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SHORT COMMUNICATION

THE FIRST DENTARY OF *LISBOASAURUS* (CROCODYLOMORPHA, ?MESOEUCROCODYLIA) FROM THE LOWER CRETACEOUS (BARREMIAN) OF UÑA, CUENCA PROVINCE, SPAIN

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Lisboasaurus is a small-sized and poorly understood crocodylomorph from the Upper Jurassic (Kimmeridgian) Guimarota fossil locality in Portugal (Buscalioni et al., 1996; Schwarz and Fechner, 2004). The holotype for the type species *L. estesi* is an incomplete right maxilla with one in situ tooth. Referred material of *L. estesi* is restricted to a maxillary fragment and a box of isolated teeth (Milner and Evans, 1991; Buscalioni et al., 1996; Schwarz and Fechner, 2004). In his original descriptions, Seiffert (1970, 1973) erected two species, *L. estesi* and *L. mitracostatus*, for material from Guimarota. Because *L. mitracostatus* was based on extremely fragmentary cranial material of both lacertilians and crocodylomorphs, it was considered a nomen dubium for a long time (Milner and Evans, 1991; Buscalioni et al., 1996). A recent revision of the crocodylomorphs from Guimarota transferred the crocodylomorph specimens originally attributed to *L. mitracostatus* to the genus *Lusitanisuchus* (Schwarz and Fechner, 2004), which left *L. estesi* as the only valid species of *Lisboasaurus*.

The phylogenetic relationships of *Lisboasaurus* have long been debated. *Lisboasaurus* originally was described as an anguimorph lacertilian (Seiffert, 1970, 1973), but this interpretation was later questioned (Estes, 1983). *Lisboasaurus* next was interpreted as an archosaurian, most probably a maniraptoran theropod (Milner and Evans, 1991). Most recently, a phylogenetic analysis placed *Lisboasaurus* within the clade of mesoeucrocodylian crocodylomorphs (Buscalioni et al., 1996).

Recently, an incomplete crocodylomorph dentary with in situ teeth virtually identical to those of *Lisboasaurus estesi* was identified in collections from the Lower Cretaceous Spanish locality of Uña (Fig. 1). This find extends the spatial and temporal range of *Lisboasaurus* considerably. Even more importantly, this first known dentary of *Lisboasaurus* increases our knowledge about the cranial morphology of this taxon, which currently is diagnosed exclusively by maxillary characters, and supports assigning *Lisboasaurus* to the Crocodylomorpha. The objectives of this paper are to describe this new dentary, provide a revised diagnosis for *Lisboasaurus*, and discuss how the new dentary furthers our understanding of the genus.

The Uña locality is an abandoned coal mine in the village of Uña, in east-central Spain (Fig. 1). The sediments of the coal mine belong to the Barremian age Uña Formation, which is an alternating sequence of limestones and vertebrate fossil-bearing, lignite-coal lenses that are interstratified with marls (Gierlowski-Kordesch and Janofske, 1989; Brinkmann, 1992). The beds are interpreted to be limnic and fluviatile in origin and to have been deposited under warm, seasonal climatic conditions (Gierlowski-Kordesch and Janofske, 1989; Schudack, 1989; Brinkmann, 1992). The fossil vertebrate assemblage from Uña includes fish, amphibians, lacertilians, crocodylomorphs, dinosaurs, and mammals (Henkel and Krebs, 1969; Brinkmann, 1992; Kriwet, 1999; Rauhut, 2002). Fossils reported in this paper are housed in the Paleontology Section, Institute of Geological Sciences, Freie Universität Berlin (**IPFUB**), in Berlin, Germany.

