

THAUMASTOSAURUS BOTTII DE STEFANO, 1903, AN ANURAN WITH GONDWANAN AFFINITIES FROM THE EOCENE OF EUROPE

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ABSTRACT—*Thaumastosaurus bottii* De Stefano, 1903 is an anuran from the phosphorites of Quercy (upper Eocene, SW France). It was originally described as a saurian reptile, on the basis of the posterior part of the skull. The type material was lost and the original description was insufficient. In the present paper, description of new material from the locality La Bouffie is given, which made it possible to define the genus as well as to designate the neotype and paratypes. Revision of its taxonomic assignment confirmed Rage's conclusion that it has Gondwanan affinities. The possible paleogeographic connections between Gondwana and Laurasia in the Eocene and pre-Eocene times are briefly summarized; the Late Cretaceous terrestrial route between North and South America appears as the most probable.

INTRODUCTION

In 1903, De Stefano erected the new genus *Thaumastosaurus* for a supposed saurian reptile found in the phosphorites of Quercy (Eocene of SW France). Nopcsa (1908) considered the similar name *Thaumattosaurus* v. Meyer, 1841 a homonym, and this is why he proposed the new name *Enigmatosaurus*. Hoffstetter (1945) correctly recognized that this animal is in fact an anuran, and Rage (1981) placed it in Ceratophryinae (Leptodactylidae). However, in accordance with the Article 56(b) of the International Code of Zoological Nomenclature (3rd edition), the names *Thaumastosaurus* and *Thaumattosaurus* are not homonyms and therefore the first name is valid and has the priority over *Enigmatosaurus*. The original material from the localities Caylux and Lamandine, which was, together with other material from the collection Rossignol (acquired in 1893 by the Muséum National d'Histoire Naturelle in Paris) described by De Stefano (prooticocooccipitals and posterior part of the frontoparietals; see De Stefano, 1903: pl. I, figs. 11, 15), was lost (Rage, 1981:76).

In the course of several years, one of us (P.L.) collected much new material from a site called La Bouffie (lower Ludian, upper Eocene; Crochet et al., 1981: 248) that makes it possible to describe the anatomical structure of this anuran in more detail. These specimens also include the same elements that De Stefano used to erect this taxon and allow us to designate a neotype to define the genus, and to revise its taxonomic position.

SYSTEMATIC PALEONTOLOGY

ANURA Giebel, 1845

LEPTODACTYLIDAE Werner, 1896

THAUMASTOSAURUS BOTTII De Stefano, 1903

Thaumastosaurus Bottii, De Stefano, 1903, p. 414, pl. 9, figs. 11 and 15.

Enigmatosaurus, Nopcsa, 1908, p. 39.

Thaumastosaurus (= *Enigmatosaurus*)—Nopcsa, 1926, p. 180.

Enigmatosaurus Bottii—Hoffstetter, 1945, p. 167.

Enigmatosaurus bottii—Crochet et al., 1981, tab. 2.

Holotype—Not explicitly stated; material on the basis of which this taxon was erected (see De Stefano, 1903: pl. 1, figs. 11 and 15) was lost (Rage, 1981:76).

Neotype—Prooticocooccipitals with coossified posterior part of the frontoparietals and parasphenoid, coll. No. LB 106, deposited in the Muséum d'Histoire Naturelle, Toulouse (Fig. 2).

Referred Material—Sphenethmoid with coossified nasals, LB 107 (Fig. 1); anterior part of the frontoparietals and posterolateral tip of the right nasal, coossified with the sphenethmoid, LB 105 (Fig. 3B, C); left frontoparietal with its posterior part broken off, and with the rest of the coossified sphenethmoid and prooticocooccipital, LB 101 (Fig. 3D, E); left maxilla with its anterior part broken off closely behind the processus frontalis, LB 32 (Fig. 4G); anterior part of the left maxilla, LB 39 (Fig. 4F); right squamosal with its ramus zygomaticus and processus posterolateralis broken off, LB 85 (Fig. 5B, C). All are deposited in the Muséum d'Histoire Naturelle, Toulouse, France.

Type Locality—Originally stated as Caylux or Lamandine, Quercy, SW France (De Stefano, 1903). It is not known to what contemporary site these names correspond (Rage, in litt.). Restricted here to La Bouffie, near the village Bach (Lot, SW France).

Type Horizon—See Type Locality. Restricted to MP 17, lower Ludian, upper Eocene.

Diagnosis—Dermal roofing bones heavily sculptured with pit-and-ridge sculpture; nasals and frontoparietals of the left and right side coossified in large individuals; frontoparietals and nasals in contact, sphenethmoid exposed even in large individuals; frontoparietals and nasals coossified with sphenethmoid and prooticocooccipitals in large individuals; frontopar-

