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Redescription of the Cranial Morphology of *Mariliasuchus amarali*, and Its Phylogenetic Affinities (Crocodyliformes, Notosuchia)

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ABSTRACT

The cranial morphology of *Mariliasuchus amarali*, a poorly known notosuchian from the Late Cretaceous of Southeastern Brazil, is redescribed based on new material. Its phylogenetic affinities within Crocodylomorpha are evaluated through a parsimony analysis involving 46 taxa and 198 characters. *Mariliasuchus* is nested well inside the clade Notosuchia, as the sister group of *Comahuesuchus*, a derived notosuchian from the Late Cretaceous of Argentina. Both taxa share the following unambiguous synapomorphies: ventral half of the lacrimal tapering posteroventrally, not contacting or only slightly contacting the jugal; presence of a large foramen on the lateral surface of the anterior part of the jugal; presence of procumbent premaxillary and anterior dentary alveoli; and ectopterygoids that do not participate of the palatine bar. The presence of procumbent premaxillary teeth, specialized tooth crown morphology, and fore–aft jaw movements suggests that this group presented complex jaw movements related to specialized feeding habits.

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INTRODUCTION

Sediments of the Bauru Basin, located in Southeastern Brazil, held one of the most diverse Upper Cretaceous Crocodyliform fauna known so far (Kellner, 1998). This diversity is predominantly of Notosuchian taxa, with some highly specialized forms such as *Sphagesaurus huenei* (Price, 1950; Pol, 2003) and *Mariliasuchus amarali* (Carvalho and Bertini, 1999). Despite the exquisite state of conservation of several fossil crocodilians unearthed from the Bauru Basin, few have been described in detail. Although the description of *Mariliasuchus amarali* was based on a specimen with an almost complete skull and partially preserved postcranium, the authors provided little details of its anatomy. Additionally, the originally description is based on a juvenile specimen (Carvalho and Bertini, 1999). Carvalho and Bertini (1999) concluded that *M. amarali* is more closely related to *Notosuchus terrestris* than to any other notosuchian, allocating it in the family Notosuchidae along with the genera *Notosuchus* and *Malawisuchus*. We present here a redescription of the species based on mostly complete skulls of a subadult and two adult specimens found in the same locality from which the type specimen was collected. The new material described here allows a more careful evaluation of the phylogenetic affinities of *Mariliasuchus amarali*.

GEOLOGICAL SETTING

The fossil remains of *Mariliasuchus amarali* reported here as well as the holotype described by Carvalho and Bertini (1999) were collected in a road cut at the right margin of the Água Formosa creek (coordinates 22°20′28″S and 49°56′46″W), 10 km south from the urban area of Marília, about 500 m from the secondary road between this city and the locality of Ocauçu (São Paulo State), in the southeastern part of the Bauru Basin. This basin is a large cratonic depression developed during the Late Cretaceous in the central-southeastern portion of the South American Platform (Fernandes and Coimbra, 1996). With an area of about 370,000 km^2 (fig. 1A) and a maximum preserved thickness of 300 m of clastic deposits, the Bauru Basin contains a sedimentary sequence—the Bauru Group—made up mostly of sandy continental deposits, overlying the Early Cretaceous basaltic lava flows of the Serra Geral Formation (Riccomini, 1997). The depocenter of the basin is coincident with the maximum thickness of the volcanic pile of the Serra Geral Formation, in the region of confluence between the Paraná and Paranapanema rivers (fig. 1A), indicating that the basin formed by slow and gradual subsidence in response to the loading of its substrate (Riccomini, 1997).

The classical stratigraphic division of the Bauru Group in the state of São Paulo was proposed by Soares et al. (1980) and encompasses the Caiuá (cross-bedded sandstone), Santo Anastácio (massive to slightly stratified sandstone), Adamantina (massive to slightly stratified sandstone interlayered with mudstones), and Marília (sandstone and conglomerates with limestone cement) formations. Suguio (1981) and Fernandes and Coimbra (2000) also recognized the Araçatuba (layers of sandstone, siltstone, and mudstone) and the Presidente Prudente (sandstone and mudstone) Formations, respectively.

The stratigraphic relationships of the units along a WNW–ESE section in the southeastern part of the basin are depicted in figure 1B. The Caiuá and Santo Anastácio formations are believed to be deposited in a paleodesert, the former representing the inner part of a sand sea and the latter the marginal sand sheets. The Araçatuba Formation probably represents a paleoswamp (Fernandes et al., 2003), whereas the Adamantina Formation comprises sand sheets, loess, and wadi deposits of a peripheral desert (Fernandes and Coimbra, 2000). The desertic conditions in this unit decreases upward. Castro et al. (1999) described lacustrine deposits in the medium to upper part of the Adamantina Formation, northeast of the basin depocenter. Isotopic δ^{18}O data from ostracod carapaces present in these deposits suggest the predominance of freshwater conditions (Castro et al., 1999).

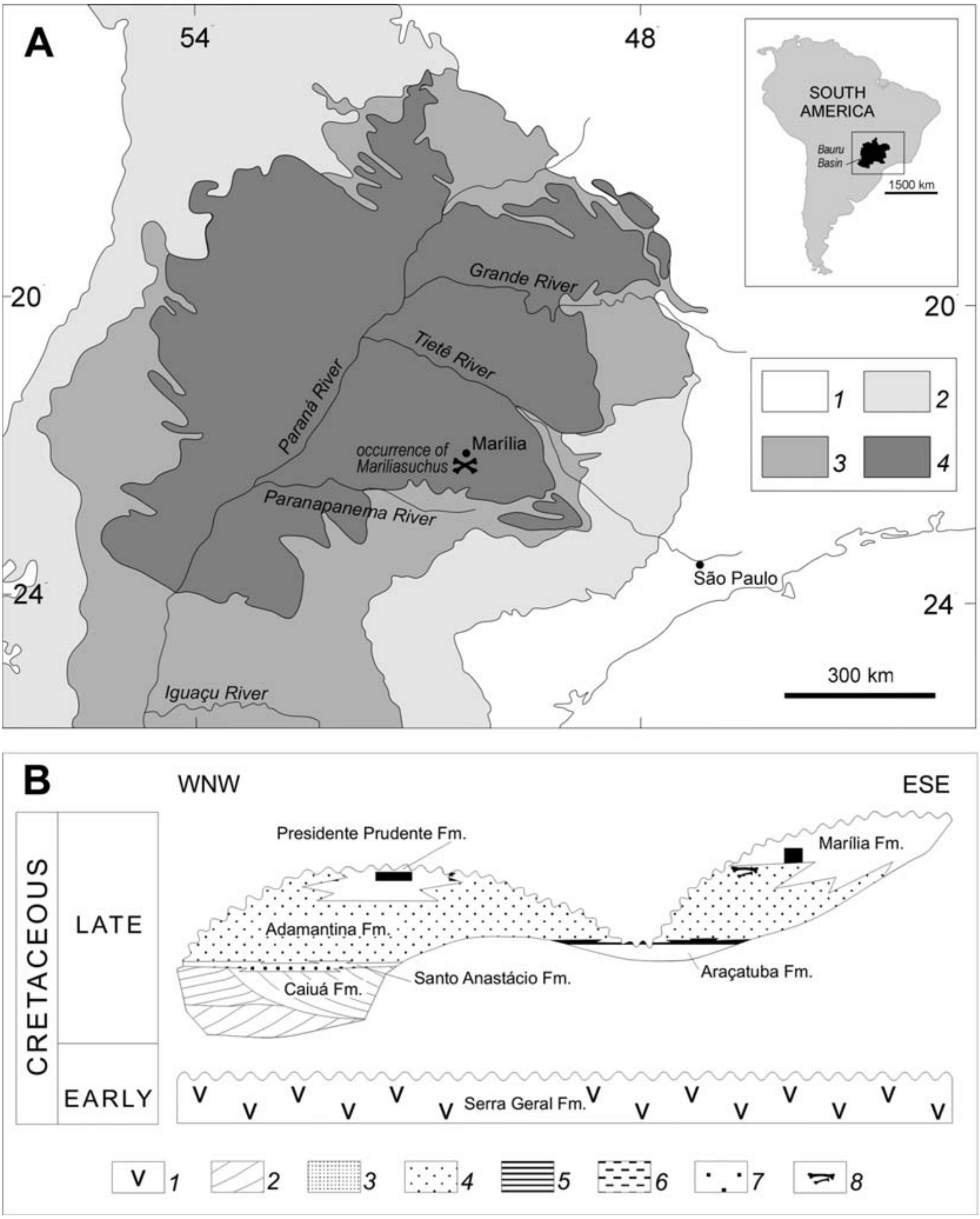


Fig. 1. **A**. Location of the *Mariliasuchus* occurrence in the Bauru Basin (after Riccomini 1997, modified): **1,** Precambrian basement rocks; **2,** Paraná Basin (Ordovician to Triassic); **3,** Serra Geral Formation (Early Cretaceous); **4,** Bauru Basin (Late Cretaceous). **B**. Stratigraphic relationships of the Bauru Group in the southeastern part of the Bauru Basin: **1,** basaltic rocks; **2,** cross-bedded sansdstone; **3,** massive to slightly stratified sandstone; **4,** massive to slightly stratified sandstone interlayered with mudstones; **5,** sandstone, siltstone, and mudstone; **6,** sandstone and mudstone; **7,** sandstone and conglomerate with limestone cement; **8,** position of *Mariliasuchus* remains.

Deposition of the Presidente Prudente Formation took place in a shallow fluvial meandering system (Fernandes and Coimbra, 2000). The Marília Formation, uppermost unit of the Bauru Group, represents an influx of alluvial fans associated with the uplift of the eastern border of the Bauru Basin (Riccomini, 1997).

The depositional age of the Bauru Group is still poorly defined. It was first established as Senonian on the basis of the dinosaur remains found in both the Adamantina and Marília Formations (Huene, 1939). Calcareous microfossils (ostracods) of the Adamantina Formation near the city of Presidente Prudente (western part of the state of São Paulo) were assigned to the Turonian–Santonian time interval (Dias-Brito et al., 2001). The Marília Formation was considered of Maastrichtian age, based on vertebrate fossils (Fernandes and Coimbra, 2000). Considering the transitional stratigraphic relationships between the Adamantina and the overlying Marília Formation, it is probable that the Adamantina Formation is younger in the southeastern part of the Bauru Basin.

The outcrop previously described by Carvalho and Bertini (1999), and referred to the Adamantina Formation, is redescribed in the present work (fig. 2). The exposure comprises about 1.2 m of brown massive to slightly stratified mudstone, a loess deposit, covered by about 3.7 m of massive to slightly stratified sandstones of sand-sheets. Sand-sheets include decimetric intercalations of discontinuous laminae of shale interbedded with sandstone, which probably corresponds to ephemeral shallow ponds, and massive or cross-bedded sandstone with shale intraclasts representing, respectively, sand-sheet and ephemeral stream (wadi) with reworked shallow pond deposits. This facies association is representative of the upper part of the Adamantina Formation and typical of a peripheral desert with sporadic (seasonal?) rainfall and restricted flooding in ephemeral ponds.

Besides *Mariliasuchus*, the fossil record in the sand-sheet facies includes articulated amphibian remains, eggs, ostracods, ganoid scales, coprolites, and vertical burrows (*Skolithos*). Disarticulated vertebrate fossils (representing remains of *Mariliasuchus*, unidentified fishes, and an undescribed amphibian) are associated with reworked deposits, whereas the holotype of *Mariliasuchus amarali* was found just above the sedimentary record of ephemeral ponds.

Based on the stratigraphic position of the studied section, at the upper part of the Adamantina Formation (fig. 2), and its relationship with the overlying Marilia Formation, it is possible to consider a Campanian to Maastrichtian age for the studied samples of *Mariliasuchus amarali*.

SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES CLARK, 1986

MESOEUCROCODYLIA WHETSTONE AND WHYBROW, 1983

Mariliasuchus amarali Carvalho and Bertini, 1999

Figures 3–10

HOLOTYPE: Universidade Federal do Rio de Janeiro, Departamento de Geologia (DG/UFRJ) 50-R, a partially complete articulated individual with a nearly complete skull and partially preserved axial and appendicular skeletons.

REFERRED SPECIMENS: Museu de Zoologia da Universidade de São Paulo (MZSP-PV) 50 and 51, Museu Nacional do Rio de Janeiro (MN) 6298-V and 6756-V (see appendix 1 for institutional acronyms used throughout the text).

LOCALITY AND HORIZON: All the *Mariliasuchus* specimens were collected in a road cut at the left margin of the Peixe River, 18 km from the city of Marília, state of São Paulo, from the upper part of the Adamantina Formation, Bauru Group, southeastern part of the Bauru Basin. Based on the stratigraphic position of the studied section, possibly of Campanian to Maastrichtian age.

AMENDED DIAGNOSIS: The lacrimal is barely exposed on the lateral surface of the snout (figs. 3, 5), the ectopterygoid contacts the jugal and the maxilla extensively on its lateral edge, forming the medial border of at least the last maxillary alveolus on a ventral plane (fig. 4); dentary rami forming a mandibular symphysis that projects anteriorly to form an elongated

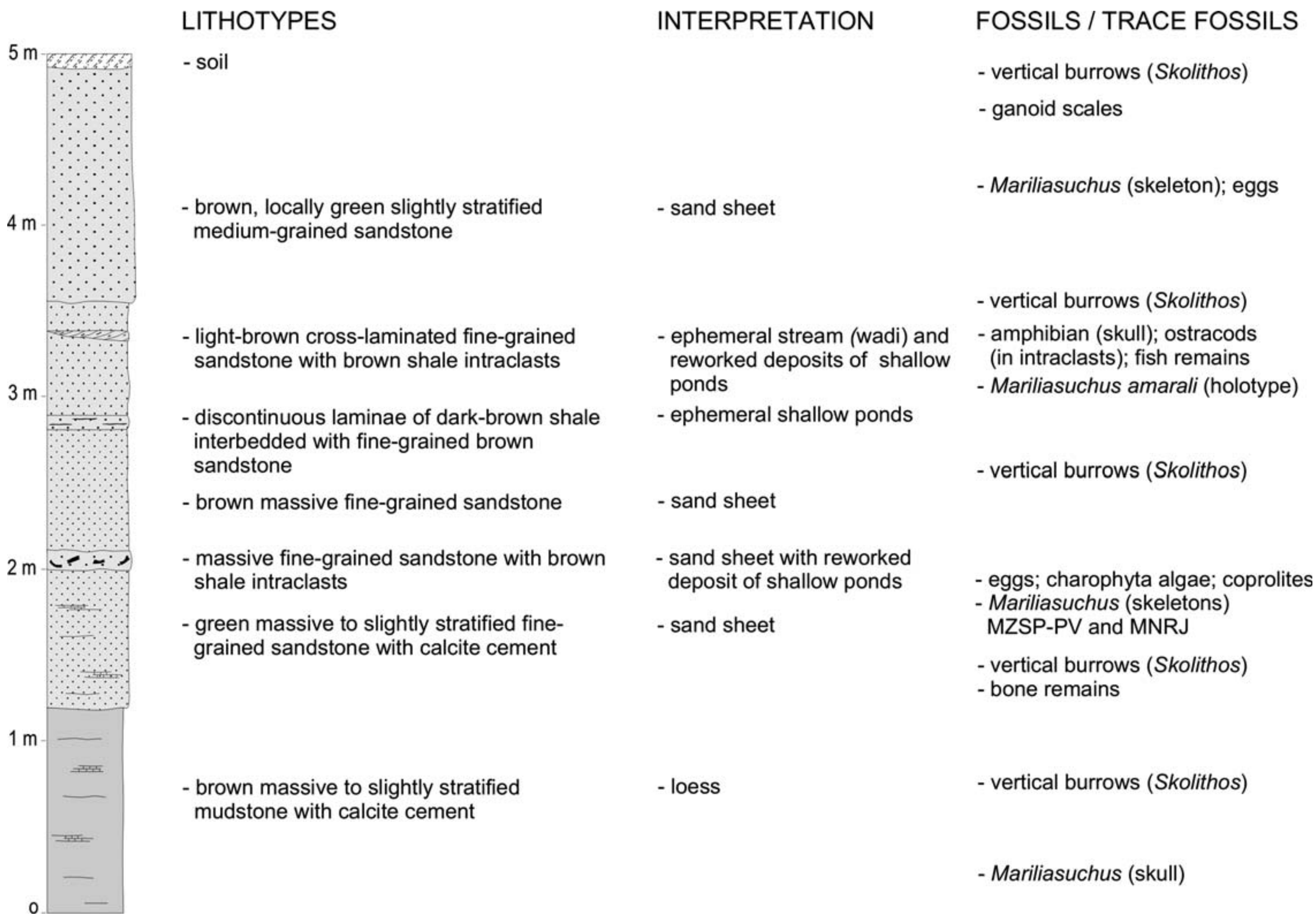
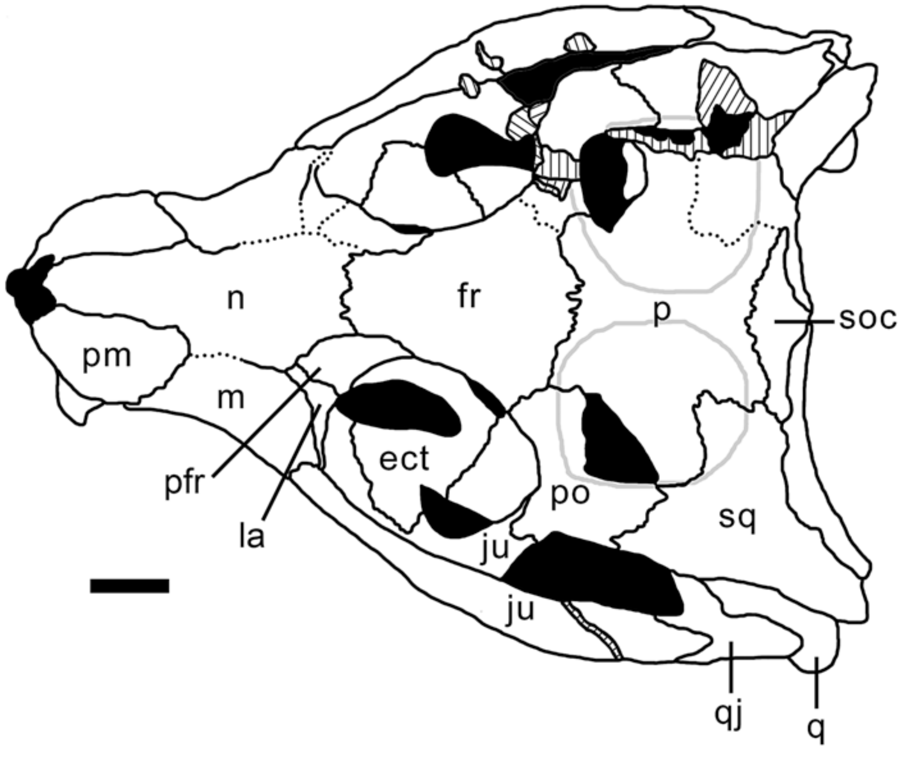


