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# REVISION OF THE ANGUINE LIZARD *PSEUDOPUS LAURILLARDI* (SQUAMATA, ANGUIDAE) FROM THE MIOCENE OF EUROPE, WITH COMMENTS ON PALEOECOLOGY

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ABSTRACT—A revision of the Early-Middle Miocene anguine, *Pseudopus laurillardi* (Lartet, 1851), is presented based on a detailed anatomical analysis of one newly discovered articulated specimen and numerous disarticulated cranial and postcranial elements from several localities in Germany, as well as on the restudy of the original skeletal material of Lartet. The articulated specimen represents the first record of an articulated anguine from the Neogene. We demonstrate that the contemporaneous anguine *Propseudopus fraasii* (=*Pseudopus fraasi*, *Pseudopus moguntinus* or *Ophisaurus moguntinus*) from Germany and elsewhere in Europe represents a junior synonym of *P. laurillardi*. Three species of *Pseudopus* can by discriminated in the Cenozoic of Eurasia: *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). Eleven morphological characters of the skull have been identified that distinguish *Pseudopus laurillardi* from *P. pannonicus* and *P. apodus*. Four of these characters regard the frontal and parietal bones, whereas all other characters regard the dentary and dentition. The genus *Pseudopus* represents the largest and most robust taxon in the subfamily Anguinae and first occurs in central Europe at the beginning of MN 4 (~18.5 Ma). In contrast to the extant species, *P. apodus*, the fossils *P. laurillardi* and *P. pannonicus* had a greater ecological plasticity and lived in various types of environments. The fossil remains of these taxa are most frequently found in localities characterized by sub-humid to humid climate, which may indicate that their preferential habitats include forested environments.

## INTRODUCTION

THE ANGUINE anguids have a long evolutionary history in the Cenozoic of Eurasia (Fejérváry-Lángh, 1923; Klembara, 1979, 1981; Rieppel, 1980; Gauthier, 1982; Rage and Augé, 1993; Conrad, 2008; Augé and Smith, 2009). The earliest fossil evidence, although fragmentary, has been reported from Early Eocene sediments in Belgium and attributed to the genus *Ophisaurus* s. l. (Augé, 1990a). The skeletal remains attributed to *Anguis* have been found in the Early Eocene of France (Augé, 1990b). Moreover, several skeletal remains have been described from the Late Eocene of Switzerland and assigned to *Parapseudopus picketi* (Hoffstetter, 1942). More recently, Augé (2005) erected a new generic name, *Helvetisaurus*, for this species. Several complete skeletons of the anguine *Ophisauriscus quadrupes* have been described from the Middle Eocene of Germany (Kuhn, 1940; Klembara, 1981; Sullivan et al., 1999), whereas the Oligocene of Europe has yielded only disarticulated, fragmentary remains of anguines that are attributable to the genera *Anguis* and *Ophisaurus* (Hecht and Hoffstetter, 1962; Augé, 1992; Augé and Smith, 2009). The Miocene record is richer than that from the Oligocene but usually consists of disarticulated remains. The Miocene specimens have been referred to the genera *Pseudopus* (e.g., Boettger, 1875; Klembara, 1981; Böhme, 1999, 2002; Roček, 1984; Augé and Rage, 2000; Miklas, 2004; Rage and Bailon, 2005; Venczel, 2006), *Ophisaurus* (e.g., Jörg, 1965; Bachmayer and Mlynarski, 1977; Klembara, 1979, 1981, 1985, 1986a; Roček, 1984; Böhme, 1999, 2002; Rage et al., 2002; Venczel, 2007), and *Anguis* (e.g., Bolkay, 1913; Klembara, 1981; Miklas, 2004). Augé (2005) replaced the generic name *Ophisaurus* with *Dopasia*, a name originally used by Gray (1853) for the Recent anguine *Dopasia gracilis* from southeast Asia, and suggested that this name be used for all fossil and living Eurasian and North African species of the genus *Ophisaurus*. The results from DNA analysis of Recent members of Anguinae presented by Macey et al. (1999), however, do not support subdivision of the species traditionally included in *Ophisaurus* from Eastern Asia and North America into two genera. In the Pliocene and Pleistocene, only the remains of *Pseudopus* (e.g., Kormos, 1911; Fejérváry-Lángh, 1923; Mlynarski, 1962; Mlynarski et al., 1984; Klembara, 1986b; Rauscher, 1992; Miklas, 2004) and *Anguis* (e.g., Rauscher, 1992; Mlynarski et al., 1984; Klembara, 1986b) have been recorded with certainty. Bailon and Blain (2007) mention the presence of cf. *Ophisaurus* from the Middle Pliocene of the Iberian Peninsula but do not provide a description or illustrations of the fossils. Five anguine genera have been recorded for the Cenozoic of Europe to date: *Helvetisaurus*, *Ophisauriscus*, *Ophisaurus*, *Anguis* and *Pseudopus*. Of these, *Ophisaurus*, *Anguis* and *Pseudopus* persist in Eurasia to the present time; the genus *Ophisaurus* also occurs in North Africa (Morocco, Libya) and North America.

The genus *Pseudopus* represents the most robust anguine in Eurasia. The robust anguine *Anguis*? *laurillardi* was first described by Lartet (1851) from the Middle Miocene of Sansan in France. In a detailed historical and taxonomical revision of the genera *Ophisaurus* and *Pseudopus*, which include both fossil and extant taxa, Fejérváry-Lángh (1923) regarded *Anguis*? *laurillardi* as a very problematic taxon, and synonymized this species, although with a question mark, with *Ophisaurus moguntinus* (Boettger, 1875). On the other hand, Estes (1983) referred to this species as *Ophisaurus*? *laurillardi* and considered it to represent a nomen dubium. According to Mlynarski (1962), *Anguis*? *laurillardi* is a synonym of *O. moguntinus*. Klembara (1979) reintroduced Merrem's (1820) name *Pseudopus* for the last species as well as *O. pannonicus*

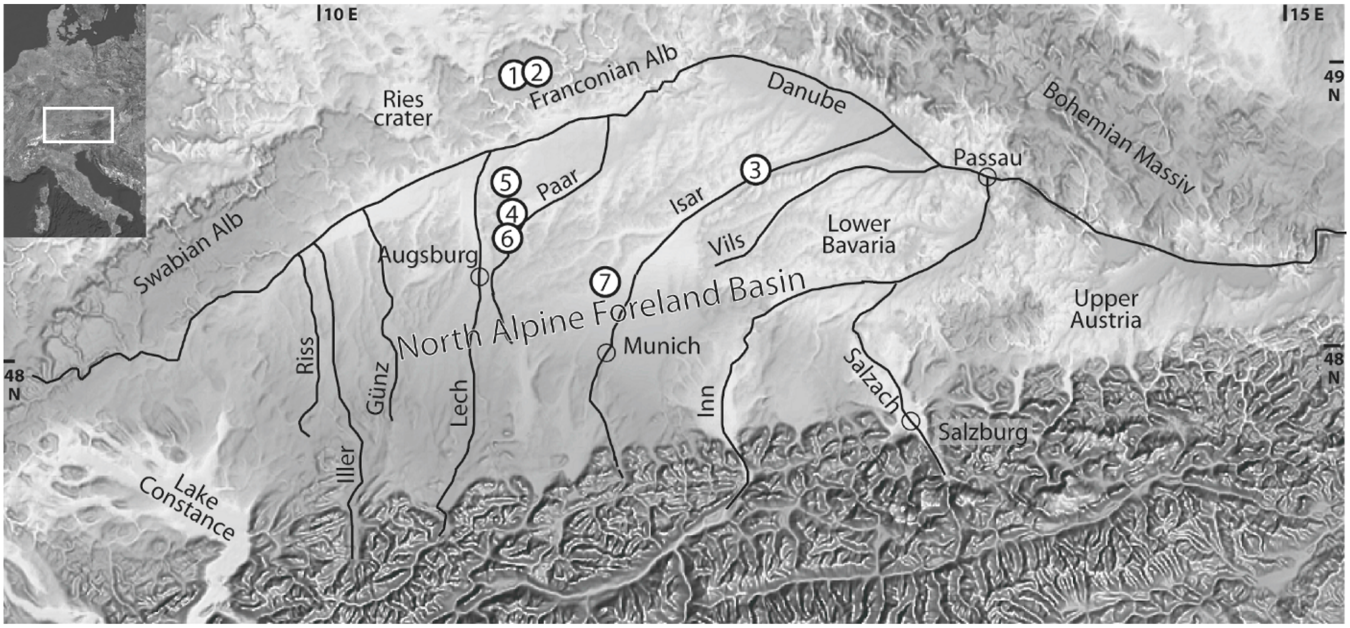

FIGURE 1—Digital elevation model of southern Germany (from Kuhlemann et al., 2006) and location of *Pseudopus* localities. 1 – Erkertshofen, 2 – Petersbuch, 3 – Niederaichbach, 4 – Sainbach, 5 – Walda, 6 – Griesbeckerzell, 7 – Kleineisenbach.

and the Recent *O. apodus* and demonstrated that both genera, the smaller and more gracile *Ophisaurus* and the large and robust *Pseudopus*, coexisted during the Miocene in Europe. Recently, Augé and Rage (2000) recognized that *Anguis*? *laurillardi* represents a separate species of *Pseudopus*, *P. laurillardi*, which differs in some cranial characters from the Miocene *P. moguntinus*, the Pleistocene *P. pannonicus*, and the Recent *P. apodus*. Later, Rage and Bailon (2005) described additional specimens of *P. laurillardi*, including remains of the braincase. Augé and Rage (2000) and Rage and Bailon (2005) suggested that *P. moguntinus* could be a junior synonym of *P. laurillardi*. However, neither Augé and Rage (2000) nor Rage and Bailon (2005) provided a list of significant differences to differentiate *P. moguntinus* from *P. laurillardi*. As a result, this problem remains unresolved.

In this paper we 1) describe abundant new material of a robust anguine from several Early and Middle Miocene localities in Germany (Fig. 1). The fossils are assigned to *Pseudopus laurillardi*, and we provide a revision of the material previously attributed to its junior synonym *Propseudopus fraasii* (=*Pseudopus moguntinus*); 2) compare the cranial anatomy of *Pseudopus laurillardi* with that seen in two other species, i.e., *P. pannonicus* and *P. apodus*, in order to define all three species in the genus *Pseudopus* based on anatomical characters and clarify the stratigraphical range and geographical distribution of the genus; and 3) attempt to evaluate the palaeoecology of fossil *Pseudopus* species by applying a method known as palaeoprecipitation reconstruction (Böhme et al., 2006) to *Pseudopus*-bearing localities.

Institutional acronyms: BSPG: Bayerische Staatssammlung für Paläontologie, Munich, Germany; DE: Department of Ecology, Faculty of Natural Sciences, Comenius University in Bratislava, Slovakia; MNHN: Muséum National d'Histoire Naturelle, Paris, France; NMA: Naturmuseum Augsburg, Augsburg, Germany.

## GEOLOGICAL SETTING

The skeletal remains of *Pseudopus* described here come from twelve South German localities situated in Bavaria (Fig. 1). Six of these sites represent fissure fillings from the Frankonian Alb, and the remaining six sites are stratified localities from the Upper Freshwater Molasse (UFM) of the North Alpine Foreland Basin (NAFB). The NAFB is a classical foreland basin situated at the northern margin of the Alps. The youngest basin infill represents the late Early to early Late Miocene UFM. The UFM sedimentary facies is characterized by a pronounced temporal and lateral variability with radial alluvial fan sedimentation in the southern part of the basin and east-to-west fluvial alluvial sedimentation more northward along the basin axis (Doppler, 1989). The local biostratigraphy based on small mammals distinguishes six faunal units (Heissig, 1997; Böhme et al., 2002, Abdul-Aziz et al., 2008): OSM ("Obere Suesswasser Molasse"; Upper Freshwater Molasse) A, B, C + D (Older Series) and OSM E, E' and F (Middle Series).

The stratigraphically oldest UFM locality occurs at Niederaichbach in Lower Bavaria. The overbank deposits lithostratigraphically belong to the lower part of the Nördlicher Vollschotter unit (Abdul-Aziz et al., 2008, fig. 2). The small mammal fauna contains a typical sized *Megacricetodon bavaricus* and can thus be correlated biostratigraphically with the fauna of Langenmoosen and Bellenberg (Schötz, 1993), which correspond to the faunal unit OSM B (MN 5). Correlation with biomagnetostratigraphically dated sections suggest an age of about 17.1 My (Abdul-Aziz et al., 2008).

The sandy channel fill sediments at the locality Walda 2 belong to the lithostratigraphic unit Fluviatile Untere Serie (Doppler, 1989; Doppler et al., 2005). Based on the size of the more advanced *Megacricetodon* aff. *bavaricus* and the absence of *M.* aff. *minor*, this fauna can be correlated with the faunas of Puttenhausen classic and Bubenhausen (personal information of J. Prieto; Wu, 1982; Boon, 1991), which correspond to the earlier part of unit OSM C + D (MN 5), suggesting an age of about 16.9 My (Abdul-Aziz et al., 2008 and unpublished results).

In the newly discovered locality Sainbach (a sand pit located ca. 1 km south of the village of Sainbach) sandy channel fill sediments indicate the lithostratigraphic position within the

Fluviatile Untere Serie unit (fossiliferous level at 465 m above sea level). These sands overlie the youngest marls of the Older Series biostratigraphical unit (top of the marls at 463 m a.s.l. in the locality Oberbernbach 2.5 km SSE of the Sainbach outcrop) and are positioned below the Ries boulder horizon (Brock horizon), which is found in this region between 480 and 485 m a.s.l. (Doppler et al., 2002; Böhme et al., 2007). The inferred stratigraphy for the Sainbach *Pseudopus* is therefore the early, pre-riesian part of the Middle Series, which corresponds to the unit OSM E (MN 5).

The locality Griesbeckerzell contains two fossiliferous levels. Level 1a represents the Ries boulder horizon that accumulated during the Ries meteorite impact. A recent $^{40}$Ar/$^{39}$Ar dating of impact glasses, along with palaeomagnetic studies of the sediments, suggests an impact age of between 14.77 and 14.78 My (Abdul-Aziz et al., 2008). According to biostratigraphy, the Ries boulder horizon marks the beginning of unit OSM F (Böhme et al., 2002). Fossiliferous level 1b is situated in channel fill sediments of the Fluviatile Untere Serie unit, five to six meters below the Ries boulder horizon, and therefore suggests an age of between level 1a and Sainbach (OSM E or E').

The youngest studied UFM locality is Kleineisenbach, which belongs to the Younger Series. According to Fahlbusch (1964), the fossiliferous level contains the cricetid *Deperetomys hagni* and thus correlates to MN 8. A recent study of the small mammal fauna (Prieto, 2007) indicates a slightly younger biostratigraphical age than estimated for the reference locality for MN 8 (Anwil in Switzerland).

Karstic fissure fillings from the Jurassic limestone quarry-field around Petersbuch/Erkertshofen are exceptionally rich in vertebrate remains (Rummel, 1993; Bolliger and Rummel, 1994). The stratigraphy of the fissures is based on their small mammal content (Rummel, 1995, 2000). The oldest samples are from Petersbuch 2 and 29, which belong to the mammal-"zone" MN 4a (Heissig, 1978; Ziegler and Fahlbusch, 1986). Slightly younger (MN 4b) are the fissures Erkertshofen 1 (Fahlbusch, 1966) and Petersbuch 38-Boden (based on the occurrence of *Ligerimys florancei*, *Megacricetodon* aff. *collongensis*, and *Democricetodon franconicus*; Rummel, unpublished), whereas Petersuch 39 III is correlated with MN 5 (based on *Megacricetodon* aff. *bavaricus*, *Democricetodon gracilis*, *D. mutilus*, and *Keramidomys thaleri*; Rummel, unpublished). Middle Miocene fissures containing *Pseudopus* include Petersbuch 68 (MN 6 based on *Megacricetodon* aff. *germanicus*, *Cricetodon* sp., Rummel and Prieto, unpublished) and Petersbuch 73 (MN 7/8 based on *Parasorex socialis*, *Deperetomys* sp., and *Cricetodon* cf. *jumaensis*; Rummel, unpublished).

## MATERIAL

The descripsion is based on the articulated specimen NMA 2009/1/2060, which represents an adult (Fig. 2). The specimen is partly broken and damaged but is significant since it represents the only record of an articulated fossil of the subfamily Anguinae from the Neogene. The premaxilla, septomaxilla, nasal, postorbital and ectopterygoid are not preserved. The specimen serves as a reference for the identification of disarticulated bones. Moreover, our material was compared to the type material of *Pseudopus laurillardi* (in the Museum d'Histoire Naturelle de Paris) described by Lartet (1851) and revised by Augé and Rage (2000) and Rage and Bailon (2005). In addition, we compared Lartet's and our specimens with those of *Propseudopus fraasii* (Hilgendorf, 1883, 1885) deposited in the Museum für Naturkunde at Berlin (Germany). We conclude that the material of *P. laurillardi* and *P. fraasii*, as well as our material, represent one species – *Pseudopus laurillardi* (Lartet, 1851).

Isolated parietals and dentaries occur in various sizes, which reflect ontogenetic sequences. They have been assigned to *Pseudopus laurillardi* based on the presence of the diagnostic features seen in NMA 2009/1/2060. Moreover, the morphology of marginal teeth is consistent regardless of growth stage.

For comparison, the following specimens of Recent anguine taxa have been considered: *Pseudopus apodus* (DE 1, 2–13, 22, 23, 29, 52; BSPG 1982 X 2383), *Ophisaurus harti* (DE 31, 36, 37), *O. gracilis* (DE 42), *O. koellikeri* (DE 30, 41), *O. attenuatus* (DE 32, 33, 43, 44), *O. ventralis* (DE 34, 35, 38), *O. mimicus* (DE 49), *O. compressus* (DE 50) and *Anguis fragilis* (DE 14–21, 24, 25, 45–48).

The terminology used to describe the individual bone features is based on Fejérváry-Lang (1923), Oelrich (1956), Klembara (1979, 1981) and Conrad (2004); several terms are new. The term otoccipital (fused opisthotic and exoccipital) is used in the sense of Bellairs and Kamal (1981) here.

## SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811
ANGUIMORPHA Fürbinger, 1900
ANGUIDAE Gray, 1825
ANGUINAE Gray, 1825
PSEUDOPUS Merrem, 1820

*Type species.*—*Pseudopus apodus* (Pallas, 1775)

PSEUDOPUS LAURILLARDI (LARTET, 1851).
Figures 2, 3.1, 3.2, 4.1–4.3, 5–8.2, 9–12.2, 13–14.2, 15–17.1, 17.3, 18.1, 19–21

*Anguis*? *Laurillardi* LARTET, 1851, p. 40
non *Pseudopus moguntinus* BOETTGER, 1875, p. 79
non *Pseudopus moguntinus* BOETTGER, 1876/1877, p. 216
*Propseudopus Fraasii* HILGENDORF, 1883, p. 139
*Propseudopus Fraasii* HILGENDORF, 1885, p. 358
non *Ophisaurus ulmensis* GERHARDT, 1903, p. 67
*Propseudopus* cf. *Fraasii* WEGNER, 1913, p. 212
*Ophisaurus moguntinus* FEJÉRVÁRY-LÁNGH, 1923, p. 141

For a complete list of synonyms of the above taxon up to 1923, see the synonymy list for *Ophisaurus moguntinus* in Fejérváry-Lángh (1923, p. 141).

*Ophisaurus fraasi* BACHMAYER AND MLYNARSKI, 1977, p. 290
*Pseudopus* sp. KLEMBARA, 1981, p. 136 - in part (specimen Nr. 1030, pl. 4, fig. 2)
*Ophisaurus* cf. *moguntinus* MLYNARSKI, SZYNDLAR, ESTES AND SANCHIZ, 1982, p. 111
*Ophisaurus*? *Laurillardi* ESTES, 1983, p. 143
*Pseudopus laurillardi* AUGÉ AND RAGE, 2000, p. 276
*Pseudopus* aff. *fraasi* BÖHME, 2002, p. 345
*Pseudopus moguntinus* AUGÉ, 2005, p. 251
*Pseudopus laurillardi* RAGE AND BAILON, 2005, p. 422

*Neotype.*—MNHN Sa 23604, left dentary (Augé and Rage, 2000, p. 277, fig. 9), Sansan, Gers, France. Astaracien, MN 6, Middle Miocene.

*Locality, age and referred specimens.*—The material described here comes from 13 localities in Germany (Figs. 1, 22).

1) Petersbuch 2 (MN 4a): Parietal, BSPG 1976 XXII 11002–11004; Maxilla, BSPG 1976 XXII 11005,11007, 11010, 11019, 11022, 11026; Dentary, BSPG 1976 XXII 11045, 11049, 11060, 11067.

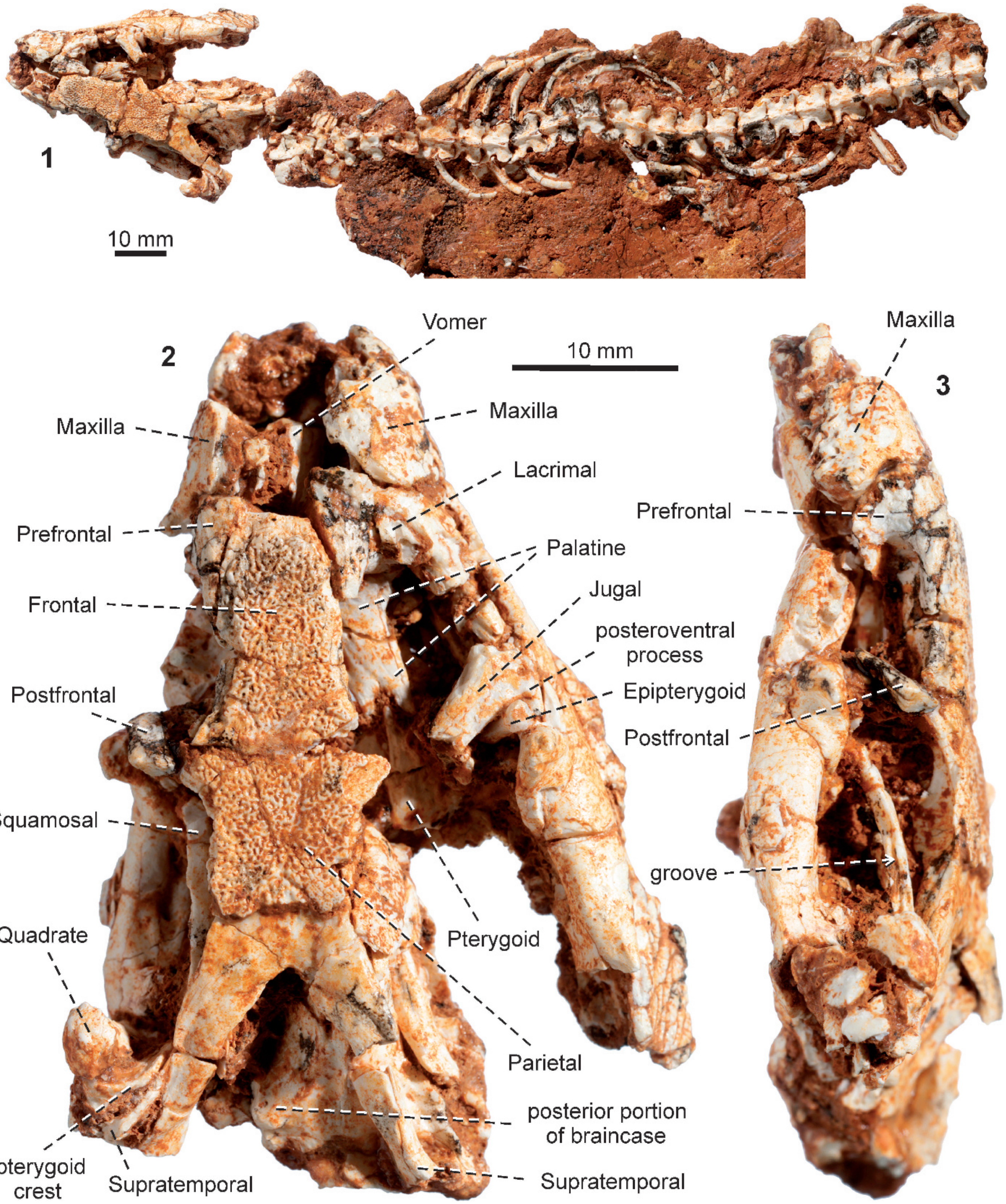

FIGURE 2—*Pseudopus laurillardi* (Lartet, 1851), NMA 2009/1/2060. *1*, skeleton in dorsal view; *2*, skull in dorsal view; *3*, skull in left lateral view; *4*, skeleton in ventral view; *5*, skull in ventral view.

