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New material of *Ophisaurus*, *Anguis* and *Pseudopus* (Squamata, Anguidae, Anguinae) from the Miocene of the Czech Republic and Germany and systematic revision and palaeobiogeography of the Cenozoic Anguinae

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Abstract – Four species of *Ophisaurus*, *O. fejfari*, *O. spinari*, *O. robustus* and *O. holeci*, are recognized on the basis of parietals from the Early Miocene of the Czech Republic and Germany. The fifth species, *O. acuminatus*, is described from the Late Miocene of Germany, but its parietal is not preserved. This paper describes new *O. fejfari*, *O. spinari*, *O. robustus* and *O. holeci* specimens from the Early and Middle Miocene of the Czech Republic and Germany. The *O. fejfari* and *O. holeci* parietals from Germany are the first records of these species outside the Czech Republic. This paper provides a significant contribution to the understanding of both interspecific and intraspecific *Ophisaurus* variability in the Cenozoic of Europe. A well-preserved parietal of *Anguis rarus* sp. nov. is described from the Early Miocene of Germany. This is the first record of the parietal of *Anguis* in the Cenozoic. A new parietal from the Middle Miocene of Germany is described as *Pseudopus* sp. It differs from the contemporaneous *P. laurillardi* only in the absence of the large and distinctly laterally projecting anterolateral processes of the parietal. In the Miocene, *Ophisaurus* and *Pseudopus* exhibit a higher diversity than that of the preceding geological periods of the Cenozoic. Besides, *Ophisaurus* emigrates from Europe to (1) Asia and via the Bering Strait to North America, and (2) North Africa during the Oligocene and Miocene. By contrast, *Anguis* and *Pseudopus* are limited to Eurasia. The palaeobiogeography of members of Anguinae is discussed.

Keywords: Anguimorpha, Central Europe, Tertiary, skull, taxonomy.

1. Introduction

The family Anguinae has three living genera: *Pseudopus* (Eurasia), *Ophisaurus* (Southeast Asia, North Africa and North America) and *Anguis* (Europe, Southwest Asia) (see reviews in Augé, 2005; Gvoždík *et al.* 2010; Klembara, Hain & Dobiašová, 2014). *Ophisaurus* fossils come from Eurasia North Africa and North America, while *Anguis* and *Pseudopus* are currently reported from Europe (Fejérváry-Lángh, 1923; Holman, 1970; Augé, 2005; Klembara, Böhme & Rummel, 2010; Klembara, 2012, 2015; Blain *et al.* 2013).

Cenozoic anguine fossils are mostly disarticulated with the exception of *Ophisauriscus quadrupes* skeletons and osteoderms from the Middle Eocene of Geiseltal (Kuhn, 1940; Meszoely & Haubold, 1975; Klembara, 1981) and from Messel (Sullivan, Keller & Habersetzer, 1999), both in Germany. Later revisions, however, have questioned their classification as Anguinae (Sullivan, Keller & Habersetzer, 1999; Conrad, 2008; Conrad *et al.* 2011). A further exception is *Pseudopus laurillardi* from the Early Miocene of Germany which has an articulated skull and well-preserved portions of the vertebral column and integument (Klembara, Böhme & Rummel, 2010). This is the reference species for abundant disarticulated skeletal elements attributed to *Pseudopus* discovered at other Early and Middle Miocene localities in Central and Western Europe. Also recorded are: (1) a partly preserved skull of *Ophisaurus acuminatus* from the German lower Late Miocene (Jörg, 1965); (2) a specimen with a partly articulated skull from the Miocene of Catalonia (Ne Iberian Peninsula) briefly described by Bolet *et al.* (2013); and (3) *Ophisaurus* sp. described from the Middle Miocene sediments of Slovakia by Klembara (1986*a*) which has a short vertebral column section and osteoderms. Recently, the cranial and postcranial remains of *Ophisaurus spinari* have been described from the late Middle Miocene of Austria (Böhme & Vasilyan, 2014). Although not articulated, the parietal, several other cranial elements, vertebrae and osteoderms were attributed to this species by the authors (however, see below).

All other Cenozoic anguine species of Europe (see below), North Africa (Blain *et al.* 2013) and North America (Holman, 1970; Estes, 1983) were described

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on the basis of the disarticulated cranial elements. This is especially relevant for *Ophisaurus* species described mainly from parietals; and to a lesser extent to *Pseudopus* and *Anguis* descriptions. Recently, an incomplete parietal from the Late Eocene of Spain was attributed to Anguinae indet (Bolet & Evans, 2013). A further Paleogene find of parietal attributed to *Ophisaurus* comes from the Late Eocene of the Hampshire Basin of southern England. However, because this parietal exhibits no specific features it was described as *Ophisaurus* sp. (Klembara & Green, 2010). From the same locality, the parietal of *Headonhillia parva* was also described (Klembara & Green, 2010). An Oligocene species of the genus *Ophisaurus* is represented by *O. roqueprunensis* from the Early to Late Oligocene of France and Belgium (Augé, 1992, 2005; Augé & Smith, 2009), later attributed to the genus *Dopasia* (Augé, 2005) and reallocated to *Ophisaurus* by Čerňanský, Klembara & Müller, (2016). Within the new material of this species described from Belgium, a partially preserved parietal is present (Augé & Smith, 2009). Four species of the genus *Ophisaurus* were described from the Early Miocene of the Czech Republic and Germany: *O. fejfari*, *O. spinari* and *O. robustus* from the locality Dolnice (MN 4) (Klembara, 1979, 1981) and *O. holeci* from the locality Merkur (MN 3) (Klembara, 2015). In *O. holeci* it was possible to associate the frontals with the parietals. Importantly, an *O. spinari* parietal was described from Germany (Čerňanský, Rage & Klembara, 2015). Unfortunately, the parietal of *O. acuminatus* (Jörg, 1965) is not preserved. One partial parietal was described from the late Middle Miocene (MN 7–8) sediments of the Pannonian Basin in Hungary and determined as *Ophisaurus* cf. *spinari* (Hír *et al*. 2001). Later, more abundant material of anguines from the same region was described (Venczel & Hír, 2013). In this disarticulated material, several other parietals were described and also attributed to *Ophisaurus* cf. *spinari* (Venczel & Hír, 2013). *Ophisaurus canadensis* from the Late Miocene of Canada is based on one vertebra (Holman, 1970).

Another partially preserved parietal was described from the Late Pliocene of Italy as *Dopasia* sp. (Delfino, Bailon & Pitruzzella, 2011). Augé (2005) started to use the generic name *Dopasia*, originally used by Gray (1853) for the extant anguine *D. gracilis* from Southeast Asia, instead of *Ophisaurus.* Augé (2005) applied the name *Dopasia* for all extinct and extant species previously described as *Ophisaurus* from the Cenozoic of Eurasia and North Africa. However, the latest phylogenetic analysis of extant Anguinae showed that it would be more prudent to use the name *Ophisaurus* for all species living in Southeast Asia, North America and North Africa (Klembara, Hain & Dobiašová, 2014).

Three *Dopasia* (=*Ophisaurus*) species, *D. roqueprunensis*, *D. coderetensis* and *D. frayssensis* from the Oligocene of France, were described on the basis of dentaries (Augé, 2005). There is also one parietal attributed to *D. coderetensis* (Augé, 2005); unfortunately its preservation is very poor and does not allow any detailed comparisons. The species *D. coderetensis* and *D. frayssensis* have been assigned to the genus *Ophisauromimus* by Čerňanský, Klembara & Müller (2016).

Crusafont Pairó & Vallalta (1952) mentioned the record of the *Ophisaurus* skull from the Miocene locality Vallès-Penedès Basin in Catalonia; a revision of this find is needed. Bailon & Augé (2012) described a new anguine genus and species, *Ragesaurus medasensis* from the Lower Pleistocene of Spain. This new taxon is based on one right dentary.

The recognition of two species of *Pseudopus*, *P. ahnikoviensis* (Klembara, 2012) and *P. rugosus* (Klembara, 2015; however, see below), from the Early Miocene locality Merkur (the Czech Republic) helped to re-evaluate Early Miocene anguines from Slovakia and the Czech Republic previously attributed to *Ophisaurus* on the basis of parietals (Klembara, 1986*a* and see below).

The aims of this paper are: (1) to re-describe four previously reported Miocene species of *Ophisaurus* named on the basis of parietals from the Czech Republic and Germany on the basis of new material; (2) to describe new *Ophisaurus*, *Anguis* and *Pseudopus* specimens from the Early and Middle Miocene Czech and German localities through better understanding of their intraspecific and interspecific variability; and (3) to perform systematic revision of all *Ophisaurus*, *Anguis* and *Pseudopus* species previously described from the Cenozoic in Europe, North Africa and North America. Consequently, our aim is to present precise understanding of *Ophisaurus*, *Anguis* and *Pseudopus* diversity in the Cenozoic of Eurasia, North Africa and North America and to confirm their palaeobiogeography.

2. Materials and methods

The material described here is disarticulated. Several parietals were coated with ammonium chloride before taking photographs.

For comparisons, the skeletons of the following Anguinae species were used: *Anguis fragilis* (DE 14–21, 24, 25, 45–48); *Ophisaurus ventralis* (DE 34, 35, 38; AMNH 73057; UF 52539; CM 1411), *O. attenuatus* (DE 32, 33, 43, 44), *O. compressus* (DE 50), *O. mimicus* (DE 49), *O. koellikeri* (DE 30, 41), *O. harti* (DE 36, 37, 56, 57, 86; AMNH 34956), *O. gracilis* (DE 42), *Pseudopus apodus* (DE 1, 3–13, 22, 23, 29, 52–54, 58, 59; BSPG 1982 X 2383).

The terminology of the anatomical structures is from Fejérváry-Lángh (1923), Oelrich (1956), Klembara (1979, 1981), Conrad (2004), Evans (2008) and Klembara, Böhme & Rummel (2010).

Institutional abbreviations. AMNH – American Museum of Natural History, New York, USA; BMNH, NHM – Natural History Museum, London, England; BSPG – Bayerische Staatssammlung für Paläontologie, Munich, Germany; CM – Carnegie Museum of Natural History, Pittsburgh, PA, USA; DE – Department of Ecology, Faculty of Natural Sciences, Comenius

Table 1. List of fossil Cenozoic species of Anguinae, their geological age and type localities. The species are listed in the same sequence as described in the text.

Ophisaurus fejfari Klembara, 1979	Lower Miocene (MN 4), Dolnice, Czech Republic
Ophisaurus spinari Klembara, 1979	Lower Miocene (MN 4), Dolnice, Czech Republic
Ophisaurus robustus Klembara, 1979	Lower Miocene (MN 4), Dolnice, Czech Republic
Ophisaurus holeci Klembara, 2015	Lower Miocene (MN 3), Merkur, Czech Republic
Ophisaurus acuminatus Jörg, 1965	Upper Miocene (MN9/10), Heweneg/Hegau, Germany
Ophisaurus canadensis Holman, 1970	Upper Miocene, Kleinfelder Farm, Wood Mountain Formation, Saskatchewan, Canada
Ophisaurus roqueprunensis Augé, 1992	Middle Oligocene (MP 23), Roqueprune, Phosphorites du Quercy; France
Anguis rarus sp. nov.	Lower Miocene (MN 3), Petersbuch 62 (Bavaria, South Germany)
?*Anguis polgardiensis* Bolkay, 1913	Upper Miocene, Polgárdi, Bányahegy, Hungary
Anguis stammeri Brunner, 1957	Upper Pleistocene, Fuchloch, Siegmannsbrunn, Germany
Pseudopus confertus sp. nov.	Lower Miocene (MN 3), Merkur, Czech Republic
Pseudopus ahnikoviensis Klembara, 2012	Lower Miocene (MN 3), Merkur, Czech Republic
Pseudopus laurillardi (Lartet, 1851)	Middle Miocene (MN 6), Sansan, Gers, France
Pseudopus pannonicus (Kormos, 1911)	Upper Miocene (MN 13), Polgárdi 2, Hungary
Ophisauromimus coderetensis (Augé, 2005)	Upper Oligocene (MP 30), Coderet, Phosphorites du Quercy, France
Ophisauromimus frayssensis (Augé, 2005)	Upper Oligocene (MP 28), Pech-du Fraysse, Phosphorites du Quercy, France
Ragesaurus medasensis Bailon and Augé, 2012	Lower Pleistocene, Meda Grande, îles Medas, Catalonia, Spain
Headonhillia parva Klembara & Green, 2010	Late Eocene, Ludian (Priabonian); Bed 6, Bembridge Limestone Formation, Headon Hill, Isle of Wight, UK
Ophisauriscus quadrupes Kuhn, 1940	Grube Cecilie site VII (Ce VII), upper middle coal MP 13, Geiseltal, Germany.

University in Bratislava, Slovakia; DP FNSP – Department of Palaeontology, Faculty of Natural Sciences, Charles University, Prague, Czech Republic; GM – Geiseltal Museum, Halle, Germany; IRsNB – Institut royal des sciences naturelles de Belgique, Bruxelles; MNHN – Muséum National d'Histoire Naturelle, Paris, France; NMA – Naturmuseum Augsburg, Germany; NMP Pb and Pv – National Museum, Prague, Czech Republic; ROM – Royal Ontario Museum, Toronto, Canada; SMNK (LNK) – Staatliches Museum für Naturkunde Karlsruhe (Landessamlungen für Naturkunde Karlsruhe), Germany; SNM PP – Slovak National Museum, Bratislava, Slovakia; UCBL – Université Claude Bernard, Lyon, France; UF – University of Florida, Gainesville, USA; UM MED – Université de Montpellier, France.

3. Systematic palaeontology

In this section, new specimens of *Ophisaurus*, *Anguis* and *Pseudopus* are described and the revision of all fossil species of these genera is given (see also Table 1).

Order SQUAMATA Oppel, 1811
Infraorder ANGUIMORPHA Fürbringer, 1900
Family ANGUIDAE Gray, 1825
Subfamily ANGUINAE Gray, 1825
Genus *Ophisaurus* Daudin, 1803
Ophisaurus fejfari Klembara, 1979
Figures 1, 2a, b

1979 *Ophisaurus fejfari* Klembara, p. 164, pl. 1, fig. 1, pl. 2, fig. 1.

1981 *Ophisaurus fejfari* Klembara, p. 125.

1981 *Ophisaurus spinari* Klembara, p. 128, specimen DP FNSP 1023.

Holotype. Parietal DP FNSP 1013 (Klembara, 1979, pl. 1, fig. 1, pl. 2, fig. 1); Fig. 1a, b. Dolnice (near the city of Cheb, west Bohemia, Czech Republic), Early Miocene (Ottnangian), middle Orleanian, zone MN 4 (Fejfar & Kvaček, 1993).

