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A new species of Metoposaurus from the Late Triassic of Portugal and comments on the systematics and biogeography of metoposaurid temnospondyls

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ARTICLE

A NEW SPECIES OF *METOPOSAURUS* FROM THE LATE TRIASSIC OF PORTUGAL AND COMMENTS ON THE SYSTEMATICS AND BIOGEOGRAPHY OF METOPOSAURID TEMNOSPONDYLS

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ABSTRACT—Metoposaurids are a group of temnospondyl amphibians that filled crocodile-like predatory niches in fluvial and lacustrine environments during the Late Triassic. Metoposaurids are common in the Upper Triassic sediments of North Africa, Europe, India, and North America, but many questions about their systematics and phylogeny remain unresolved. We here erect *Metoposaurus algarvensis*, sp. nov., the first *Metoposaurus* species from the Iberian Peninsula, based on several new specimens from a Late Triassic bonebed in Algarve, southern Portugal. We describe the cranial and pectoral anatomy of *M. algarvensis* and compare it with other metoposaurids (particularly other specimens of *Metoposaurus* from Germany and Poland). We provide a revised diagnosis and species-level taxonomy for the genus *Metoposaurus*, which is currently represented with certainty by three European species (*M. diagnosticus, M. krasiejowensis, M. algarvensis*). We also identify cranial characters that differentiate these three species, and may have phylogenetic significance. These include features of the braincase and mandible, which indicate that metoposaurid skulls are more variable than previously thought. The new Portuguese bonebed provides further evidence that metoposaurids congregated in fluvial and lacustrine settings across their geographic range and often succumbed to mass death events. We provide an updated paleogeographic map depicting all known metoposaurid occurrences, which shows that these temnospondyls were globally distributed in low latitudes during the Late Triassic and had a similar, but not identical, paleogeographic range as phytosaurs.

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INTRODUCTION

The Late Triassic (Carnian–Rhaetian, ca. 237–201 million years ago) was a formative phase in the evolution of 'modern' terrestrial ecosystems dominated by familiar clades such as mammals, lizards, turtles, and archosaurs (e.g., Sues and Fraser, 2010). By this time, ecosystems had largely stabilized after the unprecedented devastation of the end-Permian extinction (e.g., Chen and Benton, 2012) and soon-to-be dominant groups such as dinosaurs were experiencing their initial radiations (e.g., Brusatte et al., 2010; Langer et al., 2010; Sidor et al., 2013). Although faunas were clearly 'modernizing' during the Late Triassic, some 'archaic' groups of amphibians, reptiles, and synapsids remained diverse and abundant, with some undergoing their final bursts of evolutionary radiation before being ravaged by another mass extinction at the end of the Triassic. Among the most prominent of these groups is the Metoposauridae, a clade of temnospondyl amphibians that were globally distributed in low paleolatitudes during the Late Triassic (particularly during the early Carnian–middle Norian), achieved mid- to large size (1.25–3 m body length), and filled crocodile-like predatory niches in lacustrine and fluvial environments (e.g., Hunt, 1993; Schoch and Milner, 2000).

Metoposaurids are some of the most common and characteristic non-marine vertebrates from the Late Triassic, and their distinctly ornamented skulls, spool-shaped vertebrae, and atrophied limb elements are found at numerous sites in Africa (e.g., Dutuit, 1976), Europe (e.g., Meyer, 1842; Fraas, 1913; Kuhn, 1933; Sulej, 2002, 2007; Milner and Schoch, 2004), India (e.g., Chowdhury, 1965; Sengupta, 1992), and North America (e.g., Case, 1931; Sawin, 1945; Romer, 1947; Colbert and Imbrie, 1956; Hunt, 1993; Long and Murry, 1995). Metoposaurid specimens from the Germanic Basin of Europe were some of the first temnospondyls to be described, and in the 150+ years since these original materials were studied hundreds of new specimens from Germany and Poland have helped shed light on the paleoecology (Bodzioch and Kowal-Linka, 2012), intraspecific and ontogenetic variation (Sulej, 2007), bone histology (Konietzko-Meier and Klein, 2013), and growth (Sulej, 2007; Konietzko-Meier and Klein, 2013) of extinct amphibians. Despite these advances in understanding metoposaurid biology, however, many fundamental questions about metoposaurid systematics and phylogeny remain unresolved (e.g., Hunt, 1993; Schoch and Milner, 2000; Sulej, 2002, 2007). Perhaps most

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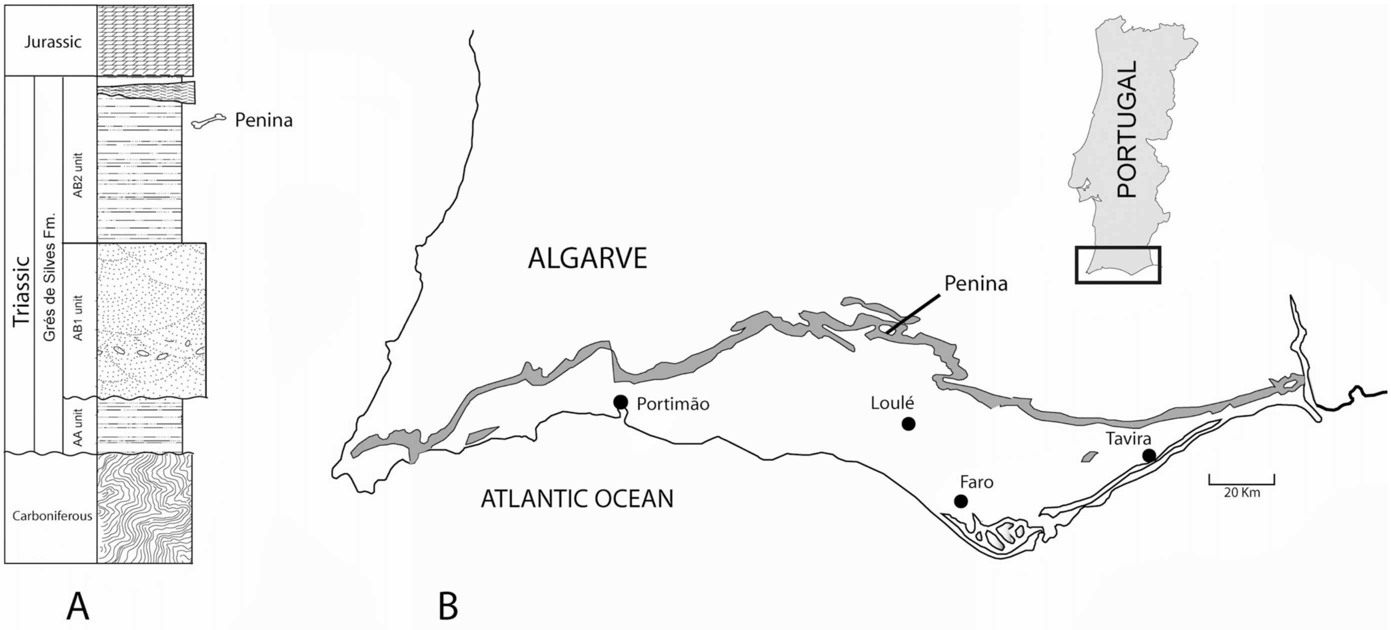

FIGURE 1. **A**, regional stratigraphic section of the Triassic sedimentary rocks of southern Portugal; **B**, location map of the Algarve Basin of southern Portugal, with the Triassic exposures shaded gray.

problematic, there is still no consensus on the alpha-level taxonomy of the group, largely because numerous species have been named over the past century and a half, often based on fragmentary material and without a detailed understanding of intraspecific variation.

We here describe new well-preserved specimens of the metoposaurid genus *Metoposaurus* from the Late Triassic of Portugal (Fig. 1), which provide new information on the anatomy, variation, and systematics of European metoposaurids. Although common in Central Europe, metoposaurids (and other temnospondyls) have previously been reported from the Iberian Peninsula based only on fragmentary material (Russell and Russell, 1977; Laurin and Soler-Gijón, 2001; Knoll et al., 2004). The new specimens come from a monodominant bonebed in the Algarve region of southern Portugal, near a site where a German geology student, Thomas Schröter, collected isolated and fragmentary temnospondyl specimens in the late 1970s–early 1980s as part of his undergraduate thesis research (Schröter, 1981). These specimens were subsequently accessioned into the collections of the Freie Universität (Berlin), and later the Museum für Naturkunde (Berlin) (F. Witzmann, pers. comm.), and described by Witzmann and Gassner (2008), who identified some of the fossils as pertaining to metoposaurids. Our team relocated the in situ bonebed in 2009 and began excavations the following year, and to date we have excavated several skulls and blocks of disarticulated postcranial material, which has been prepared at the Museu da Lourinhã (Steyer et al., 2011).

In this paper, we describe the cranial and pectoral anatomy of the new specimens, compare them with other metoposaurids (especially the German and Polish material), and provide evidence that the Portuguese specimens represent a new species of *Metoposaurus*. Based on our revision of the European metoposaurid record, we provide a revised diagnosis of the genus *Metoposaurus* and identify several cranial characters that differentiate the Portuguese, German, and Polish species. Along with the recent work of Sulej (2002, 2007), the new data help clarify the alpha-level systematics of European metoposaurids and provide a step toward the development of a stable taxonomy for metoposaurids, which is crucial to including these taxa in future cladistic analyses. We also comment on the biogeographic distribution of metoposaurids, provide an updated paleogeographic map denoting all known metoposaurid occurrences, and discuss how the Portuguese specimens lend further credence to the widespread distribution of these amphibians in fluvial and lacustrine environments in low paleolatitudes during the Late Triassic.

Institutional Abbreviations—**FCT-UNL**, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Caparica, Portugal; **NHMUK**, Natural History Museum, London, U.K.; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

SYSTEMATIC PALEONTOLOGY

TEMNOSPONDYLI Zittel, 1888, sensu Schoch, 2013
STEREOSPONDYLI Zittel, 1888, sensu Yates and Warren, 2000
METOPOSAURIDAE Watson, 1919

Comments—Although the family-level clade Metoposauridae is well defined by multiple characters (such as a very short preorbital region, enlarged nares, a greatly enlarged quadrate foramen, and a very broad and flattened cultriform process of the parasphenoid; see Hunt, 1993; Schoch and Milner, 2000; Sulej, 2007), numerous species have been erected on the basis of poorly preserved material, leaving open questions about the number of valid species, the diagnostic qualities of holotype specimens, and the referral of individual species to well-diagnosed taxa (e.g., Hunt, 1989, 1993; Long and Murry, 1995; Schoch and Milner, 2000; Sulej, 2002, 2007; Spielmann and Lucas, 2012). A systematic and phylogenetic revision of Metoposauridae is therefore needed, but given the large amount of material of different ontogenetic stages from Triassic sites across the globe, such a revision requires a specimen-level analysis that is outside of the scope of this paper. This is especially true of the North American metoposaurids, which are usually classified as members of the genera *Koskinonodon* (= *Buettneria*; see Mueller, 2007) and

Apachesaurus. In this paper, we do not comment on the systematics of the North American specimens and do not refer to individual species when making comparisons between these specimens and European taxa, unless we are referring to specific comparisons made by previous authors.

METOPOSAURUS Lydekker, 1890
(Figs. 2–12)

Type Species—*Metoposaurus diagnosticus* (Meyer, 1842).

Diagnosis—(Modified from Schoch and Milner, 2000; Sulej, 2002, 2007; Milner and Schoch, 2004.) Metoposaurid temnospondyls with the following combination of characters: lacrimal forms part of the orbital margin (also present in *Koskinonodon perfecta*); opisthotic unossified; and interclavicle with a small region of hexagonal pits at its center, the mediolateral width of which is less than half of the total width of the interclavicle.

Content—The genus *Metoposaurus* is commonly held to include two species (or subspecies, see below) from the late Carnian–middle Norian of Europe: *M. diagnosticus* from Germany (Meyer, 1842; Fraas, 1889; Schoch and Milner, 2000; Sulej, 2002, 2007; Milner and Schoch, 2004) and *M. krasiejowensis* from Poland and Germany (Sulej, 2002, 2007; Milner and Schoch, 2004). To these we add the new species from Portugal described here. *M. santaecrucis* from the Triassic of the Alps is of disputed validity and may not be a metoposaurid (e.g., Koken, 1913; Hunt, 1993; Schoch and Milner, 2000). A putative species from the Carnian–early Norian of India, '*M.*' *maleriensis* Chowdhury, 1965, has also been assigned to the metoposaurid genus *Buettneria* (= *Koskinonodon*) (Hunt, 1993; Schoch and Milner 2000; Sengupta, 2002). Because we did not observe the Indian specimens firsthand, we do not make any comments on the systematic position of this species relative to the European *Metoposaurus* species, although we note that the interclavicular sculpture appears to be consistent with referral to *Buettneria*/*Koskinonodon* (Sengupta, 2002). Some authors (Hunt, 1993; Long and Murry, 1995; Schoch and Milner, 2000) have considered a North American Carnian species to be referable to *Metoposaurus*, '*M.*' *bakeri* (Case, 1931), but this has more recently been considered a species of *Buettneria* (= *Koskinonodon*) (Sulej, 2007). Furthermore, one putative species of *Metoposaurus* ('*M.*' *ouazzoui* Dutuit, 1976) from the Carnian of Morocco has been placed in its own genus, *Dutuitosaurus* Hunt, 1993, whereas another ('*M.*' *azerouali*) is considered a nomen dubium (Hunt, 1993).

In this paper, our concept of *Metoposaurus* is therefore that of a clade including the three recently reassessed European species *M. diagnosticus, M. krasiejowensis*, and the new Portuguese species described here. The potential inclusion of *M. santaecrucis* within this clade requires further work. Our diagnosis of *Metoposaurus* reflects this concept, because we follow other recent authors (e.g., Sulej, 2002, 2007; Milner and Schoch, 2004) in recognizing a distinct combination of features that, based on present knowledge, are shared by the European taxa exclusive of other metoposaurids. We hypothesize that this combination of features diagnoses a *Metoposaurus* clade, but this remains to be tested by future cladistic analyses, which are outside of the scope of this work, and which must await alpha-level taxonomic revisions of the North American, Moroccan, and Indian specimens.

Remarks—The above diagnosis is a differential diagnosis that includes one character that is seen in *Metoposaurus* and a small number of additional taxa (the lacrimal character) and two autapomorphies of *Metoposaurus* (the opisthotic and interclavicle characters), following Sulej (2002) and Milner and Schoch (2004). Sulej (2007:128) diagnosed *Metoposaurus* relative to other metoposaurids based on the following: "the interclavicle with relatively long posterior part and small 'centre' of sculpture consisting of isometric pits; the glenoid of scapula directed posterolaterally; the braincase weakly ossified; the humerus, scapula, and fibula relatively slender." Of the bones mentioned in this diagnosis, only the interclavicle and braincase are present among the Portuguese specimens described here. We therefore do not comment on characters of Sulej (2007) relating to the scapula, humerus, and fibula. These are not included in our diagnosis here, but this is only because we have not critically reassessed these features or compared them among a range of metoposaurid specimens, and not because we necessarily disagree with them.

Interclavicle Characters—The Portuguese specimens are similar to the Polish and German ones in possessing a small region of hexagonal, isometric pits on the ventral surface of the interclavicle. The remainder of the ornamented portion of the ventral interclavicle is formed by pronounced ridges and grooves. This differs from the condition in the North American *Koskinonodon* and *Apachesaurus*, which have a proportionally larger area of hexagonal pits and a smaller area of grooves and ridges (e.g., Sulej, 2002). Sulej (2002:fig. 6) quantified this difference: in the North American taxa, the region of hexagonal pits is wider than half of the mediolateral width of the ventral surface of the interclavicle, whereas in the European *Metoposaurus* specimens it is considerably less than half of the total width of the bone. The difference between small and large pitted regions has long been recognized as a diagnostic distinction between the North American genera and the European *Metoposaurus* species (Colbert and Imbrie, 1956; Long and Murry, 1995; Sulej, 2002, 2007; Milner and Schoch, 2004). We agree that this is a legitimate difference between the European and North American metoposaurids, but note that this feature has not been well studied in metoposaurids from Africa (e.g., *Dutuitosaurus*) and India (but see above). We therefore provisionally recognize the small region of hexagonal pits as a diagnostic feature of *Metoposaurus*, but note that detailed study of other taxa is required to confirm its diagnostic condition.