2) Petersbuch 29 (MN 4a): Articulated skeleton, NMA 2009/1/2060.
3) Petersbuch 38-Boden (MN 4b): Parietal, NMA-2007-66/2035.
4) Petersbuch 39-III (MN 5): Parietal, NMA-2007-68/2035, 2007-70/2035, 2007-71/2035; Maxilla, NMA-2007-72/2035, 2007-73/2035; Dentary, NMA-2007-74/2035, NMA-2007-92/2035.

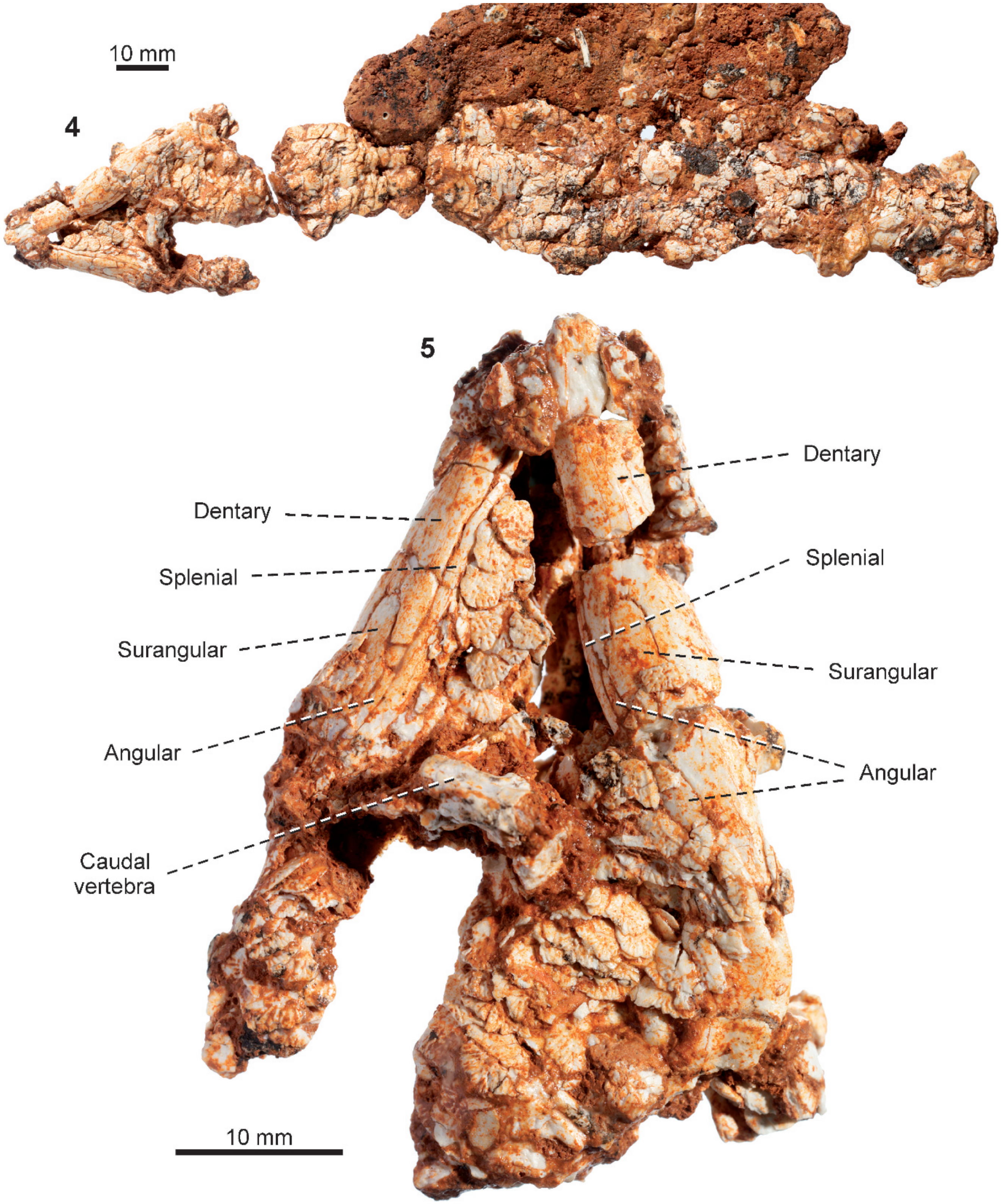

FIGURE 2—Continued.

5) Petersbuch 68 (MN 6): Maxilla, BSPG 2008 V 1-2, NMA-2007-75/2035; Frontal, NMA-2007-76/2035, 2007-77/2035; Parietal, NMA-2007-79/2035 - 2007-84/2035; Dentary, NMA-2007-85-91/2035, 2007-93-99/2035.
6) Petersbuch 73 (MN 7/8): Frontal, NMA-2007-87/2035.
7) Erkertshofen 1 (MN 4b): Parietal, BSPG 1962 XIX 2715; Frontal, BSPG 1962 XIX 2716; Palatine, BSPG 1962 XIX 2706; Pterygoid, BSPG 1962 XIX 2707; posterior portion of braincase, BSPG 1962 XIX 2709.
8) Niederaichbach (MN 5): Dentary, BSPG 1963 XXV 54.

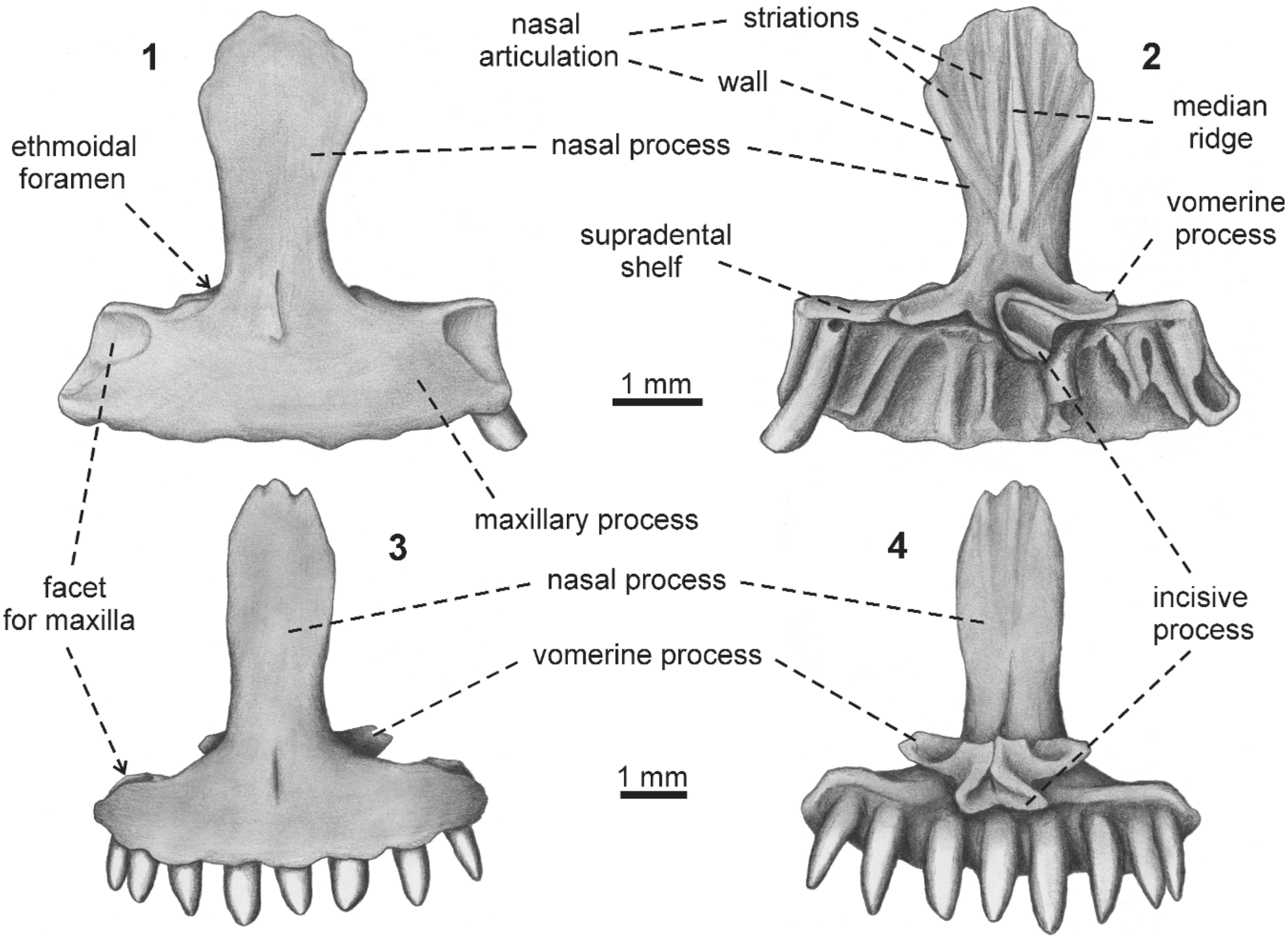

FIGURE 3—Premaxilla in external (*1*, *3*) and internal (*2*, *4*) view. *1*, *2* - *Pseudopus laurillardi* (Lartet, 1851), BSPG 1990 XXII 9; *3*, *4* - *Pseudopus apodus* (Pallas, 1775), DE 29.

9) Sainbach (MN 5/6): Dentary, BSPG 2008 I 1.
10) Walda 2 (MN 5): Premaxilla, BSPG 1990 XXII 9; Parietal, BSPG 1990 XII 10; Maxilla, BSPG 1990 XXII 19–21, 27, 29; Palatine, BSPG 1990 XXII 11–13; Dentary, BSPG 1990 XXII 30–33, 35–36, 39–41; vertebrae, BSPG 1990 XXII 17–18.
11) Griesbeckerzell 1a (MN 5/6): Maxilla, BSPG 1997 XIII 467–468, 470, 472–473, 475–476; Dentary, BSPG 1997 XIII 477, 479–482, 486.
12) Griesbeckerzell 1b (MN 5/6): Dentary, BSPG 1997 XIII 484–485, 490.
13) Kleineisenbach (MN 8): Parietal, BSPG 1972 XVI 2131; Maxilla, BSPG 1972 XVI 2133.

The skeletal remains attributed to *Pseudopus laurillardi* from the German locality of Sandelzhausen were recently described by Böhme (in press).

*Repository*.—Bayerische Staatssammlung für Paläontologie und Geologie, Munich (specimen numbers preceded by BSPG) and Naturmuseum Augsburg (specimen numbers preceded by NMA).

*Revised diagnosis* (of Rage and Bailon, 2005).—*Pseudopus laurillardi* differs from *P. pannonicus* and *P. apodus* in the following characters: (1) anteriormost portion of frontal ornamented shield reaches anterolateral margin of frontal, more posteriorly positioned dorsolateral surface of orbital margin of frontal smooth; (2) lateral margin of frontal straight; (3) sulcus between frontal and frontoparietal shields slightly longer than sulcus between frontal and interfrontal shields; (4) large, laterally extending anterolateral process of parietal table; (5) subdental shelf prominently extending medially and consisting of wide and deep sulcus and massive medial ridge; (6) subdental platform of middle and posterior portion of dentary positioned in mid-height of dentary and teeth dorsally extend only slightly dorsal to crista dorsalis; (7) surrangular process short and ending nearly or completely vertically in large specimens; (8) in internal view, sinus surangularis reaches anteriorly the level of mesiobasal portion of the 2nd tooth from posterior; (9) posterior portion of dentary positioned posterior to the posteriormost tooth short (the length equals the length of two posterior teeth); (10) spina splenialis lies anteriorly to mid-length of dentary in middle sized and large specimens; (11) posterior margin of anterior inferior mandibular foramen formed by splenial.

*Discussion*.—The name *Pseudopus moguntinus* of Boettger (1875, 1876/77) is considered here to be a nomen nudum (see also Bachmayer and Mlynarski, 1977; contra Fejérváry-Láng, 1923; Estes, 1983; Augé, 2005). Boettger's (1875, 1876/77) name *Pseudopus moguntinus* is based exclusively on osteoderms from the German localities now dated as Middle Oligocene to Early Miocene. No descriptions and illustrations of the osteoderms are provided. Moreover, the number of osteoderms studied has not been indicated and no institutions are mentioned where the specimens are deposited. According to Estes (1983, p. 141) and Augé (2005, p. 251), the osteoderms are deposited in the Senckenberg Museum

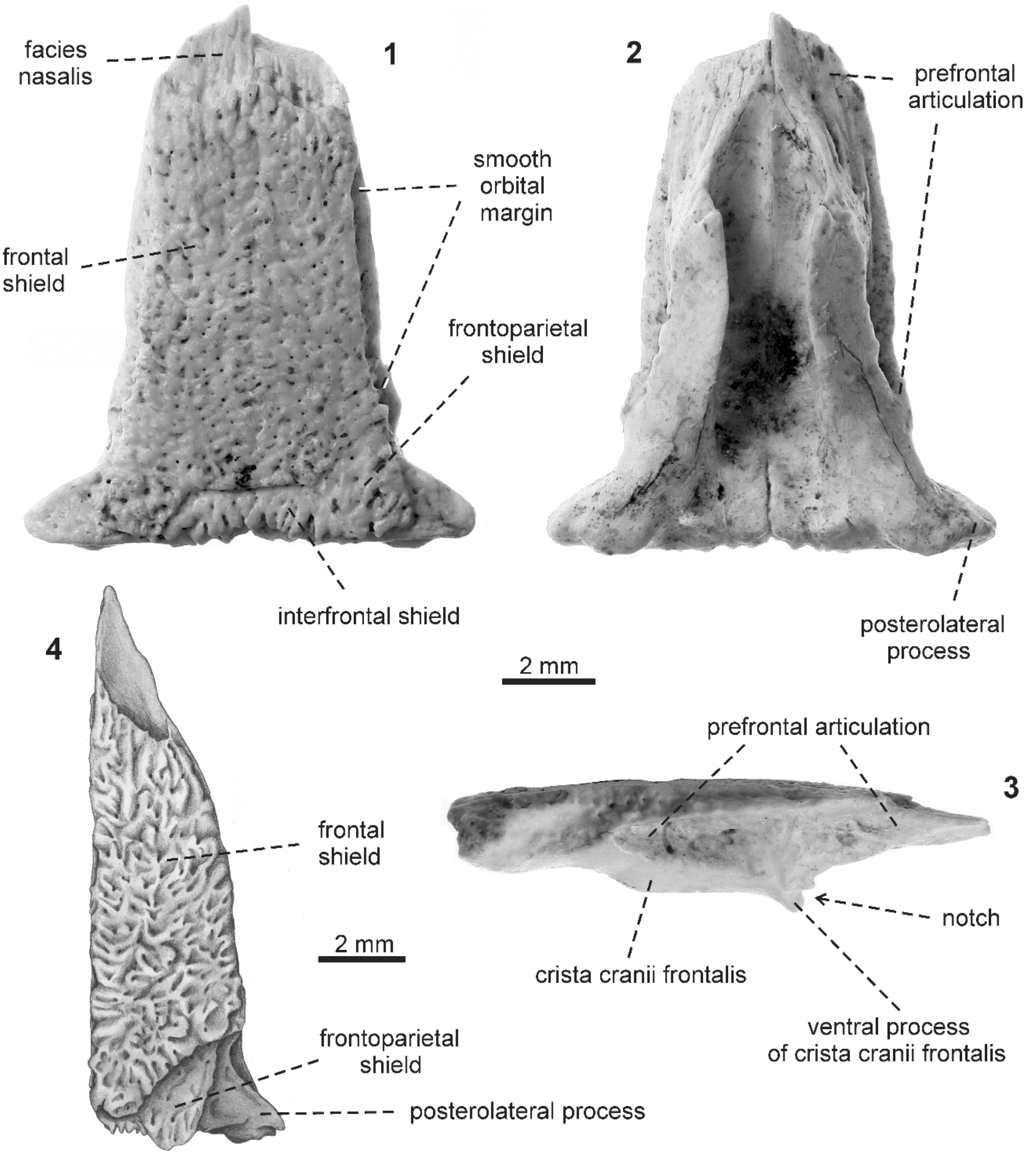

FIGURE *4—1–3*, *Pseudopus laurillardi* (Lartet, 1851), NMA-2007-87/2035, frontals in dorsal (*1*), ventral (*2*) and right lateral (*3*) view. *4*, *Pseudopus apodus* (Pallas, 1775), DE 1, right frontal in dorsal view.

(Frankfurt am Main, Germany). However, according to personal information of the curator of vertebrate collections of the Forschungsinstitut Senckenberg, Dr. R. Brocke, the osteoderms are not present in this institution and are probably lost.

Apart from a large specimen of *Propseudopus fraasii* (discovered in the pit of the Steinheim graveyard), Hilgendorf (1885) also described a second, smaller specimen that was discovered in another quarry in Steinheim (the so-called "Kopp" quarry). This specimen is represented by the parietal, maxilla, pterygoid, lower jaw and two vertebrae. Several of these elements were illustrated (Hilgendorf, 1885, figs. 5c, 5d, 8c). Hilgendorf suggested that this small specimen represents a small specimen of *P. fraasii* or a different species (Hilgendorf, 1885, p. 359). He noticed that the morphology of the parietal is very similar to that seen in *Ophisaurus*. Because the anatomy of the pterygoid (Hilgendorf, 1885, fig. 8c) does not correspond to that of *P. laurillardi* (because it lacks the mediolaterally oriented transverse process and crista oblonga, see below), but rather is reminiscent of that of the genus *Ophisaurus* (e.g., Klembara, 1981, pl. 2, fig. 2), we do not regard this small specimen as belonging to *P. laurillardi*.

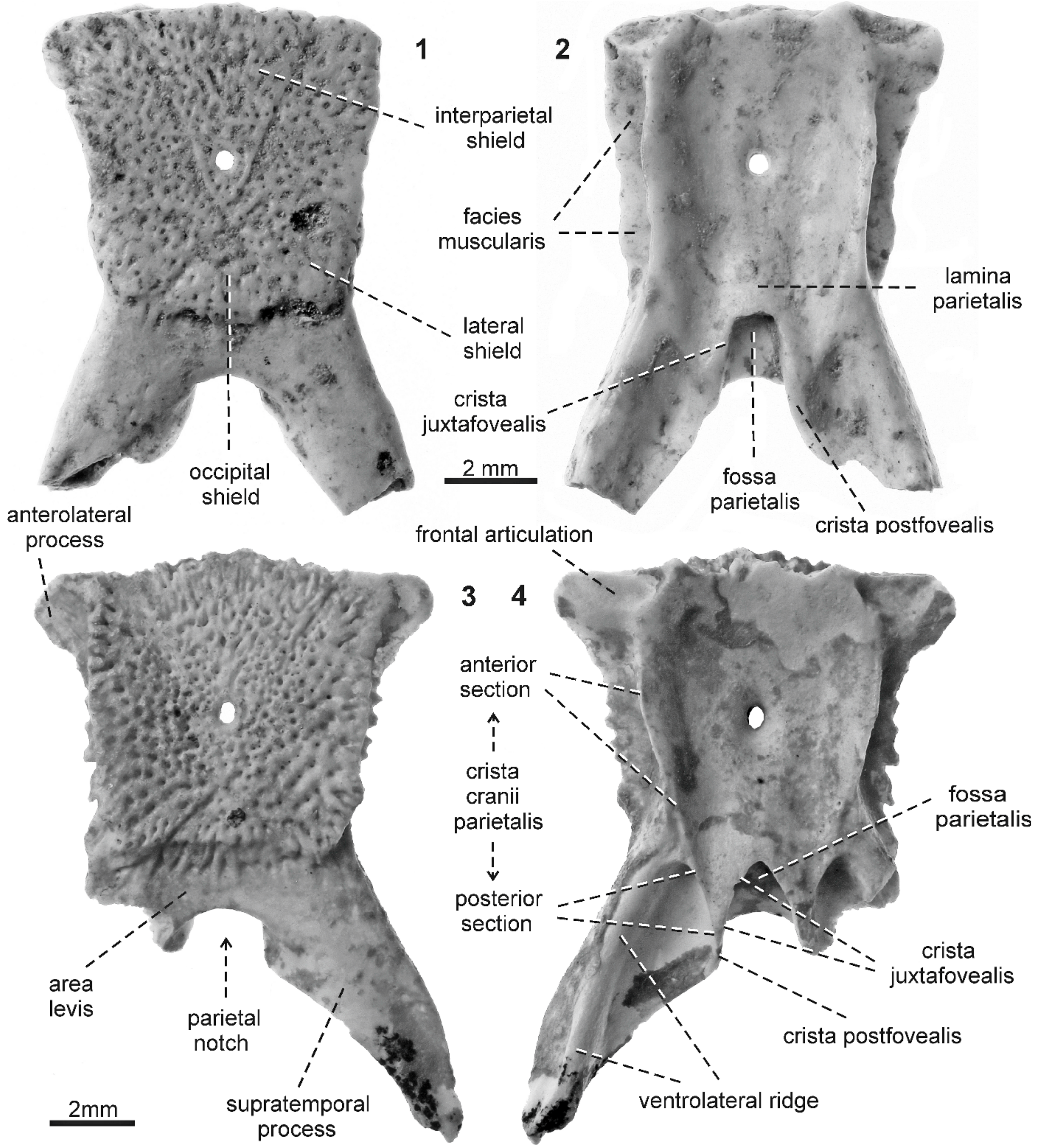

FIGURE 5—*Pseudopus laurillardi* (Lartet, 1851), NMA-2007-71/2035 (*1*, *2*), NMA-2007-66/2035 (*3*, *4*); parietals in dorsal (*1*, *3*) and ventral (*2*, *4*) view.

*Ophisaurus ulmensis* from the Early Miocene (MN 2a) of Eselsberg near Ulm was synonymized with *Propseudopus fraasii* by Fejérváry-Lángh (1923). A re-investigation of the type material (Gerhardt, 1903, fig. 4; originals to figures 1 to 3 are lost), which includes several unpublished topotypic specimens, by one of us (M. B.) revealed that *O. ulmensis* does not represent a member of the Anguidae, and thus that the material is in need of revision.

## DESCRIPTION

The description is based on the articulated specimen NMA 2009/1/2060 (Fig. 2), one almost complete lower jaw, and numerous disarticulated elements. The morphology of missing or partially damaged parts of NMA 2009/1/2060 (such as the premaxilla and parts of the pterygoid), is inferred from the original material of *Pseudopus laurillardi* (Lartet, 1851) revised

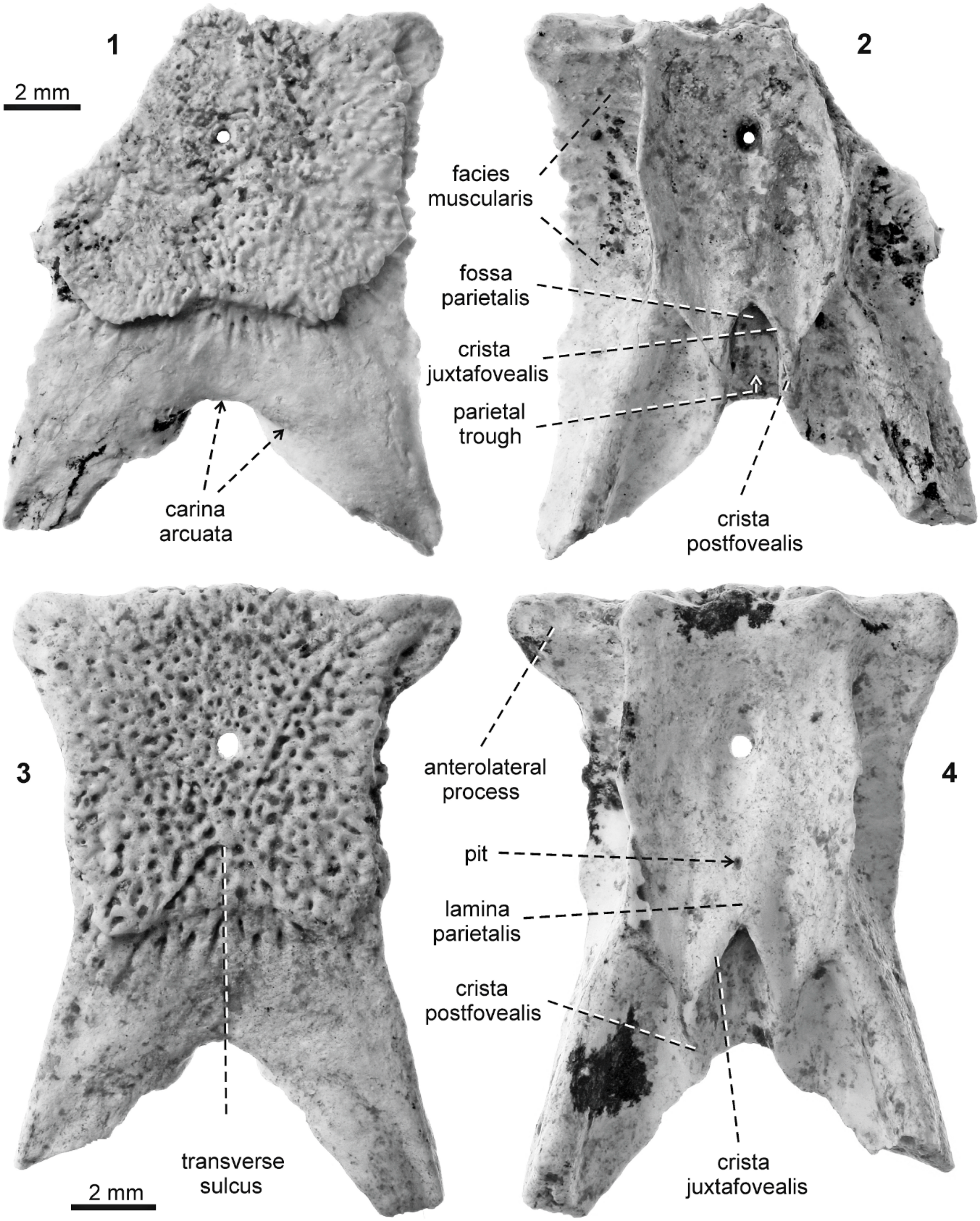

FIGURE 6—*Pseudopus laurillardi* (Lartet, 1851), NMA-2007-83/2035 (*1*, *2*), NMA-2007-84/2035 (*3*, *4*); parietals in dorsal (*1*, *3*) and ventral (*2*, *4*) view.

by Augé and Rage (2000) and *Propseudopus fraasii* (Hilgendorf, 1885).

