the lateral smooth margin of the frontal table exposed. The shield has pit, ridge and groove ornamentation. The grooves and ridges are oriented almost from the central region of the shield, being strong in the central area but less distinct anteriorly. Although the frontoparietal osteodermal shield is missing, the straight edge of the frontal shield indicates its former presence as a small element located in the posterolateral corner of the frontal table. The frontoparietal shield reached less anteriorly than the facet for the postfrontal bone located on the posterolateral edge of the frontal.

The internal surface is relatively smooth and bordered laterally by a broad frontal cranial crest. The oval facet for the parietal tab is anteroposteriorly short, mediolaterally broad, and located on the posterior edge of the frontal, medial to the cranial crest.

Dentary The posterior region of the right dentary is preserved. It is a slender bone with a shallow subdental shelf and ventromedial opening of Meckel's groove. The short splenial spine is located at the level between the fourth and fifth tooth from the rear, forming the anterodorsal margin of the splenial anterior inferior alveolar foramen. The lenticular facet for the splenial is located posterior to this on the medial margin of the subdental shelf. Further posteriorly, the facet for the coronoid becomes posterodorsally broader. These two facets are separated by a small ridge at the level of the last tooth. The rounded opening for the alveolar canal is at the second–third tooth level and medially separated from Meckel's groove by the intramandibular septum. Only a very short part of its ventral portion is free. The surangular spine lies more posterior, but only the base is preserved. The end of the dentary is divided into the small triangular coronoid process and the ventrally located, larger and blunt surangular process, which projects further posteriorly. The preserved portion of the right dental crest supports nine tooth positions, with four teeth still attached. The external dentary surface is pierced by four mental foramina, located in the mid-line.

Dorsal vertebrae Several robust dorsal vertebrae are preserved in the Oberdorf material. Lateral view indicates that the neural spine runs along the entire length of the dorsal region of the neural arch, and rises posterodorsally into the trapezoidal structure. Unfortunately, its dorsal end is broken off. The pentagonal neural canal is tall, wider anteriorly than posteriorly. Pre- and post-zygapophyseal