However, we do not agree with Sulej (2007) that there is a clear difference in the length of the posterior process of the interclavicle that distinguishes *Metoposaurus* from other metoposaurids. Sulej's (2007:128) diagnosis considered *Metoposaurus* as having an interclavicle with a "relatively long posterior part," but we have two issues with this interpretation. First, Sulej (2007:90) recognized that his data set of interclavicle proportional measurements (including the length of posterior process and width of the bone in several specimens) is "too limited to conduct (a) statistical analysis." In the absence of a quantitative analysis on the whole interclavicle, it is indeed unclear whether specimens of *Metoposaurus* have significant differences in proportions from other metoposaurids.

Second, the interpretation that *Metoposaurus* has a proportionally long interclavicle posterior process cannot easily be rectified with the numerical measurements presented in Sulej (2007: fig. 42), which is a plot of posterior process length ("Di") against the width of the ornamented region ("Si," which is essentially the width of the interclavicle). This plot shows that the German and Polish *Metoposaurus* species have a proportionally shorter Di relative to Si than *Dutuitosaurus*, not a proportionally longer Di. Additionally, many data points for *Koskinonodon* on the Di vs. Si plot overlap those for German and Polish *Metoposaurus* specimens. We do not see in this scatter plot clear evidence of European *Metoposaurus* having a proportionally longer posterior process than in other metoposaurids or, in fact, any clear difference separating the proportions of the posterior process in all European *Metoposaurus* relative to other metoposaurids. Therefore, and pending statistical analyses based on larger data sets, we do not find strong evidence for significant size differences of the posterior process of the interclavicle among metoposaurids.

Taxonomic Note—Sulej (2002, 2007) considered the German and Polish *Metoposaurus* taxa to represent different subspecies of *M. diagnosticus*: *M. diagnosticus diagnosticus* and *M.*

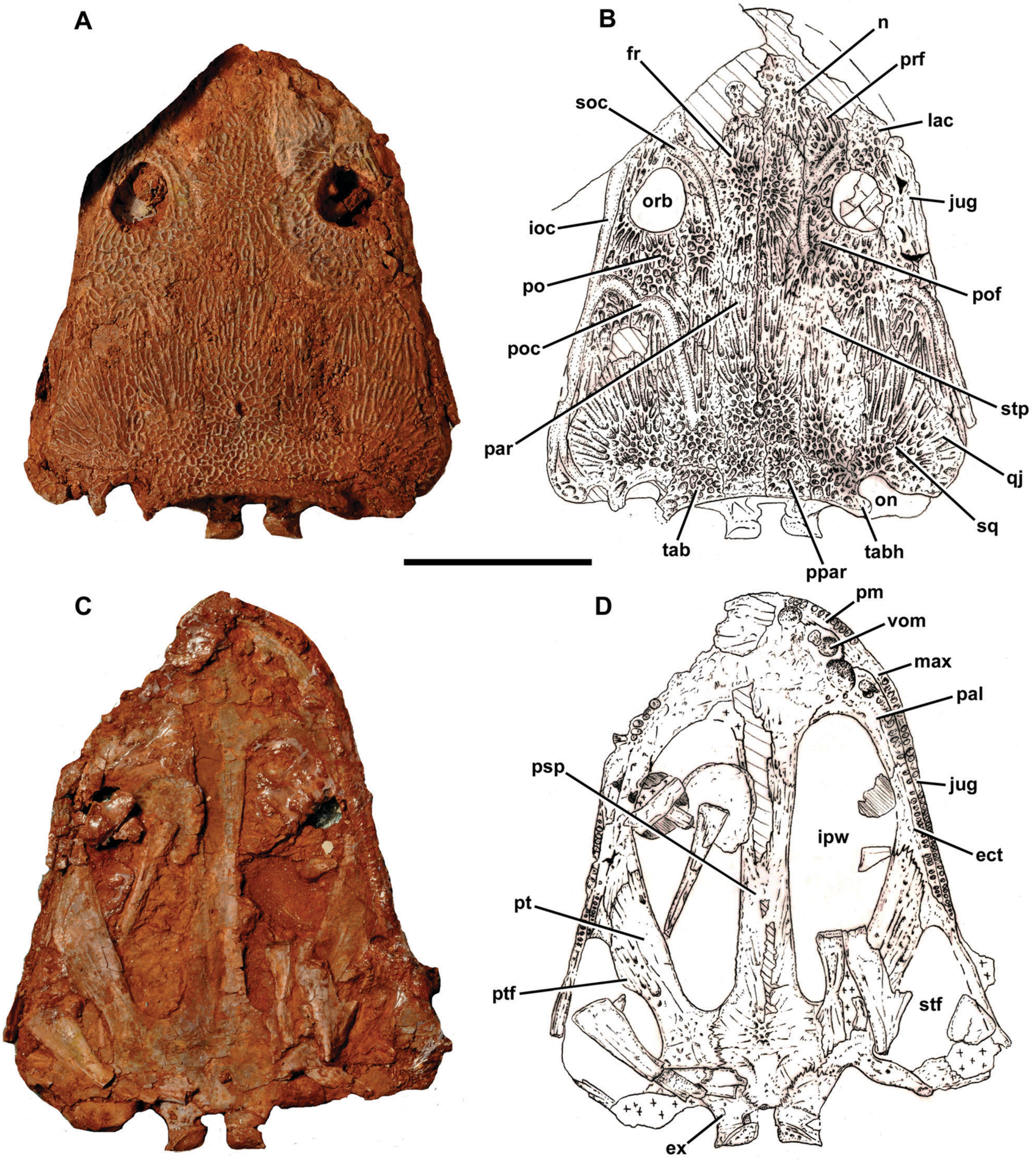

FIGURE 2. Holotype skull of *Metoposaurus algarvensis* from the Late Triassic of Portugal (FCT-UNL 600). **A**, photograph in dorsal view; **B**, drawing in dorsal view; **C**, photograph in ventral view; **D**, drawing in ventral view. **Abbreviations**: **ect**, ectopterygoid; **ex**, exoccipital; **fr**, frontal; **jug**, jugal; **ioc**, infraorbital canal; **ipw**, interpterygoid window; **lac**, lacrimal; **max**, maxilla; **n**, nasal; **on**, otic notch; **orb**, orbit; **pal**, palatine; **par**, parietal; **pm**, premaxilla; **po**, postorbital; **poc**, postorbital canal; **pof**, postfrontal; **ppar**, postparietal; **prf**, prefrontal; **psp**, parasphenoid; **pt**, pterygoid; **ptf**, pterygoid flange; **qj**, quadratojugal; **soc**, supraorbital canal; **sq**, squamosal; **stf**, subtemporal fenestra; **stp**, supratemporal; **tab**, tabular; **tabh**, tabular horn; **vom**, vomer. Scale bar equals 10 cm.

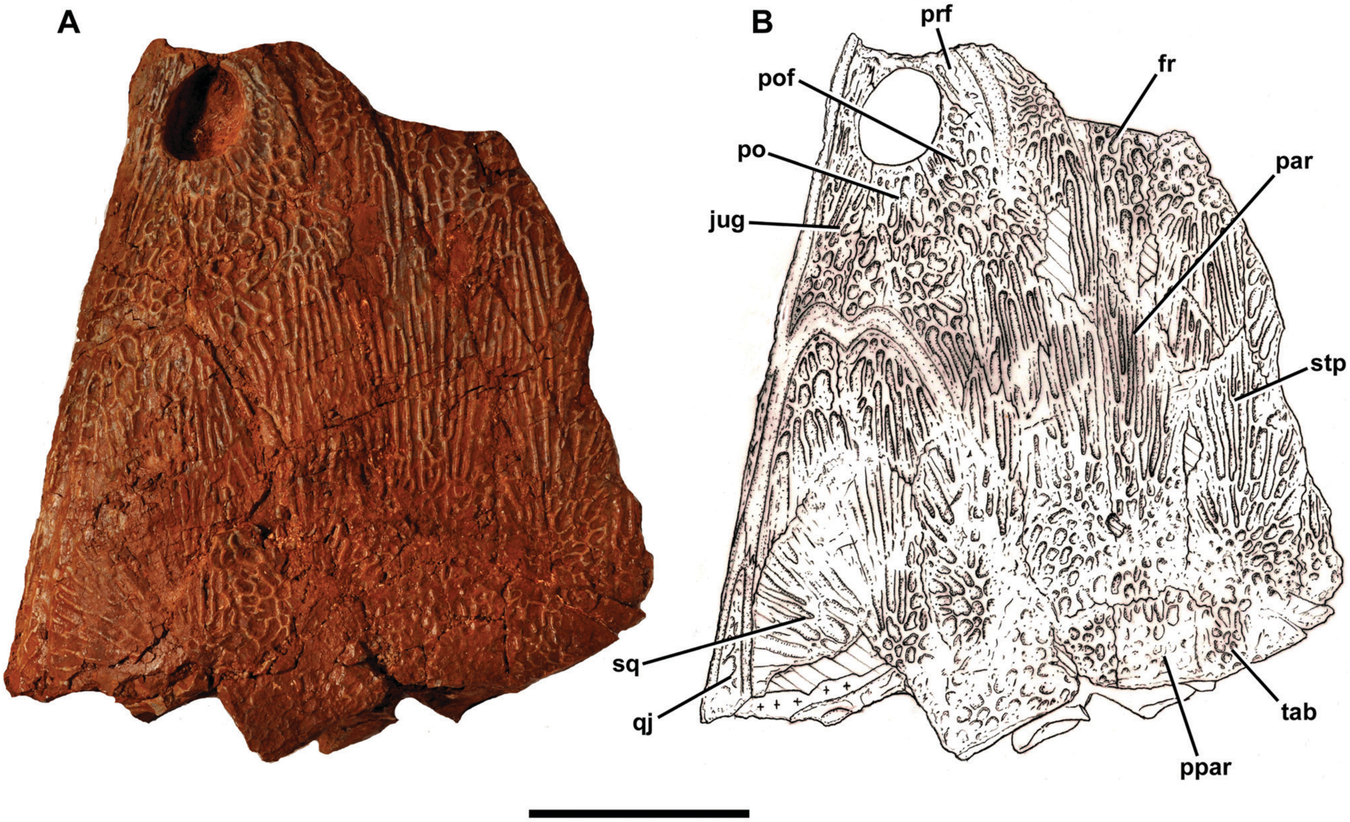

FIGURE 3. Skull of *Metoposaurus algarvensis* from the Late Triassic of Portugal (FCT-UNL 601). **A**, photograph in dorsal view; **B**, drawing in dorsal view. **Abbreviations**: **fr**, frontal; **jug**, jugal; **par**, parietal; **po**, postorbital; **pof**, postfrontal; **ppar**, postparietal; **qj**, quadratojugal; **sq**, squamosal; **stp**, supratemporal; **tab**, tabular. Scale bar equals 10 cm.

diagnosticus krasiejowensis, respectively. Because these two taxa are diagnostic relative to each other, both are distinct from the Portuguese *Metoposaurus* taxon described here, and because subspecies are rarely used in the vertebrate paleontology literature and are often erected in a stratophenetic context (see Steyer, 2000), we here refer to the German and Polish taxa as their own separate species, *M. diagnosticus* (Meyer, 1842) and *M. krasiejowensis* (Sulej, 2002), respectively. Note that Sulej (2002) and Milner and Schoch (2004) also described specimens from Germany as belonging to *M. krasiejowensis*.

METOPOSAURUS ALGARVENSIS, sp. nov.
(Figs. 2–12)

Holotype—FCT-UNL 600 (field number P-C5-11A), nearly complete skull preserving the occiput and part of the palate but lacking the anterior tip of the skull (Figs. 2, 3). The skull has a maximum anteroposterior length of approximately 270 mm, with a postorbital length of 150 mm, occipital mediolateral width of 240 mm, and width across the orbits of 175 mm. Even if the skull is not fully adult, it has been chosen as holotype because it is the best-preserved and most complete skull of our sample and is morphologically indistinguishable from other skulls referred to the species.

Referred Material—FCT-UNL 601 (field number P-C5-11B), a partial but larger skull preserved together with the holotype, and preserving part of the occiput and palate (Figs. 2, 4). The anterior and right portions of the skull are missing. The skull is estimated at approximately 450 mm in length (assuming similar proportions to those of the holotype) and is at least 290 mm wide at its posterior margin. FCT-UNL 604, a fragment of the left side of the anterior end of a skull, preserving the anterior portion of the snout and the circumnarial region (Fig. 4). FCT-UNL 605 (field number P-C6-2), the posterior portion of a large skull (Fig. 5). FCT-UNL 606 (field number P-D6-4), a relatively complete skull. FCT-UNL 607 (field number P-D7-2), the occipital region of a large skull (Fig. 6). FCT-UNL 608 (field number P-D7-5), a fragment of the palatal region of a left skull, including portions of the maxilla and jugal on the dorsal surface (Fig. 7). FCT-UNL 609 (field number P-B3-9), a well-preserved and relatively complete left mandible missing the posterior region (including the glenoid) (Fig. 8). FCT-UNL 610 (field number P-X2), the symphyseal region of a right dentary (Fig. 9). FCT-UNL 611 (field number P-A3-25), left clavicle and associated interclavicle (Fig. 10). FCT-UNL 612 (field number P-D7-8), a partial right clavicle (Fig. 10). FCT-UNL 613 (field number P-C6-5), a block of associated interclavicles. Field numbers are given here because they correspond to a numbering system that denotes the location of each specimen within the bonebed (bonebed map held on file at Museu da Lourinhã and available upon request).

Locality and Horizon—All specimens were found associated in a multi-individual, monodominant bonebed, which we refer to as the Penina Bonebed. The Penina Bonebed, which occurs in a 30–40-cm-thick mudstone unit, is located at the Penina locality, in the Municipality of Loulé, in the Algarve Region of southern Portugal (Fig. 1). The bonebed is located in the upper part of the Grés de Silves Formation (or Group), a thick sedimentary succession within the Algarve Basin, a deformed, extensional basin associated with the rifting of Pangea during the Late Triassic–Early Jurassic (Terrinha et al., 2002).

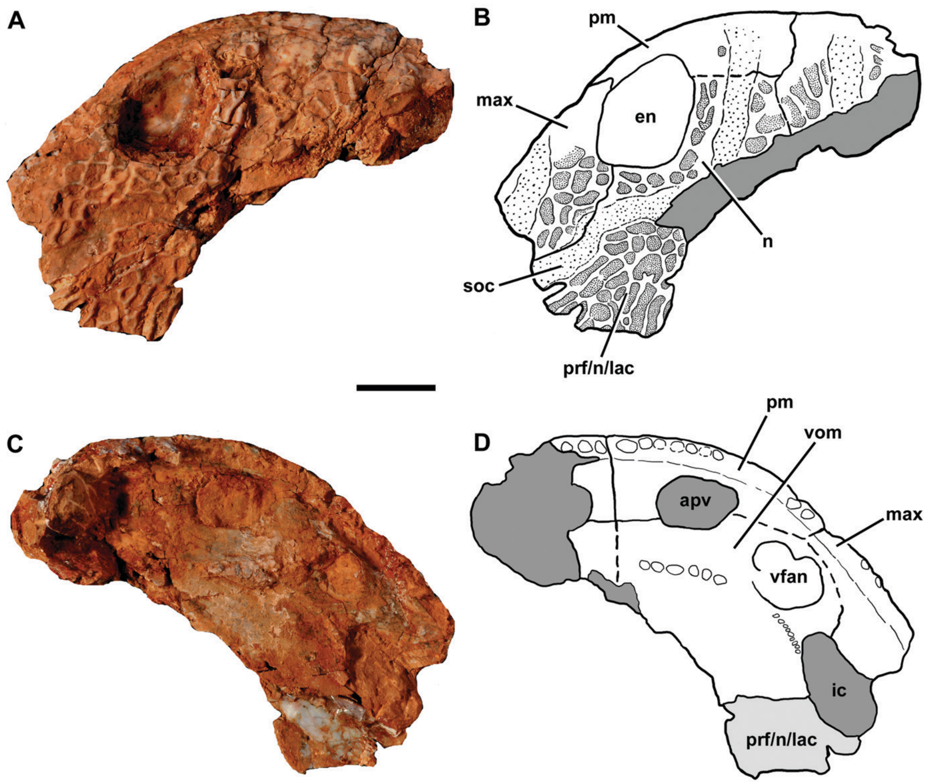

FIGURE 4. Anterior region of the snout of *Metoposaurus algarvensis* from the Late Triassic of Portugal (FCT-UNL 604). **A**, photograph in dorsal view; **B**, line drawing in dorsal view; **C**, photograph in ventral view; **D**, line drawing in ventral view. **Abbreviations**: **apv**, anterior palatal vacuity; **en**, external naris; **ic**, internal choana; **lac**, lacrimal; **max**, maxilla; **n**, nasal; **pm**, premaxilla; **prf**, prefrontal; **soc**, supraorbital canal; **vfan**, vomer fang; **vom**, vomer. Scale bar equals 2 cm.