Fig. 2. Columnar section of the studied outcrop, Araçatuba Formation, 18 km southwest from Marília (coordinates: 49°56′45″W, 22°20′32″S).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and spatulated process with parallel lateral edges (figs. 6, 7, 8, 9A); there are four premaxillary, five maxillary, and nine dentary teeth that are characterized by their heterodonty (fig. 9); most dentary and maxillary teeth with anastomosing longitudinal striations formed by enamel ridges (fig. 10); well-developed serration of the mesial and distal margins of the crown (fig. 10A); and one to six longitudinally aligned tubercles at the base of each crow, which can be well developed and ornament the whole surface of the crown base (fig. 10B).

TAXONOMIC COMMENTS: The name *Mariliasuchus amaralensis*, published in a previous contribution by Bertini and Carvalho (1999), is a *nomen nudum* according to Article 13 of the International Code of Zoological Nomenclature (ICZN, 1999), and therefore is not an available name. Several widely used taxonomic names are followed throughout the text, such as Crocodyliformes, Mesoeucrocodylia, Neosuchia, and Notosuchia. Our usage of the first three of them follows that of Clark (Benton and Clark, 1988; Clark, 1994). Notosuchia was originally created by Gasparini (1971) to cluster *Araripesuchus*, *Uruguaysuchus*, and *Notosuchus*. Later, several authors pointed out that Sebecosuchia (Pol, 2003; Sereno et al., 2003) was related to this group, or at least to some of its members (Buckley et al., 2000; Ortega et al., 2000). Sereno et al. (2001) defined this taxon using a stem-based definition of phylogenetic taxonomy. Our results and usage of Notosuchia is consistent with these propositions.

DESCRIPTION

The material available is composed of four specimens. Specimen MZSP-PV 50 (figs. 3–8) consists of an almost complete individual with skull, mandibles, and most of the postcranial skeleton. The skull and mandibles are articulated and crushed on the left side, which caused a slight displacement of elements on the parasagittal axis of the skull. The upper right temporal bar is poorly preserved. Specimen MZSP-PV 51 (fig. 9) consists of a complete skull and mandibles and the anterior part of the postcranial skeleton, including the cervical region, the anterior girdle and forelimbs, and part of the thoracic region. This skull is less distorted than MZSP-PV 50, being slightly crushed dorsoventrally. The right postorbital bar and upper temporal regions are missing. Specimen MN 6298-V consists of an almost complete individual with skull, mandible, and most of the postcranial skeleton. Both skull and mandible are compressed laterally and slightly crushed on the sagittal axis. Specimen MN 6756-V is composed of a partial skull with the naris, the orbital, and palatal regions preserved, but lacking the braincase and temporal regions.

The postcranial material of specimens MZSP-PV 50, 51, and MN 6298-V is currently under preparation and will be treated elsewhere.

All four skulls analyzed here are oreinirostral (sensu Busbey, 1994) with anteriorly facing external nares, characteristic of terrestrial forms. The snout is somewhat constricted laterally at its midpoint (at the level of the second maxillary tooth), being more conspicuous in MZSP-PV 50 and MN 6298-V. The skull widens significantly at the level of the orbital region. The orbits are large, rounded, and dorsolaterally exposed when the palpebral is removed. The temporal region is short and wide, with large, rounded supratemporal fossae (sensu Witmer, 1997) occupying most of the flat skull table. The supratemporal fossae are separated by a wide flat surface of the parietal in MZSP-PV 51 and MN 6298-V (5.92 mm) whereas this separation is markedly narrow in MZSP-PV 50 (3.33 mm). In MN 6756-V, the parietal is not entirely preserved, precluding a precise measurement. Ontogenetic variation is visible on the shape of the supratemporal fossae, being more rounded and wider in the larger specimens whereas they are more elongated and narrower in the smaller specimen MN 6298-V. The infratemporal fenestrae are large, triangular, and face latero-dorsally, being almost completely exposed on dorsal view. The skull table and

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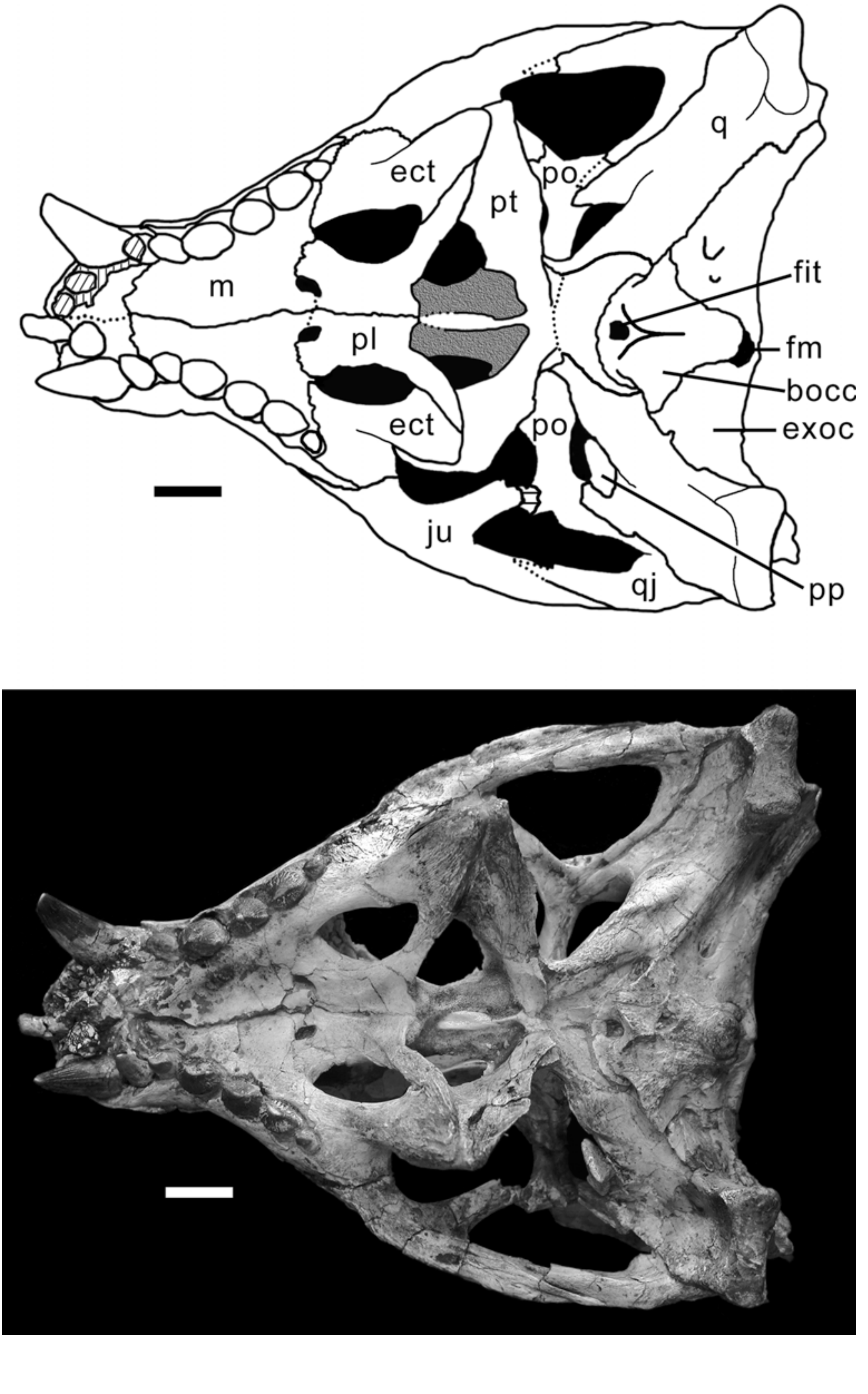
Fig. 3. Skull of MZSP-PV 50 in dorsal view. Scale bar = 1 cm. Anatomical abbreviations are listed in appendix 1.



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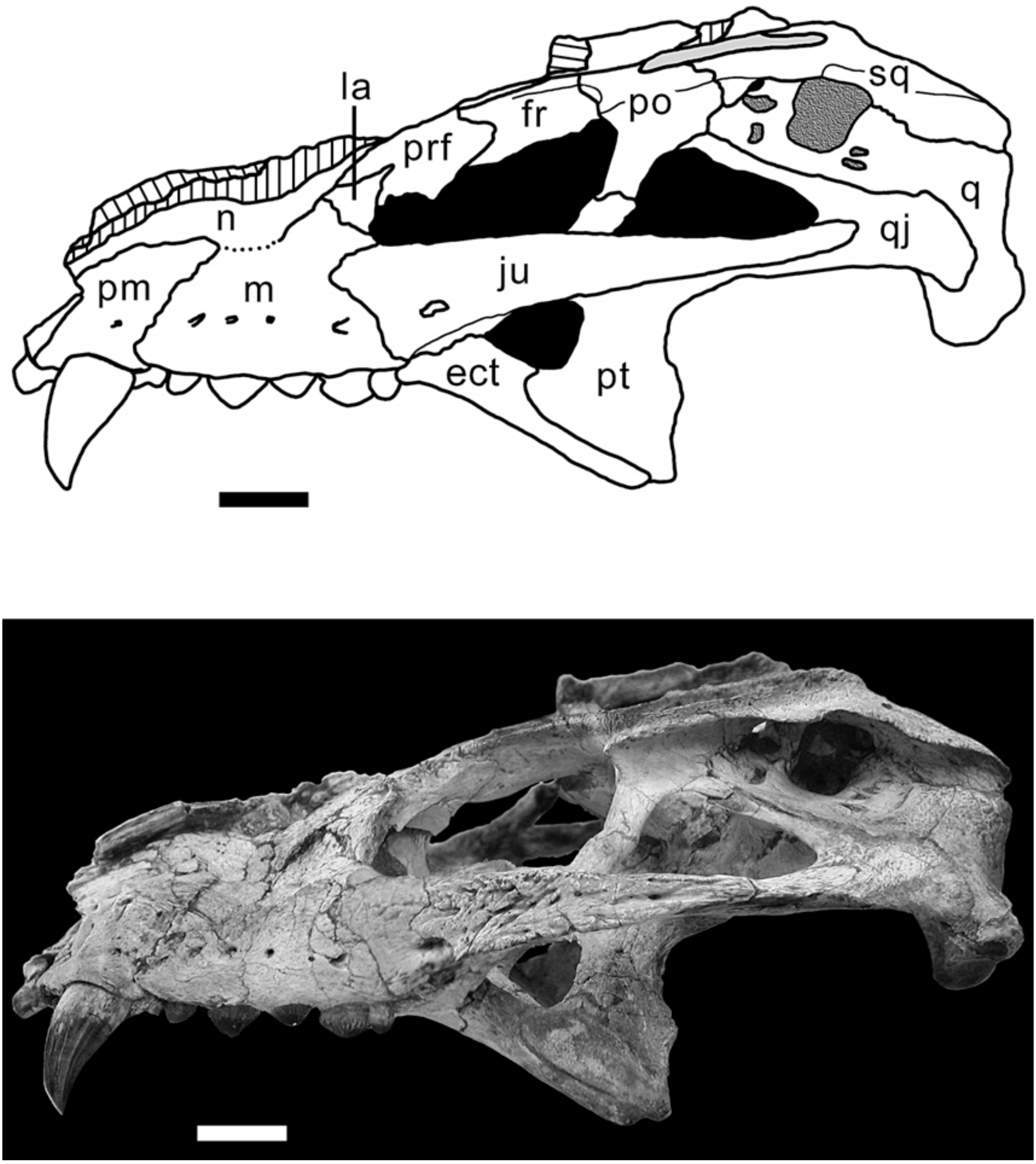

Fig. 5. Skull of MZSP-PV 50 in left lateral view. Scale bar = 1 cm. Anatomical abbreviations are listed in appendix 1.

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Fig. 4. Skull of MZSP-PV 50 in ventral view. Scale bar = 1 cm. Anatomical abbreviations are listed in appendix 1.

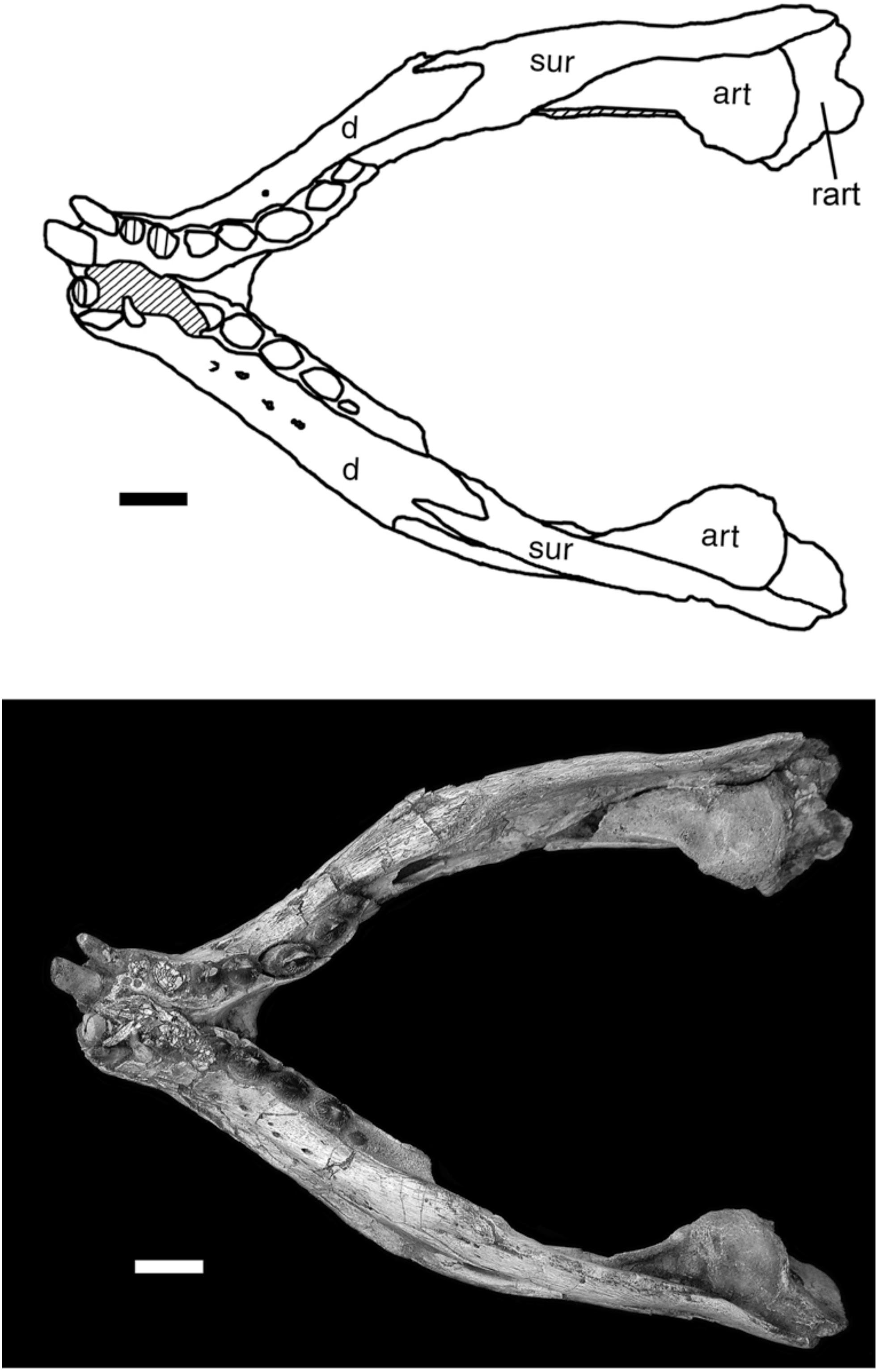
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TABLE 1
Measurements of Skulls of MZSP-PV 50, MZSP-PV 51, MN 6298-V, and MN 6756-V (in millimeters)