FIGURE 1. Map of the Iberian Peninsula showing positions of the Uña locality (Barremian) in Cuenca Province, Spain, and the Guimarota locality (Kimmeridgian) in Leiria Province, Portugal.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970 (sensu Clark, 1986)
CROCODYLIFORMES Hay, 1930 (sensu Clark, 1986)
?MESOEUCROCODYLIA Whetstone and Whybrow, 1983 (sensu Benton and Clark, 1988)
LISBOASAURUS Seiffert, 1973

Type Species and Material—*Lisboasaurus estesi* Seiffert, 1973: IPFUB Gui.37 (holotype), right maxilla with one tooth (Seiffert, 1973:fig. 27; Milner and Evans, 1991:text-fig. 1, 2A–D; Buscalioni et al., 1996:figs. 1A–D, 2; Krebs and Schwarz, 2000:fig. 10.6); IPFUB Gui L.136, box of isolated teeth (Milner and Evans, 1991:text-fig. 2E, F; Buscalioni et al., 1996:fig. 1D);

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and IPFUB unnumbered specimen, incomplete left maxilla with two teeth (Milner and Evans, 1991:text-fig. 3; Buscalioni et al., 1996:fig. 1E, F).

Holotype Locality, Unit, and Age—Guimarota coal mine, Leiria Province, Portugal; Guimarota beds, Alcobaça Formation; Late Jurassic (Kimmeridgian). All *Lisboasaurus estesi* material is from the holotype locality.

Range—Late Jurassic (Kimmeridgian), Portugal, and Early Cretaceous (Barremian), Spain.

Emended Diagnosis—Small-bodied (less than 400 mm snout–tail length) crocodylomorph differing from all other crocodylomorphs in the following unique combination of dental features of unknown polarities: teeth weakly labiolingually compressed; lingual surface of tooth crowns and roots indented by shallow vertical groove; roots inflated and broader than crowns; maxillary and post-symphyseal dentary teeth with constriction between root and crown; and symphyseal dentary teeth with narrow, cingulum-like structure around base of crown. Among Crocodyliformes most closely resembles Gobiosuchidae and Mesoeucrocodylia in having the derived feature of straight (i.e., not curved) and vertically oriented tooth crowns. Resembles derived mesoeucrocodylians in the following combination of derived features: dentaries unfused across symphysis; dentaries transversely expanded and in symphyseal region wider than high; labial surface of dentary lacking longitudinal ridge; dentary with weakly convex labial margin and more strongly convex dorsal margin; and maxillary and dentary teeth set in isolated alveoli. Differs from derived mesoeucrocodylians in primitively retaining the following features: large antorbital fenestra in maxilla; splenials forming only posteriormost part of mandibular symphysis; and anterior alveoli in maxilla and dentary not enlarged.

LISBOASAURUS sp.
(Fig. 2A–F)

Referred Specimen—IPFUB UNA 70 I-N 2-3, incomplete right dentary preserving 12 tooth positions consisting of nine in situ functional teeth, one in situ replacement tooth, and two empty alveoli (Fig. 2A–F).

Locality, Unit, and Age—Uña coal mine, Cuenca Province, Spain; Uña Formation; Early Cretaceous (Barremian).

Description—IPFUB UNA 70 I-N 2-3 (Fig. 2A–F) is the anterior two-thirds of a small, right dentary preserving 12 tooth positions with nine in situ functional teeth. The anteriormost end of the dentary and corresponding part of the tooth row are missing. As preserved, the specimen measures about 17.3 mm in maximum length, 1.5 mm in maximum height, 3.4 mm wide across the posterior limit of the symphysis, and 1.5 mm wide behind the symphysis at the level of the ninth preserved tooth position. The specimen is dorsoventrally compressed and fractured, especially along the posterior part. Coaly matrix partially infills the fractures, alveoli, and primordial canal.