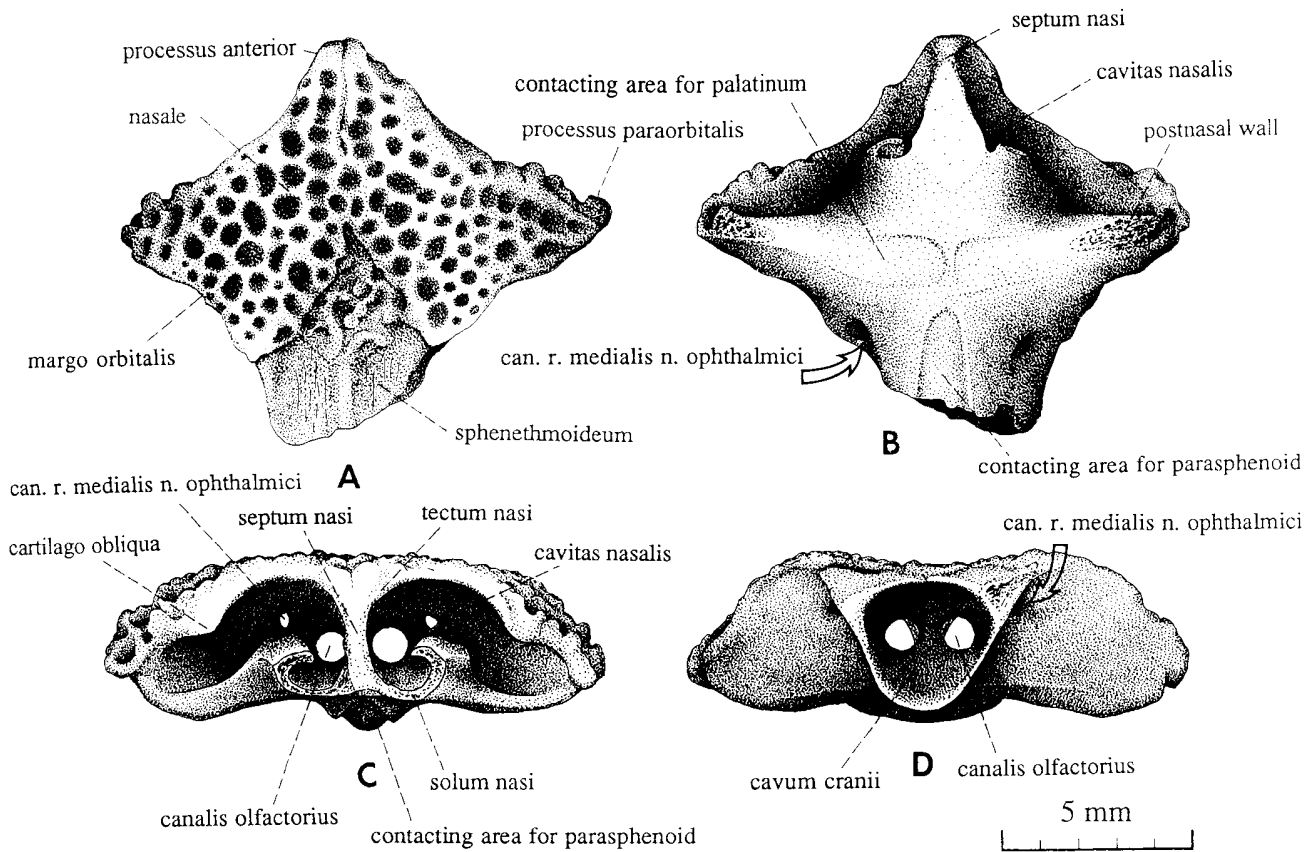


FIGURE 1. *Thaumastosaurus bottii* De Stefano, 1903. Sphenethmoid with coossified nasals. LB 107, Muséum d'Histoire Naturelle, Toulouse. A, dorsal view. B, ventral view. C, anterior view. D, posterior view.

ietal with deep vertical marginal cristae forming pars contacta; frontoparietal incrustation (sensu Jarošová and Roček, 1982) paired, its posterior part may be completely enclosed into ossified tectum synoticum; foramina pro arteriae occipitales present; frontoparietal not in contact with squamosal; spine on either side of posterior surface of prooticooccipital, medial to prominentiae ducti semicircularis posterior; the latter compressed laterally and confluent with processus paraoccipitales of frontoparietals; maxillae toothed, not fused with quadratojugals; palatines present, anterior tip of parasphenoid not extending between them.

Similar to *Eophractus* Schaeffer, 1949 from which it differs in (1) sculpture on maxilla reaching down to crista dentalis; (2) processus zygomaticomaxillaris weakly prominent; (3) different shape of anterolateral and orbital margins of nasals. Similar to *Caudiverbera* Laurenti, 1768 from which it differs in (1) robust pitted sculpture similar to that in *Eophractus* and some *Cyclorana* (however, such sculpture occurs in young individuals of *Caudiverbera*); (2) large orbits (squamoso-frontoparietal bridge absent); (3) nasals and frontoparietals of both sides fused with each other as early as in those developmental stages in which the dorsal

triangular area of the sphenethmoid is still uncovered by dermal bones; (4) anterior ramus of parasphenoid not extending between palatines; (5) frontal process of maxilla forming short contact with lateral ramus of nasal.

Similar to *Cyclorana* Steindacher, 1867 from which it differs in (1) greater extent of dermal bones (both nasals in median contact and fused in older individuals, in contact with frontoparietals); (2) frontoparietals heavily sculptured; (3) canalis pro arteria occipitalis developed. Also differs from the latter two genera in prominent spine between foramen arteriae occipitalis and dorsal margin of the occipital condyle on each side, and in having frontoparietals and nasals fused with sphenethmoid, and frontoparietals and parasphenoid fused with prooticooccipital. From *Baurubatrachus* Báez et Perí, 1989 it differs in lesser extent of dermal sculptured bones, i.e., in (1) narrow (if any) contact between nasal and processus frontalis maxillae; (2) absence of postorbital bridge; (3) small lamella alaris squamosi.