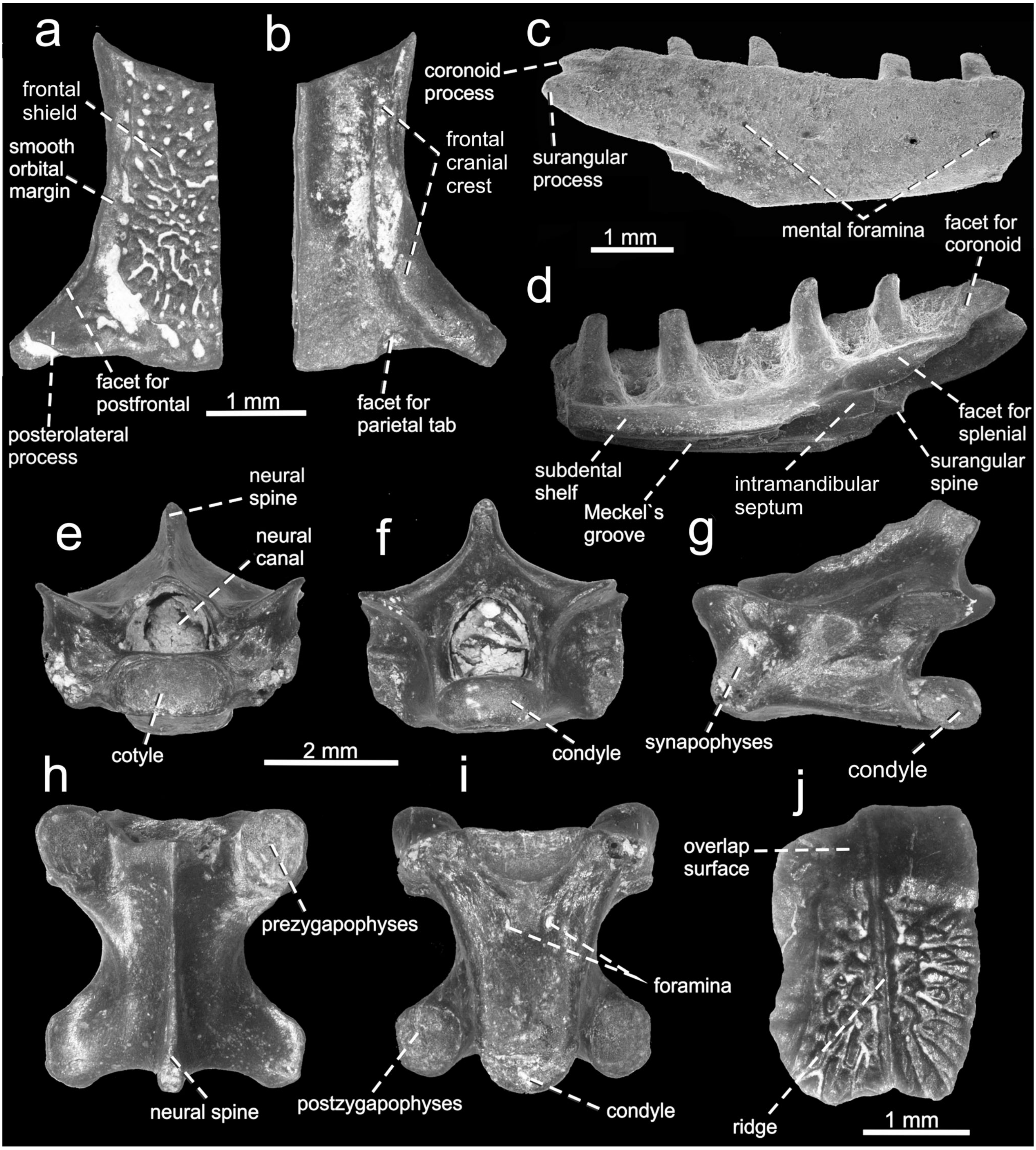

Fig. 9 *Ophisaurus* sp.; left frontal NHMW 2016/0028/0022 in **a** external and **b** internal view. Right dentary 2016/0028/0023 in **c** lateral and **d** medial view. Dorsal vertebrae 2016/0028/0024 in **e** anterior, **f** posterior, **g** lateral, **h** dorsal and **i** ventral view. Anguidae indet., osteoderm NHMW 2016/0028/0030 in **j** external view

articulation surfaces are well-rounded, expanded laterally. The inter-zygapophyseal constriction is strongly expressed. The anterior region of the lateral aspect has slightly posterodorsally inclined elliptical synapophyses. The vertebra is very broad here. The vertebral centrum is slightly anteroposteriorly elongated but gradually narrows posteriorly. Its ventral region is flat, with two foramina in the anterior quarter of the centrum. The subcentral ridges forming the lateral central margins are slightly concave. Both cotyle and condyle are strongly depressed.

Remarks

The described concave lateral walls (subcentral ridges) represent a typical character state for *Ophisaurus*. This is in contrast to the straight lateral walls in *Pseudopus* adults, or to the almost parallel walls with a slight constriction immediately posterior to the subcentral foramina as it is present in *Anguis* (Klembara 1981; fig. 3). The neural canal is taller than the cotyle in the vertebrae described here. In contrast, the reverse is true in *Pseudopus* (see Čerňanský et al. 2016b). The vertebrae described herein are therefore very similar to those of cf. *Ophisaurus* sp. (Morphotype I) described from the MN 4 Early Miocene of Dolnice (Roček 1984).

It is possible that material allocated here to *Ophisaurus* sp. belongs to the same taxon as the parietal described as from *O.* cf. *spinari*. Although this is supported by similar frontal osteodermal shield ornamentation, complete material is required for certainty.

Anguidae indet.

Figure 9j

Material and horizon Three osteoderms NHMW 2016/0028/0030-32, Oberdorf 3 and 4.

Description

Osteoderms Osteoderms are slender, rectangular elements, with a low medial ridge running along their entire central regions. The anterior overlap surface occupies almost a third of the external surface, and the lateral bevel is highest close to the gliding surface. The posterior section is ornamented with short grooves, bulges and ridges diverging from the central region. The central part of the internal surface has several small pits and foramina, and also a shallow groove which is more pronounced in the posterior section.

