SHORT COMMUNICATION

THE FIRST PHYTOSAUR (DIAPSIDA, ARCHOSAURIFORMES) FROM THE LATE TRIASSIC OF THE IBERIAN PENINSULA

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The Triassic was first defined based on the characteristic three-fold sequence of rocks that crops out across much of Europe, and many of the first records of Triassic dinosaurs, crocodile-line archosaurs, and other vertebrates were discovered in Great Britain, France, Switzerland, and Germany. These discoveries helped paint a general picture of the Triassic as a critical transitional interval in Earth's history, during which Earth recovered from a devastating extinction and more modern terrestrial ecosystems composed of dinosaurs, crocodylomorphs, squamates, and mammals were first established (e.g., Sues and Fraser, 2010). Over the past 50 years, however, the focus of Triassic vertebrate research has shifted to the fossil-rich deposits of South America and western and northeastern North America. The European record has been overshadowed, but new discoveries are stimulating a major expansion of Triassic vertebrate work across Europe, especially in Germany and Poland (e.g., Gower, 1999; Dzik, 2001; Schoch, 2006; Dzik and Sulej, 2007).

Despite considerable exposures of Triassic terrestrial sedimentary rock, the Iberian Peninsula of southwestern Europe has to date contributed little to this renewed focus on the European Triassic vertebrate record. This situation is changing with recent descriptions of Triassic terrestrial vertebrates from Spain (e.g., Fortuny et al., 2011) and Portugal (Witzmann and Gassner, 2008; Steyer et al., 2011). Here, we describe the first Iberian record of a major clade of Triassic vertebrates, the long-snouted, semi-aquatic phytosaurs that are part of the great post-Permian archosauromorph radiation (e.g., Stocker and Butler, 2013). This specimen, the posterior end of a mandible and associated teeth, was discovered in southern Portugal, 2.7 m above and about 5 m lateral to a bonebed of the temnospondyl *Metoposaurus* in a mudstone unit within the same stratigraphic section as Central Atlantic Magmatic Province (CAMP) basalts, in a classic northern Pangean rift sequence (Fig. 1). The discovery of this specimen helps to better constrain the age of the Portuguese site and provides further evidence that basal phytosaurs were widely distributed in areas with a monsoonal-type climate during the Triassic (e.g., Buffetaut, 1993; Brusatte et al., 2013).

Institutional Abbreviations—FCT-UNL, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Lisbon, Portugal; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **ZPAL**, Institute of Paleobiology, Warsaw, Poland.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903
ARCHOSAURIFORMES Gauthier, Kluge, and Rowe, 1988, sensu Nesbitt, 2011

?ARCHOSAURIA Cope, 1869, sensu Gauthier, 1986 (see Nesbitt, 2011)
PHYTOSAURIA Jaeger, 1828, sensu Sereno et al., 2005
Gen. et sp. indet.
(Figs. 2, 3)

Specimen—FCT-UNL 700, posterior end of the right hemimandible, including the posterior part of the dentary, the nearly complete surangular and angular, a complete articular, and nearly complete prearticular (Fig. 2). The splenial appears to be entirely missing from the medial surface. None of the symphysis is preserved. No teeth are preserved in situ but nine isolated teeth were recovered immediately adjacent (within 10–20 cm) to the specimen and are inferred to have disarticulated following death, given their close association and that they show no evidence for postmortem transport (Fig. 3).

Locality and Horizon—Penina locality, Municipality of Loulé, Algarve Region, southern Portugal. Stratigraphically in the upper part of the Grés de Silves Formation (or Group of some authors), in the part of the formation termed 'AB2' (Fig. 1) and previously considered to be Hettangian in age (Palin, 1979). However, the presence of the temnospondyl *Metoposaurus* suggests instead a probable late Carnian–early Norian age (Steyer et al., 2011; see below).

