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New *Araripesuchus* Remains from the Early Late Cretaceous (Cenomanian–Turonian) of Patagonia

DIEGO POL[1] AND SEBASTIAN APESTEGUIA[2]

ABSTRACT

Two new crocodyliform specimens found in a recently discovered locality from the Late Cretaceous of Patagonia (Argentina) are described herein. One of them comprises an almost complete skull found in articulation with the lower jaws, while the other consists of the anterior region of the lower jaws and fragmentary remains of the palate. These two specimens differ in the morphology of their lower jaws (e.g., height of mandibular symphysis, pattern of ornamentation on ventral surface of mandibular ramus, concavity of medial surface of splenials, shape of splenial-dentary suture on ventral surface of mandibular symphysis) and probably belong to different taxa.

The more complete specimen is considered to be a new taxon, *Araripesuchus buitreraensis*, diagnosed by the combination of the following characters (autapomorphic characters are indicated with an asterisk): long and acute anterior process of frontals extending anteriorly between the nasals; frontals extending into supratemporal fenestra; narrow parietal dorsal surface between supratemporal fossa; anterior palpebral remarkably broad; large siphoneal foramen in otic recess; T-shaped choanal septum that completely divides the internal nares, having its anterior end as broad as the midregion of the septum*; pterygoid flanges pneumatic and poorly expanded at its lateral end*; transversely elongated depression on ventral surface of pterygoid flanges close to the posterior margin of suborbital fenestra*; longitudinal groove on flat lateral surface of dentaries below toothrow.

The second, more fragmentary specimen might represent a different new taxon, although more material is needed in order to make a justified taxonomic decision. The phylogenetic relationships of both specimens are analyzed through a comprehensive cladistic analysis including 50 crocodylomorph taxa. All the most parsimonious hypotheses depict both specimens as closely related to the previously known South American species of *Araripesuchus* (*A. gomesii* and *A. patagonicus*). This group is depicted as the most basal clade of notosuchians, the most diverse group of Cretaceous mesoeucrocodylians from Gondwana.

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INTRODUCTION

Mesoeucrocodylian crocodyliforms were remarkably diverse in the Cretaceous of Gondwana, showing a wide morphological diversity that contrasts with the characteristic anatomy of extant crocodylians. The most conspicuous Cretaceous crocodyliform group from Gondwana is Notosuchia, an assemblage of small terrestrial taxa remarkably diverse in dental morphology (including multicusped teeth; Clark et al., 1989; Carvalho, 1994; Gomani, 1997; Buckley et al., 2000) and indications of fore–aft jaw movements (Clark et al., 1989; Bonaparte, 1991; Pol, 2003). Gasparini (1971) first recognized this group to include these forms and a rather generalized form from the Santana Formation, *Araripesuchus gomesii* (Price, 1959).

Buffetaut (1981) described a crocodyliform from the Early Cretaceous of Niger and referred it to this genus, *Araripesuchus wegeneri*. More recently, Ortega et al. (2000) described a third species, *Araripesuchus patagonicus*, from the Cenomanian of Patagonia. Additionally, new remains preliminarily referred to this genus were recently reported from Late Cretaceous beds of Madagascar and Niger (Buckley et al., 1997; Sereno et al., 2004; Turner, 2004b). Despite the growing knowledge on the diversity, temporal, and geographic distribution of *Araripesuchus* (and other notosuchians), the phylogenetic relationships of these forms are still disputed in current phylogenetic analyses (Clark, 1994; Wu and Sues, 1996; Buckley and Brochu, 1999; Ortega et al., 2000; Sereno et al., 2003; Pol, 2003; Turner, 2004a).

A recently discovered locality from the Cenomanian–Turonian (Corbella et al., 2004) of Rio Negro Province (Argentina) yielded new remains of crocodyliforms that, despite being fragmentary, show a combination of derived similarities exclusively present in *Araripesuchus*. Here, we describe two of these specimens, erecting a new taxon based on one of them (MPCA-PV 235). The second, more fragmentary specimen (MPCA-PV 236) is described and its taxonomic status is discussed. The relationships of these materials are analyzed through a cladistic analysis within the context of Crocodyliformes.

The following acronyms are used throughout this work:

AMNH	American Museum of Natural History, New York
BSP	Bayerische Staatssammlung für Paläontologie und Geologie, Münich, Germany
CNM	Chongqing Natural Museum, Sichuan, People's Republic of China
DGM	Departamento de Produção Mineral, Rio de Janeiro, Brazil
GMPKU-P	School of Earth and Space Sciences, Peking University, Beijing, People's Republic of China
GPIT	Institut und Museum für Geologie und Paläontologie, Universitat Tübingen, Tübingen, Germany
IGM	Mongolian Institute of Geology, Ulaan Bataar, Mongolia
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China
LACM	Los Angeles County Museum, Los Angeles
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MAL	Malawi Department of Antiquities, Malawi
MB	Institut für Palaontologie, Museum fur Naturkunde, Humbolt-Universitat, Berlin, Germany
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA
MLP	Museo de La Plata, La Plata, Argentina
MOZ	Museo Profesor J. Olsacher, Zapala, Argentina
MPCA-PV	Museo Carlos Ameghino, Cipoletti, Argentina
MUC-PV	Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina
PVL	Instituto Miguel Lillo, Tucumán, Argentina
RCL	Museo de Ciencias Naturales, Pontificia Universidade Catolica de Minas Gerais, Brazil
SAM-K	South African Museum, Cape Town, South Africa
SMNS	Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
UA	University of Antananarivo, Madagascar
UCMP	Museum of Paleontology, University of California, Berkeley
ZPAL	Instytut Paleobiologii PAN, Warszawa, Poland

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SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA HAY, 1930 (SENSU WALKER, 1970)

CROCODYLIFORMES HAY, 1930 (SENSU CLARK, 1986)

MESOEUCROCODYLIA WHETSTONE AND WHYBROW, 1983

Araripesuchus buitreraensis, new species

ETYMOLOGY: *buitreraensis*, from ''La Buitrera'', the new locality where the specimen was found.

HOLOTYPE: MPCA-PV 235, isolated skull in articulation with the lower jaws, lacking external surface of ventral region of braincase.