Diagnosis. The *Ophisaurus fejfari* parietal is distinguished from that of other extinct *Ophisaurus* species described on the basis of parietals and all extant species of the genus in the following features and their combinations: (1) a distinct divergence of bases of supratemporal processes (the longitudinal line of the basal section of the supratemporal ridge of the supratemporal process continues to the frontal tab anteriorly); (2) the arcuate edge is wedge- or arch-shaped and its lateral section runs posteriorly close to the medial margin of the supratemporal process base; and (3) the parietal cranial crest is almost straight, except for its anteriormost section.

Referred specimens, localities and horizon. Parietals DP FNSP 1501, DP FNSP 1023, Dolnice (near the city of Cheb), Early Miocene (Ottnangian), middle Orleanian, zone MN 4 (Fejfar & Kvaček, 1993). Parietal BSPG 1997 XVI 466 (Fig. 2a, b), Griesbeckerzell 1a (Bavaria, south Germany), zone MN 5/6 (according to Böhme, 2002; Abdul-Aziz *et al.* 2008).

Description. The lateral margins of the parietal table as well as its ornamented surface converge posteromedially and the parietal is constricted at the level of the transition of the parietal table and supratemporal processes (Figs 1, 2a, b). The ornamented surface is longer than it is wide. The ornamentation consists of densely arranged distinct ridges, grooves and pits occupying most of the ornamented surface. Short ridges and grooves are present only at the periphery of the ornamented surface. The anterior end of the

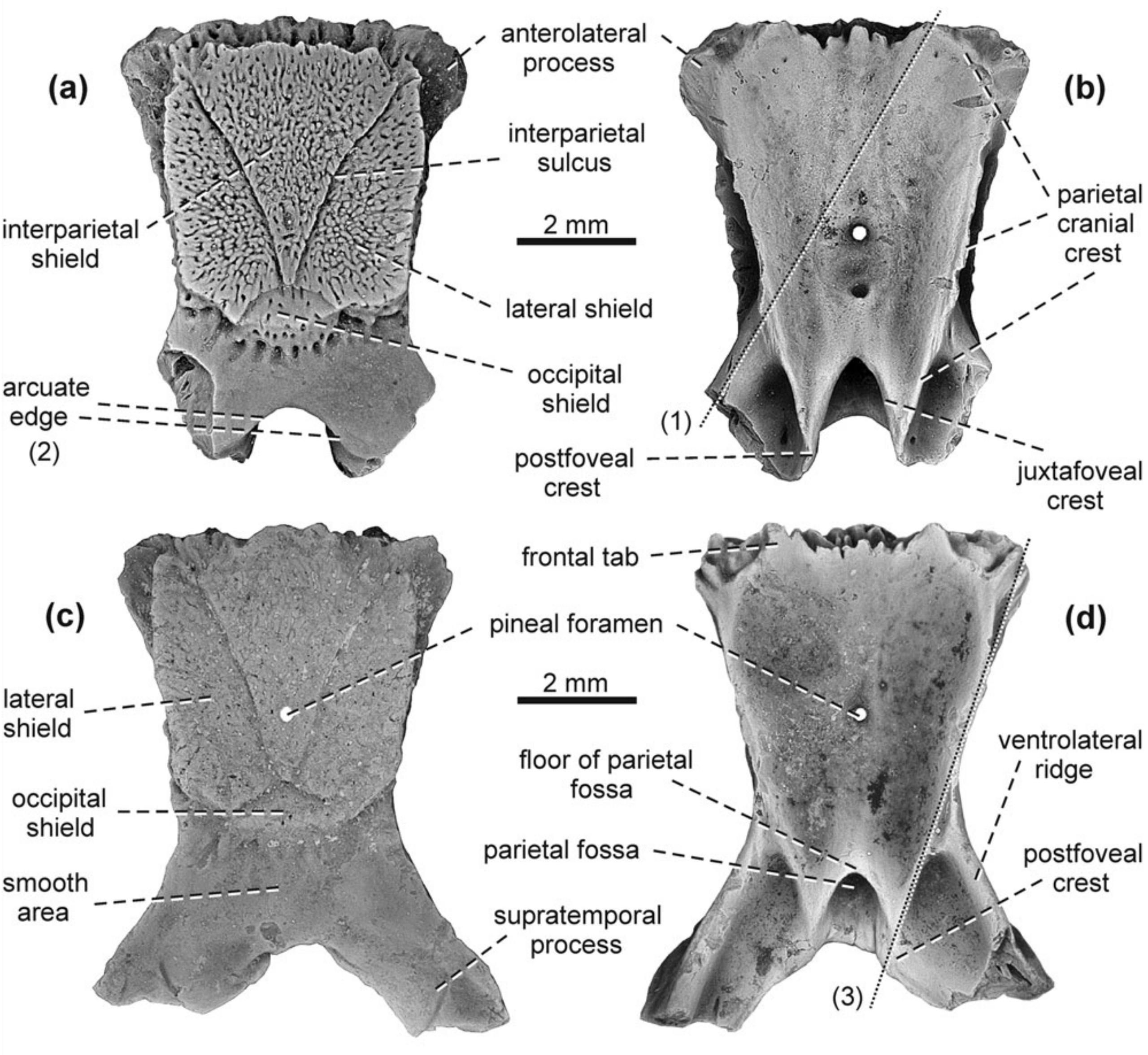

Figure 1. Photographs of parietals of *Ophisaurus fejfari* in dorsal (a, c) and ventral (b, d) views. (a, b) DP FNSP 1013, holotype; (c, d) DP FNSP 1501. Numbers 1–3 designate distinguished features of *O. fejfari* discussed in the text.

interparietal sulcus lies in the anterolateral corner of the ornamented surface. The ornamented surface consists of unpaired occipital and interparietal and paired lateral shields. The occipital shield has elliptical to quadrangular shape (Figs 1a, c, 2a). The pineal foramen lies immediately posterior to the mid-length of the ornamented surface. Measured in the median plane, the smooth area is slightly anteroposteriorly longer than the length of the occipital shield. The anterolateral process is well developed. The arcuate edge is wedge-shaped and runs posteriorly close to the medial margin of the supratemporal process base. The preserved basal portions of the supratemporal processes are massive and indicate a broad divergence of the supratemporal processes.

The parietal cranial crest forms a distinct straight wall, only its anterior section is low and turned anteromedially (Figs 1b, 2b). The frontal tab is moderately developed. The posterior tip at the junction of the posteriormost sections of the parietal cranial crest and juxtafoveal crest merges with the medial margin of the supratemporal process via a short, high and sharp postfoveal crest. The preserved anterior section of the ventrolateral ridge of the supratemporal process is massive and coincides with the lateral margin of the supratemporal process. The anterior end of the ventrolateral ridge lies at the level slightly anterior to the posteromedian margin of the floor of the parietal fossa. In the holotype parietal, there is a small, oval pit positioned posteriorly to the pineal foramen. The posterior margin of the floor of the parietal fossa is wedge-shaped. The position of the posteromedian margin of the parietal table varies slightly relative to the length of the juxtafoveal crest (cf. Fig. 1b, d).

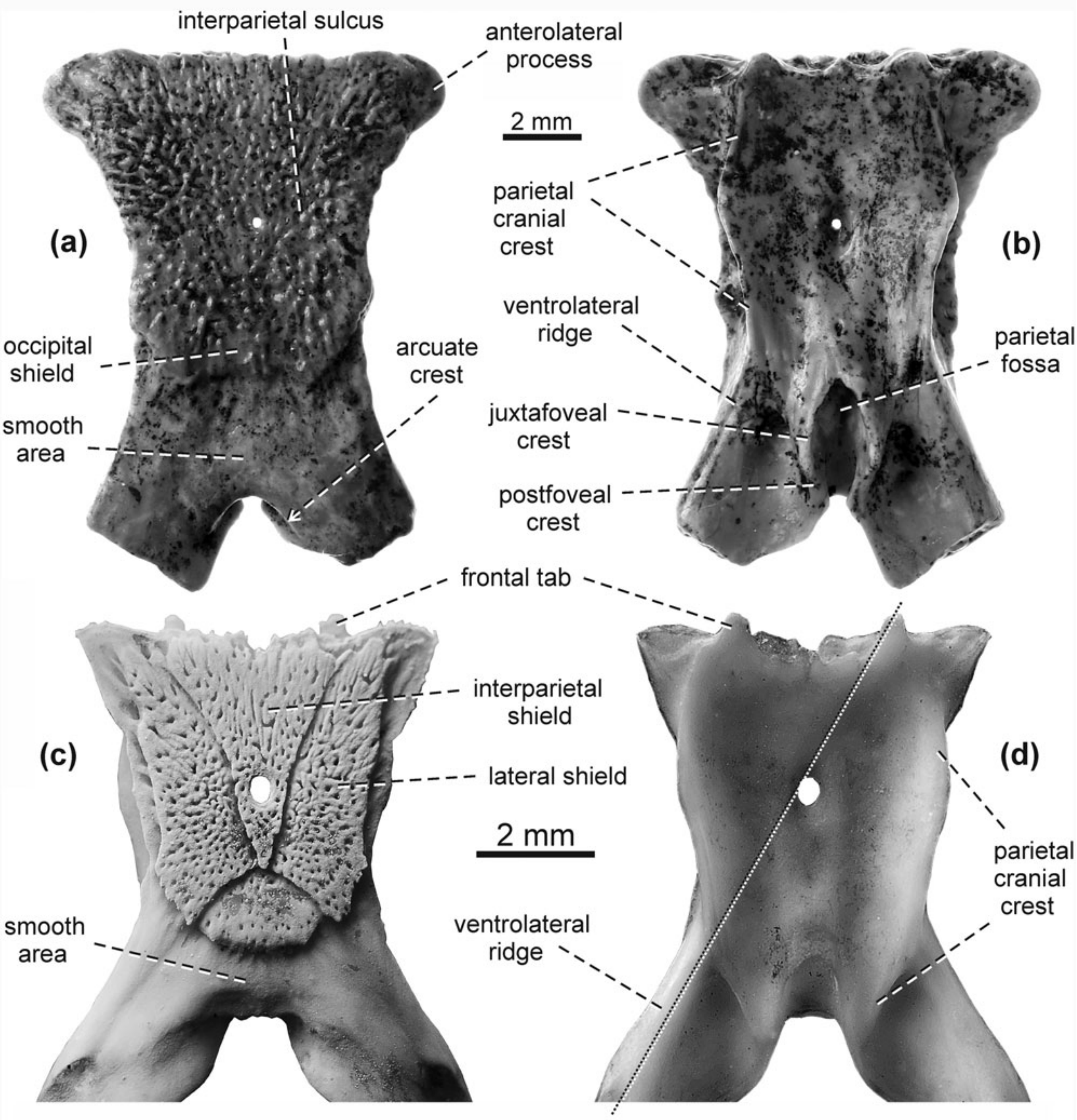

Figure 2. (a, b) BSPG 1997XVI 466, photographs of parietals of *Ophisaurus fejfari* in dorsal (a) and ventral (b) views. (c, d) UF 57121, photographs of parietal of *Ophisaurus attenuatus* in dorsal (c) and ventral (d) views.

The holotype (Fig. 1a, b) and DP FNSP 1501 (Fig. 1c, d) are of similar size. The parietal BSPG 1997 XVI 466 (Fig. 2a, b) is much larger than the other three parietals. The parietal BSPG 1997 XVI 466 differs from the holotype and DP FNSP 1501 in the following features: (1) large anterolateral processes of parietal table; (2) ornamentation of the anterolateral corner of the ornamented shield extends to the dorsal surface of the anterolateral process of the parietal table; and (3) quadrangular shape of occipital ornamented shield showing a slight variability in size and shape of the occipital shield. Probably the first two differences are connected with the larger size of the BSPG 1997 XVI 466 parietal. Unless better material is at our disposal, the parietal BSPG 1997 XVI is therefore tentatively assigned to *Ophisaurus fejfari*.

Comparisons. The parietal of *Ophisaurus fajfari* is characterized by these three features (the following numbers correspond to 1–3 in Fig. 1):

(1) A distinct divergence of bases of supratemporal processes (the longitudinal line of the basal section of the supratemporal ridge of the supratemporal process continues to the frontal tab anteriorly). In all other fossil species of *Ophisaurus*, the longitudinal line of the basal section of the supratemporal ridge of the supratemporal

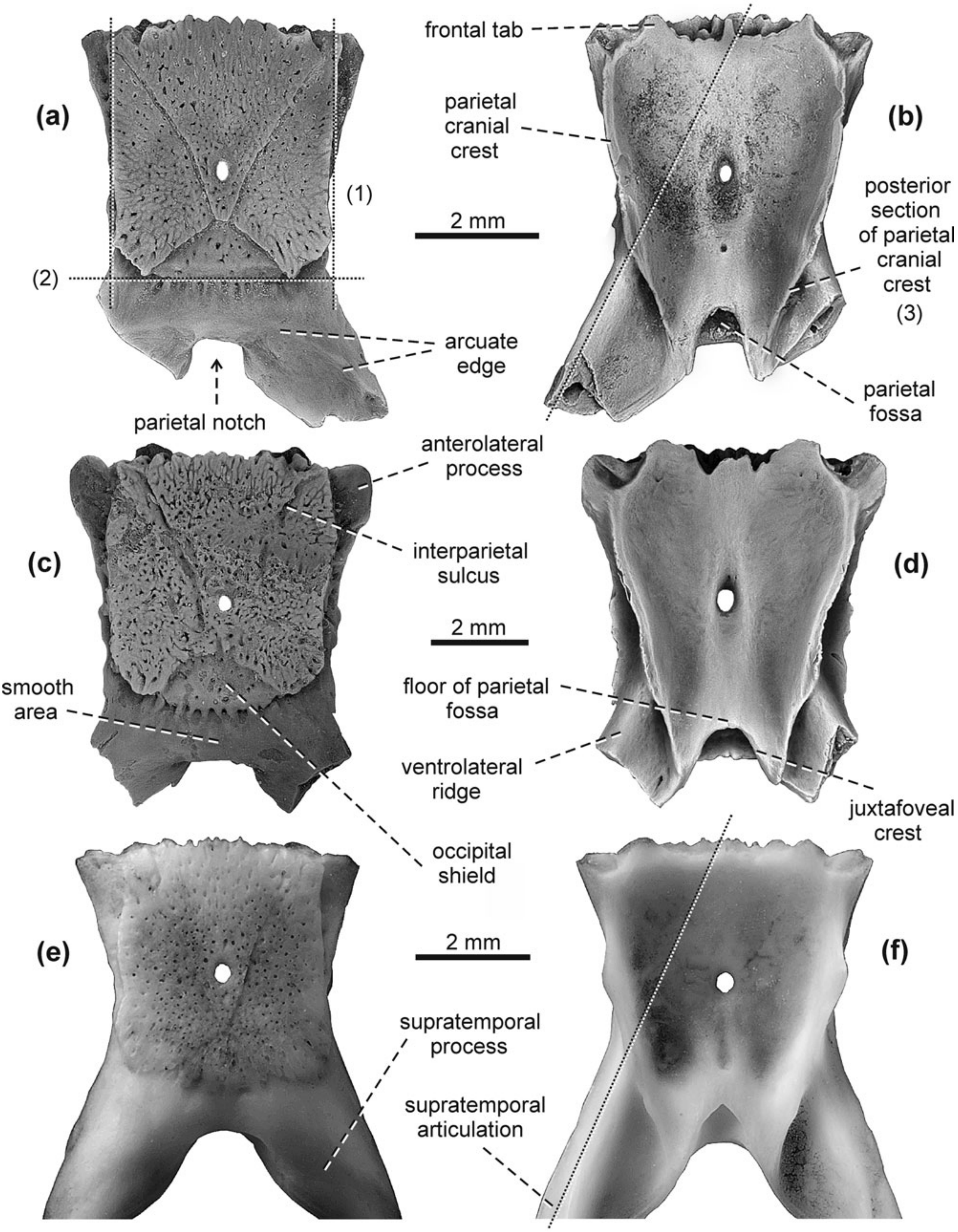

Figure 3. (a–d) Photographs of parietals of *Ophisaurus spinari* in dorsal (a, c) and ventral (b, d) views. (a, b) DP FNSP 2015, holotype; (c, d) DP FNSP 1025. (e, f) DE 35, photographs of parietals of *Ophisaurus ventralis* in dorsal (e) and ventral (f) views. Numbers 1–3 designate distinguished features of *O. spinari* discussed in the text.

process continues to or lies close to the median point of the anterior margin of the parietal (cf. Figs 1b and 3b, 5d, 8b).