*Premaxilla*.—The premaxilla consists of bilateral horizontal maxillary processes and a stout nasal process (Fig. 3.1, 3.2). The posterior portion of the nasal process is bilaterally widened and its posterior margin knurled. The internal surface of the nasal process bears massive striations subdivided by a distinct median ridge, i.e., the morphology indicating the nasal

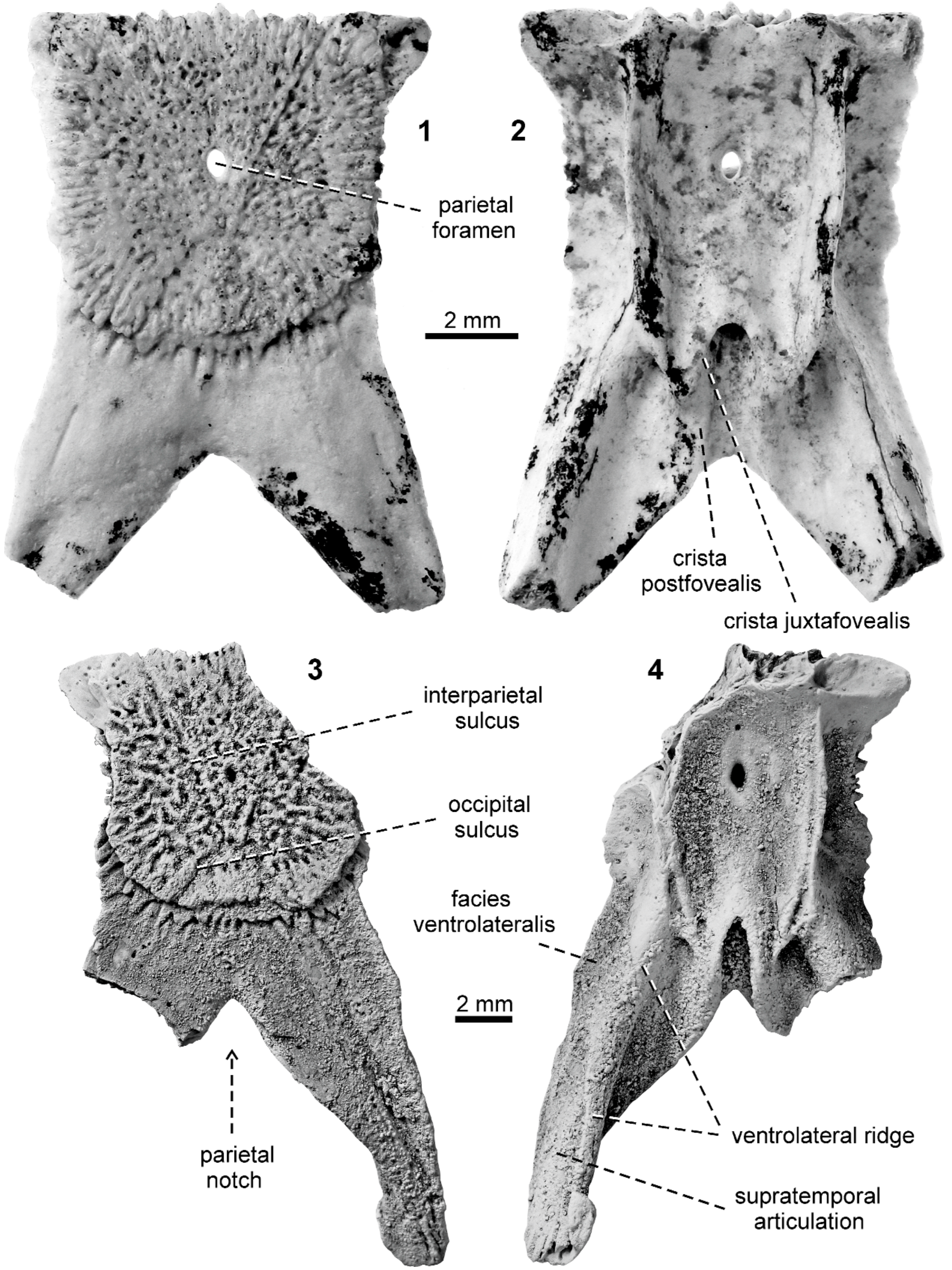

FIGURE 7—*Pseudopus laurillardi* (Lartet, 1851), NMA-2007-81/2035 (*1*, *2*), NMA-2007-82/2035 (*3*, *4*); parietals in dorsal (*1*, *3*) and ventral (*2*, *4*) view.

articulation. The external surface of the lateral end of the maxillary process bears an area for the articulation with the premaxillary process of the maxilla, by which the latter process overlaps the maxillary process of the premaxilla. The large ethmoidal foramen is located at the dorsal surface of the body of the premaxilla, at the angle between the nasal and maxillary processes. The vomerine process is laterally continuous with the supradental shelf. It forms a posteriorly

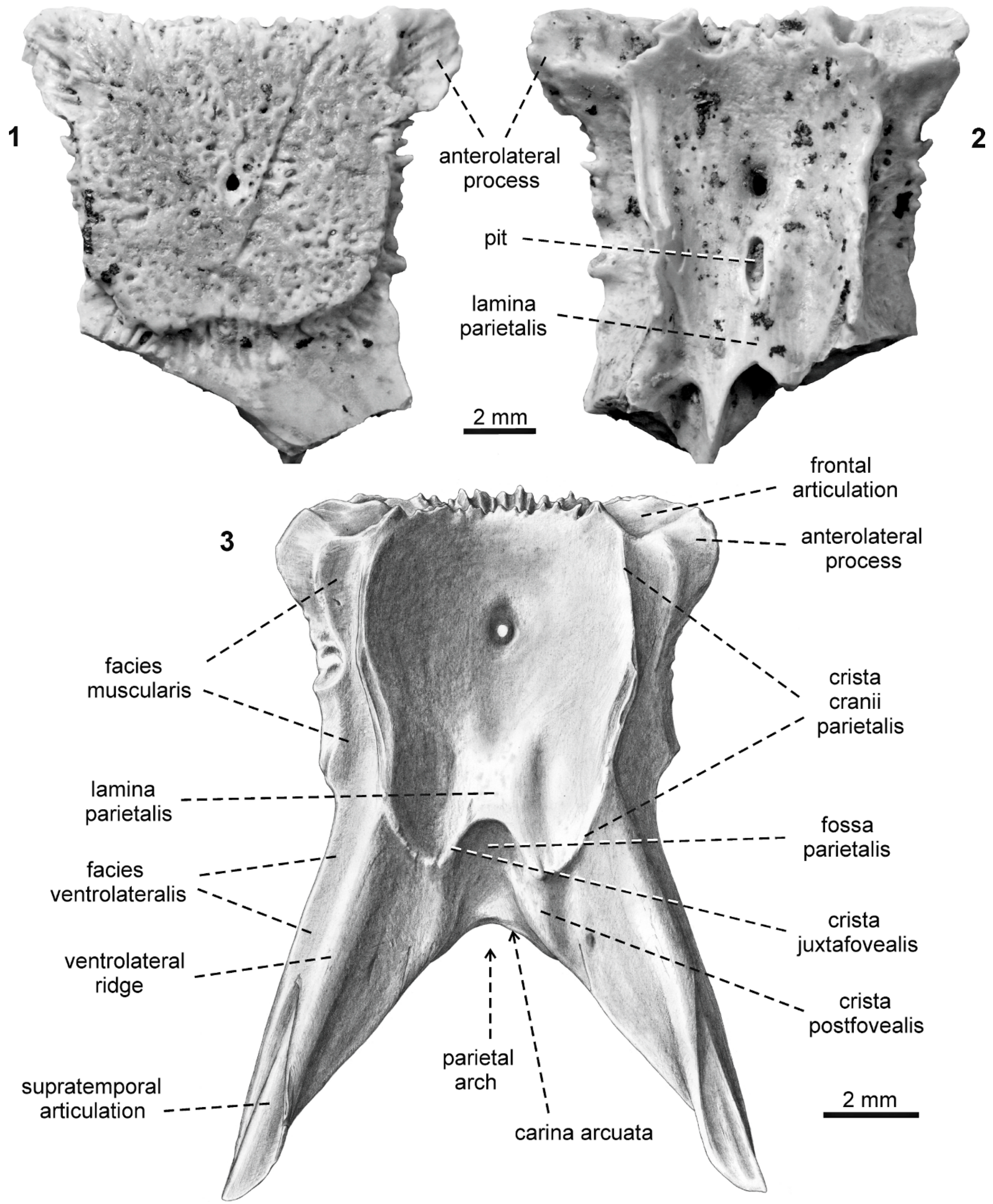

FIGURE *8*—*1–2*, *Pseudopus laurillardi* (Lartet, 1851), BSPG 1062 XIX 2715. *3*, *Pseudopus apodus* (Pallas, 1775), (DE 3), from Klembara (1981, pl. 5). Parietals in dorsal (*1*) and ventral (*2*, *3*) view.

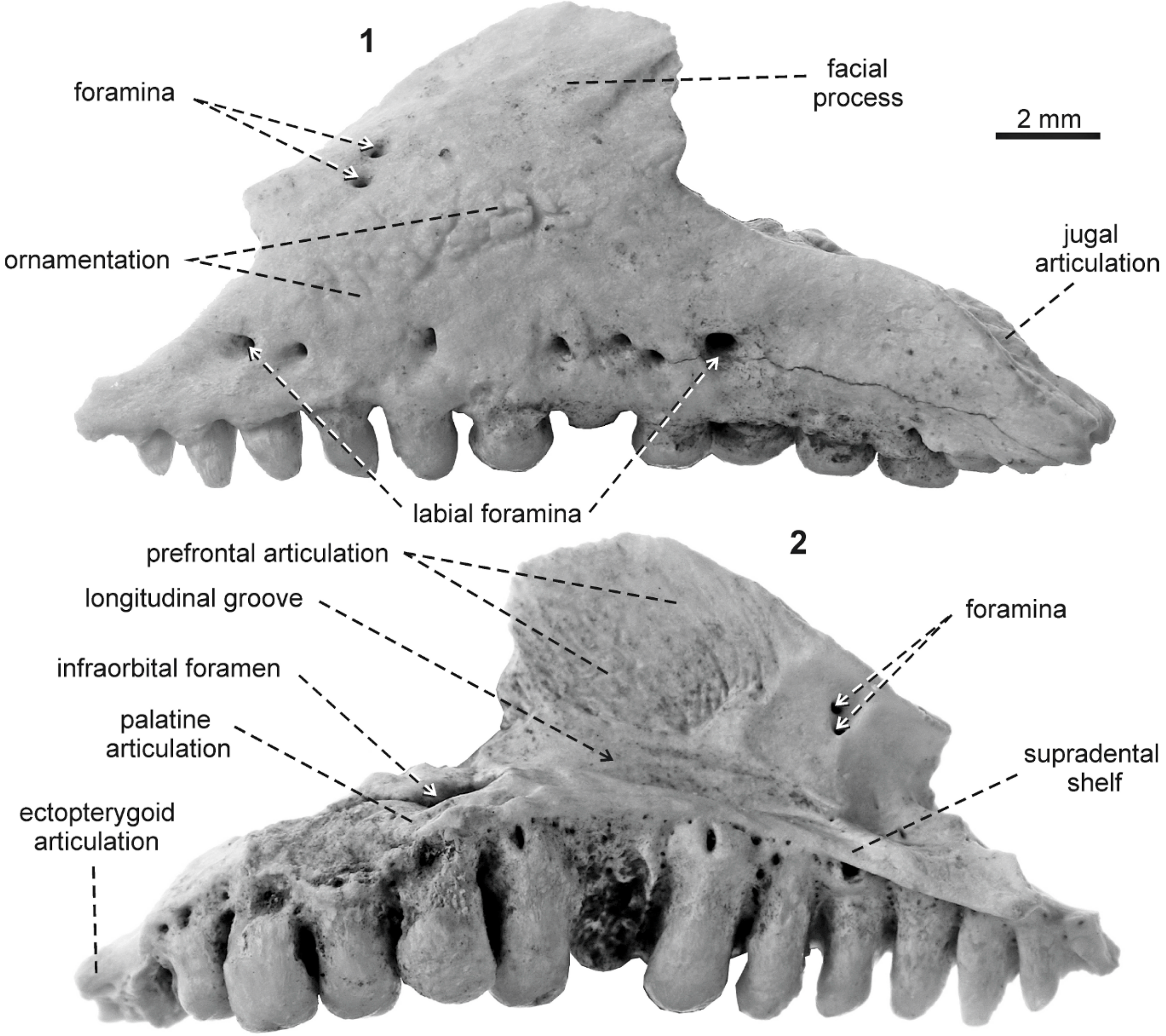

FIGURE 9—*Pseudopus laurillardi* (Lartet, 1851), NMA-2007-72/2035, maxilla in left lateral (*1*) and internal (*2*) view.

extending plate that widens mediolaterally in the posterior direction. Its medial margin is curved ventrally and extends into a short and distinct incisive process.

The premaxilla is not preserved in NMA 2009/1/2060. However, it is present in the type material of Lartet (1851) and described and figured by Augé and Rage (2000, fig. 12). The morphology of the premaxilla described here corresponds to that of the type material of Lartet (1851).

*Prefrontal.*—The right and left prefrontals are preserved in NMA 2009/1/2060 (Fig. 2.1–2.3). The prefrontal consists of a broad anterolateral portion and stout, posteriorly extending frontal process. The entire medial margin of the prefrontal is sutured with the frontal. The lateral portion of the prefrontal extends ventrally, producing a mediolaterally wide lamina that contacts the dorsal surface of the maxillary process of the palatine. Between the lateral wall of the prefrontal and the medial wall of the lacrimal, a nasolacrimal canal is present (see also below).

*Frontal.*—Both frontals are well preserved in NMA 2009/1/2060 (Fig. 2.1–2.3). The frontal is a paired and elongated bone (Fig. 4.1–4.3). Its medial and lateral margins are almost parallel. Anteriorly, the frontal extends into a pointed anteromedial process; posteriorly it forms a stout posterolateral process. The facies nasalis is large and bears anterolaterally directed ridges and grooves. The ornamentation covers most of the dorsal surface of the frontal. It consists of ridges and grooves and occasinally also of tubercles and pits. Two sulci subdivide the ornamented surface into three shields: a long interfrontal sulcus separates a large, anteroposteriorly long frontal shield from a small interfrontal shield positioned posteromedially and a large, more or less quadrangular frontoparietal shield positioned posterolaterally and partially covering the stout posterolateral process. A short sulcus divides the interfrontal and frontoparietal shields. This sulcus has an anteromedial to posterolateral course. The posterior margin of the frontal shield courses mediolaterally, whereas the long sulcus between the frontal and frontoparietal shields courses posteromedially. The posterolateral margin of the frontal shield is thus slightly longer than its posterior margin. Anteriorly, the frontal shield has a shallow notch and forms a

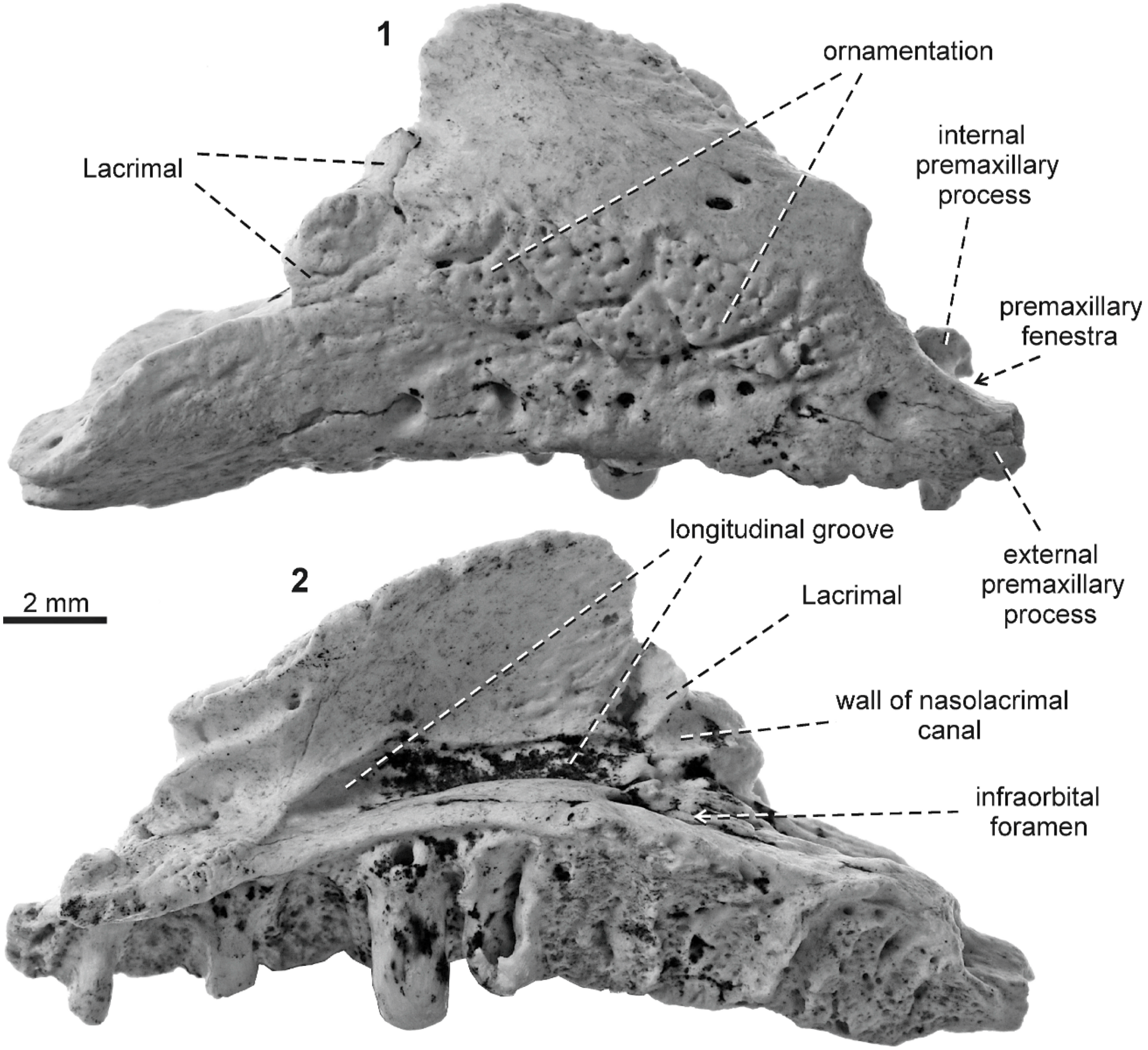

FIGURE 10—*Pseudopus laurillardi* (Lartet, 1851), BSPG 1976 XII 11005, maxilla and lacrimal in right lateral (*1*) and internal (*2*) view.

longer anteromedial and shorter anterolateral processes; between these processes, the posterior margin of the nasal is located. The anterolateral process of the frontal shield reaches the anterolateral margin of the frontal. The lateral margin of the frontal shield is straight. Between the shield and lateral margin of the frontal, a narrow strip of the dorsally uncovered surface is present, i.e., the orbital margin of the frontal is smooth.

On the ventral surface, a high and medially flexed crista cranii frontalis dominates. It forms a high wall in the middle third of the frontal length and surrounds an elongated brain excavation from the lateral side. The posterior section of the crista cranii is low and rounded. Its anterior margin gradually declines anteriorly and forms a small, but distinct and pointed ventral process which is separated from the anterior section of the crista cranii by a narrow notch (Fig. 4.3). The ventrolateral surface of the frontal and external surface of the crista cranii are deeply striated in longitudinal direction, indicating the articular area for the prefrontal. The prefrontal articulation almost reaches the posterior margin of the crista cranii frontalis.

*Postfrontal.*—On the left side of NMA 2009/1/2060, immediately lateral to the posterolateral process of the frontal and the anterolateral process of the parietal, a small, plate-like fragment is present (Fig. 2.1–2.3). Comparisons of this fragment with the cranial elements of the morphologically similar *Pseudopus apodus* indicate that the plate-like element represents the frontal process of the postfrontal. The posteromedial margin of the element bears a distinct, roughened groove, which indicates the articulation with the posterolateral process of the frontal.

*Parietal.*—The parietal is well preserved in NMA 2009/1/2060 (Fig. 2.1–2.3). Figures 5–8.2 show the morphology and variability of the shape of the parietal, its individual structures and intensity of ornamentation; here, the parietals are arranged according to the length of their parietal tables (from the shortest one – Fig. 5.1, 5.2 to the longest one – Fig. 8.1, 8.2). The parietal is an anteroposterioly elongated rectangular table from the posterolateral corners of which the supratemporal processes extend posterolaterally. The surface of the dorsal portion of the parietal table is ornamented. The parietal foramen occurs in the anterior half of the parietal table and in

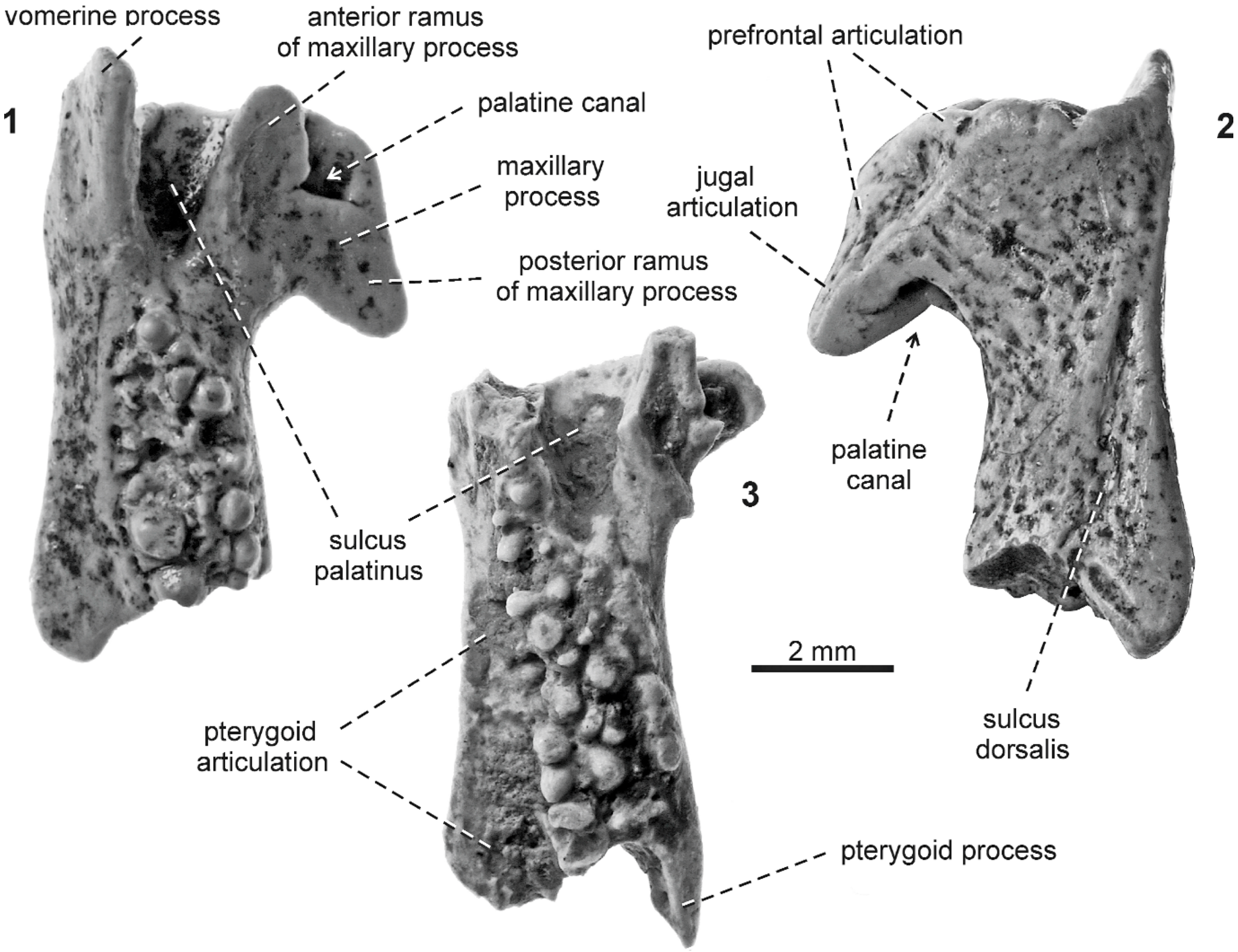

FIGURE *11*—*Pseudopus laurillardi* (Lartet, 1851). *1*, *2*, BSPG 1990 XII 11, left palatine in ventral (*1*) and dorsal (*2*) view. *3*, BSPG 1962 XIX 2706, left palatine in ventral view.

approximately the mid-length of the ornamented surface. The ornamented surface is roughly square-shaped but with a rounded posterior margin. The ornamentation is formed by distinct pits, tubercles, ridges and grooves. The radiating ridges and grooves are restricted to the periphery of the ornamented surface. There are distinct sulci that subdivide the ornamented surface into four smaller shields: (i) the interparietal sulcus borders a median triangular interparietal shield and a pair of lateral shields in bilateral position (Fig. 7.3); (ii) an occiptal sulcus that borders the posteriorly positioned bilaterally broad, triangular occipital shield, and participates in the formation of distinct borders around the posterior portions of the lateral shields (Fig. 7.3); and (iii) an occasionally present transverse sulcus positioned posteriorly to the parietal foramen (Fig. 6.3); in most specimens, this short sulcus, which forms the border between the interparietal and occipital shields, is substantially reduced, so that both shields have only a single-point contact (Fig. 5.1, 5.3). The anterior end of the interparietal sulcus occurs slightly medially to the anterolateral corner of the ornamented surface. The posterior end of the occipital sulcus terminates in the posteromedial corner of the ornamented surface. Although there is a slight variation regarding the shape of the occipital shield, its posterior margin is mostly straight and aligned with the posterior tips of the lateral shields. In some specimens, the posterior margin of the occipital shield is slightly convex (Figs. 5.1, 7.1), whereas in some specimens it is concave (Figs. 5.3, 6.1, 6.3, 8.1). Such variation of the posterior margin of the occipital ornamented shield is present also in *Pseudopus apodus*: in specimens DE 3 and DE 29 the margin is concave, whereas in DE 9 a DE 22 it is slightly convex. The ornamentation of the anterolateral corner of the lateral shield slightly extends to the root portion of the anterolateral process of the parietal. Posteriorly to the ornamented surface, a smooth surface (area levis) covers the posterior portion of the parietal table.

