New finds of anguines (Squamata, Anguidae) from the Early Miocene of Northwest Bohemia (Czech Republic)

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RESEARCH PAPER

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Abstract New material on anguines is described from two Lower Miocene localities in Northwest Bohemia in the Czech Republic: Merkur (MN 3) and Dolnice (MN 4). Although the material is disarticulated, it was possible to assign several elements to one species based on similar ornamentation of the skull roof bones and similar morphology of the teeth. Two new species, *Ophisaurus holeci* nov. sp. and *Pseudopus rugosus* nov. sp. are described. *Pseudopus rugosus* becomes the second species of the genus *Pseudopus* described from the Merkur locality. In addition to the new *Ophisaurus* species above, the species *O. spinari* is described on the basis of the parietal and *Ophisaurus* sp. 1 and *Ophisaurus* sp. 2 on the basis of the frontal bones. A further five anguines, designated Anguine morphotypes 1 to 6, are described on the basis of the marginal teeth bearing elements (premaxilla, maxilla and dentary) and on the pterygoid, the angular bone and elements forming the posterior portion of the lower jaw. The described specimens present a relevant contribution to our knowledge of the diversity of anguines in the Early Neogene of Europe.

Keywords Anguimorpha · Anguinae · Lower Miocene · Skull bones · Anatomy

Kurzfassung Neues Material von Anguinen aus zwei untermiozänen Lokalitäten, Merkur (MN 3) und Dolnice (MN 4), im nordwestlichen Böhmen in der Tschechischen Republik wird beschrieben. Obwohl das Material disartikuliert ist, war es möglich, einige Elemente aufgrund ähnlicher Ornamentation der Schädeldachknochen und ähnlicher Morphologie der Zähne zu einer Art zuzuordnen. Zwei neue Arten, *Ophisaurus holeci* nov. sp. und *Pseudopus rugosus* nov. sp., werden beschrieben. *Pseudopus rugosus* ist die zweite Art der Gattung *Pseudopus*, die aus der Lokalität Merkur beschrieben wird. Abgesehen von der neue Art von *Ophisaurus* wird die Art *O. spinari* anhand von Parietalknochen beschrieben und *Ophisaurus* sp. 1 und *Ophisaurus* sp. 2 anhand der Frontalknochen. Fünf weitere Anguinen, bezeichnet als Anguine Morphotyp 1 bis 6, werden anhand von zahntragenden Elementen (Premaxillare, Maxillare und Dentale) sowie dem Pterygoid, dem Angulare und den Elementen des posterioren Unterkiefers beschrieben. Die beschriebene Anguinen präsentieren einen relevanten Beitrag zu unserer Kenntnis der Diversität von Anguinen in dem unteren Neogen von Europa.

Schlüsselwörter Anguimorpha · Anguinae · Unter-Miozän · Schädelknochen · Anatomie

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Introduction

The family Anguidae consists of four subfamilies: Anguinae, Glyptosaurinae, Gerrhonotinae and Diploglossinae. The position of Anniellinae, sometimes considered a fifth subfamily of Anguidae, is not resolved at this juncture (see Conrad et al. 2011; Gauthier et al. 2012; Klembara et al. 2014). The skeletal remains of Gerrhonotinae and Diploglossinae are not currently recorded from Europe or Asia. Besides Anguinae, only one possible member of the subfamily Glyptosaurinae, cf. *Xestops* sp. has been recognized in the Miocene of Europe (Roček 1984). However, this determination was questioned by Augé (2005). If Augé

(2005) is correct, the members of Glyptosaurinae are undoubtedly restricted to the Late Cretaceous–Late Oligocene localities in North America, Europe and Asia (Sullivan 1979; Estes 1983; Böhme 2007). Hence, within Anguidae, only the presence of Anguinae has been unequivocally confirmed in the Miocene of Europe. This conclusion is also supported by the fact that among hundreds of osteoderms and vertebrae found in various Neogene European localities, no other member of Anguidae, besides those attributable to Anguinae, is currently recorded (Klembara 1979, 1981, 1985; Estes 1983; Roček 1984; Rage and Augé 1993; Böhme 1999, 2010; Augé 2005; Rage and Bailon 2005; Böhme and Ilg 2008; Klembara et al. 2010; Klembara 2012, and references therein).

The anguine material was recorded in two Early Miocene localities in the Northwest territory of the Czech Republic and it provides a significant contribution to our knowledge of the morphology and diversity of the Cenozoic lizards of Europe. The first locality at Dolnice has deposits of the Lower Miocene (MN 4), and the second at Merkur contains slightly older deposits of the Lower Miocene (MN 3) (Fejfar and Kvaček 1993). The discussed anguine material from both localities is disarticulated. Most anguines have currently been described from the Dolnice locality (Klembara 1979, 1981; Roček 1984), with only a few specimens described from Merkur (Vejvalka 1997; Klembara 2012).

The aims of this paper are to describe new anguine skull and lower jaw material from the Merkur locality and to highlight the significance of additional knowledge herein on other Miocene anguines recorded in European localities.

Materials and methods

The material is disarticulated and the following bones are described: premaxilla, frontal, parietal, maxilla, pterygoid, dentary, compound articular + prearticular + surangular and angular. It was possible to associate the frontal and parietal bones to one species based on the type of ornamentation present. The premaxilla, maxilla and dentary are associated with one species on the basis of tooth morphology.

Most of the bones were photographed using scanning electron microscopy, and the remainder were coated with ammonium chloride prior to photography.

The skeletons of the following Anguidae species were used for comparative purposes. Anguinae: *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). Gerrhonotinae: *Abronia graminea* (DE 67), *Barisia rudicollis* (DE 68–70), *B. imbricata* (NHMUK 92.9.5.32), *Mesaspis monticola* (DE 71, 72). Diploglossinae: *Diploglossus monotropis* (BMNH 1901.6.27.4), *Celestus occiduus* (BMNH 63.2.21.17) and *Ophiodes striatus* (BMNH 44.3.7.62).

The terminology for individual structures of the given bones is mainly derived from Fejérváry-Lángh (1923), Oelrich (1956), Klembara (1979), Conrad (2004), Evans (2008) and Klembara et al. (2010, 2014).

Localities and horizon (1) The Merkur-North Opencast mine (near the city of Chomutov in North Bohemia), the earliest part of the Early Miocene (Eggenburgian), Lower Orleanian, zone MN 3 (Fejfar and Kvaček 1993). (2) Dolnice (near the city of Cheb in West Bohemia), Early Miocene (Ottnangian), middle Orleanian, zone MN 4 (Fejfar and Kvaček 1993).

Institutional abbreviations The following acronyms are used to refer to institutional specimen repositories: AMNH, American Museum of Natural History, New York, NY, USA; BSPG, Bayerische Staatssammlung für Paläontologie, Munich, Germany; CM, Carnegie Museum of Natural History, Pittsburg, PA, USA; DE, Department of Ecology, Comenius University in Bratislava, Faculty of Natural Sciences, Slovakia; DP FNSP, Department of Palaeontology, Faculty of Natural Sciences, Charles University, Prague, Czech Republic; NHMUK(BMNH), Natural History Museum, London, England; MNHN, Laboratoire de paléontologie, Muséum national d'Histoire naturelle, Paris, France; NMA, Naturmuseum Augsburg, Augsburg, Germany; NMP Pb and Pv, National Museum, Prague (Czech Republic); UF, University of Florida, Gainesville, FL, USA.

Systematic palaeontology

Remarks Although the skull and lower jaw elements described below are disarticulated, they are assigned to the subfamily Anguinae on the basis of very similar morphology to the Recent and fossil species of *Ophisaurus* and *Pseudopus*. Regarding usage of the generic names *Ophisaurus*, *Anguis* and *Pseudopus*, see Klembara et al. (2014).

Order Squamata Oppel, 1811
Infraorder Anguimorpha Fürbringer, 1900
Family Anguidae Gray, 1825
Subfamily Anguinae Gray, 1825
Genus *Ophisaurus* Daudin, 1803

Ophisaurus holeci nov. sp.
Figures 1a–c, 2
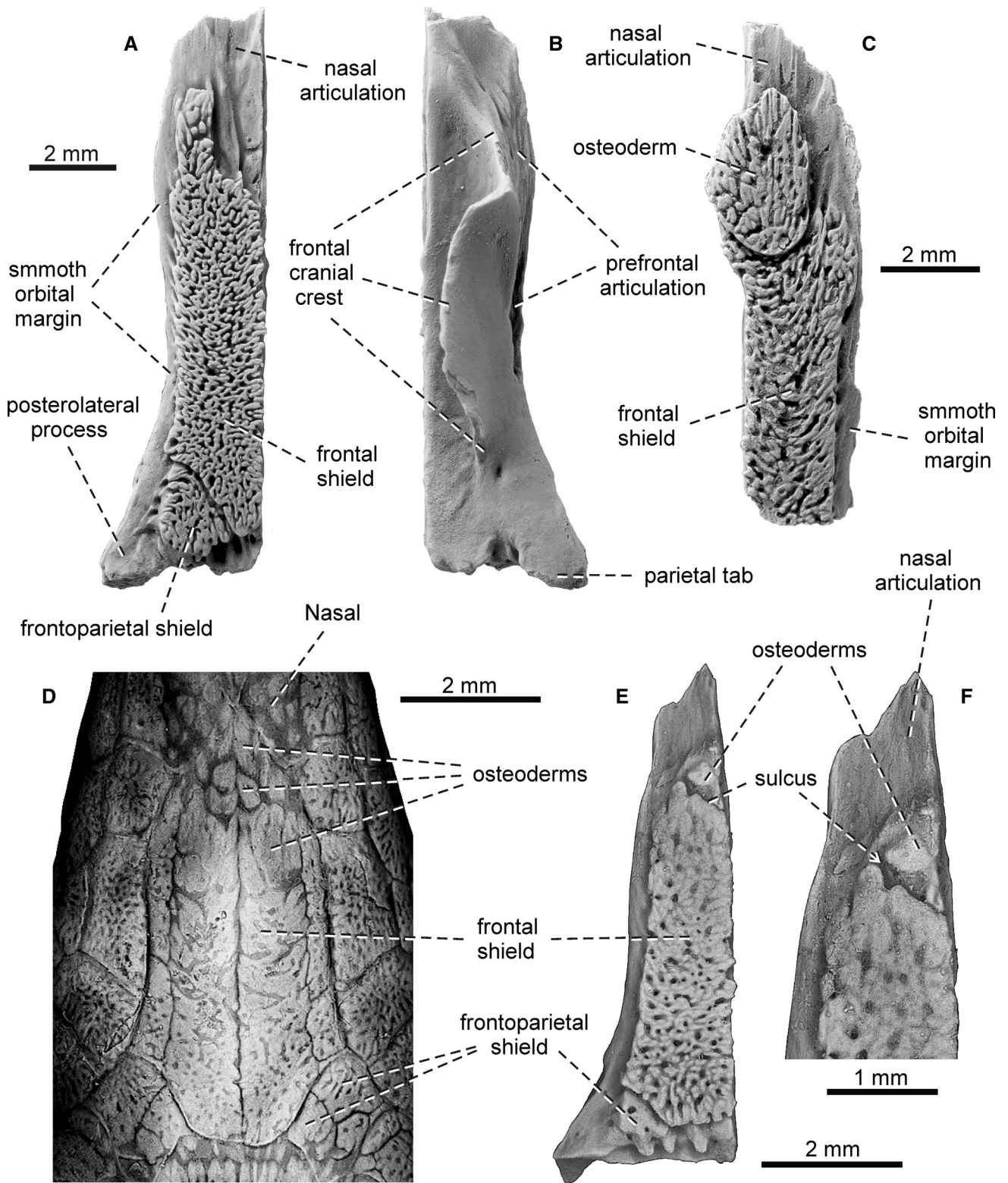
Fig. 1 *Ophisaurus holeci* sp. nov.: **a**, **b** NMP Pb 02030, frontal in *dorsal* (**a**) and *ventral* (**b**) *views*; **c** NMP Pv 10022, frontal in *dorsal view*. **d** *Ophisaurus attenuatus*, DE 44, partial skull roof in *dorsal view*. **e**, **f** *Ophisaurus harti*, DE 36, frontal (**e**) and *close-up view* of anterior portion of frontal (**f**) in *dorsal view*
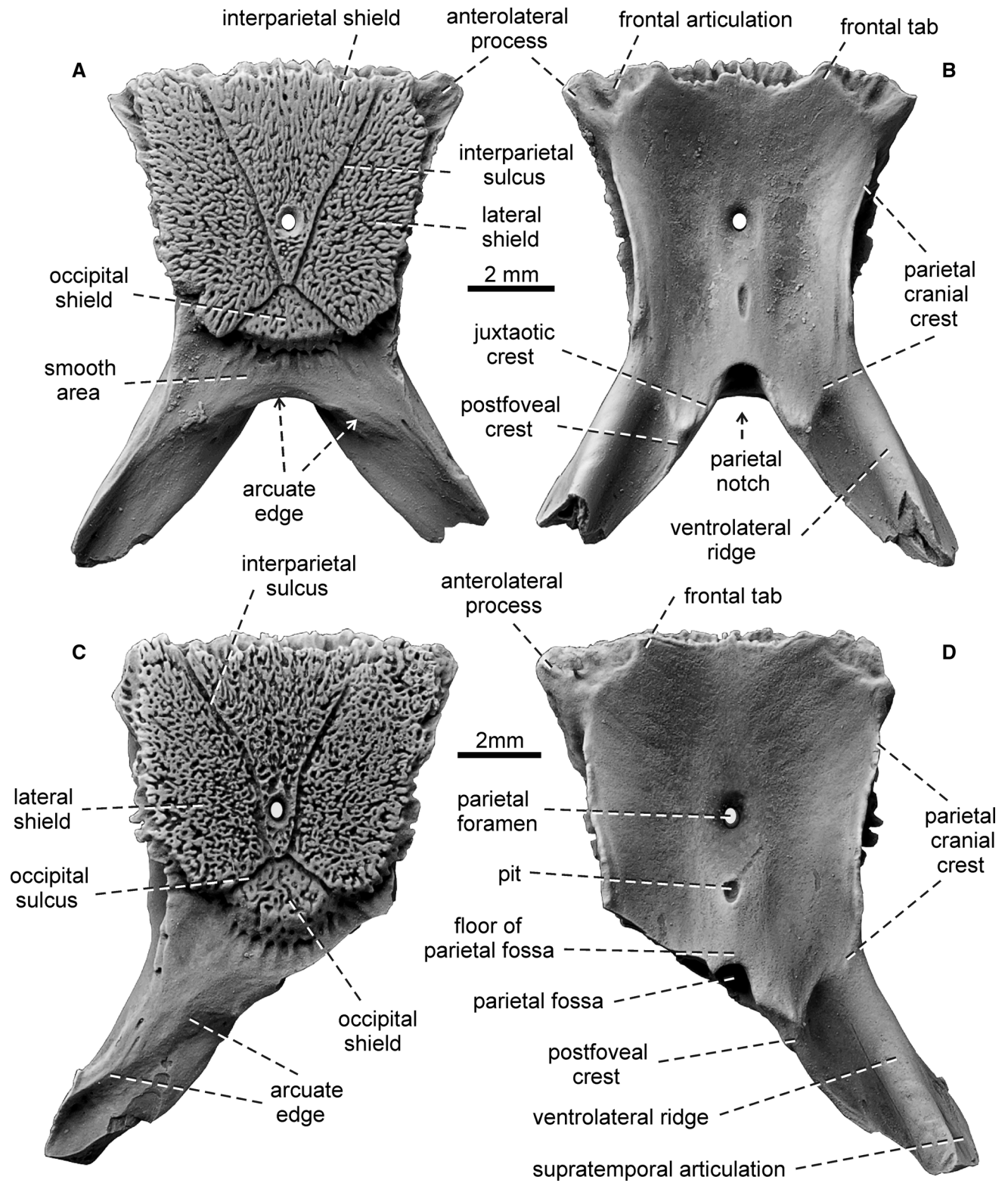
Fig. 2 *Ophisaurus holeci* sp. nov.: **a**, **b** NMP Pb 02027 (holotype), parietal in *dorsal* (**a**) and *ventral* (**b**) *views*. **c**, **d** NMP Pb 02028, parietal in *dorsal* (**c**) and *ventral* (**d**) *views*