Remarks

This morphology corresponds to *Ophisaurus*, but it lacks distinctive synapomorphy for certainty, and therefore alternative allocation cannot be excluded.

Squamata indet. 1

Figure 10

Material and horizon Right nasal NHMW 2016/0028/0033 (O4), two left frontals NHMW 2016/0028/0034-35; Oberdorf 4. Two right frontals NHMW 2016/0028/0036-37; Oberdorf 3.

Description

Nasal The right nasal bone is preserved. This is roughly rhomboidal, wider anteriorly, and its external aspect has a shallow depression in the posterior mid-region. The external surface has ornamentation of isolated but close island-like structures which vary in shape and size. The anterior region protrudes into a short blunt medial process. The internal surface is slightly convex dorsally in cross-section, with a ventral bent in the lateral portion. The facet for the maxilla is present here. Unfortunately, it is unclear whether the prefrontal reached the nasal or if such a contact was excluded by maxilla-frontal contact. A short facet for the nasal process of the premaxilla is present in the anterior part of the medial margin. It does not extend far posteriorly, and the huge facet for the frontal bone forms almost a third of the internal posterior surface. The remaining two-thirds of the nasal are smooth.

Frontal Four frontals are preserved. These are in different ontogenetic stages, most likely early juvenile, late juvenile and two adults. Description here is based mainly on specimen NHMW 2016/0028/0037 (see Fig. 10e–g); it depicts this almost complete right frontal which is boot-shaped and anteroposteriorly elongated with a slightly expanded posterolateral corner. Unfortunately, the anterior portion of the mid-region in front of the subolfactory process is broken off. In the dorsal aspect, the lateral margin is concave. While the dorsal surface is covered by osteodermal shields, the lateral and posterior regions of the frontal table are exposed, with the lateral area sloping slightly ventrally. The *sulcus interfacialis* forms the border between the frontal and frontoparietal shields, and this groove is only shallowly developed, almost straight and posteromedially oriented. The osteodermal shields are strongly ornamented with pits, grooves and wormy ridges on the frontoparietal shield, while the frontal shield is relatively fragmented with close but isolated island-like structures of varied shape and size. This ornamentation is also identical on the nasal bone. While the contact with the parietal is almost straight in dorsal aspect, the lateral frontal margin has wedge-shaped facets for the postfrontal and a distinctly larger one for the prefrontal. These facets do not contact each other, and therefore the frontal has a free lateral margin, which forms part of the dorsal border of the orbit.

The ventral aspect of the frontal has a frontal cranial crest forming a well-developed ridge along its entire lateral aspect. It is steeply sloped on both sides, and the lateral slope has a round foramen in its mid-region. The ridge is deflected ventrally to form the subolfactory process slightly in front of the posterior end of the prefrontal facet. Unfortunately, the end of the process is broken off. The internal surface, located medially to the cranial crest, has several mediolaterally oriented grooves and is pierced by several small foramina. The contact with the parietal on the ventral aspect has a wave-like surface, and the facet for the parietal tab appears to be very small.