Based on the orientation of the preserved part of the symphyseal articular surface on IPFUB UNA 70 I-N 2-3, we estimate that in life the mandibular rami diverged posteriorly from one another at an angle of approximately 30°. The preserved part of the symphysis bears a replacement tooth at the first preserved tooth position and an intact, full-sized tooth at the second tooth position. Behind the posterior limit of the symphysis, the lingual surface of the dentary narrows for a distance of about five alveoli and then is of uniform thickness to the broken posterior end. When seen in dorsal view, the labial surface of the dentary beside each tooth position bulges outward slightly. In labial view, the dorsal margin of the dentary is weakly sinuous. The dorsal margin is convex immediately behind the symphysis and its apex is at the level of the first preserved tooth position; this is the highest point along the dentary. From the second to eighth tooth positions, the dorsal edge is concave and the bone is shallowest between the fifth and sixth tooth positions. The posterior part of the dorsal edge is broadly and shallowly convex, with the highest point in this region being at about the level of the eighth alveolus and then declining gently to the broken posterior end.

The labial and ventral surfaces of the dentary are ornamented (Fig. 2A). In the symphyseal region, the labioventral surface of the bone bears regularly spaced, small, and deep subcircular pits. More posteriorly, the pits become larger and their outlines become increasingly oval and anteroposteriorly elongate. Parallel to and below the dorsal margin of the dentary is a row of anteroposteriorly elongate and deep nutritive foramina.

At the mandibular symphysis, the lingual face of the dentary bears a flattened, rugose articular surface for sutured contact with the opposite dentary (Fig. 2B). Behind the symphysis, the primordial canal extends along the ventral third of the bone and cuts deep into the lingual face of the dentary. A longitudinally oval foramen perforates the floor of the primordial canal immediately behind the symphysis. Above the primordial canal and directly behind the symphysis, the lingual face of the dentary is indented by a longitudinal depression. Below the primordial canal is a rugose articular surface for contact with the splenial. The extent of the splenial and its pattern of contact with the dentary cannot be observed directly. Judging by the width and medial curvature of the symphyseal portion of the dentary and the position of the splenial articular surface along the lingual face of the dentary, the splenials likely were not wedged between the symphyseal surfaces of the right and left dentaries. Instead, the anterior end of each splenial probably lay just behind the dentary symphysis and must have comprised a relatively small part of the inter-mandibular joint.

The preserved alveoli are separated from each other by low ridges of interalveolar bone. Lingual to the bases of teeth along the anterior part of the tooth row, the interalveolar bone is perforated by regularly spaced nutritive foramina. The teeth possess conical tooth crowns (Fig. 2C) that are weakly labiolingually compressed (Fig. 2D), with the labial face shallowly convex, the lingual face nearly flat, and the apex bluntly pointed. The enamel is smooth on both the lingual and labial faces. No denticulate carinae are present. In all preserved teeth the base is inflated, so that the root is wider than the crown, and has a fairly roughened surface. A median groove extends along the lingual face of each tooth, from the ventral part of the crown to the exposed base of the root (Figs. 2C–F). This groove widens ventrally down the face of the root. In the anteriormost two functional teeth (i.e., at preserved positions 2 and 3), the base of the crown is slightly inflated relative to the more distal part of the crown, but there is no constriction between the root and crown (Fig. 2C). All more posterior teeth have a constriction between the root and crown (Figs. 2E, F). Teeth along the posterior part of the dentary are approximately 10% larger than the more anterior teeth.

DISCUSSION

Teeth in the dentary reported here resemble those in many other archosaurs. A median, vertical depression in the lingual surface of the teeth occurs in both theropod dinosaurs (Milner and Evans, 1991) and crocodylomorphs (Buscalioni et al., 1996). Teeth of derived coelurosaurian theropods also resemble the more posterior teeth in IPFUB UNA 70 I-N 2-3 in having a constriction at the base of their crowns (e.g., Norell et al., 1994:fig. 2; Currie and Dong, 2001:fig. 2; Xu et al., 2001:fig. 1). IPFUB UNA 70 I-N 2-3 exhibits the following combination of three dental features that is typical of crocodylomorphs, but is not known in any theropod: basal constriction; lingual depression; and no denticulate carinae. The deeply pitted ornament on the labial and ventral surfaces of IPFUB UNA 70 I-N 2-3 further supports assigning the dentary to the Crocodylomorpha.