1981 *Ophisaurus spinari* Klembara: 128, specimen DP FNSP 1026.

Derivation of specific name In honour of Prof. Peter Holec (the former member of the Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University in Bratislava) and his distinguished contribution to vertebrate palaeontology.

Holotype Parietal (NMP Pb 02027) (Fig. 2a, b).

Referred specimens Frontal (NMP Pb 02030, NMP Pv 10020–10023), parietal (NMP Pb 02028, NMP Pv 10008–10018, DP FNSP 1026).

Diagnosis Ophisaurus holeci differs from all species of the genus *Ophisaurus* in the following features and the combination of features: (1) middle section of frontal cranial crest is deep, almost reaching medial margin of frontal; (2) distinct ornamentation consists of short and distinct anastomosing ridges and deep grooves and pits; (3) anterior end of interparietal sulcus lies medial to anterolateral corner of ornamented surface; (4) anterior end of ventrolateral ridge of supratemporal process joins parietal cranial crest at level of or slightly posterior to posteromedian margin of floor of parietal fossa; (5) posterior section of parietal cranial crest is very low, especially at its junction with ventrolateral ridge of supratemporal process which is also very low at that point; (6) a short postfoveal crest is present; and (7) supratemporal process is straight.

Description: *Frontal* The frontal is a long bone distinctly constricted in its posterior half (Fig. 1a, b). The ornamentation is very distinct and consists of distinct ridges and deep grooves and pits. The entire orbital margin is smooth. The nasal articulation is roughened and bears rather distinct longitudinal grooves and ridges. The posterolateral process is massive, and the frontal tab is well-developed. The frontoparietal shield is large and subquadrangular in shape. The posteromedial margin of the frontal shield follows a transverse course and is very short relative to the long posterolateral margin of the bone. The morphology of the anterior portion of the frontal shield varies slightly, as follows; (1) In NMP Pb 02030, the ornamented surface forms an anterolateral extension, and an unornamented and roughened surface remains between it and a medial margin of the frontal (Fig. 1a), (2) In NMP Pv 10022, the anterolateral extension of the ornamented surface is short and an oval ornamented osteoderm is present immediately medially covering the anteromedial portion of the frontal (Fig. 1c), and (3) In NMP Pv 10023, the anterolateral extension is absent and the morphology of the ornamentation indicates fusion of the oval osteoderm with the frontal shield and also the frontal bone.

The frontal cranial crest, referred to as the subolfactory process by some authors, is high and strongly medially flexed; almost reaching the midline (Fig. 1b). The posterior portion of the crest is almost perpendicular, with a slanting margin. The anterior section of the crest gradually declines anteriorly to a low sharp wall. Longitudinal ridges and grooves on the lateral surface of the frontal indicate a strong prefrontal articulation.

Parietal The parietal table is covered dorsally with a well-developed ornamented surface (Fig. 2a, c). The lateral margins of the parietal table and ornamented surface closely coincide, with the ornamented surface being only slightly narrower. The lateral margins of the parietal table and the ornamented surface converge slightly posteriorly. The ornamented surface is slightly longer than wide, when measured at mid-length and at the ornamented surface's mid-width. The ornamentation consists of distinct anastomosing ridges and deep grooves and pits. The radiating ridges and grooves are present at the periphery of the ornamented surface which is divided by distinct sulci into unpaired interparietal and occipital shields and paired lateral shields. The anterior end of the interparietal sulcus lies medial to the anterolateral corner of the ornamented surface. The sulcus representing the junction of the interparietal and occipital shields is very short and transversally oriented. The occipital shield is triangular in shape and its posterior margin morphology varies slightly: (1) in the holotype specimen (Fig. 2a), this margin is straight and lies at the level of the posterior corners of the lateral shields; and (2) in NMP Pb 02028 (Fig. 2c), it is convex and extends more posteriorly relative to the level of the posterior tips of the lateral shields. When measured in the median plane, the anteroposterior length of the smooth area of the parietal table is approximately the same as the anteroposterior length of the occipital shield. The anterolateral process is well-developed. The completely preserved left supratemporal process is straight in NMP Pv 10008 (not depicted herein). The arch-like arcuate edge is distinctly developed on the dorsal surface of the anterior halves of the supratemporal processes.

The frontal tab is well-developed (Fig. 2b, d). The parietal cranial crest lies almost at the level of the lateral margin of the parietal table. Hence, the muscular surface typical in *Pseudopus*, is absent. The parietal cranial crest is high and sharp only in its mid-length, with very low anterior and posterior sections, with the posterior section lowest at its junction with the ventrolateral ridge of the supratemporal process. The postfoveal crest is very short anteroposteriorly and low dorsoventrally. The arcuate edge lies approximately at the level of the mid-length of the juxtafoveal crest. The supratemporal processes are straight and diverge posteriorly. The ventrolateral ridge of the

supratemporal process is massive and coincides with the process's lateral margin anterior to the supratemporal articulation. The anterior end of the supratemporal process joins the posterior section of the parietal cranial crest at the level or slightly posterior to the posteromedian margin of the floor of the parietal fossa. An elongated rugosity situated approximately at the supratemporal process lateral margin's mid-length indicates the supratemporal articulation. Further posteriorly, a short longitudinal crest separates the supratemporal articulation from the slightly shorter and posteromedial articulation with the paroccipital process of the opisthotic (this is preserved in NMP Pv 10008, not depicted herein).

Comparisons Ophisaurus holeci is distinguished from other species of *Ophisaurus* by the morphology of its parietal and frontal bones. Although they are separate elements, these bones are interpreted as belonging to one species on the basis of their distinct and very similar ornamentation. An interesting feature is the presence of an independent oval osteoderm covering the anteromedial portion of the frontal bone (Fig. 1c). The only recorded example of a similar condition was recently described in the frontals of *Ophisaurus* sp. from the Wiesbaden (Germany) MN 2 locality, in the oldest finds of anguine frontals in the Miocene (Čerňanský et al. 2014). The anterior portion of the frontal in the DE 44 subadult specimen of the extant *O. attenuatus* is covered by several small osteoderms (Fig. 1d). These are distinctly divided from a large frontal ornamented shield. A small osteoderm is also present in the anterior portion of the left frontal of the DE 36 subadult *O. harti* (Fig. 1e, f). In this specimen, a distinct sulcus divides the small osteoderm from a large frontal shield. However, the frontal shield forms one complete unit in adult specimens of these extant species of *Ophisaurus*. The fact that such an originally independent osteoderm is present in the oldest records of *Ophisaurus* indicates that the conditions present in *O. holeci* and *Ophisaurus* sp. from Wiesbaden are primitive (at least in some species of *Ophisaurus*), and that the anterior portion of the frontal shield was formed in the phylogeny by the secondary fusion of an originally independent osteoderm(s) to the anterodorsal surface of the frontal, and consequently to the anterior margin of the frontal ornamented shield itself. However, this hypothesis has to be proved by the phylogenetic analysis of anguines which will be published separately.

Only a few frontals from the Cenozoic of Europe have been attributed to *Ophisaurus*. Klembara (1981) attributed several frontals to *Ophisaurus* sp. from the Early Miocene locality of Dolnice in the Czech Republic. Delfino et al. (2011) described the posterior half of the right frontal as *Dopasia* (=*Ophisaurus*) sp. from the Late Pliocene of Italy. The posterior margin of the frontal shield of this frontal is rounded (Delfino et al. 2011) and thus quite different from that of *O. holeci* (Fig. 1a, b).

Although the *O. fejfari*, *O. spinari* and *O. robustus* fossil species of the genus *Ophisaurus*, previously described on the basis of parietals, come from the Early Miocene locality of Dolnice in the Czech Republic (Klembara 1979, 1981), one *Ophisaurus spinari* parietal from the Merkur locality is described herein (Fig. 3a, b). Additional parietal designations include (1) an incomplete parietal and several other skeletal elements assigned to *Dopasia* (=*Ophisaurus*) sp., described from the Late Pliocene of Italy (Delfino et al. 2011); (2) a very poorly preserved parietal from the Late Oligocene of France, attributed to *Dopasia* (=*Ophisaurus*) *coderetensis* by Augé (2005); (3) an incomplete parietal of *Dopasia* (=*Ophisaurus*) *roqueprunensis*, described from the Late Oligocene of Belgium (Augé and Smith 2009); (4) a parietal, described as *Ophisaurus* sp., from the Late Eocene of the Hampshire Basin in southern England (Klembara and Green 2010); and (5) an incomplete parietal from the Late Eocene of Spain, attributed to Anguinae indet. (Bolet and Evans 2013). *Ophisaurus holeci* differs from all these fossil species, as well as the extant species of *Ophisaurus*, in the following features and the combination of features:

1. A deep, middle section of the frontal cranial crest (subolfactory process) almost reaches the medial margin of the frontal in ventral view. *Remarks* Although the morphology of the frontal of *Ophisaurus holeci* is of the *Ophisaurus* type, the middle section of the frontal cranial crest in all other extinct and extant species of *Ophisaurus* never extends as far medially as in *O. holeci* (Fig. 1b).

2. The ornamentation on both the parietal and frontal consists of short, pronounced anastomosing ridges and grooves and distinct pits, with relatively longer, radiating ridges most conspicuous at the periphery of the ornamented shields. *Remarks* While the type of ornamentation of the parietal of *Ophisaurus holeci* is most similar to that of *Ophisaurus fejfari* (Klembara 1979: Pl. 1, Fig. 1), the latter's parietal differs from that of *O. holeci* in the absence of characteristics described in points 4, 5 and 7 below. The ornamentation of the parietal of *O. holeci* is somewhat similar to that of the Late Eocene *Ophisaurus* sp. (Klembara and Green 2010), but the grooves and ridges are much more densely arranged in *O. holeci*'s ornamentation. Meanwhile, the parietal ornamentation in both *Dopasia* (=*Ophisaurus*) *roqueprunensis* (Augé and Smith 2009) and *Dopasia* (=*Ophisaurus*) sp. (Delfino et al. 2011) is poorly preserved.