(2) The arcuate edge is wedge- or arch-shaped and its lateral section runs posteriorly close to the medial margin of the supratemporal process base.

(3) The parietal cranial crest is almost straight, except for its anteriormost section.

The general shape of the parietal described as *Dopasia coderetensis* (Augé, 2005, fig. 165a, b) from the Late Oligocene of France is somewhat similar to that of *Ophisaurus fejfari*. However, the parietal from France is poorly preserved and does not allow detailed comparisons.

Among the extant species of *Ophisaurus*, the *O. fejfari* parietal is most similar to that of *O. attenuatus* (Fig. 2c, d). The parietal of *O. attenuatus* shares three features with that of *O. fejfari*: (1) the lateral margins of the parietal table converge posteriorly and a distinct constriction is present at the transition of the parietal table and bases of supratemporal processes; (2) there is a distinct divergence of the bases of supratemporal processes, the same as is in *O. fejfari* (cf. Figs 1b, 2d); and (3) besides its anteriormost section, the parietal cranial crest is almost straight. In contrast, the parietal of *O. attenuatus* lacks the postfoveal crest and the anterior end of the interparietal sulcus lies medially to the anterolateral corner of the ornamented surface.

Ophisaurus spinari Klembara, 1979
Figures 3a–d, 4

1979 *Ophisaurus spinari* Klembara, p. 164, pl. 1, fig. 2, pl. 2, fig. 2.

1981 *Ophisaurus spinari* Klembara, p. 128, specimen DP FNSP 1029.

2011 *Dopasia* sp. Delfino, Bailon and Pitruzzella, p. 368, fig. 5C, D.

2015 *Ophisaurus spinari* Čerňanský, Rage & Klembara, p. 107, fig. 8A, B.

2015 *Ophisaurus spinari* Klembara, p. 178, fig. 3A, B.

Holotype. Parietal DP FNSP 2015 (Klembara, 1979, pl. 1, fig. 2, pl. 2, fig. 2); Fig. 3a, b. Dolnice (near the city of Cheb), Early Miocene (Ottnangian), middle Orleanian, zone MN 4 (Fejfar & Kvaček, 1993).

Diagnosis. Ophisaurus spinari parietal differs from all extinct species of *Ophisaurus* described on the basis of parietals and extant species of *Ophisaurus* in the following features and combination of features: (1) the ornamented surface is quadrangular, longer than it is wide and its width is approximately the same along its entire anteroposterior length; (2) the occipital ornamented shield is triangular with an almost straight posterior margin; and (3) the posterior section of the parietal cranial crest has a concave course.

Referred specimens, locality and horizon. Parietals DP FNSP 1014, DP FNSP 1019, DP FNSP 1021, 1022, DP FNSP 1025 (Klembara, 1981, fig. 1; pl. 2, fig. 1), DP FNSP 1028, Dolnice (near the city of Cheb), Early Miocene (Ottnangian), middle Orleanian, zone MN 4 (Fejfar & Kvaček, 1993). Parietals NMA-2015-32/2196, Petersbuch 39 III, zone MN 5 (Bavaria) (Klembara, Böhme & Rummel, 2010) (Fig. 4a, b); NMA-2015-36/2196, Petersbuch 62, zone MN 3 (Bavaria) (Abdul-Aziz *et al*. 2008) (Fig. 4b, c).

Description. The parietal table is covered by a quandrangular ornamented surface (Figs 3a, c, 4a, c). This ornamentation is densely arranged. The elongated grooves and ridges are present only at the periphery of the ornamented surface. The anterior end of the interparietal sulcus lies in the anterolateral corner of the ornamented surface. The occipital shield is triangular. Its posterior margin is almost straight. The pineal foramen lies immediately posterior to the mid-length of the ornamented surface. The length of the smooth area measured in the median plane approximates that of the occipital ornamented shield. The arcuate edge is arch-shaped and the anterolateral process is moderately developed.

The parietal cranial crest is deep and distinctly developed in its entire course (Figs 3b, d, 4b, d). Its anterior and middle sections have a convex course; only its posterior section is typically more or less distinctly concave. Laterally, the parietal cranial crest reaches the lateral margin of the parietal table (measured at the level of the pineal foramen). The frontal tab is distinct. The anterior end of the ventrolateral ridge of the supratemporal process lies anterior to the posteromedian margin of the floor of the parietal fossa. The ventrolateral ridge coincides with the lateral margin of the supratemporal process. The supratemporal articulation extends anteriorly to the level of the posteromedian margin of the parietal table (Fig. 4b). The paroccipital process of the opisthotic articulation has an elongated shape (Fig. 4b).

Comparisons. Three features characterize the parietal of *Ophisaurus spinari* (the following numbers correspond to 1–3 in Fig. 3):

(1) The ornamented surface of the parietal is quadrangular, longer than it is wide and its width is approximately the same along its entire anteroposterior length. A similar shape of the ornamented surface is present in extant *Ophisaurus ventralis* (Fig. 3e). However, in *O. ventralis* the ornamentation is indistinctly developed. The ornamented surface of the adult *O. ventralis* parietal consists of very indistinct and almost flat tubercles; between them, many small pits are present (e.g. CM 1411, DE 35). Longer ridges and grooves at the periphery of the ornamented shield are also very low and indistinct.

(2) The occipital ornamented shield is triangular with an almost straight posterior margin. *Ophisaurus fejfari* (Fig. 1c) and *O. holeci* (Figs 7a, c, 8a, c further below and Klembara, 2015) have a roughly similar shape of the occipital ornamented shield. However, in contrast to *O. fejfari*, the parietal of *O. spinari* (i) lacks a distinct constriction between the bases of the

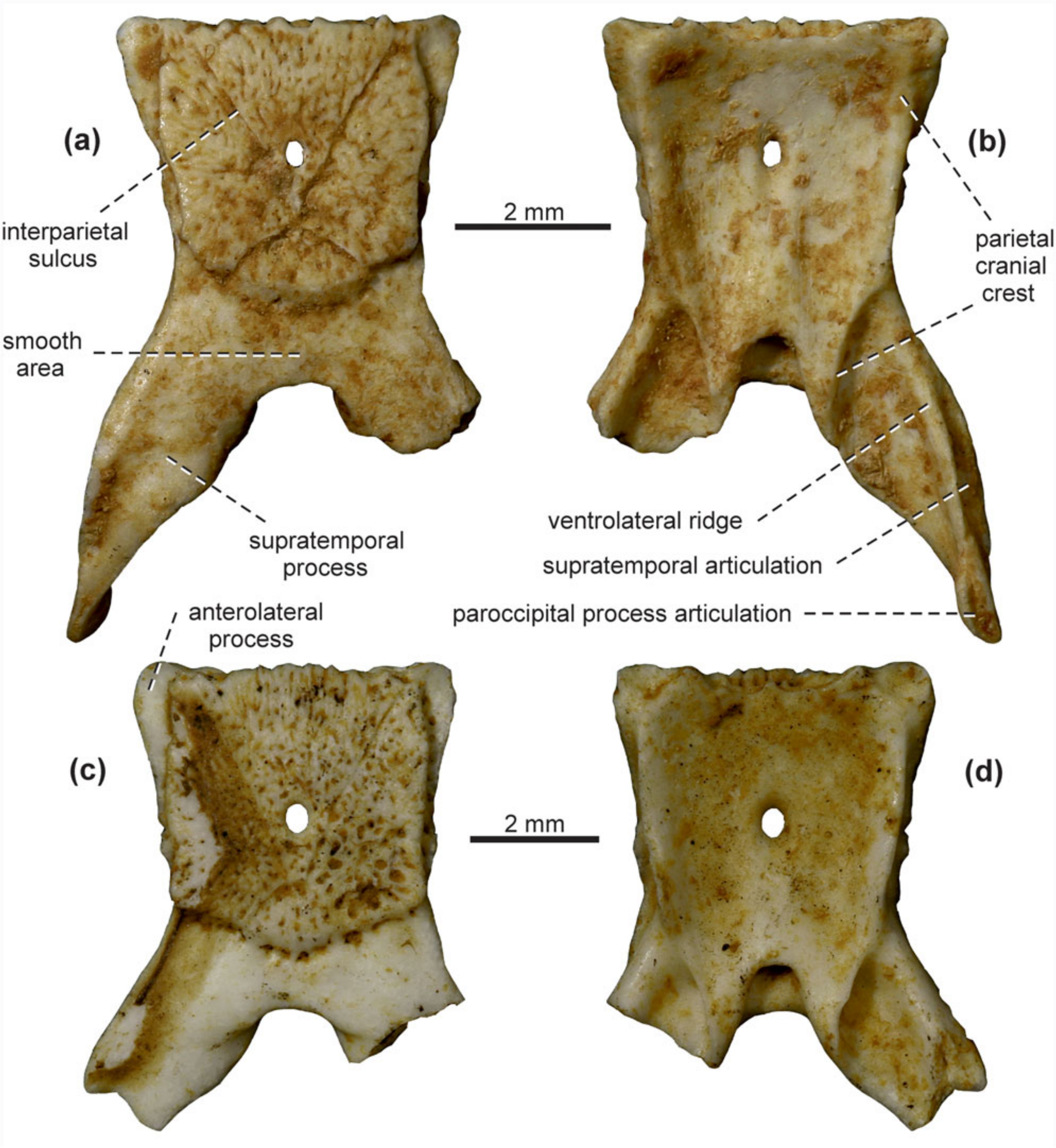

Figure 4. (Colour online) Photographs of parietals of *Ophisaurus spinari* in dorsal (a, c) and ventral (b, d) views. (a, b) NMA-2015-32/2196; (c, d) NMA-2015-36/2196.

supratemporal processes and the parietal table; (ii) lacks distinct divergence of the supratemporal processes bases (as in *O. fejfari*, in which the longitudinal line of the basal section of the supratemporal ridge of the supratemporal process is continued with the frontal tab anteriorly, Fig. 1b); in all other fossil species of *Ophisaurus*, the longitudinal line of the basal section of the supratemporal ridge is continuous with or lies close to the median point of the anterior margin of the parietal, e.g. Fig. 3b); and (iii) its cranial crest is not straight in its middle and posterior sections. In contrast to *O. holeci*, in the parietal of *O. spinari* (i) the anterior end of the interparietal sulcus lies in the anterolateral corner of the ornamented surface; (ii) the ventrolateral ridge of the supratemporal process joins the parietal cranial crest anterior to the posteromedian margin of the floor of the parietal fossa; and (iii) the posterior section of the parietal cranial crest has a concave course.

(3) The posterior section of the parietal cranial crest has a concave course. This is in contrast to the straight course of this section of the parietal cranial crest in other species of *Ophisaurus*.

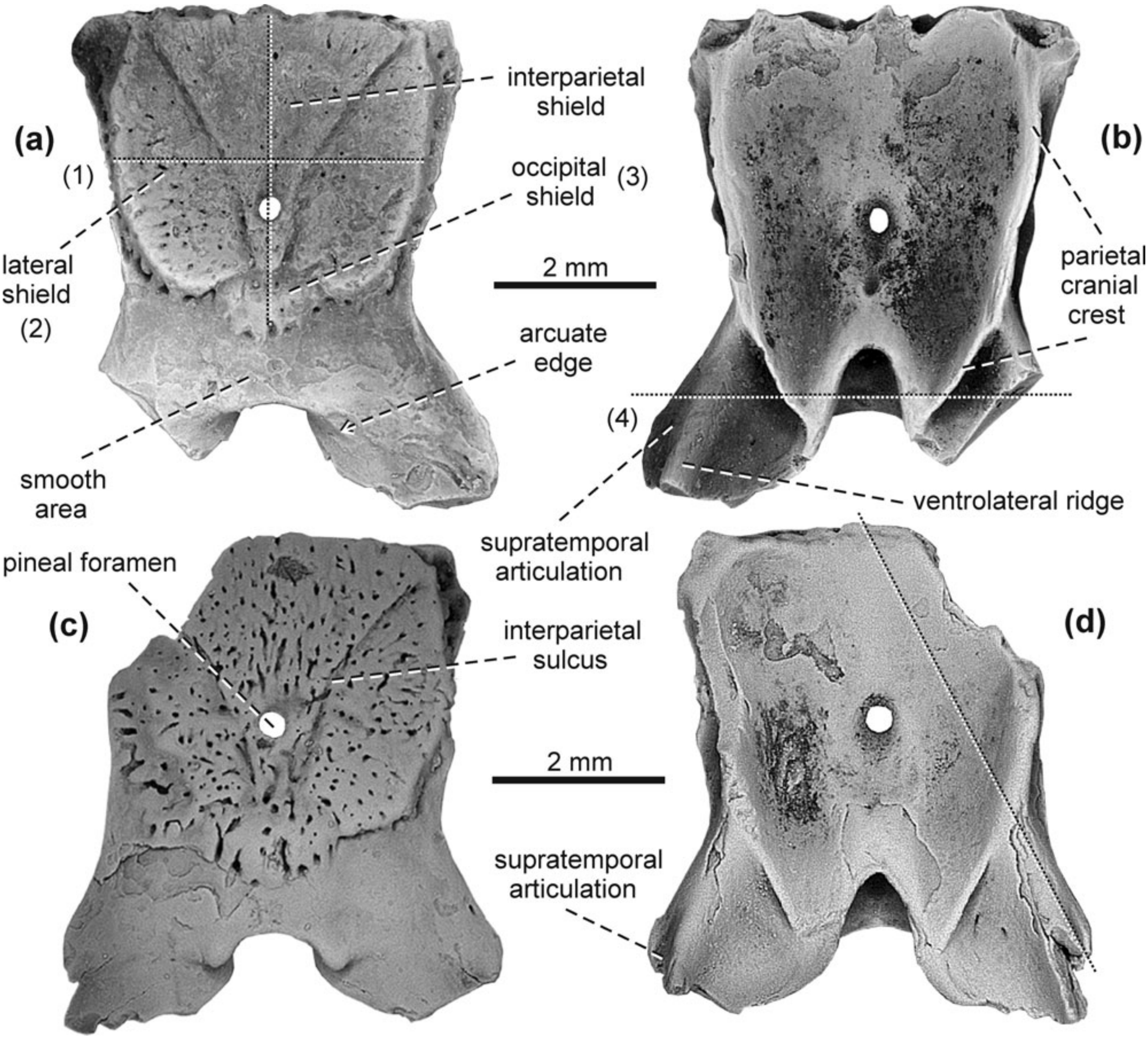

Figure 5. Photographs of parietals of *Ophisaurus robustus* in dorsal (a, c) and ventral (b, d) views. (a, b) DP FNSP 1018, holotype; (c, d) DP FNSP 1020. Numbers 1–4 designate distinguished features of *O. robustus* discussed in the text.