We relocated the Penina Bonebed, originally identified by Schröter (1981), in 2009. The Bonebed represents the “western locality” of Witzmann and Gassner (2008). All specimens described here were excavated during field seasons in 2010 and 2011. Work is ongoing at the Penina Bonebed, and to date we have excavated ~3–4 m^2 of material. Remains of temnospondyls constitute more than 95% of the macroscropic vertebrate remains in the bonebed, but it is currently not clear if all temnospondyl fossils (especially isolated postcranial elements) belong to one or multiple taxa. Rare archosauromorph and potential sarcopterygian remains have been discovered in the bonebed and a phytosaur mandible was discovered 2.7 m stratigraphically above and about 5 m lateral to the *Metoposaurus* bonebed, in the same sedimentary sequence (Mateus et al., 2014).

The Penina Bonebed is located in the part of the Grés de Silves Formation termed ‘AB2’ (Fig. 1) and previously considered to be Rhaetian–Hettangian (latest Triassic–earliest Jurassic) in age (Palain, 1979; see also Witzmann and Gassner, 2008). The bonebed is most likely older than Jurassic, however, because it is located considerably below Central Atlantic Magmatic Province (CAMP) basalts in local section. The Portuguese CAMP basalts have been radioisotopically dated at 198.1 Ma, which would place the basalts in the earliest Jurassic (Sinemurian) (Nomade et al., 2007; Verati et al., 2007). However, these dates need to be corrected for decay constant bias and are likely to be a few million years older. In any event, the Portuguese basalts are likely somewhat younger than many other radioisotopically dated CAMP sections in North America and North Africa (Blackburn et al., 2013). A more precise Triassic age determination of the bonebed is not currently possible, because the stratigraphy and geochronology of the Grés de Silves Formation have only been studied in cursory detail. Our research group is currently revising the geology of the formation (Kasprak et al., 2010), and we recently tentatively proposed, based on vertebrate biostratigraphy, that at least part of the ‘AB2’ unit (i.e., that containing the Penina Bonebed) is likely to be late Carnian–Norian in age (Mateus et al., 2014). The bonebed preserves fossils of *Metoposaurus*, and a possible basal phytosaur was recovered at a nearly identical stratigraphic level. Both of these taxa are characteristic of late Carnian–middle Norian sedimentary units at many sites across the globe (e.g., Dutuit, 1977; Dzik, 2001), although metoposaurids and phytosaurs are both known to range later in the Triassic (e.g., Hunt, 1993; Long and Murry, 1995; Parker and Martz, 2011). Future work on isotopic and cyclostratigraphy should help better correlate the Portuguese units to other CAMP sections and thus better constrain the age of the bonebed.

Etymology—‘From Algarve’ (Latin), the region in southern Portugal where all the specimens described here came from.

Diagnosis—*Metoposaurus*, which possesses the following autapomorphies within the genus (which are absent in the Polish *M. krasiejowensis* and the German *M. diagnosticus;* with asterisks denoting features that cannot be assessed in *M. diagnosticus* due to poor preservation or unknown elements): large foramen on the midpoint of the occipital (posterior) surface of the occipital pillar of the braincase (Fig. 6); two accessory foramina along the lateral edge of the occipital pillar of the braincase* (Fig. 6); small posttemporal and paraquadrate foramina on the posterior surface of the occiput*; and dorsal and ventral portions of the subdivided foramen magnum that are essentially equal in dorsoventral depth (Fig. 6). The following additional autapomorphies are preserved on the associated specimens only: mandible maintaining a relatively constant dorsoventral depth at its anterior end* (Fig. 8); mandible with a concave ventral margin at its anterior end* (Fig. 8); labial parapet of the mandible extending considerably further dorsally than the lingual parapet* (Fig. 8); presence of two accessory foramina above the anterior Meckelian window on the medial (lingual) surface of the mandible* (Fig. 8); and

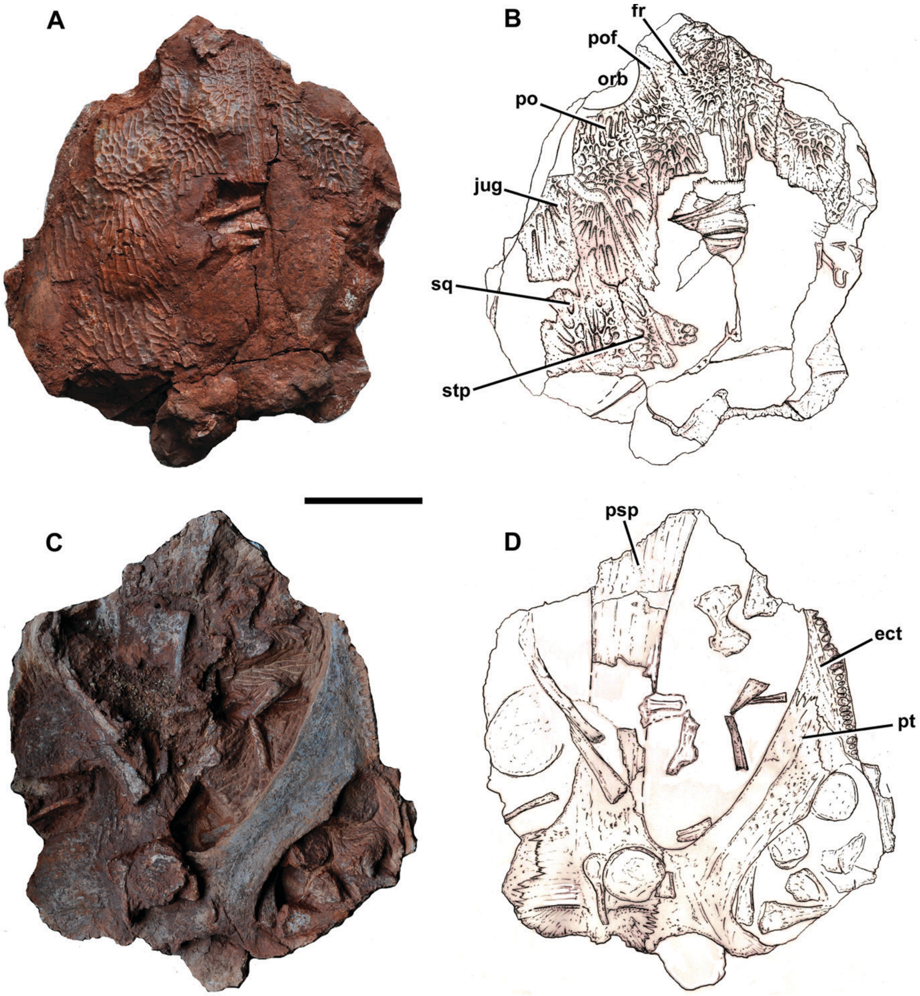

FIGURE 5. Skull of *Metoposaurus algarvensis* from the Late Triassic of Portugal (FCT-UNL 605). **A**, photograph in dorsal view; **B**, drawing in dorsal view; **C**, photograph in ventral view; **D**, drawing in ventral view. **Abbreviations: ect**, ectopterygoid; **fr**, frontal; **jug**, jugal; **orb**, orbit; **po**, postorbital; **pof**, postfrontal; **psp**, parasphenoid; **pt**, pterygoid; **sq**, squamosal; **stp**, supratemporal. Scale bar equals 10 cm.

rounded anterior extremity of the ornamented region of the interclavicle* (Fig. 10).

Comments—In addition to the autapomorphies described above, *M. algarvensis* can be distinguished from *M. krasiejowensis* in a number of features (see illustrations in Sulej, 2007). In dorsal view, the quadratojugal of *M. algarvensis* has a straight lateral margin that smoothly merges with the jugal, whereas that of *M. krasiejowensis* has a strongly convex lateral margin that is offset from the straight lateral margin of the jugal anteriorly (Figs. 3, 12). The postorbital canal of *M. algarvensis* has a pronounced 'W'-shaped kink along its anterior margin, where it traverses the postorbital, whereas this portion of the canal is smoothly convex anteriorly or is marked by only a very minor kink in *M. krasiejowensis*. Additionally, the Portuguese specimens have a smaller angle between the left and right parietal-supratemporal sutures (10–15°) than the Polish specimens (20–30°).

The occipital surfaces of the Polish and Portuguese taxa differ in several details. All observable Portuguese specimens lack the "marked pit" (Sulej, 2007:37) on the occipital surface of the postparietal immediately above the foramen magnum, which is described by Sulej (2007) as characteristic of *M. krasiejowensis*. The Polish specimens also possess much larger posttemporal and paraquadrate foramina than do all known Portuguese specimens. Furthermore, the Portuguese taxon exhibits a large foramen beneath the posttemporal foramen, as well as two small foramina along the lateral edge of the occipital pillar of the braincase, but these are absent in the Polish specimens. In the latter specimens, the dorsal portion of the subdivided foramen magnum is subtriangular and much shallower dorsoventrally than the ventral portion, unlike the condition in the Portuguese specimens in which the two portions of the foramen magnum are approximately equal in depth and the dorsal portion is rectangular. The occipital condyles are shaped like mediolaterally elongate ovals, which are widely spaced on the midline, in the Portuguese specimens (Fig. 6). In the Polish taxon, however, the condyles are larger, more spherical, and placed closer together on the midline.

There are also noticeable differences between the Polish and Portuguese *Metoposaurus* species in the mandible. The mandible tapers in depth and has a straight ventral margin anteriorly in *M. krasiejowensis*, whereas it maintains a relatively constant depth anteriorly and has a concave ventral margin in *M. algarvensis*. In medial view, the labial parapet extends much higher than the lingual parapet in the Portuguese taxon but terminates relatively lower in the Polish material. Finally, two accessory foramina are located above the anterior Meckelian window on the medial surface of the maxilla in the Portuguese taxon, but these are absent in *M. krasiejowensis*.

In addition to the autapomorphies described above, *M. algarvensis* can be distinguished from *M. diagnosticus* by a handful of features. First, *M. diagnosticus* lacks the large foramen ventral to the posttemporal foramen that is seen in the Portuguese taxon.

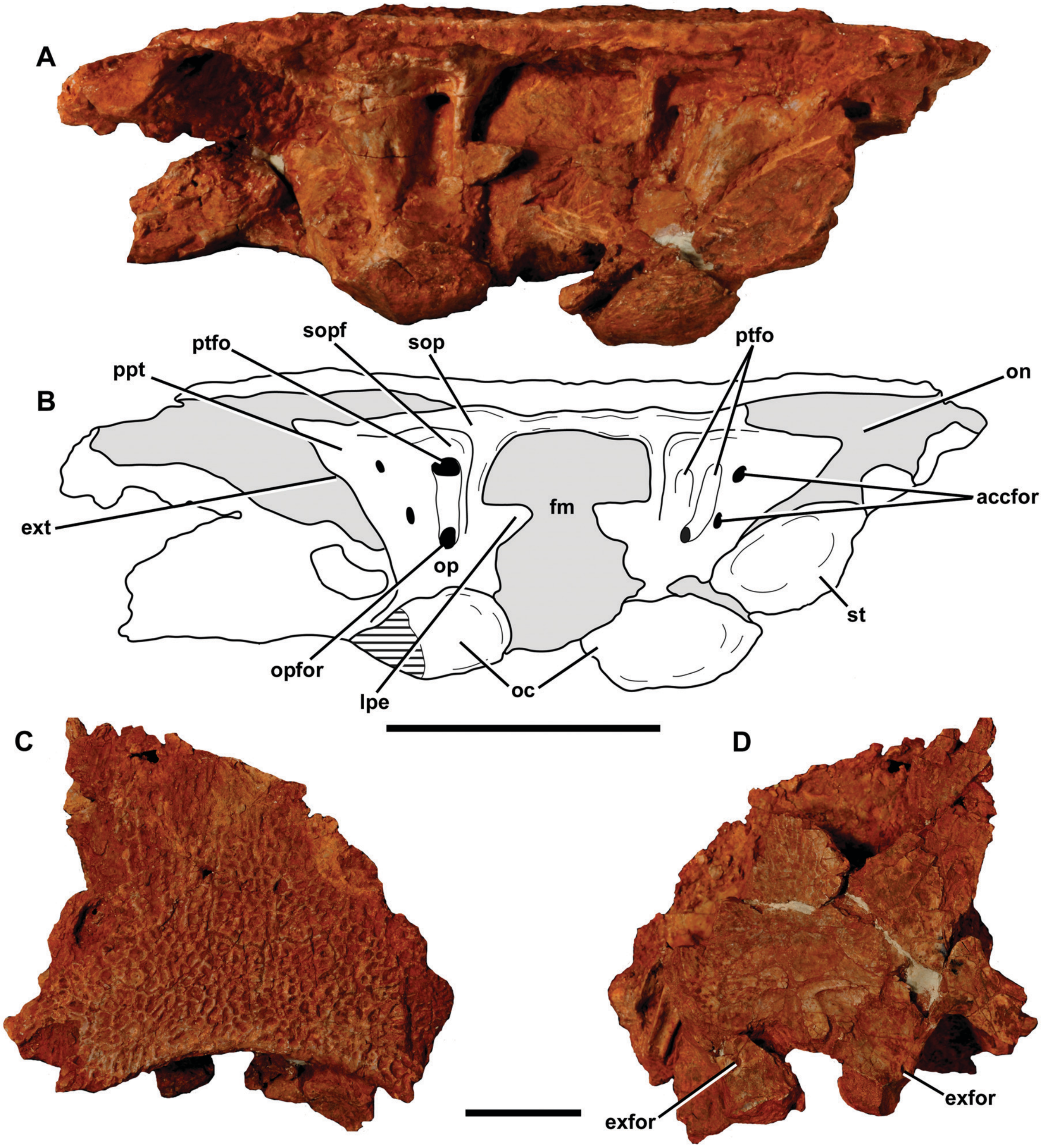

FIGURE 6. Posterior skull and occipital region of *Metoposaurus algarvensis* from the Late Triassic of Portugal (FCT-UNL 607). **A**, photograph in posterior (occipital) view; **B**, line drawing in posterior (occipital) view; **C**, photograph in dorsal view; **D**, photograph in ventral view. **Abbreviations**: **accfor**, accessory foramina on occipital pillar; **exfor**, foramen on ventral surface of exoccipital; **ext**, external tabular crest; **fm**, foramen magnum; **lpe**, lamellose process of exoccipital; **oc**, occipital condyle; **on**, otic notch; **op**, occipital pillar; **opfor**, foramen on occipital pillar; **ppt**, parotic process of tabular; **ptfo**, posttemporal foramen; **sop**, supraoccipital process of supraoccipital; **sopf**, fossa on supraoccipital process; **st**, stapes. Scale bars equal 5 cm.

Second, the ventral portion of the foramen magnum is slightly dorsoventrally deeper than the dorsal portion in *M. diagnosticus*, unlike the condition in *M. algarvensis* in which the two portions are essentially equal. The relative depth of the ventral portion of the foramen magnum in *M. diagnosticus*, however, does not reach the extreme degree that it does in *M. krasiejowensis* (Sulej, 2007) and *Koskinonodon* (Sawin, 1945). Furthermore, the shape of the dorsal portion of the foramen magnum of *M. diagnosticus* (referred specimen SMNS 4943) is flattened ovoid, unlike that of *M. algarvensis*, which is rectangular.