Description—Sphenethmoid (LB 107, Fig. 1A–D; LB 105, Fig. 3C). Most of its dorsal surface is covered by nasals. In LB 107, the nasals are synostotically fused

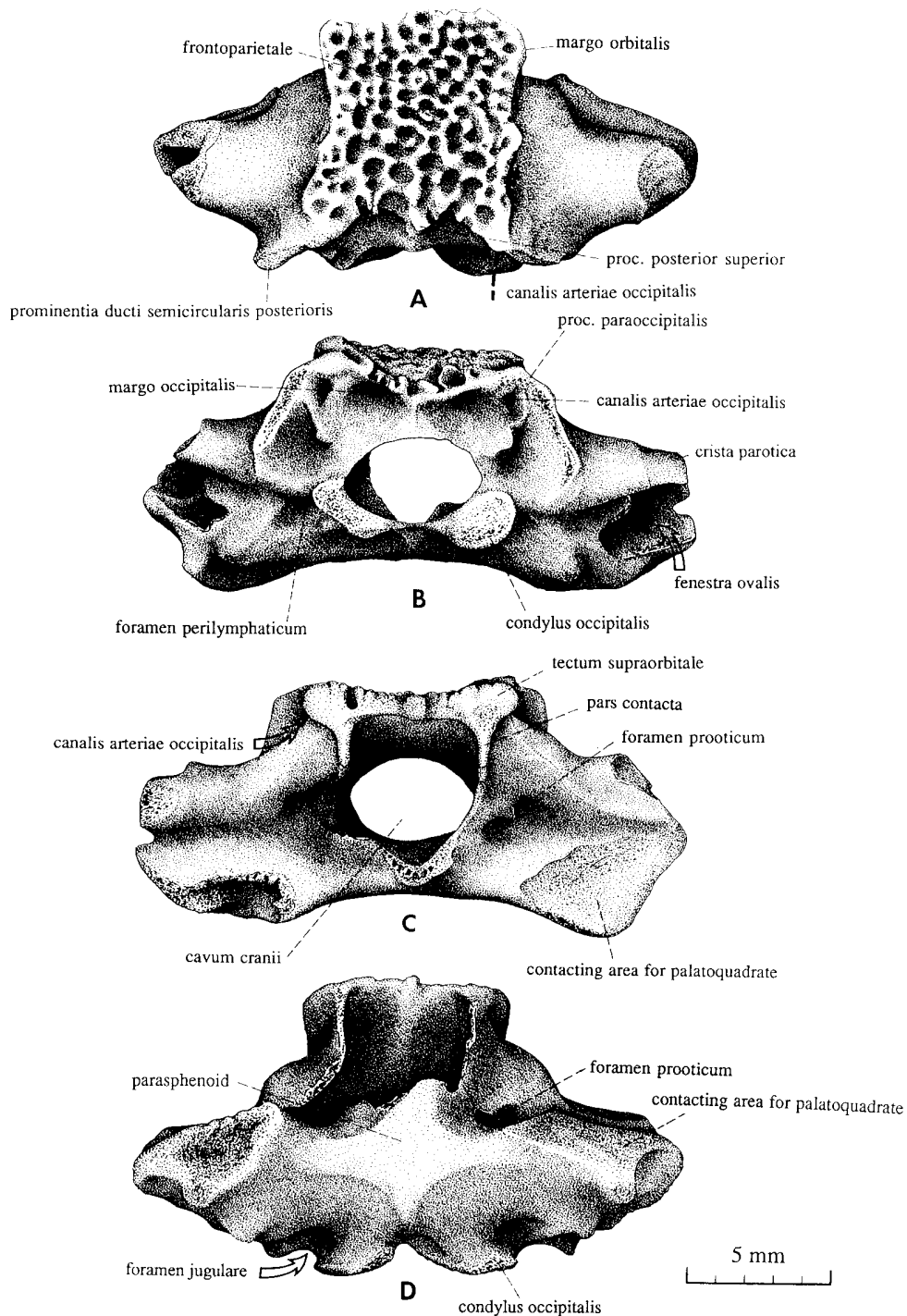


FIGURE 2. *Thaumastosaurus bottii* De Stefano, 1903, neotype. Prooticooccipitals with coossified frontoparietal and parasphenoid. LB 106, A, dorsal view. B, posterior view. C, anterior view. D, ventral view.

to it (in contrast to the frontoparietals and parasphenoid). The posterior part of the dorsal surface (contact area for the frontoparietals) is striated anteroposteriorly, with a low rounded ridge in the midline. In LB 105, which is slightly larger than LB 197, the fronto-

parietals (but not the parasphenoid) are also coossified with the sphenethmoid. Between the posteromedial margins of the nasals and anteromedial margins of the frontoparietals there is a clearly delimited rhomboid area with sculpture like that on the nasals but more