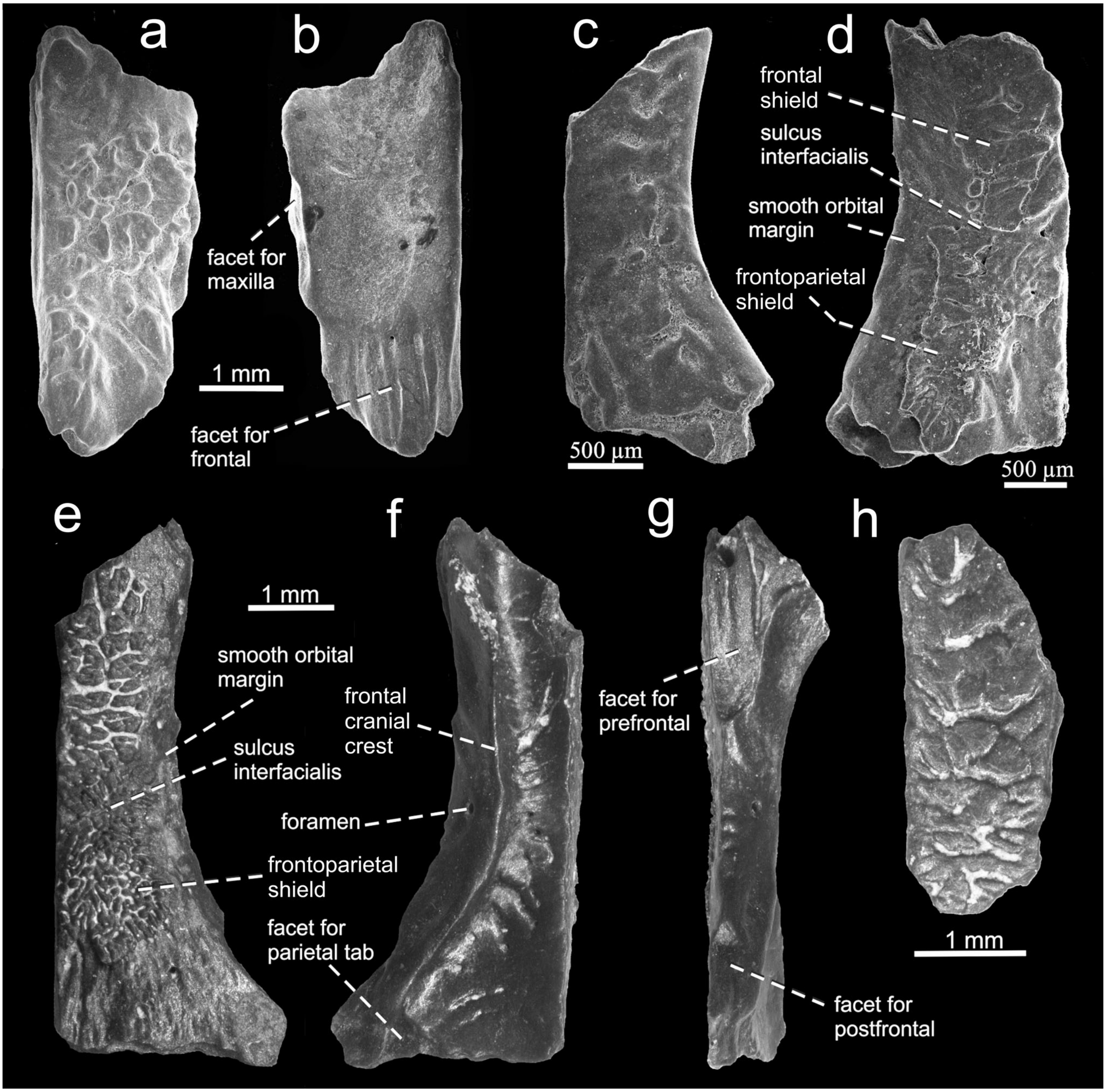

Fig. 10 Squamata indet. 1; right nasal NHMW 2016/0028/0033 in **a** external and **b** internal view. Right frontal NHMW 2016/0028/0036 in **c** external view. Left frontal NHMW 2016/0028/0034 in **d** external view. Right frontal NHMW 2016/0028/0037 in **e** external, **f** internal and **g** lateral view. Anterior region of left frontal NHMW 2016/0028/0035 in **h** external view

Remarks

The frontal ornamentation is similar to that in the extant scincids *Eumeces* and *Amphiglossus* (Digimorph 2002–2012), but a change in ornamentation character of the osteodermal shields of frontal can be observed in the lacertid *Dalmatolacerta oxycephala* as well (see Rauscher 1992: p. 119, fig. 21-1). The following differences are also noted: (1) the posterior margin of the frontal in *Dalmatolacerta* and other lacertids is not straight but has strong interdigitation, and (2) lacertid osteodermal shields completely cover the frontal table. They reach the lateral margin, so there is no frontal table exposure or ventral sloping. While the condition of the Oberdorf specimen precludes certainty that the interparietal shield reaches the frontal bone, the Oberdorf nasal and frontal morphology indicates affinity to scincids or cordyliforms. It is also important to note that the general morphology slightly resembles that of members of the Anguidae clade, but there are distinguishing features. For example, the groove