The Portuguese taxon differs from the species of the North American *Koskinonodon* (and *Apachesaurus*) based on several features (see illustrations in Case, 1931; Sawin, 1945; Hunt, 1993; Spielmann and Lucas, 2012). The posttemporal and paraquadrate foramina on the occiput are larger in *Koskinonodon* and *Apachesaurus*, but these taxa lack the large foramen ventral to

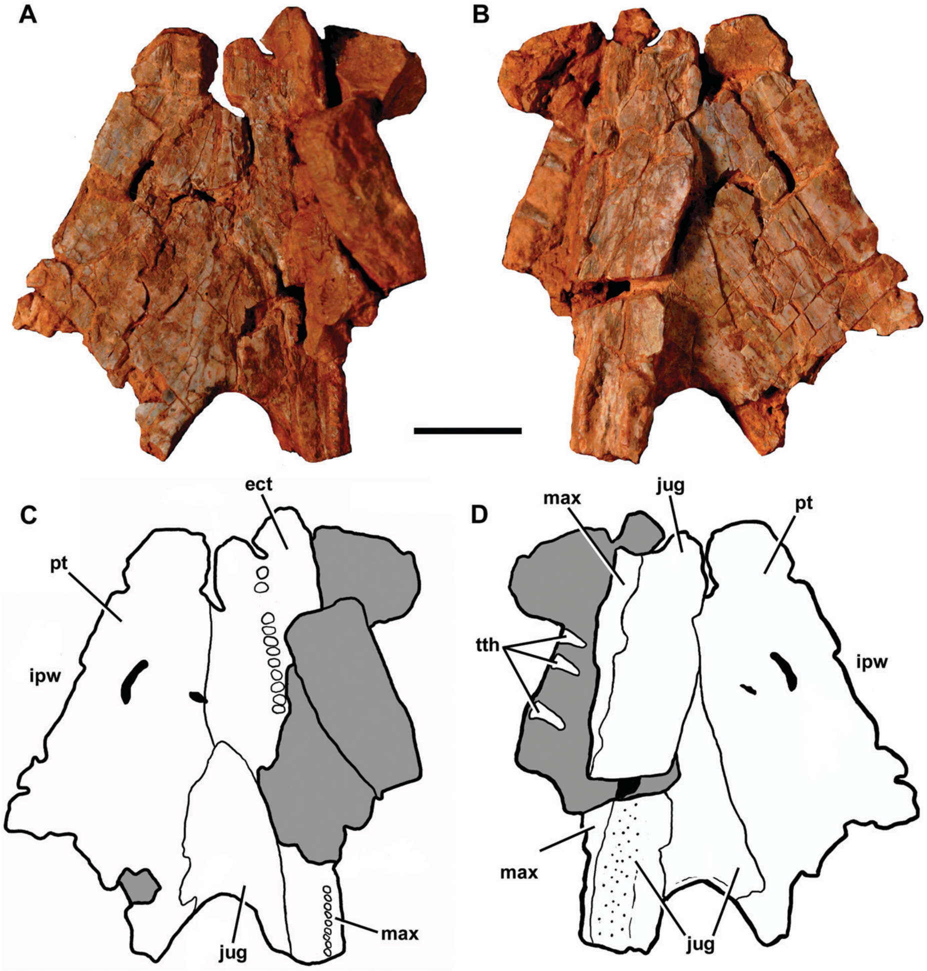

FIGURE 7. Anterior region of the palate of *Metoposaurus algarvensis* from the Late Triassic of Portugal (FCT-UNL 608). **A**, photograph in ventral view; **B**, photograph in dorsal view; **C**, line drawing in ventral view; **D**, line drawing in dorsal view. **Abbreviations**: **ect**, ectopterygoid; **ipw**, interpterygoid window; **jug**, jugal; **lac**, lacrimal; **max**, maxilla; **pt**, pterygoid; **tth**, teeth. Scale bar equals 2 cm.

the posttemporal foramen and the two lateral accessory foramina on the occipital pillar that are characteristic of *M. algarvensis*. The occiput of *Koskinonodon* is more similar to that of *M. krasiejowensis* than that of *M. algarvensis* in having a dorsal portion of the foramen magnum that is ovoid to subtriangular in shape (not rectangular) and much shallower than the ventral portion, and occipital condyles that are spherical and closely placed on the midline. The occiput of *Apachesaurus* is drastically different from *M. algarvensis*, as well as other metoposaurids, in having a triangular foramen magnum that is not divided into dorsal and ventral portions (keyhole-shaped) (Spielmann and Lucas, 2012). The mandibles of *Koskinonodon* and *Apachesaurus* taper in depth anteriorly and have a concave ventral margin along the anterior portion of the bone, which is not the case in the Portuguese taxon. Finally, *Koskinonodon* possesses a more extreme degree of sculpturing on the ventral surface of the palate, on both the cultriform process of the parasphenoid and the pterygoid.

DESCRIPTION

Skull Roof

General Comments—Several skulls have been recovered, and many of these are well preserved, although none is complete (Figs. 2–4, 6, 12). The skull roof bones are relatively thick and show a strong degree of ossification. Together with closed fusion of the cranial sutures, these characters are typical for an adult somatic age (e.g., Steyer, 2000).

As is characteristic for metoposaurids, the skull is dorsoventrally compressed, mediolaterally broad posteriorly, and gradually tapers in width anteriorly before terminating in a broadly rounded snout. The orbits are positioned just anterior to the anteroposterior midpoint of the skull and are placed along the lateral margins of the skull, such that they are widely separated on the skull roof. They are small and ovoid, with a long axis that is oriented slightly anteromedially-posterolaterally. The external nares are subtriangular in shape (as seen in FCT-UNL 604). The small pineal foramen is positioned near the posterior end of the skull. The posterior edge is marked by distinct otic notches, between which the posterior margin of the skull table is broadly and smoothly concave.

The most distinctive feature of the skull roof bones is the extreme dermal sculpturing on their dorsal surfaces, as seen in other metoposaurids and other temnospondyls. This sculpturing varies between two end-member conditions that grade into each other: small, irregularly sized, honeycomb-like pits and longitudinal grooves that are mostly oriented in an anteroposterior (or slightly oblique to anteroposterior) direction. The elongate grooves are especially concentrated in the postorbital portion of the skull, whereas the hexagonal pits are more commonly anteriorly, in the region of the orbits and the external nares. Sulej (2007) and Steyer (2003) described these longitudinal grooves as being formed in regions of fast bone growth (see also Bystrow,

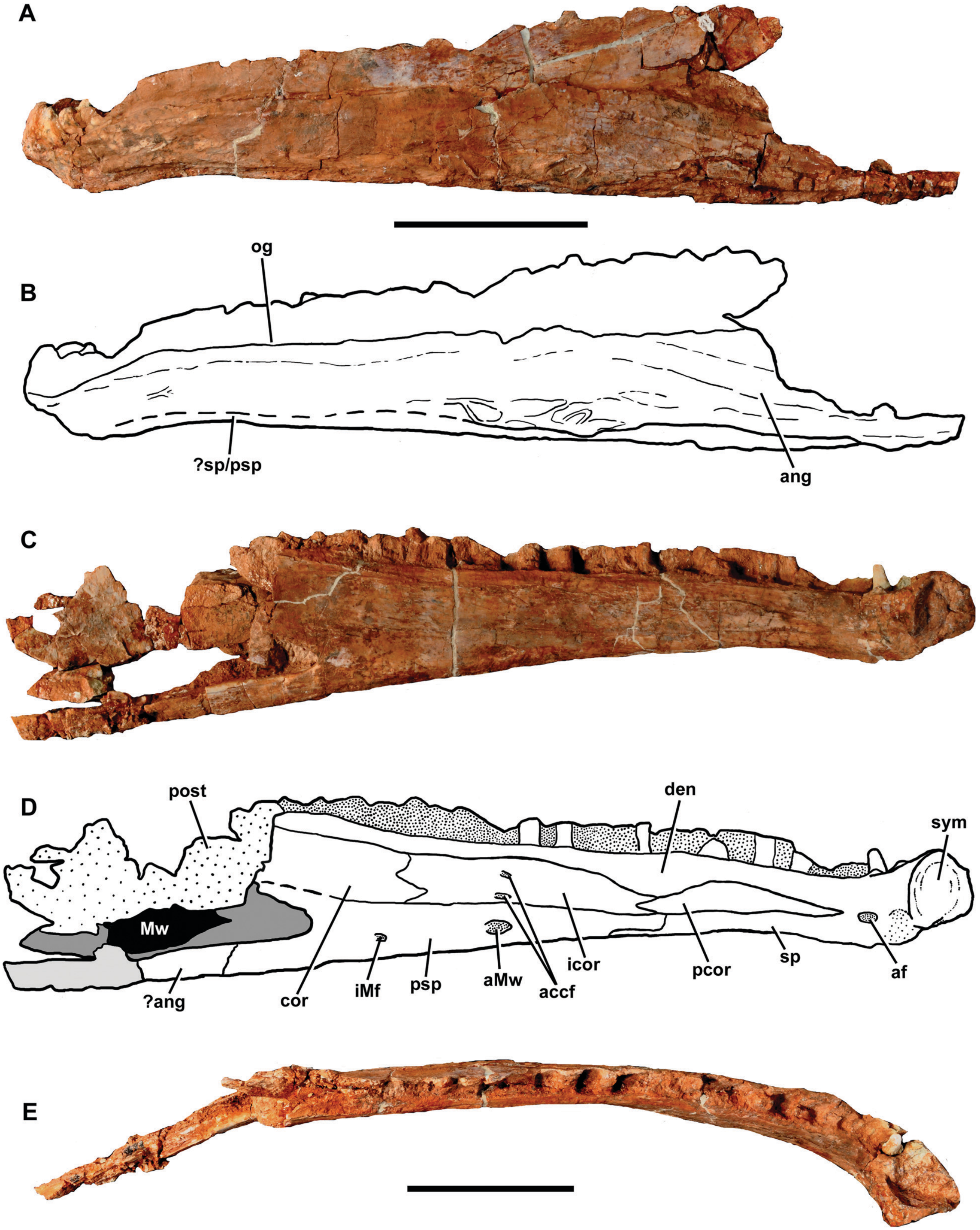

FIGURE 8. The mandible of *Metoposaurus algarvensis* from the Late Triassic of Portugal (left mandible, FCT-UNL 609). **A**, photograph in lateral view; **B**, line drawing in lateral view; **C**, photograph in medial view; **D**, line drawing in medial view; **E**, photograph in dorsal view. **Abbreviations**: **accf**, accessory foramina on intercoronoid; **af**, anterior foramen in region of dentary-spenial suture; **aMw**, anterior Meckelian window; **ang**, angular; **cor**, coronoid; **den**, dentary; **icor**, intercoronoid; **iMf**, intermeckelian foramen; **Mw**, Meckelian window; **og**, oral groove; **pcor**, precoronoid; **post**, posterior fragment of mandible; **psp**, postsplenial; **sp**, splenial;**?sp/psp**, splenial and/or postsplenial; **sym**, symphysis. Scale bars equal 10 cm. Top scale bar for **A**–**B**, bottom scale bar for **C**–**E**.

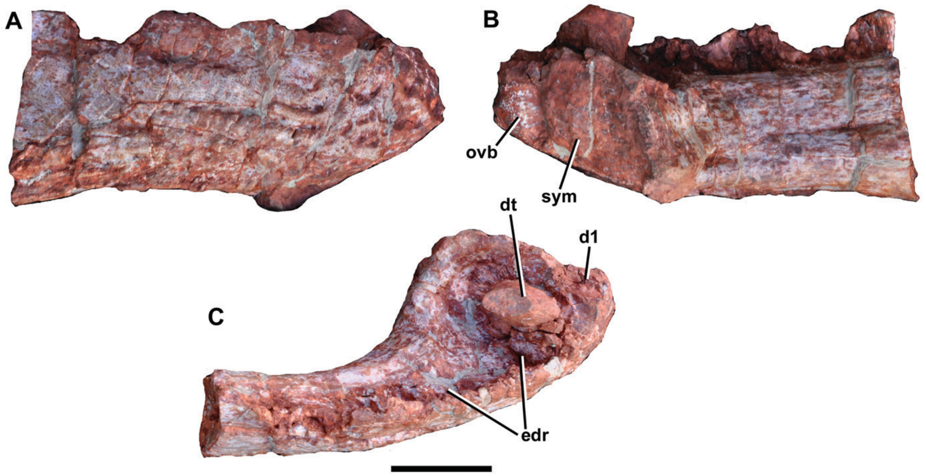

FIGURE 9. The mandible of *Metoposaurus algarvensis* from the Late Triassic of Portugal (anterior portion of right mandible, FCT-UNL 610). **A**, photograph in lateral view; **B**, photograph in medial view; **C**, photograph in dorsal view. **Abbreviations**: **d1**, first dentary alveolus; **dt**, dentary tusk; **edr**, edentulous region; **ovb**, ovoid bulge; **sym**, symphysis. Scale bar equals 2 cm.

1935). The pattern of dermal sculpturing of the Portuguese specimens is nearly identical to that in the Polish *M. krasiejowensis* (see Sulej, 2007). Similar texturing is also present on other metoposaurids (e.g., Branson and Mehl, 1929; Colbert and Imbrie, 1956; Dutuit, 1976; Hunt, 1993; Schoch and Milner, 2000).

There are three principal dermosensory canals on the skull roof, which are inset as smooth grooves that extend across several bones (e.g., Steyer, 2002). A similar pattern of canals is also present in other metoposaurids (Sulej, 2002, 2007), although there are noticeable differences between taxa that may have diagnostic significance.

The postorbital canal (also called the temporal canal by Sulej, 2007) begins at the posterolateral corner of the skull roof, on the quadratojugal (Fig. 2). From here, it extends straight anteroposteriorly across the quadratojugal and onto the jugal and then deflects medially near the midpoint of the jugal posterior to the orbit. It continues as an anteriorly convex loop that traverses the postorbital in the mediolateral direction, dividing this bone into roughly equal anterior and posterior portions and then loops back into an anteroposterior orientation before terminating on the supratemporal, approximately level to the pineal foramen. The anteroposteriorly extending portion of the postorbital canal along the lateral margin of the skull merges smoothly with the infraorbital canal at the inflection point on the jugal, where the postorbital canal loops medially onto the postorbital. On the large skull FCT-UNL 601, the postorbital canal is bifurcated into two parallel canals by a central ridge along its quadratojugal portion, but this bifurcation ends as the canal extends onto the jugal. This bifurcation is also present on the Polish (Sulej, 2007) and German (SMNS 4939) *Metoposaurus*.

Both FCT-UNL 600 and 601 exhibit a somewhat ‘W’-shaped portion of the postorbital canal that extends mediolaterally across the postorbital. This is the ‘double-looped’ condition, which is due to a pronounced kink in the canal. It is also present in *M. diagnosticus* (SMNS 4943), but not in the vast majority of the Polish *Metoposaurus* specimens (Sulej, 2007). The double

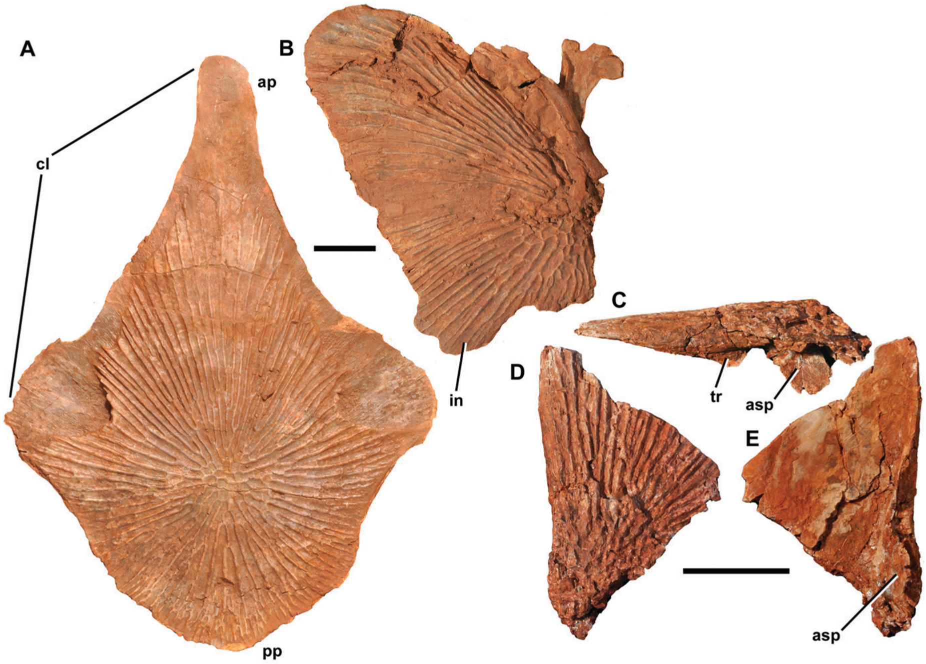

FIGURE 10. Pectoral bones of *Metoposaurus algarvensis* from the Late Triassic of Portugal. **A**, interclavicle (FCT-UNL-611) in ventral view; **B**, left clavicle (FCT-UNL-611) in ventral view; **C**, right clavicle (FCT-UNL-612) in lateral view; **D**, right clavicle (FCT-UNL-612) in ventral view; **E**, right clavicle (FCT-UNL-612) in dorsal view. Interclavicle and clavicle in **A** and **B** shown disarticulated but in-life position. **Abbreviations**: **ap**, anterior process; **asp**, ascending process; **cl**, sutural surface for the clavicle; **in**, ‘indentation’ at posteromedial corner of clavicle for articulation with interclavicle; **pp**, posterior process; **tr**, trough on lateral surface of clavicle. Scale bars equal 5 cm. Smaller scale bar for **A**–**B**; larger scale bar for **C**–**E**.