Description—The mandible (Fig. 2) is not strongly crushed in any dimension and the external bone texture is generally well preserved, although some sutures are not visible because of either poor preservation or fusion. The entire specimen is 420 mm long anteroposteriorly as preserved, but comparisons with other phytosaur specimens (e.g., Huene, 1911:fig. 11; Camp, 1930:fig. 41; Hungerbühler, 1998:fig. 2.26) indicate that approximately the front half of the mandible is missing, meaning that the complete specimen may have reached up to 800 mm in length. The mandible is 40 mm deep dorsoventrally at the anterior-most point at which the entire dorsoventral depth of the dentary is preserved (although the unpreserved splenial would have made this depth slightly greater than preserved). The mandible reaches a maximum depth of 107 mm at a point approximately level to the most posterior margin of the external mandibular fenestra. The mediolateral width at the anterior broken edge is 17 mm, the maximum width of the glenoid is 49 mm, and the width of the retroarticular process is 15 mm.

The most salient feature of the mandible in lateral view is a large external mandibular fenestra, which is elongated anteroposteriorly, as is typical of phytosaurs (Huene, 1911; Camp, 1930; Hungerbühler, 1998, 2001) and some other archosauriforms (Nesbitt, 2011). The margins of the fenestra are nearly complete and well preserved, except for parts of the dorsal margin. Therefore, the size and shape of the fenestra as preserved are likely
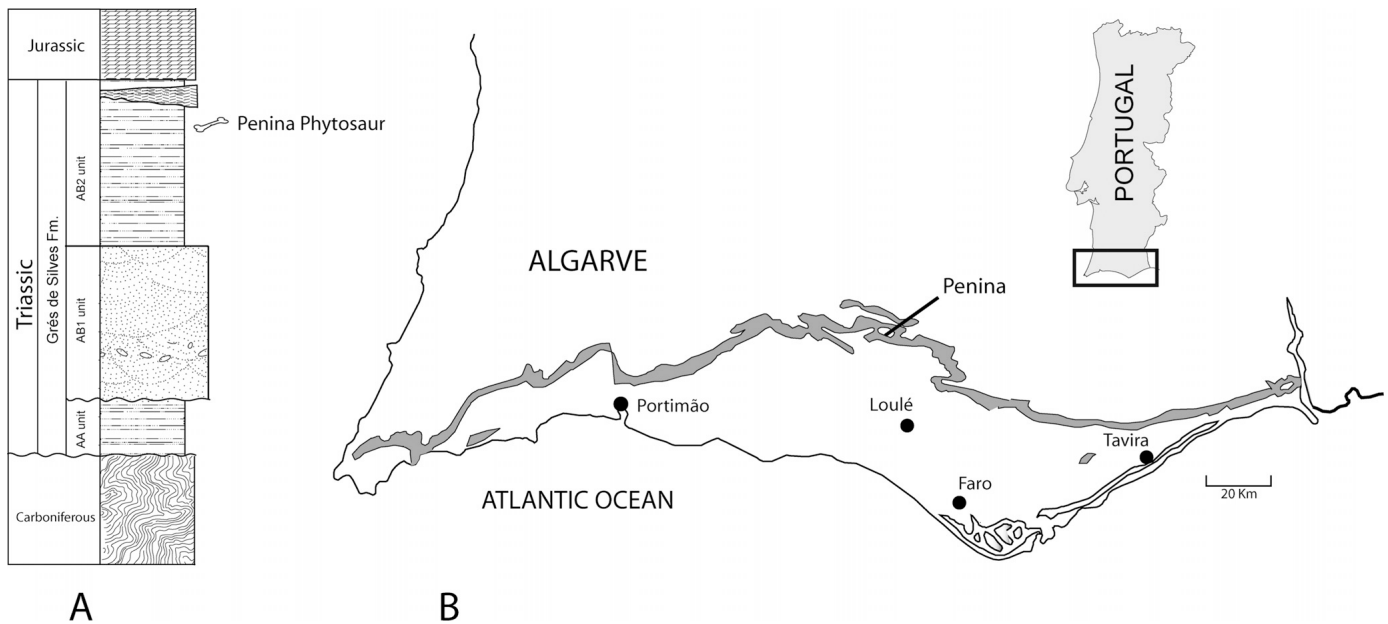
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FIGURE 1. Regional (**A**) stratigraphy and (**B**) location map of the Algarve Basin, in Portugal, with the Triassic in shaded area.

close to original. The fenestra is 190 mm long anteroposteriorly and approximately 30 mm deep dorsoventrally at its center.