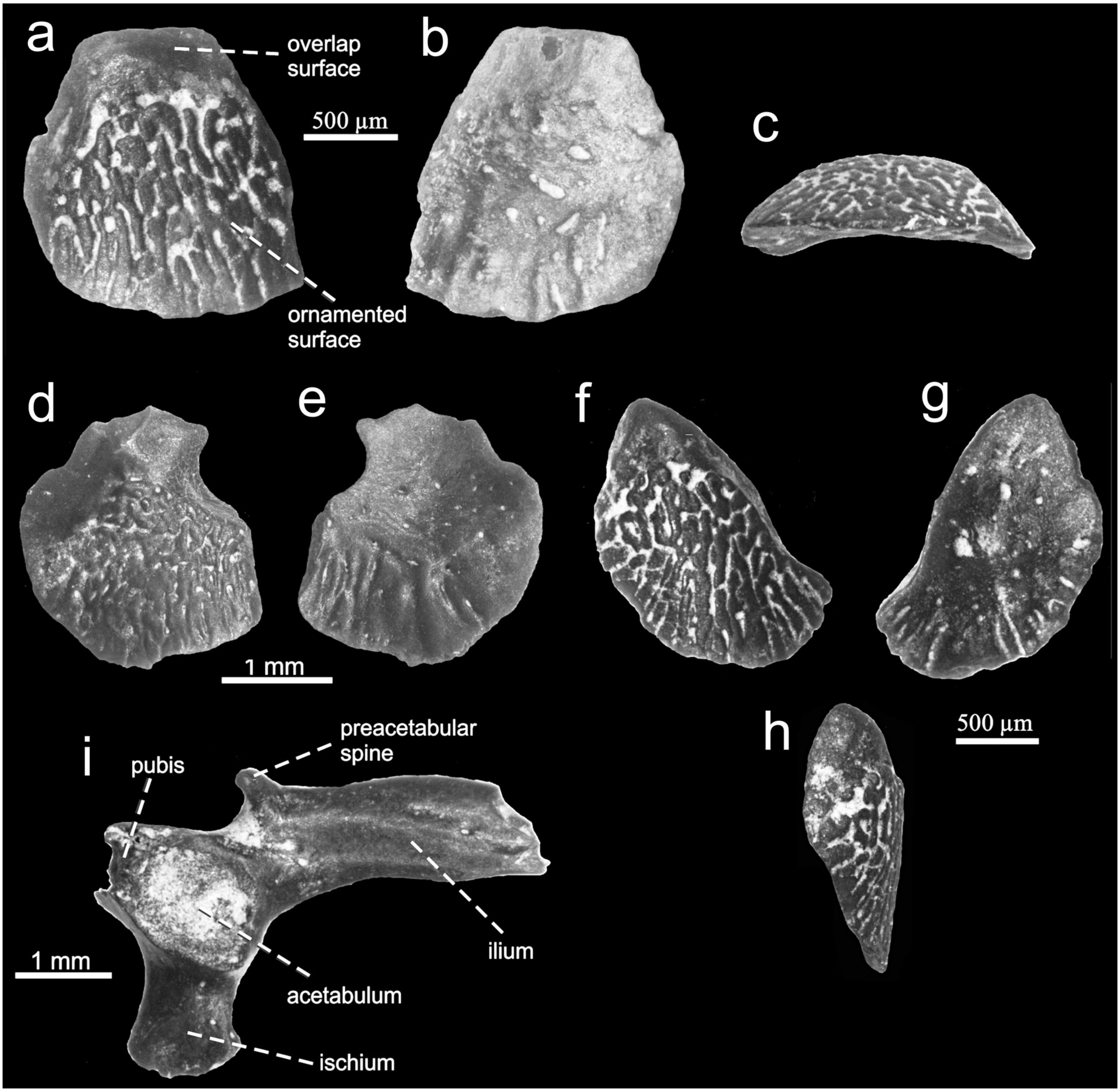

Fig. 11 Squamata indet. 2; osteoderm NHMW 2016/0028/0038 in **a** external, **b** internal and **c** posterior view. Osteoderm NHMW 2016/0028/0039 in **d** external and **e** internal view. Osteoderm NHMW 2016/0028/0040 in **f** external, **g** internal and **h** lateral view. Squamata indet. 3; right pelvis NHMW 2016/0028/0041 in **i** lateral view

separating the large frontal shield from the small posterolateral portion of the frontoparietal shield in Anguidae is located much more posteriorly than in the Oberdorf frontals. Moreover, this groove is strongly curved posteriorly and does not reach the medial margin of the frontal (see, e.g., Klembara 2015; fig. 1). In any case, the material is described here only as Squamata indet.