Delfino, Bailon & Pitruzzella (2011, fig. 5C, D) described a right portion of the parietal from the Late Pliocene of Italy as *Dopasia* sp. The parietal cranial crest of this parietal is well preserved and its posterior section is clearly concave. This feature is present only in *Ophisaurus spinari* (Figs 3b, d, 4b, d). The posterolateral portion of the ornamented surface of the parietal from Italy is rectangular, indicating that the posterior width of the ornamented surface is about the same as that of the anterior portion of the ornamented surface. This is also typical for *O. spinari*. Thus, the parietal from Italy described as *Dopasia* sp. (Delfino, Bailon & Pitruzzella, 2011) is assigned to O. *spinari* here and it represents the youngest record of this species.

Special attention is required for the parietal attributed recently to *Ophisaurus spinari* from the late Middle Miocene of Austria (Böhme & Vasilyan, 2014). The parietal from Austria exhibits features which are not preserved in similarly sized parietals of *O. spinari* (Figs 3a–d, 4; Klembara, 1979, 1981, 2015; Čerňanský, Rage & Klembara, 2015). These features are:

(1) The ornamental surface of parietal gradually widens anteriorly. In *O. spinari*, the surface is rectangular and never exhibits distinct gradual widening of its anterior portion.

(2) The parietal table is distinctly anteriorly widened bilaterally. This widening is absent in *O. spinari* and all other *Ophisaurus*, *Anguis* and *Pseudopus* species.

(3) The anteroposterior length of the smooth area measured in the medial plane is less than the anteroposterior length of the occipital ornamented shield. This condition is typical for *Anguis* (Fig. 9c further below; see also Klembara, 1979, 2015).

(4) The parietal cranial crests diverge distinctly anteriorly and the anteriormost section of this crest runs

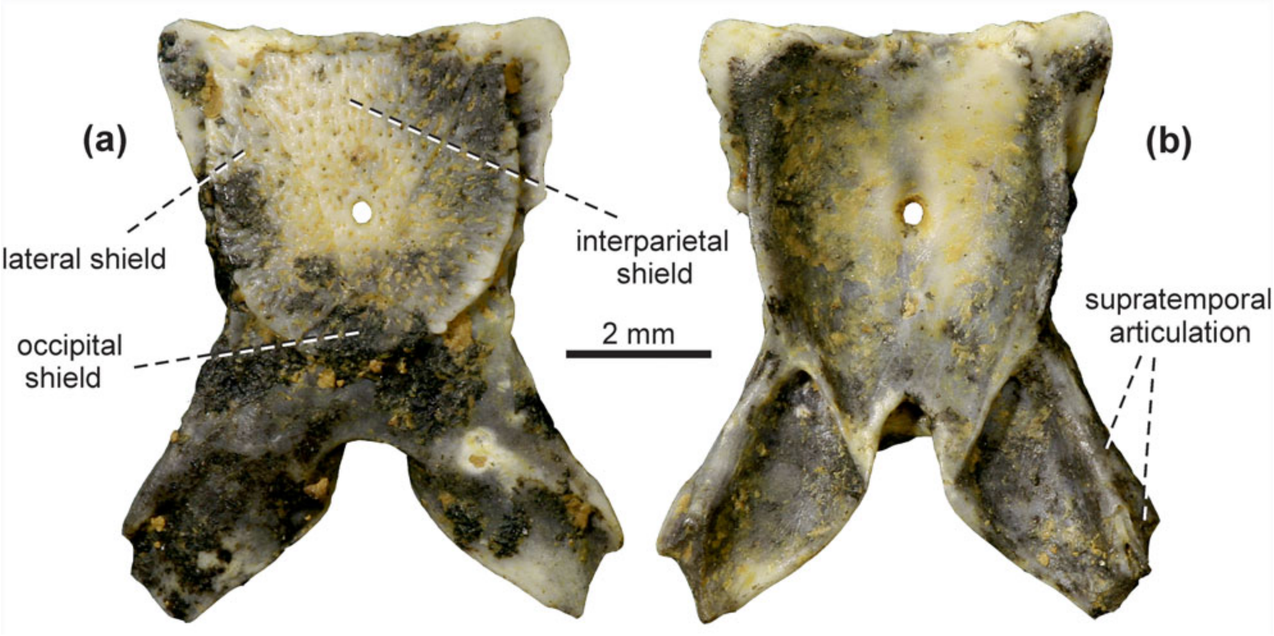

Figure 6. (Colour online) Photographs of parietal NMA-2015-37/2196 of *Ophisaurus robustus* in dorsal (a) and ventral (b) views.

laterally. In *Ophisaurus spinari*, the anteriormost section of this crest turns distinctly medially. Such course of the anterior section of the parietal crest as present in Austrian parietal is never observed in *Ophisaurus*, *Anguis* and *Pseudopus*.

(5) The presence of a muscular surface (facies muscularis). Although the lateral margins of the parietal plate of the Austrian parietal are slightly damaged, the presence of a narrow muscular surface is clearly distinguishable. The muscular surface is a typical feature of *Pseudopus* (Klembara, 1979, 1981, 2012, 2015; Klembara, Böhme & Rummel, 2010).

(6) The supratemporal process has a smooth ventrolateral surface continuous with the muscular surface of the parietal table, and the ventrolateral ridge of the supratemporal process runs medial to the lateral margin of the supratemporal process. This ventrolateral surface/muscular surface continuity is typical for *Pseudopus* (Klembara, 1979, 1981, 2012, 2015; Klembara, Böhme & Rummel, 2010).

The above analysis confirms that the parietal from the Austrian locality Gratkorn (Böhme & Vasilyan, 2014) does not represent the *Ophisaurus spinari* species. The parietal from Austria exhibits a mixture of features of *Ophisaurus*, *Anguis* and *Pseudopus*, and two characters (2 and 4 above) are not exhibited by the parietals of any known anguine (*Ophisaurus*, *Anguis* and *Pseudopus*). A complete revision of the parietal from the late Middle Miocene of Austria (Böhme & Vasilyan, 2014) is required.

Of all Recent *Ophisaurus* species, the parietal of *O. spinari* is most similar to that of *O. ventralis* (Fig. 3e, f). The parietal of *O. ventralis* shares two similar characters with that of *O. spinari*: (1) the ornamented surface is quadrangular, longer than it is wide and is of approximately equal width along its length; and (2) the occipital ornamented shield is triangular, with an almost straight posterior margin.

Ophisaurus robustus (Klembara, 1979)
Figures 5, 6

1979 *Anguis robustus* Klembara, p. 165, pl. 3, fig. 1, pl. 4, fig. 1.

1981 *Ophisaurus spinari* Klembara, p. 128, specimen DP FNSP 1020.

1981 *Ophisaurus* (?) *robustus* (cf. *Anguis*) Klembara, p. 130.

2013 *Ophisaurus* cf. *spinari* Venczel & Hír, p. 140, text-fig. 100d.

Holotype. Parietal DP FNSP 1018 (Klembara, 1979, pl. 3, fig. 1, pl. 4, fig. 1); Fig. 5a, b. Dolnice (near the city of Cheb), Early Miocene (Ottnangian), middle Orleanian, zone MN 4 (Fejfar & Kvaček, 1993).

Diagnosis. The parietal of *Ophisaurus robustus* differs from all extinct *Ophisaurus* species described on the basis of parietals and extant species of *Ophisaurus* in the following features and their combinations: (1) the ornamented shield is equal in length and width or wider than it is long; (2) the lateral margins of the lateral ornamented shields are distinctly rounded; (3) a small, elliptical occipital ornamented shield is present; and (4) the supratemporal articulation reaches the level or slightly anterior to the level of the posteromedian margin of the parietal table.

Referred specimens, locality and horizon. Parietals DP FNSP 1020, Dolnice (near the city of Cheb), Early Miocene (Ottnangian), middle Orleanian, zone MN 4

(Fejfar & Kvaček, 1993). Parietal NMA-2015-37/2196, Petersbuch 62, zone MN 3 (Bavaria) (Abdul-Aziz *et al.* 2008) (Fig. 6).

Description. The lateral margins of the ornamented surface of the parietal converge posteromedially and are distinctly rounded (Figs 5a, c, 6a). A more or less wide uncovered surface is present between the lateral margins of the ornamented surface and the parietal table. The ornamented surface is equal in length and width or wider than it is long. The anterior end of the interparietal sulcus lies in the anterolateral corner of the ornamented surface. The occipital shield is oval with the long axis running transversely. The ornamentation consists of pits, short grooves and faint ridges radiating from the centre of the ornamented surface. The position of the pineal foramen varies; it lies slightly anterior or posterior to the mid-length of the ornamented surface. The anterolateral process is moderately developed. The arcuate edge is arch-like.

The parietal cranial crest is well developed in its entire arch-like course. The postfoveal crest is absent. The ventrolateral ridge of the supratemporal process coincides with the lateral margin of the supratemporal process. The anterior end of the ventrolateral ridge of the supratemporal process joins the parietal cranial crest anterior to the level of the posteromedian margin of the parietal fossa floor. A small pit is present posterior to the pineal foramen. The frontal tab is moderately developed.

Comparisons. The *Ophisaurus robustus* parietal was originally described as *Anguis robustus* because of similarity of the parietals in both taxa, although that of *O. robustus* is more robustly constructed (Klembara, 1979). In addition, in *Anguis* the anteroposterior extent of the parietal occipital ornamented shield is greater than the anteroposterior length of the smooth area, when measured in the median plane (Fig. 9c and see below). Although there is a slight individual variability of this feature in *A. fragilis*, the smooth area is very short in most specimens of this species. This condition, typical for adult *Anguis*, is present in the juveniles of *Ophisaurus* (e.g. *O. attenuatus*, Klembara & Green, 2010, fig. 3A, B).

The following features distinguish the *Ophisaurus robustus* parietal from all extinct *Ophisaurus* species described on the basis of parietals and *Ophisaurus* extant species (the following numbers correspond to 1–4 in Fig. 5):

(1) The ornamented surface of parietal is equal in length and width or wider than it is long. This is in contrast to the always more or less longer than wide ornamented surface in adult specimens of other *Ophisaurus* species.

(2) The lateral margins of the lateral ornamented shield are distinctly rounded.

(3) A small, elliptical occipital ornamented shield. A shield of similar morphology is present in *Anguis fragilis* (e.g. Klembara, 1979, pl. 3, fig. 2). However, the lateral margin of the lateral ornamented shield is straight in *A. fragilis* (Fig. 9c further below).

(4) The supratemporal articulation lies at or slightly anterior to the level of posteromedian margin of the parietal table.

The parietal NMA-2015-37/2196 (Fig. 6) represents the first record of *Ophisaurus robustus* in Germany.

The morphology of the ornamented surface of *Ophisaurus robustus* parietal is similar to that of small specimens of extant *Ophisaurus*; in them, the ornamented surface is anteriorly and posteriorly rounded (e.g. *O. attenuatus*, Klembara & Green, 2010, fig. 3A). However, in small *O. attenuatus* the parietal is less robust, the smooth area is much shorter relative to the length of the occipital ornamented shield and the parietal cranial crest and juxtafoveal crest are very weakly developed relative to the adult specimen (Klembara & Green, 2010, fig. 3). In contrast, known *O. robustus* parietals are well developed with an equally long anteroposterior smooth area and occipital ornamented shield measured in the median plane. All these features confirm that the *O. robustus* parietals are adult specimens.

Hír *et al.* (2001) and Venczel & Hír (2013, text-fig. 100d) described a well-preserved middle portion of the parietal from the late Middle Miocene of Hungary as *Ophisaurus* cf. *spinari*. This parietal differs from that of O. *spinari* (Fig. 3a, c) by posteromedially converging and posterolaterally rounded lateral margins of the ornamented shield. These conditions are typical for the *Ophisaurus robustus* parietal (Klembara, 1979) and Figures 5a, c, 6a, the ornamented surface of which has equal width and length or is slightly wider than it is long. Unfortunately, the anteriormost portion of the parietal from Hungary is missing, so it is impossible to measure its length. Besides this, the posterior section of the parietal cranial crest of the parietal of *O. spinari* is typically concave. In contrast, it is straight in the figured parietal from Hungary (Venczel & Hír, 2013, text-fig. 100d). Thus, this parietal from Hungary is assigned to *O. robustus* here and it represents the youngest record of this species.

Ophisaurus holeci Klembara, 2015
Figures 7, 8

1981 *Ophisaurus spinari* Klembara, p. 128, specimens DP FNSP 1026, DP FNSP 1027.

2015 *Ophisaurus holeci* Klembara, p. 172, figs 1A–C, 2.

Holotype. Parietal NMP Pb 02027 (Klembara, 2015, fig. 2A, B). Opencast mine Merkur-North (near the city of Chomutov, north Bohemia, Czech Republic), North Bohemian Basin, earlier part of the Early Miocene (Eggenburgian), lower Orleanian, zone MN 3 (Fejfar & Kvaček, 1993).