Only a small portion of the posterior end of the dentary is preserved. The dentary-surangular contact, distinctly visible on the lateral surface, is positioned approximately 85 mm posterior to the anterior edge of the external mandibular fenestra. This contact is less clear medially but may be positioned immediately posterior to the last alveolus. If this is correct, the dentary laterally overlaps the surangular and extends further posteriorly on the lateral surface of the mandible than on the medial surface, as in other phytosaurs (Huene, 1911; Camp, 1930; Hungerbühler, 1998; Stocker, 2012).

As is characteristic for archosauriforms (e.g., Nesbitt, 2011:character 164), the dentary overlapped a flat facet on the angular beneath the anteroventral corner of the external mandibular fenestra. Although the dentary has shifted somewhat dorsally relative to the angular, if the two bones were preserved in natural articulation, then their suture would have intersected the ventral margin of the external mandibular fenestra on the lateral surface, approximately 55 mm posterior to the anterior edge of the fenestra. From this point, the dentary-angular suture slopes posteroventrally (differing from the anteroventral slope reported in *Protome batalaria*; Stocker, 2012) and intersects the ventral surface of the mandible anterior to the fenestra. The morphology and position of this suture is basically identical to that figured in most other phytosaurs (e.g., *Mystriosuchus*: Huene, 1911:fig. 11; *Brachysuchus*: Case, 1930:fig. 2; *Smilosuchus adamanensis*: Camp, 1930:pl. 2; *Nicrosaurus kapffi*: SMNS 5730, Hungerbühler, 1998). Ventral to the dentary-angular contact, a lateral exposure of the splenial would probably have been present but has broken away.

A conspicuous longitudinal groove on the lateral surface of the dentary extends anteroposteriorly subparallel to the alveolar margin. It is located approximately 8 mm ventral to the margin and maintains a relatively straight contour across its length. The lateral surface of the dentary dorsal to the groove is essentially flat, but ventral to the groove it is laterally convex. The convex surface of the dentary is traversed by a second anteroposteriorly extending groove at approximately the midheight of the

element. These paired grooves on the dentary were observed by Maisch and Kapitzke (2010) in *Mystriosuchus* and *Nicrosaurus meyeri* and proposed as a distinctive phytosaur feature. Indeed, these grooves are widespread in phytosaurs (e.g., *Smilosuchus adamanensis*: Camp, 1930:pl. 2; *Brachysuchus megalodon*: Case, 1930:fig. 2; *Smilosuchus gregorii*: Camp, 1930:pl. 6; *Paleorhinus*: ZPAL Ab III 112).

On the medial surface, the last nine dentary alveoli are visible. The medial walls of the alveoli would have been formed by the splenial (Hungerbühler, 1998), but this element is missing. As a result, the alveoli are open in medial view. The alveoli are variable in size, with the more distal (posterior) ones being slightly smaller in the mesiodistal direction than those located further mesially (anteriorly). The alveoli are all labiolingually compressed (the fourth alveolus from the posterior end of the jaw, which is complete, is 10 mm mesiodistally by 6 mm labiolingually) and they are separated by subtle vertical septa on the medial surface of the dentary. The medial surface of the dentary beneath the alveoli is flattened for the overlap of the splenial.