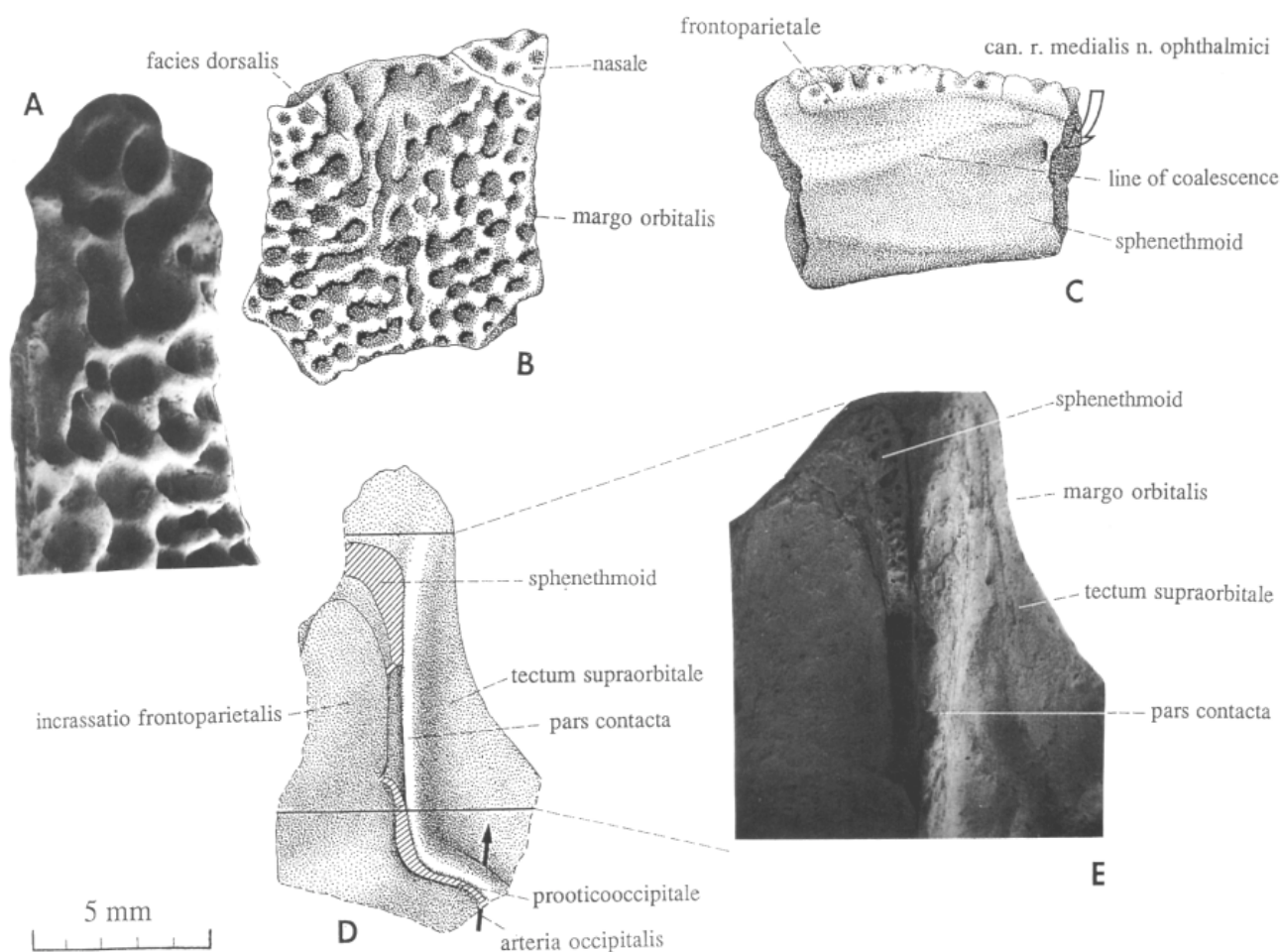


FIGURE 3. *Thaumastosaurus bottii* De Stefano, 1903. A, anterior part of right frontoparietal in dorsomedial view. LB 98. B, anterior part of frontoparietals coossified with posterior part of sphenethmoid in dorsal view. LB 105, paratype. C, same in lateral view. D, left frontoparietal in ventral view. LB 101, paratype. Broken surface of sphenethmoid and prooticooccipital hatched. E, part of the former. A and E slightly enlarged.

irregular. This is the exposed part of the sphenethmoid. In ventral view, imprints of dermal bones are noteworthy. That of the anterior section of the parasphenoid is rather deeply indented whereas those of the palatines are delimited by faint ridges. The palatines were neither fused with the vomers nor with maxillae (as can be judged from the structure of the latter elements), almost in contact in the midline, and the tip of the parasphenoid reaches posterior to them. The ossified septum nasi reaches the level of the anterior tips of both nasals. The lateral margin of the solum nasi is raised and turned medially. The ossified tectum nasi, if viewed from above, tapers anteriorly. The ossified cartilago obliqua is slender. Periosteum-free surface of the most lateral part of the bone (similar to that on the tip of the ossified septum nasi and anterior margin of the solum nasi) suggests that the lateral section of the postnasal wall was cartilaginous, as was the

septum nasi. However, this is not the case with the lamina supraorbitalis, which was poorly (if at all) developed.

Prooticooccipitals (LB 106; Fig. 2). Elements of both sides are fused with each other, which is well visible in the posterior view. The median surface dorsal to the foramen magnum is moderately thickened; there is a low and indistinct ridge running down from the posterior margin of the facies dorsalis of the frontoparietal. The prominentia ducti semicircularis posterioris on either side is compressed mediolaterally and is dorsally confluent with the processus paraoccipitalis. Underneath the orifice of the canalis arteriae occipitalis is a conspicuous spine, dividing a depression dorsolaterally adjacent to the foramen magnum into its superior and inferior parts. The foramen jugulare is partly overlapped by the lateral margin of the occipital condyle. The wall between this foramen and the otic capsule is