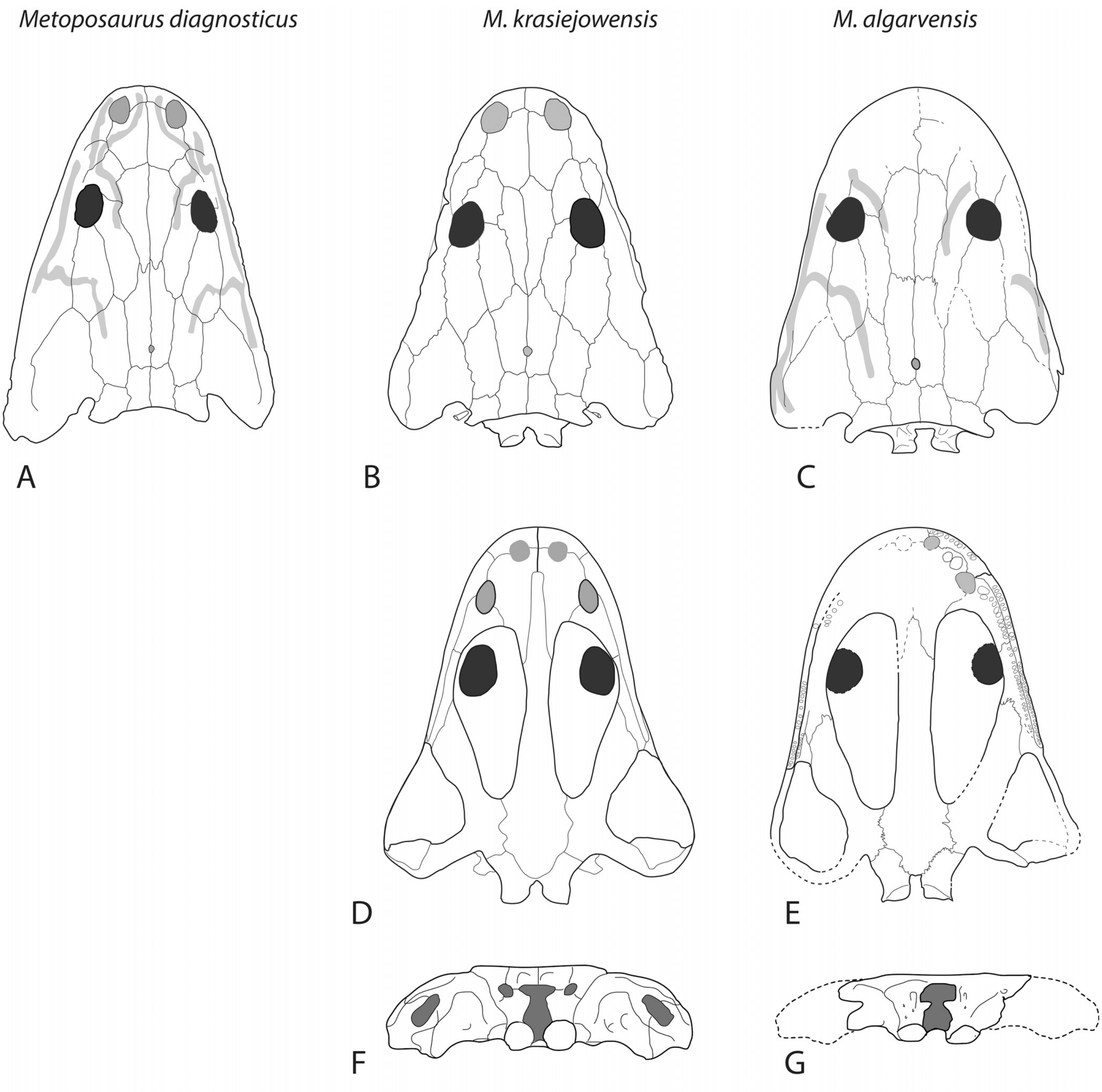

FIGURE 11. Comparison of the reconstructed skulls in **A**–**C**, dorsal; **D**, **E**, palatal; and **F**, **G**, occipital views of the Portuguese *M. algarvensis* (this work), the German *M. diagnosticus*, and the Polish *M. krasiejowensis* (based on Sulej, 2002, 2007).

loop is clearly absent in the holotype of the Polish species (ZPAL Ab III 358), as well as several other specimens (e.g., ZPAL 994/1-2, 1632/4, 893, 870, 880, 1953, 992/1, 4, 11, 11941, 1192). In these specimens, the anterior edge of the postorbital canal is smoothly convex anteriorly, without any midline kink that results in a 'W'-shape. The exceptions are two specimens: ZPAL 683, which exhibits a slightly double-looped postorbital canal on the well-preserved left side, and ZPAL 1113, which shows a weakly developed 'W'-shaped canal on the left side but a non-kinked canal on the right side. In neither of these cases is the 'W'-shape as pronounced as in the Portuguese and German material.

The infraorbital canal is positioned along the lateral margin of the skull (Fig. 2). Specimen FCT-UNL 604 shows that this canal begins near the tip of the snout, immediately posterolateral to the external naris. It extends posteriorly lateral to, and underneath, the orbit onto the maxilla and the jugal, where it merges with the postorbital canal as described above.

The supraorbital canal begins on the premaxilla near the anterior tip of the snout, immediately medial to the anterior edge of

FIGURE 12. Life reconstruction of *Metoposaurus algarvensis* from the Late Triassic of Portugal by Marc Boulay (www.cossima-productions.com).

the external naris (FCT-UNL 604) (Fig. 2). In FCT-UNL 600, it loops posterolaterally around the naris onto the nasal and then loops back posteromedially around the orbit, crossing the lacrimal, prefrontal, and postfrontal, terminating on the postfrontal immediately posterior to the orbit. This canal does not extend onto the frontal but makes contact with the lateral surface of the frontal as it crosses the prefrontal and postfrontal. It does not connect to the postorbital canal behind the orbit, but rather these canals are widely separated from each other. These canals are connected in many temnospondyls but are characteristically separated from each other in metoposaurids (Sulej, 2002).

Premaxilla—The main body of the premaxilla is rectangular, and a small process extends laterally to define the anterior end of the external naris (Fig. 4). On its palatal surface, the premaxilla bears a series of small, conical teeth along the entirety of its anterior margin. These teeth are mostly broken. A large, ovoid anterior palatal vacuity is present between the premaxilla and the vomer (Fig. 4). This vacuity would have accommodated the tusk at the anterior tip of the dentary when the jaws were closed.

Maxilla—A small portion of the anterior part of the left maxilla is present in FCT-UNL 604 (Fig. 4). It forms the posterolateral corner of the external naris on the dorsal surface and the lateral margin of the internal choana on the palatal surface. A marginal row of small teeth is located along the edges of the palatal surface of the maxilla. The ventral surfaces of the left and right maxillae are preserved on the holotype (FCT-UNL 600), and the ventral surface of part of the left maxilla is preserved on FCT-UNL 601 and 605.

Nasal—Parts of the nasal are preserved on FCT-UNL 600 and 604 (Fig. 2). Unfortunately, preservation on neither specimen is sufficient enough to determine whether there was a nasal-lacrimal contact.

Frontal—On the dorsal surface of the wedge-shaped frontals, ornamentation consists of polygonal pits slightly anterior to the center of the bone in all known skulls. In FCT-UNL 600, almost the entire sculpturing is composed of polygonal pits, but along the extreme anterior and posterior edges of the bone the pits transition into elongate ridges. In the larger skulls FCT-UNL 601 and 605, these ridges become more elongate in the posterior portion of the bone; thus, the central polygonal region becomes smaller.

Parietal—The parietal is anteroposteriorly elongate and rectangular (Figs. 3, 4). The pineal foramen is located within the posterior fourth of the bone, as is the case in the Polish and German *Metoposaurus* (e.g., Sulej, 2007). The region of the dorsal surface anterior to the pineal foramen is ornamented almost entirely by anteroposteriorly elongate ridges and grooves. The region posterior to, and surrounding, the foramen, however, is ornamented solely by polygonal pits.

Sulej (2002, 2007) described diagnostic differences between the parietals of various metoposaurids, both relative to each other and to other temnospondyls. Some differences relate to the shape of a crest on the ventral surface of the bone, but this cannot be observed in the Portuguese specimens because the ventral parietal is always obscured by underlying palatal bones. Sulej (2002) described the Polish *Metoposaurus* as having a proportionally shorter prepineal region of the parietal relative to the total anteroposterior length of the bone than the German *Metoposaurus*. These differences, however, are subtle and overlapping, and only become apparent with large numbers of specimens that can be analyzed statistically (Sulej, 2002: fig. 10B). When the holotype of *M. algarvensis* is included in Sulej's (2002: fig. 10B) plot of prepineal length vs. posterior skull width, it falls within the large cloud of Polish specimens. Furthermore, Sulej (2002:fig. 10A) noted that the Polish specimens have a larger "expansion angle" (i.e., the angle between the left and right parietal-supratemporal sutures) than the German ones. The holotype of *M. algarvensis* has an 'expansion angle' of approximately 10–15°, similar to the German material but distinct from the 20–30° measurements of the Polish material.

Postparietal—The postparietal is small and rectangular. Its posterior surface forms part of the smoothly concave posterior margin of the skull table in dorsal view (Figs. 2, 3), and a small process of the bone (the supraoccipital process) extends ventrally in occipital view to form the central dorsal portion of the occipital surface. In dorsal view, the contact between the postparietal and tabular is roughly parasagittal in the holotype FCT-UNL 600 but is slightly oblique to the midline in the isolated occiput (FCT-UNL 607). Similar variability was also noted in the Polish material by Sulej (2007), who considered it to be random intraspecific variation. The sculpturing of the dorsal surface consists of polygonal pits only, even in the largest specimens. Sulej (2007) mentioned that some of the largest Polish specimens are ornamented with elongate ridges and grooves, located on the anterior part of the bone.

Sulej (2007) mentioned an oblique crest on the ventral surface that he interpreted as a possible autapomorphy of the Polish material, but this region cannot be observed in any of the Portuguese specimens. The postparietal is also visible in posterior view, where it constitues part of the dorsal portion of the occiput. This is described below in the Occiput section.

Lacrimal—The posterior portion of the lacrimal is preserved on both sides of the holotype (FCT-UNL 600) but is better preserved and has more discernible sutures on the right side (Fig. 2). The posterior edge of the lacrimal participates in the anterior margin of the orbit, for a length of approximately 18 mm on the right side. The lacrimal usually contributes to the orbital rim in the Polish *Metoposaurus*, although in a few abnormal skulls it does not (Sulej, 2007). Fraas (1889) described the lacrimal as being excluded from the orbit in the German *Metoposaurus*, which would be an unusual feature among metoposaurids. Sulej (2002), however, reassessed the German material and noted that in the holotype of *Metoposaurus diagnosticus* (SMNS 10825), as well as other specimens, the lacrimal does contribute to the anterior rim of the orbit. We agree with this interpretation based on our study of the *Metoposaurus* collection in Stuttgart. As discussed by Sulej (2002, 2007), the lacrimal is genuinely excluded from the orbital margin in some North American (e.g., *Koskinonodon bakeri, Apachesaurus gregorii*) and African (e.g., *Arganasaurus lyadizi, Dutuitosaurus ouazzoui*) taxa. Note that Lucas et al. (2007) disputed Sulej's (2002) description of the lacrimal as contributing to the orbit in the Polish *Metoposaurus*, but Sulej (2007) clearly documented that 53 out of 55 skulls from Krasiejów exhibit a lacrimal that contributes to the orbit. Our personal observations of many of these specimens confirm Sulej's (2007) exhaustive descriptions. The lacrimal contribution to the orbit is not an unambiguous *Metoposaurus* synapomorphy, however, because it is also present in some of the North American species referred to *Koskinonodon*, as discussed by Sulej (2007).

Prefrontal—The subrectangular prefrontal is well preserved on the left side of FCT-UNL 601 and on both sides of the holotype (FCT-UNL 600) (Figs. 3, 4). On the holotype, the dorsal ornamentation of the prefrontal consists mainly of polygonal pits posterior to the supraorbital canal, and somewhat elongate ridges and grooves anterior to the canal, although these are not as elongated and pronounced as those ridges on the frontal and parietal.

FCT-UNL 600 and 601 appear to have different sutural patterns between the prefrontal and postfrontal. In the smaller holotype skull, the suture is oriented almost straight mediolaterally and is located nearly at the midpoint of the medial margin of the orbit. In the larger referred skull, the suture is oriented obliquely (anterolaterally) and intersects the orbit at a much more anterior position, at its anteromedial corner. As a result, the prefrontal makes a smaller contribution to the orbit in the larger skull. There is some variability in the shape and position of this suture in the Polish skulls (see Sulej, 2007), but in no case is the suture located so extremely anteriorly on the orbital margin, and in no case is it oriented so obliquely. The holotype of *Metoposaurus diagnosticus* (SMNS 10825) exhibits a condition similar to the large Portuguese skull, in that the suture extends obliquely and is positioned anteriorly along the medial orbital margin.

Postfrontal—The holotype of *M. algarvensis* clearly has a postfrontal-supratemporal suture on the left side, but the sutural relationships between the postfrontal, supratemporal, and postorbital are not clear on the right side (Figs. 3, 4, 6). The postfrontal and supratemporal make contact in ~70% of the Polish *Metoposaurus* skulls (Sulej, 2007) and in a well-preserved referred specimen of *Metoposaurus diagnosticus* from Germany (SMNS 4943). In both the large and small skulls of *M. algarvensis* (FCT-UNL 600, 601), the anterior region of the dorsal surface is ornamented by polygonal pits and the posterior region by elongate ridges and grooves.

Postorbital—The posterior end of the large, subrectangular postorbital terminates at a blunt point (Figs. 3, 4, 6). This point is sharpest in FCT-UNL 600 and 601 but is a mere rounded edge on the left side of the largest skull, FCT-UNL 605 (the right side of this skull is poorly preserved). Similar variability in the Polish *Metoposaurus* is noted by Sulej (2007): the posterior end of the postorbital ranges from a pointed tip to a broadly rounded edge. Sometimes, the shapes of the left and right postorbitals are different on the same skull (e.g., Sulej, 2007: fig. 6). On the dorsal surface, the portion anterior to the kinked postorbital canal is mostly covered by polygonal pits in all known Portuguese skulls (FCT-UNL 600, 601, 605), whereas the portion posterior is covered by elongate ridges.

Supratemporal—In all known Portuguese skulls (FCT-UNL 600, 601 605), the dorsal surface of the anteroposteriorly elongate and rectangular supratemporal is sculptured by polygonal pits posteriorly and elongate ridges anteriorly (Figs. 3, 4, 6). On FCT-UNL 600 and 601, the postorbital canal, which extends onto the supratemporal, terminates posteriorly at approximately the same point that the anterior region of elongate anterior ridges transitions to the posterior region of polygonal pits. This is also the case in the German (e.g., SMNS 4943) and Polish (Sulej, 2007) *Metoposaurus*.