3. The anterior end of the interparietal sulcus lies medially to the anterolateral corner of the ornamented
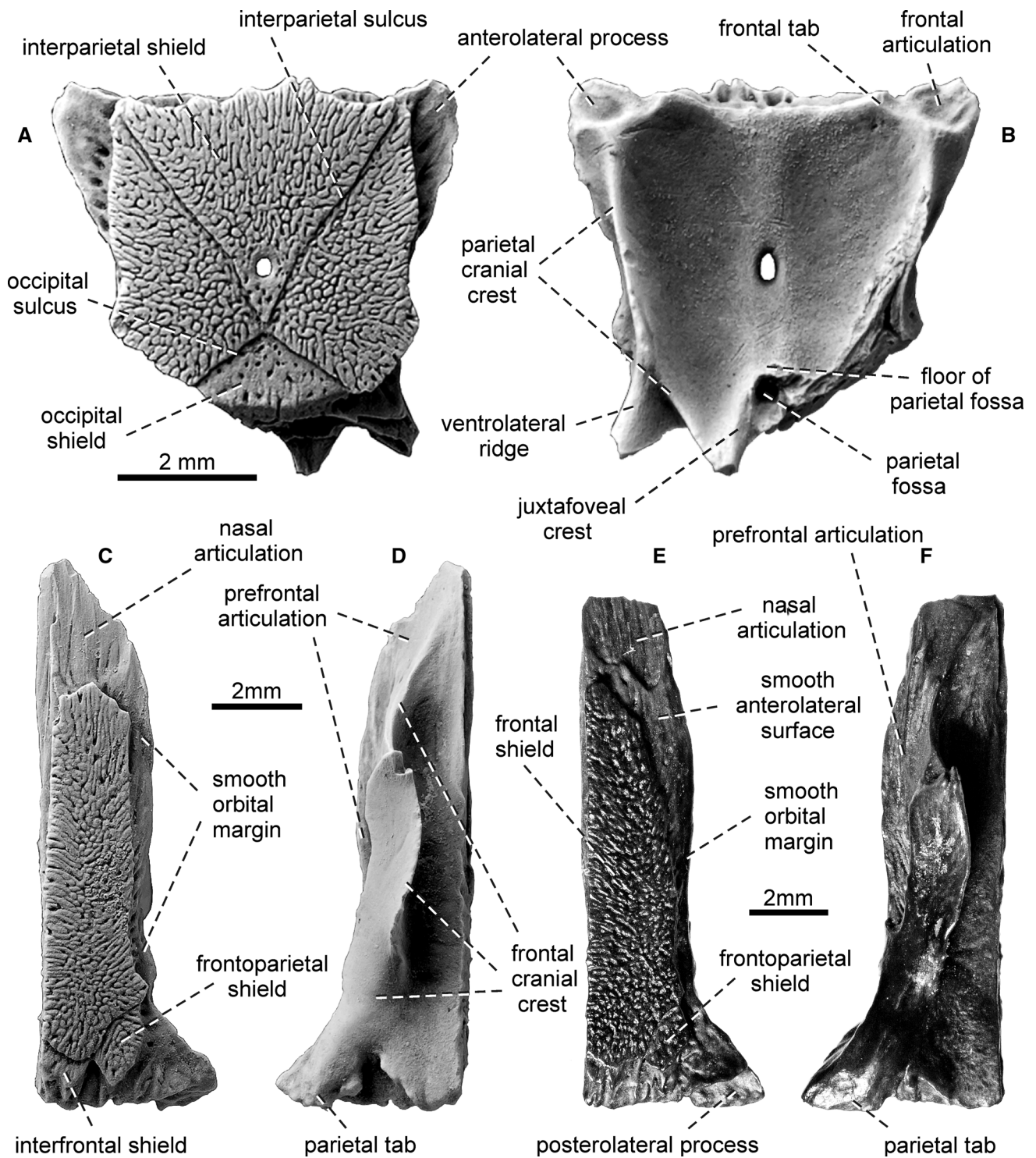
Fig. 3 **a**, **b** *Ophisaurus spinari*: NMP Pv 10019, parietal in *dorsal* (**a**) and *ventral* (**b**) views. **c**, **d** *Ophisaurus* sp. 1: NMP Pv 10024, frontal in *dorsal* (**c**) and *ventral* (**d**) views. **e**, **f** *Ophisaurus* sp. 2: NMP Pb 01872, frontal in *dorsal* (**e**) and *ventral* (**f**) views

surface. *Remarks* The anterior ends of interparietal sulci in *Ophisaurus fejfari*, *O. spinari* and *O. robustus* lie in the anterolateral corner of the ornamented surface, or closely medial to it. Although the extant *O. ventralis* and *O. attenuatus* species of the genus *Ophisaurus* and also *Anguis fragilis* have a similar position of the interparietal sulcus as that in *O. holeci*, the *Ophisaurus* and *Anguis* species differ from *O. holeci* in the absence of character 2 described above and 4 and 5 described below. The anterior parietal

portions of *Ophisaurus* sp. (Klembara and Green 2010) and both *Dopasia* (=*Ophisaurus*) *roqueprunensis* and *Dopasia* (=*Ophisaurus*) sp. (Delfino et al. 2011) are not preserved.

4. The anterior end of the ventrolateral ridge of the supratemporal process joins the parietal cranial crest at the level of the posteromedian margin of the floor of the parietal fossa or slightly posterior to it. *Remarks* While the anterior end of the posterolateral ridge of the supratemporal process lies relatively anterior to the level of the posteromedian margin of the floor of the parietal fossa in all Neogene to Recent species of *Ophisaurus*, *Anguis* and *Pseudopus*, the level of the junction of the anterior end of the ventrolateral ridge and parietal cranial crest in the Early Oligocene *Dopasia* (=*Ophisaurus*) *roqueprunensis* (Augé and Smith 2009: Fig. 6B) and Late Eocene *Ophisaurus* sp. (Klembara and Green 2010: Fig. 4B) is the same as that in *O. holeci*.

5. The posterior section of the parietal cranial crest is very low, especially at its junction with the postero-lateral ridge of the supratemporal process. *Remarks* Although this crest section is more distinct and forms a relatively sharp perpendicular crest in *Ophisaurus fejfari*, *O. spinari* and *O. robustus*, in the Early Oligocene *Dopasia* (=*Ophisaurus*) *roqueprunensis* (Augé and Smith 2009: Fig. 6B) and Late Eocene *Ophisaurus* sp. (Klembara and Green 2010: Fig. 4B) this section is very low, precisely as seen in *O. holeci*.

6. The presence of a short postfoveal crest. *Remarks* The postfoveal crest was first described by Fejérváry-Lángh (1923) for the anteroposteriorly directed crest which extends from the posterior junction of the parietal cranial crest and juxtafoveal crest to the medial margin of the base of the supratemporal process. The postfoveal crest is a typical feature of all species of *Pseudopus* (Klembara 1979; Klembara et al. 2010). Besides those, the postfoveal crest is present in the following anguines: (1) a very short postfoveal crest was described in the *Headonhilia parva* anguine from the Late Eocene in the Hampshire Basin of Southern England (Klembara and Green 2010), (2) a very short and low postfoveal crest is evident in *Ophisaurus holeci* and (3) a short and relatively higher postfoveal crest is also present in *Ophisaurus fejfari* (Klembara 1979: Pl. 2, Fig. 1). However, the parietal of *O. fejfari* differs from that of *O. holeci* by the absence of characters 3–5 described above, and the postfoveal crest is absent in all other fossil and Recent species of *Ophisaurus* and *Anguis*.

7. The supratemporal process is straight. *Remarks* While the posterior portions of the supratemporal process are always somewhat medially flexed in the extant species

of *Ophisaurus*, *Anguis* and *Pseudopus*, the corresponding portions in the fossil forms of these genera are mostly broken (e.g. Klembara 1979, 1981; Augé 2005; Augé and Smith 2009; Klembara and Green 2010; Delfino et al. 2011). These portions, however, are present in *Pseudopus laurillardi*, and here they are also relatively medially flexed (Klembara et al. 2010).

Ophisaurus spinari Klembara, 1979
Figure 3a, b

Referred specimen Parietal (NMP Pv 10019).

Description There is only one parietal present. The ornamented surface of the parietal is slightly longer than wide (Fig. 3a). The ornamentation consists of short ridges and grooves in the central portion of the ornamented shield, but distinct radiating grooves and ridges are present at its periphery. The anterior end of the interparietal sulcus lies in the anterolateral corner of the ornamented surface. The occipital shield is large and triangular in shape, with a slightly convex posterior margin. The anterolateral process is elongated anteroposteriorly. The parietal foramen lies immediately posterior to the mid-length of the ornamented surface.

The parietal cranial crest is low anteriorly, but it becomes deep and sharp posteriorly (Fig. 3b). It extends laterally to the level of the parietal table, and lacks a muscular surface. The frontal tab is moderately developed. The ventral surface of the basal-most portion of the right supratemporal process is partly preserved, and it indicates that the anterior end of the ventrolateral ridge joins the posterior section of the parietal cranial crest at a level anterior to the posteromedian margin of the floor of the parietal fossa.

Comparisons Although the *Ophisaurus spinari* parietal exhibits most morphological features of the holotype (Klembara 1979: Pl. 1, Fig. 2), that of NMP Pv 10019 differs slightly from it in two features. The latter has (1) a slightly larger anterolateral process of the parietal table, and (2) its ornamented shield is only slightly longer than wide. These features are considered to demonstrate individual variability.

Ophisaurus sp. 1
Figure 3c, d

Referred specimens Frontal (NMP Pv 10024–10027).

Description The frontal is a paired bone of triangular shape (Fig. 3c). The ornamentation consists of ridges and grooves radiating from the central portion of the ornamented surface. A wide, smooth mediolateral orbital margin is present and the frontal ornamented shield gradually narrows mediolaterally into a wedge-shaped anterior margin. The

posteromedial margin of the frontal shield proceeds in an anteromedial–posterolateral direction, and it is substantially shorter than the posterolateral margin which is oriented in the anterolateral–posteromedial direction. Posterolaterally, the frontal shield forms a small laterally extending process. In NMP Pv 10024 (Fig. 3c) and NMP Pv 10025, there are small interfrontal and larger subquadrangular frontoparietal shields present. In specimens NMP Pv 10026 and NMP Pv 10027, the frontals of the left and right sides are co-ossified; the line of fusion is visible. The nasal articulation is large and bears a series of longitudinal ridges and grooves, while the posterolateral process of the frontal is massive and extends into a small parietal tab at the posterolateral margin.

As seen on the ventral surface illustrated in Fig. 3d, the anterior section of the frontal cranial crest is low, and it rapidly deepens posteriorly. The middle section of the crest is the deepest and is flexed ventromedially. Its anterior portion extends into a small, but distinct and pointed ventral process. The posterior section of the frontal cranial crest is low and massive. The prefrontal articulation reaches slightly posterior to the mid-length of the bone.

Comparisons The general morphology of the frontal of *Ophisaurus* sp. 1 corresponds to that of *Ophisaurus* sp. 2 (Fig. 3e, f) and to the extant species of the genus *Ophisaurus*. The orbital margin is smooth along the entire lateral margin of the bone, a feature typical for *Ophisaurus* and *Anguis* but contrasted to that in *Pseudopus* (see below). However, the ornamentation of the frontal of *Ophisaurus* sp. 1 differs substantially from that of the extant species of *Ophisaurus*, where it is less distinct and the ridges and grooves are not so densely arranged. The ornamentation of the frontal of *Ophisaurus* sp. 1 is similar to that in *Ophisaurus* sp. 2 (see below). The frontal of *Ophisaurus* sp. 1 differs from that of *Ophisaurus* sp. 2 in the following features: (1) the frontal is not constricted in its posterior half, (2) the anterior margin of the frontal ornamented shield is wedge shaped, and (3) the smooth anterolateral surface of the frontal dorsal surface is relatively narrower. It may be that *Ophisaurus* sp. 1 and *Ophisaurus* sp. 2 are the same species; however, until variability in the frontals of these anguines is unequivocally established, I leave them as separate species.

Ophisaurus sp. 2
Figure 3e, f
1997 *Pseudopus* cf. *P. moguntinus* Vejvalka: 52, Pl. 12, Figs. 3 and 4.

Referred specimen Frontal (NMP Pb 01872).

Description The frontal is triangular in shape, but distinctly constricted at approximately the middle of the posterior half of the bone (Fig. 3e, f). The entire orbital margin is smooth. The nasal articulation is large and bears distinct longitudinally oriented ridges and grooves. The frontal ornamented shield covers most of the dorsal surface of the bone, where its posterior portion is widest, but this narrows anteriorly leaving a substantial portion of the anterolateral surface smooth. The anterior end of the frontal shield is pointed. The posteromedial margin of the frontal shield has an anteromedial–posterolateral orientation and is much shorter than the posterolateral margin which follows an anterolateral–posteromedial course. The subquadrangular frontoparietal shield covers most of the dorsal surface of the posterolateral process. The interfrontal shield is very small and the parietal tab is well-developed.

The frontal cranial crest is also well-developed (Fig. 2f), and its morphology is very similar to that of *Ophisaurus* sp. 1 described above (Fig. 3d).