LOCALITY AND HORIZON: ''La Buitrera'' is a recently discovered locality of the Candeleros Formation (Cenomanian, Hugo and Leanza, 2001; Cenomanian–Turonian, Corbella et al., 2004). These outcrops are located 30 km NE from Cerro Policia, Río Negro Province (NW Patagonia). The faunal assemblage recovered in this locality includes dryolestoid mammals, theropod dinosaurs, crocodyliforms, snakes, fragmentary remains of frogs and fishes, and sphenodontians (Apesteguia and Novas, 2003). Up to now a variegated fauna has been known from the exposures of Candeleros Formation in Neuquén Province, including titanosaurian and diplodocoid sauropods (Calvo and Bonaparte, 1991; Calvo and Salgado, 1995), carcharodontosaurid theropods (Coria and Salgado, 1995; Calvo and Coria, 1998), chelid turtles (Broin et al., 1997), pipoid anurans (Baez et al., 2000), and the crocodyliform *Araripesuchus patagonicus* (Ortega et al., 2000). However, La Buitrera's fauna differs from others, including abundant remains of small body-sized vertebrates.

DIAGNOSIS: This new taxon is diagnosed by the combination of the following characters (autapomorphic characters are indicated with an asterisk): long and acute anterior process of frontals extending anteriorly between the nasals; frontals extending into supratemporal fenestra; narrow parietal dorsal surface between supratemporal fossa; anterior palpebral remarkably broad on its anterior end; large siphoneal foramen anterior to the otic notch; T-shaped internal nares septum that completely divides the choanal opening, the ventral surface of which is as broad anteriorly as in the midregion of the septum*; pterygoid flanges pneumatic and poorly expanded at its lateral end*; transversely elongated depression on ventral surface of pterygoid flanges, close to the posterior margin of suborbital fenestra*; longitudinal groove on flat lateral surface of dentaries below toothrow.

DESCRIPTION

The specimen MPCA-PV 235 consists of a skull in articulation with its lower jaws. The anterior tip of the snout is missing and the external surface of most skull bones is partially damaged. The external surface of the braincase has not been preserved, although fragments of the exoccipitals and supraoccipital are partially exposed.

The anteroposterior length of the skull is almost entirely preserved (130 mm), being the largest specimen of all the described *Araripesuchus* species. Although the external surfaces of the skull bones are poorly preserved, the original ornamentation pattern has been preserved in some elements. This pattern varies depending on the skull region, being composed either by small circular pits (e.g., anterior palpebral, ventral surface of mandibular symphysis) or by shallow grooves and ridges (e.g., posterior region of nasals, anterior region of frontal, dorsal surface of postorbital). The snout is oreinirostral (sensu Busbey, 1994), being slightly wider than high, and its anteroposterior length is approximately equal to the remainder of the skull. The dorsal surface of the rostrum is slightly concave in lateral view, although this could be accentuated by the poor preservation of the nasals. Most of the rostral region has a constant lateromedial width, except at its anterior tip that tapers anteriorly (at the premaxilla-maxilla contact) and its posterior end where the skull broadens gradually. The lateromedial width of the skull increases toward the posterior region of the orbit, where it reaches its maximum width. Posteriorly, along the temporal region, the skull has a rather constant width. The skull roof has a flat and wide dorsal surface, as in all crocodyliforms (Clark, 1994).

The orbits are rather large, occupying approximately one-fourth of the skull's antero-

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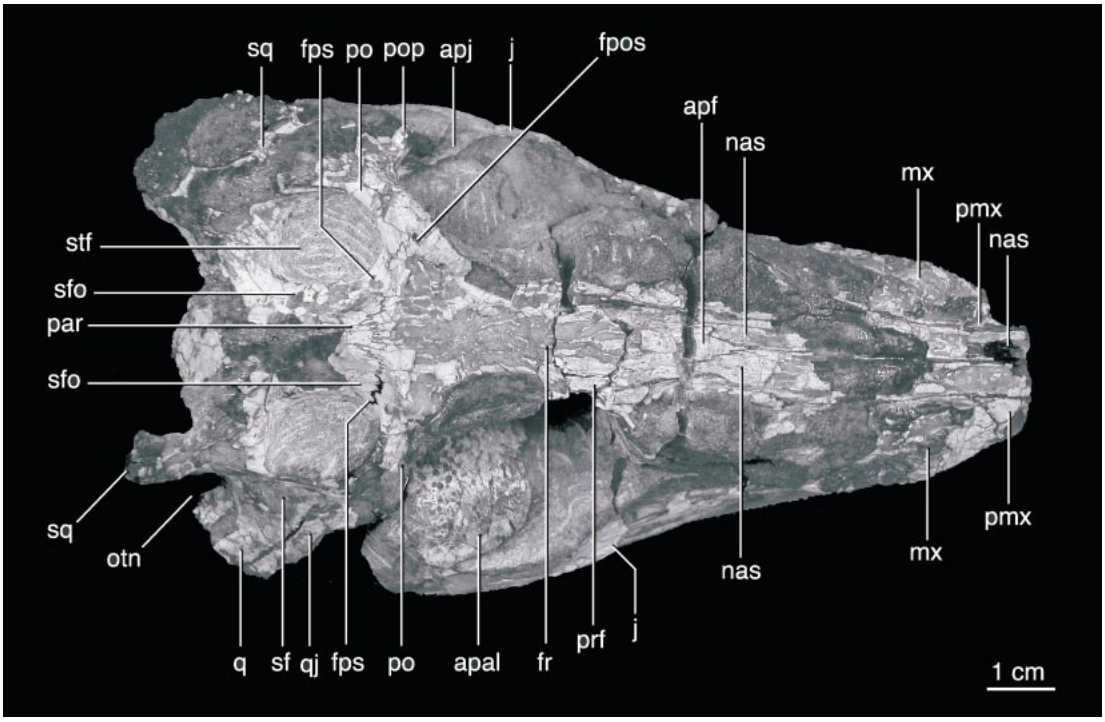

Fig. 1. Holotype of *Araripesuchus buitreraensis* MPCA-PV 235 in dorsal view. See appendix 4 for abbreviations.

posterior length. The external margins of the supratemporal fossae are not preserved. The supratemporal fenestrae are subcircular, being slightly longer than their lateromedial width. The infratemporal fenestrae face laterally and are triangular, being slightly longer than high. The antorbital fenestrae are not preserved due to poor preservation of the lateral surfaces of the lacrimals and maxillae. The suborbital fenestrae are large and elongated, being approximately three times longer than wide. The choanal opening is long, narrow, and completely septated. The external mandibular fenestrae were not preserved.