The surangular, which is widely exposed on the lateral surface of the mandible, forms the posterior and posterodorsal margins of the external mandibular fenestra and contributes to the lateral surfaces of the retroarticular process and the glenoid. The most conspicuous feature of the lateral surface of the surangular is a prominent, anteroposteriorly extending ridge that is positioned just dorsal to the midheight of the mandible. This ridge is typically present and well developed in phytosaurs (e.g., *Mystriosuchus*: Huene, 1911:fig. 11; *Brachysuchus*: Case, 1930:fig. 2; *Smilosuchus adamanensis*: Camp, 1930:pl. 2; *Nicrosaurus kapffi*: SMNS 5730, Hungerbühler, 1998; *Paleorhinus* sp.: ZPAL Ab III 678; *Protome batalaria*: Stocker, 2012:fig. 9). The ridge begins anteriorly along the dorsal margin of the posterior portion of the external mandibular fenestra and becomes increasingly prominent (offset laterally from the surface of the surangular) as it extends posteriorly. At its greatest development, it is offset 7 mm lateral to the adjacent lateral surface of the bone. The ridge is orientated relatively horizontally for most of its length. It is 4 mm in dorsoventral depth at its midpoint and gradually
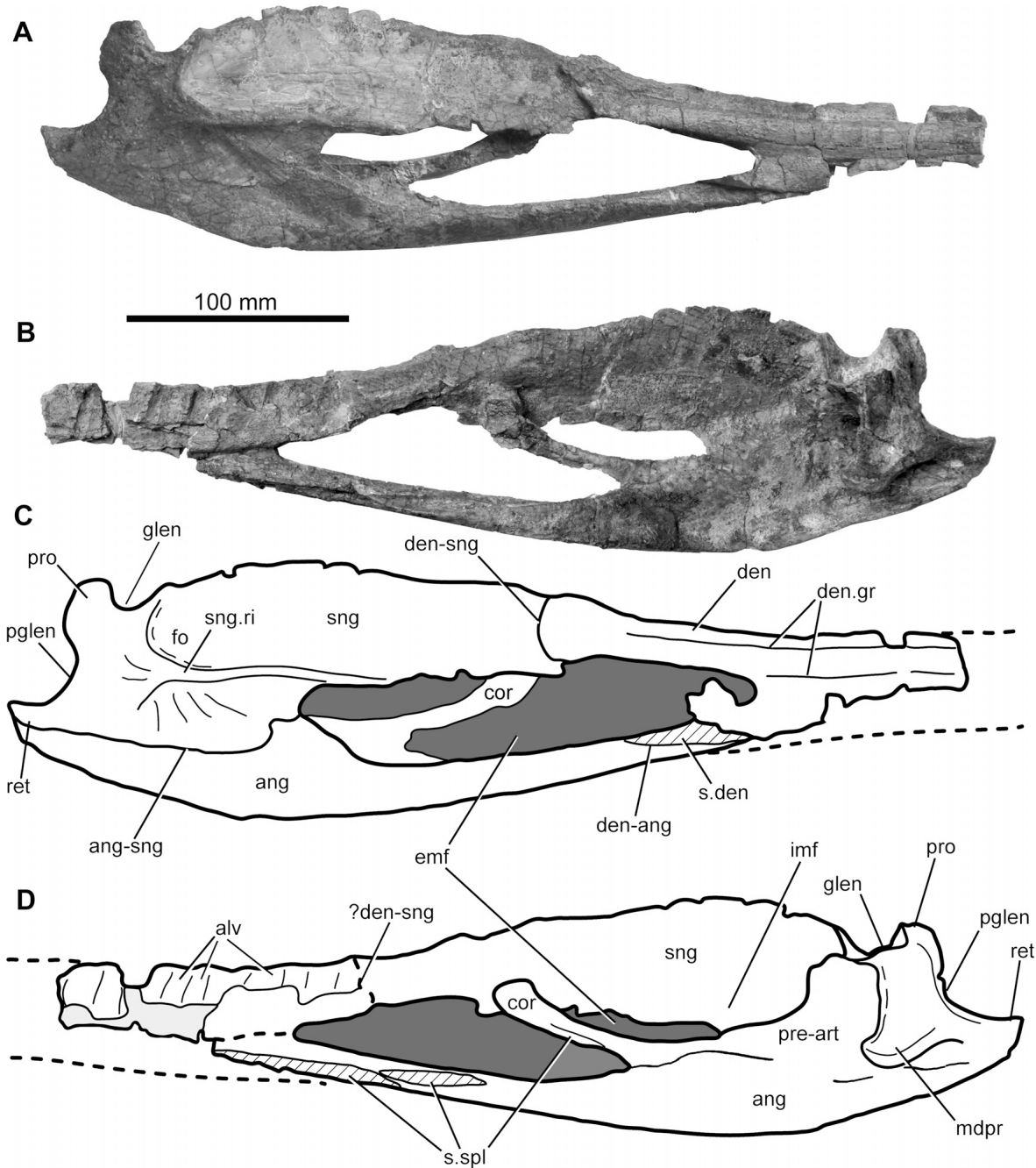
FIGURE 2. Phytosauria, gen. et sp. indet., incomplete right hemimandible (FCT-UNL 700) from the Late Triassic of Algarve, Portugal. **A**, **B**, photographs of the specimen in lateral (**A**) and medial (**B**) views; **C**, **D**, interpretative line drawings in lateral (**C**) and medial (**D**) views. **Abbreviations**: **alv**, alveoli; **ang**, angular; **ang-sng**, angular-surangular sutural contact; **co**, 'coronoid'; **den**, dentary; **den-ang**, inferred position of dentary-angular sutural contact; **den.gr**, grooves on lateral surface of dentary; **den-sng**, dentary-surangular sutural contact; **emf**, external mandibular fenestra; **fo**, fossa on lateral surface of surangular; **glen**, glenoid; **imf**, internal mandibular fenestra; **mdpr**, medial process of articular; **pglen**, postglenoid facet; **pre-art**, prearticular-articular complex; **pro**, dorsal projection of surangular; **ret**, retroarticular process; **s.den**, surface on anterior end of angular for overlap of dentary; **sng**, surangular; **sng.ri**, ridge on lateral surface of surangular; **s.spl**, surface for splenial.