A distinct anterolateral process extends from the anterolateral corner of the parietal table. Posterior to this process, the lateral margin of the parietal table and its ornamented surface coincide, or a very narrow strip of dorsally exposed surface, facies dorsolateralis, may be present. The lateral margins of the parietal table are irregularly indented to varying degrees. The basal portion of the supratemporal process is broad and gradually becomes narrower posteriorly. The carina arcuata is usually distinct on the dorsal surface of the supratemporal process. In the median plane, the carina arcuata coincides with the posterior margin of the parietal table and is wedge- or arch-shaped. The dorsomedial margin of the supratemporal process forms a sharp ridge.

The most prominent structure on the ventral surface of the parietal is the crista cranii parietalis, which is slightly convex

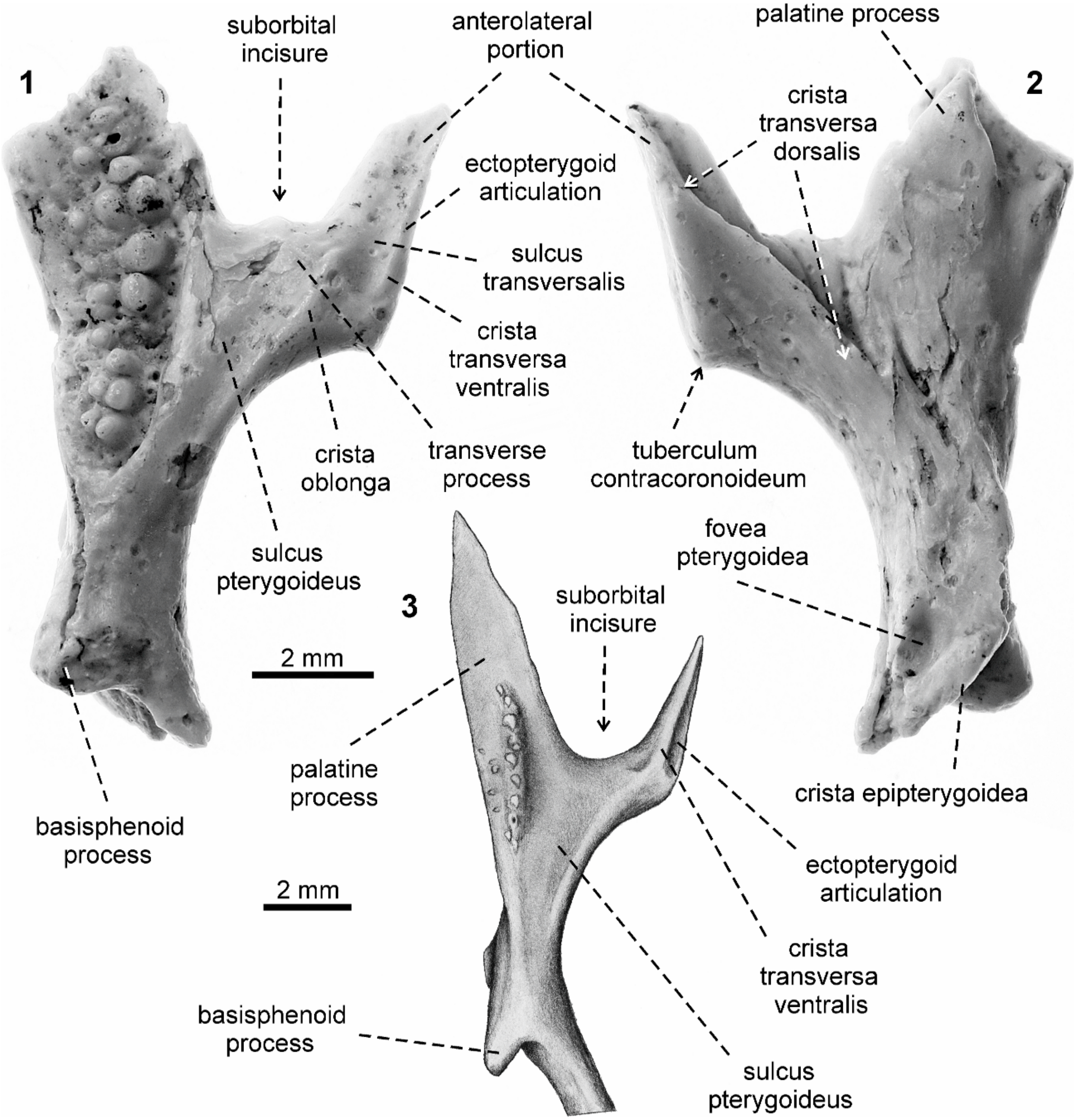

FIGURE *12*—*1*, *2*, *Pseudopus laurillardi* (Lartet, 1851), BSPG 1962 XIX 2707, left pterygoid in ventral (*1*) and dorsal (*2*) view. *3*, *Pseudopus apodus* (Pallas, 1775), DE 1, left pterygoid in ventral view.

laterally. The crista cranii and lateral margin of the parietal table do not coincide, but a strip of a smooth surface, the facies muscularis, is present between these structures. The crista cranii forms a high and sharp wall. Both cristae cranii enclose a deep excavation. The lamina parietalis, located in the posterior portion of this excavation, is deep and forms the roof of a deep fossa parietalis. The posterior margin of the lamina parietalis varies from inverse U-shaped (Fig. 7.2) to inverse V-shaped (Fig. 7.4). Such variation is present also in *Pseudopus apodus*: in DE 29, the margin is V-shaped, whereas in DE 1 it is U-shaped. The lamina parietalis bears a small pit located in the anterior portion of the surface. This pit is, however, not always present, and if present, the degree of its development varies from a small pit (Fig. 6.4) to an elongated depression (Fig. 8.2). The crista juxtafovealis is a sharp crest forming the lateral margin of the fossa parietalis (Figs. 5.4, 6.4, 7.2). The crista juxtafovealis, together with the posterior section of the crista cranii parietalis, form a triangular wedge. The posterior tip of this wedge continues posteriorly in the form of an anteroposteriorly short, but dorsoventrally high and sharp crest, the crista postfovealis, which merges into the medial margin of the basal portion of the supratemporal process. The space between the cristae postfoveales forms an anteroposteriorly elongated parietal trough leading to the parietal fossa (Figs. 5.4, 6.2, 7.2). Between the cristae postfoveales and the posterior margin of the parietal table, a short parietal notch is located. The depth of this notch slightly varies among the specimens. In most specimens, it is usually shallow and broad, regardless of the size of the specimen (Figs. 5, 6), whereas in some of the large specimens it may assume an inverse V-shape

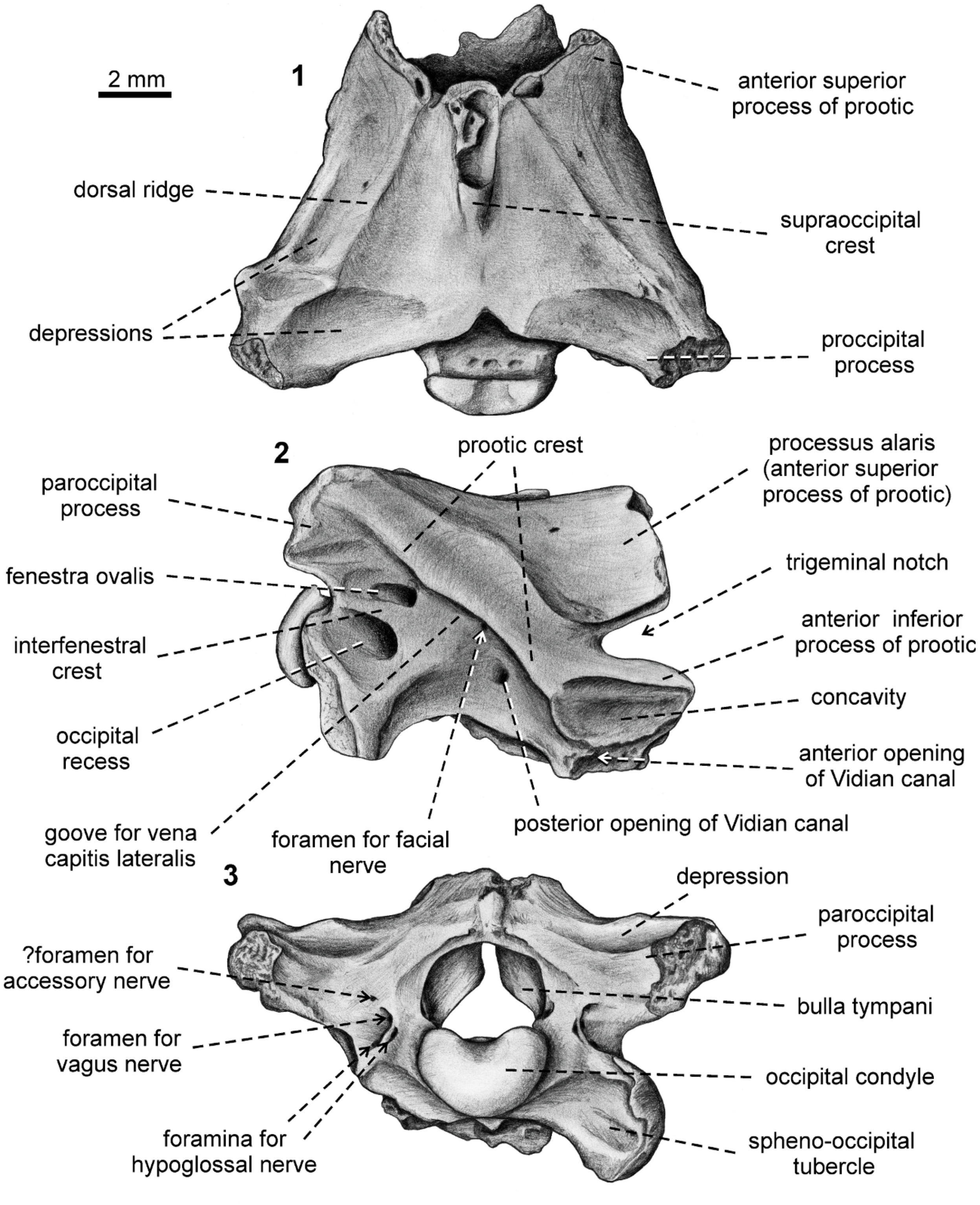

FIGURE *13*—*Pseudopus laurillardi* (Lartet, 1851), BSPG 1962 XIX 2709, posterior portion of braincase in dorsal (*1*), right lateral (*2*) and posterior (*3*) view.

(Fig. 7.3, 7.4). Along the lateral margin of the supratemporal process occurs a massive ventrolateral ridge (crista ventrolateralis). The anterior end of this ridge occurs about at the level of the posteromesial margin of the lamina parietalis. The ventrolateral ridge courses medially to the lateral margin of the supratemporal process. As a result, a smooth ventrolateral surface (facies ventrolateralis) remains between the ridge and the lateral margin of the supratemporal process. On the

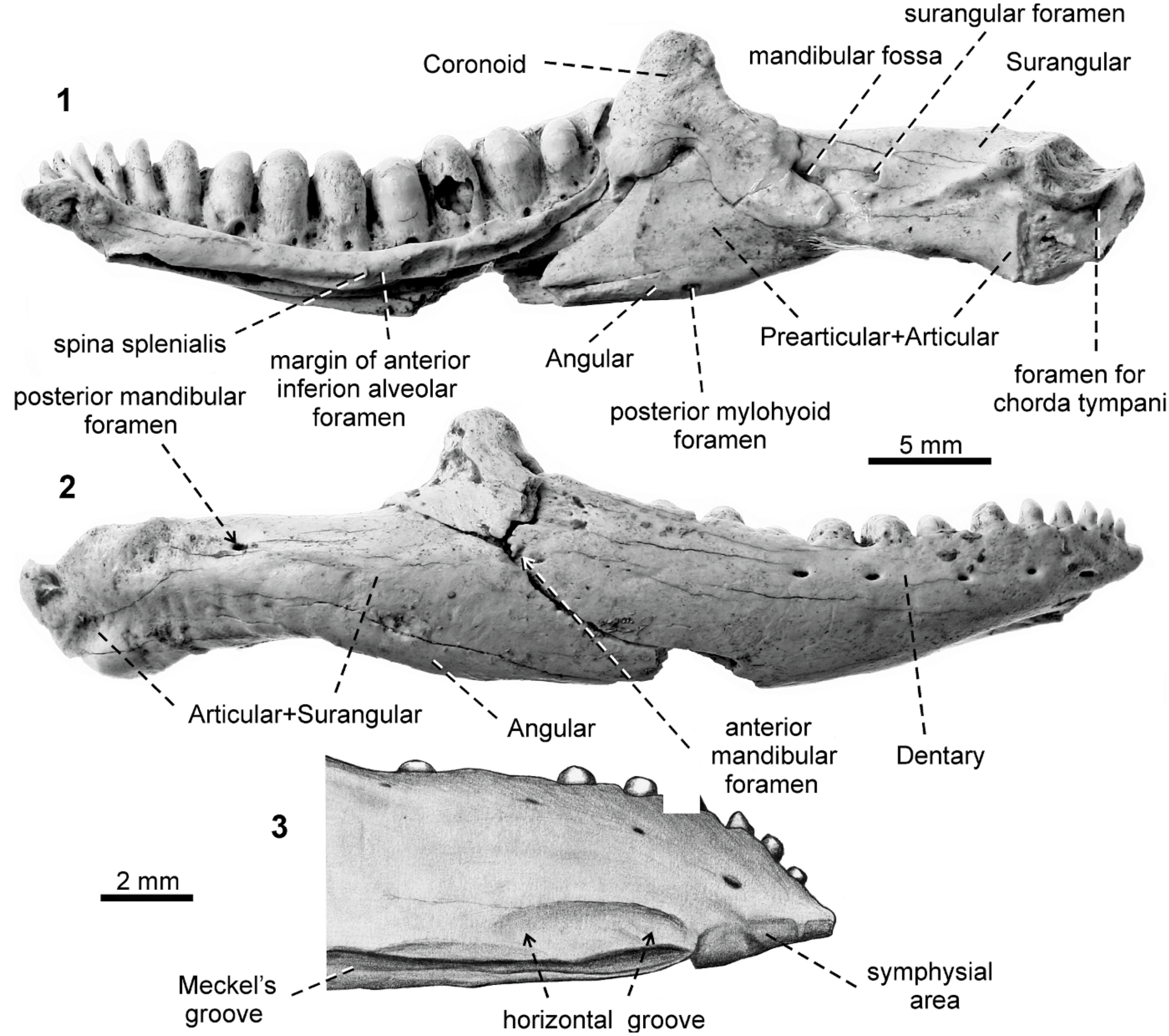

FIGURE *14*—*Pseudopus laurillardi* (Lartet, 1851), MNA-2007-85/2035, lower jaw in internal (*1*) and external (*2*) view; *3*, anterior portion of dentary in ventrolateral view.

ventrolateral wall of the supratemporal process, an anteroposteriorly elongated roughening indicates the supratemporal articulation.

The length of the parietal table of the smallest specimen (NMA-2007-71/2035) is 8.3 mm (Fig. 5.1, 5.2), whereas that of the largest specimen (BSPG 1962 XIX 2715) is 12.3 mm (Fig. 8.1, 8.2). Specimens displaying intermediate parietal table lengths include: 8.5 mm in NMA-2007-66/2035 (Fig. 5.3, 5.4), 10.2 mm in NMA-2007-83/2035 (Fig. 6.1, 6.2), 10.4 in NMA-2007-84/2035 (Fig. 6.3, 6.4), 11.0 mm in NMA-2007-81/2035 (Fig. 7.1, 7.2) and 12.2 in NMA-2007-82/2035 (Fig. 7.3, 7.4). Although parietals of various sizes show several ontogenetic changes, their distinctive features remain consistent regardless of growth stage. The following ontogenetic changes of the parietal have been observed:

1) The ornamentation becomes more pronounced with increased size; the pits and grooves are deeper and ridges more massive (cf. Fig. 5.3 and Fig. 7.3).
2) The parietal ornamented shield becomes wider. In large specimens, the parietal ornamented shield is more or less square-shaped; only in the smallest specimens it is slightly longer than wide. In two large specimens (NMA-2007-79/2035, NMA-2007-83/2035), however, the ornamented surface is wider than long (Fig. 6.1). Moreover, in these specimens the ridges, grooves and tubercles representing the ornamentation are fused together in many instances and form regions of indistinct ornamentation, and the sulci in the ornamented shield start to obliterate, which is often observed in old *P. apodus* individuals (e.g., DE 13) (see feature 3 below).
3) Widening of the facies muscularis. In smaller specimens, the width of the facies muscularis is about half of that of the crista cranii parietalis-median plane width. However, in the large specimen NMA-2007-83/2035, the width of the facies muscularis nearly corresponds to the width of the crista cranii

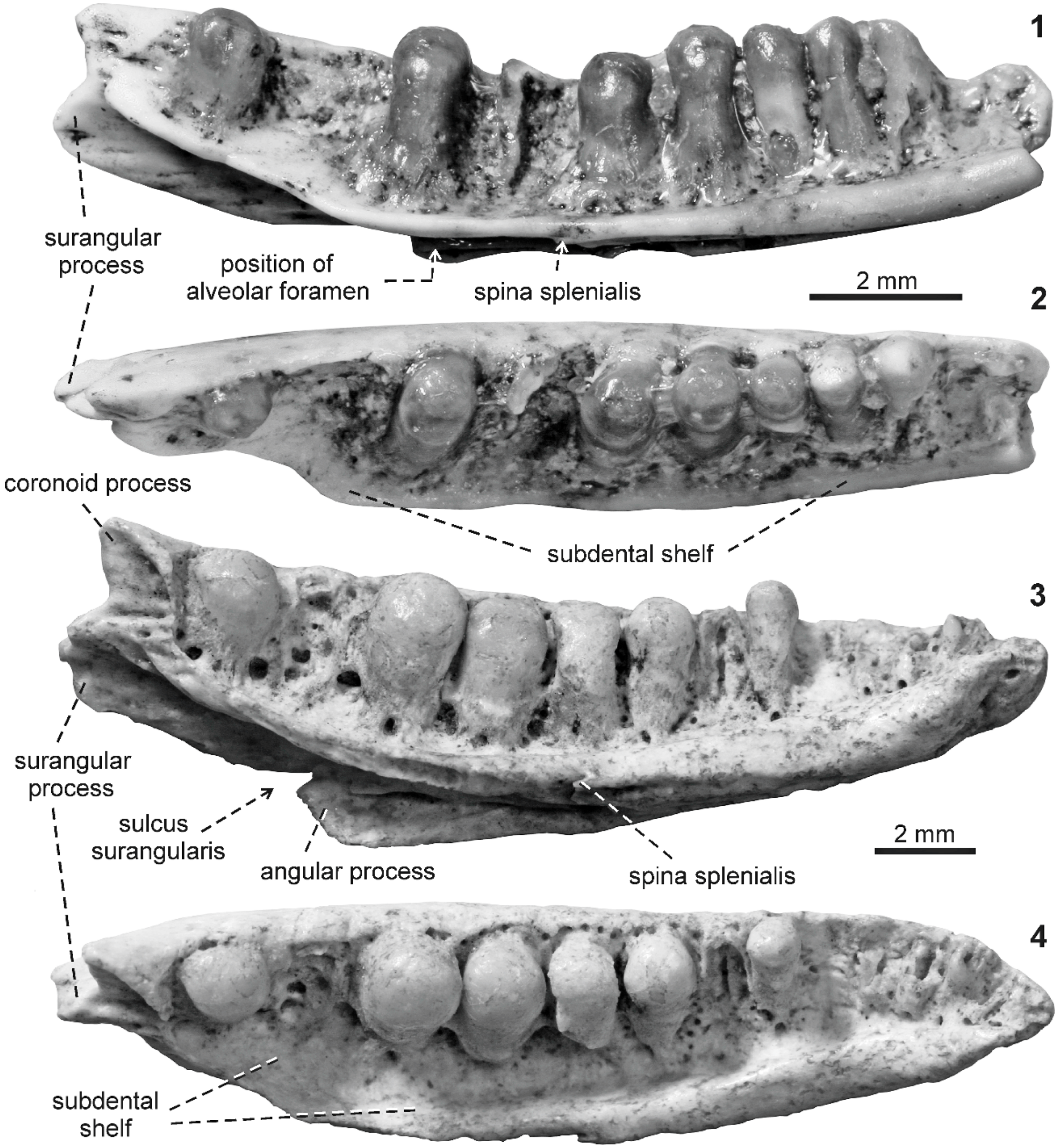

FIGURE 15—*Pseudopus laurillardi* (Lartet, 1851). *1*, *2*, BSPG 1997 XIII 482, left dentary in internal (*1*) and dorsal (*2*) view; *3*, *4*, NMA-2007-97/2035, left dentary in internal (*3*) and dorsal (*4*) view.

parietalis-median plane (Fig. 6.2). Moreover, the parietal ornamented shield is wider than long (feature 2 above). These conditions, i.e., wide facies muscularis and ornamented shield wider than long, are typical for *Pseudopus pannonicus* (Bachmayer and Mlynarski, 1977; Klembara, 1986b). However, specimen NMA-2007-83/2035 comes from MN 6, a stratum that has to date not produced other bones establishing the presence of *P. pannonicus* in these early strata. Until the presence of *P. pannonicus* in MN 6 is demonstrated beyond doubt, such morphology of the parietal has to be considered as within the range of intraspecific variability of *P. laurillardi*, restricted to large and old individuals. The same trend, i.e., the widening of the facies muscularis with size and age of the animal has also been observed in *P. apodus* (among all of the specimens of *P. apodus* included in this study, the facies muscularis is the widest in the largest specimen, DE 13; the presence of the indistinct regions of ornamentation and partial obliteration of parietal sulci indicate that it is an old individual).