Diagnosis. The parietal of *Ophisaurus holeci* differs from all extinct *Ophisaurus* species described on the basis of parietals and extant *Ophisaurus* species in the

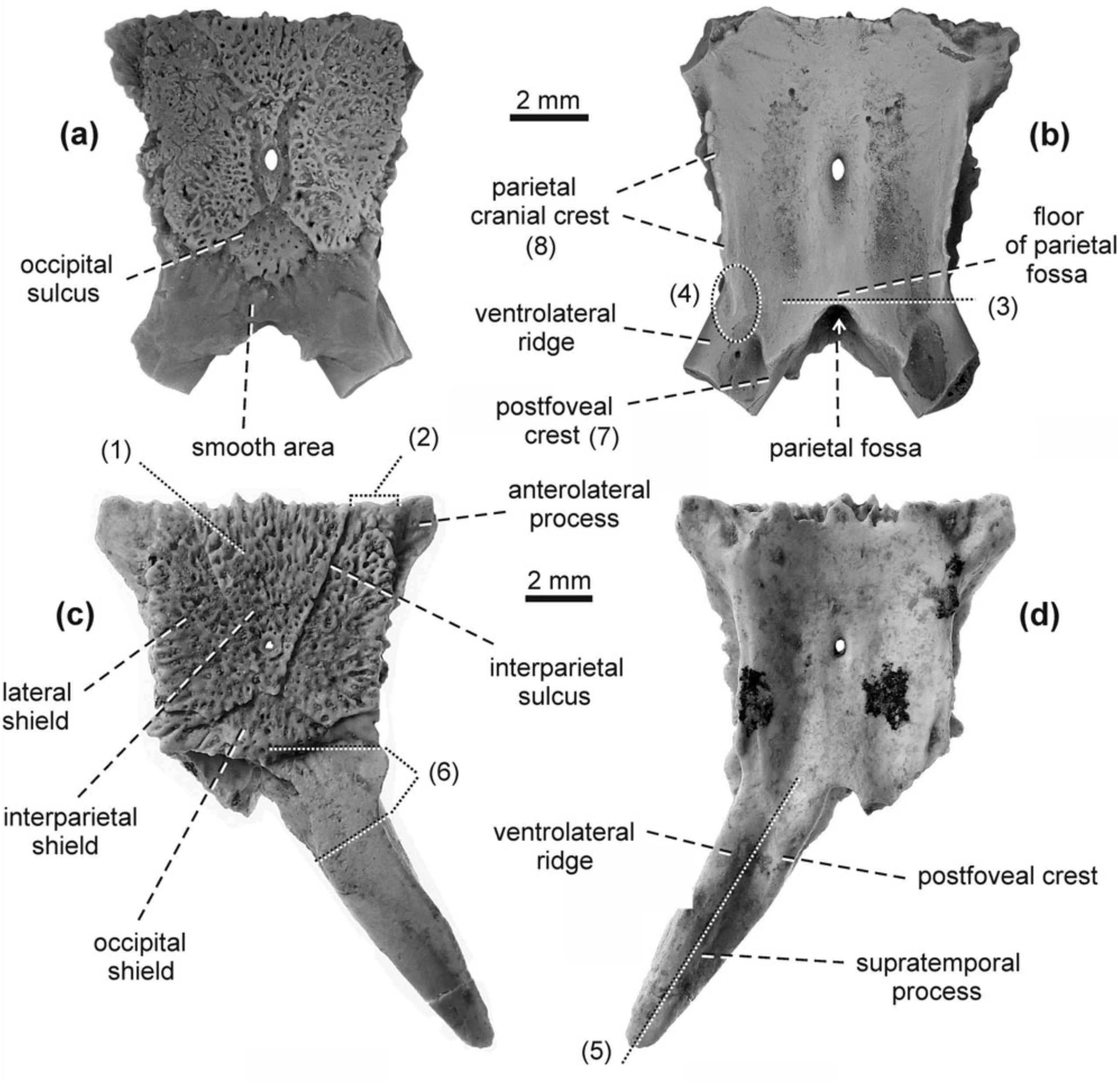

Figure 7. Photographs of parietals of *Ophisaurus holeci* in dorsal (a, c) and ventral (b, d) views. (a, b) DP FNSP 1026; (c, d) NMA-2007-69/2035. Numbers 1–8 designate distinguished features of *O. holeci* discussed in the text.

following features and their combinations (for details, see Klembara, 2015): (1) the parietal and frontal ornamentation has short, pronounced anastomosing ridges and grooves and distinct pits; (2) the anterior end of the interparietal sulcus lies medial to the anterolateral corner of the ornamented surface; (3) the anterior end of the ventrolateral ridge of the supratemporal process joins the parietal cranial crest at or slightly posterior to the posteromedian margin of the parietal fossa floor; (4) the posterior section of parietal cranial crest is very low, especially at its junction with the ventrolateral ridge of the supratemporal process; (5) the supratemporal process is straight; (6) the base of the supratemporal process is mediolaterally narrow; (7) a short postfoveal crest is present; and (8) a long anterior section of parietal cranial crest is more or less distinctly concave or straight.

Referred specimens, locality and horizon. Parietals DP FNSP 1026 (Fig. 7a, b), ?DP FNSP 1027, ?DP FNSP 1029, Dolnice (near the city of Cheb), Early Miocene (Ottnangian), middle Orleanian, zone MN 4 (Fejfar & Kvaček, 1993). Parietal NMA-2007-69/2035, Petersbuch 39-III (Bavaria), zone MN 5 (Klembara, Böhme & Rummel, 2010) (Fig. 7c, d). Parietals NMA-2015-33/2196 (Fig. 8a, b) and NMA-2015-35/2196 (Fig. 8c, d), Petersbuch 62, zone MN 3 (Bavaria) (Abdul-Aziz *et al.* 2008).

Description. The parietal DP FNSP 1026 (Fig. 7a, b) and those from Germany (Fig. 8) are similar in size

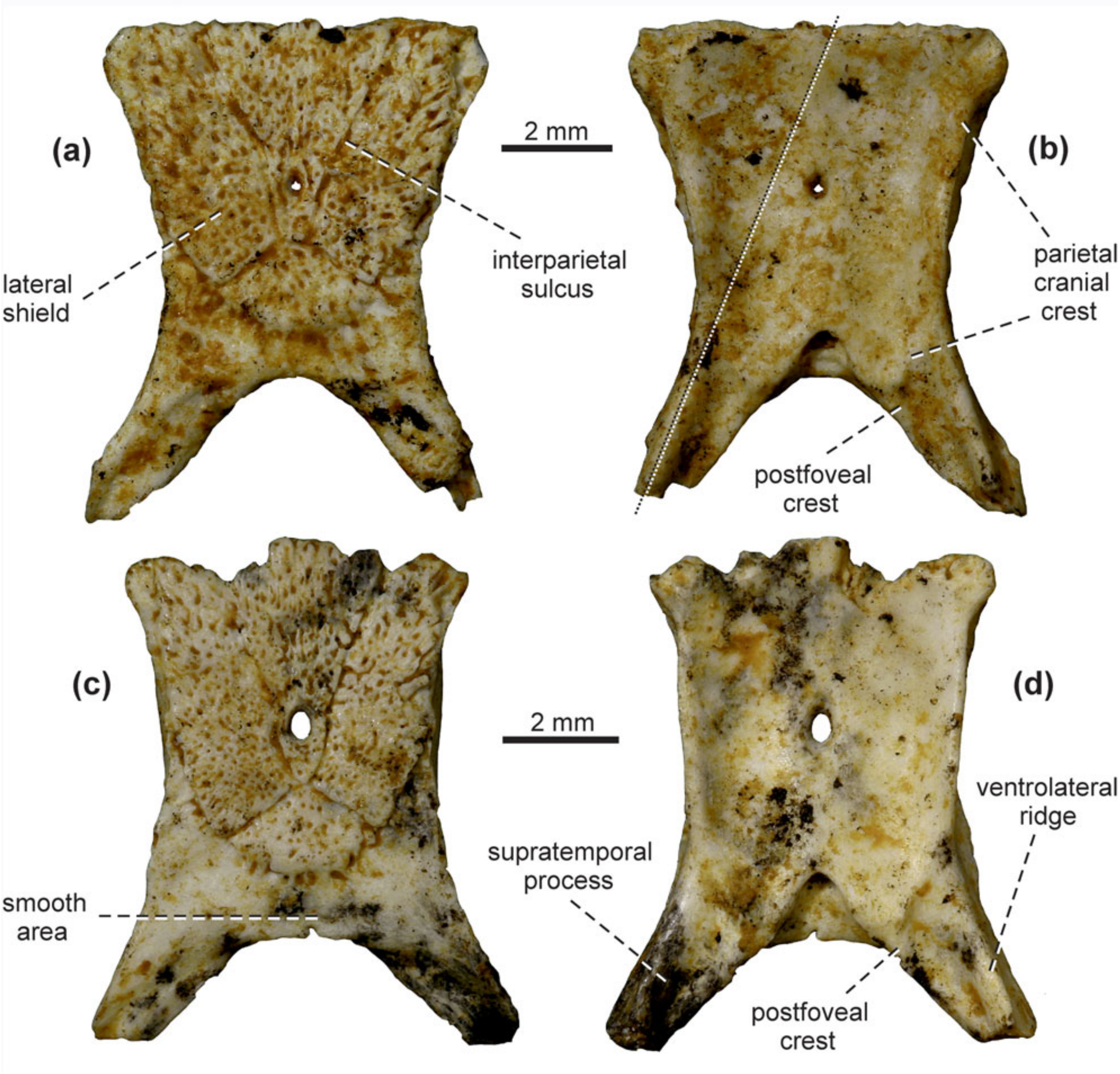

Figure 8. (Colour online) Photographs of parietals of *Ophisaurus holeci* in dorsal (a, c) and ventral (b, d) views. (a, b) NMA-2015-33/2196; (c, d) NMA-2015-35/2196.

and morphology to those described recently (Klembara, 2015). Specimen NMA-2007-69/2035 (Fig. 7c, d) from Germany represents the largest parietal of *Ophisaurus holeci*. The ornamented surface is slightly longer than it is wide and its lateral margins converge slightly posteromedially. The anterior end of the interparietal sulcus lies medial to the anterolateral corner of the ornamented surface. The occipital ornamented shield is a more or less wide triangle with a slightly convex posterior margin. The anterolateral process is distinctly developed. A small pineal foramen lies immediately posterior to the mid-length of the ornamented shield. The right supratemporal process is completely preserved in NMA-2007-69/2035 (Fig. 7c, d) and is typically straight. The bases of the supratemporal processes are typically mediolaterally narrow relative to those of other species of *Ophisaurus*.

The posterior section of the parietal cranial crest is very indistinct, especially at the junction with the anterior end of the ventrolateral ridge of the supratemporal process. This junction lies at the level of or slightly posterior to the posteromedian margin of the parietal fossa floor. The ventrolateral ridge of the supratemporal process coincides with the lateral margin of the supratemporal process. A short postfoveal crest is present.

Comparisons. The parietal of *Ophisaurus holeci* is distinguished by the following features and their combinations (the following numbers correspond to 1–8 in Fig. 7):

(1) The parietal and frontal ornamentation has short, pronounced anastomosing ridges and grooves and distinct pits.

(2) The anterior end of the interparietal sulcus lies medial to the anterolateral corner of the ornamented surface. In *O. fejfari*, *O. spinari* and *O. robustus*, the anterior end of the interparietal sulcus lies in the anterolateral corner of the parietal ornamented shield. In the Recent *O. attenuatus*, the condition is almost the same as in *O. holeci*; however, *O. holeci* differs from *O. attenuates* in features 3–7 listed below.

(3) The anterior end of the ventrolateral ridge of the supratemporal process joins the parietal cranial crest at or slightly posterior to the posteromedian margin of the parietal fossa floor. In contrast, in all other species of *Ophisaurus* the anterior end of the ventrolateral ridge of the supratemporal process joins the parietal cranial crest anteriorly to the level of the posteromedian margin of the parietal fossa floor.

(4) The posterior section of the parietal cranial crest is very low, especially at its junction with the ventrolateral ridge of the supratemporal process. In all other species of *Ophisaurus*, the parietal cranial crest is a distinct ridge at its junction with the ventrolateral ridge of the supratemporal process.

(5) The supratemporal process is straight. In other species of *Ophisaurus* there is always an angle between the base and the posterior section of the supratemporal process.

(6) The base of the supratemporal process is mediolaterally narrow (the width of the base is less than half the width of the parietal table measured at the level of maximum constriction of the parietal table – at the level of the posterior portion of the occipital ornamented shield).

(7) A short postfoveal crest is present (a similar crest is present also in *O. fejfari*; however, the parietal of *O. fejfari* lacks characteristics 1–6 above).

(8) A long anterior section of the parietal cranial crest is more or less distinctly concave (see also Klembara, 2015, fig. 2B, D). In *Ophisaurus fejfari*, this section of the crest is straight and in *O. spinari* and *O. robustus* is convex.

The parietal NMA-2007-69/2035 (Fig. 7c, d) from Germany differs from smaller specimens by its slightly larger anterolateral process and wider occipital ornamented shield. This parietal represents the largest specimen of *O. holeci*, and together with two other parietals from Germany (Fig. 8) represents the first record of this species outside the Czech Republic.

The parietal of *Ophisaurus holeci* is similar to those of *Ophisaurus roqueprunensis* from the Early to Late Oligocene of France and Belgium (Augé & Smith, 2009) and *Ophisaurus* sp. from the Late Eocene of the Hampshire Basin described by Klembara & Green (2010) in two features: (1) the anterior end of the ventrolateral ridge of the supratemporal process joins the posterior section of the parietal cranial crest slightly posteriorly to the level of the posteromedian margin of the parietal fossa floor; and (2) the posterior section of the parietal cranial crest is very low, especially at its junction with the posterolateral ridge of the supratemporal process. These two features are recognized only in these three taxa; the conditions in *Ophisauriscus quadrupes* from the Middle Eocene of Germany (Sullivan, Keller & Habersetzer, 1999) require revision in this respect. On the other hand, the parietals of *Ophisaurus roqueprunensis* and *Ophisaurus* sp. differ from the parietal of *O. holeci* by the two following characters: (1) the smooth area of the parietal of *O. roqueprunensis* and *Ophisaurus* sp. is slightly longer than the length of the occipital ornamented shield, when measured in the median plane; and (2) the postfoveal crest is absent in *O. roqueprunensis* and *Ophisaurus* sp. (Augé & Smith, 2009; Klembara & Green, 2010). These two latter features need to be revised also in *Ophisauriscus quadrupes*.

Ophisaurus acuminatus Jörg, 1965

Holotype. Partial skull SMNK-PAL.8561; Heweneg/Hegau (near city Öhningen), Germany.

Diagnosis. After Jörg (1965).

Locality and horizon. Heweneg/Hegau (near city Öhningen), Germany; lower Late Miocene, zone MN 9 – MN 10.

Remarks. The general morphology of preserved cranial elements of *Ophisaurus acuminatus* corresponds to that in fossil or extant species of *Ophisaurus*. The maxillary and dentary teeth of *O. acuminatus* are most similar to those in Anguine morphotype 1 from the Early Miocene locality Merkur (MN 3; the Czech Republic) (Klembara, 2015). The teeth are recurved posteriorly and their apices bear anterior and posterior cutting edges. Although the parietal bone is missing in this species, the ornamented surfaces of frontal and nasal bones are preserved. Comparison of equal-sized bones of *O. acuminatus* with those of all other species of *Ophisaurus* described here shows that the ornamentation of the preserved skull roof bones in *O. acuminatus* is much more robustly developed.

Ophisaurus canadensis Holman, 1970

Holotype. Dorsal vertebra ROM 7705, Upper Miocene, Kleinfelder Farm locality of the Wood Mountain Formation near Rockglen, Saskatchewan, Canada.

Diagnosis. After Holman (1970).

Locality and horizon. Kleinfelder Farm locality of the Wood Mountain Formation near Rockglen, Saskatchewan, Canada. Upper Miocene.