Tabular—The posterolateral corner of the small, rectangular tabular is expanded into a rounded horn that defines the posteromedial boundary of the otic notch (Fig. 3). In both FCT-UNL 600 and 601, the dorsal surface of the tabular is ornamented by polygonal pits and not elongate grooves and ridges. Polygonal pits, and not elongate grooves, are also present on the tabulars of the Polish and German material (SMNS 4943; Sulej, 2007), indicating that this type of ornamentation is conservative among European metoposaurids.

The tabular horn is larger and more dorsoventrally thickened in the isolated occiput (FCT-UNL 607) than the smaller holotype skull (FCT-UNL 600). Unfortunately, the tabular horn is broken on both sides of FCT-UNL 601. Similar differences in tabular horn size and shape are described as the result of ontogenetic transformation by Sulej (2007) in the Polish *Metoposaurus*. The tabular contributes to the dorsal region of the occipital surface and is therefore also visible in occipital view. This portion of the tabular is described in the Occiput section below.

Jugal—The elongate and rectangular jugal constitutes much of the lateral edge of the skull in dorsal view (Figs. 3, 4, 6). Its dorsal surface is ornamented by polygonal pits in the center and elongate ridges and grooves anteriorly and posteriorly. This pattern is also present in the Polish (Sulej, 2007) and German (e.g., SMNS 4943) *Metoposaurus* material. On the palatal surface, a small triangular portion of the jugal wedges between the maxilla, ectopterygoid, and pterygoid but does not bear palatal teeth (Fig. 7).

Squamosal—The large and subtriangular squamosal forms the anterior margin of the otic notch, and the notch itself is a deep concave indentation in the posterior margin of the squamosal (Figs. 3, 4, 6). The extreme posterior edge of the squamosal joins with the posterior edge of the quadratojugal to form a thin but distinct falciform crest (= crista falciformis) that slightly overhangs the occipital surface of the skull. This crest is the extreme dorsal margin of the occipital surface itself. The squamosal is also broadly visible in the occipital view (see below).

Quadratojugal—The quadratojugal forms the posterolateral corner of the skull (Figs. 3, 4), the lateral margin of the subtemporal fenestra in ventral view, and the dorsolateral region of the occiput in posterior view. Sulej (2007) described the occipital surface of the quadratojugal as being composed of three processes, but none of the Portuguese skulls are preserved well enough to clearly distinguish these.

There is a marked difference in the shape of the quadratojugal in dorsal view that distinguishes the Portuguese and German material from the Polish material (Fig. 11). For the Polish material, Sulej (2007) described the quadratojugal as forming a slightly convex posterolateral corner of the skull. In other words, the lateral margin of the quadratojugal is convex and offset from the straight lateral margin of the more anterior skull, formed by the jugal and maxilla. This morphology is confirmed by our observations of all the Polish ZPAL specimens that we personally examined, but it is not present in the Portuguese (FCT-UNL 600, 601) or German *Metoposaurus* (SMNS 4943). Instead, these taxa have a quadratojugal with a lateral margin that is essentially straight and smoothly confluent with the lateral margin of the jugal. The North American *Koskinonodon* and *Apachesaurus* are similar to the German and Portuguese material, and do not possess the laterally convex shape of the quadratojugal (Sawin, 1945; Hunt, 1993; Spielmann and Lucas, 2012).

Palate

Choana—The choana, located between the premaxilla and vomer, is ovoid in shape, with a long axis extending posterolaterally-anteromedially (Fig. 4). It is slightly larger than the anterior palatal vacuity.

Interpterygoid Window—The interpterygoid window (= fenestra or vacuity) is an enormous opening that is somewhat teardrop-shaped, with the tapered end of the tear extending posteriorly (Fig. 2).

Vomer—The vomer forms the posterior margin of the anterior palatal vacuity and the anteromedial edge of the internal choana (Figs. 3, 5). In ventral view, its anterolateral corner houses an enormous alveolus for a tusk-like palatal tooth, which is more than 10 times the size of adjacent alveoli (Fig. 4). A circum-vomerine tooth row is divided into two partitions by the intervening tusk alveolus. The first of these partitions, the transvomerine tooth row, crosses the vomer medial to the tusk alveoli. The second, the anterochoanal tooth row, follows the medial margin of the choana anteriorly and continues posterolaterally to the tusk alveolus. The transvomerine teeth are larger than the anterochoanal teeth. The entire circum-vomerine tooth row parallels the contours of the marginal tooth row along the lateral edges of the premaxilla and maxilla, but these two tooth rows are separated by approximately 20 mm.

Parasphenoid—The basal plate is subcircular in shape and underlies the brain and the auditory capsules. The cultriform process extends from the basal plate anteriorly as an elongate, rectangular sheet of bone. The cultriform processes of metoposaurids, including the Portuguese specimens, are proportionally mediolaterally broader than in close outgroups such as *Callistomordax* (Schoch, 2008).

The ventral surface of the basal plate is ornamented by a series of very faint longitudinal ridges and grooves that radiate outwards from a central series of polygonal pits. This ornamentation is so subtle that it is only visible when the specimens are held at a low angle to light, and it clearly does not continue anteriorly past the base of the cultriform process. A similar degree of ornamentation, which is subtle and restricted mostly to the basal plate region, is present in the Polish *Metoposaurus* (Sulej, 2007), whereas the North American *Koskinonodon* has more pronounced ornamentation that extends far anteriorly onto the cultiform process (Sawin, 1945: fig. 3). Shallowly impressed muscle scars are visible on the ventral surface of the basal plate adjacent to the contact with the exoccipitals, which are nearly identical in size and position to those reported by Sulej (2007). Sulej (2007) also described a number of distinct crests, mostly for muscle attachments, on the dorsal surface of the basal plate in the Polish specimens, but none of the Portuguese specimens can be observed in dorsal view.

Palatine—Teeth are present in two regions of the palatine (Fig. 2). A main longitudinal row continues posteriorly on the ectopterygoid and runs parallel to the maxillary tooth row on the lateral edge of the skull. In all Portuguese specimens where the teeth can be observed, the teeth of the palatine/ectopterygoid row are markedly larger than those of the lateral row, with basal diameters more than twice those of the adjacent maxillary teeth. Sulej (2007:fig. 1) illustrated the palatine/ectopterygoid and maxillary teeth of the Polish taxon as being approximately equal in size, but many individual specimens that we examined are too poorly preserved to measure individual teeth. The specimen figured by Sulej (2007:fig. 6) does, however, possess palatine/ectopterygoid teeth that are noticeably larger than adjacent maxillary teeth. The palatine and ectopterygoid teeth of *Koskinonodon* are also larger than the adjacent maxillary teeth (Sawin, 1945: fig. 3). Sulej (2007) described a pair of palatine tusks, but these cannot be observed in the Portuguese specimens due to poor preservation. A second, very short row of denticles (small teeth) is present on the central portion of the palatine anterior to the interpterygoid window. This row extends parallel to the edge of the internal choana.

Ectopterygoid—This bone forms part of the lateral margin of the interpterygoid window and bears a single row of teeth on its ventral surface that is continuous with the primary row on the palatine anteriorly (Figs. 3, 6, 7). This tooth row is described above.

Pterygoid—This bone has a typical triradiate shape, with a posteromedially projecting basipterygoid ramus, a laterally and somewhat posteriorly extending quadrate ramus, and an anterolaterally projecting palatine ramus (Figs. 3, 6, 7). Additionally, the lamina ascendens, a dorsally projecting sheet extending from the dorsal surface of the quadrate ramus, is visible on the isolated Portuguese occiput specimen FCT-UNL 607. It was also described by Sulej (2007) in the Polish *Metoposaurus*. The ventral surface of the region where the palatine and quadrate rami diverge is marked by a series of very faint bumps. Sawin (1945) figured a noticeable degree of ventral sculpturing, mostly on the palatine ramus in the North American *Koskinonodon*.

In FCT-UNL 601, the narrowest width of the palatine ramus is 43 mm, whereas in a similarly sized Polish skull (skull length 480 mm) this process is 33 mm in minimum width. This suggests that the Portuguese taxon may have a proportionally wider palatine process than the Polish taxon, although a larger sample is needed to confirm this. On all Portuguese specimens that preserve this region, a prominent convex flange on the lateral margin of the palatine ramus projects as a small tab into the suborbital fenestra (Fig. 2). This flange is present in *Koskinonodon* (Sawin, 1945: fig. 3), *Apachesaurus* (Spielmann and Lucas, 2012: fig 10B), the Polish *Metoposaurus* (Sulej, 2007), and the German *Metoposaurus* (SMSN 4939), but not in the close metoposaurid outgroup *Callistomordax* (Schoch, 2008). In the Portuguese specimens and other metoposaurids, the medial margin of the palatine ramus is smooth and essentially straight, without any discrete flanges. In *Callistomordax*, by contrast, the medial margin is strongly convex (Schoch, 2008).

Sulej (2007) described for the first time a ‘small prominence’ on the ventral surface of the basipterygoid ramus that continues onto the palatine. We are unable to recognize this feature on any of the Portuguese specimens. This may be a diagnostic difference, but it is also possible that this is a subtle feature that is easily obscured by damage or is individually variable. The pterygoid is visible on the occipital surface of the skull, lateral to the occipital pillar formed by the exoccipital, tabular, and postparietal. Here, the pterygoid depression (sensu Sulej, 2007) is deep and well defined.

Occiput

General Comments—The Portuguese specimens appear very similar to the Polish specimens in their degree of braincase ossification, notably the lack of a clear ossified opisthotic. This is true of all Polish and Portuguese specimens, regardless of skull size. Other metoposaurids, specifically *Dutuitosaurus ouazzoui* and *Koskinonodon perfecta*, possess ossified opisthotics. Sulej (2007) described the sphenethmoid as unossified or extremely small in the Polish *Metoposaurus*, differing from the condition in *Dutuitosaurus* in which this bone is composed of two ossified blades that lie on the dorsal surface of the parasphenoid cultriform process. Unfortunately, the dorsal surface of the cultriform process cannot be observed in any of the Portuguese specimens, so the presence or absence of an ossified sphenethmoid cannot be determined.

Posttemporal Foramina—The shapes of the posttemporal foramina are well visible on the isolated occiput (FCT-UNL 607) (Fig. 6). There is clear left-right asymmetry on this specimen: the left foramen is larger, more ovoid in shape, and has a long axis that trends mediolaterally. The right foramen is smaller, more circular, and has a long axis that trends dorsoventrally. On the right side, a small pocket is separated dorsolaterally from the foramen by a strut of bone. This is not the case on the occiput of the smaller holotype (FCT-UNL 600), which apparently possesses a relatively larger right posttemporal foramen (although the left is damaged). Therefore, it is possible that the small pocket on the right side of FCT-UNL 607 may represent part of a larger, subdivided right temporal foramen. Sulej (2007) described a horizontal-to-vertical reorientation of the foramen during ontogeny, and also described the shape of the opening as generally variable. The Portuguese occiput (FCT-UNL 607) shows that the size and shape, and possibly the number, of foramina is variable on the left and right sides of a single specimen, meaning that the morphology of the fenestra may not be controlled solely by ontogeny.

In any case, there is a clear difference in the size of the posttemporal foramina between the Portuguese and Polish specimens, because the foramina in both the smaller holotype and the larger referred occiput are much smaller than those in multiple Polish specimens of different skull size (e.g., Sulej, 2007: fig. 16; ZPAL 358, ZPAL 1680). The morphology and size of the posttemporal foramina are unfortunately not observable in the German *Metoposaurus* due to poor preservation and obscuring matrix. The North American *Koskinonodon* exhibits large posttemporal foramina, as in the Polish *Metoposaurus* (Sawin, 1945: fig. 4).

Tabular—The tabular contributes to the dorsal region of the occipital surface. Along the lateral margin of the tabular on the occipital surface is a ventrally descending projection, which Sulej (2007) refers to as the parotic process. This process forms the lateral margin of the posttemporal foramen and therefore also part of the lateral margin of the broad fossa on the occipital surface of the regions lateral to the foramen magnum and above the basipterygoid processes. This region is composed of the tabular, postparietal, and exoccipital and is referred to here as the occipital pillar. The ventral edge of the parotic process contacts the dorsolateral pedestal of the exoccipital at the ventrolateral margin of the posttemporal foramen.

The tabular horn is connected to the parotic process by the external tabular crest (= crista tabularis externa) (Fig. 6). This crest is thin, sharp, and pronounced in all known Portuguese skulls (FCT-UNL 600, 601, 607) but is relatively stouter and more robust in the largest of these skulls (FCT-UNL 601). This crest forms the lateral margin of the occipital pillar in occipital view and thus also delimits the medial edge of the otic notch in occipital view.

Supraoccipital—In occipital view, the supraoccipital process roofs the foramen magnum dorsally and also forms part of the dorsal border of the posttemporal foramen (Fig. 6). The supraoccipital process contacts the exoccipital ventrally, but the contact between these two bones is not apparent in occipital view in either FCT-UNL 600 or 607. On the occipital surface of the supraoccipital process, immediately above the posttemporal foramen and the foramen magnum, a mediolaterally wide fossa is visible (Fig. 6). The fossa is bordered ventrally by the raised dorsal margins of the foramen magnum and posttemporal foramen and dorsally by a lamina of bone that forms the posterior edge of the skull table. It is this lamina that largely defines the fossa, due to the fact that the posterior edge of the skull roof dramatically overhangs the foramen magnum and adjacent occipital surface dorsally. This fossa is also present in the German (SMNS 4943) and Polish (Sulej, 2007) material. None of the Portuguese specimens preserving the occiput (i.e., FCT-UNL 600, 607) exhibit the ‘marked pit’ on the occipital surface of the postparietal immediately above the foramen magnum and within the aforementioned fossa, which Sulej (2007) describes in several Polish *Metoposaurus* specimens. Because the pits are absent in these two Portuguese skulls of differing size, but present in Polish skulls of varying size, we consider this a diagnostic difference between the two sets of specimens.

Squamosal—Because the lateral corners of the occiputs are broken in all specimens except the holotype (FCT-UNL 600; although the far lateral edge of its right lateral corner is missing), it is difficult to comment on the size, shape, and position of the paraquadrate and accessory paraquadrate foramina. However, a large, ovoid region on the left side of the occiput of FCT-UNL 600 appears to bear a large paraquadrate foramen, as in the Polish *Metoposaurus* (Sulej, 2007: figs. 1, 16). A portion of this foramen, also filled with matrix, is present on the right side. These paraquadrate foramina are large, but not so large as those of some Polish specimens (e.g., ZPAL 358) and of the North American *Koskinonodon* (Sawin, 1945: fig. 4) and African *Dutuitosaurus* (Dutuit, 1976: fig. 7; Spielmann and Lucas, 2012: fig. 11C).

Epipterygoid, Quadrate, and Sphenethmoid—These bones cannot be observed on any of the Portuguese specimens because they are obscured by surrounding bones that are in articulation.

Stapes—The stapes is present in articulation within the otic notch on the right side of the isolated occiput FCT-UNL 607 (Fig. 6). This bone has a somewhat rod-like shape but is incomplete: its posterior end is broken and its anterior end is hidden from view. It is dorsoventrally flattened and expands slightly transversely towards its anterior end. At the midpoint of the exposed surface, it is 8 mm in mediolateral width but only 1.5 mm in dorsoventral thickness. Its ventral surface is deeply concave due to a groove that covers nearly the entire surface. The shape of the stapes is very similar to that figured by Sulej (2007:fig. 1) for the Polish *Metoposaurus*.

Exoccipital—On the occipital surface, the vertical column of the exoccipital, which bifurcates dorsally, contacts the postparietal and tabular to form the ventral part of the occipital pillar (Fig. 6). The occipital surface of the vertical column is pierced by a foramen, located beneath the posttemporal foramen, at approximately midheight of the vertical column (Fig. 6). This foramen is confluent dorsally with a groove that leads into the posttemporal foramen. The foramina are absent in several Polish *Metoposaurus* specimens (Sulej, 2007: fig. 16), and we did not observe them on any of the ZPAL specimens we studied. They also are absent on the German SMNS 4939 and on the North American *Koskinonodon* (Case, 1931:pl. 2; Sawin, 1945: fig. 4) and *Apachesaurus* (Spielmann and Lucas, 2012: figs. 11, 16). They are present, however, in the close metoposaurid outgroup *Callistomordax* (Schoch, 2008), but in this taxon there are two foramina in this region: one larger, ovoid opening placed dorsolaterally to a smaller, circular foramen. Therefore, the presence of a single foramen is apparently unique to the Portuguese specimens among European metoposaurids and close outgroups. Two additional small foramina are also visible along the lateral edge of the occipital pillar in the Portuguese taxon, one on the tabular dorsally and the other on the exoccipital ventrally (Fig. 6). These are present on both left and right sides of FCT-UNL 607 but are not present in any of the Polish material figured by Sulej (2007: fig. 16) or examined during our study, nor on *Koskinonodon* figured by Case (1931:pl. 2) or Sawin (1945:fig. 4), nor on *Apachesaurus* figured by Spielmann and Lucas (2012:figs. 11, 16). The presence or absence of these foramina cannot be confirmed in the German specimens because of poor preservation.