4) Prolongation of the crista postfovealis.

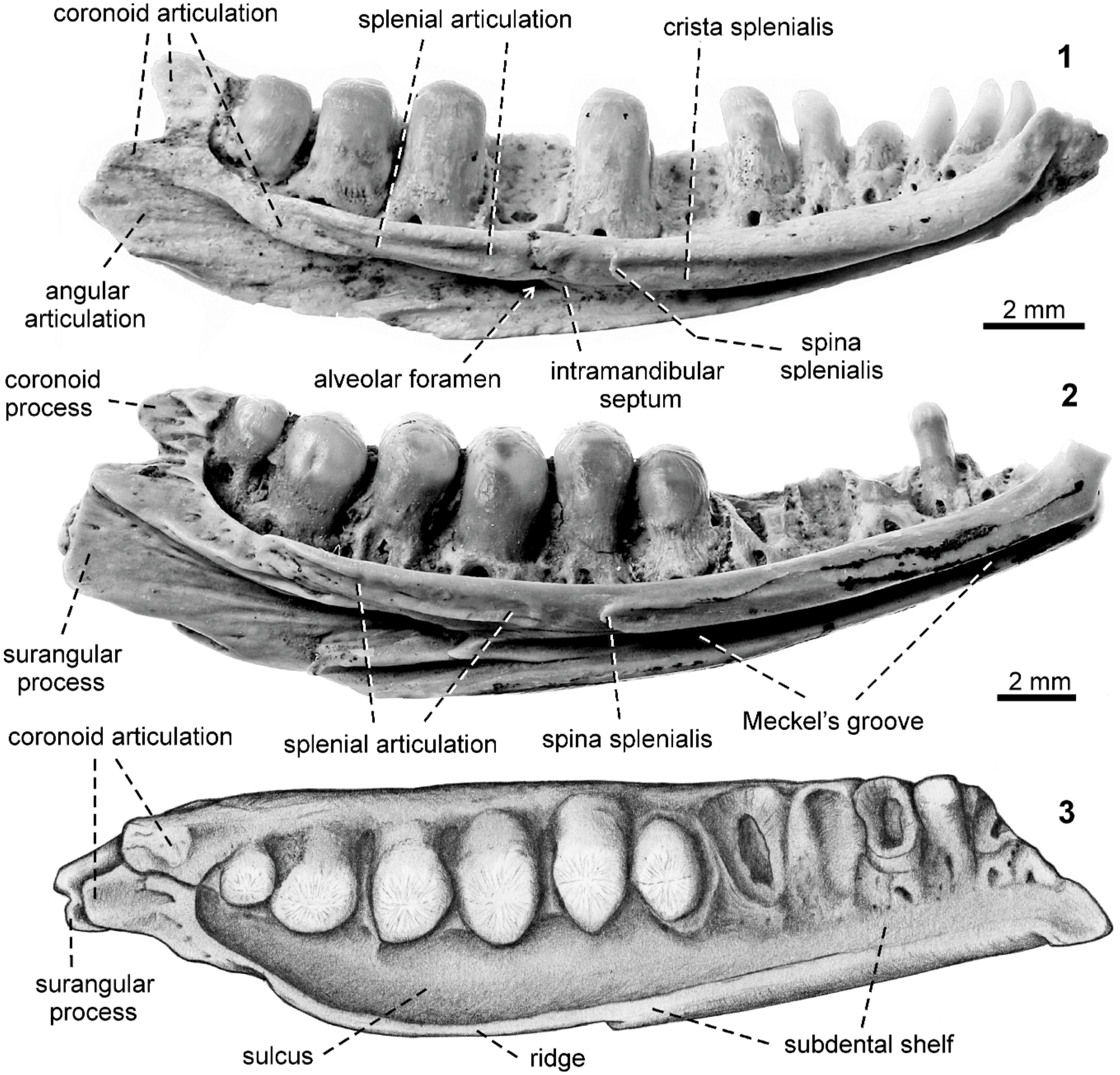

FIGURE *16*—*Pseudopus laurillardi* (Lartet, 1851). *1*, NMA-2007-96/2035, left dentary in internal view; *2*, *3*, NMA-2007-90/2035, left dentary in internal view (*2*), drawing of the same dentary in dorsal view (*3*).

5) Widening of the surface (facies ventrolateralis) interposed between the lateral margin and ventrolateral ridge of the supratemporal process.

*Supratemporal.*—The right and left supratemporals are present in NMA 2009/1/2060 (Fig. 2.2). The left supratemporal exhibits the presence of the mediolaterally broadened posterior portion with a distinct dorsal ridge, whereas the right supratemporal has a well preserved, anteriorly extending plate-like portion. The entire medial surface of the supratemporal is sutured with the lateral wall of the posterior half of the supratemporal process of the parietal.

*Maxilla.*—Although broken in part, both maxillae are present in NMA 2009/1/2060 (Fig. 2.1–2.3). Two of the many variously sized isolated maxillae are almost completely preserved (Figs. 9, 10). The facial process is posterodorsally elongate and forms a high wall that dorsomedially extends from the dental portion. The anterodorsal margin bears a distinct rugose articulating area for the nasal; the anteroventral margin is sutured with the lacrimal (see below). The external surface of the facial process is variously ornamented and most pronounced in the region immediately dorsal to the labial foramina. The ornamentation consists of several osteoderms fused to the external surface of the maxilla that have pits and very short irregular grooves on the surface. The ornamentation is most pronounced in the largest specimens. Usually, two foramina perforate the anterior portion of the facial process immediately dorsal to the ornamented surface. There are usually 7–8 labial foramina, the posteriormost of which typically is the largest. Both the external and internal premaxillary processes are almost completely preserved in NMA-2007-72/2035 (Fig. 9) and BSPG 1976 XII 11005 (Fig. 10); only the anterior tips are lacking. The maxilla-premaxillary aperture is present.

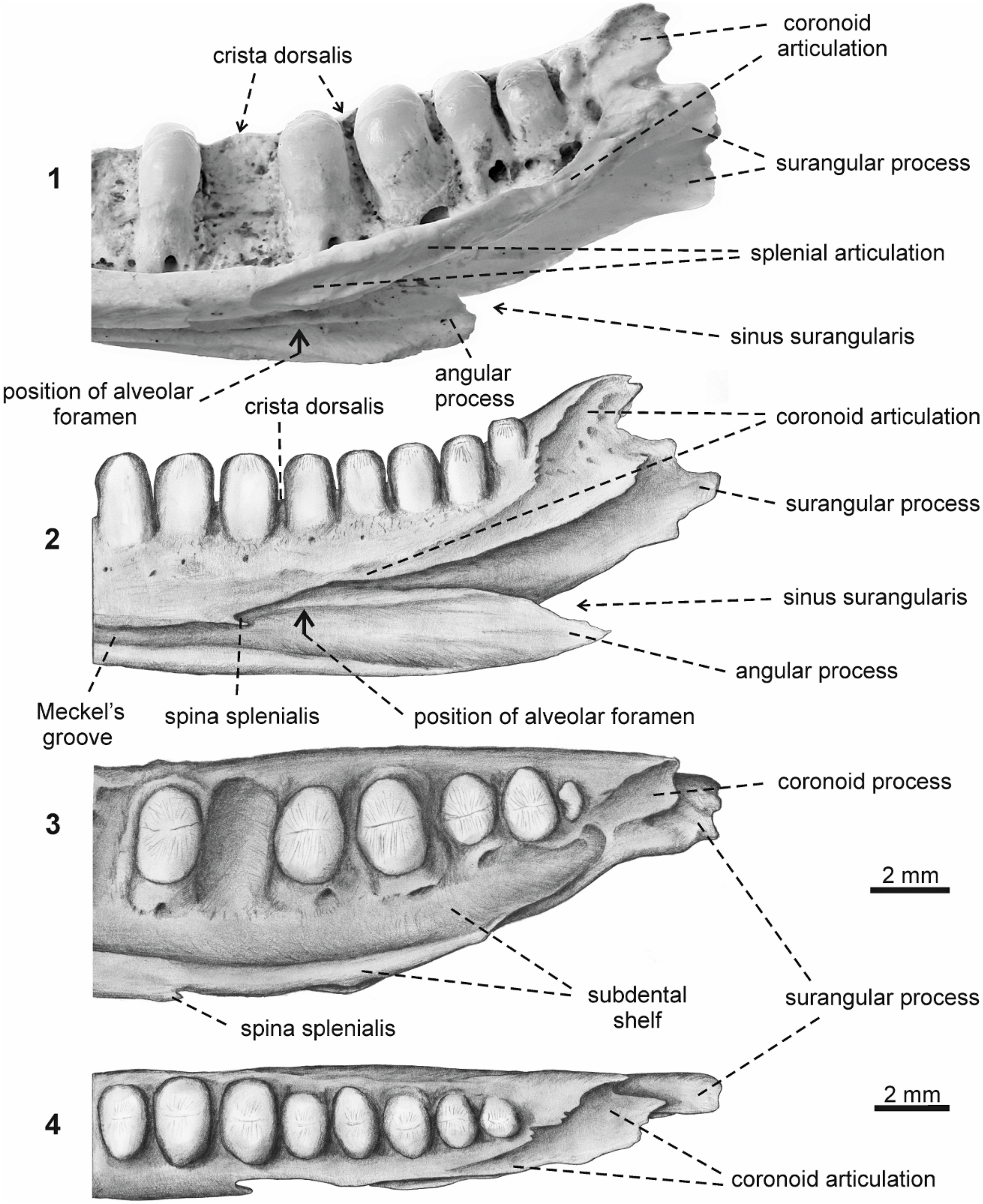

FIGURE 17—*1*, *3*, *Pseudopus laurillardi* (Lartet, 1851), NMA-2007-91/2035, posterior half of right dentary in internal (*1*) and dorsal (*3*) view. *2*, *4*, *Pseudopus apodus* (Pallas, 1775), DE 13, posterior half of right dentary in internal (*2*) and dorsal (*4*) view.

The dorsal surface of the posterior section of the maxilla bears an elongated and deep groove that serves for the articulation with the anterior ramus of the jugal. On the posterior and posteromedial surfaces of the posterior end of the maxilla, a distinct facet for the articulation with the ectopterygoid is present.

On the internal surface of the maxilla, the palatal process is well developed, and its dorsal surface has a large and roughened area for the articulation with the palatine. The maxilla is distinctly concave at this level. Immediately anterolateral to the articular area for the palatine, an infraorbital foramen is located that occurs in the level of, or

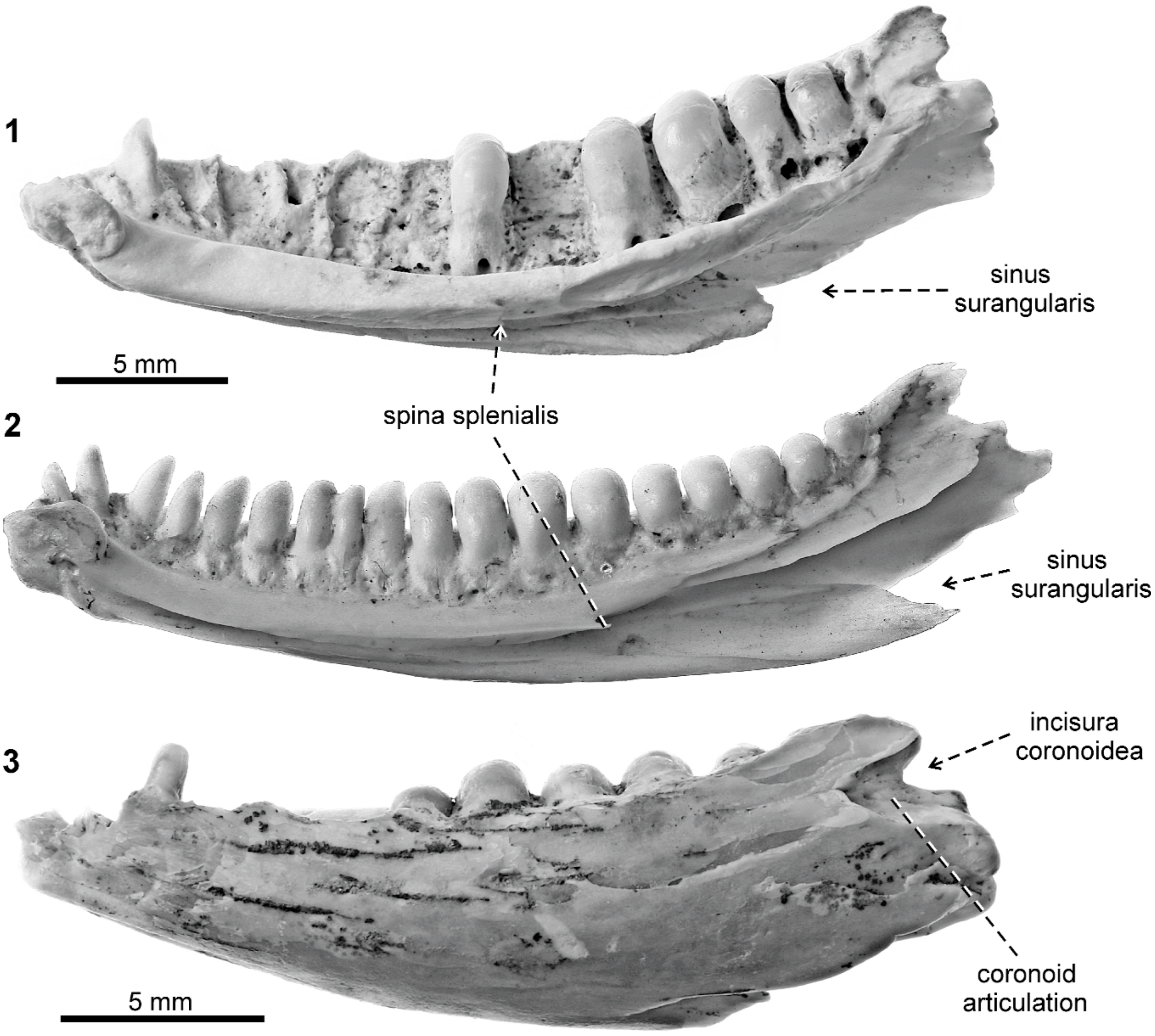

FIGURE 18—*1*, *3*, *Pseudopus laurillardi* (Lartet, 1851); *1*, NMA-2007-91/2035, *3*, NMA-2007-90/2035. *2*, *Pseudopus apodus* (Pallas, 1775), DE 13. Dentaries in internal (*1*, *2*) and external (*3*) view.

immediately posterior to, the posterior margin of the facial process. Anterior to the alveolar foramen, the supradental shelf is mediolaterally narrow and strongly convex, together with the entire anterior portion of the maxilla. The posterior half of the internal surface of the facial process displays a large and massive rugosity for the articulation with the prefrontal that consists of long ridges and intervening grooves. Immediately ventral to the prefrontal articulation and dorsal to the supradental shelf, the internal wall of the maxilla bears a distinct longitudinal groove (Fig. 9.2). The groove is posteriorly continuous with the wall of the nasolacrimal canal of the lacrimal (Fig. 10.2).

*Lacrimal*.—The partial lacrimal is preserved on the right side of NMA 2009/1/2060 (Fig. 2.2). Moreover, a completely preserved lacrimal is present in BSPG 1976 XII 11005 (Fig. 10). It is a small bone sutured to the posteroventral margin of the facial process and dorsal margin of the maxilla immediately posterior to the facial process. The external surface of the lacrimal is ornamented. The ornamentation consists of delicate depressions, elevations and pits. The internal surface of the lacrimal displays a smooth groove that forms the wall of the nasolacrimal canal.

*Jugal*.—The ventral half of the postorbital portion of the right jugal is well preserved in NMA 2009/1/2060 (Fig. 2.1, 2.2). It is a dorsoventrally elongated and plate-like bone. A short posteroventral process extends from the ventral portion of the jugal.

*Squamosal*.—The left squamosal is present in NMA 2009/1/2060 (Fig. 2.1–2.3). However, it is turned over anteroposteriorly, and thus the more robust posterior portion lies anteriorly in the specimen. The bone is a slender and arch-like rod that participates in the formation of the upper temporal arch. The grooves and ridge indicating the articulation with the postorbital are well preserved along the anterior half of the medial margin of the squamosal (visible in lateral view of the specimen).

*Vomer*.—A fragment of the anteriormost portion of the left vomer is preserved in NMA 2009/1/2060 (Fig. 2.2). The bone is trough-like in transverse section, precisely as in *Pseudopus apodus*. Its medial wall is high and positioned perpendicular to the horizontally oriented ventral wall; the medial wall is slightly higher than the lateral wall. Unfortunately, no other anatomical data are accessible.

*Palatine*.—The right palatine is preserved in NMA 2009/1/2060 (Fig. 2.2); it is well recognizable in dorsal view and partially in ventral view, including several well preserved teeth. The body of the palatine is anteroposteriorly elongated (Fig. 11). The posteromedial portion of the ventral surface contains a triangular area for the junction with the pterygoid. The posterolateral corner of the palatine extends into a pointed pterygoid process. Between this process and the posterolateral corner of the palatine, an anteriorly oriented wedge-like notch occurs. The vomerine process is long and pointed. The maxillary process is anteroposteriorly elongated. The anterior ramus of the maxillary process has a rounded tip. The posterior ramus of the maxillary process is large, with a rugose ventral surface representing the area for the articulation with the dorsal surface of the palatine process of the maxilla. The root of the posterior ramus of the maxillary process contains a large palatine canal. Between the maxillary and vomerine processes, a deep sulcus palatinus is present. The narrow ventral and dorsal surfaces of the anterior margin of the palatine and the dorsolateral surface of the maxillary process bear distinct rugose articulating areas for the junction with the prefrontal, and slightly more posterolaterally, a smaller elongated area is present for the articulation with the jugal. The dorsal surface of the palatine is smooth, but it has an obliquely positioned groove, the sulcus dorsalis. In the bottom of this groove, several foramina occur that are arranged one after another.

*Pterygoid*.—Only the anterior half of the palatine process and the partial quadrate ramus of the right pterygoid are preserved in NMA 2009/1/2060 (Fig. 2.2). However, a well preserved pterygoid occurs in Hilgendorf's (1885) material of *Propseudopus fraasii*; this pterygoid morphologically corresponds with that of our material. Moreover, the transverse break of the pterygoid in NMA 2009/1/2060 shows that the teeth are low, stout and blunt, exactly as in the isolated pterygoid described here (Fig. 12.1).

The palatine process is mediolaterally broad and the preserved portion of its ventral surface is covered by teeth (Fig. 12.1). The tooth rows extend posteriorly slightly posterior to the root of the transverse process. In all specimens, the anterior tips of the palatine processes are broken off. The transverse process is shorter than the palatine process. The lateral surface of the transverse process displays a strong striation for the articulation with the ectopterygoid. The transverse process has a mediolateral course and forms an acute angle with the anterolaterally extending portion of the process. The posterior margin of the suborbital incissure is straight (Fig. 12.1, 12.2). The tuberculum contracoronoideum is distinct. Moreover, the ventral surface of the transverse process has an anteroposteriorly coursing crest, here termed a crista oblonga, which posteriorly merges into the lateral margin of the body of the pterygoid. This crest is more distinctly developed in large specimens, and reached the posterolateral margin of the suborbital incisure. Between the crista oblonga and the lateral margin of the denticulate field, a narrow sulcus pterygoideus is present. Interposed between the crista oblonga and the lateral crista transversa ventralis of the anterolateral portion of the transverse process is a distinct anteroposteriorly oriented groove, the sulcus tranversalis. The basisphenoid process is small and terminally blunt. The

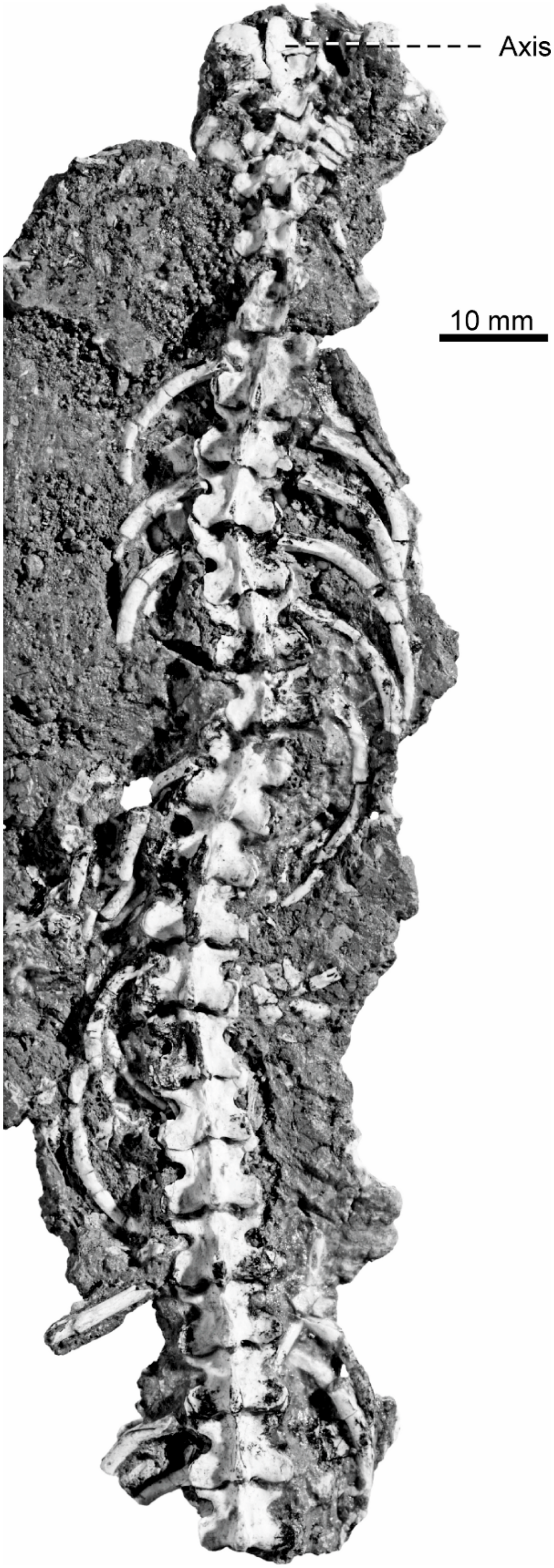

FIGURE 19—*Pseudopus laurillardi* (Lartet, 1851), NMA 2009/1/2060, vertebral column in dorsal view.

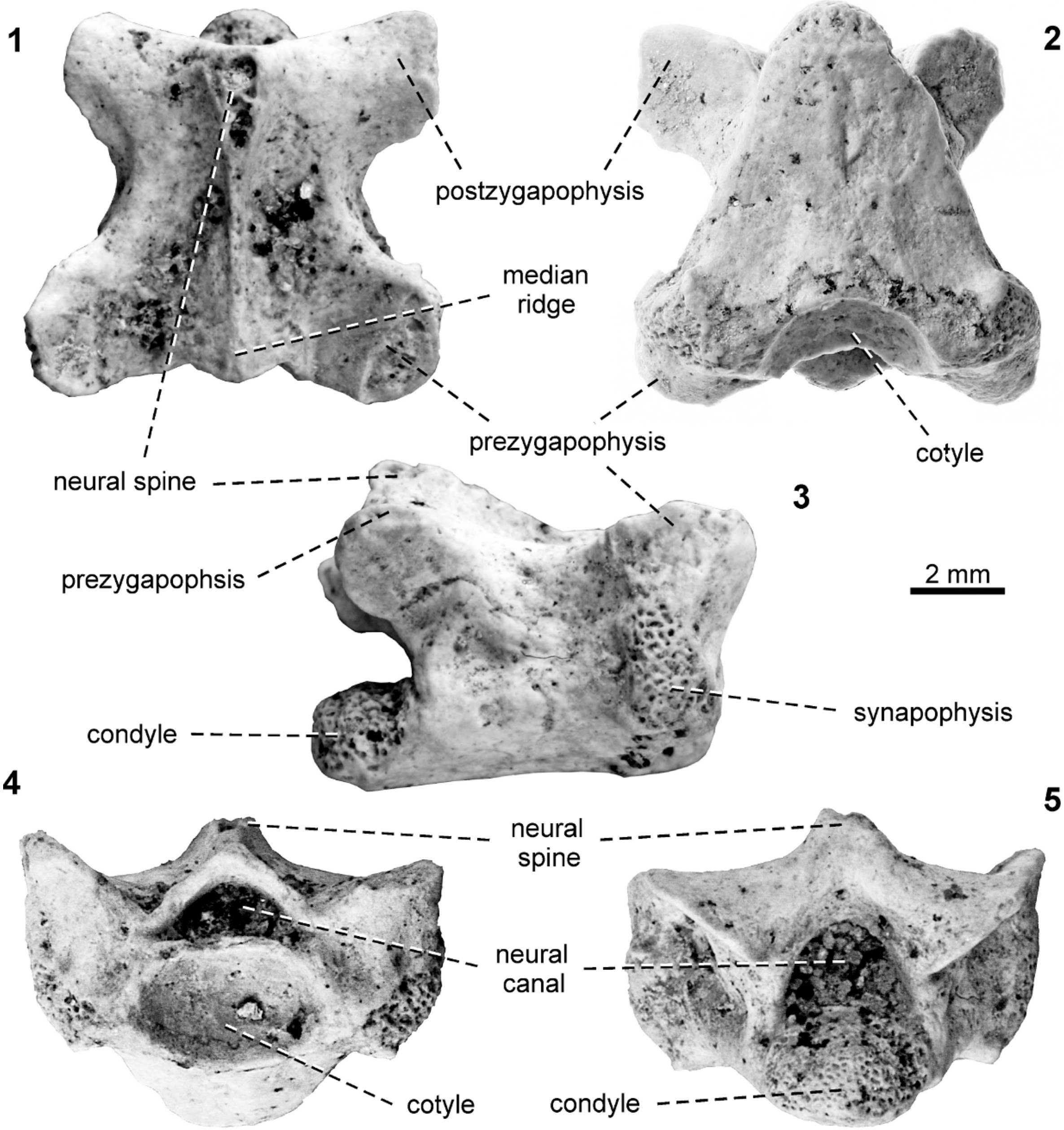

FIGURE 20—*Pseudopus laurillardi* (Lartet, 1851), BSPG 1990 XXII 17, dorsal vertebra in dorsal (*1*), ventral (*2*) lateral (*3*), anterior (*4*) and posterior (*5*) view.

posterolateral wall of the quadrate ramus bears a distinct groove indicating the articulation with the quadrate.