Most of the *premaxillae* are missing, except for their posterodorsal process. This process is smooth and is exposed on the dorsal surface of the rostrum. The posterodorsal process is long, acute, and wedges between the maxilla and nasal (fig. 1). The external surface of the left *maxilla* of MPCA-PV 235 is damaged, but the anterior and posteroventral regions of the right element are well preserved. Most of the maxilla is vertically oriented except for its dorsal region, which is dorsally deflected, facing dorsolaterally. The anterior region of the maxilla bulges laterally at the level of the enlarged maxillary tooth and seems to be constricted at the premaxilla-maxilla contact (fig. 1). Posterior to its contact with the posterodorsal process of the premaxilla, the maxilla is bordered by the nasal along a straight suture that is longitudinally oriented. The buccal edge of the maxilla is concave posterior to the enlarged maxillary tooth, as in *A. gomesii* (AMNH 24450). Posteriorly, the maxilla is overlapped by the jugal and extends posterior to the anterior orbital margin. Unfortunately, its posterodorsal region and its contact with the lacrimal have not been preserved in MPCA-PV 235. The palatal processes of the maxillae meet on the midline, forming an extended secondary palate. Posterolaterally, they contact the anterolateral process of the ectopterygoids and posteromedially they receive the rounded anterior process of the palatines (fig. 2). The posterior edges of the palatal branches of the maxillae form the anterolateral margins of the suborbital fenestra.

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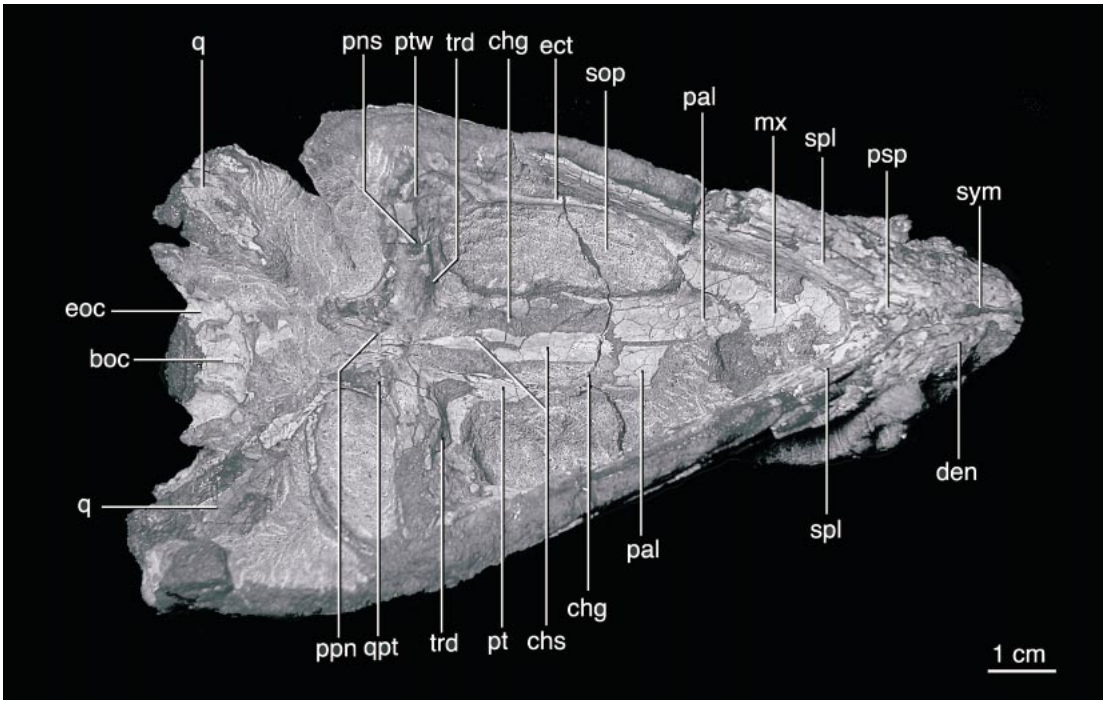

Fig. 2. Holotype of *Araripesuchus buitreraensis* MPCA-PV 235 in ventral view. See appendix 4 for abbreviations.

The *nasals* are narrow and elongated, having their lateral edges subparallel to each other (fig. 1). Their lateromedial width increases slightly along the posterior region of the nasal-maxilla suture; however, the nasals narrow markedly at their posterior end (along their contact with the prefrontals). The posterior edge of each nasal is anteromedially oriented, receiving a long and acute anterior process of the frontal. This morphology contrasts with the transverse and interdigitated suture present in *A. gomesii* (AMNH 24450) and *A. patagonicus* (MUC-PV 269). The nasal-lacrimal contact cannot be determined since the latter element has not been preserved in MPCA-PV 235.

Only the medial regions of the *prefrontals* are well preserved in MPCA-PV 235. These elements are long and narrow, extending longitudinally on the dorsal surface of the skull (fig. 1). They form the anterior half of the dorsal margin of the orbits and extend anteriorly to them along the prefrontal-nasal contact. Their lateral region is badly preserved, although they seem to be depressed for the articulation with the large anterior palpebral. The right anterior *palpebral* was preserved dislocated, inside the orbit. The preserved portion of this element is subrounded and remarkably broader than in other species of *Araripesuchus*. The anterior palpebral of *A. patagonicus* (MUC-PV 269) and *A. gomesii* (AMNH 24450) has a moderately broad anterior edge and rapidly tapers posteriorly, forming a wing-shaped, acute, and elongated posterior process. The dorsal surface of the anterior palpebral of MPCA-PV 235 is ornamented on its anteromedial region with small and well-separated pits (fig. 1). The anterior edge is straight and the medial margin is slightly convex and probably overlapped the prefrontal. The extensive width of the anterior palpebral would have covered most of the orbit.