The medial surface of the exoccipital gives rise to a discrete lamellose process, which projects into the foramen magnum to divide it into separate dorsal and ventral regions that together constitute a keyhole shape (Fig. 6). In the best-preserved occiput, FCT-UNL 607, each lamellose process is as mediolaterally wide as the gap between the left and right processes on the midline. The keyhole shape of the foramen magnum is also present in capitosaurians (e.g., Steyer, 2003) and most other metoposaurids (except for *Apachesaurus*; Spielmann and Lucas, 2012), which share with the Portuguese specimens the large and pronounced lamellose processes that define the keyhole. Sulej (2007) considered the large size of the lamellose process to be characteristic of metoposaurids, and these processes are indeed much smaller in the close outgroup *Callistomordax* (Schoch, 2008).

There are differences in the size and shape of the foramen magnum among metoposaurids. In the Polish material, including four specimens ranging in size and figured by Sulej (2007: fig. 16), the dorsal portion of the subdivided foramen is much shallower dorsoventrally than the ventral portion. This is also the case in the North American *Koskinonodon* (Sawin, 1945: fig. 4). In the Portuguese specimens, as best exemplified by FCT-UNL 607 but also present in FCT-UNL 600 and 601, the dorsal and ventral regions are of approximately equal dorsoventral height. The German SMNS 4939, although perhaps slightly crushed, also exhibits dorsal and ventral regions of approximately equal height. Furthermore, in the three Portuguese specimens, the dorsal region is approximately rectangular in shape, due to lamellose processes that project nearly straight medially to define the ventral edge of the dorsal portion and lateral walls of the dorsal portion that are nearly straight vertically. A more rectangular shape is also apparently present in SMNS 4949; in this specimen, the lamellose process clearly extends approximately horizontally, but the shape of the lateral walls cannot be determined due to encrusting matrix. The Polish specimens and *Koskinonodon*, on the other hand, possess more ovoid dorsal regions due to lamellose processes that extend obliquely ventromedially-anterodorsally and lateral edges that are rounded. One potential difference between the Portuguese and German specimens is that, in SMNS 4949, the dorsal portion is dorsoventrally deeper than the ventral portion, whereas in the Portuguese specimens the ventral portion is slightly deeper than the dorsal portion.

The occipital condyles are mediolaterally elongate ovals in all three Portuguese skulls (Fig. 6), whereas in the Polish material (Sulej, 2007), *Koskinonodon* (Case, 1931:pl. 2; Wilson, 1941: fig.12; Sawin, 1945: fig. 4), and *Apachesaurus* (Spielmann and Lucas, 2012: fig. 11), they are more spherical. The German SMNS 4939 and *Dutuitosaurus* (Dutuit, 1976: fig. 7) possess dorsoventrally shallow and mediolaterally elongate occipital condyles similar to those in the Portuguese specimens. Additionally, the left and right condyles are widely spaced on the midline in the Portuguese and German specimens and *Dutuitosaurus* but are more narrowly spaced in the Polish material (Sulej, 2007: fig. 16) and *Koskinonodon.* This is likely due to the large shape of the condyles in the Polish specimens and *Koskinonodon.*

On the ventral surface of the exoccipital, the subtympanic process projects laterally to contact the pterygoid. Smooth contact surfaces for the cartilaginous basisphenoid are visible on the ventral surface of the exoccipitals and basal plate of the parasphenoid. On FCT-UNL 607, small foramina are visible on the ventral surface of the exoccipitals, posterior to the occipital condyles (Fig. 6). These foramina are asymmetrically placed, because the left one is close to the lateral edge of the exoccipital and located only a few millimeters behind the condyle, whereas the right one is centered mediolaterally on the bone and positioned farther posteriorly. On the palatal surface of the skull, the exoccipital, parasphenoid, and pterygoid all meet each other in strong, interdigitating, but unfused sutures, even in the smallest skull (FCT-UNL 600).

Mandible

General Comments—Two partial mandibles were found associated (but not articulated) with the skull material from the Penina Bonebed (Figs. 9, 10). Both specimens are very similar in size, shape, and proportions to the mandibles of other metoposaurids (e.g., Sulej, 2007) but differ from other temnospondyls such as cyclotosaurids (e.g., Sulej and Majer, 2005). FCT-UNL 609, the most complete, is a left mandible that is approximately 60% complete in anteroposterior length but broken posteriorly, at the level of the middle of the Meckelian window (Fig. 8). A strip of bone continues posteriorly underneath the Meckelian window, preserving much of the ventral margin of the window and part of the articular region of the mandible. Nearly the entire tooth row is preserved. Very few teeth, however, are preserved in situ. FCT-UNL 610 is a small fragment of the anterior end of the mandible that preserves the symphysis, the large anterior alveolus bearing the dentary tusk, and the first 6–7 alveoli behind the tusk (Fig. 9). The symphysis of FCT-UNL 610, although smaller, is nearly identical in morphology to that of FCT-UNL 609. The following description is based primarily on the more complete mandible FCT-UNL 609.

FCT-UNL 609, as preserved, is 525 mm in anteroposterior length when measured as a straight line parasagittally (this measurement includes the posterior strip that continues underneath and behind the Meckelian window). The mandible is strongly laterally convex, however, and is 570 mm in anteroposterior length when measured along the contours of the lateral surface (its outer curve). By comparison with complete *Metoposaurus* mandibles from Poland (Sulej, 2007), we estimate the total length of the Portuguese mandible as approximately 600–650 mm. In dorsal view, the mandible arches medially as it continues anteriorly. As a result, the left and right conjoined mandibles would have formed a broad ‘U’-shape when in articulation. When the lingual surface of the symphysis is held so that it faces completely medially, the labial surface of the mandible seems to twist along its length. It faces completely labially (laterally) along the first half of the tooth row and then gradually reorients so that it faces dorsolaterally along the posterior half of the tooth row. As a result, the mesial (anterior) teeth project straight dorsally, whereas the more distal (posterior) teeth extend somewhat dorsomedially into the oral cavity.

In lateral (labial) view, the dorsal and ventral margins of the mandible are both fairly straight and diverge from each other posteriorly; thus, the mandible increases in dorsoventral depth as it continues posteriorly. Although straight along most of its length, the ventral margin is concave anteriorly, resulting in a slightly downturned symphyseal region. In contrast, the ventral margin is straight anteriorly in the Polish *Metoposaurus* specimens figured by Sulej (2007), and our study of the ZPAL collection confirms that none of the Polish mandibles possess the concave ventral margin and downturned symphysis seen in the Portuguese material. Additionally, the Portuguese mandible maintains a relatively constant dorsoventral depth along the anterior 150 mm of the dentary. The Polish mandibles, on the other hand, taper in depth anteriorly (Sulej, 2007). Unfortunately, there are no mandibles that can confidently be assigned to *Metoposaurus* among the German specimens that we observed in the SMNS and NHMUK collections, and none have been figured in the literature. The North American *Koskinonodon* and *Apachesaurus* are similar to the Polish specimens in possessing an anteriorly tapering mandible with a straight ventral surface (Branson and Mehl, 1929; Romer, 1947; Spielmann and Lucas, 2012).

The symphyseal region of FCT-UNL 610 is large and medially expanded (Fig. 9). The symphyseal surface is formed primarily from the dentary and probably by part of the splenial, although the suture between these bones is not clear in this region. The articular surface of the symphysis is subcircular in medial (lingual) view, surrounded by a pronounced rim, and faces strongly medially. Anterior to this articular surface, and separated from it by the rim on the symphyseal surface, is a smaller ovoid bulge that has a convex medial surface (Fig. 9). This bulge is the lingual (medial) edge of an alveolus, and it is unclear whether it would have articulated against the corresponding structure on the opposing mandible. In dorsal view, the symphyseal articular surface is nearly straight.

Dentary—The sutures between the dentary and the splenial and postsplenial are not clear, but there is a subtle change in surface texture on the lateral surface approximately 15 mm dorsal to the ventral margin (Fig. 8). This change may represent the suture between the dentary and these bones, which would be consistent with Sulej's (2007) description of these sutures as being located close to the ventral margin of the lateral dentary in the Polish *Metoposaurus*. In general, the pattern of sutures on the medial surface of the mandible is similar to that figured by Sulej (2007:fig. 3) for the Polish *Metoposaurus*.

The lateral surface of the dentary is not well preserved, but the most salient feature of this surface is a deep and anteroposterorly elongate oral groove that extends approximately parallel to the tooth row, across the entire length of the bone (Fig. 8). A weakly developed ornamentation is visible on the lateral surface of the dentary, ventral to the oral groove, but it is more subtle and random than the ordered array of polygonal pits and elongate grooves and ridges on the skull roof. The portion of the lateral dentary above the oral groove is essentially smooth, with only very minor texturing.

The dentary bears a series of large teeth that change in size and shape across the tooth row. Immediately lateral and adjacent to the symphysis is a large circular alveolus for a hypertrophied tusk-like tooth, which is much larger than the surrounding teeth (Fig. 9). This is also the case in the Polish *Metoposaurus* (Sulej, 2007) and many other temnospondyls (e.g., Schoch and Milner, 2000). In the Portuguese mandible, there is a small alveolus, positioned anteromedially to the giant alveolus, which is located directly anterior to the main symphyseal surface, at the extreme anteromedial tip of the mandible in dorsal view. Continuing along the external edge of the bone, posterolateral to this small alveolus and lateral to the tusk alveolus, is a 20-mm region that lacks teeth (Fig. 9). This small edentulous region is then followed posteriorly by the main tooth row that continues along the lateral edge of the entire preserved length of the dentary. The edentulous region lateral to the tusk alveolus is not present in the vast majority of the Polish *Metoposaurus*, in which a continuous tooth row stretches along the entire length of the dentary (Sulej, 2007: fig. 1). Our observations of numerous specimens in the Polish collection confirm this morphology (e.g., ZPAL Ab III 1693, 1663). However, Konietzko-Meier and Wawro (2007:fig. 2) described a few abnormal specimens of the Polish *Metoposaurus* that possess this edentulous region, so it is not unique to the Portuguese taxon.

The first alveolus at the anteromedial tip of the mandible is small and circular. More posterior alveoli of the primary row on the dentary, posterior to the edentulous region, are larger but still generally circular. Broken teeth, preserved in a few alveoli, are conical with circular cross-sections. The hypertrophied anterior tusk is preserved in situ in the anterior mandible fragment FCT-UNL 610, but it is broken near its tip. It has an ovoid cross-section with a long axis that approximately parallels the plane of the symphysis. This tusk does not fill the entire alveolus and is much smaller than may be expected based on the size of the alveolus alone. It is possible, therefore, that two tusks were present in this alveolus (see Konietzko-Meier and Wawro, 2007). Sulej (2007) described and figured a small row of teeth posterior to the tusk alveolus, but this region is poorly preserved in both Portuguese mandibles.

In medial view, the labial parapet of the alveolar row (formed by the lateral surface of the dentary) is distinctly higher than the lingual parapet (formed by the medial surface of the dentary). There is not as much of a marked difference between the heights of the two parapets in the vast majority of the Polish *Metoposaurus* specimens that we observed (ZPAL Ab III 858/2, 41, 167, 399, 511, 561, 855, 899, 918/3, 919, 920, 970/1, 1663, 1664, 1671, 1675/8-9, 1986, 2380/1). A single Polish mandible (ZPAL Ab III 1693), larger than most of the others, however, possesses a labial parapet that is somewhat intermediate in height between the short parapets of most Polish specimens and the high parapet of the Portuguese specimen. It is possible, therefore, that the parapet becomes taller during ontogeny, and for this reason we recognize parapet height as only a potential diagnostic difference between the Polish and Portuguese specimens.

Angular—The anteroventral region of the labial surface of the angular is heavily ornamented by a series of prominent pits, whereas posterodorsal to this region the labial surface bears a series of pronounced ridges extending approximately anterodorsally-posteroventrally (Fig. 8). This degree of texturing is greater than that seen on the dentary.

Medial Mandible—In medial view, several bones tightly fit together to define a smooth medial surface of the mandible below the tooth row (Fig. 8). The dentary forms the region immediately below the tooth row. Beneath the dentary, beginning at the front of the jaw, is a series of three bones in anteroposterior succession: the precoronoid, intercoronoid, and coronoid. Each bone is flat and sheet-like. Below this trio of bones are, again in anteroposterior succession, the splenial, postsplenial, and angular. The postsplenial and angular form the floor of the Meckelian window, whose anterior and ventral margins are preserved. This opening is clearly a large, oval fenestra, but its precise size and shape cannot be determined due to the breakage of the posterior region of the mandible. The dorsal border of the window is formed by the postsplenial and prearticular. The postsplenial bifurcates posteriorly to form the anterior end of the window as well as parts of its dorsal and ventral borders.

Several additional foramina are visible on the medial surface of the mandible anterior to the Meckelian window. Approximately 105 mm anterior to the Meckelian window is a large foramen on the postsplenial that is 15 mm in anteroposterior length (Fig. 8). This is the anterior Meckelian window of Sulej (2007). Above this foramen is a smaller, ovoid accessory foramen positioned on the intercoronoid, which is 8 mm in anteroposterior length by 4 mm in dorsoventral depth (Fig. 8). There is also a third, smaller, and more subtle foramen on the intercoronoid 10 mm directly above the accessory foramen (Fig. 8). The two latter foramina are not figured by Sulej (2007) in the Polish *Metoposaurus* and are not visible, at least as noticeable openings, on any of the ZPAL specimens we examined. Additionally, there is a fourth small foramen on the postsplenial, between the Meckelian window and anterior Meckelian window. It is located approximately 60 mm posterior to the anterior Meckelian window and is also present in the Polish material (Sulej, 2007: fig. 3). We refer to this here as the 'intermeckelian foramen' (Fig. 8). Finally, a small foramen at the far anterior end of the medial surface is present on both Portuguese specimens and appears to be at or near the border between the dentary and splenial (Fig. 8). This elongate, oval foramen is larger than the intercoronoid and intermeckelian foramina but smaller than the anterior Meckelian window. It is not figured by Sulej (2007: fig. 3) in his skull reconstruction of the Polish *Metoposaurus* taxon.

Posterior Mandible—A fragment of the posterodorsal portion of the large Portuguese mandible FCT-UNL 609 is separated from the remainder of the specimen and does not cleanly attach to it (Fig. 8). It is thin and strongly textured laterally by a set of ridges that radiate from a concentrated region of polygonal pits. Most or all of this piece belongs to the angular.

Postcranial Skeleton

General Comments—Numerous temnospondyl postcranial elements have been excavated from the Penina Bonebed, but these are generally not preserved in articulation with the *Metoposaurus* skulls described here. Because in other localities *Metoposaurus* is often associated with other temnospondyls (particularly cyclotosaurs) (e.g., Dzik and Sulej, 2007; Jalil and Peyer, 2007), it is difficult to be certain of the systematic assignment of the Portuguese postcranial material. As a result, we do not describe the vast majority of this postcranial material (mostly vertebrae) in detail here, but it will be reviewed in the future. However, we do describe the interclavicles and clavicles, which are known from several specimens that closely match the corresponding bones in the Polish *Metoposaurus*, and which have been well described by Sulej (2007).