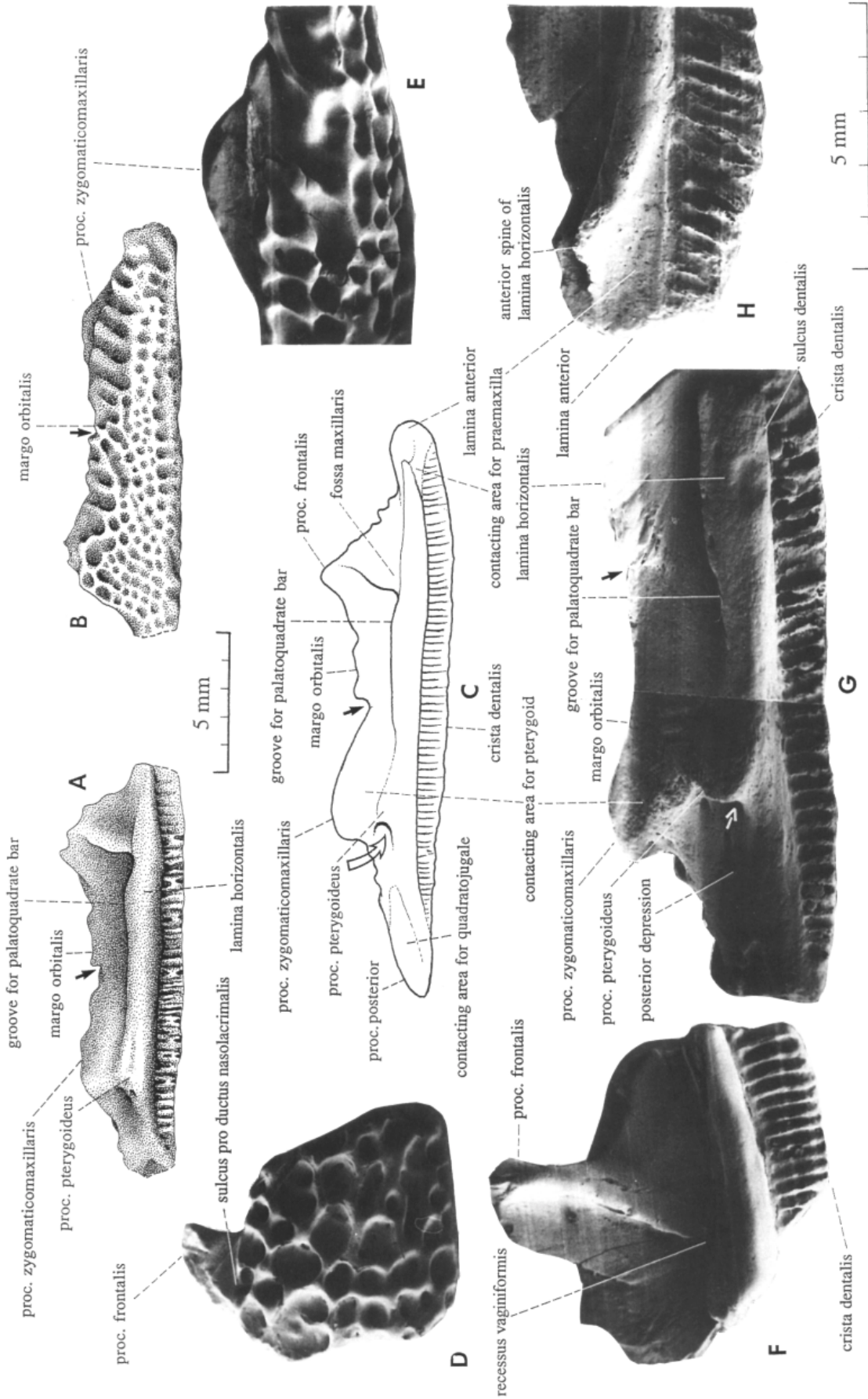


FIGURE 4. *Thaumastosaurus bottii* De Stefano, 1903. A, left maxilla in medial view with processus posterior and lamina anterior broken off. LB 33. B, same in lateral view. C, composite reconstruction of left maxilla in medial view. D, fragment of left maxilla with processus frontalis in lateral view. LB 6. E, fragment of left maxilla in dorsolateral view, with processus zygomaticomaxillaris. LB 10. F, fragment of left maxilla with processus frontalis in medial view. LB 39. G, posterior part of right maxilla in medial view. LB 32. H, anterior end of right maxilla in medial view. LB 29. Photographs slightly enlarged (see scales). Black arrows in A, B, C, G mark notch in orbital margin, open arrow in C and white arrow in G mark pit behind processus posterior.

pierced by a foramen which is subdivided by an incomplete partition into the anterior and posterior parts. Both are homologues of the foramina perilymphatica. In ventral view, there is a distinct rounded median keel running posteriorwards into the space between both condyles. Similar, but developed to a lesser degree, are ridges running laterally on the ventral surface of both otic capsules. These ridges, together with the central rhomboid elevation where they meet, form the posterior part of the parasphenoid which is coalesced with the ventral surface of the prooticooccipitals. In dorsal view, the crista parotica is widely rounded, and it was completed by cartilage extending anteroposteriorly to fit into the ramus paroticus squamosi (Fig. 5C). The most lateral part of the dorsal surface of the otic capsule is indented and delimited medially by a low ridge, which probably indicates the level reached by the margin of the ramus paroticus. The anterior surface of the otic capsule is divided by a broad horizontal groove into a robust ventral and a more delicate dorsal part. Laterally, the groove ends in an arch-like notch, whereas medially the groove ends in the foramen prooticum. The latter is entirely surrounded by bone and partly subdivided. The anterolateral surface of the lower part of the capsule is devoid of periost and served as a contact area for the palatoquadrate.