Comparisons The frontal of *Ophisaurus* sp. 2 differs from that of *Ophisaurus* sp. 1 in the following features: (1) the anterior half of the frontal ornamented shield is much more mediolaterally narrowed; (2) the frontal ornamented shield is anteriorly pointed; and (3) the posterior half of the frontal is distinctly constricted.
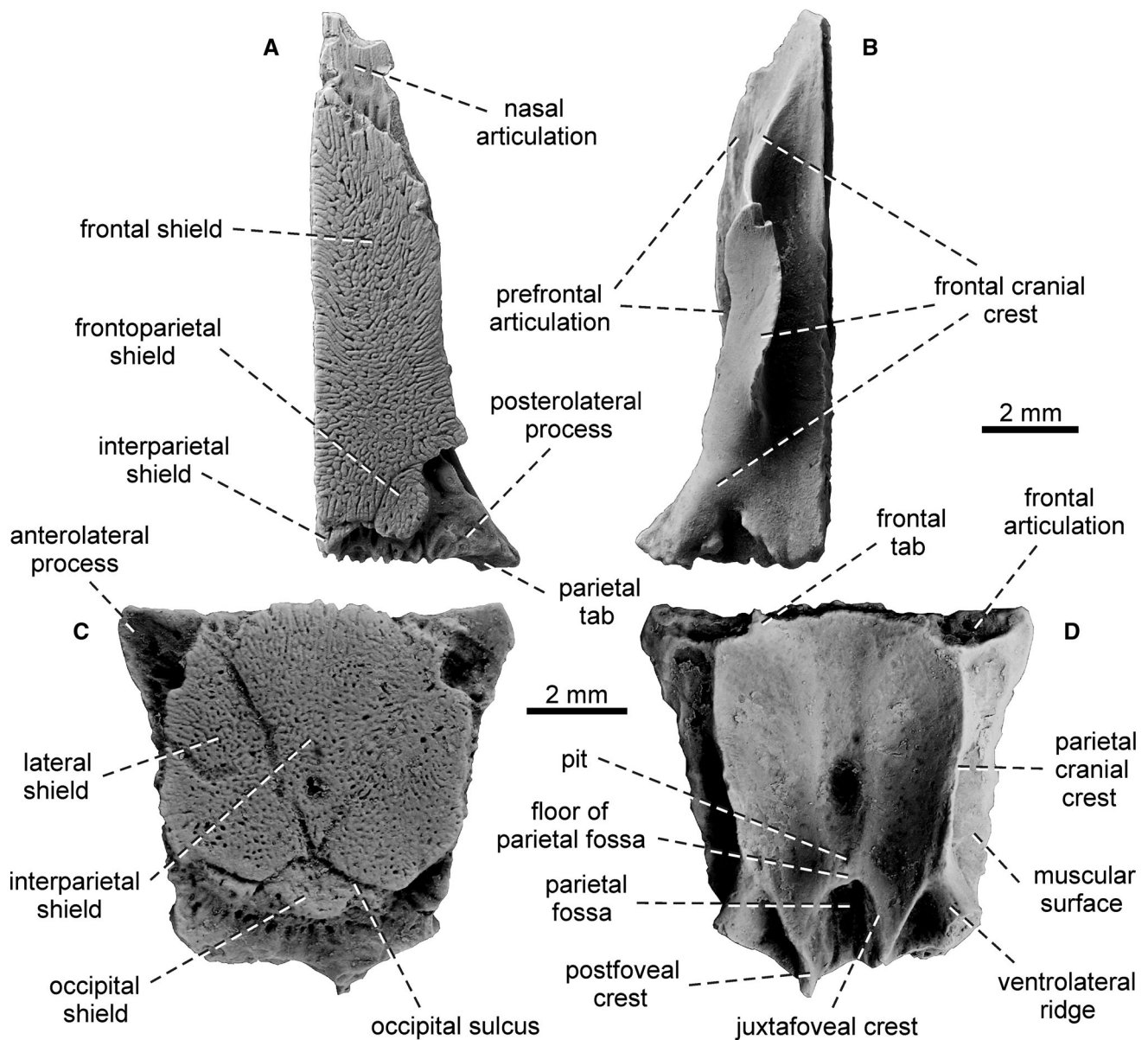
Pseudopus rugosus nov. sp.
Figure 4a–d

Derivation of specific name According to the pattern of densely arranged, distinct grooves and ridges on the ornamented surfaces of the frontal and parietal bones.

Holotype Frontal (NMP Pv 10028, Fig. 4a, b).

Referred specimen Parietal (NMP Pv 10006), Fig. 4c, d.

Diagnosis Pseudopus rugosus differs from all species of the genus *Pseudopus* in the following features and combination of features: (1) lateral margin of frontal ornamented shield reaches the lateral margin of the frontal; (2) the posteromedial margin of the frontal ornamented shield is much shorter than its posterolateral margin; (3) the anterolateral process of the parietal is moderately developed; and (4) in ventral view, the parietal foramen lies posterior to the mid-length of the distance between the anterior margin of parietal table and the posterior margin of the floor of the parietal fossa, when measured in the median plane.

Description: *Frontal* The lateral margin of the frontal shield slightly overlaps the lateral margin of the frontal, and hence no smooth orbital margin is present (Fig. 4a). The frontal shield is mediolaterally widest at the level immediately anterior to the postfrontal shield; here, the frontal shield extends into a small lateral process. Anterior to this level, the lateral and medial margins of the frontal shield run parallel, and only anteriorly the lateral margin turns gradually anteromedially. The posterolateral margin

Fig. 4 *Pseudopus rugosus* sp. nov.: **a**, **b** NMP Pv 10028 (holotype), frontal in *dorsal* (**a**) and *ventral* (**b**) *views*; **c**, **d** NMP Pv 10006, parietal in *dorsal* (**c**) and *ventral* (**d**) *views*

of the frontal shield is much longer than the transversely running and short posteromedial margin of the frontal shield. The ornamentation consists of densely arranged anastomosing ridges and grooves concentrated in the central portion of the shield. From here, the ridges radiate to the periphery of the shield. A postfrontal shield of almost oval shape is present, and the interfrontal shield is much smaller. The articular area for the nasal bears anteroposteriorly orientated ridges and grooves. The posterolateral process of the frontal is distinct and has a parietal tab at its posterolateral margin. In the ventral aspect, the middle section of the frontal cranial crest is deep and flexed ventromedially (Fig. 4b). The prefrontal articulation occupies

two-thirds of the length of the ventrolateral margin of the frontal. The posterolateral margin of the frontal shield is exposed in ventral view.

Parietal There is only one parietal present, with most of the parietal table preserved (Fig. 4c, d). The ornamented surface is square in shape, and consists of densely arranged anastomosing ridges and grooves which have a radiating pattern at the periphery of the lateral and interparietal shields. The parietal foramen lies slightly posterior to the mid-length of the ornamented surface. The anterior end of the interparietal sulcus lies in the anterolateral corner of the ornamented surface which almost coincides with the lateral

margins of the parietal table. The anterolateral processes are moderately developed.

The muscular surface is well-developed (Fig. 4d). A short postfoveal crest is present. The anterior end of the ventrolateral ridge of the supratemporal process coincides with the lateral margin at the base of the supratemporal process and joins the posterior section of the parietal cranial crest slightly anterior to the posteromedian margin of the floor of the parietal fossa. In ventral aspect, the parietal foramen lies posterior to the mid-distance between the anterior margin of the parietal table and the posterior margin of the floor of the parietal fossa, when measured in the median plane.

Comparisons This parietal bone is assigned to the frontal on the basis of very similar ornamentation. Although several portions of the parietal ornamented shield are eroded, the well-preserved ornamented portions clearly demonstrate a very similar pattern to that on the frontal. Although *Pseudopus rugosus* and *P. ahnikoviensis* (Klembara 2012) are two species of *Pseudopus* of the same size, age and locality, *P. rugosus* differs from all species of the genus *Pseudopus*, fossil or extant, in the following combination of features:

1. The lateral margin of the frontal ornamented shield reaches the lateral margin of the frontal. *Remarks* In *Pseudopus apodus* (Klembara et al. 2010) and *P. pannonicus* (Klembara 1986), the lateral margin of the frontal ornamented shield reaches the lateral margin of the frontal as in *P. rugosus*. However, the ornamentation of the frontal and parietal in *P. apodus* and *P. pannonicus* is quite different from those in *P. laurillardi* and *P. ahnikoviensis*. In these two former species, the ornamentation consists of distinct tubercles in the central portion of the bone with relatively distinct radiating ridges and grooves at the periphery (see also Klembara 2012). In *P. laurillardi* and *P. ahnikoviensis*, only a narrow anterolateral portion of the frontal ornamented shield reaches the lateral margin of the frontal bone and most of its orbital margin is smooth (Klembara et al. 2010; Klembara 2012). In all extant species of *Ophisaurus* and *Anguis*, the orbital margin of the frontal is consistently smooth.

2. The posteromedial margin of the frontal ornamented shield is much shorter than its posterolateral margin. *Remarks* Although these characteristics in *Pseudopus rugosus* are the same as those in *P. apodus*, *P. pannonicus* and *P. laurillardi* (Klembara 1986; Bachmayer and Mlynarski 1977; Augé and Rage 2000; Klembara et al. 2010), the ornamentation of the frontal and parietal of *P. rugosus* is quite different to that of the three *Pseudopus* species. In further contrast, the frontal ornamented shield's posteromedial and posterolateral margins are of equal length in *P. ahnikoviensis* (Klembara 2012).

3. The anterolateral process of the parietal is moderately developed. *Remarks* The size and morphology of the anterolateral process of *Pseudopus rugosus* is very similar to that of *P. apodus* and *P. pannonicus* (Klembara 1986; Klembara et al. 2010). However, as already emphasized, the parietal ornamentation type in *P. rugosus* is quite different from that in *P. apodus* and *P. pannonicus*, and the parietal anterolateral process in *P. laurillardi* (Klembara et al. 2010) and *P. ahnikoviensis* (Klembara 2012) is anteroposteriorly shorter and distinctly extended laterally. Otherwise, *P. rugosus'* parietal morphology corresponds to that of *P. ahnikoviensis* in its principal features (Klembara 2012).

4. In ventral view, the parietal foramen lies posterior to the mid-distance between the anterior margin of the parietal table and the posterior margin of the floor of the parietal fossa; when measured in the median plane. *Remarks* Although *Pseudopus ahnikoviensis* shares this feature (Klembara 2012), *P. rugosus* differs in character 3 above. Meanwhile, the pineal foramen in *P. laurillardi*, *P. pannonicus* and *P. apodus* lies anterior to this mid-distance (Klembara 1986; Klembara et al. 2010).

Anguinae indeterminate

Remarks In this section, anguine specimens which cannot be assigned to either new or existing taxa, but may belong to them, are described as Anguinae indeterminate.

Anguine morphotype 1
Figures 5, 6a

Referred specimens Maxilla (NMP Pb 01856, Pb 01871, Pb 02036, NMP Pv 10206–10208); Dentary (NMP Pb 02048, NMP Pv 10087–10100).

Description: *Maxilla* (Fig. 5a–d) The most completely preserved maxilla is NMP Pb 01871, which has only the anterior portion missing (Fig. 5a, b). The lateral surface of this maxilla has deep-furrow and high-ridge ornamentation in the region of the four preserved mental foramina. The lateral surface of the nasal process is smooth, with an oblique dorsal margin coursing in the anteroventral–posterodorsal direction. The posterodorsal corner of the nasal process extends into a small, but distinct process. Two tiny pointed processes are evident at approximately the middle of the posterior margin of the nasal process, with the maxilla gradually decreasing in height posterior to this process. The dorsal surface of the posterior portion bears an anteroposteriorly elongated and distinct groove for articulation with the jugal.
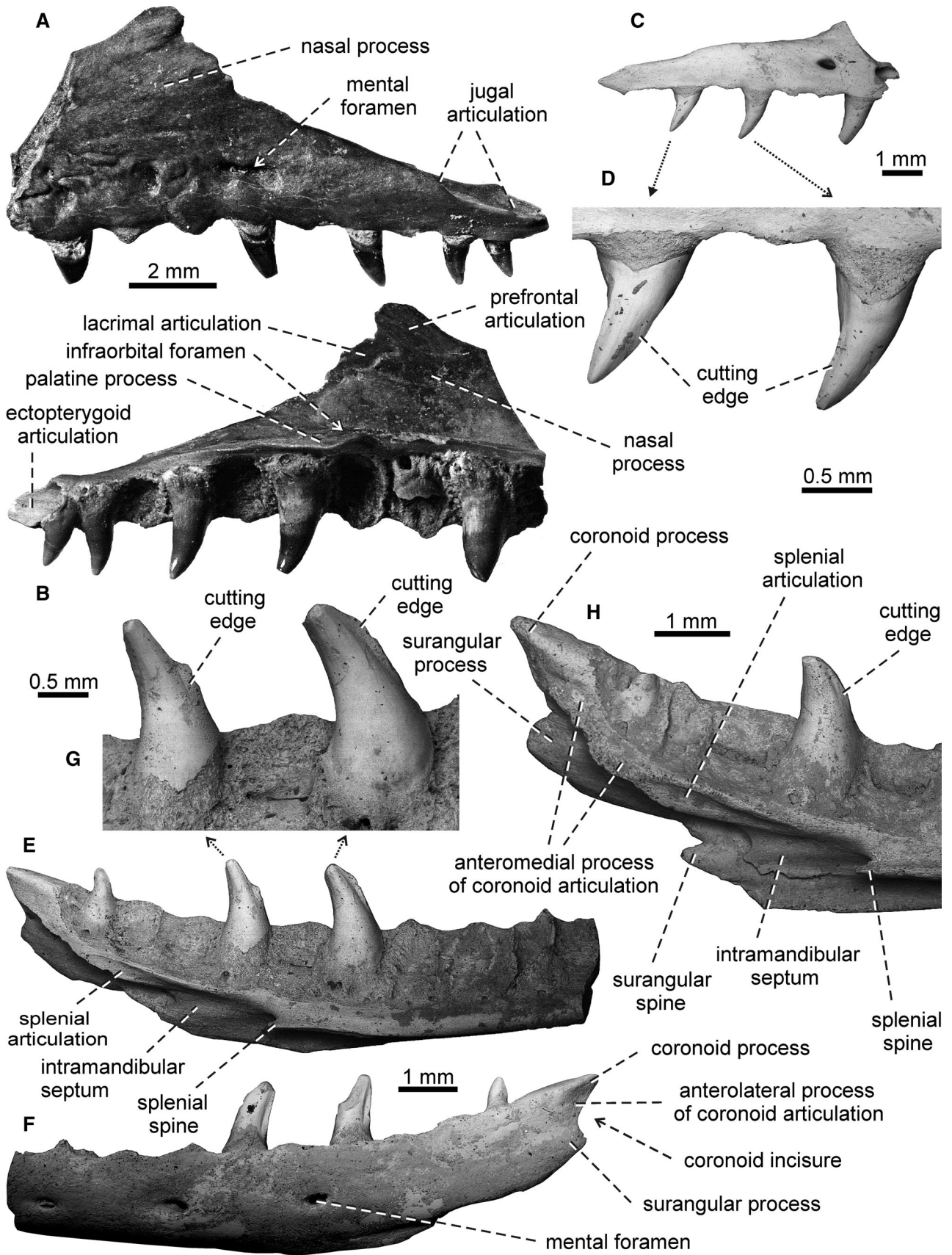
◄**Fig. 5** Anguine morphotype 1: NMP PB 01871, left maxilla in *lateral* (**a**) and *medial* (**b**) *views*; **c**, **d** NMP Pb 02036, right maxilla (**c**) and close-up of two teeth (**d**) in *lateral* views; **e**–**g** NMP Pb 02048, left dentary in *medial* (**e**) and *lateral* (**f**) *views*, and close-up of two teeth in *medial view* (**g**); **h** NMP Pv 10087, partial left dentary in *medial view*