The *frontals* are completely fused into a single element, as in all mesoeucrocodylians (Clark, 1994). Most of the external surface is damaged, except for its anterior and posterior regions. In these areas, the frontal dorsal surface is poorly ornamented. The anterior re-

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gion of the frontal extends beyond the anterior orbital margin, narrowing markedly between the prefrontals (fig. 1). The anterior end of the frontals extends between the posterior region of the nasals, forming an acute V-shaped process. Posteriorly, the frontal broadens laterally, forming the posteromedial margins of the orbit. The frontal posterior margin contacts the parietal and postorbital through a strongly interdigitated suture (fig. 1). The medial region of the frontal-parietal suture extends transversely on the skull roof, at the level of the anterior margin of the supratemporal openings. This suture extends laterally into the supratemporal fossa and reaches to the anterolateral corner of the supratemporal fenestra (fig. 1). Thus, the frontal enters widely into the supratemporal fossa, forming part of the anterolateral margin of the supratemporal fenestra. This condition contrast with that of *A. gomesii* (AMNH 24450) and *A. patagonicus* (MUC-PV 269), in which the frontal barely enters the supratemporal fossa and does not reach the supratemporal fenestra. The frontal-postorbital suture extends anterolaterally from the anterior margin of the supratemporal fenestra along the supratemporal fossa. This contact continues on the dorsal skull surface, reaching the posteromedial region of the orbital margin (fig. 1).

The *parietals* are completely fused into a single element, as in all crocodyliforms. Most of the parietal dorsal surface is damaged and its posterior region was not preserved. Its anterior margin is sutured to the frontal along a transversely oriented, interdigitated suture. This contact extends on the dorsal surface of the skull table and the smooth surface of the supratemporal fossa floor (fig. 1). The dorsal surface of the parietal is markedly restricted in MPCA-PV 235, being much narrower than the interorbital region of the frontal. Although the minimum width of the parietal dorsal surface cannot be determined due to the poor preservation of this element, the dorsal surface of this element at the frontal-parietal suture is remarkably narrow, being approximately one-third the maximum lateromedial width of the supratemporal fossa. In contrast, the parietal of *A. gomesii* (AMNH 24450) and *A. patagonicus* (MUC-PV 269) is notably wider, having this region approximately equal to the maximum lateromedial width of each supratemporal fossa. Lateral to its dorsal surface, the parietal forms a wide and smooth medial and posteromedial surface of the supratemporal fossa.

The *squamosals* are poorly preserved in MPCA-PV 235. Most of their dorsal surface has been eroded, and its posterior and occipital regions are missing. On the left element most of its lateral flange overhangs the quadrate and quadratojugal, forming a rather deep otic recess. Unfortunately, its contact with the postorbital, quadrate, and exoccipitals cannot be determined in MPCA-PV 235.

The *postorbitals* are also poorly preserved in MPCA-PV 235, although the left element has most of its dorsal surface complete. This surface is exposed horizontally, forming part of the flattened ''skull roof'' characteristic of Crocodyliformes. The medial edge of the dorsal surface of the postorbital contacts the frontal and extends posterolaterally, forming an oblique anterolateral margin of the skull roof, as in *A. gomesii* (AMNH 24450), *A. patagonicus* (MUC-PV 269), and most notosuchian crocodyliforms (e.g., *Notosuchus terrestris* MACN-RN 1037; *Malawisuchus mwakayasyunguti* MAL-45; *Simosuchus clarki* UA 8679; *Libycosuchus brevirostris* BSP 1912.VIII.574; *Baurusuchus pachecoi* DGM 299-R). The dorsal surface of the postorbital is poorly ornamented and slightly narrow toward its posterolateral region. The posterolateral end of the left postorbital of MPCA-PV 235 is damaged, and therefore its contact with the squamosal cannot be observed. The postorbital has a small, subtriangular, pointed process on its anterolateral corner (fig. 1). The dorsal surface of this process is flat and ventrally recessed from the postorbital dorsal surface. In other crocodyliforms a similar process is present and is overlapped by the posterior palpebral (e.g., *A. gomesii* AMNH 24450; *A. patagonicus* MUC-PV 269; *Notosuchus terrestris* MACN-RN 1037; *Malawisuchus mwakayasyunguti* MAL-45; *Baurusuchus pachecoi* DGM 299-R; *Libycosuchus brevirostris* BSP 1912.VIII.574; *Theriosuchus* (Clark, 1986); *Zaraasuchus shepardi* IGM 100/1321). The descending process of the postorbital is wide, smooth, and flat. Its posterior margin is sutured to the quadrate and quadratojugal. The

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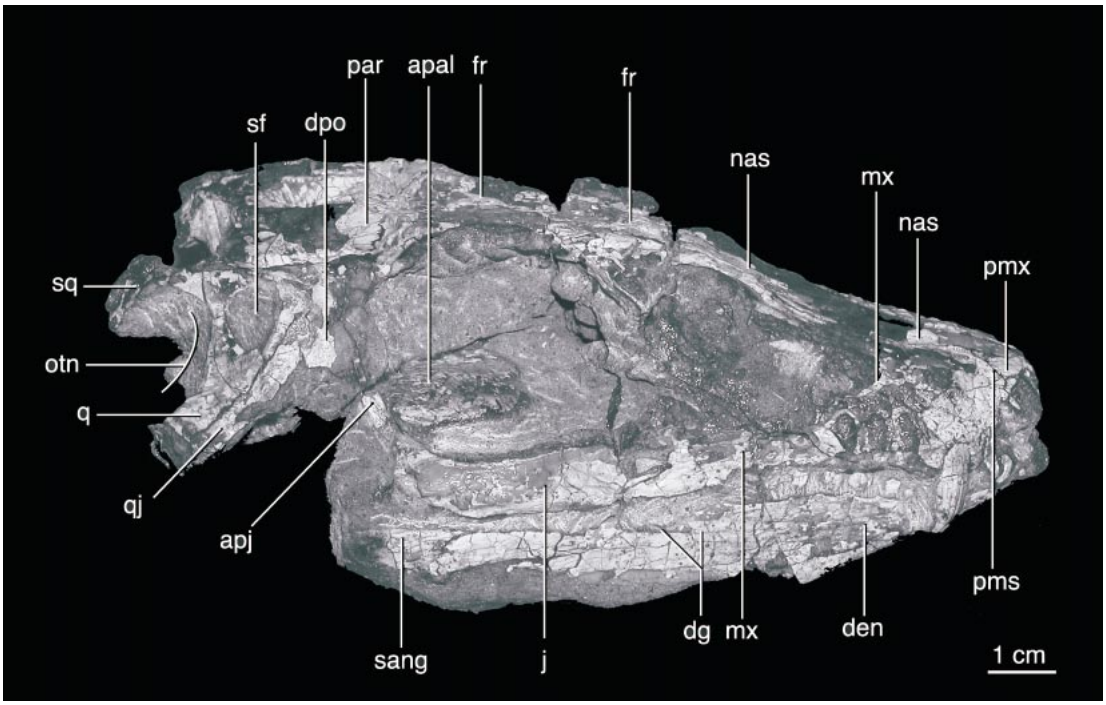