increases in dorsoventral depth posteriorly, such that it is 14 mm deep at its posterior termination underneath the anterior edge of the glenoid. The dorsal edge of the ridge curves abruptly dorsally at this point and is continuous with the thickened anterolateral margin of the glenoid fossa.

The dorsal curvature of the surangular ridge forms the posterior margin of a deep and pocket-like fossa. This invagination is

the posteroventral corner of the large attachment surface for the jaw adductors, which cover a majority of the lateral surface of the surangular. This attachment site is smooth and is demarcated both posteriorly and ventrally by the prominent ridge. The dorsal edge of the attachment facet, which is the dorsal edge of the surangular itself, is damaged but clearly has a generally convex shape.

The lateral surface of the surangular underneath the lateral ridge and posterior to the external mandibular fenestra is ornamented by a series of pronounced ridges that radiate outwards from the posteroventral corner of the ridge. Similar ridges are observed in other phytosaurs (e.g., Hungerbühler, 1998). These ridges do not extend onto the angular ventrally. The contact between the surangular and the angular on the lateral surface is visible, and the surangular clearly overlapped the angular laterally.

Description of the glenoid and postglenoid regions is complicated because the sutures between the surangular, angular, and articular are not clearly visible on the medial surface of the mandible, largely because of fusions. The glenoid is visible in lateral view as a deep, semicircular notch. In dorsal view, the glenoid is approximately 43 mm wide mediolaterally and 30 mm long anteroposteriorly at its center. It is surrounded by a raised lip of bone.

On the lateral surface of the mandible, posterior to the glenoid, a discrete and well-defined tab-like dorsal projection of the surangular is separated from the retroarticular process ventrally by a broad concave margin in lateral view. The lateral surface of this tab-like process is covered with a raised convexity. The retroarticular process terminates posteriorly at a sharp point in lateral view. Its lateral surface is formed by the surangular dorsally and angular ventrally, whereas the majority of the process is composed of the prearticular-articular complex medially. Posterior to the glenoid, the retroarticular process forms a triangular postglenoidal facet (Hungerbühler, 1998) that faces posterodorsally.

On the medial surface of the mandible, positioned medial to the glenoid and anterior to the retroarticular process, is a prominent tongue-like medial process. A similar process is present in other phytosaurs (e.g., Huene, 1911:fig. 11; Camp, 1930:fig. 41; Hungerbühler, 1998:fig. 2.26), many rauisuchians, and some other crocodile-line archosaurs (Gower, 1999; Nesbitt, 2011:character 157). As described by Gower (1999) for *Nicrosaurus*, this process in phytosaurs is more dorsoventrally elongate than the more medially expanded process of rauisuchians. In medial view, the process projects anteroventrally, with an anterior margin that is concave and a posterior margin that is straight. The medial surface of the process is strongly concave and the ventral (distal) end is slightly expanded and rugose. The process is linked to both the retroarticular process and medial surface of the glenoid by strong ridges. A dorsomedial process posterior to the glenoid is not preserved, although it is unclear if this absence is genuine or results from damage. A dorsomedial process is present in several rauisuchians and other crocodile-line archosaurs (Nesbitt,

2011:character 157), and a homologous feature may be present in *Nicrosaurus kapffi* (SMNS 5730; 'postglenoidal process' of Hungerbühler, 1998).