Interclavicle—The interclavicles match the general morphology of *Metoposaurus* (Sulej, 2007: figs. 40, 42) in that the posterior process is abbreviated compared with other temnospondyls, especially cyclotosaurids in which the elongate proportions of this process give the interclavicle an overall rhomboid shape (Sulej and Majer, 2005). The best-preserved specimen, which is representative of the morphology of the Portuguese *Metoposaurus*, is a large and essentially complete interclavicle (FCT-UNL 611) (Fig. 10). It is 465 mm in anteroposterior length and 330 mm in maximum mediolateral width, and the distance between the posterior termination of the clavicular sutural surface to the posterior end of the bone (distance 'Di' of Sulej, 2007) is 165 mm. This very thin specimen is only visible in ventral view because its dorsal surface was embedded in plaster in the field in order to stabilize it. As in the interclavicles of the Polish *Metoposaurus*, the posterior process of the Portuguese specimen is short and broadly rounded, the posterolateral margins are initially concave immediately posterior to the clavicle articulation but become convex more posteriorly, and the anterior process is elongate and bluntly rounded at its anterior termination.

The ventral surface of the main body of the interclavicles is heavily ornamented by a series of ridge-and-groove ornamentation radiating outward from an area of honeycomb-like hexagonal pits that is situated slightly posterior to the center of the element. The relative size of the area of hexagonal depressions has been used as a character of taxonomic significance within metoposaurids: these depressions cover a relatively large area in the North American *Koskinonodon* and *Apachesaurus* but are much more limited in extent in the European *Metoposaurus*, including the Polish and German specimens (Colbert and Imbrie, 1956; Sulej, 2002). The development of the hexagonal pits in the Portuguese material, and the small region that they cover, is similar to that of the Polish and German *Metoposaurus* (Sulej, 2002, 2007). One possible difference from the Polish taxon is that the ornamented area does not taper to form a sharp point anteriorly, but is more rounded, and ends at some distance (90 mm) from the anterior termination of the bone. Sulej (2007) described the shape of the anterior termination of the ornamented area to be variable in the Polish taxon, but all specimens figured in his monograph possess the tapered morphology (Sulej, 2007: figs. 40, 42).

The sutural surfaces for the clavicles are deeply incised posteriorly and become shallower anteriorly (Fig. 10). Anterior to the ornamented region, an elongate sutural surface is present, which may suggest a relatively broad midline contact between the clavicles. The sutural surfaces are covered with fine linear striations that radiate away from the area of hexagonal pitting, but are generally smoother than the heavily ornamented main body of the bone.

We compared the shape of the ornamented region of the Portuguese specimen with that of other metoposaurids by plotting it on Sulej's (2007:fig. 42) scatter plot of Di (distance between the posterior termination of the clavicular sutural surface to the posterior end of the bone) vs. Si (maximum transverse width of the ornamented region). In the Portuguese specimen, Di is 16.5 cm and Si is 30 cm. When added to Sulej's diagram, the Portuguese specimen falls above the regression lines for the other taxa. In other words, the Portuguese specimen has a larger Di than would be expected for its Si. It has a larger Di than several specimens of *Dutuitosaurus* with nearly identical Si, as well as specimens of '*Metoposaurus*' *maleriensis* and *Koskinonodon* with nearly equal or slightly larger Si measurements. This may represent a diagnostic difference between the Portuguese taxon and other metoposaurids, but it is unclear how these ratios may be related to body size.

Clavicle—The largest (maximum length 335 mm, maximum width 170 mm) and most complete clavicle (FCT-UNL 611), found associated with the large interclavicle described above, is described here (Fig. 10). It is a left clavicle, which like the corresponding interclavicle is only visible in ventral view due to the manner in which it was collected. It is similar in its overall shape to clavicles of the Polish *Metoposaurus* (Sulej, 2002, 2007).

The main body of the clavicle is relatively complete, although small parts are probably missing along its medial and posterior margins. The ascending crest, anterior plate, and dorsal process, all of which project dorsally perpendicular to the plate region to articulate with the cleithrum, are not preserved. As preserved, the medial and posterior margins of the clavicle are nearly straight and meet one another at approximately 90°, although there is a small medial projection at the posteromedial corner. This projection helps define the 'indentation' for the articulation of the interclavicle, which is present in other metoposaurids but absent in some temnospondyl clades (Warren and Marsicano, 2000; Sulej, 2007). The lateral surface of the clavicle is convex, and anteriorly the bone is rounded. It is difficult to assess the degree to which contact between the clavicles would have occurred, because there is no clear flattened surface for this contact as reported in *Metoposaurus diagnosticus* (Colbert and Imbrie, 1956).

The ventral surface of the clavicle is strongly ornamented. There is a small area of rounded-to-hexagonal pits at the posterolateral corner of the ventral surface. Curvilinear grooves and ridges radiate medially and anteromedially away from this pitted area and cover the entire ventral surface. This is nearly identical to the ornamentation in the Polish material (Sulej, 2007).

A second clavicle specimen, FCT-UNL 612, is a fragmentary right clavicle preserved in three dimensions (Fig. 10C–E) that preserves an important feature that distinguishes metoposaurids from cyclotosaurs. The base of the ascending crest is present on the dorsal surface, where it extends perpendicular to the remainder of the bone (Fig. 10). A deep trough is impressed into the lateral surface of the base of the crest, as in the Polish *Metoposaurus* (Sulej, 2007) (Fig. 10). According to Sulej (2007), this trough is not present in *Cyclotosaurus* specimens that are found alongside the Polish *Metoposaurus* specimens at Krasiejów and is a major feature that distinguishes these taxa.

DISCUSSION

Metoposaurid Systematics

The new specimens of *Metoposaurus algarvensis* from Portugal help clarify the systematics of European metoposaurids, especially when studied within the context of Sulej's (2002, 2007) recent exhaustive descriptions of the Polish *Metoposaurus* material. In particular, the Portuguese specimens permit a more confident diagnosis of the genus *Metoposaurus* (containing three species: *M. algarvensis, M. diagnosticus, M. krasiejowensis*) relative to other metoposaurids from Africa and North America. The Portuguese taxon possesses an interclavicle with a restricted region of hexagonal, isometric pits on the ventral surface, which is also seen in the German and Polish species but not on North American material. This was hypothesized by Sulej (2002, 2007) to be a diagnostic character of *Metoposaurus*, and the identification of this feature in *M. algarvensis* strengthens this argument. Furthermore, the Portuguese taxon also shares with the German and Polish *Metoposaurus* species a lacrimal that participates in the orbital margin, which is rarely seen in other metoposaurid specimens. Seeing that these characters are now observed in a range of *Metoposaurus* material from across Europe, but rarely if ever in other taxa, they can confidently be considered as diagnostic features of *Metoposaurus* based on present knowledge.

Our comparisons of the new Portuguese material with the German and Polish collections also reveal several new features that may help distinguish between metoposaurid species, particularly the European species of *Metoposaurus* (Fig. 11). Most previous metoposaurid taxonomies have separated species based on features of the skull roof, including the shapes of sutures and the orientation of the lateral line systems. We have found, however, that there is also a large amount of variation in other portions of the metoposaurid skull, particularly the braincase and the mandible. The new Portuguese species is diagnosed based on four autapomorphies of the braincase and four autapomorphies of the mandible. These features are not seen in the Polish *M. krasiejowensis* and in many cases cannot be assessed in the German *M. diagnosticus* because of poor preservation. Therefore, it remains possible that some of these features may support a clade consisting of *M. algarvensis* and *M. diagnosticus* to the exclusion of *M. krasiejowensis*. In any event, our identification of several discrete differences in the braincase and mandible between the Portuguese and Polish material indicates that metoposaurid skulls may not be as morphologically conservative (invariable) as often thought (e.g., Spielmann and Lucas, 2012).

We have also identified several features that the German and Portuguese taxa may share, which are not present in the Polish taxon. These include a 'W'-shaped postorbital loop, a small expansion angle on the parietals (the angle between the left and right parietal-supratemporal sutures), a straight lateral margin of the quadratojugal, a rectangular to subrectangular dorsal portion of the foramen magnum, dorsal and ventral portions of the foramen magnum that are approximately equal in depth, and occipital condyles that are mediolaterally elongate ovals widely separated on the midline. Some of these characters, such as the straight lateral margin of the quadratojugal, are also seen in non-European taxa such as *Koskinonodon*, so it remains uncertain whether they are truly synapomorphies of a subclade of *Metoposaurus* species or retained plesiomorphies. These conflicting hypotheses can only be tested with an inclusive, species-level phylogenetic analysis of metoposaurids. Such an analysis is outside of the scope of this paper, because it will first require careful specimen-level revision of the African and North American taxa, of the sort exemplified by Sulej's meticulous (2002, 2007) work on the Polish material. Given the lack of specimen-level, alpha-taxonomic revisions of taxa such as *Apachesaurus, Arganasaurus, Dutuitosaurus*, and *Koskinonodon*, it is not surprising that large-scale analyses of temnospondyl phylogeny often represent Metoposauridae with one or a few exemplars (e.g., McHugh, 2012; Schoch, 2013). Rectifying this situation should be a primary focus of future work on metoposaurids.

Metoposaurid Paleoecology and Paleobiogeography

The discovery of numerous associated, densely packed *Metoposaurus* individuals within a narrow stratigraphic horizon in Portugal is yet another example of a metoposaurid temnospondyl bonebed in the Late Triassic fossil record. Metoposaurid bonebeds are also known from at least five other sites in Africa (Dutuit, 1976; Jalil, 1996), Europe (Sulej, 2002, 2007), and North America (Case, 1932; Romer, 1939; Colbert and Imbrie, 1956; Zeigler et al., 2002; Lucas et al., 2010). These bonebeds differ slightly in fossil composition and preservational style. Some, such as the Lamy bonebed in New Mexico, are monodominant or monotaxic assemblages that include only the remains of metoposaurids (sometimes with a few rare specimens of other taxa), whereas others, like the Krasiejów bonebed in Poland, are a mixed assemblage of metoposaurids and other semiaquatic and terrestrial vertebrate taxa. The Portuguese bonebed appears to be monodominant at this time, but future excavations may reveal a more diverse fauna akin to Krasiejów. Furthermore, most of these bonebeds show some evidence of transport before burial, but others, most notably the Moroccan locality described by Dutuit (1976), contain articulated specimens that were probably preserved at the site of death. Additional work on the taphonomy of the Portuguese bonebed is needed to determine whether the specimens were transported before burial or died in situ. Regardless of the exact composition and preservational style of the Portuguese bonebed, it is additional evidence that metoposaurids often congregated in groups in freshwater systems and regularly succumbed to mass death events. This apparently occurred across their entire geographic range, given the widespread distribution of bonebeds.

Metoposaurus algarvensis (Fig. 12) is the first *Metoposaurus* species known from the Iberian Peninsula. The discovery of *Metoposaurus* in the Late Triassic of Portugal is also additional evidence that these large amphibians were widespread at low latitudes in the Late Triassic. All known *Metoposaurus* fossils have been discovered within a narrow belt between approximately 30°N and 30°S paleolatitude during the Late Triassic. This paleogeographic distributional pattern has long been recognized (e.g., Buffetaut and Martin, 1984; Hunt, 1993; Schoch and Milner, 2000; Witzmann and Gassner, 2008) and continues to hold with the discovery of new metoposaurid specimens in Europe and elsewhere. We here provide an updated map of all known occurrences of metoposaurid fossils (Fig. 13), based on records in the Paleobiology Database (http://paleobiodb.org).

We note that the distribution of metoposaurids is similar, but not identical, to the distribution of phytosaurs during the Late Triassic (Buffetaut, 1993; Brusatte et al., 2013; Stocker and Butler, 2013). Phytosaurs are also commonly found in the 30°N–30°S latitudinal belt, and were once thought to be restricted to these regions (Shubin and Sues, 1991), but are now known to extend into latitudes as high as 45–50°N. It is possible that metoposaurids extended into these higher latitudes but have yet to be discovered because these regions are more poorly sampled than the low latitudes, which are represented by the richly sampled Pangean rift sections in Africa, Europe, and North America. Like phytosaurs, metoposaurids are also notably rare in the southern hemisphere during the Triassic and remain completely unknown from the well-sampled Late Triassic deposits of South Africa and Argentina. Brusatte et al. (2013) hypothesized that

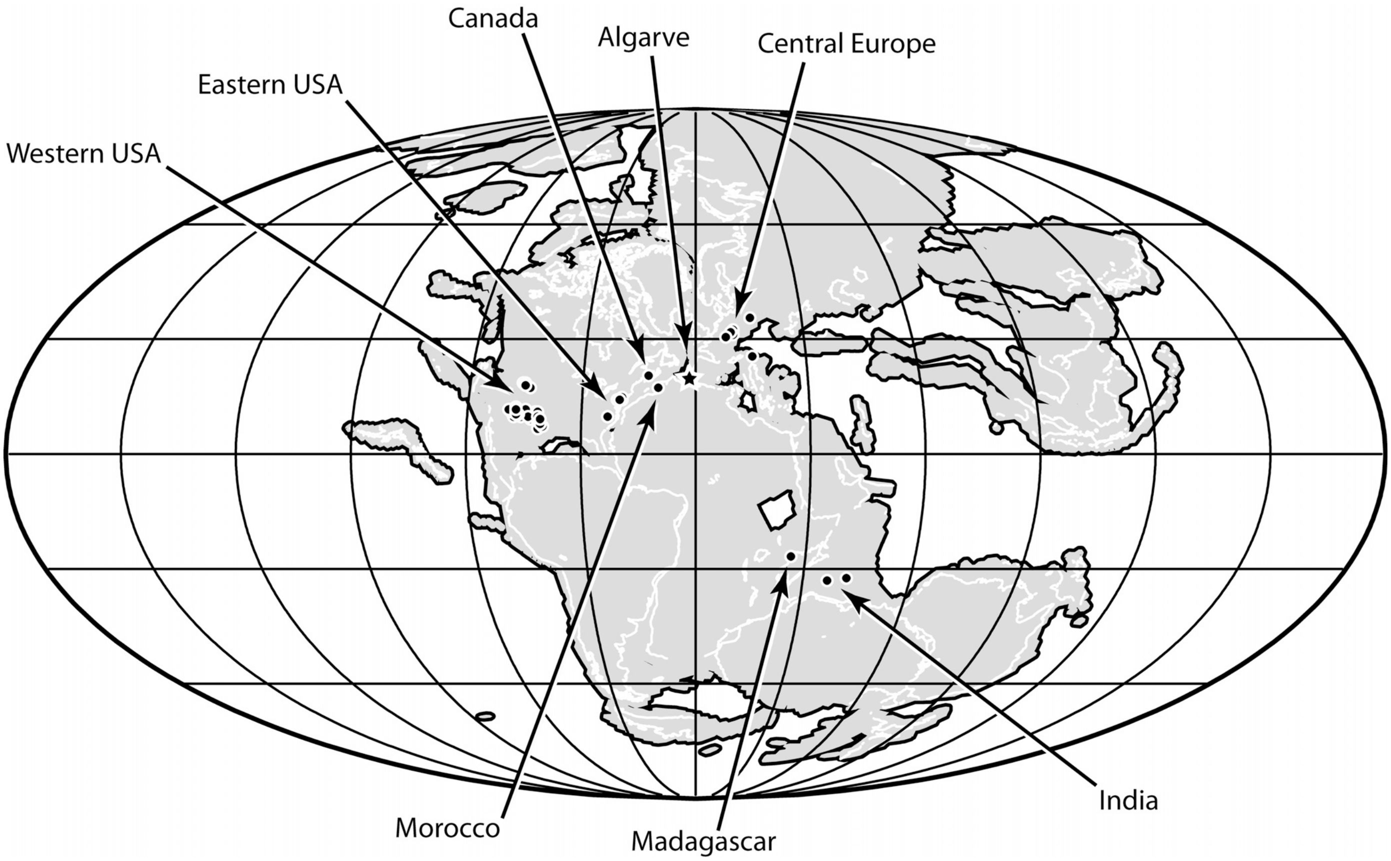

FIGURE 13. Paleogeographic map of the Late Triassic illustrating the currently known distribution of metoposaurid temnospondyls (paleomap generated using Fossilworks based upon data from the Paleobiology Database, Alroy 2013). The new record from the Late Triassic of Portugal is marked with a star.

the lack of phytosaurs in these regions may have been caused by local climatic conditions in southwestern Pangea, which is thought to have been more arid than the monsoonal environments in low-to-mid latitudes during the Late Triassic (Sellwood and Valdes, 2006). If correct, this hypothesis may also explain the absence of metoposaurids in the same faunas and may indicate that climate was a major driver of the paleoenvironmental distributions of many vertebrate groups during the Late Triassic.

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