The medial surface of the dorsal portion of the nasal process has a distinct striation, indicating a strong articulation with the prefrontal (Fig. 5b). Immediately ventral to the prefrontal articulation, a narrow dorsoventrally coursing rugosity marks the lacrimal articulation. The supradental shelf is well-developed, and the medially extending palatine process bears a distinct anteroposteriorly elongated facet for articulation with the palatine. A large infraorbital foramen lies immediately laterally to the palatine process. The entire medial surface of the posterior tip of the maxilla bears a distinct facet for articulation with the ectopterygoid (Fig. 5b).

Dentary (Figs. 5e–h, 6a) The largest completely preserved dentary is 17 mm in length (NMP Pv 10100, Fig. 6a). The external surface of this dentary is smooth and bears up to six mental foramina. The articular surface for the anterolateral process of the coronoid is short and high (Fig. 5f).

The coronoid process extends slightly more posteriorly than the surangular process (Fig. 5e, f, h). The angular process is broken in all specimens. The coronoid incisure is shallow, but distinct. The alveolar foramen lies at the level of the third posterior tooth. The posterior section of the intramandibular septum is almost vertical and fused to the internal wall of the dentary; however, the line of fusion is recognizable (Fig. 5e). While this line of fusion is clearly visible in NMP Pv 10091 and NMP Pv 10092, the posteroventral margin of the intramandibular septum in NMP Pv 10087 is free (Fig. 5h). It is clearly evident in all these specimens that the posteroventral margin of the intramandibular septum lies immediately posteroventrally to the alveolar foramen. In NMP Pv 10087 (Fig. 5h) and NMP Pv 10091, a distinct surangular spine is present (for this structure see Klembara 2012; Klembara et al. 2014). The splenial spine lies at the level of the distal portion of the fifth posterior tooth. The posterior-most section of the dental crest bears the articular facet for the anteromedial process of the coronoid, with this facet reaching the level of the last posterior tooth (Fig. 5h, e). Immediately anterior to it, the ventral margin of the dental crest forms an anteroposteriorly elongated and dorsoventrally narrow and distinct facet for articulation with the posterodorsal portion of the splenial (Fig. 5h). Thus, the anterior inferior alveolar foramen is posteriorly bordered by the splenial. The internal and ventral surface of the dental crest bears a facet for articulation with the anterior portion of the splenial

immediately anterior to the splenial spine (Fig. 6a). The symphysial facet is kidney-shaped and entered by Meckel's canal, which is open ventrally.

Dentition (Figs. 5, 6a) The largest and best preserved maxilla, NMP Pb 01871, has five well-preserved teeth and ten preserved tooth positions, so that the complete number of teeth is estimated as 15 (Fig. 5a, b). The dentary NMP Pv 10099 also has up to 15 tooth positions (Fig. 6a). The teeth are conical and posteriorly curved with mesiodistally broad bases (Figs. 5, 6a). The tips of the apices are pointed and unstriated, with well-developed mesial and distal cutting edges.

Comparisons The morphology and number of teeth are very similar to those of *Ophisaurus acuminatus* from the lower Late Miocene of Germany (Jörg 1965). However, while *O. acuminatus*' teeth are also conical with distinct mesial and distal cutting edges, the posterior portion of the Anguine morphotype 1 maxilla is longer relative to this portion in *O. acuminatus* (Jörg 1965: Fig. 1).

The teeth of Anguine morphotype 1 are also similar to those of *Dopasia* (=*Ophisaurus*) *roqueprunensis* from the Early Oligocene of France and Belgium (Augé 1992; Augé and Smith 2009) and, to a certain degree, also to *Dopasia freyssensis* and *D. coderetensis* from the Late Oligocene of France (Augé 2005). The fragmentary nature of the material from these species does not allow for a more detailed comparison.

Although the teeth are also similar in shape to those of the largest specimens of the Recent *Ophisaurus harti* and *O. koellikeri*, the apices in these extant species are striated (Klembara et al. 2014).
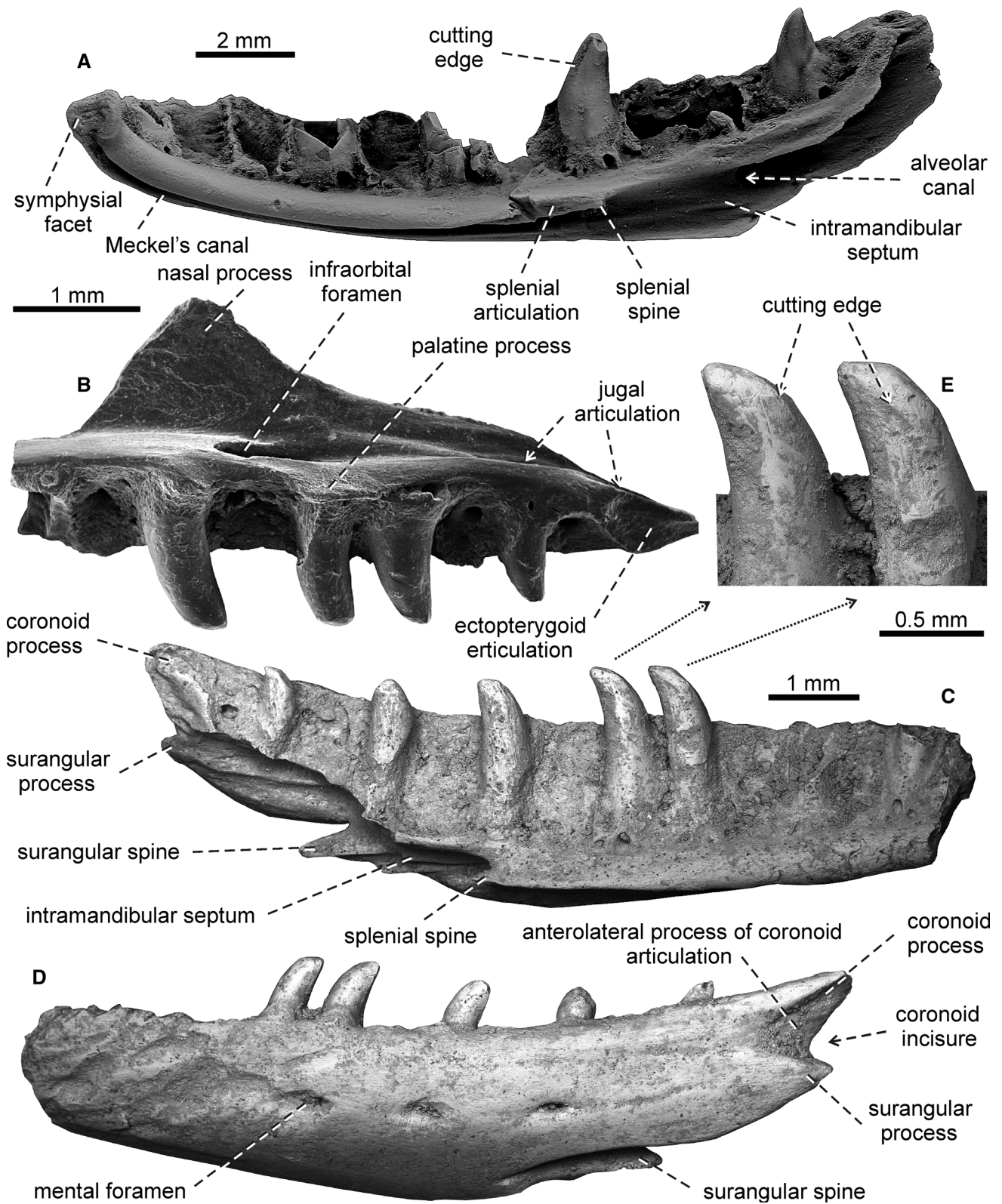
Anguine morphotype 2
Figure 6b–e

Referred specimens Maxilla (NMP Pv 10043); dentary (NMP Pb 02049).

Description: *Maxilla* Only part of the middle portion and the entire posterior portion of a single incomplete maxilla is available (Fig. 6b). The anterior portion of the preserved lateral surface of the maxilla has an ornamentation consisting of irregular shallow grooves and low ridges. Two mental foramina are present. The dorsal surface of the long posterior portion bears a deep and broad groove for articulation with the jugal.

The preserved section of the supradental shelf is well-developed (Fig. 6b), and the infraorbital foramen lies at the level of the posteroventral margin of the nasal process. The palatine process forms a plate-like medial extension of the supradental shelf at the level of the foramen. The medial surface of the posterior-most tip of the maxilla has a distinct oval facet for articulation with the ectopterygoid.

Fig. 6 **a** Anguine morphotype 1: NMP Pv 10100, right dentary in *medial view*. **b–e** Anguine morphotype 2: **b** NMP Pv 10043, right maxilla in *medial view*; **c–e** NMP Pb 02049, left dentary in *medial* (**c**) and *lateral* (**d**) *views*, and close-up of two teeth in *medial view* (**e**)

Dentary The lateral surface of the dentary is smooth and three mental foramina are preserved (Fig. 6d). The articular surface for the anterolateral process of the coronoid is anteroposteriorly short, high and slightly roughened.

The coronoid process extends slightly further posteriorly than the surangular process, and the coronoid incisure forms a shallow wedge (Fig. 6c, d). The angular process is broken. The well-developed surangular spine is a process of the posteroventral margin of the dentary, being pointed and lying at a level posterior to the alveolar foramen. The posteroventral portion of the intramandibular septum is a free vertical lamina (Fig. 6c), and this septum forms a horizontal shelf more anteriorly. While the alveolar foramen lies at the level of the fourth posterior tooth, the splenial spine is at the sixth posterior tooth level. Since the posterior section of the dental crest is damaged, it is impossible to identify the extent of the anteromedial process's articulations with the coronoid and splenial. The ventromedial margin of the dental crest bears a facet for articulation with the anterior portion of the splenial immediately anterior to the splenial spine. Meckel's canal opens ventrally.

Dentition The maxilla and dentary are associated on the basis of a very similar tooth morphology (Fig. 6b–e). The preserved portion of the maxilla bears eight tooth positions with four well-preserved teeth (Fig. 6b), while the dentary has 13 positions and five completely preserved teeth (Fig. 6c). The teeth are rod-like with almost straight shafts and slightly posteriorly curved apices, and their bases are only slightly mesiodistally broadened relative to the mesiodistal width of the tooth shafts. The mesial and distal cutting edges are weakly developed with unstriated apices.

Comparisons Although the general dentary morphology of Anguine morphotype 2 and Anguine morphotype 1 is quite similar, subtle differences in absolute tooth morphology were evident. The teeth of Anguine morphotype 2 are rod-like with posteriorly curved apices, but their shafts are almost straight and their bases are only slightly mesiodistally broadened. In addition, the apices have only very slightly developed mesial and distal cutting edges. In contrast, the teeth of Anguine morphotype 1 are conical and curved posteriorly, with broad bases mesiodistally and sharp well-developed mesial and distal cutting edges. Here, the Anguine morphotype 2 teeth are very similar to those described in specimen DP FNS 3844 as *Ophisaurus* sp. I. (Roček 1984: Pl. 10, Fig. 3).