Within the Crocodylomorpha, a median groove in the lingual

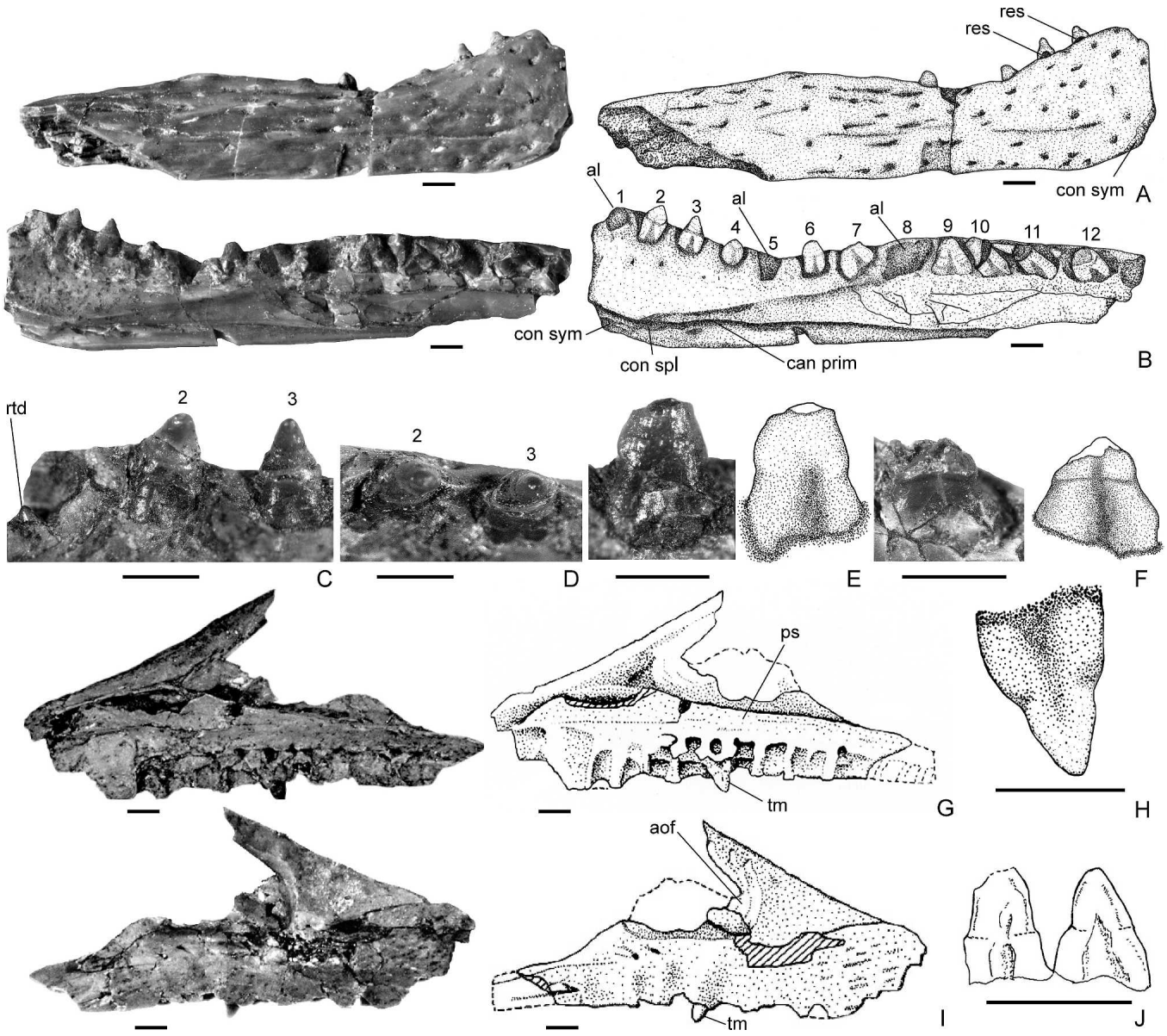

FIGURE 2. Jaws and teeth of *Lisboasaurus* Seiffert, 1973. **A–F**, *Lisboasaurus* sp., IPFUB UNA 70 I-N 2-3, rostal end of right dentary, missing anteriormost end and preserving 12 tooth positions with nine in situ functional teeth, from Uña (Barremian), Spain: **A**, **B**, photographs (left) and interpretative drawings (right) of entire specimen in (**A**) labial and (**B**) lingual views; **C**, **D**, detail photographs of in situ functional teeth at preserved positions 2 and 3 in (**C**) lingual view (note also replacement tooth crown at first preserved tooth position) and (**D**) dorsal view; **E**, detail photograph (left) and interpretative drawing (right) of in situ tooth at preserved position 6 in lingual view; **F**, detail photograph (left) and interpretative drawing (right) of in situ tooth at preserved position 12 in lingual view. **G–I** *Lisboasaurus estesi*, IPFUB Gui.37, holotype, incomplete right maxilla with one in situ tooth, from Guimarota (Kimmeridgian), Portugal: **G**, photograph (left) and interpretative drawing (right; taken from Milner and Evans, 1991:text-fig. 2B) in lingual view; **H**, interpretative drawing of the in situ maxillary tooth in lingual view; **I**, photograph (left) and interpretative drawing (right; taken from Milner and Evans, 1991:text-fig. 2C) in labial view. **J**, Drawing of two maxillary teeth in lingual view of the undescribed "Las Hoyas crocodylomorph" LH-7991 from Las Hoyas, Spain (taken from Buscalioni et al., 1996:fig. 1D; © copyright 1996 The Society of Vertebrate Paleontology; reprinted and distributed with permission of the Society of Vertebrate Paleontology). **Abbreviations**: **al**, alveolus; **aof**, antorbital fossa; **can prim**, primordial canal; **con spl**, contact surface for splenial; **con sym**, symphyseal contact surface; **ps**, palatal shelf; **res**, resorption