	MZSP-PV 50	MZSP-PV 51	MN 6298-V	MN 6756-V
SAPL	102.19	88.83	72.38	—
MWR	27.30	28.95	16.03	24.11
MFW	15.14		9.95	14.77
MPW	16.80		10.78	—
STW	63.72		41.05	—
SH	—		16.53	17.30
SL	43.72		24.20	31.14
TH	24.76		21.96	—
OL	29.19		21.87	28.05
MLSFo	24.79		18.55	—
MLSFe	13.12		10.47	—

Abbreviations: **SAPL** skull anteroposterior length; **MWR** minimum width of rostrum; **MFW** minimum frontal width; **MPW** minimum parietal width (measured within the fossae); **STW** skull table width; **SH** snout height at the level of the maximum constriction; **SL** snout length from the tip of the snout to the anterior border of the orbit; **TH** temporal height measured at the level of the temporal fossae on their dorsoventral axis; **OL** orbital length on its anteroposterior axis; **MLSFo** maximum length of supratemporal fossae, measured on its anteroposterior axis; **MLSFe** maximum length of supratemporal fenestrae, measured on its anteroposterior axis.

dorsal region of the snout of MZSP-PV 51 are ornamented by grooves and ridges that are more conspicuous in the region of the snout than in the temporal region. The other three specimens do not show the same amount of ornamentation, being barely ornamented in most of the dorsal surface of the skull. Cranial measurements are given in table 1.

Skull Elements

Rostral Region

The premaxillae (figs. 3, 4, 5, 10) form the ventral and lateral edges of the external nares and contribute to some degree to the dorsal edge. The ventral surface of the external nares bares a small dorsally directed crest formed at the premaxillary medial suture. This crest projects anteriorly to form a poorly developed narrow and pointed anterior process similar to the condition found in *Notosuchus* (MACN-RN 1040). Lateral to the external nares, the anterior surface of the premaxillae bear a smooth perinarial depression extending dorsoventrally. This depression runs parallel to the narial border, from the level of its dorsal margin toward the buccal edge. A similar condition is present in several notosuchians (e.g., *Comahuesuchus*, *Simosuchus*, *Notosuchus*, *Baurusuchus*). The lateral surface of the premaxillae is slightly convex due to the lodging of the enlarged caniniform root. This region is deflected and more ornamented dorsally to the caniniform root whereas the convex surface tends to be smooth and vertically oriented. There is at least one large neurovascular foramen located just anteriorly to the premaxilla–maxilla suture and another one at the level of the caniniform tooth. Contrary to Carvalho and Bertini's (1999) interpretation, the premaxilla–maxilla suture runs posterodorsally to meet the nasal, forming a blunt posterodorsal process of the premaxilla that contrasts with the narrow and pointed condition of *Comahuesuchus* and *Notosuchus*. At the level of the last premaxillary tooth, the maxilla extends laterally to the premaxilla, overlapping slightly the latter with a short anteriorly directed lamina as in *Notosuchus* (the condition is unknown in *Comahuesuchus*). From that point, the premaxilla–maxilla suture runs to the palatal surface, bordering the last alveolus and then curving gently anteromedially to meet its counterpart sagitally. In all specimens except MZSP-PV 50, there is evidence of a median foramen incisivum between the premaxilla–maxilla suture at the level of the sagittal plane. However, it is not possible to clarify the precise shape and number of foramina due to the poorly preserved condition of this region in all specimens. Specimen MZSP-PV 50 seems to lack any trace of foramen incisivum. The palatal branches of the premaxillae bear

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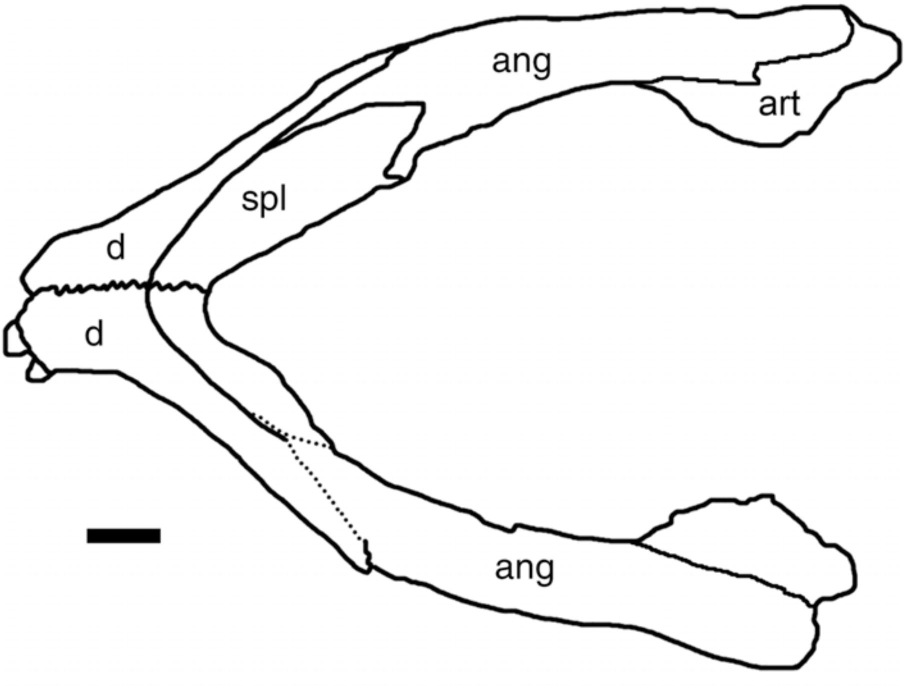
Fig. 6. Mandible of MZSP-PV 50 in dorsal view. Scale bar = 1 cm. Anatomical abbreviations are listed in appendix 1.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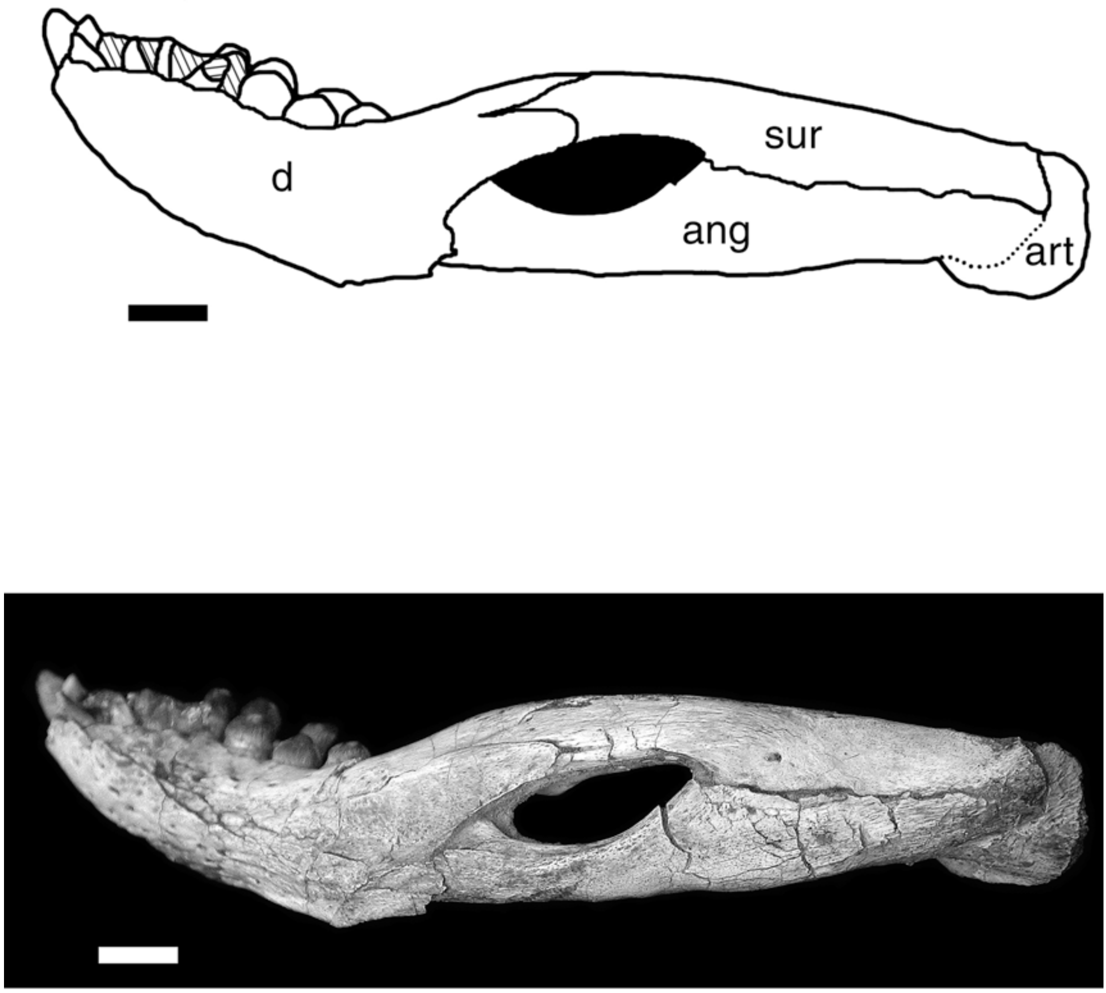

Fig. 8. Mandible of MZSP-PV 50 in left lateral view. Scale bar = 1 cm. Anatomical abbreviations are listed in appendix 1.

from 6 to 10 large alveolar foramina on the anterior part. Each premaxilla bears four teeth, with the third being caniniform (see dentition section below).

The maxillae (figs. 3, 4, 5, 10) show a tabular shape and are almost as long as high and restricted to the dorsolateral and lateral surfaces of the rostrum. As with the premaxillae, the maxillae are vertical and smooth on their ventral half and deflected with ornamentations on the dorsal half. Depending on the specimen, there are 4 to 10 large neurovascular foramina on the ventral half of the lateral surface. The suture with the nasal is anteroposteriorly directed and runs along almost all the dorsolateral side of the snout.

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Fig. 7. Mandibule of MZSP-PV 50 in ventral view. Scale bar = 1 cm. Anatomical abbreviations are listed in appendix 1.

Posteriorly, the maxilla contacts the lacrimal and participates on the orbital margin, forming its anteroventral corner. There is no vestige of an antorbital fenestra. The lateral contact between the maxilla and the jugal occurs just below the level of the anterior margin of the orbit, with the latter sending a short rounded anterior process laterally to the maxilla on its dorsal half. The maxilla-jugal contact runs ventrally toward the buccal margin where it meets the ectopterygoid. The buccal margin is straight, lacking the festooning pattern present in derived neosuchians. The palatal branches of the maxillae meet along their entire length in the sagittal line. The posterolateral border contacts the ectopterygoid along the medial margin of the last maxillary tooth (in MZSP-PV 50 and MN 6298-V) or the last two maxillary teeth (MZSP-PV 51 and MN 6756-V). Medially to this point, the border of the maxillae runs transversally and barely enters the anterior edge of the suborbital fenestrae. The maxilla–palatine suture extends anteromedially from the level of the suborbital fenestrae to the maxillo-palatine foramina where the maxilla contributes to its anterior edge. The maxilla–palatine sutures seem to run transversely to meet at the sagittal plane from the posteromedial edge of the maxillo-palatine foramina. There are five maxillary teeth on each maxilla that are located in individual alveoli that are only partially septate (i.e., the interdental plate is poorly developed). There are 6 to 10 neurovascular foramina along the lingual edge of the alveoli. In all specimens both labial and lingual margins are at the same plane, except in MZSP-PV 51 where the labial alveolar margin is much more developed ventrally than the lingual margin.

The pair of nasals (figs. 3, 5) forms most of the posterodorsal border of the external nares. They slightly widen posteriorly along their contact with the premaxillae and maxillae until reaching the anterior tip of the lacrimal. The nasal then narrows posteriorly along the contact with the anterodorsal surfaces of the lacrimal and prefrontal. The nasal–frontal suture, positioned just behind the anterior margin of the orbit, is transversally oriented and shows clear interdigitation in MZSP-PV 50, MN 6756-V, and MN 6298-V. In MZSP-PV 51, the precise position of the nasal–frontal suture cannot be determined due to the heavy ornamentation.

The lacrimal (figs. 3, 5) is barely exposed on the lateral surface of the snout and is restricted to the anterior border of the orbit. It shows a triangular shape being dorsoanteriorly expanded at the triple contact between lacrimal, maxilla, and nasal. Ventrally, the lacrimal tapers markedly along the anteroventral border of the orbit, barely contacting the expanded anterodorsal border of the jugal or not contacting at all, as in MN 6298-V. At that level the lacrimal is embraced medially by a dorsal flange of the maxilla. The lacrimal shows a posterior tuberosity exposed dorsally on its posterodorsal surface that receives the anterior tip of the palpebral. Dorsally to this tuberosity, the lacrimal contacts the prefrontal along an anteroposteriorly oriented suture. This suture continues ventromedially on the inner surface of the orbit, bordering the posterior opening of the lacrimal duct, which is completely included within the lacrimal.

Both anterior and posterior palpebrals were preserved in position in specimen MN 6298-V. Specimens MZSP-PV 50 and 51 retained right anterior palpebrals in position that were removed during preparation. A right posterior palpebral is also preserved in MZSP-PV 50, but dislocated and laying ventral to the supratemporal fenestrae along the anterodorsal process of the quadrate (fig. 4). In all specimens, the anterior palpebrals are blade-like, somewhat triangular, elongated, and strongly curved bones that are latero-posteriorly and dorsally positioned to the orbit. The dorsal surface of the anterior palpebrals is slightly ornamented. The posterior tip of the anterior palpebral lies close to the anterior tip of the posterior palpebral but does not contact the latter. The posterior palpebrals are short, broad, and somewhat triangular bones that lie along the anterior margin of the postorbital.

The prefrontal (figs. 3, 5) is positioned mostly on the anterodorsal border of the orbit, running from the dorsal midpoint of the orbit to the anterodorsal corner, where it meets the lacrimal. Anteriorly, the prefrontal expands to meet the nasal on an oblique suture. Most of the dorsal surface is ornamented by large rugosities where the palpebral articulates. The anterodorsal region of the prefrontal is much wider than the posterior region, where the prefrontal forms the orbital margin. Posteromedially, on the inner margin of the orbit, the prefrontal bears a small rounded process that overlaps the frontal. The prefrontal has well-developed prefrontal pillars strongly sutured to the palate. These are thin laminae, entirely oriented in an oblique position. Each prefrontal pillar bears a medially oriented process that meets it counterpart on the sagittal plane, forming a closed bridge below the olfactory bulbs.

Dorsal and Temporal Region

The frontals (figs. 3, 5) are completely fused and contribute to most (two-thirds) of the dorsal margin of the orbit. In all specimens except MZSP-PV 51, the dorsal surface of the frontals is flat and barely ornamented. In the latter, this surface is rugose and bears a slightly marked longitudinal ridge. A poorly defined longitudinal ridge is also present in *Comahuesuchus* and *Notosuchus*. It expands slightly posterolaterally to contact the postorbital in a strait longitudinal suture. The frontal meets the postorbital and the parietal at the anterior edge of the supratemporal fossa in MZSP-PV 50 and MN 6298-V, whereas in MZSP-PV 51 it seems to expand into the supratemporal fossa (not visible in MN 6756-V). The posterior margin of the frontal is strongly sutured to the parietal via a slightly concave, transverse, interdigitated suture. The lateral ventral flange of the frontals forms a concave and moderately developed dorsomedial inner orbital wall. Posteriorly, the flange is sutured to the postorbital and the dorsal projection of the laterosphenoid. Anteriorly, the flange is overlapped by a posterior process of the prefrontal.