Nasals (LB 107; Fig. 1A). In this specimen, both nasals are fused together and only a trace of the median suture is observable in its anterior section. The anterolateral and posterolateral margins of the bone are moderately concave so that the processus paraorbitalis forms a tip similar to the processus anterior. The posteromedial margin of the bones probably varied with the animal's age; in LB 107, both margins diverged posteriorly towards the orbital margin. The dorsal surface of the bones is deeply pitted, and the pits paralleling the orbital and narial margins are smaller and shallower. In agreement with the general shape of the sphenethmoid, the processus paraorbitalis is deflected ventrally, as is the posteromedial part of the bone.

Frontoparietals (LB 92–107; Fig. 3). In large individuals, the frontoparietals are fused with one another (not in small individuals) as well as with the prooticooccipitals and sphenethmoid. The tectum supraorbitale is narrow anteriorly and becomes wider in the posterior part of the orbit. However, because it is narrow again in the posterior part of the bone (Fig. 2A) one may suppose that there was a lateral process at the level of the posterior margin of the orbit. The frontoparietal was not in contact with the lamella alaris squamosi by means of the postorbital bridge. The arteria occipitalis entered into the skull through a broad foramen medial to the processus paraoccipitalis (Fig. 2B). As there is no suture between the frontoparietal and the prooticooccipital preserved in specimen LB 106 one cannot decide whether the foramen is within the frontoparietal or between this bone and the prooticooccipital. After a short course through the bone, the canal opens above the posterior part of the otic capsule (Fig. 2A). The further course of this artery may

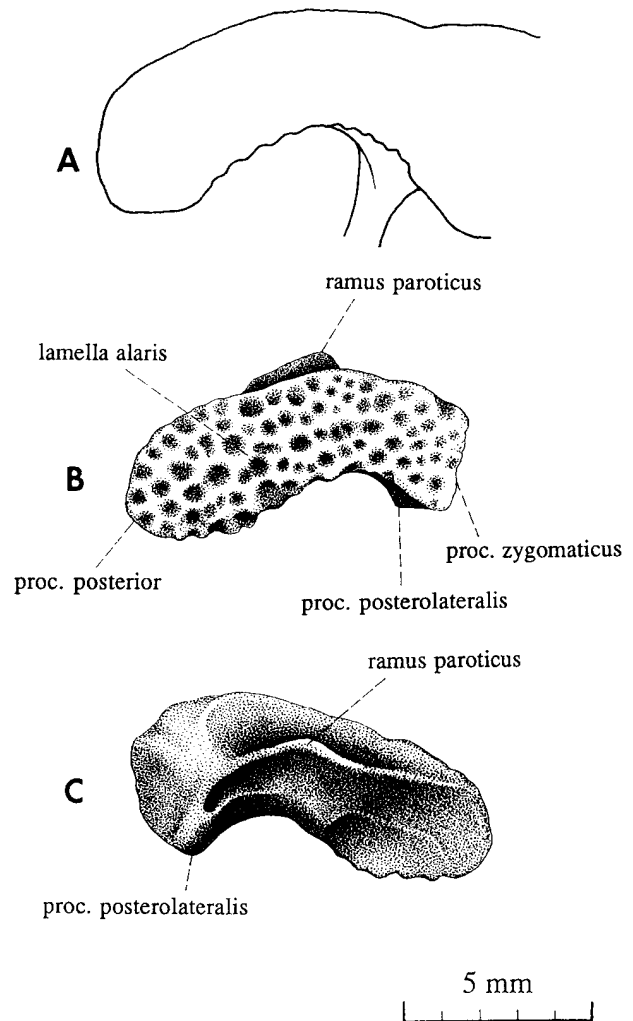


FIGURE 5. *Thaumastosaurus bottii* De Stefano, 1903. A, composite reconstruction of right squamosal in lateral view. B, posterior half of right lamella alaris squamosi in lateral view. LB 85. C, same specimen as B in medial view.

be traced through the lateral incisure (or possibly a foramen) into the laterally directed section of the pars contacta (Fig. 3D) through which this vessel passes into the orbit (as the arteria orbitonasalis). The facies dorsalis is heavily sculptured (as is the case with other dermal bones) and runs out posterolaterally onto the processus paraoccipitalis. These processes are confluent on each side with the mediolaterally compressed ridge, which represents the prominentia ducti semicircularis posterioris of the prooticooccipital (Fig. 2B). The posterior margin of the facies dorsalis runs out in a median pointed outgrowth that continues onto the posterior surface of the prooticooccipital as an indistinct ridge. The pars contacta is a prominent vertical lamina, which attaches the frontoparietal to the endoskeletal elements. In its anterior section it extends anteroposteriorly, and, at the level of the anterior wall

of the otic capsule, it abruptly turns laterally (Fig. 3D). Its lateral extent cannot be ascertained but it is pierced here by a foramen or notched for the arteria occipitalis (see above). Its course above the otic capsule cannot be traced but supposedly it follows its shape. The *incrassatio frontoparietalis* is paired and consists of the anterior and posterior parts, both of them being surrounded by the ossified endoskeletal roof of the braincase which is formed by the sphenethmoid and both prooticooccipitals (Fig. 3D, E).