Squamata indet. 2

Figure 11a–h

Material and horizon Three osteoderms NHMW 2016/0028/0038-40, Oberdorf 3 and 4.

Description

Osteoderm 1 The osteoderm is roughly trapezoidal in shape, with slight external bulging, giving a convex appearance in cross-section. While the anterior overlap surface is short, occupying only a quarter of the external surface, the posterior section has an ornamentation which diverges from the anterior region to run relatively posteriorly. The ornamentation begins with tubercles and then has ridges and grooves. The medial ridge is absent. The lateral bevel has a straight medial margin and a convex lateral one. The internal aspect of the osteoderm has several irregularly distributed pits, foramina, and a few grooves near the posterior end.

Osteoderms 2 and 3 The osteoderms are irregular in shape. Their ornamentation is similar to that of osteoderm 1, and both osteoderms 2 and 3 have irregular overlapping surfaces.

Remarks

These body osteoderms differ dramatically from the flat anguid (possibly *Ophisaurus*) osteoderms described above. The major distinguishing features are the external bulging in the central portion, sloped lateral areas, and irregular overlapping surfaces in the second and third osteoderms. The body topology also plays a major role. Irregular overlapping type is often present on the limbs. This could suggest that these osteoderms belong to animals with limbs rather than to a limbless form. While this osteoderm ornamentation resembles that in cranial material allocated to ? Scincidae indet., complete material is required for certain attribution.

Squamata indet. 3

Figure 11i

Material and horizon The right pelvis NHMW 2016/0028/0041, Oberdorf 3.

Description

Pelvis The pelvis is partially preserved. Only the posterior portion of the elongated ilium can be studied, because the rest is broken off and missing. This is an anterodorso-posteroventrally broad element, with its anterodorsal margin forming a sharp crest. The proximal section has a blunt, short triangular pre-acetabular spine. The ilium has a small foramen on the lateral aspect, slightly posterior to the spine. The elliptical acetabulum is large. The ischium is also partly preserved, and only the base of the pubis is present. This base forms part of the anterior region of the acetabulum.

Remarks

The pre-acetabular spine is present in Lacertidae, Gymnophthalmidae, *Cordylus*, *Broadleysaurus* and *Heloderma* (Gauthier et al. 2012; pers. observ. 2016), but absent in Chamaeleonidae. This pelvis can be only tentatively ascribed to “scincomorphan”.

Discussion

Faunal composition

Although the Oberdorf material is only fragmentarily preserved, it provides important information on the palaeobiodiversity and spatial distribution of lizard taxa in the Early Miocene. The Oberdorf locality presents material from the M4 interval between Petersbuch 2 (Germany; MN4a), Dolnice 1, 2 (Czech Republic; MN4a), and the MN 4b localities including Forsthart, Rembach and Rauscheröd in Germany (see Daxner-Höck 1998). The following six major lizard clades are present or likely present in Oberdorf: Gekkota, ? Chamaeleonidae, Lacertidae, ? Scincidae, Cordylidae and Anguidae. The palaeobiodiversity in Oberdorf is lower than in Dolnice. Although the chamaeleonid clade is well-documented in other MN 4 Central European localities (Moody and Roček 1980; Čerňanský 2010a, 2011), the present data indicate that it is rare in Oberdorf, where Scincoidea clade members represent an abundant component of the fauna. In addition, the anguine fauna from Dolnice contains *Anguis* sp., *Pseudopus ahnikoviensis* and at least three *Ophisaurus* taxa (Table 1), *O. fejfari*, *O. spinari* and *O. robustus* (Klembara 1979, 1981, 2012, 2015; Roček 1984). In contrast, only *O.* cf. *spinari* is identified in the Oberdorf material. From Petersbuch 2, Klembara et al. (2010) identified *Pseudopus laurillardi*. Although Böhme (2002) mentioned the occurrence of *O. fejfari* in Petersbuch 2, no *Ophisaurus* material has been officially published at the time of writing this article. As for Lacertidae, several types are reported from Dolnice—the *Lacerta viridis* group (Čerňanský 2010b), *Lacerta* sp., *Miolacerta* and the amblyodont form *Amblyolacerta* (Roček 1984)—but only *Lacerta* cf. *poncenatensis* and *Lacerta* sp. have been identified in Oberdorf. Finally, the faunal composition of the Oberdorf locality is an interesting mix of Dolnice taxa (*Ophisaurus* cf. *spinari*, a similar cordylid morphotype, and *Lacerta*) and those from Petersbuch 2 (?Scincidae).