Fig. 3. Holotype of *Araripesuchus buitreraensis* MPCA-PV 235 in lateral view. See appendix 4 for abbreviations.

postorbital descending process forms part of the dorsal and anterodorsal margins of the infratemporal fenestra and contacts the ascending process of the jugal through an oblique and posteroventrally directed suture. The postorbital descending process of MPCA-PV 235 seems to lack the large postorbital foramen present above the jugal-postorbital suture in *A. gomesii* (AMNH 24450).

The *jugal* is a triradiate bone, with its anterior (suborbital) process being approximately twice as high as its posterior (infratemporal) process. Its anterior process extends beyond the anterior orbital margin, overlapping the maxilla (fig. 3). The lateral surface of this region is badly damaged although it seems to be slightly concave below the orbit. The left jugal of MPCA-PV 235 has a moderately developed longitudinal ridge running on its lateral surface along the posterior third of the orbit, close to its buccal margin. The ascending postorbital process of the jugal of MPCA-PV 235 is located posterior to the anteroposterior midpoint of the jugal (fig. 3). This process is narrow, cylindrical, and posterodorsally directed. The base of this process is continuous with the lateral surface of the jugal on its anterior margin, as in *A. patagonicus* MUC-PV 269, instead of being inset as in *A. gomesii* AMNH 24450. The posterior margin of this process is also superficially located, although this margin is located slightly more medially than the anterior margin since the major axis of the postorbital bar is slightly deflected posteromedially. The postorbital process of the jugal forms most of the anterior margin of the infratemporal fenestra and contacts the descending process of the postorbital. The left jugal preserves most of the infratemporal bar, which is slightly flattened and forms most of the ventral margin of the infratemporal fenestra. Most of its lateral surface is smooth, except for the region below the postorbital bar. The posterior end of the jugal and its contact with the quadratojugal has not been preserved in MPCA-PV 235.

Only the ascending process of the *quadratojugal* has been preserved in MPCA-PV 235. This element is exposed dorsolaterally

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as a narrow process extending into the otic recess. The base of the ascending process of the quadratojugal is slightly constricted while its dorsal end is broader than the rest of the process. The quadratojugal forms the posterior edge of the infratemporal fenestra. Its posterior margin contacts the anterodorsal process of the quadrate along a straight suture. Dorsally, it contacts the postorbital along a slightly interdigitated suture. The anterodorsal edge of the quadratojugal's ascending process is not indented as in *A. gomesii* (AMNH 24450).

The *quadrates* of MPCA-PV 235 preserve only their anterodorsal branch. This process of the quadrate is smooth and extends into the otic recess overhung by the lateral flange of the squamosal (fig. 3). The quadrate contacts the quadratojugal along a straight suture. The anterodorsal end of the quadrate is sutured to the posterior margin of the descending process of the postorbital. The dorsal edge is badly preserved and its contact with the squamosal has not been preserved in MPCA-PV 235, except at the anterodorsal margin of the right otic notch (fig. 3). The posterodorsal edge of the anterodorsal branch of the quadrate is markedly concave, forming the anterior and ventral edges of the large otic notch. Presumably, the squamosal closed the otic aperture posteriorly as in all mesoeucrocodylians. However, this is not preserved in MPCA-PV 235. The right quadrate of MPCA-PV 235 has a remarkably large ovoid siphoneal foramen located anteriorly to the otic notch (fig. 3). This opening is significantly larger than that of *A. gomesii* (AMNH 24450). The lateral surface of the quadrate is slightly depressed posteroventral to this opening, although this depression is not as developed and does not extend around the otic notch as in *A. gomesii* (AMNH 24450).

The *ectopterygoids* of MPCA-PV 235 are only exposed in ventral view. Their posteromedial process is a thin and subcylindrical bar that extends along the lateral edge of the pterygoid flange (fig. 2). This process is slightly deflected with respect to the anterior half of the ectopterygoids, which is oriented longitudinally, forming the entire lateral margin of the suborbital fenestra. Anteriorly, the ectopterygoids contact the posterior end of the palatal process of the maxilla. Its suture with the jugal and the presence of an ectopterygoid-postorbital contact cannot be determined in MPCA-PV 235.

The *palatines* of MPCA-PV 235 are exposed ventrally in articulation with the rest of the palate. The palatines are medially sutured to each other, extending posteriorly to form the secondary palate characteristic of mesoeucrocodylians. As in *A. gomesii* AMNH 24450 and *A. patagonicus* MUC-PV 269, the anterior end of the palatines extends anterior to the suborbital fenestra, forming a rounded anterior process that fits between the palatal processes of the maxillae (fig. 2). The palatines are strongly sutured to the maxillae instead of overlapping them as in basal crocodyliforms. The palatines form the anterior and medial margins of the suborbital fenestra. The posterior edge of the palatal surface of the palatines is concave and delimits the anterior margin of the choanal opening (fig. 2). At the medial part of this margin, the palatines are sutured to the wide anterior end of the choanal septum. The posterolateral regions of the palatines form the lateral borders of the choanal groove and contact the pterygoids.