The crista transversa dorsalis forms a sharp crest on the dorsal surface. The crista epipterygoidea is distinct and its margin is rounded. The fovea pterygoidea is more or less round and occurs at the level of the posterior third of the crista epipterygoidea.

*Epipterygoid*.—On the right side of NMA 2009/1/2060 is a fragment of a slender, rod-like bone. It is circular in outline in transverse section, and represents a fragment of the epipterygoid (Fig. 2.2). In this position, the fragment of the epipterygoid is significantly out of articulation and anteriorly displaced.

*Quadrate*.—The left quadrate is preserved in NMA 2009/1/2060 (Fig. 2.1, 2.2). It is a massive bone with the stout dorsal portion. The pterygoid crest is mediolaterally broad (Fig. 2.2). Unfortunately, all other portions of the quadrate are not visible because they are covered with the osteoderms.

*Posterior portion of braincase*.—The posterior portion of the braincase is preserved in NMA 2009/1/2060 (Fig. 2.1, 2.2). Moreover, a single almost completely preserved posterior portion of the braincase is also present (BSPG 1962 XIX 2709); only the anteriormost portion of the prootic and basisphenoid and the basipterygoid processes are lacking (Fig. 13). The originally separate sphenoid, otic and occipital bones are completely fused in this specimen, and the sutures between the individual bones are hardly discernible.

In the spehenoid region, the basipterygoid processes and the region of the pituitary fossa are broken off, but in the surface of the breakage the anterior opening of the Vidian canal is visible (Fig. 13.2). The canal for the internal carotid artery is also preserved and lies dorsomedially to the anterior opening

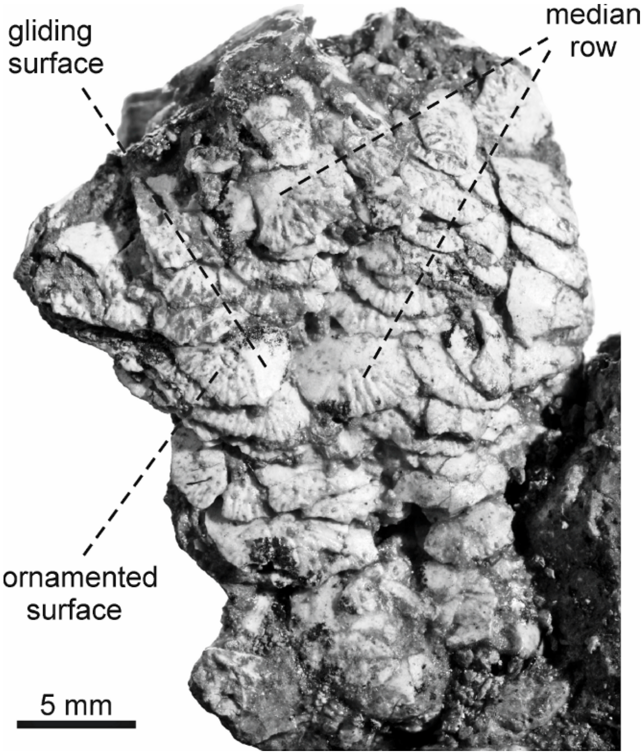

FIGURE 21—*Pseudopus laurillardi* (Lartet, 1851), NMA 2009/1/2060, articulated ventral osteoderms lying immedietely posterior to skull (cf. Figure 2.4).

of the Vidian canal. The dorsal margin of the anterior inferior process of the prootic (ventral border of the trigeminal notch sensu Rage and Bailon, 2005) is massive. The lateral wall of the anterior inferior process is characterized by a distinct concavity.

The most prominent structure of the basioccipital region is the sphenooccipital tubercle, perfectly preserved on the right side of the braincase (Fig. 13.3). It is of quadrangular shape, elongated and oriented ventrolaterally and posteroventrally. The ventral portion of the sphenooccipital tubercle is massive and its anterior wall bears a deep dorsoventrally coursing depression. The anteroventral surface of the tubercle lies at the level of the posterior wall of the fenestra ovalis (Fig. 13.2). The occipital condyle is massive and reniform (Fig. 13). Its dorsal wall bears a small but distinct median pit. On the ventral surface, there is a large rounded depression immediately anterior to the occipital condyle. The depression is separated from the rest of the ventral surface by the stout ventral margins of the sphenooccipital tubercles. Immediately anterior to the bases of the tubercles, there is a small but distinct median tubercle. From it, a short and shallow median ridge extends anteriorly. This ridge divides two depressions bilaterally limited by sharp ridges.

The most prominent structure of the dorsal surface of the supraoccipital portion of the braincase is the straight dorsal ridge that courses in anteromedial-posterolateral direction (Fig. 13.1). Although partially damaged in BSPG 1962 XIX 2709, the median ridge is also well developed and forms a high supraoccipital crest in its anterior section (better preserved in NMA 2009/1/2060, Fig. 2.2).

On the lateral surface of the posterior portion of the braincase, a distinct groove for the vena capitis lateralis is present and courses in anteroventral-posterodorsal direction (Fig. 13.2). The groove is dorsolaterally covered by a sharp prootic crest. The crest originates on the lateral surface of the posterior portion of the inferior process, extends posterodorsally onto the prootic and fades out on the ventrolateral margin of the posterior process of the prootic. About in the mid-length of the groove, a small foramen for the facial nerve is located (Fig. 13.2). On the left side, two separate facial foramina are present: the anterior foramen for the exit of the palatine branch and the posterior foramen for the exit of the hyomandibular branch. Anteroventral to the foramen for the facial nerve, a larger foramen, representing a posterior opening of the Vidian canal, is present (Fig. 13.2). The trigeminal notch is deep and dorsoventrally narrow. The anterior superior process (alar process) of the prootic is of quadrangular shape and is oriented anterodorsally. Its anterior margin lies posterior relative to the anterior margin of the anterior inferior process of the prootic. The posterodorsal surface of the prootic portion of the braincase bears an elongated depression. On the medial surface of the prootic portion of the braincase, the tympanic bulla and acoustic recess are well preserved. The facial foramen lies in the acoustic recess, ventral to the anterior auditory foramen. The large posterior auditory foramen lies posterodorsal to the anterior auditory foramen. The endolymphatic foramen lies along the dorsal margin of the tympanic bulla, about at the level of the posterior auditory foramen. There is a small foramen lying in the medial wall of the anterior portion of the prootic, about at the level of the anterior wall of the anterior

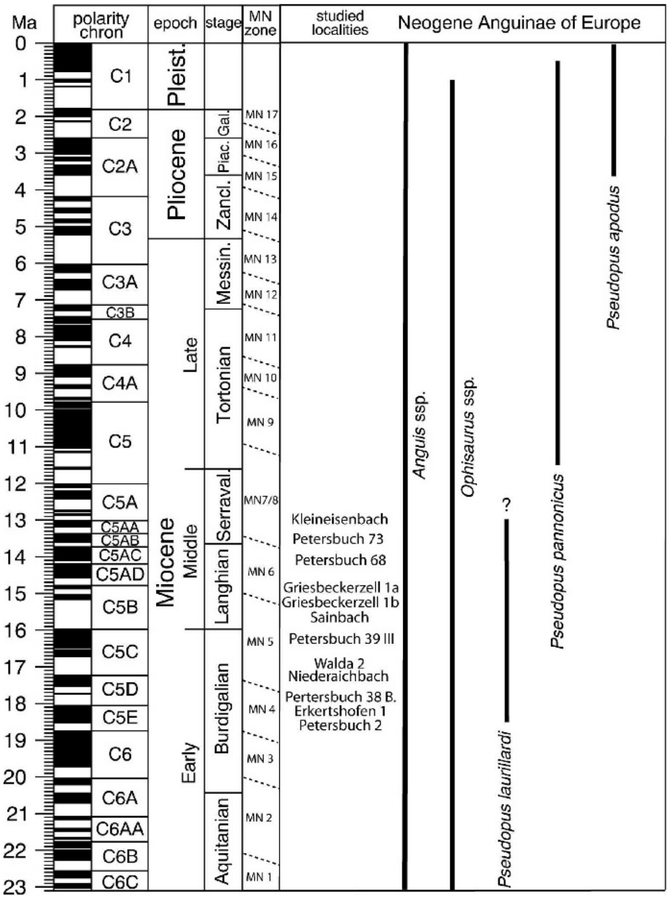

FIGURE 22—Stratigraphical occurrence of European Anguinae and stratigraphical position of study localities.

semicircular canal. The region of the recessus scalae tympani is not sufficiently accessible for description.

The paroccipital process is stout and displays a distinctly depressed posterior surface; the depression (posteromedial surface of paroccipital process sensu Rage and Bailon, 2005) is mediolaterally elongated (13.1, 13.3). Lateral to the foramen magnum, a pronounced depression is located. In its basal portion, two small hypoglossal foramina are present (Fig. 13.3). Immediately dorsal to these hypoglossal foramina, a large slit-like external opening for the vagus nerve is positioned (Fig. 13.3). Immediately dorsal to it, one small foramen probably for the accessorius nerve is present. On the lateral surface of the otoccipital region, the fenestra ovalis and occipital recess are well preserved. The fenestra and recess are separated by an anteroposteriorly elongated and dorsoventrally narrow crista interfenestralis.

*Lower jaw*.—The right and left lower jaws are preserved in NMA 2009/1/2060 (Fig. 2). Moreover, one complete mandible (Fig. 14) and many isolated dentaries are present in other specimens.

The dentary is a long, massive, and ventrally arched bone (Figs. 2.4, 2.5, 14–17.1, 17.3, 18.1, 18.3). The external surface is smooth and has up to 6 mental foramina (Fig. 14.2). The anteroventral surface bears a horizontal groove (Fig. 14.3). Posteriorly, the dentary extends into three processes. The coronoid process is posteriorly more or less pointed in smaller specimens (Fig. 15.1, 15.2), but rounded or ending irregularly in the largest specimens (Figs. 16 and 17.1 respectively). The surangular process positioned beneath the coronoid process is massive, dorsoventrally broad and has almost or complete vertical termination in large specimens (Figs. 16, 17.1). The internal surface of its dorsal portion is covered by the coronoid, and this coronoid articulation continues anteriorly on the medial margin of the subdental shelf (Fig. 16.1, 16.2). The internal side of the remaining large portion of the surangular process is covered by the surangular (Figs. 16.1, 16.2). The surangular process extends more posteriorly than the coronoid process (Figs. 15, 16). On the external surface, in the space between the two processes, a distinct, large, and roughened area for the accommodation of the anterior process of the coronoid and a shallow incisura coronoidea are developed (Fig. 18.3). The angular process, which is positioned most ventrally, is broken off in most specimens, but in several dentaries the root portions are well preserved (Figs. 15.3, 17.1). The sinus surangularis occurs in the form of a deep notch, and it can be estimated that it reached anteriorly the level of the mesial portion of the base of the 2nd tooth from posterior in the middle-sized specimens (Fig. 15.3). In one large specimen the surangular sinus reaches the mesial portion of the base of the 3rd tooth from posterior; however, the 1st tooth from posterior is very small here (Fig. 17.1). The whole ventral surface of the dentary bears a deep Meckel's groove that broadens dorsoventrally in a posterior direction (Fig. 16.2). The symphysial area is kidney-shaped and the Meckel's groove partially extends into this area. At the level of the distal wall of the sixth tooth from posterior (in the largest specimens), an anteriorly notched incisure having a ventral margin extending into a small pointed process, the spina splenialis, is present (Fig. 17.1, 17.3). The spina splenialis lies slightly anterior relative to the mid-length of the dentary in the middle sized and large specimens (Figs. 15.3, 16.1, 16.2, 18.1). The incisure and spina splenialis form the anterior wall of the anterior inferior alveolar foramen (Figs. 14.1, 16.1, 16.2). The anterior margin of the anterior inferior alveolar foramen lies at the level of the distal portion of the 6th tooth from posterior in the largest specimens (Fig. 17.1). In the smallest specimen BSPG 1997 XIII 482, the anterior margin of the anterior inferior alveolar foramen lies at the level of the mesial wall of the 4th tooth from posterior (Fig. 15.1). In medium-sized specimens, the anterior margin of the anterior inferior alveolar foramen lies at the level of the mid-length of the 5th tooth from posterior (Figs. 15.3, 15.4, 16). Immediately anterior to the anterior inferior alveolar foramen, the ventromedial margin of the subdental shelf bears an elongated articular surface for the splenial (Fig. 16.1, 16.2). The distinctive fearure of the dentary is the presence of a mediolaterally broad subdental shelf (lamina horizontalis). The medial margin of the subdental shelf forms a massive rounded ridge. The portion of the subdental shelf interposed between this medial ridge and the teeth forms a deep sulcus (Figs. 16.3, 17.3). Immediately posterior to the anterior inferior alveolar foramen, at the level between the 4th and 5th tooth from posterior, the opening of the alveolar canal, the alveolar foramen, is located (Figs. 16.1). In the smallest specimen BSPG 1997 XIII 482 (and also in two specimens of similar size: BSPG 1990 XXII 41 and BSPG 1990 XXII 32), the alveolar foramen lies at the same level as the mesial portion of the 3rd tooth from posterior (Fig. 15.1). The intramandibular septum forms an almost horizontally oriented shelf separating the Meckel's groove lying ventrally from the alveolar canal lying dorsally, and only the posterior section of the intramandibular septum is partially exposed in internal view (Fig. 16.1).

The coronoid is a biramous bone that dorsally extends into a stout process (Fig. 14.1, 14.2). The anterior portion of the anterior ramus is broken off, but the articular surface on the lingual margin of the subdental shelf shows that it reached anteriorly the mesiobasal portion of the 2nd tooth from posterior in the largest specimens (Figs. 16.1, 16.2, 17.1). The posterior ramus of the coronoid is slender and long and represents the anterior margin of the mandibuar fossa.

The splenial forms a high plate in its posterior section (well visible in the left dentary of NMA 2009/1/2060). Approximately around the 4th tooth from posterior, a small anterior mylohyoid foramen is present in the ventral portion of the splenial. More anteriorly, the splenial forms a trough-like ventral cover of the Meckel's canal extending almost to the symphysial region (Fig. 2.5).

The angular is an elongated element forming a trough-like ventral cover of the mandible at the level of the coronoid and slightly posterior to it (Figs. 2.5, 14.1, 14.2). The ventromedial portion of the angular bears the posterior mylohyoid foramen; it lies at the level of the dorsal process of the coronoid.

*The fused articular + prearticular + surangular*.—These three bones are fused posteriorly to form a single compound bone (Figs. 2.5, 14.1, 14.2). The retroarticular process is broken off. The articular surface faces posterodorsally and medially. The prearticular portion is a vertical plate forming the medial wall of the mandible immediately ventral to the coronoid. The external surface of the compound bone is smooth. It bears a posterior mandibular foramen located anterolateral to the articular surface; the anterior mandibular foramen is located in the dentary-surangular suture, immediately ventral to the coronoid. On the internal surface of the compound bone, a single small foramen for the chorda tympani occurs immeditely posteroventrally to the articular surface. The mandibular fossa is deep. Immediately posterior to the mandibular fossa, a large surangular foramen is present.

*Dentition*.—The premaxilla (BSPG 1990 XXII 9) has nine tooth positions, but only a single complete, conical tooth (i.e., the left lateralmost tooth) is present (Fig. 3.2). There are up to

14 maxillary and 15 dentary teeth (or tooth positions) present. The basic morphology of the maxillary and dentary teeth remains the same in all growth stages.

In the middle section of the dentary, the teeth are rod-like. The anteriormost teeth are slender, pointed, and slightly curved posteriorly (Figs. 14, 16.1, 18.1). The posterior teeth are densely spaced and form robust cylinders with slightly mediodistally widened blunt apical portions (Figs. 14.1–16, 17.1). In most instances, the third or fourth tooth from posterior is the largest (Figs. 15.3, 15.4, 16.2, 16.3). The surface of the crown tip of the largest teeth has a delicate mesiodistal crest; a very fine lingual and labial striation converge to the apex of the crest (Figs. 16.3, 17.3). In the teeth of both small and large specimens, these striae are very delicate.

On the ventral surface of the palatine, immediately lateral to the suture with the pterygoid, three to four anteroposterior rows of teeth are present (Fig. 11.1, 11.3). There are up to ten teeth in each row, and the teeth in the medial row are most robust. The pterygoid teeth are arranged in three to four anteroposteriorly oriented rows on the ventral surface of the bone (Fig. 12.1). The teeth of the lateral row are the largest. The teeth of the remaining rows are usually smaller, and in some specimens they may be densely spaced. The teeth of both the palatine and pterygoid are low, stout, blunt, and some of them bear very fine apical striae (e.g., palatine BSPG 1962 XIX 2706; pterygoid BSPG 1962 XIX 2707).

*Vertebrae.*—A complete series of 25 presacral vertebrae is preserved in NMA 2009/1/2060 (Fig. 19). The atlas is broken, but it is recognizable from the transverse section that this bone consisted of two separate halves (not figured), similar to that seen in *Pseudopus apodus*. A slender neural arch extends from the centrum dorsomedially. The axial neural spine is anteroposteriorly elongated and forms a high, fan-shaped crest. The neural spines of the other vertebrae are quadrangular in shape and extend dorsally from the posterior section of the median ridge. The pre- and postzygapophyses are well developed. Otherwise, the morphology of the observable portions of the vertebrae is very similar to that in *Pseudopus pannonicus* (Klembara, 1986b) and *Pseudopus apodus*. Unfortunately, none of the vertebrae are exposed in ventral view because they are embedded in the matrix. There is a single caudal vertebra present that was secondarily dislodged to the space between the mandibles (Fig. 2.5). It displays the root portion of the left transverse process and the partially preserved roots of the haemapophysis.

There are two additional isolated presacral vertebrae present. The morphology of the dorsal portions of these vertebrae is similar to that in NMA 2009/1/2060; however, they are more robust (Fig. 20). The lateral margins of the body are straight so that the shape of the body is triangular in ventral view. This feature is typical for the genus *Pseudopus*; in the genera *Ophisaurus* and *Anguis*, however, the lateral margins of the body are more or less concave (Klembara, 1981, fig. 3A). On the dorsal side, the spinal process is low and unfinished. There is no difference in morphology between our material and the vertebrae of *Propseudopus fraasii* described and figured by Hilgendorf (1885).

*Ribs.*—The first of the preserved ribs is associated with the eighth vertebra in NMA 2009/1/2060 (Figs. 2.1, 19). The condylar portions are partially exposed in several ribs, and their morphology, as well as the morphology of all other ribs, corresponds to that seen in *Pseudopus pannonicus* and *P. apodus* as detailed by Fejérváry-Lángh (1923).

*Osteoderms.*—The osteoderms are usually preserved in the region between the lower jaws and on the ventral portion of the body (Fig. 2.4, 2.5). Although they are articulated in some places, they are mostly damaged substantially. As a result, it is not possible to describe the changes of their morphology in bilateral and posterior directions. Several isolated osteoderms are attached to the ventral surface of the right lower jaw (Fig. 2.5). They are approximately quadrangular in shape and, with the exception of the lateral margins, ornamented. The ornamentation consists of grooves and ridges radiating from the ossification center of the osteoderm. Immediately posterior to the head, a small portion of the articulated ventral osteoderms is preserved (Figs. 2.4, 21). The osteoderms in the median row are bilaterally widened and their lateral margins converge anteriorly. The anterior and lateral portions of the osteoderms are smooth, representing the overlapping-gliding surfaces. The osteoderms situated lateral to the median row display their gliding surfaces in the lateral and anterior portions. This type of arrangement of ventral osteoderms corresponds to that seen in *Pseudopus apodus* (Fejérváry-Lángh, 1923, fig. 26; personal observation of J. K.).

## COMPARISONS AND DISCUSSION

Augé and Rage (2000) and Rage and Bailon (2005) consider *Pseudopus laurillardi* a separate species that differs from the contemporaneous *Propseudopus fraasii* (Hilgendorf, 1885). According to the diagnosis of *P. laurillardi* (Rage and Bailon, 2005, p. 422), only two features are believed to discriminate the two species. Firstly, the presence of larger anterolateral processes of the parietal in *P. laurillardi*. However, the parietal of *P. fraasii* (Hilgendorf, 1885, pl. 15, fig. 1) displays large anterolateral processes, which are typical for *P. laurillardi* (Augé and Rage, 2000, fig. 11) and not present in *P. pannonicus* and *P. apodus*. In the latter two taxa, the process is relatively small and its posteromedial margin more or less gradually passes into the lateral margin of the parietal table (see analysis below). Secondly, the presence of a short horizontal groove on the lateroventral margin of the anterior part of the dentary in *P. laurillardi* [Augé and Rage, 2000, fig. 9l; Rage and Bailon, 2005, fig. 4A(r)]. However, a groove in this position is present in *P. fraasii* (Hilgendorf, 1885, pl. 15, fig. 13), the dentaries of *P. laurillardi* described above (Fig. 14.3), *P. pannonicus* (Miklas, 2004, pl. 6g), and *P. apodus* (Rauscher, 1992, fig. 19-2a, and personal observations of J. K.). All other features used to characterize *P. laurillardi* in the diagnosis of Rage and Bailon (2005, p. 422) may also occur in *P. pannonicus* and *P. apodus*. As a result, we conclude that *Propseudopus fraasii* is a junior synonym of *P. laurillardi*. This is also the case in all other fossils of this robust anguine that have been described by various authors from the Early and Middle Miocene localities of Europe under different names such as *Ophisaurus moguntinus*, *Ophisaurus fraasi*, *Pseudopus moguntinus*, and *Pseudopus fraasi* (see the synonymy list above).

*Pseudopus laurillardi* differs from *P. pannonicus* and *P. apodus* with regard to the following features:

1) Anteriormost portion of frontal ornamented shield reaches anterolateral margin of frontal, the more posteriorly positioned dorsolateral surface of orbital margin of frontal smooth (Figs. 2.2, 4.1; Augé and Rage, 2000, fig. 12). In *P. pannonicus* (Klembara, 1986b, pl. 3, figs. 5–8) and *P. apodus* (Fig. 4.4), the lateral margin of the frontal ornamented shield reaches the lateral margin of the frontal.