The unpaired parietal (fig. 3) forms a dorsal table that is constricted between the supratemporal fossae, the constriction being wider in MZSP-PV 51 and MN 6298-V than in the other two specimens. In MZSP-PV 50, the parietal table represents only a thin string of slightly ornamented bone running between the fossae, whereas in MZSP-PV 51 and MN 6298-V this surface is much broader and ornamented, being almost as wide as the frontal at its narrower orbital constriction. Anteriorly, the parietal contacts the frontal on a broad and slightly concave suture. The parietal contacts the postorbital within the supratemporal fossa. Posterior to this contact, the parietal forms the entire medial surface of the supratemporal fossa, being bordered ventrally by the laterosphenoid and the ascending anterodorsal process of the quadrate. The laterosphenoid and the quadrate ascending processes form the medial wall of the supratemporal fenestra. Lateroposteriorly, within the supratemporal fossa, the parietal contacts the squamosal on an interdigitated suture that passes medially to the anterior temporal orbital foramen, which is totally enclosed within the squamosal. Posterior to this point the parietal meets the supraoccipital on the dorsal surface of the skull table.

The squamosal (figs. 3, 5) is triradiate, with the anterior branch contacting the postorbital, the medial branch contacting the parietal, and the posterolateral branch contacting the exoccipital and quadrate. In MZSP-PV 50 and MN 6298-V, the anterior branch is wide laterally and has a smooth dorsal surface whereas the medial branch is very narrow and ornamented dorsally. In MZSP-PV 51, both branches are ornamented. The postorbital–squamosal contact is directed posteromedially from the lateral margin of the skull table to the lateral margin of the supratemporal fossa, meeting the anterodorsal process of the quadrate on a longitudinal suture positioned at the inner edge of the supratemporal fenestra. Then, the squamosal suture runs posteriorly along the inner posterolateral surface of the supratemporal fossa to meet the parietal in a triple contact with the latter and the anterodorsal process of the quadrate. The lateral margin of the postorbital and squamosal overhangs the quadrate and quadratojugal, forming a deep otic recess. The squamosal is extensively sutured to the quadrate within the otic recess, forming the dorsal and posterior margins of the otic aperture. The posterolateral branch is almost smooth on both specimens, showing a median crest that divides the branch in two distinct lateral surfaces: one dorsolaterally oriented and the other dorsoposteriorly oriented. The dorsoposterior surface meets the paroccipital process of the exoccipital on a broad contact that runs mediolaterally along the occipital surface of the skull.

The postorbital (figs. 3, 4, 5) is also triradiate, with a narrow medial branch contacting the frontal and parietal and separating the supratemporal fossa from the orbit, a posterior branch that contacts the squamosal, and a descending branch that forms the dorsal half of the postorbital bar separating the infratemporal fenestra from the orbit. Both medial and posterior branches constitute the anterolateral border of the supratemporal fossa that is somewhat L-shaped. The anterolateral border of the postorbital shows a triangular peglike process forming a step positioned just below the level of the skull roof. This process is also present in *Notosuchus*, *Simosuchus*, and *Araripesuchus*, where the posterior palpebral articulates. The posterior branch articulates with the squamosal dorsally (see description of the squamosal) and ventrally, within the otic recess. Also within the otic recess and anteriorly to the otic notch, the postorbital articulates with the quadrate and sends a small posteroventral process that overlaps the ascending process of the quadratojugal. The ventral branch forming the dorsal half of the postorbital bar is smooth and somewhat cylindrical. It embraces the ascending process of the jugal anteriorly and contacts in a straight transversally oriented suture the same process of the jugal posteriorly.

The jugal (figs. 3, 4, 5) is triradiate, sending a cylindrical ascending branch directed posterodorsally and that meets the postorbital (see description of postorbital), a broad anterior branch that contacts the maxilla and ectopterygoid, and a posterior branch that contacts the quadratojugal. The lateral surface of the jugal is densely ornamented (except for the ascending branch) in all specimens. The anterior branch reaches the level of the anterior margin of the orbit, where it is dorsoventrally tall. The anterior edge of the jugal contacts the maxilla in an extensive and sinuous suture, overlapping slightly the latter. The lateral surface of the anterior branch presents a large foramen that is also present in *Comahuesuchus* (as in MOZ P 6131). The ventral surface of the anterior branch of the jugal becomes sutured to the extensive posterolateral process of the ectopterygoid. Posteriorly, the jugal tapers gradually to form a thin posterior branch that overlaps laterally the anterior branch of the quadratojugal. Both branches contribute to form a dorsoventrally flattened infratemporal bar.

The quadratojugal (figs. 3, 4, 5) has an anterior process that forms the posterior half of the infratemporal bar, lying medial to the jugal in an extensive longitudinally directed suture. It expands posteriorly to form a broad contact with the quadrate and sends a narrow anterodorsally ascending process that forms most of the posterior border of the infratemporal fenestra. The ascending process meets dorsally with the postorbital in a narrow suture. The posterior and posterodorsal borders of the quadratojugal are solidly sutured to the anterior border of the quadrate. The posteroventral tip of the quadratojugal does not reach the articular condyle of the quadrate, thus not contributing to the craniomandibular articulation.

The quadrate (figs. 3, 4, 5) shares most synapomorphies of the notosuchian clade. The anterodorsal branch is laterally exposed on the otic recess whereas the distal body of the quadrate is projected ventrally at 90° in respect to the longitudinal axis of the skull. The distal body of the quadrate is anteroposteriorly thin and lateromedially wide and bears a well-developed ridge on its posterior surface running from the medial condyle to the distal tip of the posterolateral process of the squamosal. A large foramen aereum is located just medially to this ridge. The distal body of the quadrate is projected ventrally in posterior view rather than ventrolaterally as in most neosuchians. The anterior surface of the distal body of the quadrate is concave and smooth, lacking the ridges for the origin of the adductor bundles. The anterodorsal branch of the quadrate is broadly exposed laterally on the otic recess and forms the ventral and anterior margin of the otic notch. Four accessory pneumatic foramina are present: Three are located posteroventrally and one anteriorly to the otic notch. In addition, there is a siphoneal foramen located near the postorbital–quadrate suture. Anteroventrally, the pterygoid process of the quadrate is strongly sutured to the exoccipital, running anteromedially to meet the basioccipital, basisphenoid, and pterygoid on a longitudinal somewhat interdigitated suture.

The single supraoccipital (fig. 3) is briefly exposed on the skull table, representing only its posterior margin. This exposed part is lightly ornamented. The supraoccipital is exposed on the occiput as a triangular surface, wedging ventrally between the exoccipitals. The ventral border is excluded from the dorsal edge of the foramen magnum by the exoccipitals. The occipital surface of the supraoccipital is smooth and bears a sagittal ridge. The postemporal fenestrae are extremely small and bordered medially by the supraoccipital, dorsally by the occipital flange of the squamosal, and laterally by the exoccipital.

Braincase

The exoccipitals (figs. 3, 4) show two distinct surfaces: one vertically exposed and located dorsal to the foramen magnum and the other one exposed posteroventrally and at the level of the foramen magnum. Both surfaces are separated by a transversely oriented ridge. The vertically oriented surface extends laterally as the paroccipital process, which is dorsally and laterally bordered by the occipital flange of the squamosal and ventrally by the quadrate. MN 6298-V is a young individual that shows ontogenetically variable traits on the occiput. In the latter, the dorsal surface of the exoccipitals is less concave and more anteriorly deflected instead of being vertically oriented as in the larger specimens. A large cranio-quadrate passage is present ventral to the paroccipital process and medial to the triple contact between the squamosal, quadrate, and paroccipital process. The posteroventral surface extends laterally to meet the distal body of the quadrate, ventrally to the cranio-quadrate passage. On its medial surface, it forms the dorsal and lateral edges of the foramen magnum and contributes to the occipital condyle by sending a lateral flange. Lateral to the foramen magnum and on the proximal part of the posteroventral surface, there are five foramina for the exit of the posterior cranial nerves: The two medial-most foramina are interpreted to be paired exits for the XIIth cranial nerve (only visible in MZSP-PV 50 and 51). Lateral to these there is a larger foramen subdivided internally by a transverse wall and a separate smaller, lateral foramen, which are interpreted as representing the common passage for the IX, X, and XI cranial nerves. We failed to find a convincing interpretation for accommodating the internal carotid, its course remaining uncertain on several notosuchian crocodyliforms.

The basioccipital (fig. 4) is exposed posteroventrally in the same plane as the posteroventral surface of the exoccipitals. The basioccipital forms most of the occipital condyle and the ventral margin of the foramen magnum. Anterior to the condyle, the basioccipital expands laterally, forming a rhomboid element that laterally contacts the quadrate and anteriorly the basisphenoid. There is a Y-shaped, low sagittal crest that diverges anteriorly to surround laterally the foramen intertympanicum located at the basioccipital–basisphenoid suture. This sagittal crest is barely marked in MN 6298-V due to its early ontogenetic stage. Lateral to this foramen, the basioccipital–basisphenoid suture is interrupted by the lateral Eustachian foramen that is enclosed by these two bones in MZSP-PV 51, whereas in MZSP-PV 50 and MN 6298-V the Eustachian foramina are enclosed by the quadrate and basioccipital. In MZSP-PV 50, the basisphenoid may also have a marginal participation on the border of the Eustachian foramina, but this cannot be confirmed unambiguously on the specimen.

The basisphenoid (fig. 4) is crescentic and widely exposed on the ventral surface of the braincase. The lateral margins of the basisphenoid are bordered by the pterygoid process of the quadrate posteriorly and by the ascending process of the pterygoid anterolaterally and anteriorly. Its ventral surface is flat near the lateral edges and becomes deeply concave transversely on its central region. The concave surface is wide posteriorly and narrows markedly anteriorly to contact on a narrow suture the posteromedial surface of the ascending processes of the pterygoids. The basisphenoid contacts posteriorly the basioccipital in a concave suture interrupted by the lateral Eustachian foramina, which are located at the posterolateral end of the bone. The basisphenoid of *Mariliasuchus* resembles the condition present in *Sphagesaurus*, in which the bone is widely exposed ventrally with a slightly concave posterior margin and with the Eustachian and intertympanicum foramina aligned transversely. This contrasts with the condition found in *Notosuchus*, in which the posterior border is markedly concave and the foramina are not aligned in the same transversal plane.

Palate

The palatines (figs. 4, 5) are flat and wide anteriorly, where they are sutured to each other, forming the secondary palate, and narrow and divergent posteriorly, where they send a barlike process that contacts the ectopterygoid and pterygoid. The anterior border of the palatines is positioned slightly anteriorly to the suborbital fenestrae, suturing with the maxilla medially to the latter. The suture is anteromedially directed, reaching the anterolateral border of the maxillo-palatine fenestra. Medially to the maxillo-palatine fenestra, the suture between the palatine and the maxilla cannot be located with certainty. The lateral border of the palatine forms the entire median margin of the elongated suborbital fenestra. At the level of the posteromedial border, the palatines are slightly deflected ventrally, each one sending a dorsoventrally flattened bar in a posterolateral direction. The posterior half of this bar meets the medial branch of the ectopterygoid and the pterygoid flange. The lateral edge of the posterior half of this process is strongly sutured to the medial branch of the ectopterygoid. These two elements overlap and are sutured to the ventral surface of the pterygoid flange on its anterolateral region. These palatine bars form the lateral and anterior margins of the choanal opening, separating it from the suborbital fenestra. The palatine bars are also present in *Comahuesuchus*, *Notosuchus*, and *Baurusuchus*. In *Comahuesuchus* and *Mariliaschus* the palatine bars stand posteriorly to the suborbital fenestrae, whereas in *Notosuchus* and *Baurusuchus* these bars are much shorter contacting an anteromedially directed process of the ectopterygoid at the level of the suborbital fenestrae, that is, the latter process of the ectopterygoid does contribute to the palatine bar in *Notosuchus* and *Baurusuchus*, a very distinct condition from the one present in *Comahuesuchus* and *Marialiaschus*.

As previously described, the ectopterygoid (Figs. 3, 4) contacts the jugal and the maxilla extensively on its lateral edge, and on a ventral plane, forming the medial border of at least the last maxillary alveolus (two alveoli in MZSP-PV 51). The contact with the jugal extends slightly posterolaterally and fails to project into the medial surface of the postorbital bar, being restricted to the suborbital region. The lateral edge of the ectopterygoid contacts the maxilla on its dorsomedial surface, forming a broad and flat flange of bone that overlaps the mediodorsal surface of the maxilla laterally to the suborbital fenestra. The medial edge of the ectopterygoid forms the lateral margin of the suborbital fenestra, being slightly constricted at this point. The posterior end of the ectopterygoid that overlaps the ventral surface of the lateral region of the pterygoid flange is broader and massive with a striated (rugose) ventral surface. It is bordered medially by the palatine bar.

The pterygoids (figs. 4, 5) are fused and have a posterior ascending process that contacts the basisphenoid and the quadrate on the ventral and lateral surfaces of the braincase. Medially and ventrally, the pterygoids narrow markedly, forming a posterior notch that is continuous to the medial depression on the ventral surface of the basisphenoid. The pterygoid flanges are thin and ventrolaterally oriented, being medially narrow and expanding laterally to form a large bladelike process that receives the ectopterygoid and palatine on the ventral surface of its lateral edge. Anteriorly, each pterygoid forms a trough-shaped choanal groove that projects toward the palatines. The choanal groove is partially septated by an anterior process of the pterygoid that broadens anteriorly to become sutured to the dorsal surface of the secondary palate.

Dentition

There are four premaxillary, five maxillary, and nine dentary teeth, which are characterized by their heterodonty (figs. 4, 6, 9). Specimens MN 6298-V and 6756-V lack most of their premaxillary teeth, which are well preserved in MZSP-PV 50 and 51. Maxillary teeth are preserved in all four specimens, except in MN 6756-V, which lacks two teeth on the right row, MZSP-PV 51, which lacks the last tooth on each row, and MN 6298-V, which lacks the last tooth of the right row. The mandible of MN 6756-V is not preserved, but tooth rows are complete on the dentaries of all three other specimens, except for MZSP-PV 51 and MN 6298-V, which lack one of the anteriormost dentary teeth. Except for MN 6298-V, which is a young specimen and for this reason shows less marked serrations and thinner enamel coat, all other specimens agree in most details. The specimens MZSP-PV 50 and 51 have preserved better dentition; therefore we will focus our detailed description below on these two specimens.