The *pterygoids* of MPCA-PV 235 are exposed in ventral view. Anteriorly, the pterygoids are markedly depressed, forming a trough-shaped choanal groove. This elongated depression extends posteriorly up to the anteroposterior midpoint of the pterygoid flanges (figs. 2, 4A). In contrast, in *A. gomesii* (AMNH 24450) and *A. patagonicus* (MUC-PV 269), the posterior limit of the choanal opening is located anterior to the pterygoid flanges (fig. 4). The lateral walls of the choanal groove are thin and subparallel to each other, forming the medial margins of the suborbital fenestra and reaching the posterolateral projections of the palatines.

The choanal groove bears a sagittally oriented process formed by the pterygoids that reaches the posterior edge of the palatines. This choanal septum completely divides the choanal groove, from the roof of the nasopharyngeal passage to its palatal surface, resembling the condition of *A. gomesii* (AMNH 24450), *A. patagonicus* (MUC-PV 269), and *Simosuchus clarki* (UA 8679). The choanal septum is T-shaped in cross section,

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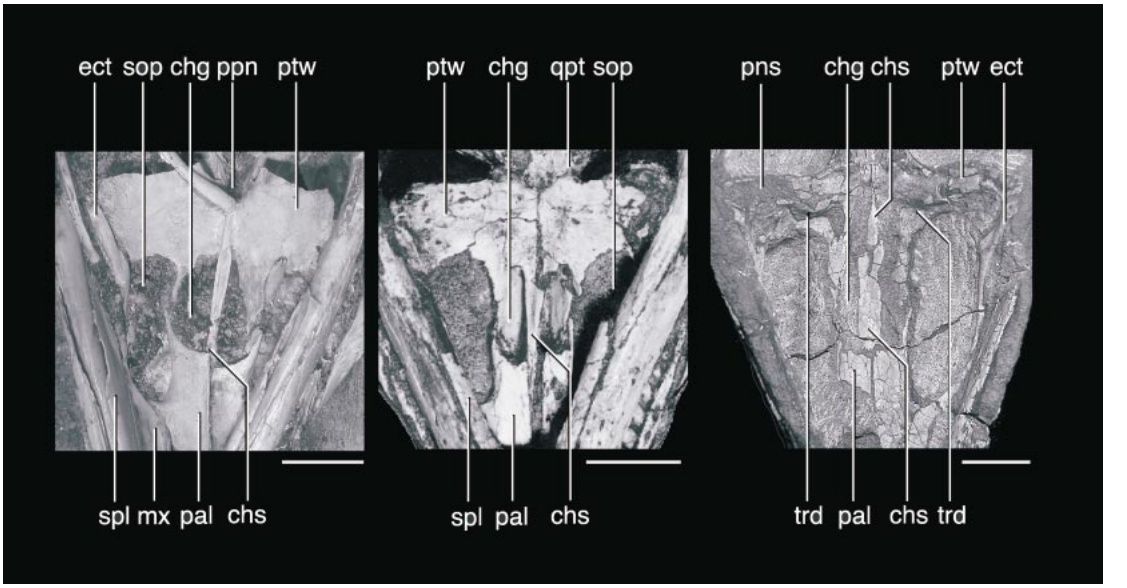

Fig. 4. Choanal opening of *Araripesuchus* in ventral view. **Left.** *Araripesuchus buitreraensis* MPCA-PV 235. **Middle.** *Araripesuchus gomesii* AMNH 24450. **Right.** *Araripesuchus patagonicus* MUC-PV 269 (after Ortega et al., 2000). Scale bar = 1 cm. See appendix 4 for abbreviations.

having its palatal surface flat and lateromedially wider than the rest of the septum (fig. 4). This condition is exclusively shared with *A. gomesii* (AMNH 24450), *A. patagonicus* (MUC-PV 269), and *Simosuchus clarki* (UA 8679). However, the flat palatal surface of the choanal septum of *A. gomesii* (AMNH 24450) and *A. patagonicus* (MUC-PV 269) tapers anteriorly, while in *Simosuchus* UA 8679 and MPCA-PV 235 it is broad anteriorly and tapers posteriorly (fig. 4).

The choanal groove is closed posteriorly by the pterygoids, which seem to be completely fused at this point. The pterygoid flanges extend laterally and are slightly deflected ventrally. The ventral surfaces of these flanges are smooth and anteroposteriorly narrower in comparison with those of *A. gomesii* (AMNH 24450) and *A. patagonicus* (MUC-PV 269). The anterior margins of the pterygoid flanges are markedly concave while their posterior margins are oriented transversely and are only slightly concave (fig. 4). The posterior half of the pterygoid flanges of MPCA-PV 235 bulges ventrally, indicating pneumatic spaces within them (exposed in the broken areas of both pterygoids; fig. 4A). Anterior to these swollen areas, the ventral surface of the pterygoid flanges bears a transversely elongated depression running parallel to the posterior margin of the suborbital fenestra (fig. 4A). This suite of characters of the pterygoid flanges of MPCA-PV 235 is absent in *A. gomesii* (AMNH 24450) and *A. patagonicus* (MUC-PV 269). In these taxa, the pterygoid flanges are broad and laminar, lacking the pneumatic spaces described above (fig. 4).

The lateral edges of the pterygoid flanges of MPCA-PV 235 are sutured to the posteromedial process of the ectopterygoids. At the posteromedial region, the pterygoids are deeply notched as in the other species of *Araripesuchus* and other mesoeucrocodylians. The base of the quadrate processes of the pterygoids is markedly narrow as in most mesoeucrocodylians (fig. 4), although further details of this region and its contact with the quadrate and basisphenoid have not been preserved in MPCA-PV 235.