Further comparison can be made with the teeth of *Ophisaurus* sp. from Dolnice which have an almost straight shaft and slightly curved apices (Klembara 1981: Pl. 3, Figs. 1–3), in addition to well-developed medial and distal cutting edges. In contrast, although *Ophisaurus* sp. teeth are similar to those of Anguine morphotype 2, the latter's cutting edges are only very slightly developed.
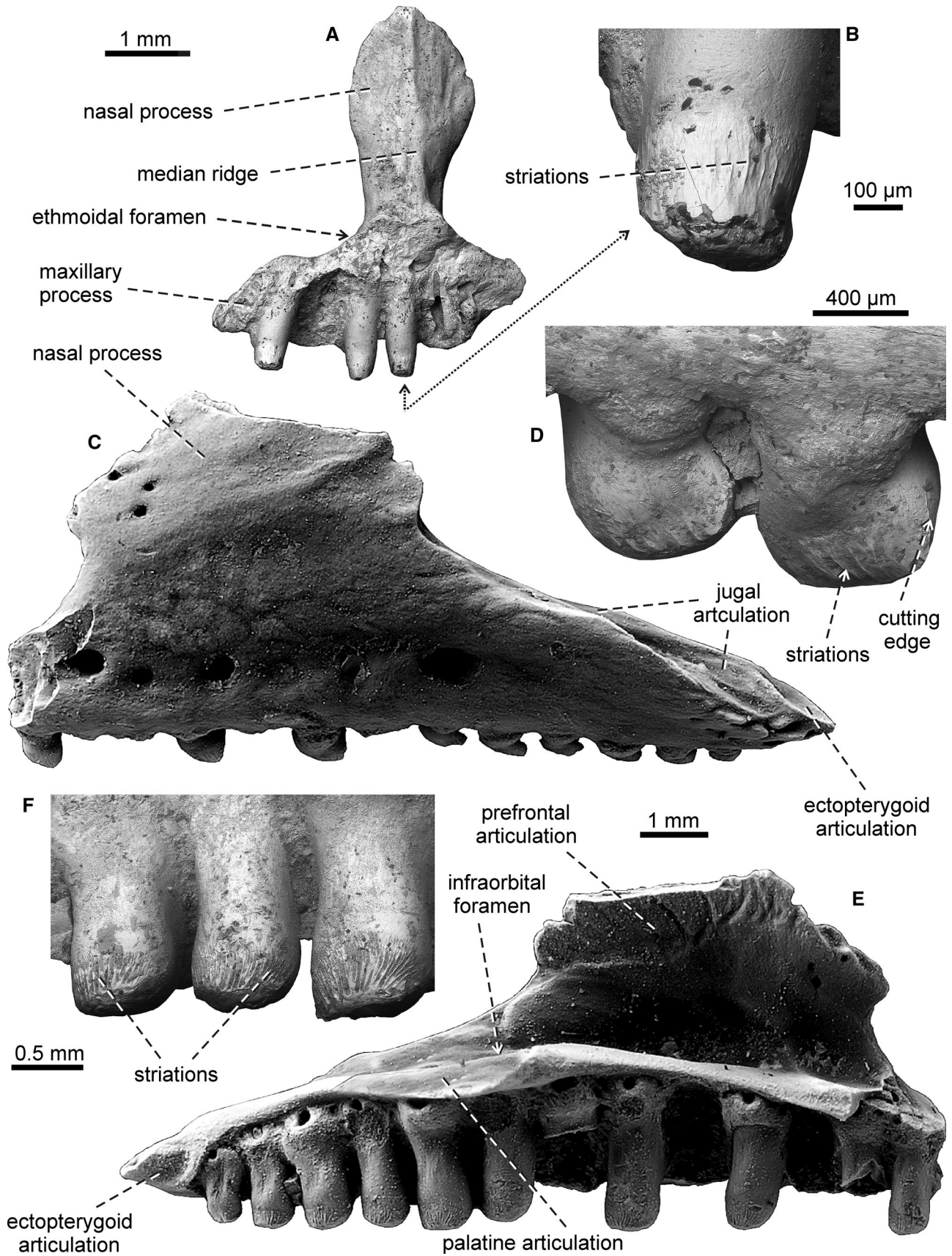
Anguine morphotype 3
Figures 7, 8, 9

Referred specimens Premaxilla (NMP Pb 02035, NMP Pv 10044–10045); maxilla (NMP Pb 02031–02034, NMP Pb 02037, MP Pv 10031–10042); dentary (NMP Pb 02038–02040, NMP Pb 02047, NMP Pv 10046–10055, NMP Pv 10056–10064, NMP Pv 10066).

Description: *Premaxilla* The best preserved premaxilla shows well-developed nasal and maxillary processes (Fig. 7a). The posterior portion of the nasal process is expanded, its posterior tip is pointed and its internal surface has a longitudinal median ridge. The dorsolateral surface of the maxillary process bears an area for articulation with the premaxillary process of the maxilla, and this latter process overlaps the maxillary process of the premaxilla. The large ethmoidal foramen is located on the dorsal surface of the premaxilla body, at the angle between the nasal and maxillary processes.

Maxilla (Figs. 7c–f, 8) Although three of the 17 maxillae are almost completely preserved, all premaxillary processes are largely incomplete. The nasal process forms a high lateral wall of the nasal capsule, and has distinctly irregular grooves and ridges ornamenting its external surface immediately dorsal to the mental foramina (Figs. 7c, 8a). There are up to six mental foramina, of which the posterior foramen is generally the largest. The external ramus of the premaxillary process is completely preserved in NMP Pv 10037 (Fig. 8a) and NMP Pv 10042 (Fig. 8d). Its anterior tip is slightly flexed dorsally indicating that it overlaps the maxillary process of the premaxilla. Although the root portion of the internal premaxillary process is preserved in NMP Pv 10040 and NMP Pv 10052, further morphological details are unavailable. The notch between both premaxillary processes indicates the presence of the premaxillary–maxillary fenestra.

The prefrontal articulation is well-preserved on the internal surface of the nasal process (Fig. 7e) and the supradental shelf is distinct (Figs. 7e, 8c, d). The palatine process is well-developed and its dorsal surface bears a large, anteroposteriorly elongated and slightly roughened area for articulation with the palatine (NMP Pv 10031, Fig. 7e). Here, the maxilla is slightly concave, and the infraorbital foramen is located immediately lateral to the articulation area for the palatine. Anterior to the infraorbital foramen, the supradental shelf is mediolaterally narrow and the entire anterior portion of the maxilla is strongly convex in shape. The dorsal surface of the posterior section of the supradental shelf bears an elongated

◀**Fig. 7** Anguine morphotype 3: **a**, **b** NMP Pv 10044, premaxilla (**a**) and close-up view of one tooth (**b**) in *medial views*; **c**–**f** NMP Pv 10031, maxilla (**c**) and close-up view of the second and third teeth from posterior (**d**) in *lateral views*, maxilla (**e**) and close-up of the third to fifth tooth from posterior (**f**) in *medial views*

and deep groove for articulation with the anterior ramus of the jugal (Figs. 7c, 8a), and its surface bears up to two small foramina. The dorsomedial surface of the posterior tip on the posterior portion of the maxilla in NMP Pv 10031, NMP Pv 10032 and NMP Pv 10037 bears a distinct facet for articulation with the ectopterygoid (Figs. 7c, e, 8c).

Dentary (Fig. 9) The dentary is a long, ventrally arched bone (Fig. 9a). The external surface is smooth and bears up to seven mental foramina. A triangular, slightly roughened area for articulation with the anterolateral process of the coronoid is distinctly developed (Fig. 9d).

Posteriorly, the dentary extends into three processes (Fig. 9b, d). (1) The coronoid process is massive and posteriorly pointed; (2) the surangular process is wedge-shaped, and the posterior tip of the surangular and coronoid processes extend approximately the same length with a shallow coronoid incisure between them; and (3) the angular process is posteriorly pointed and reaches the level of the distal margin of the second posterior tooth. The surangular sinus is deep and dorsoventrally broad. The surangular spine is shorter than the angular process, but it is well-developed, wedge-shaped and projects posteriorly into the space of the surangular sinus. The posteroventral portion of the intramandibular septum is free in the largest dentary (Fig. 9a). In other specimens it is fused to the inner wall of the dentary, however, the line of fusion is clearly visible in most of them (as in NMP Pv 1059, NMP Pv 10062 and NMP Pv 10064). Further anteriorly, the intramandibular septum forms a horizontal shelf. While the alveolar foramen is located at the level of the fourth posterior tooth in NMP Pb 02047, it is at the level of the fifth posterior tooth in the largest specimen, NMP Pv 100048 (Fig. 9a). Meckel's groove widens dorsoventrally in a posterior direction. The symphysial facet is kidney-shaped, with Meckel's groove partly entering it. The splenial spine lies at the level between the fifth and sixth posterior tooth in NMP Pb 02047 (Fig. 9b) and between the sixth and seventh posterior tooth in NMP Pv 10048 (Fig. 9a). This spine forms the anterior margin of the anterior inferior alveolar foramen. Posterior to this foramen, the dental crest is dorsoventrally narrow and bears a shallow groove extending to the level of the posterior-most tooth, and forming the splenial's posterodorsal articular surface (Fig. 9a, b). Further posteriorly, this crest forms a roughened dorsoventrally broad facet

for the articulation with the anteromedial process of the coronoid (Fig. 9b). The crest is dorsoventrally broad and smooth anterior to the anterior inferior alveolar foramen, and the crest's ventromedial margin bears an elongated groove for articulation with the anterodorsal margin of the splenial (Fig. 9a).

Dentition The premaxilla, maxilla and dentary described above are considered to belong to one species on the basis of almost identical tooth morphology (Figs. 7, 8, 9). Four teeth and two tooth positions are preserved in premaxilla NMP Pb 02035, and three teeth are present in the premaxilla NMP Pv 10044 (Fig. 7a, b). While there are up to 16 maxillary tooth positions in NMP Pv 10032 (Fig. 8c), this is increased to 18 tooth positions in NMP Pv 10048 (Fig. 9a).

The dentary teeth of the largest specimens are rod-like and densely spaced (Fig. 9). The apices are mesiodistally widened, from which the posterior corner of the apex extends slightly distally. The entire apex bears a sharp and low cutting edge. The lingual and labial apical surfaces are distinctly striated, with this striation strikingly more distinct in large individuals. A slightly developed depression is evident on the lingual surface between the striated portion and the remaining part of the crown, and the crown's basal portions are slightly expanded lingually.

The apices of the maxillary teeth of the largest specimens are only very slightly curved posteriorly (NMP Pv 10031, NMP Pv 10033, 10034 and NMP Pv 10036–10040; Figs. 7c–f, 8a, b). While the apices are more distinctly curved posteriorly in medium-sized specimens such as NMP Pv 10032 (Fig. 8c), the entire teeth are slightly curved posteriorly in smaller specimens like NMP Pv 10041, 10042 (Fig. 8d, e). The largest teeth, mostly two or three, are positioned immediately anterior to the palatine process, and the teeth then diminish in size mesially and distally.

Comparisons The expanded nasal process of the premaxilla bearing the median keel is present in *Ophisaurus*, *Anguis* and three species of *Pseudopus* (*P. pannonicus*, *P. laurillardi*, and *P. ahnikoviensis*) (Klembara 1986, 2012; Klembara et al. 2010).