Remarks. According to Holman (1970), the dorsal vertebra is most similar to those of Recent North American *Ophisaurus ventralis* and *O. attenuatus*. However, it differs in having a rounded anterior portion of neural arch which extends almost as far as the anterior edges of prezygapophyses; prezygapophyses are not so dorsally extended (see Estes, 1983). While additional material is required to confirm feature validity and justify the species existence, this dorsal vertebra documents *Ophisaurus* presence in the Late Miocene of North America and its distinction as the oldest currently recognized *Ophisaurus* record in North America.

Ophisaurus roqueprunensis Augé, 1992

1992 *Ophisaurus roqueprunensis* Augé, p. 160, fig. 1A, B.

2005 *Dopasia roqueprunensis* Augé, p. 234.

2009 *Dopasia roqueprunensis* Augé & Smith, p. 152.

2016 *Ophisaurus roqueprunensis* Čerňanský, Klembara & Müller, p. 23.

Holotype. Left dentary IRScNB No. R120, Middle Oligocene (zone MP 23), Roqueprune, Phosphorites du Quercy, France.

Diagnosis. After Augé (1992); emended diagnosis (Augé & Smith, 2009).

Localities and horizons. Early Oligocene, Boutersem, Hoogbutsel (MP 21), Belgium; Early Oligocene – Late Oligocene, Phosphorites du Quercy (MP 23 – MP 28), Roqueprune (MP 23), Belgarric (MP 25), Rigal-Jouet (MP 25), Pech du Fraysse (MP 28), France.

Remarks. This species is present from the Early to Late Oligocene of France and Belgium and is based on dentaries, maxillae, one incomplete parietal, dorsal and caudal vertebrae and numerous osteoderms (Augé & Smith 2009).

Genus *Anguis* Linnaeus, 1758

Anguis rarus sp. nov.

Figure 9a, b

Holotype. Parietal NMA-2015-34/2196, Petersbuch 62 (Bavaria, south Germany), zone MN 3 (Fig. 9a, b).

Diagnosis. The parietal of *Anguis rarus* sp. nov. differs from the parietal of *A. fragilis* by the following combination of features: (1) more diverging bases of supratemporal processes; (2) the anterior end of the interparietal sulcus lies in the anterolateral corner of the parietal ornamented shield; and (3) the anterior end of the supratemporal articulation reaches anterior to the level of the posteromedian margin of the parietal table.

Derivation of name. From the Latin *rarus* – rare, indicating very rare record of *Anguis* in the Miocene.

Locality and horizon. Petersbuch 62 (Bavaria), zone MN 3 (Abdul-Aziz *et al.* 2008) (Fig. 9a, b).

Description. The parietal is almost completely preserved; only the posterior tip of the right supratemporal process is broken (Fig. 9a). The parietal table is anteroposteriorly elongated and its lateral margins converge slightly posteromedially. The anterolateral processes are moderately developed. The ornamented surface is longer than it is wide and covers most of the surface of the parietal table. Ornamentation consists of low tubercles and short ridges, and deep pits with longer ridges and grooves present only on the anterolateral margin of the ornamented surface. The anterior end of the interparietal sulcus lies in the anterolateral corner of the ornamented surface. The lateral margin of the parietal ornamented shield reaches the lateral margin of the parietal table. The occipital ornamented shield is triangular, but its posterior margin is slightly rounded. The smooth area of the parietal table immediately posterior to the ornamented surface is anteroposteriorly shorter than the anteroposterior length of the occipital shield (measured in the median plane). The supratemporal processes extend posterolaterally. The arcuate crest forms a shallow arch and its posterior end gradually passes into the medial margin of the supratemporal process.

The parietal cranial crest forms a moderate convex arch and reaches the lateral margin of the parietal table (Fig. 9b). The anterior section of the ventrolateral ridge of the supratemporal process coincides with the lateral margin of the supratemporal process. The anterior end of the ventrolateral ridge joins the parietal cranial crest anterior to the level of the posteromedian margin of the parietal fossa floor. The anterior end of the supratemporal articulation reaches the level of the posteromedian margin of the parietal table.

Comparisons. Specimen NMA-2015-34/2196 is the only parietal of *Anguis* from the Miocene and together with the vertebrae (Klembara, 1981) unambiguously documents the presence of *Anguis* in this geological period.

As already indicated earlier (Klembara, 2015), the parietals of *Anguis* and *Ophisaurus* are very similar, but they differ in one feature: in *Anguis*, the anteroposterior length of the smooth area lying immediately posterior to the ornamented surface of the parietal table is distinctly shorter than the anteroposterior length of the occipital ornamented shield (when measured in the median plane). This is quite apparent in both the extant *Anguis* and the parietal described here (Fig. 9a, c). Although this feature is evident in distinguishing the parietals of *Ophisaurus* and *Pseudopus* on the one hand and *Anguis* on the other, there is a slight variability as for the anteroposterior length of the occipital ornamented shield and the length of the smooth area of the parietal table (measured in the median plane). In most specimens of *A. fragilis*, the occipital ornamented shield is two or sometimes three times longer than the smooth area (Fig. 9c). In all specimens of *A. fragilis* studied here, however, the occipital shield is always slightly longer than the smooth area. Occasionally, in specimens of some *Ophisaurus* species the conditions may be similar to those of *Anguis*. For example, in the parietal NMA-2015-33/2196 of *O. holeci* the occipital ornamented shield is longer than the smooth area. This condition is mostly due to a secondary fusion of a small more posteriorly lying osteoderm to the posterior margin of the occipital ornamented shield (Fig. 8a). However, taking into account other parietal characters for

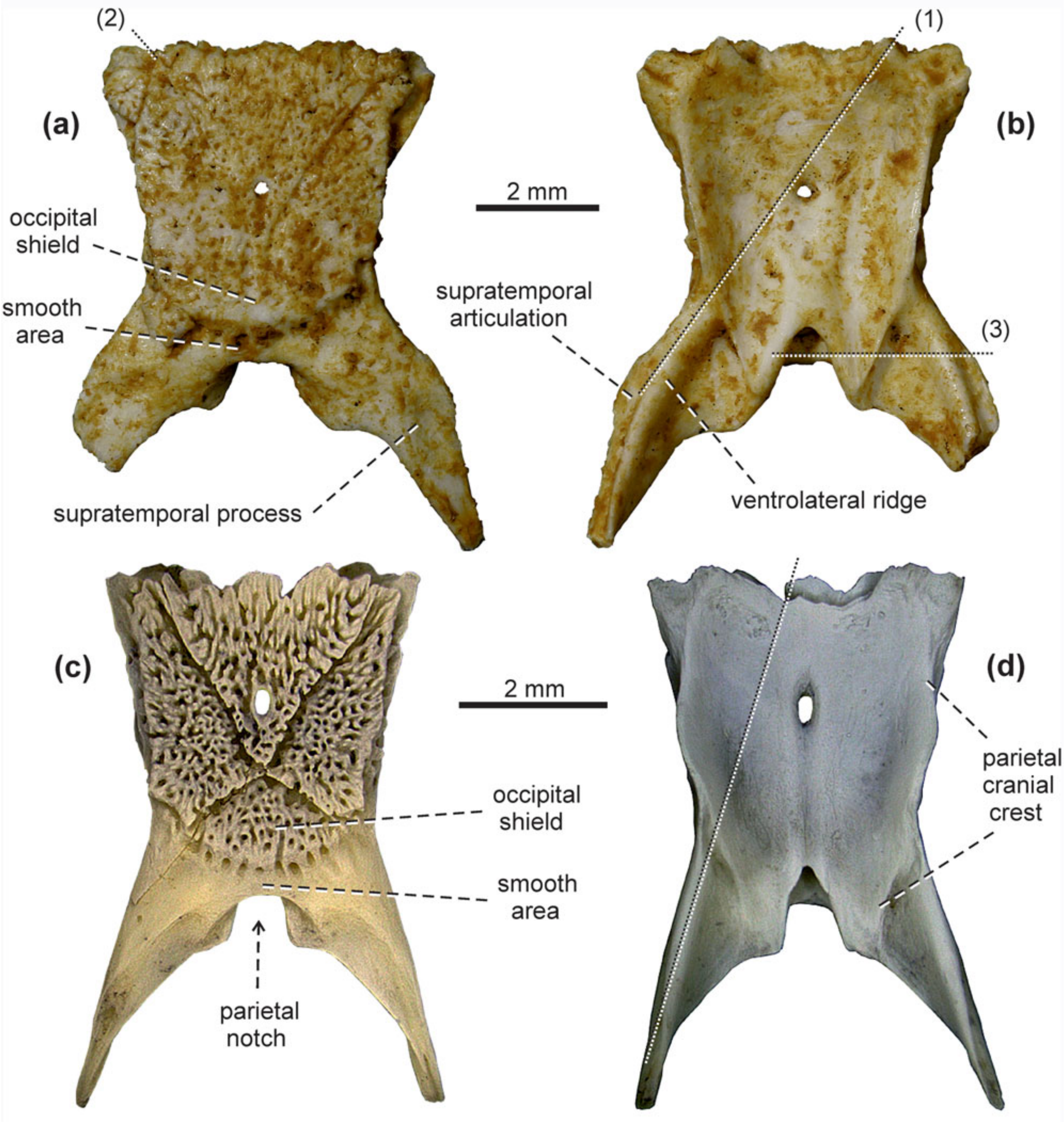

Figure 9. (Colour online) (a, b) NMA 2015-34/2196, photographs of parietal of *Anguis rarus* sp. nov. in dorsal (a) and ventral (b) views; numbers 1–3 designate distinguished features of *A. rarus* discussed in the text. (c, d) DE 19, photographs of parietal of *Anguis fragilis* in dorsal (c) and ventral (d) views.

comparison it is evident that the parietal NMA-2015-33/2196 cannot represent the species of *Anguis*.

The comparisons below do not include *Anguis polgardiensis* from the Late Miocene of Hungary (Bolkay, 1913). As analysed recently (Klembara, 2015), it is not possible to decide unambiguously whether the incomplete parietal of this species represents *Anguis* or *Ophisaurus*.

The parietal of *Anguis rarus* sp. nov. exhibits no autapomorphy. However, it differs from the parietal of *A. fragilis* by the following combination of features (the following numbers correspond to 1–3 in Fig. 9a, b):

(1) Strongly diverging bases of the supratemporal processes. This is the same as in *Ophisaurus fejfari* (cf. Figs 1b and 9b); however, contrary to *A. rarus*, *O. fejfari* exhibits the following characteristics: (i) the lateral margins of the parietal table converge posteriorly and a distinct constriction is present at the transition of the parietal table and the bases of the supratemporal processes; (ii) the parietal cranial crest is almost straight, except for its anteriormost section; and (iii) a short postfoveal crest is present.

(2) The anterior end of the interparietal sulcus lies in the anterolateral corner of the parietal ornamented

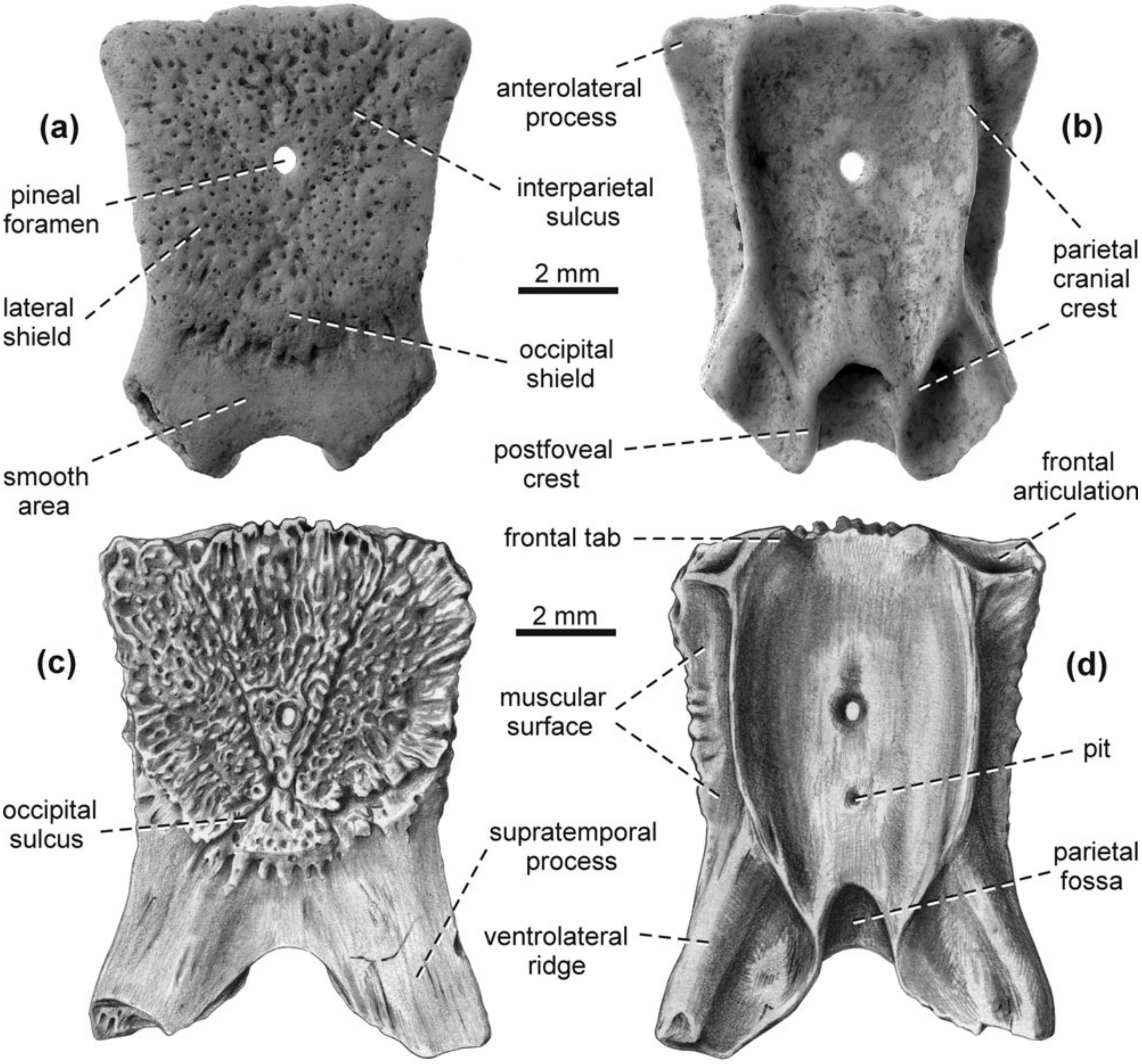

Figure 10. Photographs (a, b) and drawings (c, d) of parietals of *Pseudopus* sp. in dorsal (a, c) and ventral (b, d) views. (a, b) NMA-2007-86/2035; (c, d) SNM PP 1393 (from Klembara, 1986*a*, pl. 1).

shield. In *Anguis fragilis*, the anterior end of the interparietal sulcus lies slightly medial to the anterolateral corner of the parietal ornamented shield (Fig. 9c and Klembara, 1979, pl. 3, fig. 2). The same condition as that of *A. rarus* is present in several species of *Ophisaurus* (see above) and *Pseudopus ahnikoviensis* (Klembara, 2012); however, in *A. rarus* (and *A. fragilis*) the anteroposterior length of the occipital ornamented shield is about twice the anteroposterior length of the smooth area (measured in the median plane).