Palaeoecological comments

Differences in fauna composition here are explained by the different local environments, which have a huge impact on ectothermic vertebrate animals. The German localities and Dolnice in the Cheb Basin represented more or less inland environments, while Oberdorf was much closer to the Central Meso-Paratethys sea. Ebner and Stingl (1998) identified the Styrian basin deposits as paleogeographically

Table 1 List of taxa examined from Oberdorf, Dolnice and Petersbuch 2 (based on Klembara 1979, 1981, 2012; Klembara et al. 2010; Roček 1984; Kosma 2004; Čerňanský 2010a, b, 2011)

	Oberdorf (Styrian basin)	Dolnice (Cheb basin)	Petersbuch 2 (Bavarian basin)
Gekkota	Gekkota indet.	–	?
Chamaeleonidae	?	*Chamaeleo andrusovi*	?
	Chamaeleonidae indet.	Two dentary morphotypes	Chamaeleonidae indet.
Lacertidae	*Lacerta* cf. *poncenatensis*	–	
	Lacerta sp.	*Lacerta* sp.	?
		Lacerta viridis group	
	–	*Amblyolacerta dolnicensis*	
	–	*Miolacerta tenuis*	
Cordylidae	Cordylidae indet.	*Palaeocordylus bohemicus*	–
	–	–	*“Bavaricordylus ornatus”*
? Scincidae	? Scincidae indet.	–	*“Bavariascincus mabuyaformis”*
Anguidae	*Ophisaurus* cf. *spinari*	*Ophisaurus spinari*	?
	–	*Ophisaurus fejfari*	?
	–	*Ophisaurus robustus*	?
	–	*Anguis* sp.	?
	–	*Pseudopus ahnikoviensis*	–
	–	–	*Pseudopus laurillardi*

part of the Central Paratethys region (for the Central Paratethys region, see, e.g., Seneš and Marinescu 1974; Steininger and Wessely 2000; Harzhauser et al. 2003). Furthermore, petrographical and palynological studies highlight the differences between Oberdorf and Dolnice localities.

The Oberdorf paleoenvironmental conditions are interpreted as a rare pond-like habitat, close to wet forest swamp paleoenvironment (Daxner-Höck et al. 1998, Haas 1998). Lignite originated here from a low-lying mire in a wet-forest swamp environment. Here, Taxodiaceae–Cupressaceae forest-swamp pollen dominates with pollen from plants living in a mixed mesophytic forest, and pollen from aquatic and reed plants is rare. Paleoclimatic reconstructions based on the ratio of presumed deciduous and evergreen plants confirm warm-temperate subtropical and humid conditions (Kolcon and Sachsenhofer 1999; Kovar-Eder et al. 2001). Haas et al. (1998) estimated the Oberdorf paleoclimatic conditions at 14–17 °C mean annual temperature and 1000–2000 mm mean annual precipitation, while only 374 mm precipitation has been estimated for Dolnice (Vida 2015).

The presence of *O.* cf. *spinari* fits perfectly with previous paleoenvironmental interpretations. Böhme (2002) asserts that this taxon is found especially in fluviolacustrine basin sediments, while *O. fejfari* is more adapted to environments with low levels of groundwater. Therefore, the reported presence of *O. spinari* in both localities suggests that this taxon occurs across wider environmental conditions than *O. fejfari*.