The majority of the concave ventral margin of the internal mandibular fenestra is formed by the prearticular. Anteriorly, a strut of bone (the coronoid process of the prearticular) that is continuous with the prearticular forms the anteroventral border of the internal mandibular fenestra. Camp (1930) identified a separate coronoid ossification in this area in *Smilosuchus*, but Hungerbühler (1998) was unable to confirm this observation for *Nicrosaurus*. Stocker (2012) questioned the presence of a coronoid ossification in phytosaurs. The medial surface of this strut of bone is marked by a subtle depression along its ventral margin, which was likely overlapped in life by the splenial. The accessory internal mandibular fenestra (e.g., Hungerbühler, 1998) is not preserved because of the lack of preservation of the splenial.

The angular is widely visible in lateral view. Its ventral margin is smoothly convex along its entire length. Its lateral surface is slightly depressed near the articulation with the surangular, relative to both the overlapping surangular and the ventral part of the lateral surface of the angular. The medial surface of the angular is relatively flat over most of its surface, but facets are present for articulation with the splenial anteriorly. The splenial would have covered the medial surface of the angular anteroventral to the internal mandibular fenestra, and extended anteriorly to cover the medial surface of the dentary.

Two of the isolated teeth preserve the root and most of the crown, five are shed crowns, and two are portions of a root. All are relatively poorly preserved, obscuring fine details of surface texture and making it difficult to comment on the morphology of the carinae and denticles. Some of the teeth, especially the larger and more triangular crowns, have been crushed labiolingually. Precise measurements are difficult for most teeth because of incomplete preservation.

The teeth differ drastically in size and shape (Fig. 3). Two teeth are apicobasally elongate but mesiodistally thin, and resultantly have a spear-like shape in labial or lingual view (Fig. 3A). These teeth have a cross-section that grades between nearly circular to ovoid, and are slightly longer mesiodistally than labiolingually. The one well-preserved crown among this series is convex labially and flat lingually. Two teeth, which are noticeably larger than the remaining teeth, have mediolaterally thin crowns that are apicobasally short, giving a subtriangular shape in labial or lingual view (Fig. 3C). In these teeth, the mediolateral dimension is much larger than the labiolingual dimension, and both labial
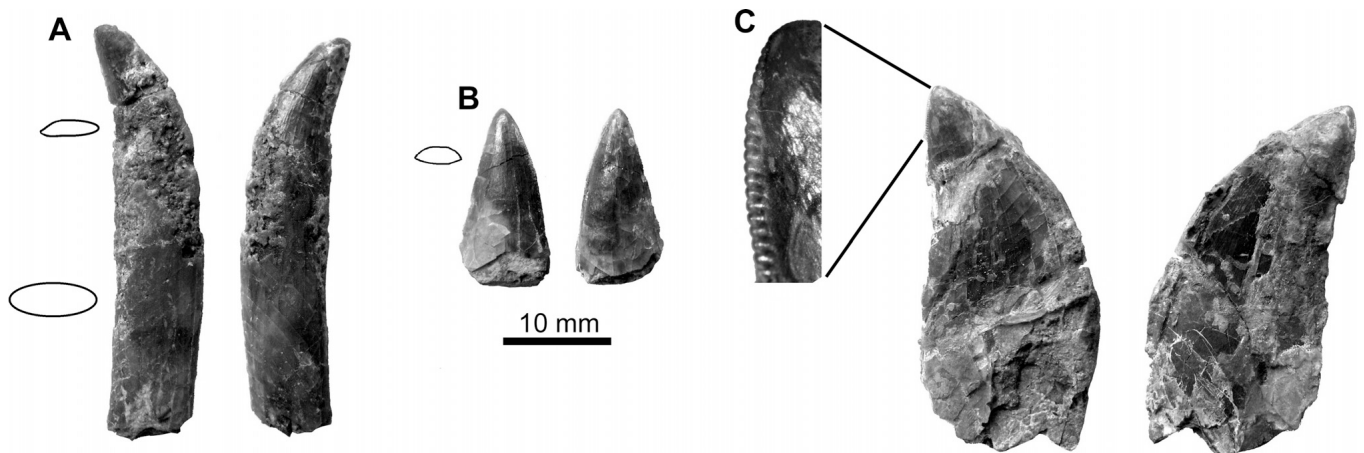