2) Lateral margin of frontal straight (Fig. 4.1, 4.2; Augé and Rage, 2000, fig. 13). In *P. pannonicus* (Klembara, 1986b, pl. 3, figs. 5–8) and *P. apodus* (Fig. 4.4), the lateral margin of the frontal is slightly convex.
3) Sulcus between frontal and frontoparietal shields slightly longer than sulcus between frontal and interfrontal shields (Fig. 4.1; Augé and Rage, 2000, fig. 13). In *P. pannonicus* (Klembara, 1986b, pl. 3. figs. 5, 6) and *P. apodus* (Fig. 4.4), the sulcus between the frontal and frontoparietal shields is always much longer than the sulcus between the frontal and interfrontal shields.
4) Large, laterally extending anterolateral process of parietal table. Although there may be some variability with regard to the size of this process (Figs. 2.2, 5–7; Augé and Rage, 2000, fig. 11; Hilgendorf, 1885, pl. 15, figs. 1–2), in *P. laurillardi* this process is generally larger and extends further laterally (Figs. 2.2, 8.1, 8.2) than that seen in *P. pannonicus* (Fejérváry-Lángh, 1923, pl. 1, fig. 1; Bachmayer and Mlynarski, 1977, pl. 1, figs. 3–5; Klembara, 1986b, pl. 1, pl. 2, fig. 4; Rauscher, 1992, pl. 7, fig. 6) and *P. apodus* (Fig. 8.3), in which the transition of the root portion of the process to the lateral margin of the parietal table is more or less gradual.
5) Subdental shelf distinctly extending in medial direction and consisting of wide and deep sulcus and massive medial ridge (Figs. 15.4, 16.3, 17.3; Higendorf, 1885, pl. 15, fig. 13). During growth, the subdental shelf progressively widens: in the smallest specimen, the subdental shelf is relatively narrow (Fig. 15.2) in comparison to that of a medium-sized specimen (Fig. 15.4). In *P. pannonicus* (Fejérváry-Lángh, 1923, pl. 2, fig. 4a) and *P. apodus* (Fig. 17.4), this subdental shelf is absent.
6) Subdental platform of middle and posterior portion of dentary positioned in mid-height of dentary and teeth dorsally extend only slightly dorsal to crista dorsalis (Fig. 15.3, 16.1, 17.1; Higendorf, 1885, pl. 15, fig. 13; Augé and Rage, 2000, fig. 9). This is probably connected with the wide and deep subdental shelf (see character 5 above). In *P. pannonicus* (Bachmayer and Mlynarski, 1977, pl. 2, figs. 14, 15) and *P. apodus* (Figs. 17.2, 18.2), the subdental platform is positioned in the dorsal half of the dentary height, and the teeth extend to about one half of their length over the crista dorsalis.
7) Surangular process short, dorsoventrally broad and ending nearly or completely vertically in large specimens (Figs. 16, 17.1). Although the smallest specimen BSPG 1997 XIII 482 already has the adult morphology of the surangular process, it is still gracile (Fig. 15.1); in slightly larger specimens, the surangular process becomes dorsoventrally broader (Fig. 15.3). In *P. pannonicus* (Bachmayer and Mlynarski, 1977, pl. 2, fig. 14; Miklas, 2004, pl. 6, figs. g, h) and in *P. apodus* (Figs. 17.2, 18.2), the surangular process is longer and pointed or rounded.
8) Viewed from the inside, the sinus surangularis reaches anteriorly the level of the mesiobasal portion of the 2nd tooth from posterior (Fig. 15.3). In *P. pannonicus* (Bachmayer and Mlynarski, 1977, pl. 2, fig. 14; Miklas, 2004, pl. 6, figs. g, h) and *P. apodus* (Fig. 17.2), the sinus surangularis reaches anteriorly the level immediately posterior to the last tooth.
9) Posterior portion of dentary, posterior to the posteriormost tooth, short (the length equals the length of two last teeth) (Figs. 15, 16, 17.1; Augé and Rage, 2000, fig. 9; Rage and Bailon, 2005, fig. 4A). In *P. apodus*, the length of the posterior portion of the dentary equals the length of the four last teeth in the dentary of large specimens (Fig. 17.2, 17.4). In *P. pannonicus*, the situation is similar to that seen in large *P. apodus* (Bachmayer and Mlynarski, 1977, pl. 2, fig. 14).
10) Spina splenialis lies anterior to mid-length of dentary in the middle sized and large specimens (Figs. 15.3, 16.1, 16.2, 17.1). In *P. pannonicus* (Bachmayer and Mlynarski, 1977, pl. 2, fig. 15; Rauscher, 1992, pl. 5, fig. 3b; Miklas, 2004, pl. 6, fig. h) and *P. apodus* (Figs. 17.2, 17.4, 18.2), the spina splenialis lies posterior to the mid-length of the dentary.
11) Posterior margin of anterior inferior mandibular foramen formed by splenial. Although the anterior ramus of the coronoid is not preserved in the specimens studied here, it is seen on most dentaries that the coronoid articulation extended anteriorly to the mesiobasal portion of the 2nd tooth from posterior (Fig. 16.1, 16.2). In the specimen described by Hilgendorf (1885, pl. 15, fig. 13b), the anterior ramus of the coronoid is present, and its length corresponds to the anterior extent of the coronoid articulation in the dentaries described here. Besides this, the splenial-dentary articulation anterior to the anterior ramus of the coronoid is preserved in this specimen (Hilgendorf, 1885, pl. 15, fig. 13b). It means that the posterior margin of the anterior inferior mandibular foramen is formed by the splenial, similar to that of *Ophisaurus* and *Anguis*. In *P. pannonicus* (Bachmayer and Mlynarski, 1977, pl. 2, fig. 15; Rauscher, 1992, pl. 5, fig. 3b) and *P. apodus* (Fig. 17.2, 18.2 and articulated specimens DE 4, 6, 8, 10, 12), the posterior wall of the anterior inferior mandibular foramen is formed by the anterior margin of the anterior ramus of the coronoid.

*Pseudopus pannonicus* differs from *P. laurillardi* and *P. apodus* in the following features:

1) *Pseudopus pannonicus* is the largest and most robust species of the genus *Pseudopus* and probably grew to a similar size as *P. apodus*; however, the bones, marginal teeth and the palatine and pterygoid teeth of the former species are more robust.
2) Ornamented surface of parietal wider than long (Fejérváry-Lángh, 1923, pl. 1, fig. 1; Bachmayer and Mlynarski, 1977, pl. 1, figs. 3–5; Klembara, 1986b, pl. 1, pl. 2, fig. 4; Rauscher, 1992, pl. 7, fig. 6). In *P. laurillardi*, the ornamented surface of parietal is more or less square-shaped (Figs. 5.3, 6.3, 7.1, 7.3, 8.1; Hilgendorf, 1885, pl. 15, fig. 1), although in a few large and old individuals, the ornamented surface of parietal may be slightly wider than long (Fig. 6.1; see above). In *P. apodus*, the ornamented surface of parietal is square-shaped.
3) In large specimens, occipital shield of parietal ornamented surface large; its junction with interparietal shield lies close or in mid-length of ornamented surface (Fejérváry-Lángh, 1923, pl. 1, fig. 1; Klembara, 1986b, pl. 1, pl. 2, fig. 4B; Bachmayer and Mlynarski, 1977, pl. 1, fig. 3). In *P. laurillardi*

(Figs. 2.2, 5.1, 5.3, 6.3, 7.1, 7.3, 8.1) and *P. apodus* (J. K. personal observations), the occipital shield is always smaller and its length equals one third of the length of the ornamented surface.

4) Facies muscularis wide. In *P. pannonicus*, the width of the facies muscularis nearly equals the distance from the crista cranii parietalis to the median plane (Klembara, 1986b, pl. 1, figs. 1B, 2B, pl. 3, fig. 4A). In *P. apodus* (Fig. 8.3) and *P. laurillardi* (Figs. 5.2, 5.4, 7.2, 8.2), the width of the facies muscularis is approximately equal to half of the distance between the crista cranii parietalis and the median plane. Only in some of the largest specimens of *P. laurillardi* (Fig. 6.2), the relative width of the facies muscularis is next to identical to that in *P. pannonicus* (see above).

The largest anguine, *Pseudopus pannonicus*, morphologically represents a transitional form between *P. laurillardi* and *P. apodus*. It shares several features with *P. laurillardi*, but, at the same time, it is very similar in many respects to the Recent *P. apodus*. The fossil record does at present not indicate a stratigraphic overlap of *P. laurillardi* and *P. pannonicus* (Fig. 22 and see below).

*Pseudopus apodus* differs from *P. pannonicus* and *P. laurillardi* in the following features:

1) Lateral margins of nasal process of premaxilla parallel (Fig. 3.3, 3.4). The bilaterally widened dorsal portion of the nasal process is present in *P. laurillardi* (Fig. 3.1, 3.2; Augé and Rage, 2000, fig. 12) and *P. pannonicus* (Bachmayer and Mlynarski, 1977, pl. 1, fig. 7; Miklas, 2004, pl. 6d).
2) Interfrontal shield of frontal reduced or absent. The interfrontal shield is present rarely and mostly in the largest specimens (DE 3, DE 13). In the middle sized and small specimens, the interfrontal shield is mostly absent (Fig. 4.4). In *P. laurillardi* (Fig. 4.1; Augé and Rage, 2000, fig. 13d) and *P. pannonicus* (Klembara, 1986b, pl. 3, figs. 5, 6), the interfrontal shield is well developed.
3) Crista postfovealis of parietal low and rounded (Fig. 8.3). In *P. pannonicus* (Fejérváry-Lángh, 1923, pl. 1, fig. 1a; Bachmayer and Mlynarski, 1977, pl. 1, fig. 5; Klembara, 1986b, pl. 1, figs. 1B, 2B, pl. 2, fig. 4A) and *P. laurillardi* (Figs. 5.2, 5.4, 6.2, 6.4, 7.2, 7.4; Hilgendorf, 1885, pl. 15, fig. 1a; Augé and Rage, 2000, fig. 11v), the crista postfovealis forms a sharp and high wall.
4) Absence of a parietal notch, but instead a parietal arch is present (Fig. 8.3). The parietal notch is a structure located immediately posterior to the posterior margin of the parietal table formed by the carina acruata and between the anteromedial margins of the supratemporal processes (Meszoely and Haubold, 1975; Klembara, 1981, p. 138). The parietal notch is a typical feature of the genera *Ophisaurus* and *Anguis* (Klembara, 1981). In *P. laurillardi* (Figs. 5–7; Hilgendorf, 1885, pl. 15, fig. 1; Augé and Rage, 2000, fig. 11) and *P. pannonicus* (Fejérváry-Lángh, 1923, pl. 1, fig. 1; Bachmayer and Mlynarski, 1977, pl. 1, figs. 3, 5; Klembara, 1986b, pl. 1, fig. 1), the parietal notch is present although it is never as deep as in *Ophisaurus* and *Anguis* (Klembara, 1979), and its presence in *P. laurillardi* and *P. pannonicus* morphologically represents an intermediate condition between *P. apodus*, and *Ophisaurus* and *Anguis*. *P. apodus* does not possess a distinct parietal notch, but instead a parietal arch is present; only a very shallow anteromedian emargination of the carina arcuata may be present (Fig. 8.3).
5) Posteroventral process of jugal absent. A short posteroventral process of jugal is present in *P. laurillardi* (Fig. 2.2; Hilgendorf, 1885, pl. 15, figs. 4, 4a) and *P. pannonicus* (Fejérváry-Lángh, 1923, pl. 1, figs. 6, 6a).
6) Palatine and pterygoid teeth are gracile, posteriorly curved and pointed. In *P. laurillardi* (Figs. 10.1, 10.3, 11.1) and *P. pannonicus* (Fejérváry-Lángh, 1923, pl. 1, fig. 7; Bachmayer and Mlynarski, 1977, pl. 1, fig. 6; Miklas, 2004, pl. 6c), these teeth are low, stump-like, and blunt.
7) Suborbital incisure is U-shaped (Fig. 12.3). In *P. apodus*, the transverse process has a posteromedial-anterolateral course and its transition to the anterolaterally extending portion of the transverse process is gradual. In *P. laurillardi* (Fig. 12.1, 12.2) and *P. pannonicus* (Bachmayer and Mlynarski, 1977, pl. 1, fig. 6), the transverse process has a mediolateral course and a straight anterior margin. The transverse process has obtuse but sharp angles with both the anterolaterally extending portion of the transverse process and with the palatine process. Thus, the posterior margin of the suborbital commissure is straight.
8) Absence of crista oblonga on transverse process of pterygoid (Fig. 11.3). In *Pseudopus laurillardi* (Fig. 12.1) and *P. pannonicus* (Bachmayer and Mlynarski, 1977, pl. 1, fig. 6), the ventral surface of the transverse process bears an anteroposterior crista oblonga. In *P. apodus*, the transverse process is relatively slender; its anterolateral portion is mediolaterally narrow and the crista oblonga and sulcus transversalis are absent (Fig. 12.3).
9) Anterior superior process of prootic long. In *P. apodus*, the anterior margin of the anterior superior process of the prootic (crista alaris) extends more anteriorly relative to the level of the anterior margin of the anterior inferior process of the prootic. In *P. laurillardi* (Fig. 13.1, 13.2; Rage and Bailon, 2005) and *P. pannonicus* (Fejérváry-Lángh, 1923, pl. 2, figs. 1, 1a, 1b), the anterior superior process of the prootic does not reach the level of the anterior margin of the anterior inferior process of the prootic.
10) Posterior teeth of dentary are lightly construted (Figs. 17.2, 17.4, 18.2). In *P. laurillardi* (Figs. 14–16, 17.1, 17.3, 18.1, 18.3; Hilgendorf, 1885, pl. 15, fig. 1; Augé and Rage, 2000, fig. 11) and *P. pannonicus* (Fejérváry-Lángh, 1923, pl. 1, fig. 7; Bachmayer and Mlynarski, 1977, pl. 1, fig. 6; Miklas, 2004, pl. 6c), the corresponding teeth are much more robust.

Based on the preceding considerations, we conclude that the genus *Pseudopus* is comprised of three Euroasiatic species: *P. laurillardi* (Lartet, 1851; Early-Middle Miocene of Europe), *P. pannonicus* (Kormos, 1911; Late Miocene-Middle Pleistocene of central and eastern Europe) and *P. apodus* (Pallas, 1775; Late Pleistocene-Recent, from eastern Europe to central Asia). *P. pannonicus* is the largest of these three species. *P. laurillardi* and *P. apodus* are similar in size, but the cranial bones and teeth of *P. laurillardi* are more robust than in *P. apodus*. The genus *Pseudopus* represents the most robust member of the subfamily Anguinae.

## BIOSTRATIGRAPHY AND BIOGEOGRAPHY

Our reevaluation of *Pseudopus moguntinus* Boettger (1875) from the Oligocene of the Mainz Basin has shown that this taxon is a nomen nudum. As a result, Paleogene members of the genus *Pseudopus* remain unknown. The latest Oligocene (MP 30) postcranial anguine remains from Rott near Bonn in Germany are difficult to refer to a particular genus (Klembara, 1985). The Late Oligocene to Early Miocene (MP 27 to MN 3) anguins from Europe include the genera *Ophisaurus* (=*Dopasia*) and *Anguis* (Augé, 2005; Böhme and Ilg, 2008; Böhme, 2008). The first occurrence of the genus *Pseudopus* (*P. laurillardi*) has been recorded for the beginning of MN 4 (MN 4a) at Petersbuch 2, which is approximately 18.5 Ma in age (Fig. 22). During this time, which is known as the "Proboscidian Datum Event", an important faunal renewal occurred in Europe that was characterized by the first appearance of several new mammals (e.g., proboscidians, bovids; van der Made, 1999), as well as amphibians, reptiles (e.g., bufonids, lizards, snakes; Böhme, 2001; Ivanov, 2001; Rage and Baillon, 2005), and freshwater fishes (e.g., cyprinins, channids; Böhme, 2001, 2004) of both African and Asian origin (see Harzhauser et al., 2007 for palaeogeographic details). Up to the late Middle Miocene, *P. laurillardi* fossils have frequently been recorded for localities in western, central, and eastern Europe (but to date only north of the Alpine orogen) without displaying any notable morphologic change. The youngest records of this species come from MN 8 of Kleineisenbach (Fig. 22) and probably from Anwil in Switzerland (unpublished material). Both localities are approximately 13 Ma in age or slightly younger (Prieto, 2007). The material cf. *Pseudopus* sp. described from Tasad in Romania (Early Sarmatian, ~12.4 Ma; Hir et al., 2001) is fragmentary (one osteoderm), and thus it remains unclear as to whether it belongs to *P. laurillardi*. We conclude, that, during the last 1 to 1.5 million years of the Middle Miocene (Sarmatian), *Pseudopus* continues to be unknown in Europe (in contrast to *Ophisaurus*, Fig. 22). The stratigraphically younger species *P. pannonicus* has first been documented from the very base of the Late Miocene (oldest record Hammerschmiede, MN 9; Böhme unpublished). During the Late Miocene and Pliocene, *P. pannonicus* was a widespread species that, during the Late Pliocene and Pleistocene, even has been reported from northern and central Italy and northeastern Spain (Delfino, 2002; Blain and Bailon, 2006). During this time interval, this species is contemporaneous with *P. apodus*, which has been described from MN 15 at Ivanovce in Slovakia (Klembara, 1986b).

## PALEOECOLOGY

The extant *Pseudopus apodus* is the largest living anguine lizard. It feeds on land snails, slugs and large insects. The present-day geographical distribution (Obst, 2004) includes southeastern Europe (Balkan Peninsula, Anatolia), West Asia and central Asia (Kazakhstan, Kyrgyzstan), where it lives in open, sparsely vegetated environments of arid to sub-humid climate zones.

To understand the humidity dependence of fossil *Pseudopus* species, we estimated the palaeoprecipitation at the *Pseudopus*-bearing loalities by using the method outlined in Böhme et al. (2006). The key components of this method are briefly summarized below (for details see Böhme et al., 2006, 2008). The distribution and spatial occurrence of amphibians and reptiles depends on environmental conditions at various scales, ranging from habitat to global scale (Zug et al., 2001). It is assumed that distribution of species at a given spatial scale is in equilibrium with their environment (Guisan and Theurillat, 2000; Guisan and Hofer, 2003). Precipitation serves as a direct predictor for the herpetofaunal distribution and species richness and yields robust and widely applicable modelling results (Austin, 2002). The most important environmental factors for amphibian and reptilian distribution are sunlight availability as the ultimate heat source, and water availability for reproduction and as a buffering medium against thermal extremes. Accordingly, amphibians and reptiles have evolved several different ecophysiological strategies and adaptations to maintain thermoregulation, water balance, and gas exchange. Böhme et al. (2006) assigned recent amphibians and reptiles to six groups based on their ecophysiological strategies. The relative frequency of these groups in recent communities is used to establish an ecophysiological index for the communities, which shows a highly significant correlation with mean annual precipitation ($r^2 = 0.88$).

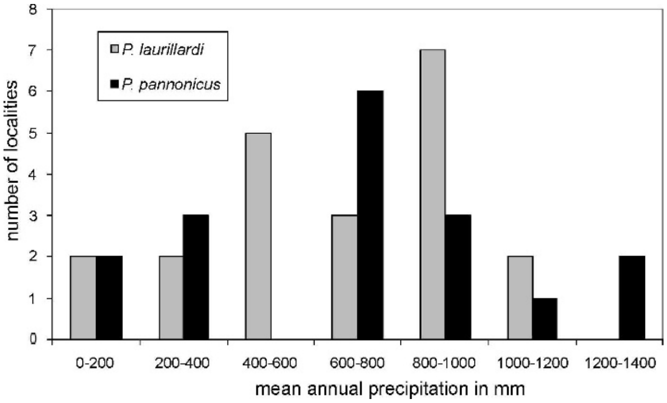

FIGURE *23*—Palaeoprecipitation estimates (based on Böhme et al., 2006) for 38 Neogene *Pseudopus* localities.

We applied this method to the 38 *Pseudopus*-bearing localities (21 with *P. laurillardi*, 17 with *P. pannonicus*). The taxonomic data sets for these localities (Table 1 and Table 2) were converted into mean annual paleoprecipitation estimates using Eq. (6) in Böhme et al. (2006). The results show that, unlike the Recent species, both fossil *Pseudopus* species can occur in a wide range of humidity conditions, i.e., from arid to perhumid climates (Fig. 23). This suggests a much greater ecological plasticity for the extinct *Pseudopus* species than exhibited by the living *P. apodus*. However, the majority of analyzed localities represent sub-humid to humid climates between 400 and 1,000 mm. These values may indicate that the preferential habitats of the fossil *Pseudopus* species include forested environments, such as have been reconstructed for southern Germany during some periods of the Miocene Climatic Optimum (subtropical semi-deciduous limestone forest, subtropical oak–laurel forest; Böhme, 2003; Böhme et al., 2007). This interpretation is supported by the faunal elements that co-occur with *Pseudopus* in many localities, including crocodiles, a variety of amphibians and several groups of aquatic turtles (see Table 1 and Table 2).

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TABLE *1*—Data set of fossil amphibian and reptile species (from Böhme and Ilg, 2008) and paleoprecipitation estimates (according to Eq. 6 in Böhme et al., 2006) for 21 localities containing *Pseudopus laurillardi*. 1 – Petersbuch 2, 2 – Beon 1, 3 – Erkertshofen 1, 4 – Rembach, 5 – Forsthart, 6 – Eitensheim, 7 – Langenmoosen, 8 – Niederaichbach, 9 – Ichenhausen 3, 10 – Schönenberg, 11 – Walda 2, 12 – Puttenhausen B, 13 – Sandelzhausen B-C3, 14 – Sandelzhausen D1-E, 15 – Burtenbach 1b + 1c, 16 – Untereichen-Altenstadt 565 m, 17 – Griesbeckerzell 1a, 18 – Laimering 2 + 3, 19 – Sansan, 20 – Kleineisenbach, 21 – Anwil.

|  | Petersbuch 2 | Beon 1 | Erkertshofen 1 | Rembach | Forsthart | Eitensheim | Langenmoosen | Niederaichbach | ICH 3 |
|---|---|---|---|---|---|---|---|---|---|
|  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| taxon | MN4a | MN4b | MN4b | MN4b | MN4b | MN5 | MN5 | MN5 | MN5 |
| *Albanerpeton inexpectatum* | 0.0917 |  | 0.0917 |  |  | 0.0917 |  | 0.0917 |  |
| *Mioproteus caucasicus* |  |  |  |  |  |  | 1 |  | 1 |
| *Mioproteus* sp. |  |  |  |  |  | 1 |  |  |  |
| *Salamandrina* sp. | 0.9768 |  |  |  |  |  |  |  |  |
| *Chioglossa meini* | 0.9768 |  | 0.9768 |  |  |  |  |  |  |
| aff. *Mertensiella* sp. | 0.9768 |  |  |  |  |  |  |  |  |
| *Salamandra sansaniensis* | 0.3918 |  | 0.3918 |  |  |  |  |  |  |
| *Chelotriton paradoxus* | 0.3918 |  |  |  |  |  |  |  |  |
| *Chelotriton* aff. *pliocaenicus* | 0.3918 |  |  |  |  |  |  |  |  |
| *Chelotriton* sp. |  | 0.3918 | 0.3918 |  |  |  | 0.3918 | 0.3918 | 0.3918 |
| Salamandridae indet. |  |  |  |  |  |  |  |  |  |
| *Triturus vulgaris* |  |  |  |  |  |  |  |  |  |
| *Triturus* cf. *marmoratus* |  | 0.513 |  |  |  |  |  |  |  |
| *Triturus* sp. | 0.3918 | 0.3918 |  |  |  |  |  |  |  |
| *Triturus* cf. *helveticus* | 0.3918 | 0.3918 |  |  |  |  |  |  |  |
| *Triturus* aff. *vittatus* | 0.513 |  |  |  |  |  |  |  |  |
| *Latonia gigantea* |  |  |  |  |  | 0.3918 | 0.3918 |  |  |
| *Latonia ragei* | 0.3918 | 0.3918 |  |  |  |  |  |  |  |
| *Latonia* sp. |  |  |  |  |  |  |  |  |  |
| Discoglossidae indet. |  |  |  |  |  |  |  | 0.3918 | 0.3918 |
| Palaeobatrachidae sp. 1 | 1 |  |  |  |  |  |  |  |  |
| Palaeobatrachidae sp. 2 | 1 |  |  |  |  |  |  |  |  |
| Palaeobatrachidae indet. |  |  |  |  |  |  |  |  |  |
| *Bufo* (cf.) *viridis* | 0 |  | 0 |  |  |  |  |  |  |
| *Bufo* sp. indet. |  |  |  |  |  |  |  |  |  |
| *Pelophylax* sp. | 0.513 | 0.513 | 0.513 |  |  |  | 0.513 |  | 0.513 |
| *Rana* s.l. sp. |  |  |  |  | 0.513 | 0.513 |  |  |  |
| *Ranidae* indet. |  |  |  |  |  |  |  |  |  |
| *Pelodytes* sp. |  |  | 0.3918 |  |  |  |  |  |  |
| *Eopelobates* sp. | 0.3918 |  |  |  |  | 0.3918 |  |  |  |
| *Pelobates* sp. | 0.0917 |  | 0.0917 |  | 0.0917 | 0.0917 |  | 0.0917 | 0.0917 |
| *Pelobates* cf. *decheni* |  |  |  |  |  |  |  |  |  |
| *Diplocynodon* sp. |  | 1 |  |  |  |  | 1 |  | 1 |
| *Mauremys* sp./*sophiae* |  |  |  |  |  |  |  | 1 |  |
| Emydidae indet. |  |  |  |  |  | 1 |  |  | 1 |
| *Trionyx* sp. |  |  |  |  |  |  | 1 |  |  |
| *Chelydropsis* sp. |  |  |  |  |  |  |  |  |  |
| *Chelydropsis sansanensis* |  |  |  |  |  |  |  |  |  |
| *Clemmydopsis turnauensis* |  |  |  |  |  |  |  |  |  |
| aff. *Clemmydopsis* sp. |  |  |  | 0.3918 |  |  |  |  |  |
| *Ptychogaster sansaniensis* |  |  |  |  |  |  |  |  |  |
| *Ptychogaster batalleri* |  |  |  |  |  |  |  |  |  |
| *Ptychogaster* sp. | 0.3918 | 0.3918 | 0.3918 |  |  |  |  | 0.3918 |  |
| *Palaeotestudo canetotiana* |  |  |  |  |  |  |  |  |  |
| *Testudo rectangularis* |  |  |  |  |  |  |  |  |  |
| *Testudo* sp. | 0 | 0 | 0 |  | 0 | 0 | 0 |  |  |
| *Geochelone*/*Ergilemys* sp. | 0.513 | 0.513 |  |  |  |  |  |  |  |
| *Blanus* sp. |  |  |  | 0.0917 |  |  |  | 0.0917 |  |
| *Blanus antiquus* |  |  |  |  |  |  |  |  |  |
| *Palaeoblanus* nov. sp. |  |  |  |  |  |  |  |  |  |
| Amphisbaenidae indet. |  | 0.0917 | 0.0917 |  |  |  |  |  |  |
| Scolecophidia indet. |  | 0.0917 |  |  |  |  |  |  |  |