It is surprising that only one find, tentatively attributed to chameleons, would represent these arboreal specialists in the fluviatile and swampy Oberdorf habitat, because their rich occurrence is recognized from the older Merkur-North Czech locality in the Most basin (MN3a; Fejfar and Schleich 1994; Čerňanský 2010a). The Merkur locality is interpreted as area flooded by rivers, with run-off spreading into flatlands and creating swamps and shallow lakes, and hence a swamp ecosystem (Kvacek et al. 2004). The hypothetical explanation for this might be proximity to the sea and the different types of trees thriving there.

In contrast, an abundant component of the Oberdorf material is formed by members of the clade Scincoidea. The occurrence of cordylid lizards is not suited to the Oberdorf environment because of the modern ecology of this strictly endemic African reptile clade. These are terrestrial, thermophilous, predominantly arid-land species of scrub forest and grasslands, and often occur in boulder fields and rocky outcrops (see Branch 1988; Jacobsen et al. 1990; Bauer 1998). However, the habitat preferences of Early Miocene forms in Central Europe are unknown, so if their autochthony (at the very local scale) is assumed, we cannot exclude their adaptation to more humid conditions. Their record is also documented from Dolnice and Merkur in the Czech Republic (Roček 1984; Čerňanský 2012). In addition, altitudinal differences are unknown in studied geographic regions where micro-habitats such as elevations and dry plateaux could be common. These factors play an important role in the vertical distribution of species. Unfortunately, all European cordyloid finds are very limited. Moreover, within the clade Scincoidea, Cordylidae, Gerrhosauridae and Scincidae are often difficult to distinguish (see, e.g., Gao and Fox 1996). A new, more complete material of these lizards and a revision of the previously described specimens are crucial for understanding their taxonomy and palaeoecology.

Böhme (2003) regarded geckos ("Gekkonidae" in her terminology) as animals adapted to dry habitats. However, their occurrence is documented in Oberdorf and in the older Merkur-North locality (Čerňanský and Bauer 2010: the clade Sphaerodactylidae as for Gekkota). Albanerpetontid amphibian (*Albanerpeton inexpectatum*) has been reported from both aquatic and wet environments (see Gardner and Böhme 2008). The occurrence of this taxon is documented from Oberdorf and Merkur (see Sanchiz 1998; Čerňanský 2010c).

According to Szyndlar (1998), the Oberdorf snake fauna is very similar to those described from Dolnice and Petersbuch 2 (for the snake fauna of these localities, see Szyndlar 1987; Szyndlar and Schleich 1993). However, *Bransateryx*, an erycine boid, is not reported from Oberdorf and Böhme (2003) considers it a dry-adapted form. This taxon is absent in Merkur as well (for Merkur snakes, see Ivanov 2002).

The state of the preserved Oberdorf material precludes strong conclusions. Sanchiz (1998) previously reported that many of the fossils are badly preserved and broken, and Daxner-Höck (1998) stressed that bone fragments of small vertebrates are sporadically distributed among large mammal remains, and no articulated skeletons have been found.

Finally, other interesting consequences certainly exist. If such poor preservation could indicate transported material, for example by river, caution would be essential, because the fauna, or some part of it, could be allochthonous. The same principle applies to presence resulting from predation, especially by birds of prey. The preserved tooth crowns from Oberdorf do not negate these possibilities.

Acknowledgments The author is indebted to U. Göhlich (the Natural History Museum, Vienna) for access to material described in this paper. I also thank J. Klembara (Comenius University in Bratislava), R. Kosma (Staatliches Naturhistorisches Museum, Braunschweig) and K. Smith (Senckenberg Research Institute, Frankfurt am Main) for helpful advice. M. Reich (Bayerische Staatssammlung für Paläontologie und Geologie Munich) and S. Kirchhof (Museum für Naturkunde, Berlin) helped with the German abstract. SEM pictures were taken by N. Halašiová (Slovak Academy of Sciences). For critical reading of the manuscript I thank J.-C. Rage (Muséum National d'Histoire Naturelle), K. Rauscher (Universität Wien) and M. Reich (Bayerische Staatssammlung für Paläontologie und Geologie Munich).

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