All teeth are covered by a thick layer of enamel that is preserved with a dark-brown coloration (figs. 9, 10). The two anteriormost premaxillary teeth are facing anteroventrally rather than ventrally as in other crocodyliforms (fig. 9A). These elements are smooth, conical, and gently curved downward. The third premaxillary tooth is caniniform and conical, being smooth in MZSP-PV 51 but showing clear longitudinal striation all on its surface in MZSP-PV 50 (fig. 9B). The fourth premaxillary tooth is the smallest of the four, showing a blunt but conical shape with barely developed longitudinal striations. The general shape of all five maxillary teeth is of a blunt aspect, with the labial side being more convex than the lingual side. The first maxillary tooth is similar in size to the last premaxillary tooth. The three following maxillary teeth are larger, whereas the last one is reduced (being the smallest element of the maxillary tooth row). They show well-developed serrations on the mesial and distal margins of the crown, except for the first tooth, which lacks a well-developed serration on its mesial margin. The serration is composed of a series of rounded tubercles, instead of the sharp denticles present in ziphodont crocodyliforms (see Prasad and de Broin, 2002). These tubercles are mainly formed by the thickening of the enamel coat. All the maxillary teeth have anastomosing longitudinal striations formed by enamel ridges. At the base of each crown, some of these ridges bear one to six longitudinally aligned tubercles similar to the ones that form the marginal serration. These tubercles can be well developed and ornament the whole surface of the crown base, being more conspicuous at the third and fourth maxillary teeth (fig. 10B). The distal serrated margin of the second and third maxillary teeth is directed posteromedially rather than posteriorly (a condition more developed in MZSP-PV 50). Both specimens show extensive wear facets on the lingual surface of some of their maxillary teeth. In MZSP-PV 50, the wear facet is located apically on the lingual surface, being extended both anteriorly and posteriorly in the second right and fourth teeth on both sides. The second left maxillary tooth shows a wear facet that extends more posteriorly and basally than in the other teeth. This latter pattern is also present in the second right, third, and fourth teeth of MZSP-PV 51. The second left tooth of MZSP-PV 51 bears a reduced wear facet that is located anteroapically. Where visible in the wear facet, the striae are directed obliquely from the anterodistal margin of the wear facet toward its posterobasal margin. Such striae suggest a significant anteroposterior movement of the lower jaws, which is congruent with the presence of an anteroposteriorly enlarged articular surface for the quadrate condyles (see description of the mandible). The two anteriormost teeth of the dentary are conical and directed horizontally in a markedly procumbent position. Posteriorly along the tooth row, the mandibular teeth shift progressively to a more erect position. The third and fourth dentary teeth are conical and have slightly serrated distal and mesial margins, being still directed anterodorsally. Posterior to this point, the remaining dentary teeth are erect and blunt shaped. The size and shape of these crowns as well as the enamel surface closely match the morphology of their corresponding maxillary teeth. The wear facets are well developed and visible only on the sixth to eighth dentary teeth. These wear facets are located on the labial surface of the crowns and perfectly match the shape and extension of the

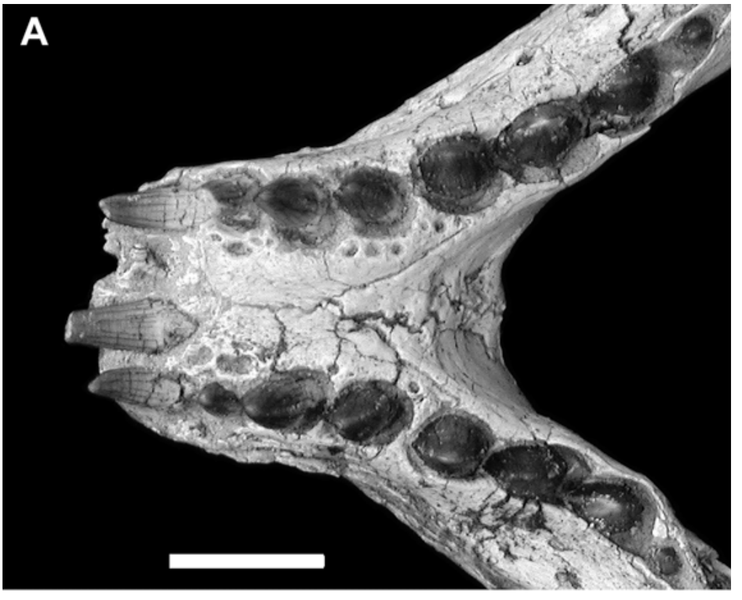
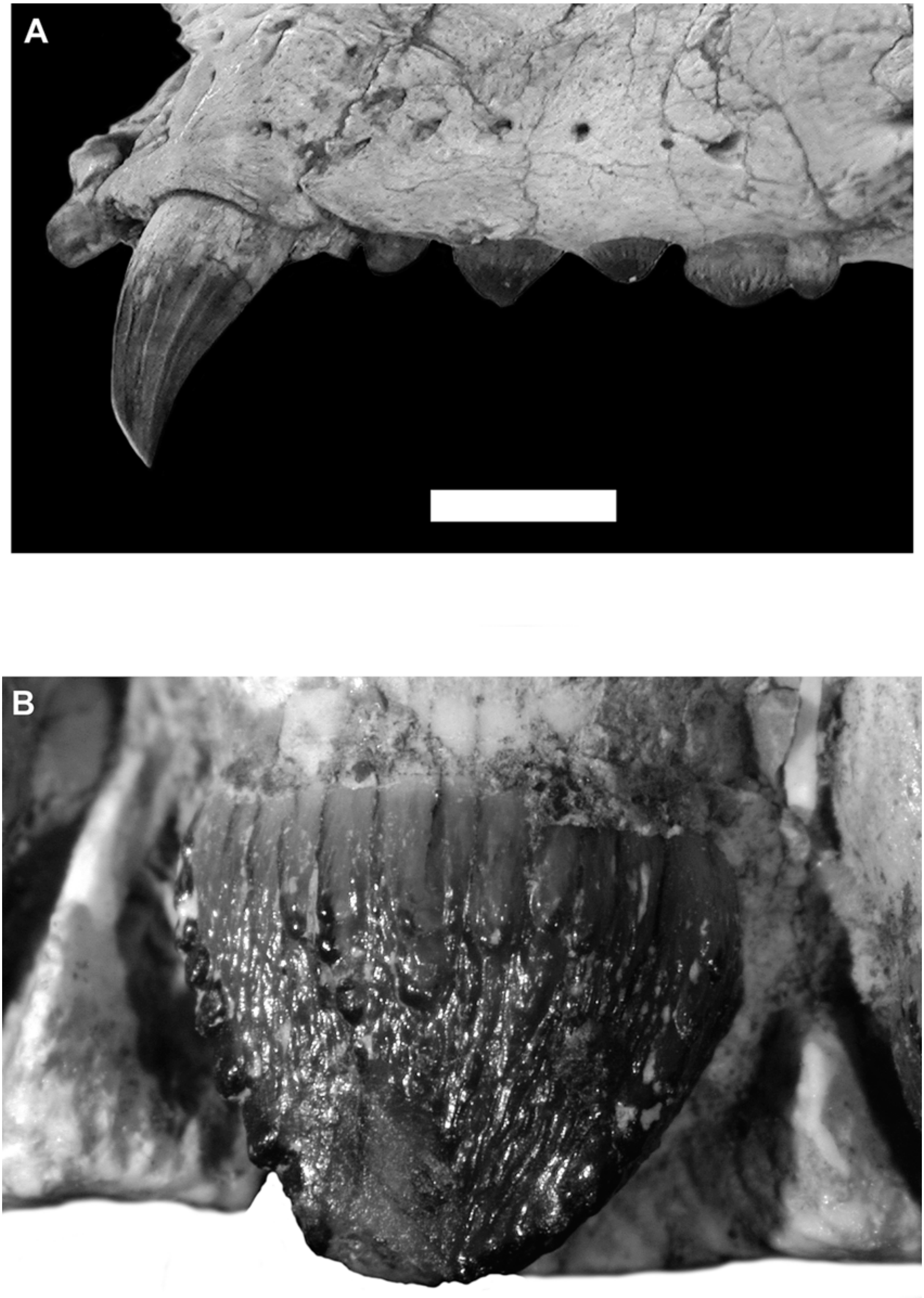


Fig. 9. **A**. Dorsal view of mandibular symphysis of MZSP-PV 51. **B**. Ventral view of anterior palatal region of the skull of MZSP-PV 51.


A
B

wear facets present in the corresponding maxillary teeth, implying that a pattern of tooth-to-tooth occlusion was present in *Mariliasuchus amarali*. Such a pattern was only found previously in *Sphagesaurus huenei* among crocodyliforms (Pol, 2003).

To accommodate the highly autapomorphic position of the two anteriormost teeth, the corresponding alveoli of both premaxillae and dentaries are in an almost horizontal position, with an enlarged labial wall and a highly reduced lingual wall.

Mandible

The complete mandible is preserved in MZSP-PV 50 (figs. 6, 7, 8), MZSP-PV 51, and MN 6298-V. The dentaries are dorsoventrally low and laterally convex at the mandibular symphysis. The dentary rami converge to meet and form a mandibular symphysis that tapers anteriorly along its posterior half. Anteriorly, the symphyseal region is elongated and spatulated, with parallel lateral edges. At this point, the symphyseal region has a peculiar, large, and flattened dorsal surface between the two parallel tooth rows. In all three specimens the ventral surface of the symphysis is ornamented, whereas the lateral surface is smooth and bears several large neurovascular foramina, varying from four to eight. Just posterior to the mandibular symphysis, the dentaries diverge and the tooth rows (last four teeth) are medially inset on their ramus, being lingually bordered by a thin lamina of the splenial. The lateral surface of the posterior half of the dentary is mostly smooth and lateromedially broad in the larger specimens. The dorsal posterior process of the dentary is forked, receiving an acute anterior process of the surangular in an interdigitated suture. The ventral branch of the dorsal posterior process forms the anterodorsal margin of the external mandibular fenestra, and contacts the angular at the anterior edge of the mandibular fenestra. The ventral posterior process of the dentary is extremely reduced and fails to extend underneath the mandibular fenestra, the angular–dentary suture being directed dorsoventrally.

The splenials (fig. 7) represent thin laminae that form the posterior third of the dorsal surface of the mandibular symphysis. The splenial participation on the ventral surface of the symphysis is much more restricted, constituting only the posterior tip of the symphysis ventrally, where it forms a peglike protuberance on the sagittal midline. The posterior surface of the symphysis is notably high and is entirely formed by the splenials, which contact each other on a solid interdigitated suture. Posterior to the symphysis, the splenials contribute to the ventral surface of the mandibular rami on their anterior half, curving gently dorsally and being restricted to the medial surface of the rami on their posterior half. The medial surface of the mandibular rami is covered by a flat lamina of the splenial that bears a moderately large foramen intramandibularis oralis posterior to the mandibular symphysis, located at the level of the seventh dentary tooth. The posterior edge of the splenials forms the anterior border of the internal mandibular fenestra. Its posteroventral margin contacts the anterior process of the angular that wedges between the dentary and splenial.

The surangular (figs. 6, 8) is an elongated bone that forms the dorsal margin of the posterior half of the mandibular rami. The anterior process is forked like the posterior dorsal process of the dentary with which it interdigitates. The medial surface of the anterior branch extends anteriorly between the dorsal margin of the splenial and the dentary, reaching the lateral border of the last dentary alveolus. At the level of the anterodorsal border of the inner mandibular fenestra, the anterior process of the surangular has a concave and spatulate rugose surface that projects medially and ventrally. This surface might represent the coronoid bone

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Fig. 10. **A**. Left lateral view of the skull of MZSP-PV 50 showing the buccal side of the premaxillary and maxillary tooth rows. **B**. Detail of the second maxillary tooth of MZSP-PV 51 in lingual view. Scale bar = 1 cm.

that fused to the surangular. However, there is no unambiguous evidence that the coronoid was present in any of the examined specimens. Posterior to this spatulate process, the surangular broadens markedly along its contact with the lateral surface of the articular. The surangular projects a ventrally directed pointed process that forms the posterior margin of the external mandibular fenestra. This process is mostly overlapped laterally by the angular. The surangular forms the upper lateral surface of the postdentary region of the mandible, joining the angular in a straight suture oriented anteroposteriorly. The posterior tip of the surangular reaches the dorsolateral surface of the retroarticular process, covering it partially.

The angular (fig. 7) forms the ventral margin of the postdentary ramus of the mandibles as well as the ventral half of their lateral surface, posterior to the external mandibular fenestra. Its anterior part forms the entire ventral margin of the mandibular fenestra and wedges anteriorly between the splenial and the dentary, forming a pointed, anteriorly directed process on the ventral surface of the mandible. The lateral lamina of the angular also forms most of the anterior margin of the external mandibular fenestra, being overlapped by the dentary anteriorly to this region. Posterior to the mandibular fenestra, the angular is smooth, extending caudally to overlap laterally the ventrolateral surface of the articular and retroarticular process.

The articular (fig. 6) is roughly triangular, having an acute tip that extends anteriorly to the articular facet for the quadrate, deflecting ventrally, being bordered laterally by the surangular and fitting into the U-shaped angular surface located posteriorly and medially to the mandibular fenestra. The facet is anteroposteriorly long and broadens posteriorly. Its dorsal surface is convex, lacking a well-developed longitudinal ridge that fits between the quadrate condyles. The ventral surface of the articular facet projects medially as a shelf, overhanging the ventral surface of the angular. The retroarticular process (figs. 6, 7, 8) has a broad, rounded, and slightly concave surface that projects posteroventrally from the articular facet.

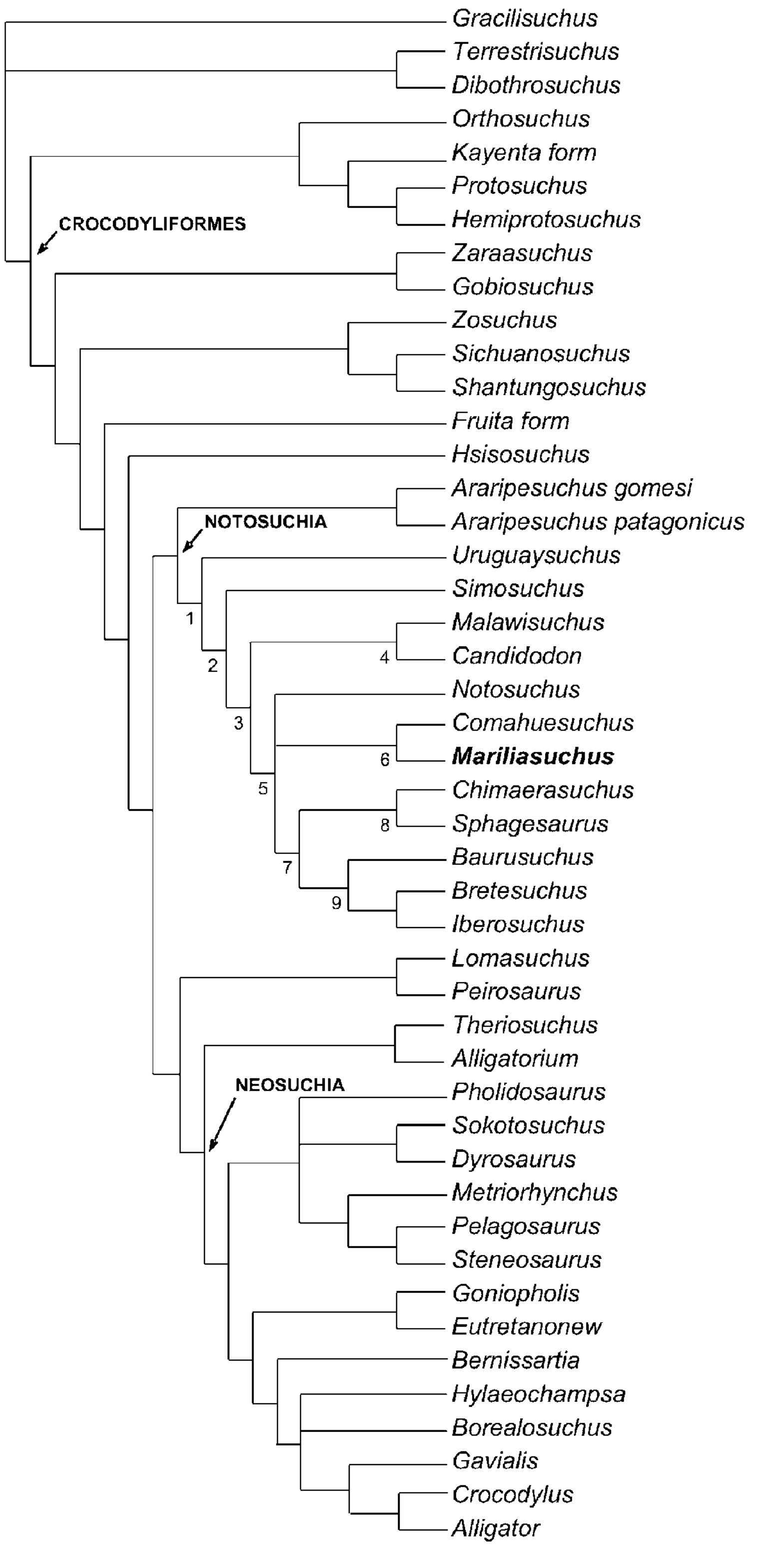
DISCUSSION

Assignment of Specimens to *Mariliasuchus amarali*

The four specimens described herein share all the diagnostic features present in the type specimen and exemplified in the Amended Diagnosis. However, the former specimens differ from the latter in numerous aspects that are ontogenetically related, since the type specimen is a juvenile whereas the material described here consists of two subadults and two adults. Specimens MN 6298-V, MN 6756-V, and MZSP-PV 50 are very similar in most aspects, the former representing a younger adult. Although MZSP-PV 51 shares all autapomorphic traits of the species, it shows several significant morphological differences, such as the presence of a foramen incisivum (absent in the other three specimens), a dense ornamentation of the skull table and dorsal region of the snout (only poorly ornamented in MN 6298-V, MN 6756-V, and MZSP-PV 50), a wider parietal width between the supratemporal fossae, and the presence of a longitudinal ridge on the frontal (absent in MN 6298-V, MN 6756-V, and MZSP-PV 50). These differences might suggest that MZSP-PV 51 belongs to a different species from the other three specimens. Alternatively, these differences may be related to sexual dimorphism or individual variation. Here MZSP-PV 51 is referred to *Mariliasuchus amarali*, provisionally accepting the latter hypotheses to explain the observed differences. However, more material is needed in order to clarify this issue.