FIGURE 3. Phytosauria, gen. et sp. indet., teeth from the Late Triassic of Algarve, Portugal (FCT-UNL 700) in labial and lingual views. **A**, mesial tooth with cross-sectional outlines; **B**, intermediate tooth with cross-sectional outline; **C**, distal tooth with inset details of the distal denticles.

and lingual faces of the crown are relatively flat. The remaining three teeth form a gradational series between the spear-like and triangular teeth (Fig. 3B). These are mediolaterally thicker than the triangular teeth but not quite as thick as the spear-like teeth. Their apicobasal height is approximately intermediate between the spear-like and triangular teeth, and their labial surfaces are highly convex but lingual surfaces approximately flat.

Differences in the size and shape of teeth within a single phytosaur skull are common, because many phytosaurs possess a strongly heterodont dentition in which the size, shape, and other features of the dentition differ between the upper and lower jaws and along the tooth rows (Hungerbühler, 1998, 2000). Hungerbühler (1998, 2000) described in detail how the dentition of *Nicrosaurus* changes in morphology along the tooth rows, and how it differs between different regions of the upper and lower jaws. Such detailed studies have yet to be carried out on other taxa; it is therefore uncertain if a *Nicrosaurus*-like pattern of heterodonty is also present in other phytosaurs. This makes it difficult to use Hungerbühler's description to identify the jaw position of isolated phytosaur teeth, although this has been attempted in some cases (e.g., Brusatte et al., 2013).

Denticles are well preserved on only two teeth. First, denticles are preserved along the mesial and distal carinae near the tip of the large triangular crown, but only the distal denticles are preserved well enough to measure (Fig. 2C). These denticles are symmetrical and small, with eight occurring per millimeter. Second, denticles are preserved on the small transitional crown along the medial carina near the crown tip and these are similar in size and shape to those on the triangular tooth. As with the triangular tooth, there are eight denticles per millimeter. It is unclear if the denticles were continuous over the tip, but there clearly are no deep interdenticular sulci ('blood grooves') between them (see Currie et al., 1990, for an example of these in theropod dinosaurs) and there are no clear transverse 'wrinkles' on the labial or lingual surface of the tooth, as described in theropod dinosaurs (Brusatte et al., 2007), crocodylomorphs (Andrade et al., 2010), and some phytosaurs (Brusatte et al., 2013).

DISCUSSION

Published descriptions of phytosaur mandibles are sparse, limiting comparative observations and the recognition of systematically important variation. The presence and development of the lateral ridge on the surangular, the depressed lateral surface of the surangular above this ridge, the tab-like process posterior to the glenoid, the well-developed ventrally extending medial process, the nature of the surangular/dentary articulation anteroventral to the external mandibular fenestra, and the paired grooves on the lateral surface of the dentary are all characters that are shared with a range of other phytosaur species. Many of these are likely synapomorphies of Phytosauria, but most have not been explicitly used in numerical cladistic analyses, which generally concentrate solely on characters of phytosaur crania (e.g., Hungerbühler, 1998, 2002; Stocker, 2010). As more phytosaur mandibles are discovered and historic specimens are redescribed, the systematic importance of mandibular characters should become clearer.

Currently, the referral of the Portuguese hemimandible and associated teeth to Phytosauria is supported by the above-listed characters, general morphological similarities, and one explicit feature that has been described as a phytosaur synapomorphy: the presence of paired grooves on the lateral surface of the dentary (Maisch and Kapitzke, 2010). Other proposed mandibular synapomorphies of Phytosauria that have been specifically outlined in the literature, primarily relating to the relative lengths of the tooth-bearing and non-tooth-bearing parts of the mandible and the length and nature of the mandibular symphysis

(Hungerbühler, 1998, 2001), cannot be assessed in the Portuguese specimen because the relevant parts of the specimen are not preserved.