(3) The anterior end of the supratemporal articulation reaches anterior to the level of the posteromedian margin of the parietal table. A similar condition is present in *Ophisaurus robustus*; however, the ornamented shield of the parietal of *O. robustus* has distinctly rounded anterolateral and posterolateral corners. This feature is absent in *Anguis rarus*.

Młynarski (1962) reported the presence of jaw fragments, osteoderms and vertebrae of *Anguis* at several Pliocene and Pleistocene localities in Poland. He figured the left dentary from the Pliocene locality Węże I and designated it as *Anguis* cf. *fragilis* (Młynarski, 1962, pl. 14, fig. 3). Unfortunately, he gives no detailed description, and the posterior portion of the dentary is not visible on the photograph of this bone. Thus, it is not visible whether the dentary has the surangular spine or not. This spine is present in *Ophisaurus*, but absent in *Anguis* (Klembara, Hain & Dobiašová, 2014). However, the morphology of the robust teeth, the position of the splenial spine at the level of the third tooth from posterior and a much longer coronoid process than the surangular process of the dentary could indicate that this dentary may belong to *Ophisaurus*. A dentary of similar morphology, including teeth, was described by

Venczel (2006) from the Late Miocene (MN 13) of Hungary. Anyway, the revision of the dentary from Poland is needed.

Augé (2005) and Rage & Augé (2010) described one left dentary from the Middle Eocene (MP 14) of Lissieu (France) as *Anguis* sp. (figured in Augé, 2005, fig. 161). From the point of the determination, this dentary exhibits the following important features: (1) sharp, pointed teeth strongly recurved distally and lingually; (2) absence of a surangular spine; and (3) splenial spine lying at the level of the second tooth from the posterior. These features strongly indicate that this dentary is from *Anguis*.

Augé (2005) also described a parietal from the Middle Eocene (MP 16) locality Le Bretou in France as *Anguis* sp. However, (1) the smooth area of this parietal is long anteroposteriorly and much longer than that of the occipital ornamented shield; and (2) the parietal does not have a distinct parietal notch. These characteristics reflect partial similarity of this Middle Eocene parietal to the Late Eocene *Headonhillia parva* (Klembara & Green, 2010).

?*Anguis polgardiensis* Bolkay, 1913

1983 *Ophisaurus pannonicus* Estes, p. 141, fig. 34A.

Holotype. Not designated. Polgárdi, Bányahegy, Late Miocene, Hungary.

Diagnosis. After Bolkay (1913).

Referred specimens, locality and horizon. All specimens (parietal, 2 maxillae, fragment of dentary) of this species were lost (personal information of Professor L. Kordos of the Hungarian Geological Museum in Budapest, Hungary). Polgárdi, Bányahegy, Late Miocene (MN 13), Hungary.

Remarks. This species is based on one incomplete parietal, two maxillae and a fragment of the dentary. The morphology of this species parietal was recently revised by Klembara (2015) who concluded that it is impossible to decide now whether this parietal belongs to *Anguis* or *Ophisaurus*. The teeth of maxilla and dentary described by Bolkay (1913) are more robust than those of *A. fragilis*, thus indicating the *Ophisaurus* affinity (Venczel, 2006).

Anguis stammeri Brunner, 1954

Holotype. Right dentary (BSPG; number not assigned), Late Pleistocene, Fuchsloch, Siegmannsbrunn, Germany.

Diagnosis. After Brunner (1954, 1957) and Estes (1983).

Locality and horizon. Upper Pleistocene, Fuchloch, Siegmannsbrunn, Germany.

Remarks. This species is based on the right dentary. According to Brunner (1957), the robust teeth differ from those of the extant *Anguis fragilis*. According to Młynarski (1962), the dentary of *A. stammeri* belongs to *Ophisaurus*. However, the teeth of the specimen described as *Anguis* cf. *fragilis* by Młynarski (1962) are similar to those of *A. stammeri*. Revision of *A. stammeri* is therefore required.

Genus *Pseudopus* Pallas, 1775
Pseudopus sp.
Figure 10

1986*a Ophisaurus spinari* Klembara, p. 189, figs 1, 2, pl. 1.

Referred specimens, locality and horizon. Parietal NMA-2007-86/2035, Petersbuch 73 (Bavaria), zone MN 7/8 (Klembara, Böhme & Rummel, 2010), Fig. 10a, b; parietal SNM PP 1393, Devínska Nová Ves (west Slovakia), zone MN 6 (Klembara, 1986*a*), Fig. 10c, d.

Description. The parietal table and bases of the supratemporal processes are well preserved in both specimens (Fig. 10). The ornamented surface has equal length and width or is slightly longer than it is wide. Its lateral margins converge slightly posteromedially. The ornamented surface is eroded, but short ridges, grooves and pits are easily recognizable. Several short grooves are clear at the periphery of the ornamented surface. The anterior end of the interparietal sulcus lies slightly medial to the anterolateral corner of the ornamented surface. The ornamentation of the lateral shield slightly extends to the surface of the anterolateral process of the parietal table. In NMA-2007-86/2035, the pineal foramen lies slightly anterior to the mid-length of the ornamented surface (Fig. 10a), whereas in SNM PP 1393 the pineal foramen lies slightly posterior to the mid-length of the ornamented surface (Fig. 10c). The occipital shield is triangular with a slightly convex posterior margin. The arcuate edge forms a shallow arch. The anterolateral process is moderately developed.

The parietal cranial crest forms a high and sharp wall. The muscular surface is present. The ventrolateral ridge of the supratemporal process is well developed. It joins the parietal cranial crest anterior to the posteromedian margin of the parietal fossa floor. There is a small, shallow pit posterior to the pineal foramen. A well-developed postfoveal crest is present.

Comparisons. Both parietals are very similar to that of *Pseudopus laurillardi*, but they have less distinctly developed anterolateral processes of the parietal table than those in *P. laurillardi* (Klembara, Böhme & Rummel, 2010) when compared with similar size specimens. Distinctly extending anterolateral processes of the parietal are also present in *P. ahnikoviensis*, but the parietal ornamentation is completely different in the latter species (Klembara, 2012). The poorly developed anterolateral processes of the parietal are present in the Early Miocene *P. rugosus* (Klembara, 2015; however, see below), but *Pseudopus* sp. differs from *P. rugosus* in two features: (1) the ornamentation of the parietal comprises short ridges and grooves that are not so densely arranged as those in the parietal of *P. rugosus*; and (2) in ventral view, the pineal foramen lies anterior to the mid-distance between the anterior margin of the parietal table and the posteromedian margin of the parietal fossa floor, when measured in the median plane.

The parietals of *Pseudopus* sp. have similar geological age and are contemporaneous with the latest documented records of *P. laurillardi* (Klembara, Böhme & Rummel, 2010). The poorly developed anterolateral processes are the only feature distinguishing *Pseudopus* sp. and *P. laurillardi*, so we have not created a new specific name for this anguine pending availability of more complete material.

Pseudopus confertus sp. nov.

2015 *Pseudopus rugosus* Klembara, p. 179, fig. 4.

Holotype. Frontal NMP Pv 10028; Merkur-North opencast mine (near Chomutov city, north Bohemia, Czech Republic).

Diagnosis. After Klembara (2015).

Localities and horizons. Merkur-North opencast mine (near Chomutov), the earliest part of the Early Miocene (Eggenburgian), lower Orleanian, zone MN 3 (Fejfar & Kvaček, 1993).

Derivation of name. From the Latin *confertus* – squeezed-in, indicating the densely arranged ridges and grooves on the ornamented surface of the frontal and parietal.

Remarks. Recently, Klembara (2015) described a new species of *Pseudopus*, *P. rugosus*, from the Merkur locality. Although Troschel (1860) previously applied this name to a snake-like reptile from the Late Oligocene locality of Rott bei Bonn (Germany), it was also similar to the one he described as *Thoracophis rugosus* from the same locality (see Rage & Augé, 1993). Troschel (1860) further noted that the new animal from Rott is more like the modern *Pseudopus* lizard than a snake. This was probably the reason to replace the generic name *Thoracophis* with *Pseudopus*. Fejérváry-Láng (1923) and Estes (1983) suggested that the name *Pseudopus rugosus* could be a senior synonym of *Ophisaurus moguntinus* (Boettger, 1875), that is, *Pseudopus laurillardi* (Klembara, Böhme & Rummel, 2010). But the specimen is presumably lost and no description, depiction or photograph exists. There is therefore doubt about which animal Troschel named *P. rugosus*. Theoretically, the animal he referred to as *Pseudopus rugosus* may be rediscovered, proving his appellation valid, and therefore we have created the new name, *Pseudopus confertus* sp. nov., for the Merkur anguine (Klembara, 2015, p. 179, fig. 4).

Pseudopus ahnikoviensis Klembara, 2012

Holotype. Parietal NMP Pb 02026. Opencast mine Merkur-North (near Chomutov).

Diagnosis. Pseudopus ahnikoviensis is distinguished from all other species of *Pseudopus* by the following features and the combination of features: (1) the length of a sulcus between the frontal and frontoparietal ornamented shields equals the length of the sulcus between the frontal and interfrontal shields; (2) the ornamented surface of the parietal consisting of densely arranged very fine ridges, grooves, and pits; (3) the ventrolateral ridge of the supratemporal process of the parietal coincides with the lateral margin of the supratemporal process; (4) the presence of the surangular spine of dentary; (5) the apices of crowns of robust bulbous teeth smooth; and (6) the posterior margin of the anterior inferior alveolar foramen formed by a splenial. For the analysis of these characteristics, see Klembara (2012).

Localities and horizons. Opencast mine Merkur-North (near Chomutov), North Bohemian Basin, earlier part of the Early Miocene (Eggenburgian), lower Orleanian, zone MN 3 (Fejfar & Kvaček, 1993).

Pseudopus laurillardi (Lartet, 1851)

Neotype. Left dentary MNHN Sa 23604. Sansan, Gers, France.

Diagnosis. After Klembara, Böhme & Rummel (2010).

Localities and horizons. Sansan, Gers, France. Astaracien, zone MN 6, Middle Miocene (Augé & Rage, 2000, p. 277, fig. 9).

Pseudopus pannonicus (Kormos, 1911)

Neotype. Mandible (number not assigned) deposited in the Hungarian Geological Institute, Budapest, Hungary.

Diagnosis. After Kormos (1911) and Fejérváry-Lángh (1923). As for lower jaw, see Klembara, Böhme & Rummel (2010).

Localities and horizons. Polgárdi 2 (Hungary), Upper Miocene (Turolian), zone MN 13 (Kormos, 1911; Tempfer, 2009).

Genus *Ophisauromimus* Čerňanský, Klembara & Müller, 2016

Ophisauromimus coderetensis (Augé, 2005)

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

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

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

2016 *Ophisauromimus coderetensis* Čerňanský, Klembara & Müller, p. 23, fig. 14.

Holotype. Right dentary (UCBL No. 97684), Upper Oligocene (MP 30), Coderet, France.

Diagnosis. After Augé (2005).

Localities and horizons. Itardies, Lower Oligocene (MP 23) and Coderet, Upper Oligocene (MP 30), Phosphorites du Quercy, France.

Remarks. This species is based on dentaries, maxilla fragments, one parietal and a mandible posterior portion. The parietal attributed to this species is so poorly preserved that comparisons are impossible (Augé, 2005, fig. 165a, b). Recently Rage & Augé (2015) have described an anguine as *Dopasia* s.l. sp. on the basis of one dentary and several trunk and caudal vertebrae from the Early Oligocene (MP 22) Valbro locality of France (Quercy).

Ophisauromimus frayssensis (Augé, 2005)

2005 *Dopasia frayssensis* Augé, p. 235, fig. 154.

2016 *Ophisauromimus frayssensis* Čerňanský, Klembara & Müller, p. 22.

Holotype. Right dentary NMHN No. PFR11003. Pech-du Fraysse, Phosphorites du Quercy, Upper Oligocene (MP 28), France.

Diagnosis. After Augé (2005) and Čerňanský, Klembara & Müller (2016).

Localities and horizons. Pech-du Fraysse and Pech Desse, Upper Oligocene (MP 28), Phosphorites du Quercy, France.

Remarks. This species is based on dentaries and dorsal vertebrae (Augé 2005).

Genus *Ragesaurus* Bailon & Augé, 2012
Ragesaurus medasensis Bailon & Augé, 2012
aff. *Ophisaurus* Bailon (unpub. Ph.D. thesis, Univ. Paris, 1991)

Holotype. Right dentary UM MED-121. Meda Grande, îles Medas, Catalonia, Spain.

Diagnosis. After Bailon & Augé (2012).

Locality and horizon. Lower Pleistocene; Meda Grande, îles Medas, Catalonia, Spain.

Remarks. The dentary of this Lower Pleistocene species is like that of the Oligocene species of *Ophisauromimus* in similar morphology of the intramandibular septum forming a large, perpendicular septum extending posteriorly to a small process, and the ventrolateral margin of the septum is free (Čerňanský, Klembara & Müller, 2016). These features are not present in *Ophisaurus*. *Ragesaurus medasensis* differs from all other anguines in which the marginal dentition is preserved in the following features (Bailon & Augé, 2012): (1) the anterior inferior alveolar foramen is medially bordered by a small perpendicular septum; (2) the Meckelian groove is very narrow in the mid-length of the dentary in ventral view; and (3) the teeth are conical and their bases are not mediodistally widened; their apices are unstriated and their mesial and distal cutting edges are absent.

Genus *Headonhillia* Klembara & Green, 2010
Headonhillia parva Klembara & Green, 2010

Holotype. Parietal BMNH R13522. Bembridge Limestone Formation, Headon Hill, Isle of Wight, UK.

Diagnosis. Headonhillia is distinguished from other anguines on the basis of the following combination of features: (1) small size (the smallest of all the anguines; it approaches the size of *Anguis fragilis* and juveniles of *Ophisaurus*); (2) large smooth area of parietal table (twice the length of the occipital shield, and anteroposteriorly the longest of any anguine); and (3) short postfoveal crest which is about a quarter of the length of the posterior section of the parietal cranial crest. For the analysis of these characters, see Klembara & Green (2010).

Locality and horizon. Late Eocene, Ludian (Priabonian); Bed 6, Bembridge Limestone Formation, Headon Hill, Isle of Wight, UK.

Genus *Ophisauriscus* Kuhn, 1940
Ophisauriscus quadrupes Kuhn, 1940

Holotype. Almost complete specimen GM Ce VII-804; upper middle coal MP 13, Geiseltal, Grube Cecilie site VII (Ce VII), Germany.