Phylogenetic Affinities of *Mariliasuchus amarali*

To test the phylogenetic affinities of *Mariliasuchus amarali*, we used an extended version of the data matrix furnished by Pol and Norell (2004b), including all notosuchian taxa relevant for the analysis (see appendices 2 and 3). A total of 46 taxa were scored for 198 characters. Parsimony analysis, using PAUP 4.0 (beta 10) (Swofford, 2003) with a heuristic search strategy (100 replicates of Wagner trees followed by TBR branch swapping, resulted in 12 most parsimonious trees with 658 steps (CI


Gracilisuchus
Terrestrisuchus
Dibothrosuchus
Orthosuchus
Kayenta form
Protosuchus
Hemiprotosuchus
CROCODYLIFORMES
Zaraasuchus
Gobiosuchus
Zosuchus
Sichuanosuchus
Shantungosuchus
Fruita form
Hsisosuchus
Araripesuchus gomesi
Araripesuchus patagonicus
NOTOSUCHIA
Uruguaysuchus
Simosuchus
1
Malawisuchus
Candidodon
4
2
Notosuchus
3
Comahuesuchus
Mariliasuchus
6
5
Chimaerasuchus
Sphagesaurus
8
Baurusuchus
7
Bretesuchus
9
Iberosuchus
Lomasuchus
Peirosaurus
Theriosuchus
Alligatorium
NEOSUCHIA
Pholidosaurus
Sokotosuchus
Dyrosaurus
Metriorhynchus
Pelagosaurus
Steneosaurus
Goniopholis
Eutretanonew
Bernissartia
Hylaeochampsa
Borealosuchus
Gavialis
Crocodylus
Alligator

= 0.36; RI = 0.67), the strict consensus of which is presented in figure 11. The 12 phylogenetic hypotheses differ in the relationships of some neosuchian crocodyliforms (e.g., *Hylaeochampsa*, *Borealosuchus*, and *Pholidosaurus*) and the alternative position of *Notosuchus* either as the sister group of clade 6 or clade 7 within Notosuchia (or Ziposuchia sensu Ortega et al., 2000). In contrast to some previous phylogenetic analyses (e.g., Clark, 1994; Buckley et al., 2000; Ortega et al., 2000; Turner, 2004), the genus *Araripesuchus* appears as the basalmost notosuchian instead of being a basal member of Neosuchia, as in a recent analysis (Pol and Apesteguía, 2005).

According to the present analysis, *Mariliasuchus* appears nested well inside the clade Notosuchia, as the sister group of *Comahuesuchus*, a derived and highly autapomorphic notosuchian from the Late Cretaceous of Argentina. These two taxa share four unambiguous synapomorphies: the ventral half of the lacrimal tapering posteroventrally, not contacting or only slightly contacting the jugal (character 192 [1]), the presence of a large foramen on the lateral surface of the anterior part of the jugal (character 193 [1]), the presence of procumbent premaxillary and anterior dentary alveoli [character 194 (1)], and ectopterygoids that do not participate of the palatine bar (character 196 [0]). Character 194 confers to both *Mariliasuchus* and *Comahuesuchus* an unusual condition in which the anteriormost (premaxillary and dentary) teeth are set horizontally instead of vertically. These peculiar characteristics, related to specialized dental crown morphology and the presence in derived notosuchians of fore–aft jaw movements, suggests that this group presented complex jaw movements related to specialized feeding habits still poorly understood for the majority of the taxa.

Jacobs et al. (1990) and, more recently, Nobre and Carvalho (2002) suggested that *Candidodon itapecuruense* from the Lower Cretaceous Parnaíba basin is more closely related to *Malawisuchus* than to any other notosuchian, due to their similarities in dental morphology (i.e., lingual base of the crown ornamented with a cuspidate cingulum; Clark et al., 1989; Gomani, 1997; Carvalho and Bertini, 2000). Similarly, one could interpret the complex lingual cuspidate ornamentation at the base of the crown of *Mariliasuchus* as homologous to the lingual cuspidate cingula in the teeth of *Candidodon* and *Malawisuchus*. However, such similarity may well be superficial, as recent works documented a high diversity of complex crown morphologies among crocodyliforms (Clark et al., 1989; Wu and Sues, 1996; Gomani, 1997; Wu et al., 1997; Larsson and Sidor, 1999; Buckley et al., 2000; Pol, 2003). The present analysis supports the hypothesis previously proposed by Jacobs et al. (1990) and Nobre and Carvalho (2002), with *Candidodon* and *Malawisuchus* forming a clade (4) supported by five ambiguous synapomorphies (9 [1], 122 [0], 140 [0], 149 [0], 161 [2]; *contra* Carvalho et al., 2004).

Although the recently described notosuchian *Anatosuchus minor* was hypothesized to be the sister group of *Comahuesuchus* (Sereno et al., 2003), it was not included in this analysis, awaiting a more detailed description. However, Sereno et al.'s (2003) preliminary description of the skull shows that *Anatosuchus* may lack the synapomorphies supporting clade 6 (fig. 11), suggesting that it might not represent the sister group of *Comahuesuchus*. A more detailed phylogenetic analysis including *Anatosuchus*, as well as *Comahuesuchus*, *Mariliasuchus*, and *Candidodon*, is needed before any more accurate taxonomic or biogeographic conclusions concerning these taxa can be drawn.

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Fig. 11. Strict consensus of the 12 most parsimonious topologies that resulted from a strict parsimony analysis using PAUP 4.0 (beta 10). Unambiguous synapomorphies for the labeled nodes are: Node 1: 95 (0), 104 (2), 151 (1). Node 2: 1 (1), 74 (1), 79 (0), 106 (1). Node 3: 78 (1), 107 (1), 141 (1). Node 4: 140 (0). Node 5: 195 (1), 198 (1). Node 6: 192 (1), 193 (1), 194 (1), 196 (0). Node 7: 121 (1), 130 (1), 134 (1), 148 (1). Node 8: 105 (3), 124 (1). Node 9: 3 (0), 9 (2), 79 (1), 80 (1), 106 (0), 118 (1), 120 (0), 128 (0), 155 (0), 158 (1).

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APPENDIX 1

Institutional Acronyms and Anatomical Abbreviations

Institutional

DG/UFRJ	Departamento de Geologia, Universidade Federal do Rio de Janeiro, Brazil.
MZSP-PV	Museu de Zoologia, Universidade de São Paulo, Brazil.
MN	Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil.
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina.

Anatomical

ang	angular
art	articular
bocc	basioccipital
d	dentary
ect	ectopterygoid
exoc	exoccipital
fit	foramen intertympanicum
fm	foramen magnum
fr	frontal
ju	jugal
la	lacrymal
m	maxilla
n	nasal
p	parietal
pm	premaxilla
pl	palatine
po	postorbital
pp	posterior palpebral
prf	prefrontal
pt	pterygoid
q	quadrate
qj	quadratojugal
rart	retroarticular process
soc	supraoccipital
spl	splenial
sq	squamosal
sur	surangular

APPENDIX 2

Character List Corresponding to Data Matrix Used in Phylogenetic Analysis

Character definitions 1–101 were taken from Clark (1994) and have the same numeration as in the original publication. Character 5 was excluded from the analysis (because it depends on the modified definition of character 6); however, its inclusion does not affect the outcome of the analysis (except for the tree length). The additional characters are also listed here and their respective source is cited along with the character number of the original publication. Characters 1, 3, 6, 23, 37, 45, 49, 65, 67, 69, 73, 77, 79, 90, 91, 96, 97, 103, 104, 105, 107, 126, 143, 149, and 165 were set as ordered characters (marked "+" in this list).

Character 1 (modified from Clark, 1994; character 1). + External surface of dorsal cranial bones: smooth (0), slightly grooved (1), and heavily ornamented with deep pits and grooves (2).

Character 2 (modified from Clark, 1994; character 2). Skull expansion at orbits: gradual (0) or abrupt (1).

Character 3 (modified from Clark, 1994; character 3). + Rostrum proportions: narrow oreinirostral (0) or broad oreinirostral (1) or nearly tubular (2) or platyrostral (3).

Character 4 (Clark, 1994; character 4). Premaxilla participation in internarial bar: forming at least the ventral half (0) or with little participation (1).

Character 5 (Clark, 1994; character 5). Premaxilla anterior to nares: narrow (0) or broad (1).

Character 6 (modified from Clark, 1994; character 6). + External nares facing: anterolaterally or anteriorly (0), dorsally not separated by premaxillary bar from anterior edge of rostrum (1), or dorsally separated by premaxillary bar (2).

Character 7 (Clark, 1994; character 7). Palatal parts of premaxillae: do not meet posterior to incisive foramen (0) or meet posteriorly along contact with maxillae (1).

Character 8 (Clark, 1994; character 8). Premaxilla–maxilla contact: premaxilla loosely overlies maxilla (0) or sutured together along a butt joint (1).

Character 9 (modified from Clark, 1994; character 9). Ventrally opened notch on ventral edge of rostrum at premaxilla–maxilla contact: absent (0) or present as a notch (1) or present as a large fenestra (2).

Character 10 (Clark, 1994; character 10). Posterior ends of palatal branches of maxillae anterior to palatines: do not meet (0) or meet (1).

Character 11 (Clark, 1994; character 11). Nasal–lacrimal contact: (0) or do not contact (1).

Character 12 (Clark, 1994; character 12). Lacrimal contacts nasal along: medial edge only (0) or medial and anterior edges (1).

Character 13 (Clark, 1994; character 13). Nasal contribution to narial border: yes (0) or no (1).

Character 14 (Clark, 1994; character 14). Nasal–premaxilla contact: present (0) or absent (1).

Character 15 (modified from Clark, 1994; character 15). Descending process of prefrontal: does not contact palate (0) or contacts palate (1).

Character 16 (Clark, 1994; character 16). Postorbital–jugal contact: postorbital anterior to jugal or postorbital medial to jugal (1) or postorbital lateral to jugal (2).

Character 17 (Clark, 1994; character 17). Anterior part of the jugal with respect to posterior part: as broad (0) or twice as broad (1).

Character 18 (Clark, 1994; character 18). Jugal bar beneath infratemporal fenestra: flattened (0) or rod-shaped (1).

Character 19 (Clark, 1994; character 19). Quadratojugal dorsal process: narrow, contacting only a small part of postorbital (0) or broad, extensively contacting the postorbital (1).

Character 20 (Clark, 1994; character 20). Frontal width between orbits: narrow, as broad as nasals (0) or broad, twice as broad as nasals (1).

Character 21 (Clark, 1994; character 21). Frontals: paired (0), unpaired (1).

Character 22 (Clark, 1994; character 22). Dorsal surface of frontal and parietal: flat (0) or with midline ridge (1).

Character 23 (modified from Clark, 1994; character 23; by Buckley and Brochu, 1999; character 81). + Parieto-postorbital suture: absent from dorsal surface of skull roof and supratemporal fossa (0) or absent from dorsal surface of skull roof but broadly present within supratemporal fossa (1) or present within supratemporal fossa and on dorsal surface of skull roof (2).

Character 24 (Clark, 1994; character 24). Supratemporal roof dorsal surface: complex (0) or dorsally flat "skull table" developed, with postorbital and squamosal with flat shelves extending laterally beyond quadrate contact (1).

Character 25 (modified from Clark, 1994; character 25). Postorbital bar: sculpted (if skull sculpted) (0) or unsculpted (1).

Character 26 (modified from Clark, 1994; character 26). Postorbital bar: transversely flattened (0) or cylindrical (1).

Character 27 (Clark, 1994; character 27). Vascular opening in dorsal surface of postorbital bar: absent (0), present (1).

Character 28 (modified from Clark, 1994; character 28). Postorbital anterolateral process: absent or poorly developed (0) or well developed, long, and acute (1).

Character 29 (Clark, 1994; character 29). Dorsal part of the postorbital: with anterior and lateral edges only (0) or with anterolaterally facing edge (1).

Character 30 (Clark, 1994; character 30). Dorsal end of the postorbital bar broadens dorsally, continuous with dorsal part of postorbital (0) or dorsal part of the postorbital bar constricted, distinct from the dorsal part of the postorbital (1).

Character 31 (Clark, 1994; character 31). Bar between orbit and supratemporal fossa broad and solid, with broadly sculpted dorsal surface (0) or bar narrow, sculpting restricted to anterior surface (1).

Character 32 (modified from Clark, 1994; character 32). Parietal: with broad occipital portion (0) or without broad occipital portion (1).

Character 33 (Clark, 1994; character 33). Parietal: with broad sculpted region separating fossae (0) or with sagittal crest between supratemporal fossae (1).

Character 34 (Clark, 1994; character 34). Postparietal (dermosupraoccipital): a distinct element (0) or not distinct (fused with parietal?) (1).

Character 35 (Clark, 1994; character 35). Posterodorsal corner of the squamosal: squared off, lacking extra "lobe" (0) or with unsculptured "lobe" (1).

Character 36 (modified from Clark, 1994; character 36). Posterolateral process of squamosal: poorly developed and projected horizontally at the same level of the skull (0) or elongated, thin, and posteriorly directed, not ventrally deflected (1) or elongated, posterolaterally directed, and ventrally deflected (2).

Character 37. (Clark, 1994; character 37). + Palatines: do not meet on palate below the narial passage (0) or form palatal shelves that do not meet (1) or meet ventrally to the narial passage, forming part of secondary palate (2).

Character 38 (Clark, 1994; character 38). Pterygoid: restricted to palate and suspensorium, joints with quadrate and basisphenoid overlapping (0) or pterygoid extends dorsally to contact laterosphenoid and form ventrolateral edge of the trigeminal foramen, strongly sutured to quadrate and laterosphenoid (1).

Character 39 (modified from Clark, 1994; character 39). Choanal opening: continuous with pterygoid ventral surface except for anterior and anterolateral borders (0) or opens into palate through a deep midline depression (choanal groove) (1).

Character 40 (Clark, 1994; character 40). Palatal surface of pterygoids: smooth (0) or sculpted (1).

Character 41 (Clark, 1994; character 41). Pterygoids posterior to choanae: separated (0) or fused (1).

Character 42 (modified from Clark, 1994; character 42; by Ortega et al., 2000; character 139). Depression on primary pterygoidean palate posterior to choana: absent or moderate in size being narrower than palatine bar (0) or wider than palatine bar (1).

Character 43 (Clark, 1994; character 43). Pterygoids: do not enclose choana (0) or enclose choana (1).

Character 44 (modified from Clark, 1994; character 44). Anterior edge of choanae situated near posterior edge of suborbital fenestra (or anteriorly) (0) or near posterior edge of pterygoid flanges (1).

Character 45 (Clark, 1994; character 45). + Quadrate: without fenestrae (0) or with single fenestrae (1) or with three or more fenestrae on dorsal and posteromedial surfaces (2).

Character 46 (Clark, 1994; character 46). Posterior edge of quadrate: broad medial to tympanum, gently concave (0) or posterior edge narrow dorsal to otoccipital contact, strongly concave (1).

Character 47 (Clark, 1994; character 47). Dorsal, primary head of quadrate articulates with: squamosal, otoccipital and prootic (0) or with prootic and laterosphenoid (1).

Character 48 (Clark, 1994; character 48). Ventrolateral contact of otoccipital with quadrate: very narrow (0) or broad (1).

Character 49 (Clark, 1994; character 49). + Quadrate, squamosal, and otoccipital: do not meet to enclose cranioquadrate passage (0) or enclose passage near lateral edge of skull (1) or meet broadly lateral to the passage (2).

Character 50 (Clark, 1994; character 50). Pterygoid ramus of quadrate: with flat ventral edge (0) or with deep groove along ventral edge (1).

Character 51 (Clark, 1994; character 51). Ventromedial part of quadrate: does not contact otoccipital (0) or contacts otoccipital to enclose carotid artery and form passage for cranial nerves IX–XI (1).

Character 52 (Clark, 1994; character 52). Eustachian tubes: not enclosed between basioccipital and basisphenoid (0) or entirely enclosed (1).

Character 53 (Clark, 1994; character 53). Basisphenoid rostrum (cultriform process): slender (0) or dorsoventrally expanded (1).

Character 54 (Clark, 1994; character 54). Basipterygoid process: prominent, forming movable joint with pterygoid (0) or basipterygoid process small or absent, with basisphenoid joint suturally closed (1).

Character 55 (modified from Clark, 1994; character 55; by Ortega et al., 2000; character

68). Basisphenoid ventral surface: shorter than the basioccipital (0) or wide and similar to or longer in length than basioccipital (1).

Character 56 (Clark, 1994; character 56). Basisphenoid: exposed on ventral surface of braincase (0) or virtually excluded from ventral surface by pterygoid and basioccipital (1).

Character 57 (Clark, 1994; character 57). Basioccipital: without well-developed biltaeral tuberosities (0) or with large pendulous tubera (1).

Character 58 (Clark, 1994; character 58). Otoccipital: without laterally concave descending flange ventral to subcapsular process (0) or with flange (1).

Character 59 (Clark, 1994; character 59). Cranial nerves IX–XI: pass through common large foramen vagi in otoccipital (0) or cranial nerve IX pass medial to nerves X and XI in separate passage (1).

Character 60 (Clark, 1994; character 60). Otoccipital: without large ventrolateral part ventral to paroccipital process (0) or with large ventrolateral part (1).

Character 61 (Clark, 1994; character 61). Crista interfenestralis between fenestrae pseudorotunda and ovalis nearly vertical (0) or horizontal (1).