One character discussed briefly by Hungerbühler (2001) as potentially variable among phytosaurs, and therefore systematically useful, is the relative length of the external mandibular fenestra. Some non-phytosaurid phytosaurs retain the likely-plesiomorphic condition of a relatively anteroposteriorly short fenestra that terminates posterior to the tooth row (Mehl, 1928:fig. 1; Chatterjee, 1978:fig. 3). By contrast, Hungerbühler (2001) proposed that a synapomorphy of Phytosauridae is the presence of an elongate slit-like fenestra that extends below the posterior tooth row, as in the Portuguese specimen. However, a specimen of the non-phytosaurid *Paleorhinus* from Krasiejów in Poland (ZPAL Ab III 112) clearly possesses a similarly elongate and slit-like external mandibular fenestra, likely invalidating this character as diagnostic for Phytosauridae. It may, however, diagnose another more inclusive phytosaur ingroup clade.

Two anatomical characters that may be worthy of further investigation as additional data on phytosaur mandibles come to light are the length of the retroarticular process and the outline of the dorsal margin of the surangular in lateral view. The retroarticular process is elongate and tapers to a point in the Portuguese specimen and some basal phytosaur species (e.g., *Angistorhinus talainti*: Dutuit, 1977:pl. 5F, G; *Paleorhinus* sp. from Krasiejów: ZPAL Ab III 678, 2368), whereas it is strongly reduced and blunt in lateral view in a number of other phytosaurid species (e.g., *Rutiodon carolinensis*: Colbert, 1947:fig. 12; *Protome batalaria*: Stocker, 2012:fig. 9; *Nicrosaurus kapffi*: SMNS 5730; *Smilosuchus* spp.: Camp, 1930:pls. 2, 6).

In lateral view, the dorsal surface of the surangular is gently convex along its entire length in the Portuguese specimen and the non-phytosaurids *Paleorhinus* (Krasiejów: ZPAL Ab III 678) and *Parasuchus* (Chatterjee, 1978:fig. 3). By contrast, in the clade Leptosuchomorpha + *Protome*, the dorsal surface of the surangular is flat to gently concave in lateral view along most of its length, but rises to a distinct apex immediately posterior to the contact with the dentary (*Protome batalaria*: Stocker, 2012:fig. 9; *Nicrosaurus kapffi*: SMNS 5730; *Smilosuchus lithodendrorum*: Camp, 1930:fig. 41; *Smilosuchus gregorii*: Camp, 1930:pl. 6; *Mystriosuchus planirostris*: SMNS unnumbered).

In summary, these mandibular characters are most consistent with the identification of the Portuguese specimen as a relatively basal member of Phytosauria, potentially as a non-phytosaurid or a basal phytosaurid outside the Leptosuchomorpha + *Protome* clade of Stocker (2012). This phylogenetic hypothesis requires verification via discovery of more complete material. Because morphologically similar basal phytosaur taxa are present in the late Carnian–early Norian worldwide (e.g., Dutuit, 1977; Dzik, 2001), the Portuguese phytosaur specimen casts doubt on the hypothesis of Witzmann and Gassner (2008) that the Portuguese Penina locality is of latest Triassic or even earliest Jurassic age. This suggestion was solely based on the presence of the Penina locality within the same section as CAMP basalts of earliest Jurassic age, but our field observations indicate that the Penina locality is placed stratigraphically some distance below these basalts. Non-vertebrate, biostratigraphically useful fossils are currently lacking. The recent recognition of a new species of the typically late Carnian–early Norian temnospondyl genus *Metoposaurus* at the Penina locality further undermines a latest Triassic or basal Jurassic age (Steyer et al., 2011). Future field efforts should focus on determining more precisely the stratigraphic position of the Penina bonebeds relative to the CAMP basalts within the Algarve Basin. Regardless of its exact age, the Portuguese specimen is another example of a basal phytosaur from the mid-latitudinal monsoonal belt of the Late Triassic, lending further evidence that phytosaurs were widely distributed in this type of climate zone, and that phytosaurs and metoposaurids often coexisted in these

biomes (e.g., Buffetaut, 1993; Brusatte et al., 2013; Stocker and Butler, in press).

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