Only the dentaries, splenials, and a fragment of the surangular have been preserved from the lower jaw of MPCA-PV 235. The mandibular symphysis is moderately long and tapers anteriorly in its dorsoventral and lateromedial dimensions (figs. 3, 5). The ven-

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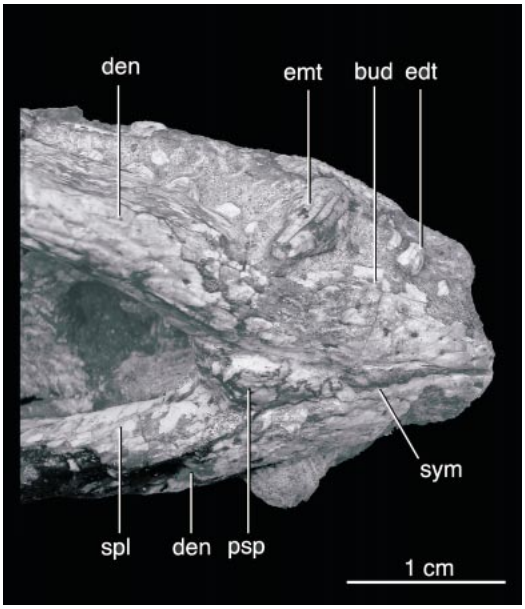

Fig. 5. Mandibular symphysis of *Araripesuchus buitreraensis* MPCA-PV 235 in ventral view. See appendix 4 for abbreviations.

tral surface of the *dentaries* is slightly ornamented with small and well-spaced circular pits. On this surface, the dentaries form the anterior two-thirds of the mandibular symphysis, while the posterior third is formed by the splenials. The lateral margins of the dentaries diverge posteriorly at the anterior symphyseal region, and they are moderately bulged at the enlarged anterior dentary tooth (fig. 5). In lateral view, the dentaries gradually increase the dorsoventral height of the mandibular symphysis.

Posterior to the mandibular symphysis, the buccal margin of the dentaries protrudes dorsally, although it seems to lack the abrupt step present in *Araripesuchus gomesii* (DGM 423-R; AMHN 24450) and MPCA-PV 236 (see below). The lateral surfaces of the dentaries are flat, vertically oriented, and lack the ornamentation present on their ventral surface. This smooth region also seems to lack neurovascular foramina. In contrast, the lateral surface of *A. gomesii*, *A. patagonicus*, and neosuchians is laterally convex below the alveolar region (Ortega et al., 2000). The dentaries of MPCA-PV 235 bear a slightly marked longitudinal groove that runs parallel to the buccal edge on the posterior region of the toothrow (fig. 3). The left dentary has preserved its contact with the anterior branch of the surangular, being a vertically directed sinusoidal suture. Unfortunately, the posteroventral region of the dentaries and their contact with the angular has not been preserved in MPCA-PV 235.

The *splenials* are involved in the mandibular symphysis, contacting the dentaries through a U-shaped suture (fig. 5), in contrast to the acute V-shaped suture present in *A. gomesii* (AMNH 24450), *A. patagonicus* (MUC-PV 269), and most other crocodyliforms (except for *Notosuchus terrestris* MACN-RN 1037 and *Comahuesuchus brachybuccalis* MOZ P 6131). The splenials have a blunt-ended peg on the posterior edge of the symphysis (fig. 5), similar to the condition of *A. patagonicus* MUC-PV 269 and other basal mesoeucrocodylians (e.g., *Uruguaysuchus aznarezi* (Rusconi, 1933; fig. 19); *Notosuchus terrestris* MACN-RN 1037, 1040; *Malawisuchus mwakayasyunguti* MAL-49; *Simosuchus clarki* UA 8679). This posterior peg, however, is absent in *A. gomesii* (AMNH 24450). Lateral to this peg, the splenial is pierced by the anterior foramen for the mandibular branch of the trigeminal nerve.

Posterior to the mandibular symphysis, the splenials expand dorsally to cover the entire medial surface of the mandibular rami. This splenial lamina is medially convex and dorsoventrally high, extending from the alveolar margin to the ventral surface of the mandibular ramus. The splenial lamina lacks any signs of a posterior opening for the mandibular branch of the trigeminal nerve (such as those present in derived alligatoroids).

The *dentition* of MPCA-PV 235 is poorly preserved. None of the premaxillary teeth has been preserved and most of the maxillary tooth crowns are missing. The anterior maxillary teeth seem to be implanted in discrete alveoli, and the second preserved maxillary tooth is markedly enlarged with respect to the other maxillary teeth (fig. 3). All the preserved maxillary teeth are conical, with smooth enamel surfaces, and they seem to lack serrations or denticles on their mesial and distal margins. The dentary teeth are mostly hidden by the upper dentition. The

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anterior dentary teeth seem to be small except for a slightly enlarged tooth located at the level of the premaxilla-maxilla contact, which produces a moderate swelling of the dentaries (fig. 5). Probably, there were two or three teeth anterior to this element.

DESCRIPTION OF MPCA-PV 236

The specimen MPCA-PV 236 was found in the same locality and horizon as MPCA-PV 235 and consists of the anterior half of the lower jaws and fragmentary remains of the palate. This specimen differs from MPCA-PV 235 and the other described species of *Araripesuchus* in the morphology of the medial surface of splenials. In MPCA-PV 236 this surface is markedly concave, in contrast to the flat or slightly convex surface of all other species of *Araripesuchus*. Additionally, the medial edge of the posterior half of the alveolar groove (formed by the splenial) is dorsally located with respect to the lateral alveolar edge formed by the dentary. In contrast, in *A. gomesii* (AMNH 24450) the medial and lateral alveolar edges are located at the same level. Unfortunately, this information is not available for the other three species of *Araripesuchus*. Although these differences may suggest that MPCA-PV 236 belongs to a different taxon, its fragmentary nature prompted us to wait for more complete remains in order to make a formal taxonomic decision. Despite the fragmentary nature of this specimen, it shows several characters that suggest close phylogenetic affinities with the *Araripesuchus* clade (see below).