Character 62 (Clark, 1994; character 62). Supraoccipital: forms dorsal edge of the foramen magnum (0) or otoccipitals broadly meet dorsal to the foramen magnum, separating supraoccipital from foramen (1).

Character 63 (Clark, 1994; character 63). Mastoid antrum: does not extend into supraoccipital (0) or extends through transverse canal in supraoccipital to connect middle ear regions (1).

Character 64 (Clark, 1994; character 64). Posterior surface of supraoccipital: nearly flat (0), or with bilateral posterior prominences (1).

Character 65 (modified from Clark, 1994; character 65). + One small palpebral present in orbit (0) or one large palpebral (1) or two large palpebrals (2).

Character 66 (Clark, 1994; character 66). External nares: divided by a septum (0) or confluent (1).

Character 67 (Clark, 1994; character 67). + Antorbital fenestra: as large as orbit (0) or about half the diameter of the orbit (1) or much smaller than the orbit (2) or absent (3).

Character 68 (modified from Clark, 1994; character 68; by Ortega et al., 2000; character 41). Supratemporal fenestrae extension: relatively large, covering most of surface of skull roof (0) or relatively short, fenestrae surrounded by a flat and extended skull roof (1).

Character 69 (modified from Clark, 1994; character 69). + Choanal groove: undivided (0) or partially septated (1) or completely septated (2).

Character 70 (Clark, 1994; character 70). Dentary: extends posteriorly beneath mandibular fenestra (0) or does not extend beneath fenestra (1).

Character 71 (modified from Clark, 1994; character 71). Retroarticular process: absent or extremely reduced (0) or very short, broad, and robust (1) or with an extensive rounded, wide, and flat (or slightly concave) surface projected posteroventrally and facing dorsomedially (2) or posteriorly elongated, triangular shaped and facing dorsally (3) or posteroventrally projecting and paddle shaped (4).

Character 72 (Clark, 1994; character 72). Prearticular: present (0) or absent (1).

Character 73 (modified from Clark, 1994; character 73). + Articular without medial process (0) or with short process not contacting braincase (1) or with process articulating with otoccipital and basisphenoid (2).

Character 74 (Clark, 1994; character 74). Dorsal edge of surangular: flat (0) or arched dorsally (1).

Character 75 (Clark, 1994; character 75). Mandibular fenestra: present (0) or absent (1).

Character 76 (Clark, 1994; character 76). Insertion area for M. pterygoideous posterior: does not extend onto lateral surface of angular (0) or extends onto lateral surface of angular (1).

Character 77 (modified from Clark, 1994; character 77). + Splenial involvement in symphysis in ventral view: not involved (0) or involved slightly in symphysis (1) or extensively involved (2).

Character 78 (Clark, 1994; character 78). Posterior premaxillary teeth: similar in size to anterior teeth (0) or much longer (1).

Character 79 (modified from Clark, 1994; character 79). + Maxillary teeth waves: absent, no tooth size variation (0) or one wave of teeth enlarged (1) or enlarged maxillary teeth curved in two waves ("festooned") (2).

Character 80 (Clark, 1994; character 80). Anterior dentary teeth opposite premaxilla–maxilla contact: no more than twice the length of other dentary teeth (0) or more than twice the length (1).

Character 81 (modified from Clark, 1994; character 81). Dentary teeth posterior to tooth opposite premaxilla–maxilla contact: equal in size (0) or enlarged dentary teeth opposite to smaller teeth in maxillary tooth row (1).

Character 82 (modified from Clark, 1994; character 82; by Ortega et al., 2000; character 120). Anterior and posterior scapular edges: symmetrical in lateral view (0) or anterior edge more strongly concave than posterior edge (1) or dorsally narrow with straight edges (2).

Character 83 (modified from Clark, 1994; character 83; by Ortega et al., 2000; character 121). Coracoid length: up to two-thirds of the scapular length (0) or subequal in length to scapula (1).

Character 84 (Clark, 1994; character 84). Anterior process of ilium: similar in length to posterior process (0) or one-quarter or less of the length of the posterior process (1).

Character 85 (Clark, 1994; character 85). Pubis: rodlike without expanded distal end (0) or with expanded distal end (1).

Character 86 (Clark, 1994; character 86). Pubis: forms anterior half of ventral edge of acetabulum (0) or pubis at least partially excluded from the acetabulum by the anterior process of the ischium (1).

Character 87 (Clark, 1994; character 87). Distal end of femur: with large lateral facet for the fibula (0) or with very small facet (1).

Character 88 (Clark, 1994; character 88). Fifth pedal digit: with phalanges (0) or without phalanges (1).

Character 89 (Clark, 1994; character 89). Atlas intercentrum: broader than long (0) or as long as broad (1).

Character 90 (modified from Clark, 1994; character 90). + Cervical neural spines: all anteroposteriorly large (0), only posterior ones rodlike (1), or all spines rodlike (2).

Character 91 (modified from Clark, 1994; character 91; by Buscalioni and Sanz, 1988; and by Brochu, 1997; character 37 and character 7, respectively). + Hypapophyses in cervicodorsal vertebrae: absent (0) or present only in cervical vertebrae (1) or present in cervical and the first two dorsal vertebrae (2) or present up to the third dorsal vertebra (3) or up to the fourth dorsal vertebrae (4).

Character 92 (Clark, 1994; character 92). Cervical vertebrae: amphicoelous or amphyplatian (0) or procoelous (1).

Character 93 (Clark, 1994; character 93). Trunk vertebrae: amphicoelous or amphyplatian (0) or procoelous (1).

Character 94 (Clark, 1994; character 94). All caudal vertebrae: amphicoelous or amphyplatian (0) or first caudal biconvex with other procoelous (1) or procoelous (2).

Character 95 (Clark, 1994; character 95). Dorsal osteoderms: rounded or ovate (0) or rectangular, broader than long (1) or square (2).

Character 96 (modified from Clark, 1994; character 96; and Brochu, 1997; character 40). + Dorsal osteoderms without articular anterior process (0) or with a discrete convexity on anterior margin (1) or with a well-developed process located anterolaterally in dorsal parasagittal osteoderms (2).

Character 97 (modified from Clark, 1994; character 97; by Ortega et al., 2000; characters 107 and 108). + Rows of dorsal osteoderms: two parallel rows (0) or more than two (1) or more than four with "accessory ranges of osteoderms" (sensu Frey, 1988) (2).

Character 98 (Clark, 1994; character 98). Osteoderms: Some or all imbricated (0) or sutured to one another (1).

Character 99 (Clark, 1994; character 99). Tail osteoderms: dorsal only (0) or completely surrounded by osteoderms (1).

Character 100 (Clark, 1994; character 100). Trunk osteoderms: absent from ventral part of the trunk (0) or present (1).

Character 101 (Clark, 1994; character 101). Osteoderms: with longitudinal keels on dorsal surfaces (0) or without longitudinal keels (1).

Character 102 (Wu and Sues, 1996; character 14). Jugal: participating in margin of antorbital fossa (0) or separated from it (1).

Character 103 (modified from Wu and Sues, 1996; character 23). + Articular facet for quadrate condyle: equal in length to the quadrate condyles (0) or slightly longer (1) or close to three times the length of the quadrate condyles (2).

Character 104 (modified from Wu and Sues, 1996, and Wu et al., 1997; character 24 and character 124, respectively). + Jaw joint: placed at level with basioccipital condyle (0) or below basioccipital condyle about above level of lower tooth row (1) or below level of tooth row (2).

Character 105 (modified from Wu and Sues, 1996, and Ortega et al., 2000; character 27 and character 133, respectively). + Premaxillary teeth: five (0), four (1), three (2), or two (3).

Character 106 (modified from Wu and Sues, 1996; character 29). Unsculptured region along alveolar margin on lateral surface of maxilla: absent (0) or present (1).

Character 107 (modified from Wu and Sues, 1996; character 30). + Maxilla: with eight or more teeth (0) or seven (1) or six (2) or five (3) or four (4) teeth.

Character 108 (Wu and Sues, 1996; character 33). Coracoid: without posteromedial or ventromedial process (0) or with elongate posteromedial process (1) or distally expanded ventromedial process (2).

Character 109 (Wu and Sues, 1996; character 40). Radiale and ulnare: short and massive (0) or elongate (1).

Character 110 (Wu and Sues, 1996; character 41). Postacetabular process: directed posteroventrally or posteriorly (0) or directed posterodorsally and much higher in position than preacetabular process (1).

Character 111 (modified from Gomani, 1997; character 4). Prefrontals anterior to orbits: elongated, oriented parallel to anteroposterior axis of the skull (0) or short and broad, oriented posteromedially–anterolaterally (1).

Character 112 (modified from Gomani, 1997; character 32). Basioccipital and ventral part of otoccipital: facing posteriorly (0) or posteroventrally (1).

Character 113 (Buscalioni and Sanz, 1988; character 35). Vertebral centra: cylindrical (0) or spool shaped (1).

Character 114 (modified from Buscalioni and Sanz, 1988; character 39). Transverse process of posterior dorsal vertebrae dorsoventrally low and laminar (0) or dorsoventrally high (1).

Character 115 (Buscalioni and Sanz, 1988; character 44). Number of sacral vertebrae: two (0) or more than two (1).

Character 116 (Buscalioni and Sanz, 1988; character 49). Supra-acetabular crest: present (0) or absent (1).

Character 117 (Buscalioni and Sanz, 1988; character 54). Proximal end of radiale expanded symmetrically, similarly to the distal end (0) or more expanded proximomedially than proximolaterally (1).

Character 118 (Ortega et al., 1996; character 5). Lateral surface of the dentary: without a longitudinal depression (0) or with a longitudinal depression (1).

Character 119 (Ortega et al., 1996; character 9). Ventral exposure of splenials: absent (0) or present (1).

Character 120 (Ortega et al., 1996, 2000; characters 11 and 100, respectively). Tooth margins: with denticulate carinae (0) or without carinae or with smooth or crenulated carinae (1).

Character 121 (modified from Pol, 1999a, and Ortega et al., 2000; character 133 and character 145, respectively). Lateral surface of anterior process of jugal: flat or convex (0) or with broad shelf below the orbit with triangular depression underneath it (1).

Character 122 (Pol, 1999a; character 134). Jugal: does not exceed the anterior margin of orbit (0) or exceeds (1).

Character 123 (Pol, 1999a; character 135). Notch in premaxilla on lateral edge of external nares: absent (0) or present on the dorsal half of the external nares lateral margin (1).

Character 124 (Pol, 1999a; character 136). Dorsal border of external nares: formed mostly by the nasals (0) or by both the nasals and premaxilla (1).

Character 125 (Pol, 1999a; character 138). Posterodorsal process of premaxilla: absent (0) or present extending posteriorly wedging between maxilla and nasals (1).

Character 126 (Pol, 1999a, and Ortega et al., 2000; character 139 and character 9, respectively). + Premaxilla–maxilla suture in palatal view, medial to alveolar region: anteromedially directed (0) or sinusoidal, posteromedially directed on its lateral half and anteromedially directed along its medial region (1) or posteromedially directed (2).

Character 127 (Pol, 1999a; character 140). Nasal lateral border posterior to external nares: laterally concave (0) or straight (1).

Character 128 (Pol, 1999a; character 141). Nasal lateral edges: nearly parallel (0) or entirely oblique to each other converging anteriorly (1) or oblique to each other diverging anteriorly (2).

Character 129 (Pol, 1999a; character 143). Palatine anteromedial margin: exceeding the anterior margin of the palatal fenestrae wedging between the maxillae (0) or not exceeding the anterior margin of palatal fenestrae (1).

Character 130 (Pol, 1999a; character 144). Dorsoventral height of jugal antorbital region respect to infraorbital region: equal or lower (0) or antorbital region more expanded than infraorbital region of jugal (1).

Character 131 (Pol, 1999a; character 145). Maxilla–lacrimal contact: partially included in antorbital fossa (0) or completely included (1).

Character 132 (Pol, 1999a; character 146). Lateral eustachian tube openings: located posteriorly to the medial opening (0) or aligned anteroposteriorly and dorsoventrally (1).

Character 133 (Pol, 1999a; character 147). Anterior process of ectopterygoid: developed (0) or reduced–absent (1).

Character 134 (Pol, 1999a; character 148). Posterior process of ectopterygoid: developed (0) or reduced–absent (1).

Character 135 (Pol, 1999a, and Ortega et al., 2000; character 149 and character 13, respectively). Small foramen located in the premaxillo-maxillary suture in lateral surface (not for big mandibular teeth): absent (0) or present (1).

Character 136 (Pol, 1999a; character 150). Jugal posterior process: exceeding posteriorly the infratemporal fenestrae (0) or not (1).

Character 137 (Pol, 1999a; character 151). Compressed crown of maxillary teeth: oriented parallel to the longitudinal axis of skull (0) or obliquely disposed (1).

Character 138 (Pol, 1999a; character 152). Large and aligned neurovascular foramina on lateral maxilary surface: absent (0) or present (1).

Character 139 (modified from Pol, 1999a; character 153). External surface of maxilla and premaxilla: with a single plane facing laterally (0) or with ventral region facing laterally and dorsal region facing dorsolaterally (1).

Character 140 (Pol, 1999a, and Ortega et al., 2000; character 154 and character 104, respectively). Maxillary teeth: not compressed laterally (0) or compressed laterally (1).

Character 141 (Pol, 1999a; character 155). Posteroventral corner of quadratojugal: reaching the quadrate condyles (0) or not reaching the quadrate condyles (1).

Character 142 (Pol, 1999a; character 156). Base of postorbital process of jugal: directed posterodorsally (0) or dorsally (1).

Character 143 (Pol, 1999a; character 157). + Postorbital process of jugal: anteriorly placed (0), in the middle (1), or posteriorly positioned (2).

Character 144 (Pol, 1999a, and Ortega et al., 2000; character 158 and character 36, respectively). Postorbital–ectopterygoid contact: present (0), absent (1).

Character 145 (Pol, 1999a; character 161). Quadratojugal: not ornamented (0) or ornamented in the base (1).

Character 146 (Pol, 1999a; character 162). Prefrontal–maxillary contact in the inner anteromedial region of orbit: absent (0) or present (1).

Character 147 (Pol, 1999a; character 163). Basisphenoid: without lateral exposure (0) or with lateral exposure on the braincase (1).

Character 148 (Pol, 1999a; character 165). Quadrate process of pterygoids: well developed (0) or poorly developed (1).

Character 149 (modified from Pol, 1999a, and Ortega et al., 2000; character 166 and character 44, respectively). + Quadrate major axis directed: posteroventrally (0) or ventrally (1) or anteroventrally (2).

Character 150 (Pol, 1999a; character 167). Quadrate distal end: with only one plane facing posteriorly (0) or with two distinct faces in posterior view, a posterior one and a medial one bearing the foramen aereum (1).

Character 151 (Pol, 1999a; character 168). Anteroposterior development of neural spine in axis: well developed, covering all the neural arch length (0) or poorly developed, located over the posterior half of the neural arch (1).

Character 152 (Pol, 1999a; character 169). Prezygapophyses of axis: not exceeding anterior edge of neural arch (0) or exceeding the anterior margin of neural arch (1).

Character 153 (Pol, 1999a; character 170). Postzygapophyses of axis: well developed, curved laterally (0) or poorly developed (1).

Character 154 (modified from Pol, 1999b; character 212). Shape of dentary symphysis in ventral view: tapering anteriorly forming an angle (0) or U shaped, smoothly curving anteriorly (1) or lateral edges longitudinally oriented, convex anterolateral corner, and extensive transversally oriented anterior edge (2).

Character 155 (Pol, 1999b; character 213). Unsculpted region in the dentary below the tooth row: absent (0) or present (1).

Character 156 (Ortega et al., 1996, and Buckley et al., 2000; character 13). Cheek teeth: not constricted at base of crown (0) or constricted (1).

Character 157 (Ortega et al., 2000; character 42). Outer surface of squamosal laterodorsally oriented: extensive (0) or reduced and sculpted (1) or reduced and unsculpted (2).

Character 158 (Ortega et al., 2000; character 74). Length/height proportion of infratemporal fenestra: higher than wide or equal (0) or very antero-posteriorly elongated (1).

Character 159 (Ortega et al., 2000; character 90). Foramen intramandibularis oralis: small or absent (0) or big and slotlike (1).

Character 160 (Ortega et al., 2000; character 146). Ectopterygoid medial process: single (0) or forked (1).

Character 161 (modified from Gomani, 1997, and Buckley et al., 2000; character 46 and character 113, respectively). Cusps of teeth: unique cusp (0), one main cusp with smaller cusps arranged in one row (1) or one main cusp with smaller cusps arranged in more than one row (2) or several cusps of equal size arranged in more than one row (3) or multiple small cusps along edges of occlussal surface (4).

Character 162 (Pol and Norell, 2004a; character 164). Cross section of distal end of quadrate: mediolaterally wide and anteroposteriorly thin (0) or subquadrangular (1).