Diagnosis. After Kuhn (1940) and Sullivan, Keller & Habersetzer (1999).

Locality and horizon. Grube Cecilie site VII (Ce VII), upper middle coal MP 13, Geiseltal, Germany.

Remarks. Meszoely & Haubold (1975) were the first to note the affinity of *Ophisauriscus quadrupes* to Anguinae. Klembara (1981) came to a similar conclusion. Sullivan, Keller & Habersetzer (1999) revised all finds assigned to Anguidae by Kuhn (1940) and assigned *O. quadrupes* as belonging to ?'Anguinae', the taxon based on plesiomorphies and thus no support for its homology. Conrad (2008) and Conrad *et al.* (2011) questioned the affinity of *O. quadrupes* to Anguinae. Because there is no convincing anatomical evidence that would clearly pose *O. quadrupes* outside Anguinae, here it is included tentatively in Anguinae. However, a review of *O. quadrupes* is required to resolve its relationships.

It is necessary to emphasize that there are two features of the parietal which are similar in the Oligocene species *Ophisaurus roqueprunensis* (France and Belgium) and the Eocene taxa *Ophisaurus* sp., *Headonhillia parva* (England) and *Ophisauriscus quadrupes* (Germany): (1) the smooth area is longer than that of the occipital shield, when measured in the median plane; and (2) the anterior end of the ventrolateral ridge of the supratemporal process joins the posterior section of the parietal cranial crest at or slightly posterior to the level of the posteromedian margin of the parietal fossa floor. To evaluate these similarities, the revision of the skeletal material of *O. quadrupes* is needed.

4. Discussion

To summarize, there are six species of *Ophisaurus* coming from the Miocene of Europe and Canada. Four species of *Ophisaurus* from the Early Miocene of the Czech Republic and Germany are described on the basis of parietals: *O. fejfari*, *O. spinari*, *O. robustus* (Klembara, 1979, 1981; Čerňanský, Rage & Klembara, 2015) and *O. holeci* (Klembara, 2015). The fifth species of *Ophisaurus*, *O. acuminatus* from the lower Late Miocene of Germany (Jörg, 1965), is based on partially articulated cranial elements without a parietal. The same is true for the sixth species, *O. canadensis*, based on one vertebra from the Late Miocene of Canada (Holman, 1970). Recently, a new find of *Ophisaurus,* described as *Dopasia* (=*Ophisaurus*) sp., has been recorded in the Late Miocene of North Africa (Blain *et al.* 2013) and represents the earliest remains of this genus in Africa.

From the Oligocene of France, one parietal is present for *Ophisaurus roqueprunensis* (Augé, 1992, 2005; Augé & Smith, 2009).

From the Eocene, a parietal of *Ophisaurus* sp. is described from the Late Eocene of the Hampshire Basin in southern England (Klembara & Green, 2010).

Further isolated skeletal elements (mainly comprising dentaries, vertebrae and osteoderms) have been described from various Cenozoic localities of Europe and attributed with some certainty to the genus *Ophisaurus* (e.g. *Ophisaurus* sp., Rage & Sen, 1976; Roček, 1984; Augé, 1990; Böhme, 1999, 2008; Augé & Rage, 2000; Murelaga *et al.* 2002; Rage & Bailon, 2005; Venczel, 2006, 2007; *Dopasia* sp., Delfino, Bailon & Pitruzzella, 2011; Blain *et al.* 2013; Venczel & Hír, 2015; Čerňanský, Klembara & Müller, 2016). *Dopasia* s.l. sp. from the Oligocene of France is described on the basis of one dentary and several trunk and caudal vertebrae (Rage & Augé, 2015); however, Čerňanský, Klembara & Müller (2016) consider these skeletal elements as belonging to a new genus *Ophisauromimus*.

There are four fossil species of the genus *Pseudopus*, *P. laurillardi* and *P. pannonicus* (Early Miocene to Pleistocene of Europe and Central Asia; for review see Klembara, Böhme & Rummel, 2010) and *P. ahnikoviensis* and *P. confertus* from the Early Miocene of Merkur (Klembara, 2012, 2015), and two parietals of *Pseudopus* sp. from Germany and Slovakia are described herein.

Previously, two Cenozoic species of the genus *Anguis* were described: *A. stammeri* from the Late Pleistocene of Germany and *A. polgardiensis* from the Late Miocene of Hungary. However, *A. stammeri* requires revision and in the case of *A. polgardiensis* it is not clear whether this species belongs to *Anguis* or *Ophisaurus*. The third species is *Anguis rarus* sp. nov. described here from the Early Miocene of Germany.

Together, six species of *Ophisaurus*, four species of *Pseudopus* and one species of *Anguis* are recognized in the Miocene of Europe and Canada.

There are many isolated skeletal elements (mostly dentaries and vertebrae) and osteoderms described as cf. *Anguis* or *Anguis* sp. from various Cenozoic localities of Europe. The earliest come from the Early Eocene of France and Belgium (Augé, 1990, 2005; Rage & Augé, 1993; Rage, 2006). Dentaries, vertebrae and osteoderms designated as *Anguis* sp. were also described from the Early and Middle Eocene of France (Augé *et al.* 1997; Rage & Augé, 2010). The vertebrae unambiguously belonging to *Anguis* come from the Early Miocene (MN 4) of Dolnice in the Czech Republic (Klembara, 1981, fig. 3C). It must be emphasized, however, that as in the case of *Ophisaurus* (see below) it is no certainty that these skeletal elements or their fragments from the Eocene really represent the genus *Anguis*. Only better-preserved specimens can help to resolve this taxonomic problem.

As previously mentioned, a detailed comparative analysis of the studied skeletal elements is required to differentiate clearly *Anguis* and *Ophisaurus* elements. According to the genetic data, the branching event separating *Anguis* and *Pseudopus apodus* is *c.* 9 Ma old (Macey *et al.* 1999). Unfortunately, Macey *et al.* (1999) completely ignored the fossil record. Anyway, the presence of *Anguis* in the Early Miocene, that is, from *c.* 20 Ma (Klembara, 1981 and this paper), is confirmed.

Now we can conclude that the earliest find of the parietal attributable to *Ophisaurus* is represented by *Ophisaurus* sp. from the Late Eocene of the Hampshire Basin (Klembara & Green, 2010), whereas the earliest finds of vertebrae most likely belonging to *Ophisaurus* are from the Early Eocene of France (cf. *Ophisaurus*, Augé, 1990). However, as indicated above, it is not clear whether the genus *Ophisaurus* was already present in the Eocene and Oligocene. Only a more complete fossil record may elucidate this taxonomic problem. The earliest finds of *Pseudopus* are from the Early Miocene of the Czech Republic (Klembara, 2012, 2015); however, it is highly probable that the vertebrae and osteoderms described from the Late Oligocene of Herrlingen (Germany) belong to *Pseudopus* (Čerňanský, Klembara & Müller, 2016). The presence of at least five species of *Ophisaurus*, four species of *Pseudopus* and one species of *Anguis* in the Miocene of Europe documents that anguines were most likely more diversified in this geological period than in preceding Cenozoic periods. While anguines from the Oligocene are rather small and have low diversity (Augé, 2005; Augé & Smith, 2009; Čerňanský, Klembara & Müller, 2016), abundant osteoderms and vertebrae from the pre-Grande Coupure, i.e. Eocene, sediments of the Hampshire Basin are large, at least as large as in adult specimens of extant *Pseudopus apodus* (Klembara & Green, 2010). Therefore more complete anguine material from the Eocene is required to understand their size and diversity in this warm period of the Cenozoic.

4.a. Palaeobiogeography

Currently several *Ophisaurus* species live in North America and Southeast Asia, and one species lives in North Africa and several *Anguis* species have recently been identified by genetic data in Europe and Southwest Asia (Gvoždík *et al.* 2010). However, *Pseudopus apodus* is the only species of *Pseudopus* surviving today. With regard to the distribution of fossil species of *Ophisaurus* in the Cenozoic, the Eocene and Oligocene species are restricted to Western Europe (France, England, Belgium and Spain) and Central Germany while Miocene species range from the Early Miocene of Germany (Čerňanský, Rage & Klembara, 2015) and Central Europe (the Czech Republic; Klembara, 2015) to the Late Miocene *O. canadensis* of Saskatchewan (Canada) (Holman, 1970). The youngest fossil records of *Ophisaurus* are reported from various Pliocene and Pleistocene localities of Europe (M. Böhme & A. Ilg, unpub. data, 2008, www.wahre.staerke.com) and the United States (Estes, 1983). It is considered that *Ophisaurus* reached the North American continent at least in the Late Miocene, while several species persisted in the Middle and Late Miocene in Europe (e.g. *O. acuminatus*, lower Late Miocene of Germany; *Ophisaurus robustus* from the late Middle Miocene (MN 7–8) sediments of Hungary (Hír *et al.* 2001; Venczel & Hír, 2013). The oldest finding of *Ophisaurus* in North Africa also comes from the Late Miocene (Blain *et al.* 2013). In the Pliocene, *Ophisaurus* is present in southern Italy (Delfino, Bailon & Pitruzzella, 2011 and this paper) and the youngest finds of *Ophisaurus* in Europe come from the Early Pleistocene (south of the Iberian Peninsula: Barranco León 5 and Fuente Nueva 3; Bailon & Blain, 2007).

No anguine fossil specimens were recorded in the Palaeocene, and it is surmised that the Anguinae ancestor came to Europe from North America via a land bridge connecting them (via Greenland) between the Late Cretaceous and Early Eocene (Klembara, 1981). In addition to *Ophisaurus* and *Anguis*, the anguine *Headonhilia parva* was also described in the Eocene (Klembara & Green, 2010) and the further potential anguine, *Ophisauriscus quadrupes*, was present in the Middle Eocene of Germany (Kuhn, 1940; Sullivan, Keller & Habersetzer, 1999; however, see Conrad, 2008 and Conrad *et al.* 2011).

Such palaeogeographic distribution of *Ophisaurus* indicates that *Ophisaurus* probably originated in Western Europe where it is represented by *Ophisaurus* sp. from the Late Eocene of southern England (Klembara & Green, 2010), although several skeletal elements probably belonging to *Ophisaurus* come from the Early Eocene of France (cf. *Ophisaurus*; Augé, 1990). Later it spread to central and eastern regions of Europe. Because the Turgai Strait became dry land during the Early Oligocene (Rögl, 1998; Hou *et al.* 2011), *Ophisaurus* might have spread to the east. Recent unique finds of several skeletal elements from the Middle Miocene and Early Pleistocene deposits of northern Kazakhstan document the presence of fossil *Ophisaurus* in Asia (*Ophisaurus* sp.; Vasilyan, Böhme & Klembara, 2016). The extant species of *Ophisaurus* of Southeast Asia are considered descendants of the European Neogene species of *Ophisaurus*. From East Asia, *Ophisaurus* most likely emigrated via the Bering Strait to North America as documented by the dorsal vertebra in the Late Miocene of Canada (Holman, 1970). From here, *Ophisaurus* spread to the middle and southern territories of North America (Estes, 1983). This indicates that *Ophisaurus* originated in Europe and only later migrated, via Asia, to North America. During the Miocene, *Ophisaurus* probably migrated to North Africa as documented by several cranial and postcranial remains in the Late Miocene deposits of Morocco (Blain *et al.* 2013). As suggested by Blain *et al.* (2013), *Ophisaurus* may have entered North Africa during or prior to the Middle Miocene via the land bridge between the Afro-Arabian Plate and Eurasia established from the Early Miocene onwards. Only the one species, *Ophisaurus* (=*Hyalosaurus*) *koellikeri* (Günther, 1873), survives in North Africa today.

Such a scenario of the evolution and palaeobiogeography of *Ophisaurus* and other anguines, although on the basis of a much limited fossil record, was first published in 1981 (Klembara, 1981). Macey *et al.* (1999) came to the same palaeobiogeographic scenario of *Ophisaurus* evolution based on the genetic data. However, they ignored the results published previously (Klembara, 1981).

As previously mentioned, the earliest skeletal elements considered to be *Anguis* come from the Early Eocene of France and Belgium: *Anguis* sp., together with the remains of *Ophisaurus* (Augé, 1990, 2005). This means that the earliest record of this taxon is from Western Europe, similar to that of *Ophisaurus* (Rage & Augé, 1993). In the Early Miocene, *Anguis* is already present in Germany (this paper) and the Czech Republic (Klembara, 1981). The recent morphological analysis of the parietal of *A. polgardiensis* from the Late Miocene of Hungary (Bolkay, 1913) found that it was impossible to positively distinguish it as *Anguis* or *Ophisaurus* (Klembara, 2015). Later, *Anguis* is recorded in the Pliocene localities in Poland (Młynarski, 1962) and the Plio-Pleistocene deposits at various localities of Western Europe (Bailon & Blain, 2007). All these recordings document that *Anguis* originated in Western Europe but later immigrated to Eastern European areas. Today, the most easterly occurrence of *Anguis* is in Southwest Asia (Georgia, Russia, Iran) (Gvoždík *et al.* 2010). Anyway, the presence of fossils strongly indicates that Western and Central Europe are the places of origin of *Anguis* and *Ophisaurus*.

The oldest species of *Pseudopus*, *P. ahnikoviensis*, comes from the Early Miocene (MN 3) locality in the Czech Republic (Klembara, 2012). More recently, the fragments of dentary and osteoderms belonging to *Pseudopus* sp. were identified from the German locality Wiesbaden–Amöneburg (MN 2) (Čerňanský, Rage & Klembara, 2015). *Pseudopus laurillardi* (Augé & Rage, 2000; Klembara, Böhme & Rummel, 2010) comes from France and Germany. The oldest record is from the Early Miocene deposits (zone MN 4) of Germany, while the youngest finds of this species are from the late Middle Miocene of Germany (Klembara, Böhme & Rummel, 2010). Here, *Pseudopus* sp. is described from Slovakia (zone MN 6) and south Germany (zone MN 7/8). The largest species of *Pseudopus* is *P. pannonicus* first described from Hungary (Kormos, 1911). This species ranges from the Late Miocene to the Early Pleistocene of Europe (e.g. Fejérváry-Lángh, 1923; Bachmayer & Mlynarski, 1977; Klembara, 1986*b*; Rauscher, 1992; Delfino & Bailon, 2000; Tempfer, 2004; Klembara, Böhme & Rummel, 2010). The recent species, *Pseudopus apodus*, was found in the Early and Late Pleistocene (M. Böhme & A. Ilg, unpub. data, 2008, www.wahre.staerke.com) and was more likely present in the Middle Pliocene (Zanclean, MN 15) of Slovakia (Klembara, 1986*b*). It lives in arid and semi-arid territories from the Balkan region of Europe to Kazakhstan. As in *Ophisaurus* and *Anguis*, the fossil record of *Pseudopus* highlights west–east spreading of this genus from the Early Miocene to the Holocene. Macey *et al.* (1999) suggested that the *Ophisaurus* generic name for *O. apodus* should be replaced by the original *Pseudopus*, but this had already been accomplished by Klembara (1979).

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