pit in tooth; **rtd**, replacement tooth; **tm**, maxillary tooth. Arabic numbers denote positions of preserved tooth positions in dentary, numbered from anterior to posterior. Dotted lines depict parts of the holotype maxilla that were lost when the specimen was re-prepared (see Milner and Evans, 1991:504). Scale bars equal 1 mm.

face of the teeth has been reported in *Gobiosuchus* and *Candidodon* (Buscalioni et al., 1996) and in some very young, juvenile crocodylids (DS, pers. observ.). The dentary IPFUB UNA 70 I-N 2-3 was unfused to its counterpart, which is in contrast to the anteriorly fused dentaries of *Gobiosuchus* (Osmólska, 1972; Osmólska et al., 1997; Ortega et al., 2000). The maxillary and dentary teeth of *Gobiosuchus* are not constricted between the base and crown (Osmólska et al., 1997:fig. 7). Maxillary teeth in the ziphosuchian *Candidodon* possess a median, vertical groove and a cuspidate cingulum (Carvalho, 1994; Pol, 2003), but lack the inflated roots seen in IPFUB UNA 70 I-N 2-3. Labiolingually compressed teeth with a median groove also seem to occur in the

Late Jurassic shartegosuchid *Nominosuchus*, but only in the cheek region (Efimov, 1996). The dentary of *Nominosuchus* and other shartegosuchids also possesses at least one enlarged caniniform tooth (Efimov et al., 2000; Kurzanov et al., 2003), which is absent in IPFUB UNA 70 I-N 2-3. Teeth in IPFUB UNA 70 I-N 2-3 are morphologically most similar to those of *Lisboasaurus estesi* in being straight, vertically oriented, weakly labiolingually compressed, and constricted between the root and crown, in possessing a median lingual groove, and in having an inflated base (cf. Fig. 2C–F vs. H). Based on the nearly identical tooth morphologies of specimens from Guimarota and Uña and, to a lesser extent, on the close geographic proximity and ages of the two sites, we identify the dentary IPFUB UNA 70 I-N 2-3 as belonging to the genus *Lisboasaurus*.