The teeth of the maxilla from the Dolnice locality described as *Pseudopus* sp. (Roček 1984: Pl. 11, Figs. 1–3) have apical striations on their lingual and facial surfaces similar to those in Anguine morphotype 3. However, in contrast to Anguine morphotype 3 teeth, those in the Dolnice specimen are conical (Roček 1984). Although the Late Eocene Anguine B from the Hampshire Basin in Southern England (Klembara and Green 2010) is much smaller than Anguine morphotype 3, the teeth in both anguines are almost identical.
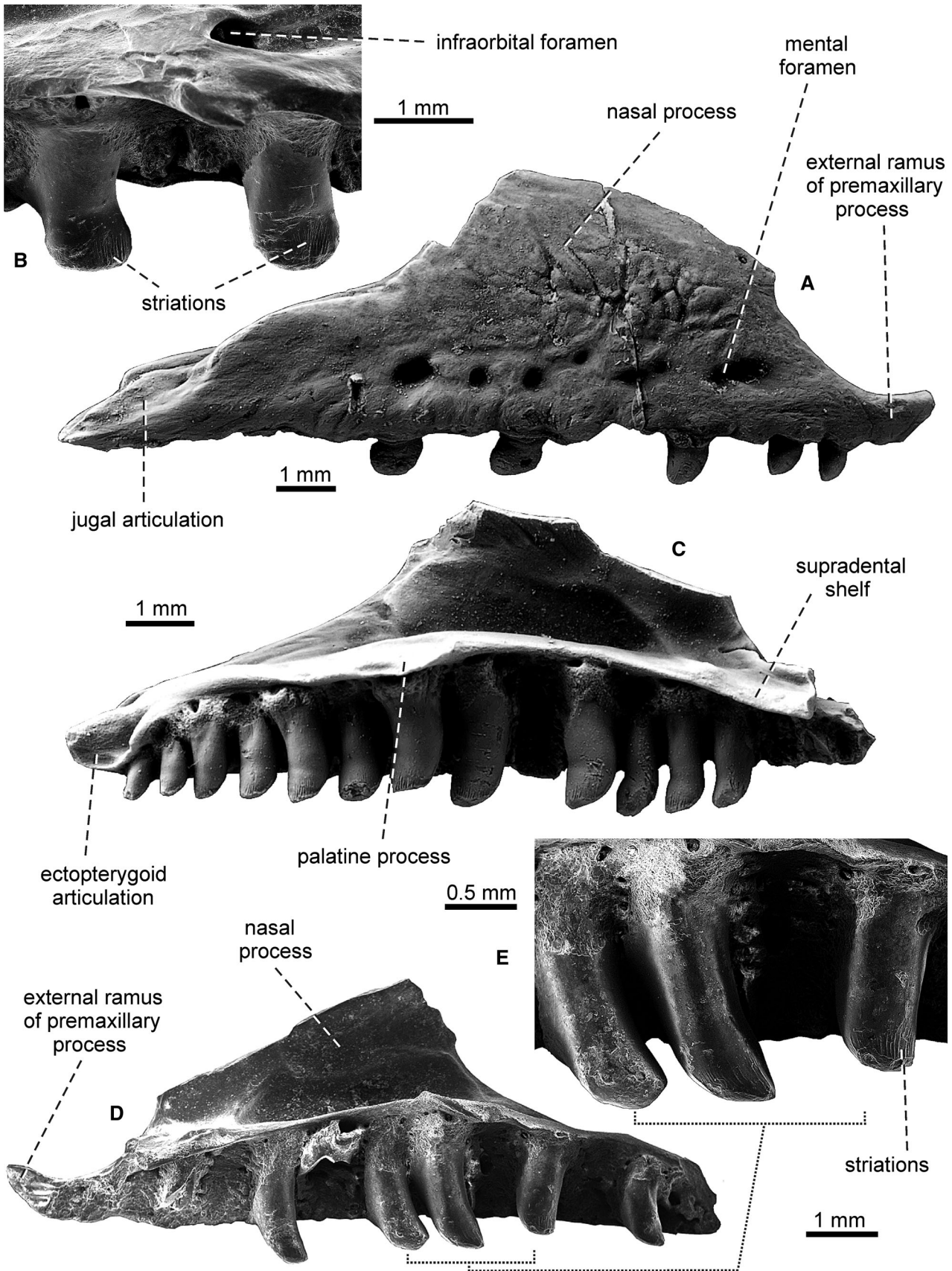
◄**Fig. 8** Anguine morphotype 3: **a**, **b** NMP Pv 10037, maxilla in *lateral view* (**a**) and two last preserved teeth from posterior in *medial view* (**b**); **c** NMP Pv 10032, maxilla in *medial view*; **d**, **e** NMP Pv 10042, maxilla (**d**) and three teeth (**e**) in *medial view*

Anguine morphotype 4
Figure 10
1981 *Ophisaurus* sp. Klembara: 133, Pl. 2, Fig. 2.

Referred specimens Pterygoid (NMP Pb 02043, NMP Pv 10067–10070, DP FNSP 4700).

Description The anteroposteriorly elongated body of the pterygoid extends into two processes anteriorly (Fig. 10). (1) The anteromedially extending one is the palatine process, which is mediolaterally wide, but, unfortunately, its tips are broken in all specimens; and (2) the antero-laterally extending transverse process is well-preserved in NMP Pb 02043 and NMP Pv 10068 (Fig. 10) and its entire medial surface bears a striated articular area for the ectopterygoid. The root of the palatine process and almost the entire ventral surface of the pterygoid body bear an elliptical denticulate field which extends posteriorly to almost the anterior level of the obtuse process. The ventral transverse crest is sharp and is positioned along the posterior margin of the transverse process. Between it and the lateral margin of the denticulate field, there is a deep pterygoid sulcus. The suborbital incisure is deeply notched posteriorly. The pterygoid body forms two processes posteriorly. While the obtuse process is small, stout and blunt, the quadrate process is long and mediolaterally flattened. This latter is well-preserved only in NMP Pv 10067, where its medial wall bears a distinct basipterygoid articulation.

On the dorsal surface of the transverse process, the dorsal transverse crest is sharp; it runs obliquely and then fades away in the central portion of the pterygoid body. The high and sharp epipterygoid crest forms a dorsal wall of the basipterygoid articulation, with its straight margin almost rectangular in shape. The crest then merges posteriorly into the sharp dorsomedial margin of the quadrate process. While the pterygoid fovea is deep and round, its posterior portion continues posteriorly as a groove in the dorsal surface of the root of the quadrate process.

The denticulate field is elliptical, with the teeth arranged in anteroposterior rows. There are up to four rows, and the lateral row always contains the largest teeth. Several teeth, medial to the main lateral tooth row, are irregularly scattered in the large, presumably aged, NMP Pv 10069 specimen. The teeth are conical with almost pointed apices.

Comparisons The pterygoid of Anguine morphotype 4 is very similar to that described as *Ophisaurus* cf. *spinari* (Roček 1984: Pl. 10, Fig. 2).

Anguine morphotype 5
Figure 11a, b

Referred specimen Fused articular + prearticular + surangular (NMP Pb 02041).

Description The articular, prearticular and surangular are indistinguishably fused posteriorly. The retroarticular process is quadrangular, and its internal surface bears a deep oval depression. The glenoid fossa faces posterodorsally and medially, with a small foramen for the chorda tympani immediately posterior to it. On the medial surface of the compound bone, one tiny foramen lies immediately anterior to the anterior margin of the glenoid fossa. The adductor fossa is anteroposteriorly elongated and a large posteromedial surangular foramen lies a short distance posterior to it. Meckel's groove is deep, and dorsal to this, a large, longitudinally striated surface indicates the strong articulation with the prearticular (Fig. 11a). Still further dorsally, there is a distinct articular surface for the coronoid. The prearticular articular surface bears two foramina. The ventrolateral margin of the surangular bears a longitudinal facet for articulation with the angular (Fig. 11b), and its anterior portion has a deep groove for articulation with the dentary.

The external surface of the compound bone is smooth. It bears a large posterior surangular foramen anterior to the anterior margin of the glenoid surface. The anterior surangular foramen lies in the anterior portion of the surangular, immediately posterior to the articular surface for the surangular process of the dentary.

Comparisons This bone is very similar to that of *Ophisaurus*. Contrary to that in *Pseudopus*, the anterior surangular foramen is located in the anterolateral wall of the surangular, which is also visible in lateral view. This is a typical condition of *Ophisaurus* and *Anguis* (Klembara et al. 2014).

Anguine morphotype 6
Figure 11c, d

Referred specimen Fused articular + prearticular + surangular and angular (NMP Pb 02042).

Description The articular, prearticular and surangular are fused posteriorly. The anterior portion of the prearticular is partly preserved in the form of a thin perpendicular plate (Fig. 11c). The glenoid fossa is only partly preserved and the retroarticular process is absent. A tiny foramen lies in the dorsomedial surface of the compound bone, immediately anterior to the anterior portion of the glenoid fossa. The adductor fossa is deep and anteroposteriorly elongated, with a large posteromedial surangular foramen posterior to it. A large roughened area dorsal to the deep Meckel's groove indicates strong articulation with the prearticular, and there is a distinct articular surface for the coronoid
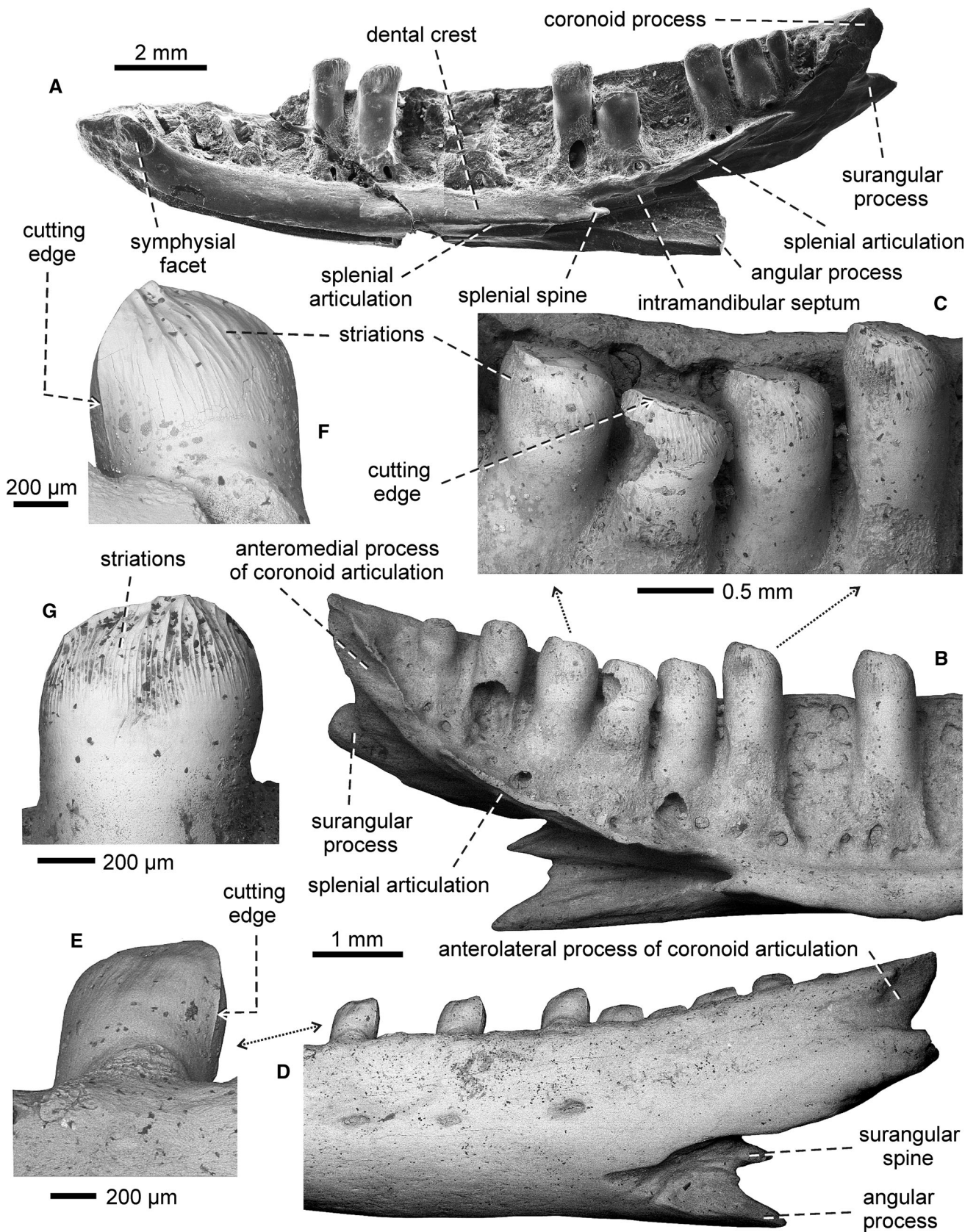
◄ **Fig. 9** Anguine morphotype 3: **a** NMP Pv 10048, dentary in *medial view*; **b–e** NMP Pb 02047, partial dentary (**b**) and close-up view of four teeth (**c**) in *medial view*, dentary (**d**) and one tooth (**e**) in *lateral view*; **f, g** NMP Pv 10046, close-up view of the sixth tooth from anterior in *lateral view* (**f**), and close-up view of the third tooth from posterior in *medial view* (**g**)

slightly dorsal to this area (Fig. 11c). The articular surface for the prearticular bears one foramen. Anteriorly, the surangular extends into a distinct dental process for articulation with the dentary.

The external surface of this compound element is smooth. A large posterior surangular foramen lies anterior to the anterior margin of the glenoid fossa, while the anterior surangular foramen is present on the anterodorsal portion of the compound bone. This latter foramen is only partly visible in lateral view (Fig. 11d).

Almost the entire posterior half of the angular is well-preserved, and it forms a ventral trough of the compound bone (Fig. 11c, d). There is a small posterior mylohyoid foramen present on the medial surface of the angular, and it is positioned at the level of the anterior portion of the coronoid articulation (Fig. 11c).