Maxillae (LB 1–72; Fig. 4). In outer view, sculpturing extends ventrally to the crista dentalis. The processus zygomaticomaxillaris and frontalis are smooth and set off from the sculptured surface. In the medial view, the processus pterygoideus is represented only by the blunt posterior end of the lamina horizontalis. From this level, the lamina, though much narrower, continues posteriorly as a gradually fading rounded ridge that joins the crista dentalis. Its lower margin delimits the tooth row posteriorly. Thus the tooth row exceeds the level of the processus pterygoideus. The pterygoid process delimits laterally a deep and large pit facing posteriorly (marked by an open arrow in Figs. 4C, G). Several (mostly two) foramina may be found in its bottom and/or walls. The processus posterior was long and slender, with a clearly indented contact facet for the quadratojugal on its medial surface. The inner surface of the maxilla dorsal to the posterior section of the lamina horizontalis is flat, slanting down from the margin of the processus zygomaticomaxillaris. The sulcus for the palatoquadrate bar is poorly (if at all) developed here, contrary to the anterior half of the margo orbitalis where it is conspicuously deep. The depth of the sulcus is also emphasized by a low edge running out dorsally from the lamina horizontalis in this section (see Fig. 4G). The surface of the margo orbitalis (if observed from above) is in its posterior half facing slightly outside whereas inside in its anterior half. Both moieties are separated by somewhat deep incisure (marked by black arrow in Figs. 4A–C, G), which continues onto the outer surface of the bone where it merges with the pattern of sculpture. The section of the margo orbitalis posterior to the incisura and the flat inner surface is the contact facet for the pterygoid and lamella alaris squamosi. The sulcus for the palatoquadrate bar turns anterodorsally when reaching the recessus vaginiformis (for the processus maxillaris anterior palatoquadrati in extant animals; see Fig. 4F), and is overlapped by a crista that runs toward the tip of the processus frontalis. The fossa maxillaris is only slightly shallower compared to the part of the bone at the level of the recessus vaginiformis. The lamina horizontalis in its most anterior part is cut off obliquely from below, resulting in a dorsoventrally compressed spine (Fig. 4H). The upper margin of the tooth row splits from the lower margin of the lamina and joins the crista dentalis anterior to the level of the tip of the spine. The triangular area between the spine and the dorsal margin of the tooth row is the articular facet for the premaxilla. The upper margin of the bone within

the anterior moiety of the margo orbitalis, the proximal part of the processus posterior, and anterior to the processus frontalis may be highly irregular, in agreement with sculpture on its outer surface.

Squamosal (LB 73–91; Fig. 5). The lamella alaris is comparatively narrow in its posterior part, but wider anteriorly, as judged from the proximal part of the processus zygomaticus (its anterior part is broken off in all available specimens). The posterior process of the lamella alaris is broadly arch-like. The lamella alaris bears sculpturing over its entire outer surface. In most specimens, the sculpturing consists of pits and rounded ridges; however, in some cases it may be tubercular as well. There is a distinct but shallow notch in the dorsal margin of the lamella alaris. No evidence exists for a squamoso-parietal contact. The processus posterolateralis is slender at its base; its distal section is broken off in all specimens. The ramus paroticus consists of two more-or-less horizontal ridges, the course of which corresponds to the shape of the crista parotica of the prooticooccipital (see above). In specimen LB 86, the distal part of the crista parotica is broken off from the prooticooccipital and coalesced with the squamosal to such an extent that, if viewed from above, the suture between the two is not discernible. However, the deep and narrow recess in the anterior part of the ramus paroticus is empty, even in this specimen, which means that the anterior section of the crista parotica remained cartilaginous even in the largest (oldest) individuals, in contrast to the posterior section of the crista parotica, which was coossified with the squamosal.

Ossification sequence. The comparatively large number of elements apparently belonging to individuals of various size (and thus age) allows restoration of the ossification sequence in adults. Hyperostosis affects not only exocranial (dermal) elements but endocranial (endochondral) ones as well, and it is manifested also in the coossification of both. As all frontoparietals that are still paired and not yet coossified with the sphenethmoid are preserved only in their anterior section, one may suppose that the median fusion of both proceeded from the back toward the front (among disarticulated frontoparietals there was none that would include also the posterior part). Also, fusion of the frontoparietal with the prooticooccipital preceded that of the former with the sphenethmoid. This is evidenced in some specimens (Fig. 3D, E) in which the posterior part of the *incrassatio frontoparietalis* is entirely surrounded by the endocranial bone without a discernible line of coalescence, whereas the anterior part of the *incrassatio* is still separated from the sphenethmoid by a suture. In the smallest individuals the *incrassatio* is devoid of endocranial parts, indicating that the latter were still cartilaginous or ossified but in synchondrotical contact with the frontoparietal. At the stage when both frontoparietals were fused with one another even anteriorly (with no trace of a median suture) the line of coalescence between the frontoparietal and the sphenethmoid is hardly discernible (Fig.

3B, C). Also both nasals fuse with one another in an anteroposterior direction (Fig. 1A). At the stage when both nasals are still separated by a vestige of a median suture anteriorly, they are coossified with the sphenethmoid, which is largely ossified as well (e.g., the cartilago obliqua; see Fig. 1C). It is noteworthy that this ossification preceded fusion between the frontoparietals, parasphenoid, and palatines with the sphenethmoid. This is evidenced by free contact areas for these bones (Fig. 1A, B). In large individuals, the parasphenoid coossified with the floor of the prootic capsules and the crista parotica with the ramus paroticus squamosi. However, in smaller ones the crista was covered with cartilage, which was inserted into the ramus paroticus. The lateral walls of the braincase between the prooticocapitals and sphenethmoid probably remained cartilaginous, regardless of the degree of ossification of other elements. The maxilla obviously remained free from all adjacent elements.