The scarcity of characters exposed in the Guimarota material and in the dentary IPFUB UNA 70 I-N 2-3 makes it impossible to determine whether the latter belongs to *Lisboasaurus estesi*. Compared with the one tooth preserved in the holotype maxilla IFPUB Gui.37 (Fig. 2G–I), teeth in IPFUB UNA 70 I-N 2-3 are slightly more labiolingually compressed. IPFUB UNA 70 I-N 2-3 also is about 10% smaller than IPFUB Gui.37. This size difference suggests that differences in relative size and tooth structure between IFPUB Gui.37 and IPFUB UNA 70 I-N 2-3 could be due to ontogenetic or individual variation, as frequently occurs in fossil and extant crocodylians (e.g., Kälin, 1933; Buscalioni and Sanz, 1990; Sullivan and Lucas, 2003). Mesial and distal carinae were described for teeth of *L. estesi* from Guimarota (Milner and Evans, 1991; Buscalioni et al., 1996), but when we examined the same specimens we saw carinae only on the referred isolated teeth IPFUB Gui L.136. None of the preserved teeth in the dentary IPFUB UNA 70 I-N 2-3 from Uña possesses carinae. Because all available material of *Lisboasaurus* is fragmentary, at present it is not possible to determine if these differences are taxonomically significant or are due to ontogenetic or individual variation.

Little new information can be obtained from the dentary IPFUB UNA 70 I-N 2-3 that decisively resolves the phylogenetic position of *Lisboasaurus*. Buscalioni et al.'s (1996) phylogenetic analysis identified *Lisboasaurus* as a basal mesoeucrocodylian and, based on four tooth apomorphies, placed *Lisboasaurus* as the sister taxon of the undescribed "Las Hoyas crocodylomorph" sensu Buscalioni et al. (1996). For comparison, two teeth from the "Las Hoyas crocodylomorph" are shown here in Figure 2J. The "Las Hoyas crocodylomorph" was the sister taxon of *Gobiosuchus* in Ortega et al.'s (2000) analysis and that sister pair formed the clade Gobiosuchidae outside of the Mesoeucrocodylia (see also Pol and Norell [2004] for a similar hypothesis on the phylogenetic position of the Gobiosuchidae). In contrast to the condition in gobiosuchids, but as in mesoeurcrocodylians, the Uña dentary is unfused anteriorly and transversely expanded, lacks a well-developed longitudinal ridge on its labial surface, and, at least in the symphyseal region, is wider than high; this combination of features also occurs in both *Araripesuchus* and the Neosuchia (Ortega et al., 2000; Pol and Apesteguía, 2005). The previously listed dentary characters support placing *Lisboasaurus* within the Mesoeucrocodylia, but this should be considered tentative because the Uña dentary exhibits no unambiguous mesoeucrocodylian synapomorphies.

The occurrence of *Lisboasaurus* in both the Upper Jurassic (Kimmeridgian) Guimarota locality and the Lower Cretaceous (Barremian) Uña locality reveals that the taxon was spatially and temporally more widely distributed than previously known. *Lisboasaurus* must have existed for at least 20 Ma on the Iberian Peninsula. The presence of *Lisboasaurus* in Uña also increases the diversity of crocodylomorphs previously reported from this locality (Brinkmann, 1992). The extremely small-bodied (ca. 40 cm snout–tail length) *Lisboasaurus* is now added to an assemblage of neosuchian crocodylomorphs that also includes the slightly larger (not more than 1 m snout–tail length) taxa *Unasuchus*, *Theriosuchus*, and *Bernissartia*, and the much larger (approximately 3 m snout–tail length) *Goniopholis*. The cooccurrence of at least five different-sized taxa implies that the Uña crocodylomorph assemblage was more ecologically diverse than hitherto assumed, which is consistent with paleoecological reconstructions of Uña as an extensive alluvial plain that contained a variety of suitable habitats for crocodylomorphs, such as braided rivers and a deep lake.

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