Comparisons The morphology of the preserved portion of the compound bone is very similar to that of *Pseudopus* (Fejérváry-Lángh 1923; Klembara et al. 2010), and it is much more robustly built than that in Anguine morphotype 5. In addition, the anterior surangular foramen in Anguine morphotype 6 lies in the anterodorsal portion of the surangular and it is not visible in lateral view, exactly as in other species of *Pseudopus* (Klembara et al. 2010, 2014).
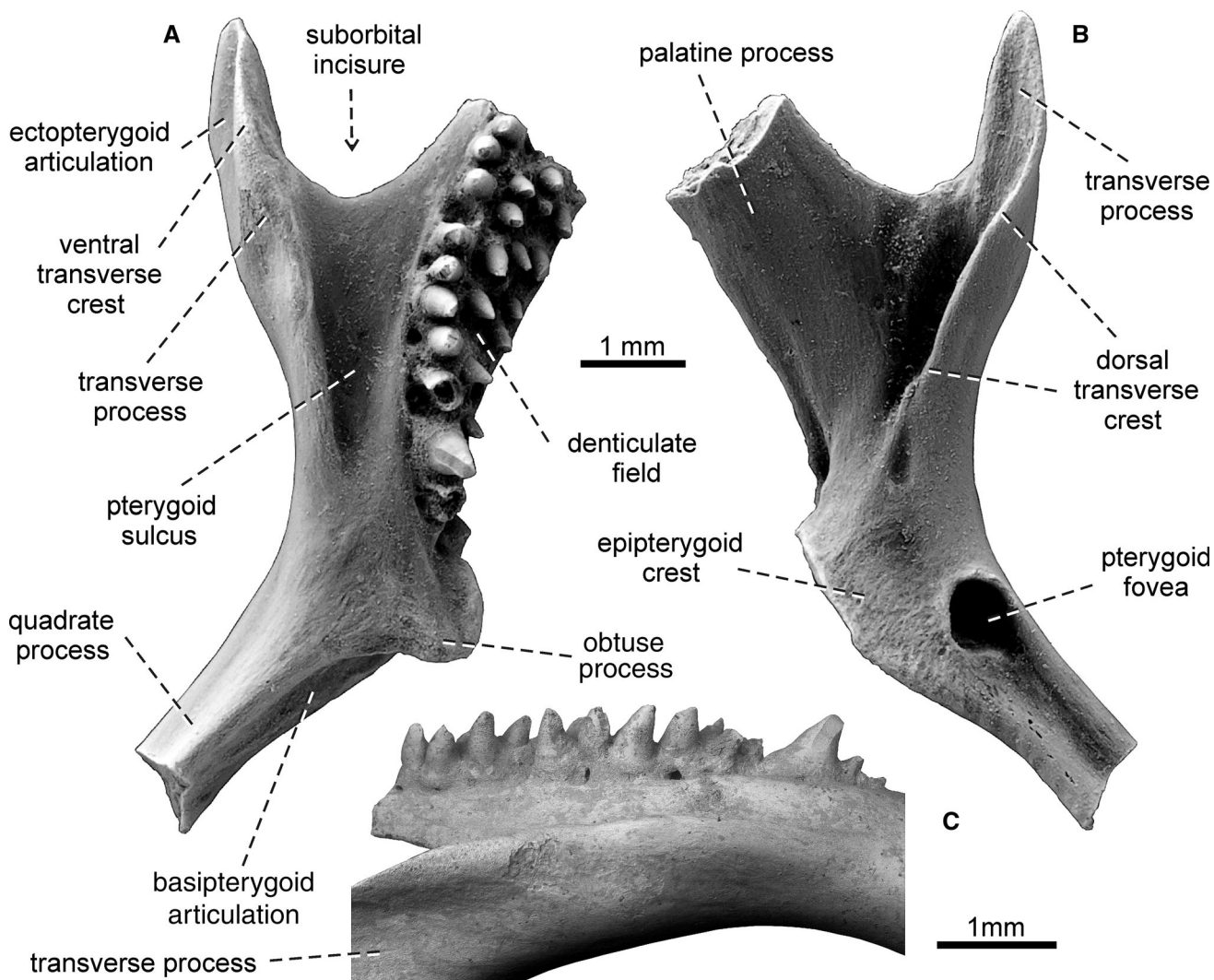
Fig. 10 Anguine morphotype 4: NMP Pv 10068, pterygoid in *ventral* (**a**) and *dorsal* (**b**) views, and middle portion of pterygoid in *lateral view* (**c**)
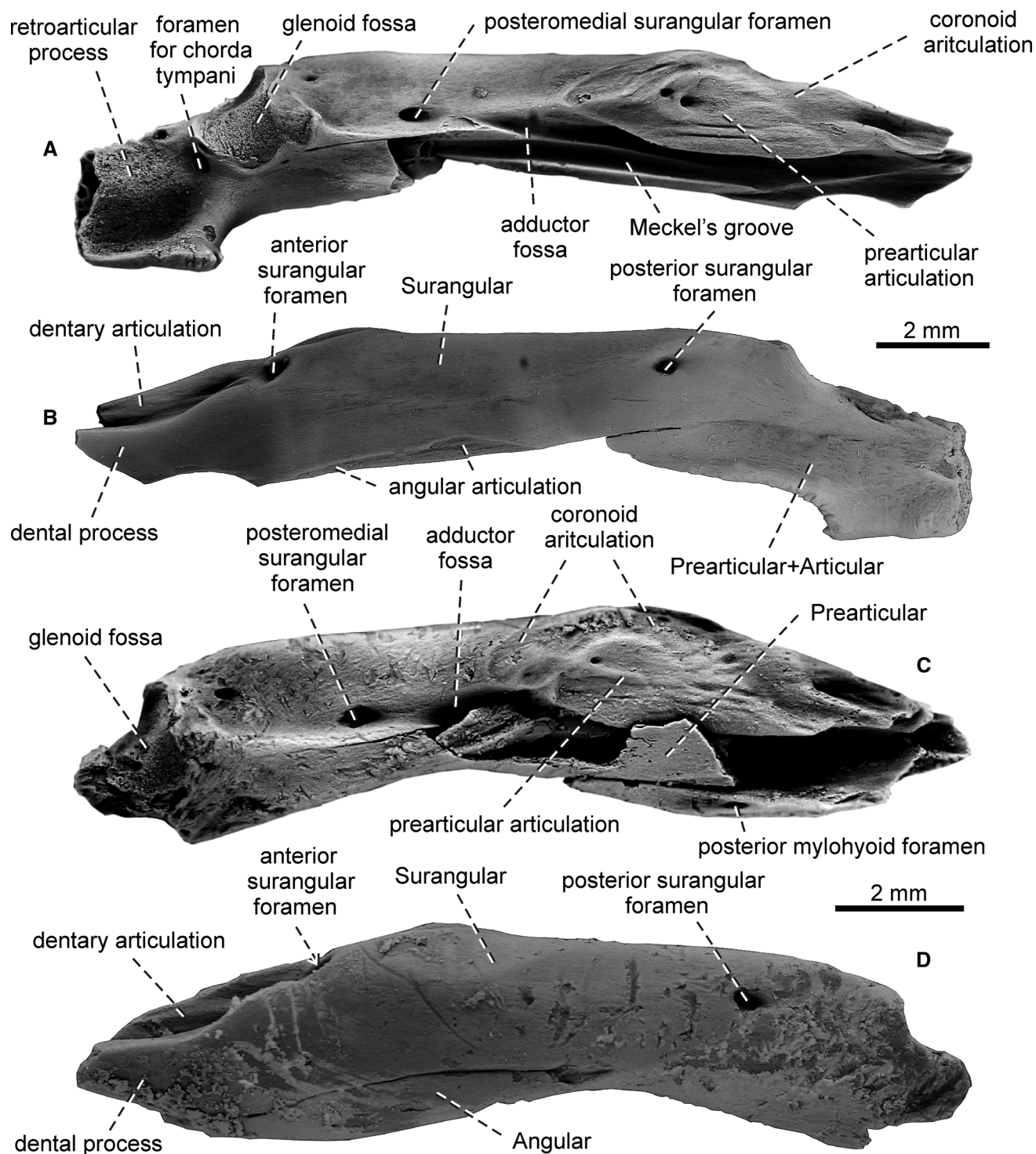
Fig. 11 **a**, **b** Anguine morphotype 5: NMP Pb 02041, posterior half of lower jaw in *medial* (**a**) and *lateral* (**b**) *views*. **c**, **d** Anguine morphotype 6: NMP Pb 02042, posterior half of lower jaw in *medial* (**c**) and *lateral* (**d**) *views*

Discussion

Several bones assigned to Anguinae from the Merkur locality were first briefly described in Vejvalka's (1997) thesis. The frontal bone, re-described and designated as

Ophisaurus sp. 2 herein (Fig. 3e, f), was originally assigned to *Pseudopus* cf. *P. moguntinus* by Vejvalka (1997). Recently, the new species of *Pseudopus*, *P. ahnik-oviensis*, which is the oldest and smallest species of this genus, was described from the Merkur locality (Klembara

2012). All other material described here is the first description of anguines from the Merkur locality. This is the second oldest Miocene anguine locality in Europe, with the oldest being in the Wiesbaden area of Germany (Lower Miocene, MN 2; Čerňanský et al. 2014).

Unfortunately, although lizard material, including anguines, from Cenozoic localities in Europe is disarticulated, it is sometimes possible to associate several bones on the basis of the ornamentation of the frontal and parietal bones or on morphology of the teeth of marginal tooth-bearing elements, which is also the case in the new species of both *Ophisaurus* and *Pseudopus* described herein. The new species of *Ophisaurus*, *O. holeci*, is the fourth Miocene species of this genus described on the basis of the parietal bone. The three other species, *O. fejfari*, *O. spinari* and *O. robustus*, were previously described from the Dolnice locality (Klembara 1979, 1981). It is highly probable that the tooth-bearing elements described herein belong to one or more species described on the basis of isolated parietals. *Ophisaurus acuminatus* was described from the early Late Miocene of Hewenegg–Hegau in Germany, but this species' parietal and frontal are missing (Jörg 1965). Although the Anguine morphotype 1 teeth described here (Figs. 5, 6a) are very similar to those in *O. acuminatus*, only a more complete specimen of the latter with preserved parietal and frontal bones could establish if it is a different species to those described on the basis of the parietals or one of the species described on the basis of the parietals will be synonymous with *O. acuminatus*. Nevertheless, there is a significant time gap between the species of *Ophisaurus* described on the basis of the parietals and *O. acuminatus*.

Another problem refers to the determination of the skull and lower jaw elements of *Anguis polgardiensis* (Bolkay 1913) which, according to Estes (1983), is synonymous with *Pseudopus pannonicus* from the Late Miocene of Hungary. *Anguis polgardiensis* was described on the basis of a single incomplete parietal, two maxillaries and a fragment of one dentary. While the preserved portion of the parietal is ~4 mm in length, the posterior portion of the smooth area and both supratemporal processes are missing. Bolkay (1913) identified this parietal as belonging to *Anguis* based on the following two features: (1) the presence of a wide triangular interparietal ornamental shield (his "scutum interparietale") where the anterior end of the interparietal sulcus lies exactly at the anterolateral corner of the ornamented parietal shield, and (2) the presence of an occipital ornamented shield (his "scutum occipitale"). Bolkay (1913) added that he did not observe his "scutum occipitale" in the extant *Anguis fragilis*. However, although there is slight individual variability in the shape of the interparietal and occipital ornamental shields, the

triangular interparietal shield and a well-developed occipital shield are always present in the *A. fragilis* parietal (see also Klembara 1979: Pl. 3, Fig. 2). In addition, (1) the morphology of the parietal ornamented shield of *A. polgardiensis* is very similar to that of *Ophisaurus spinari* (Klembara 1979: Pl. 1, Fig. 2 and Fig. 3A here), and (2) since the parietal of *A. polgardiensis* is not visible in ventral view, its morphology cannot be precisely substantiated. For example, we are not able to determine whether the muscular surface is present or not, and this is most important because the muscular surface is of characteristic shape in *Pseudopus* (Klembara 2012). According to personal information from Professor L. Kordos of the Hungarian Geological Museum in Budapest, the material of *A. polgardiensis* is lost. Therefore, precise determination of *A. polgardiensis* is impossible.

However, the most important result is that we are able to identify a new species of *Pseudopus*, *P. rugosus*, in the new material from Merkur. The genus *Pseudopus* consists of four species, *P. ahnikoviensis* (Early Miocene of Merkur; Klembara 2012), *P. laurillardi* (Early-Middle Miocene of Europe), *P. pannonicus* (Late Miocene–Middle Pleistocene of Central and Eastern Europe) and *P. apodus* (Late Pleistocene–Recent, from Eastern Europe to Central Asia) (for review see Klembara et al. 2010). Therefore, the new species *P. rugosus*, similar in size to *P. ahnikoviensis*, is now the second species identified from the Merkur locality. The identification of the fifth species of *Pseudopus* indicates that the genus *Pseudopus* was quite diverse in the Early Neogene of Europe, as witnessed also in *Ophisaurus*.

Although in most cases problems must be overcome in designation of disarticulated elements to one species, recognition of the various morphotypes enables the appreciation of the morphological variability and diversity of certain groups in certain time period. This variability was clearly established in this study by both anguine parietals and their dentaries. Profuse dentary morphotypes have been described from various European Miocene localities, including; *Ophisaurus* sp. (Klembara 1981: Pl. 3, Figs. 1–3), *Ophisaurus* cf. *spinari*, *Ophisaurus* sp. I, and *Ophisaurus* sp. II (Roček 1984) from the Early Miocene Dolnice locality in the Czech Republic, *Ophisaurus* sp. from the Early Miocene of Germany (Schleich 1988) and *Ophisaurus* sp. from the latest Early Miocene of Germany (Böhme 2010). In certain aspects, all the above dentaries are similar to those of Anguine morphotype 1 and Anguine morphotype 2 described herein. In conclusion, although articulated specimens are necessary to be able to unequivocably designate individual dentaries and other skull and lower jaw elements to one or more species, this research elucidates that the subfamily Anguinae was extremely diverse in the Miocene of Europe.

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