Comparisons—*Thaumastosaurus* is similar to *Eophractus* in the type of sculpture, in the shape of nasals, and in the exposed area of the sphenethmoid. The difference is mainly in the extent of dermal bones (as can be judged from the deep maxilla, broad processus zygomaticomaxillaris and rather small orbit). In the type of sculpture, these Eocene forms are similar to very small subadults of *Caudiverbera*, and in sculpture and morphology of the posterior surface of skull also to adult *Cyclorana australis*, though these genera were placed in different subfamilies (Lynch, 1971) or even families (Frost, 1985). As is the case with *Eophractus*, differences between *Thaumastosaurus*, *Caudiverbera*, and *Cyclorana* are mainly in the extent and degree of dermal ossification. Similarities between *Thaumastosaurus* and Ceratophryinae, as suggested by Rage (1981), occur mainly in the extent of dermal bones and the degree of hyperostosis (for instance, in *Thaumastosaurus* the frontoparietal-squamosal contact is not developed and the quadratojugal is not fused to maxilla). Similar to "*Estesius*" (described by Báez, 1991) in overall skull structure, it differs in lesser degree of dermal ossification and in lacking dermal ornamentation. Thus, the close similarity of *Thaumastosaurus* to *Eophractus*, *Caudiverbera*, and *Cyclorana* indicates that it has some relations to the Leptodactylidae (regardless of the discussions that are associated with the taxonomy of this group). It is noteworthy that these relationships are not based only on characters associated with hyperostosis but also on the structure of the posterior surface of the prooticocapital that reflects the pattern of the cervical muscles.

The only known specimen of *Eorubeta* Hecht, 1960, a supposed leptodactylid from the lower Eocene of North America, is too crushed to make any contribution to the taxonomic analysis (see also Lynch, 1971).

The early Eocene and Oligo-Miocene leptodactylids from Queensland, Australia (Tyler, 1989, 1991; Tyler and Godthelp, 1993; Tyler, Hand and Ward, 1990) are based on the ilia that do not allow any comparisons with *Thaumastosaurus*.

Geographic Occurrence—La Bouffie (this paper); Perrière, Sainte-Néboule, Coânac 1, Escamps, Rosières 2, Sindou D, perhaps also Aubrelong 2 and Malperie (Quercy, France; Crochet et al., 1981: 250; Rage, 1984:table 1). La Débruge, given by Rage (1984:table 1) seemingly as a locality for this taxon is, according to Rage (in litt.), used only as a reference locality of the standard level MP 19 and should not be placed among geographic occurrences of this anuran. It is not inconceivable that Eocene finds of *Eopelobates*, if they were identified only on the basis of pitted sculpture, may belong to *Thaumastosaurus*. The Eocene anurans from the Geiseltal and Messel, Germany, should be revised with this possibility in mind.

Stratigraphic Occurrence—Upper Eocene-Marinesian through upper Ludian (Crochet et al., 1981: 248). This span perhaps could be extended after a revision of Eocene specimens of *Eopelobates* (see above).

Concerning the pre-Eocene history of the leptodactylids, one may suppose that some leptodactylid or pre-leptodactylid stock was widely distributed in Gondwana during the Jurassic through Paleogene interval. If we take into account the paleogeographic history of Indian subcontinent then *Indobatrachus*, provided that it is really a leptodactylid, may be taken as evidence supporting this hypothesis. During the Eocene, members of the Leptodactylidae were distributed from southernmost South America, as suggested by *Eophractus casamayorensis* Schaeffer, 1949, through the Caribbean region (documented by *Eleutherodactylus*; Poinar and Cannatella, 1987) to North America (probably *Eorubeta* and another early Eocene frog; Hecht, 1960), Australia where they were represented by *Lechriodus* (Tyler and Godthelp, 1993), to India (*Indobatrachus*; Owen, 1847) and to Europe (*Thaumastosaurus*). Late Cretaceous and Paleocene finds of leptodactylids, namely *Baurubatrachus pricei* (Báez and Perí, 1989), unidentified leptodactylids from the Los Alamitos Formation, Patagonia (Bonaparte, 1986; Báez, 1987; Gayet et al., 1991), "*Estesius*" *boliviensis* from Tiupampa, Bolivia (material mentioned by de Muizon et al., 1983; described under the preoccupied generic name by Báez, 1991), and unidentified leptodactylids from Itaborai, eastern Brazil (Estes and Reig, 1973) and Laguna Umayo, Peru (Sigé, 1968) represent the earliest fossil records of the Leptodactylidae and suggest that these frogs took their origin in Gondwana. The European forms probably invaded Laurasia via a land connection between North and South America during the Late Cretaceous, similar to other vertebrates such as snakes, birds, and marsupials (Rage, 1978, 1981, 1986, 1988a, b; Buffeteaut and Rage, 1982). This connection could have been re-established temporarily in the late Paleocene, as documented by faunal interchange (Gingerich, 1985; Gayet et al., 1992). Only later, in the early Eocene, Europe became separated from North America by the Atlantic Ocean. An alternative route, South America–Africa–Europe, was suggested by Mourer-Chauviré (1981) and accepted, though with some doubts, by Gayet et al. (1992: 785). For some

reason, neither of these possible routes were used by pipids that reached the Middle East (Nevo, 1968; Estes et al., 1978), despite some local interchanges between Africa and Europe that took place during the Cretaceous-Eocene interval (Gheerbrant, 1987; Rage, 1988b). Asian leptodactylids arrived via the Indian subcontinent that joined Laurasia during the Late Cretaceous or early Paleocene (Prasad and Rage, 1991; Klootwijk et al., 1992). It is difficult to explain why they did not extend beyond Indian subcontinent, into Asia. Until now there was no evidence that leptodactylids in Europe survived the Eocene/Oligocene boundary (unlike Discoglossidae, Palaeobatrachidae, and Pelobatidae).

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