TABLE *1*—Continued.

| | Petersbuch 2 | Beon 1 | Erkertshofen 1 | Rembach | Forsthart | Eitensheim | Langenmoosen | Niederaichbach | ICH 3 |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| taxon | MN4a | MN4b | MN4b | MN4b | MN4b | MN5 | MN5 | MN5 | MN5 |
| *Albaneryx depereti* | | | | | | | | | |
| cf. *Albaneryx* sp. | | | | | | | | | |
| *Eoanilus* sp. | 0.0917 | | | | | | | | |
| *Chamaeleo* sp. | | | | 0.0917 | | | | 0.0917 | |
| *Chamaeleo bavaricus* | 0.0917 | | | | | | | | |
| *Chamaeleo caroliquarti* | 0.0917 | | 0.0917 | | | | | | |
| *Chamaeleo* cf. *sulcodentatus* | | | | | | | | | |
| Chamaeleonidae vel Agamidae | | | | | | 0.0917 | | | |
| Agamidae indet. | | | | | | | | | |
| Agamidae (aff. *Stellio*) | | | | | | | | | |
| Gekkonidae indet. | | 0 | | 0 | | | | | |
| *Edlartetia sansaniensis* | | | | | | | | | |
| *Lacerta* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Lacerta* sp. 2 | | 0 | | 0 | 0 | | | 0 | |
| *Lacerta* sp. 3 | | | | | | | | | |
| *Miolacerta* sp. | 0 | | | | | | | | |
| *Amblyolacerta* sp. | | | | | | | | | |
| Lacertidae indet. | | 0 | | | | | | | |
| aff. *Eumeces* sp. | | | 0 | | | | | | |
| *Tropidophorus bavaricus* | | | | | | | | | |
| *Bavariascincus mabuyaformis* | 0 | | | 0 | 0 | | | | |
| *Bavaricordylus molassicus* | | | | | | | | | |
| *Bavaricordylus ornatus* | 0 | | | | | | | | |
| Scincidae indet. | | | 0 | | | | | 0 | 0 |
| Scincidae indet. 2 | | | | | | | | | |
| Cordylidae indet. | 0 | | | | | | | | |
| Scincomorpha indet. | | | | | | | 0 | | |
| *Varanus* sp. | 0 | 0 | | | | | | | |
| ?*Iberovaranus* sp. | 0.513 | | | | | | | | |
| Varanidae indet. | | | | | | | | | |
| Anguidae indet. | 0 | | 0 | | | | | | 0 |
| Anguidae gen. indet. nov. sp. | | | | | | | | | |
| *Pseudopus laurillardi* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ophisaurus fejfari* | 0 | | | | | | | | |
| *Ophisaurus* cf. *spinari* | | | | | | | | | |
| *Ophisaurus* sp. 1 | | 0 | | 0 | | 0 | | 0 | |
| *Ophisaurus* sp. 2 | | | | | | | | | |
| mean index | 0.32761 | 0.24639 | 0.20826 | 0.06391 | 0.08639 | 0.31636 | 0.42966 | 0.20421 | 0.39894 |
| paleoprecipitation (in mm) | 751 | 556 | 465 | 118 | 172 | 724 | 997 | 455 | 923 |
| average error (in mm) | 253 | 252 | 252 | 259 | 258 | 252 | 257 | 253 | 255 |
| | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Station | | | | Aldersbach, Pfarrkirchen | Aldersbach, Eichendorf | Gaimersheim | Schrobenhausen, Pöttmes | Essenbach | Burgau |
| Niederschlag Station | | | | 824 | 786 | 656 | 766 | 715 | 826 |
| relative to recent | | | | 14 | 22 | 110 | 130 | 64 | 112 |

TABLE *1*—Extended.

| Schönenberg b. Jettingen | Walda 2 | PUT B | SAND unten | SAND oben | Burtenbach 1b + c | UA 565 m | GBZ1a (Brock) | Laimering 2 + 3 | Sansan | Kleineisenbach | Anwil |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
| MN5 | MN5 | MN5 | MN5 | MN5 | MN5 | MN5 | MN6 | MN6 | MN6 | MN7/8 | MN7/8 |
|  |  |  | 0.0917 |  |  |  |  |  | 0.0917 |  |  |
| 1 | 1 |  |  |  | 1 |  | 1 |  |  |  | 1 |
|  |  |  |  |  |  | 1 |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  | 0.9768 |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  | 0.3918 |  | 0.3918 |  | 0.3918 |  | 0.3918 | 0.3918 | 0.3918 |  |  |
|  | 0.3918 |  | 0.3918 | 0.3918 |  |  |  | 0.3918 | 0.3918 |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 0.3918 |  |  |  |  |  | 0.3918 | 0.3918 |  |  |  |  |
|  |  |  | 0.513 | 0.513 |  |  |  |  |  |  |  |
|  |  |  | 0.3918 | 0.3918 |  |  |  | 0.3918 |  | 0.3918 |  |
|  |  |  | 0.513 | 0.513 |  |  |  |  | 0.513 |  |  |
| 0.3918 |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  | 0.3918 |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
| 0.3918 | 0.3918 |  | 0.3918 | 0.3918 | 0.3918 | 0.3918 | 0.3918 | 0.3918 | 0.3918 |  | 0.3918 |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  | 0.3918 |  |  |  |  |  |  |  | 0.3918 |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  | 1 |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  | 1 |  | 1 |  |
|  |  |  | 0 |  |  |  | 0 | 0 |  |  |  |
|  |  |  | 0.3918 |  |  |  |  |  |  |  |  |
|  | 0.513 |  | 0.513 | 0.513 |  | 0.513 | 0.513 | 0.513 | 0.513 | 0.513 |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  | 0.513 |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  | 0.3918 |  |  |
| 0.3918 |  |  | 0.3918 | 0.3918 |  |  | 0.3918 | 0.3918 |  | 0.3918 |  |
|  | 0.0917 | 0.0917 | 0.0917 | 0.0917 |  |  | 0.0917 | 0.0917 | 0.0917 |  | 0.0917 |
|  |  |  |  |  | 0.0917 |  |  |  |  |  |  |
| 1 | 1 |  | 1 | 1 | 1 | 1 | 1 |  | 1 |  | 1 |
| 1 | 1 | 1 | 1 | 1 |  | 1 |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  | 1 |  |
| 1 | 1 |  | 1 | 1 | 1 | 1 | 1 |  |  |  | 1 |
|  | 1 |  |  |  |  |  | 1 |  |  |  |  |
|  |  |  |  |  |  |  |  |  | 1 |  |  |
| 0.3918 |  |  | 0.3918 | 0.3918 | 0.3918 |  |  |  | 0.3918 |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  | 0.3918 |  |  |
|  |  |  |  |  |  |  |  |  | 0.3918 |  |  |
|  | 0.3918 |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  | 0 |  |  |
|  |  |  | 0 | 0 |  |  |  |  |  |  |  |
| 0 | 0 | 0 |  |  | 0 | 0 | 0 | 0 |  |  |  |
| 0.513 | 0.513 |  | 0.513 |  |  | 0.513 | 0.513 |  |  |  |  |
|  |  |  |  |  |  |  |  |  | 0.0917 | 0.0917 |  |
|  |  |  |  |  |  |  |  | 0.0917 |  |  |  |
|  |  |  | 0.0917 |  |  |  |  |  |  |  |  |
|  |  | 0.0917 |  |  |  |  |  |  | 0.0917 |  |  |

TABLE *1*—Extended. Continued.

| Schönenberg b. Jettingen | Walda 2 | PUT B | SAND unten | SAND oben | Burtenbach 1b + c | UA 565 m | GBZ1a (Brock) | Laimering 2 + 3 | Sansan | Kleineisenbach | Anwil |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
| MN5 | MN5 | MN5 | MN5 | MN5 | MN5 | MN5 | MN6 | MN6 | MN6 | MN7/8 | MN7/8 |
|  |  |  |  |  |  |  |  |  | 0.0917 |  |  |
|  |  |  |  |  |  |  |  |  |  | 0.0917 |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  | 0.0917 |  |  |  | 0.0917 |  |  |  |  |  |
|  |  |  | 0.0917 |  |  |  |  | 0.0917 |  |  |  |
|  | 0.0917 |  | 0.0917 |  |  |  |  | 0.0917 |  |  |  |
|  |  |  |  |  |  |  |  | 0.0917 |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  | 0 |  |  | 0 |  |  |  |
|  |  |  |  |  |  |  |  | 0 |  |  |  |
|  |  |  |  |  |  |  |  |  | 0 | 0 |  |
|  |  |  | 0 |  |  |  |  |  | 0 | 0 |  |
| 0 |  |  | 0 | 0 |  | 0 | 0 | 0 | 0 | 0 | 0 |
|  |  |  | 0 |  |  |  | 0 |  | 0 | 0 |  |
|  |  |  | 0 |  |  |  |  |  |  |  |  |
|  |  |  | 0 |  |  |  |  | 0 |  | 0 | 0 |
|  | 0 |  |  |  |  |  |  |  | 0 |  |  |
|  |  |  |  |  | 0 |  |  | 0 |  |  |  |
|  |  |  |  |  |  |  | 0 |  |  |  |  |
|  |  |  | 0.3918 | 0.3918 |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  | 0 | 0 |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  | 0 | 0 |  | 0 | 0 | 0 | 0 | 0 |  |
|  |  |  | 0 | 0 |  |  |  |  | 0 |  |  |
|  |  |  | 0 |  |  |  |  |  |  |  |  |
| 0 |  | 0 |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  | 0 |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  | 0 |  |
|  | 0 |  |  |  |  |  |  |  |  | 0 |  |
|  |  |  | 0.0917 |  |  |  |  |  | 0.0917 |  |  |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  |  |  |  |  |  |  | 0 |  |  | 0 |  |
|  |  |  | 0 |  |  |  |  |  |  |  |  |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 |  | 0 | 0 |  | 0 |
|  |  |  | 0.0917 |  |  |  |  |  | 0.0917 |  |  |
| 0.43147 | 0.43203 | 0.16669 | 0.25693 | 0.36745 | 0.35559 | 0.42152 | 0.35184 | 0.17089 | 0.28958 | 0.21510 | 0.38706 |
| 1001 | 1002 | 365 | 582 | 847 | 819 | 977 | 810 | 375 | 660 | 481 | 894 |
| 257 | 257 | 254 | 252 | 254 | 253 | 256 | 253 | 253 | 252 | 252 | 255 |
| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Burgau | Pöttmes | Wolnzach, Rottenburg | Mainburg, interpoliert | Mainburg, interpoliert | Burgau | Illertissen | Augsburg NE | Dasing |  |  |  |
| 826 | 752 | 774 | 760 | 760 | 826 | 882 | 750 | 805 |  |  |  |
| 121 | 133 | 47 | 77 | 111 | 99 | 111 | 108 | 47 |  |  |  |
|  |  |  |  |  |  |  | Testudo v. Ziemetsh.1b<br>Trionyx, Chelydr. V. Derching |  |  |  |  |
|  |  |  |  | 52 | 50 |  |  |  |  |  |  |

TABLE 2—Data set of fossil amphibian and reptile species (from Böhme and Ilg, 2008) and paleoprecipitation estimates (according to Eq. 6 in Böhme et al., 2006) for 17 localities containing *Pseudopus pannonicus*. 1 – Hammerschmiede 1, 2 – Hammerschmiede 3, 3 – Richardhof-Golfplatz, 4 – Götzendorf, 5 – Buzhor 1, 6 – Kalfa, 7 – Suchomasty, 8 – Kohfidisch, 9 – Tardosbánya 3, 10 – Polgárdi 4, 11 – Polgárdi 2, 12 – Osztramos 1, 13 – Ivanovce, 14 – Weze 1, 15 – Weze 2, 16 – Rebielice Królewskie 1A, 17 – Deutsch-Altenburg 2C1.

| | Hammerschmiede 1 | Hammerschmiede 3 | Richardhof-Golfplatz | Götzendorf | Buzhor 1 | Kalfa | Suchomasty | Kohfidisch |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| taxon | MN9 | MN9 | MN9 | MN9 | MN9/10 | MN9/10 | MN10 | MN11 |
| *Andrias* sp. | 1 | | | | | | | |
| *Andrias scheuchzeri* | | | | 1 | | | | |
| aff. *Palaeoproteus* sp. | 1 | 1 | | | | | | |
| Batrachosauroidae indet. | | 1 | | | | | | |
| Urodela indet. | | 1 | | | | | | |
| *Mioproteus caucasicus* | | | 1 | 1 | 1 | | | 1 |
| *Mioproteus wezei* | | | | | | | | |
| *Mioproteus* aff. *wezei* | 1 | 1 | | | | | | |
| *Parahynobius kordosi* | | | | | | | | |
| *cf. Parahynobius sp.* | | | | | | | | |
| *Albanerpeton inexpectatum* | | | 0.0917 | | | | | |
| *Salamandra salamandra* | | | | | | | | |
| *Salamandra* cf. *sansaniensis* | | | | | | | 0.3918 | |
| *Mertensiella mera* | | | | | | | | |
| *Mertensiella ? caucasica* | | | | | | | | |
| *Chelotriton paradoxus* | 0.3918 | 0.3918 | | | | | | 0.3918 |
| *Chelotriton* sp. | | | | 0.3918 | | | 0.3918 | |
| *Triturus alpestris* | | | | | | | | |
| *Triturus vulgaris* | | | | | | | | 0.3918 |
| *Triturus cristatus* | | | | | | | | 0.3918 |
| *Triturus* sp. | | | 0.3918 | 0.3918 | | | | |
| *Triturus roersi* | 0.3918 | 0.3918 | | | | | | |
| *Triturus montadoni* | | | | | | | | |
| *Triturus* aff. *montadoni* | | 0.3918 | | | | | 0.3918 | |
| *Triturus ? marmoratus* | | | | | | | | |
| *Latonia gigantea* | 0.3918 | 0.3918 | 0.3918 | 0.3918 | | | 0.3918 | 0.3918 |
| *Latonia ? gigantea* | | | | | | | | |
| *Latonia ragei* | | | | | | | | 0.3918 |
| *Bombina* cf. *variegata* | | | | | | | 0.3918 | |
| *Bombina bombina* | | | | | | | | |
| *Bombina* cf. *bombina* | | | | | | | | 0.3918 |
| *Bombina* sp. | | | | | | | | |
| *Palaeobatrachus* sp. | | 1 | | 1 | | | | |
| *Pliobatrachus* cf. *langhae* | | | | | | | | |
| *Bufo* (cf.) *viridis* | | | | | | | | |
| *Bufo bufo* | | | | | | | 0.3918 | 0.3918 |
| *Bufo* sp. | | 0.3918 | | | 0.3918 | | | |
| *Hyla* sp. | 0.3918 | | | | | | | 0.3918 |
| *Hyla arborea* | | | | | | | | |
| *Hyla* cf. *arborea* | | | 0.3918 | | | | | |
| *Pelophylax* sp. | 0.513 | 0.513 | | 0.513 | | | | 0.513 |
| *Rana* s.l. sp. 1 | | | 0.513 | | 0.513 | | | |
| *Rana* s.l. sp. 2 | | | | | | | | |
| *Rana ? temporaria* | | | | | | | | |
| *Rana arvalis* | | | | | | | | |
| *Rana ? arvalis* | | | | | | | | |
| *Pelodytes* sp. | | | | | | | | |
| *Eopelobates* sp. | | 0.3918 | | | | | 0.3918 | |
| *? Eopelobates* sp. | | | | | | | | |
| *Pelobates* sp. | | | 0.0917 | | | | | |
| *Pelobates fuscus* | | | | | | | | |
| *Pelobates ? fuscus* | | | | | | | | |
| *Pelobates* cf. *cultripes* | | | | | | | | 0.0917 |
| *Pelobates* cf. *syriacus* | | | | | | | | |
| *Lazarussuchus* sp. | | 1 | | | | | | |
| *Mauremys gaudryi* | | | | | | | | 1 |
| *Sakya* sp. | | | | | 1 | | | |
| *Sarmatemys lungui* | | | | | 1 | | | |
| *Emys orbicularis* | | | | | | | | |
| *Trionyx* sp. | 1 | | | 1 | 1 | | | |
| *Chelydropsis* sp. | 1 | 1 | | 1 | 1 | | | |
| *Clemmydopsis* sp. | 0.3918 | 0.3918 | | | | | | |
| *Melanochelys mossoczyi* | | | | | | | | |
| *Melanochelys* sp. | | | | | 0.3918 | 0.3918 | | |
| *Ptychogaster (Temnoclemmys)* sp. | | | | | | | 0.3918 | |
| *Eurotestudo herrmanni* | | | | | | | | |
| *Eurotestudo globosa* | | | | | | | | |
| *Testudo* sp. | 0 | 0 | | 0 | | | 0 | |
| *Protestudo csakvarensis* | | | | | 0 | 0 | | 0 |
| Amphisbaenidae indet. | 0.0917 | | | | | | | |
| *Typhlops grivensis* | | | | | | | | 0.0917 |
| Gekkonidae indet. | | | | | | | | 0 |

TABLE *2*—Extended.

| Tardosbánya 3 | Polgárdi 4 | Polgárdi 2 | Osztramos 1 | Ivanovce | Weze 1 | Weze 2 | Rebielice Królewskie 1A | D.-Altenb. 2C1 |
|---|---|---|---|---|---|---|---|---|
| 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| MN12 | MN13 | MN13 | MN14a | MN15 | MN15 | MN15b/16a | MN16 | early Biharian |
| | | | | | | 1 | 1 | |
| | | | | | | | | |
| | 0.3918 | | | | | | | |
| 0.3918 | | | 0.3918 | | | | | |
| | | | | | | | | |
| | | | | 0.3918 | 0.3918 | | 0.3918 | |
| | | | | | | | | |
| | | | | 0.9768 | | | | |
| | | | | | | | 0.9768 | |
| | | | | | | | | |
| | | | | | | | | |
| | | | | 0.3918 | | | | |
| | | | | 0.3918 | | | | |
| | | | | 0.3918 | 0.3918 | | 0.3918 | |
| | | | | | | | | |
| | | | | | | | | |
| | | | | | | | 0.3918 | |
| | | | | | | | | |
| | | | | 0.513 | | | | |
| 0.3918 | 0.3918 | 0.3918 | 0.3918 | | | | | |
| | | | | 0.3918 | | | | |
| | | | | | | | | |
| | | | | | | | | |
| | | | | | | | 0.3918 | |
| | | | | | 0.3918 | | | |
| | | | 0.3918 | 0.3918 | | | | |
| | | | | | | 1 | | |
| | | | 1 | 1 | 1 | 1 | 1 | |
| 0 | 0 | 0 | 0 | | | | 0 | 0 |
| | | | 0.3918 | 0.3918 | 0.3918 | 0.3918 | 0.3918 | 0.3918 |
| | | | | | | | | |
| | 0.3918 | | | | | | | |
| | | | | 0.3918 | | | 0.3918 | |
| | | | | | | | | |
| 0.513 | 0.513 | 0.513 | | 0.513 | | 0.513 | | |
| | | | 0.513 | | | | | |
| | | | | 0.3918 | 0.3918 | 0.3918 | 0.3918 | |
| | | | | | | | 0.3918 | |
| | | | | | 0.3918 | | | |
| | | | | | | | 0.3918 | |
| | | | | | | | | 0.3918 |
| | | | 0.3918 | 0.3918 | 0.3918 | | | |
| | | | | | | | 0.3918 | |
| | | | | | 0.0917 | 0.0917 | | |
| 0.0917 | 0.0917 | | | | 0.0917 | 0.0917 | 0.0917 | 0.0917 |
| | | | | 0.0917 | | | | |
| | | | | | | | | |
| | | | | | | | 0.0917 | |
| | | | | | | | | |
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| | | | | | | | | |
| | | | | | | | | |
| | | | | | 1 | 1 | | |
| | | | | | | | | |
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| | | | | | | | | |
| | | | | | 0.3918 | | | |
| | | 0.3918 | | | | | | |
| | | | | | | | | |
| | | | | | 0 | | | |
| | | | | | | | | |
| | | | | | 0 | | | |
| 0 | | | 0 | | | | | |
| | 0 | 0 | | | | | | |
| | | | | | | | | |
| | | | | | | | | |
| | | | 0 | | | | | |

TABLE *2*—Continued.

| | Hammerschmiede 1 | Hammerschmiede 3 | Richardhof-Golfplatz | Götzendorf | Buzhor 1 | Kalfa | Suchomasty | Kohfidisch |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| taxon | MN9 | MN9 | MN9 | MN9 | MN9/10 | MN9/10 | MN10 | MN11 |
| *Edlartetia sansaniensis* | | | | | | | | 0 |
| *Lacerta* sp. | 0 | 0 | | 0 | | | | 0 |
| *Lacerta* sp. 2 | 0 | | | | | | | |
| *Lacerta viridis* | | | | | | | | 0 |
| *Lacerta* ? *viridis* | | | | | | | | |
| *Lacerta agilis* | | | | | | | | |
| *Lacerta vivipara* | | | | | | | | |
| *Podarcis praemuralis* | | | | | | | | |
| *Podarcis* ? muralis | | | | | | | | |
| *Podarcis* ? *sicula* | | | | | | | | |
| *Chalcides* sp. | 0 | | | | | | | |
| Scincidae indet. | | 0 | 0 | | | | | 0 |
| Scincomorpha indet. | | | | | | | 0 | |
| *Varanus hofmanni* | | | | | | 0 | | 0 |
| *Pseudopus pannonicus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pseudopus apodus* | | | | | | | | |
| *Ophisaurus* sp. | 0 | 0 | | | | | | |
| *Anguis fragilis* | | | | | | | | 0.0917 |
| mean index | 0.42021 | 0.51278 | 0.31909 | 0.55737 | 0.62966 | 0.09795 | 0.28495 | 0.26920 |
| paleoprecipitation (in mm) | 974 | 1196 | 731 | 1303 | 1477 | 200 | 649 | 611 |
| average error (in mm) | 256 | 263 | 252 | 267 | 276 | 257 | 252 | 252 |
| | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

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TABLE *2*—Continued Extended.

| Tardosbánya 3 | Polgárdi 4 | Polgárdi 2 | Osztramos 1 | Ivanovce | Weze 1 | Weze 2 | Rebielice Królewskie 1A | D.-Altenb. 2C1 |
|---|---|---|---|---|---|---|---|---|
| 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
| MN12 | MN13 | MN13 | MN14a | MN15 | MN15 | MN15b/16a | MN16 | early Biharian |
| 0 | 0 | 0 | 0 |  | 0 | 0 |  |  |
|  |  |  |  |  |  |  |  |  |
|  | 0 |  |  |  |  | 0 |  | 0 |
|  |  |  |  |  |  |  | 0 |  |
|  |  |  |  |  |  |  |  | 0 |
|  |  |  |  |  |  |  |  | 0 |
|  |  |  |  |  |  |  |  | 0 |
|  |  |  |  |  |  |  | 0 |  |
|  |  |  |  |  | 0 |  | 0 |  |
|  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  |  |  |  | 0 |  |  |  |  |
|  | 0 | 0 |  |  |  |  |  |  |
|  |  |  | 0.0917 | 0.0917 | 0.0917 | 0.0917 | 0.0917 |  |
| 0.17354 | 0.16183 | 0.16208 | 0.27413 | 0.39468 | 0.30053 | 0.42859 | 0.34142 | 0.09726 |
| 381 | 353 | 354 | 623 | 912 | 686 | 994 | 785 | 198 |
| 253 | 254 | 254 | 252 | 255 | 252 | 257 | 253 | 257 |
| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

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