Character 163 (Pol and Norell, 2004a; character 165). Palatine–pterygoid contact on palate: palatines overlie pterygoids (0) or palatines firmly sutured to pterygoids (1).

Character 164 (Wu et al., 1997; character 103). Squamosal descending process: absent (0) or present (1).

Character 165 (modified from Wu et al., 1997; character 105). + Development of distal quadrate body ventral to otoccipital–quadrate contact: distinct (0) or incipiently distinct (1) or indistinct (2).

Character 166 (Wu et al., 1997; character 106). Pterygoid flanges: thin and laminar (0) or dorsoventrally thick, with pneumatic spaces (1).

Character 167 (Wu et al., 1997; character 108). Postorbital participation in infratemporal fenestra: almost or entirely excluded (0) or bordering infratemporal fenestra (1).

Character 168 (Wu et al., 1997; character 109). Palatines: form margin of suborbital fenestra (0) or excluded from margin of suborbital fenestra (1).

Character 169 (Wu et al., 1997; character 110). Angular posterior to mandibular fenestra: widely exposed on lateral surface of mandible (0) or shifted to the ventral surface of mandible (1).

Character 170 (Wu et al., 1997; character 112). Posteroventral edge of mandibular ramus: straight or convex (0) or markedly deflected (1).

Character 171 (modified from Wu et al., 1997; character 119). Quadrate ramus of pterygoid in ventral view: narrow (0) or broad (1).

Character 172 (Wu et al., 1997; character 121). Pterygoids: not in contact anterior to basisphenoid on palate (0) or pterygoids in contact (1).

Character 173 (Wu et al., 1997; character 122). Olecranon: well developed (0) or absent (1).

Character 174 (Wu et al., 1997; character 123). Cranial table width respect to ventral portion of skull: as wide as ventral portion (0) or narrower than ventral portion of skull (1).

Character 175 (Wu et al., 1997; character 127). Depression on posterolateral surface of maxilla: absent (0) or present (1).

Character 176 (Wu et al., 1997; character 128). Anterior palatal fenestra: absent (0) or present (1).

Character 177 (Pol and Norell, 2004a; character 179). Paired ridges located medially on ventral surface of basisphenoid: absent (0) or present (1).

Character 178 (Pol and Norell, 2004a; character 180). Posterolateral end of quadratojugal: acute or rounded, tightly overlapping the quadrate (0) or with sinusoidal ventral edge and wide and rounded posterior edge slightly overhanging the lateral surface of the quadrate (1).

Character 179 (Pol and Norell, 2004a; character 181). Orientation of quadrate body distal to otoccipital-quadrate contact in posterior view: ventrally (0) or ventrolaterally (1).

Character 180 (Gasparini et al., 1991; character 3). Wedgelike process of the maxilla in lateral surface of premaxilla–maxilla suture: absent (0) or present (1).

Character 181 (Pol and Norell, 2004b; character 181). Palpebrals: separated from the lateral edge of the frontals (0) or fused to each other and the lateral margin of the frontals (1).

Character 182 (Pol and Norell, 2004b; character 182). External surface of ascending process of jugal: exposed laterally (0) or exposed posterolaterally (1).

Character 183 (Pol and Norell, 2004b; character 183). Longitudinal ridge on lateral surface of jugal below infratemporal fenestra: absent (0) or present (1).

Character 184 (Pol and Norell, 2004b; character 184). Dorsal surface of posterolateral region of squamosal: without ridges (0) or with three curved ridges oriented longitudinally (1).

Character 185 (Pol and Norell, 2004b; character 185). Ridge along dorsal section of quadrate-quadratojugal contact: absent (0) or present (1).

Character 186 (Pol and Norell, 2004b; character 186). Sharp ridge along the ventral surface of angular: absent (0) or present (1).

Character 187 (Pol and Norell, 2004b; character 187). Longitudinal ridge along the dorsolateral surface of surangular: absent (0) or present (1).

Character 188 (Pol and Norell, 2004b; character 188). Dorsal surface of osteoderms ornamented with anterolaterally and anteromedially directed ridges (fleur de lys pattern of Osmólska et al., 1997): absent (0) or present (1).

Character 189 (Pol and Norell, 2004b; character 189). Cervical region surrounded by lateral and ventral osteoderms sutured to the dorsal elements: absent (0) or present (1).

Character 190 (Pol and Norell, 2004b; character 190). Appendicular osteoderms: absent (0) or present (1).

Character 191 (Ortega et al., 2000; character 72). Supratemporal fenestra: present (0) absent (1).

Character 192. Ventral half of lacrimal: extending posteroventrally, widely contacting the jugal (0) or tapers posteroventrally, not contacting or contacting slightly the jugal (1).

Character 193. Large foramen on lateral surface of anterior jugal: absent (0) or present (1).

Character 194. Procumbent premaxilary and anterior dentary alveoli: absent (0) or present (1).

Character 195. Palatine bar: absent (0) or present (1).

Character 196. Participation of ectopterygoid on palatine bar: no (0) or yes (1).

Character 197 (Pol and Norell, 2004b; character 192). Choanal opening: opened posteriorly and continuous with pterygoid surface (0) or closed posteriorly by an elevated wall formed by the pterygoids (1).

Character 198. Ectopterygoid: projecting medially on ventral surface of pterygoid flanges barely extended (0) or widely extended, covering approximately the lateral half of the ventral surface of the pterygoid flanges (1).

APPENDIX 3

Data Matrix Used in Phylogenetic Analysis

The data matrix contains 46 taxa and 198 characters.

Gracilisuchus

000000??0?000000000000?0?000000000?0??0?-
0?00000?000???0000?0???00000?100000?00000-
000?0???0000?0?000001012?00?00????0?01?010-
00??1?01???000001002?0???0000?????0??0??000-
0?00000?0?00000000?0?0000??0??0?

Terrestrisuchus

000??00??0??000000?000?0?00?000?110?00000-
?00000?000??0?000?000???00???010??0?00000-
0?010?0000?0200000101??01100??00000?0010-
0??10?00?110?0?0??(01)110???00000???00?0??-
0???00??0?0???0???????????0?????0?

Dibothrosuchus

000?00?020??001???000000?????00110000000?-
00000?0000?00000?0?0101000?010100?0010?0-
00?????2000?0?????01010?01100?0?0000000100-
1?10?00?1?000101011100??000001??00000010-
001000100?0?00000000?000000?00??0?

Protosuchus

2100000120?00001101000210000001000100010-
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010100011100{1234}00?1200110101110210 01-
010000{01}000000?01??01??10010{01}010100-
0000???010000000012000001 1110??01000?010-
?0000?00??0?

Hemiprotosuchus

?00?00?10??????10010?0??00?0010?11?0??01??0-
020?00?11?1100101??1?2?11??1?21????01??????-
???0????1200?1?101??0??????????000?000??10?0-
0???00000??10?????00???????0?000?12???001??1-
0?0?00?01??00???0?????0?

Orthosuchus

21100001201?0001001000{01}1000001000100-
0?000?002011001111100??1?1?02011?0?0?0?00-
1000100011100000?1200100102114210 01?100-
10?100000001?0101000000000?0???00001???-
000000?12?000011110?001000?0?000?00??0??0?

Kayenta Form

(12)01110?1200000?10010?0??00????0?0???111-
10?00201001111110000101 1?2011?0102100?1-
010??0???00??0?1200101101112?????0????011-
00?00?01000111?101001?01?1000000001 1?0??-
40012??00011??0?00???00?????????????0?

Zaraasuchus

10?????????????1?01?01?1000001?10?02?????????-
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34}0??1010??0???????????0????????????????????-
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Gobiosuchus

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11?00??00

Sichuanosuchus

(12)01??0?1200(01)00?10010(01)1?110???1?00?-
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0011?1??1????000????????1?11?0?1????0??1001-
00??1??10?0????00110(01)1210??00?????1?????0-
101110111111 00?110000100?1???0?00??00

Shantungosuchus

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0020?1?011?1100?10????????101?1?000??10????-
???0????????????????1????????1?????00100??????00??-
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0?110??0???1???????????0?

Zosuchus

201??0?1200000??001010{01}110?001110?022-
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0111??1011?10111000000100???0?000?00

Fruita Form

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1?0?0100100??101?0011?01110??0??00?10?000-
0?1???000????101?0?00000?000??0???0??0

Hsisosuchus

211??????1??00000010000110001100 0?022110-
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2?1??10???????000?1000???101?0021??1?????01-
001???????0000??00??1?11?1??00????????0??0???-
{01}00?0?0111(01)?00??00?0?1000?0?0???10

Notosuchus

101?0011010100111000111111001100010221101-
10021112011?1000010?1102111112?0101110001-
{01}111?1?200001000??0122011???1100101(01)1-
101(01)0100100000011111111?000111100100-
0010111011000011101100000000000000001111

Comahuesuchus

103??0?101??00?????0112????????0010?2????1??-
11?1??????????????????131??????0?10101?????????-
??????????????{01}13???1??????0?10?101201?01?-
????011??0?1????11???11?00100?1?0??000???10-
0??0?000??0????011110?1

Mariliasuchus

101?00?10100001110001(01)0111000110010221-
10100021?12011?1000010?1?0213111210(01)0?-
11000?????????????????????22111???11?????0{01}0-
001010010?1100{01}0011110110?0011???01100-
01001100100001?1010000000000???011110?1

Uruguaysuchus

201?001101??00??10??1??1????1???01022?101?-
0011????1?????0??0???01111(12)???000110100?-
?1?1??????0000?0??01?21002100?00?000?{01}?-
??01?1?00????1?0111?11?????11?????1?0001????-
????0???10?????00????????0?????1?

Chimaeresuchus

101?0001111?00???????????????????????????????????-
?????????????????????12??0110?01010??1?1?????21-
00?00???11(12)?314210??00?0100111111011??-
????0?0110????????????10?11?????3????????????1?00-
???0????????????0?0?????

Malawisuchus

101?00?1110000?(01)10001(01){01}1100?1100-
01?22110100011??20???1000?10?1?02?111(01)-
2?0101110001????1??210000010??01(12)2111??-
?01?0???01100101?11000???110110101?0?0001-
???0?100??21110?1000011100000000000000???0-
??00?10

Candidodon

??-
??-
?????????????????????1?????????????????0??0?????????-
??????1????2??

Simosuchus

1030101100000010001011111 0?0110001021?1-
0100011?11011?1000010?1?020112121010110-
000???????02100?2010?10002010???01??????11-
0110121200001010011100211001 20???211{12-
}0001111011001{01}1?10000000000000100000?-
000?10

Sphagesaurus

101?000101??00??100?????110??????????21101?0-
0?????011?1000?????????13?2?????????100?????????-
1????????????????312????0???????1111110111111-
111111111001110111 1?0?11?0??011?0?10??01?-
?000000?00????????00?0??1?

Bretesuchus

1{01}0??01121??00????????????0????????????2???10-
011?????????1011?1???????13?1??1?00?10110?????-
????????????????????100????1???????01??0????01??0-
???0??1?0?????????????{01}0(01)?1?10?1???1??001-
??00????????????0????0?01?1?

Baurusuchus

100??0?121??00?1101????111?0110?????2?1011-
0011112011?1000?10??10??31112101011111 1?-
??????????????????????12103????1?????1101110101-
01110011001111 0110?0111???{01}0(01)11110-
11101?00001?0001000000000000???0??01111

Iberosuchus

1?0?00012?0?0011100011111 1?01?000?02??10-
100111?12??1?101??10?1????111??10?0?101101-
1??????{12}{1234}00??00???00?{12}(01)0?2??0-
000???11001101010?1?0??100?11001?0??101???-
{01}?0111?001101?0??01?1000010000000??0??0-
?00??1?

Araripesuchus gomesii

20100011010000111000101111 1011(01)00102-
21101000111112011?10000?0?11020112121000-
1101{01}{01}1{01}11111?1{234}0001000100-
11110021001001010100100100100000010011-
000210000110?0011{01}0000111101000 01110-
0?000000000000000?000?10

Araripesuchus patagonicus

201000?1010000?1{01}000101111?011100102-
2?10100011?12?11?1000??0?1?02?11212?0?011-

{01}1??1?1??????????1000??0111100???01???0?-
01?01101?010000??100110102?0??01????0??{0-
1}1000111?0100001110?000000000000000?00-
0?10

Lomasuchus

201????1211?00?11000101111??110001022?10-
10001??12??1?100??1??1??2?21????00??0(12)1-
1???????????????????1???00???00?????0?00???1?1-
10?00???00011?0??1??0??????010???0?11??10??0-
1?1000??11000??0???0?0?0?10

Peirosaurus

201?011??1??00??????10?1????????0???2?10?????-
????????????????????1??????????(12)1???????????-
????????????000????????????0????1???0???????0?1-
?????????????(01)??????0??????????????00??1????-
??????0???????

Theriosuchus

2011011111010011000011011110011001?21-
1010001?11?01111000?????1?20211?41001010-
10110111110001111200100101000 2?00?10?1-
10110(01)001?1100?00?0?00100??01??0?00??1-
0100000?11?010??01?10000??0000??????0???0-
?10

Alligatorium

?0??????1?0000?1000010?111??0?100?1????0??0-
0??11??1??1000???????20?1????00101?101?0111-
11000???1?00100???????????10??1???????????????-
????0??????????????????????0?????????????????0?-
?????????????????

Goniopholis

203?12111100101110001001 11?0010001002?1-
01000?1112011?1010?10?1?021312?4100{01}0-
(12)02011?1??1??0?00?1200?11?000002100010-
?1101101??101100?000010010001?1???000011-
0020000011001000011110?0100000000000?0-
00?10

Eutretauranosuchus

203????1?100101110001001 11?00?0001001110-
?000?1112011?1010??0?1?0?121204?00001020-
111???1??0??0?1?????????000???00?????0?101???-
?110???????0??00???1???0????10?2???001?0??000-
?1?110?01?0000000???0?00??10

Pelagosaurus

202?11111100110201010000000000000(01)100-
211010000001101111001001?10001200?30000-
020000110111?000000120001 1101?00???10???-
????1?1??????0000??010010?0010???00????0001-
00001120100001100000 1?0000000???0??00?10

Teleosauridae

(02)02?1111110011020100100000000000001100-
21?01000?001101111001011?1?00120003?000?-
200002101111?0000?1200010101 1?0???10??01-
001101??101100001100001 0100?0??0000??100-
0100001 1?010?011100010100000000000000??00?-
10

Metriorhynchidae

(02)02?121101001112010110 00?00000001100-
21?0?000?0011011110010 11?1?001200?300010-
200002101?11?0000??????0??012?0???100?0100-
1101??1011?000??000010102?0???000????0010-
00011?01000?110000010000000 0??00?00?10

Sokotosuchus

2?2???1101??10????001001???101001?012?1????-
??1112?11?1?11??0???1?1?0?????????01?????????-
?????????????????????????????1???????????????0-
??0?????????????????????0?????????????????????????-
????????????

Dyrosauridae

002??1?101?010?11?0010001 1?1010011012?10-
101001112011?1011?10?10101302?3?00??2?00-
0?????????0?00??????1???????????????????1????????-
????????0??0???????????????021?0001????0???????0-
0??1?0000000???0??00?10

Pholidosaurus

212?111101??11?11101100111?00100010?211?-
100001112111?101??10?100?1311?300???2?0??-
?11?1???0??0??2?0???????????????????????1????1?11-
0?????0?0010????????????????0?1?0001???10?001?-
100?010???0???????0???0?10

Bernissartia

203??21111??00111000?00111?001000?002????-
?0001112?11?10100?0?1???1?1??410010102011-
?1?11??020021110110100000??00????????1????-
1????????0??0?10???01???0????1?12000001????0?-
?????00??10000????0??0???0?10

Hylaeochampsa

00???????11???11????1?01???0????0?002?1?1011-?????????101??1??1?????10??????????????????????-??????????????????0???????10????????????0??0???-???0????????????2??00???????????????????????????-?0???0?1?

Borealosuchus

203?121111001011100010011 1?001000100211-01011111121111101001 0?110?131003100011 0-?011111111113111?110?00?000002110?100100-?101??11110??000000010001?1???0000110?20?-0001100100001110000100000000000???0?10

Gavialis

212?1211110011111011011111001000100211-0101101112011110110101110{01}131003100-012000001111110131112111100?000002110?1-00100?101??121100?00000001000101?1?00001-?0?20?00011001000011100001?00000000000??-00?10

Crocodylus

203012111100(01)01110001021111001000100 21-10?01111112011110100101110{01}13100310001-00101211111101311120211 00?0000021100100 1-00?101??121100?000000010011010110000 1?0?20-00001100100001110000100000000000 0?000?10

Alligator

203112?101?00011100010211110010 00?0021101-011111120111101001011 10{01}03120310001002-01211111111311120211?0?000002110010010011-01??111000?00000001001(12)01011000011(01)12-00000110010000111000010000000000000000?10

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