The fragmentary skull remains of MPCA-PV 236 are poorly preserved and only exposed in palatal view. Although the palatal branches of the premaxillae are badly damaged, they seem to meet medially, forming the anterior region of the secondary palate. The premaxilla-maxilla palatal contact cannot be precisely determined; however, the palatal branches of the *maxillae* clearly contact each other medially, forming a posteriorly extended secondary palate. The ventral surface of the maxillary secondary palate is markedly concave at its anterior third, although this was probably accentuated by preservation causes. Posteriorly, the palatal surface becomes progressively flattened toward its contact with the anterior process of the palatines. Only the ventral half of the lateral surface of the maxilla was preserved in MPCA-PV 236. As in *A. gomesii* (AMNH 24450), this surface is ornamented with closely spaced pits extending down to the buccal margin of the maxilla, lacking the smooth maxillary surface present in more derived notosuchians (e.g., *Notosuchus terrestris* MACN-RN 1037; *Malawisuchus mwakayasyunguti* MAL-52; *Sphagesaurus huenei* RCL-100). The maxillary buccal margin is straight along most of its length, but it extends ventrally at the anterior portion of the maxilla, where a hypertrophied maxillary tooth is located. The *palatines* contact each other medially and the palatal processes of the maxillae anteriorly, forming the posterior part of the secondary palate. A well-developed anterior process of the palatines projects anteriorly and laterally between the palatal branches of the maxillae, forming a semicircular anterior end. In ventral view the palatines narrow posteriorly, where they probably form the floor of the nasopharyngeal duct. At this point, the lateral edges of the palatines form the medial and anteromedial margins of the suborbital fenestra.

Both rami of the lower jaw were completely preserved from their anterior end to the caudal end of the toothrow. The mandibular symphysis is moderately long, extending along two-thirds of the mandibular toothrow and is formed by both dentaries and splenials. At the symphyseal region, the dorsoventral and lateromedial dimensions of the *dentaries* taper anteriorly (figs. 6–8). The ventral surface of the dentaries is heavily ornamented with grooves and ridges. On ventral view, the dentaries only form the anterior two-thirds of the mandibular symphysis (fig. 7). Their lateral edges diverge slightly posteriorly in the symphyseal region, but they are strongly deflected laterally posterior to the symphysis. In the symphyseal region, the dorsal surface of the dentaries forms an anteroposteriorly elongate concavity between the toothrows (fig. 6). This shallow, trough-shaped, smooth surface narrows anteriorly and is not anteriorly delimited by an elevated anterior alveolar margin. This suite of characters is also present in *A. gomesii* (DGM

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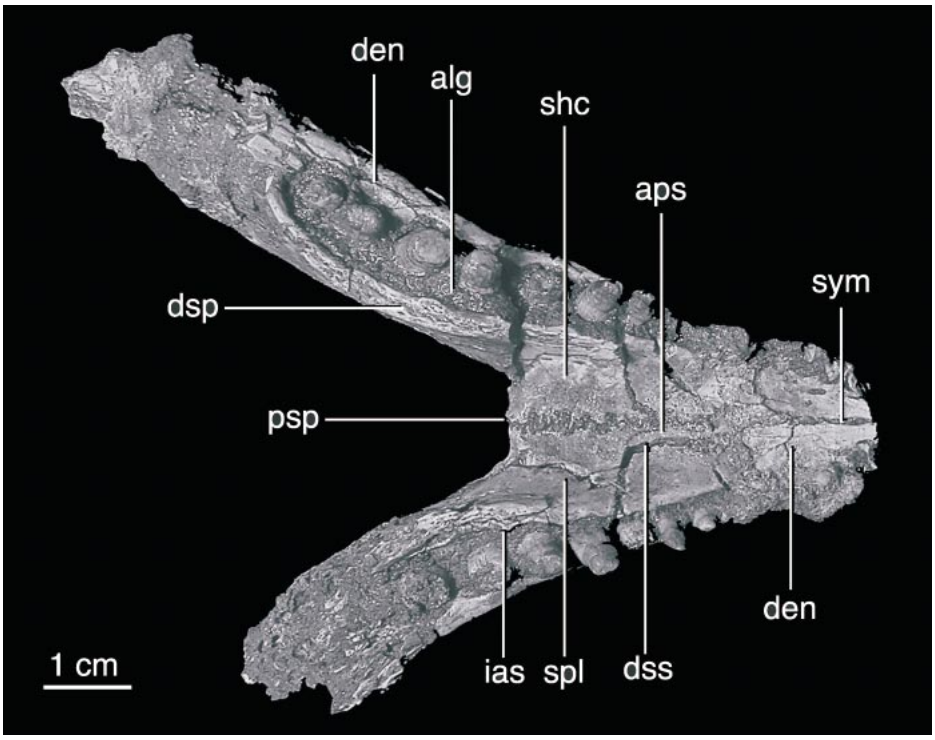

Fig. 6. Lower jaw of *Araripesuchus* sp. MPCA-PV 236 in dorsal view. See appendix 4 for abbreviations.

423-R; AMHN 24450). Posterior to the mandibular symphysis, the medial surface of the dentaries is completely hidden by the splenials.

In lateral view, the ventral edge of the dentaries extends posteroventrally, gradually increasing the dorsoventral height of the mandibular rami (fig. 8). The anterior region of the dorsal edge of the dentaries is straight and subparallel with the longitudinal axis of the mandible. However, at the level of the seventh mandibular tooth, the dorsal alveolar margin protrudes dorsally rather abruptly. This marked step causes an abrupt increase in the dorsoventral height of the dentaries, as seen in lateral view (fig. 8). Posterior to this step, the dorsal margin of the dentaries is straight and extends posterodorsally at a low angle. A similar lateral profile of the dorsal edge of the dentaries is also present in *A. gomesii* (DGM 423-R; AMHN 24450). Some other mesoeucrocodylians also have a drastic step in the dorsal margin of the dentaries (e.g., *Sebecus icaeorhinus* AMNH 3160), but this occurs at the level of the premaxilla-maxilla suture (approximately at the third mandibular alveolous), and the dorsal margin is distinctly concave posterior to this tooth. *Comahuesuchus brachybuccalis* (MOZ P 6131) also bears an abrupt step, although it is located at the posterior end of the toothrow where the enlarged dentary tooth is located. In most notosuchians, however, the dorsal edge of the dentaries is straight along the entire toothrow, having anterior dentary teeth located at the same level as the posterior teeth (e.g., *Notosuchus terrestris* MACN-RN 1037, 1040; *Mariliasuchus amarali* UFRJ 50-R; *Malawisuchus mwakayasyunguti* MAL-49). The ventral half of the lateral surface of the dentaries is ornamented with deep grooves and ridges while the dorsal half of the lateral surface of the dentaries is smooth and perforated by large neurovascular foramina (fig. 8). Posterior to the symphyseal region, the lateral surface of the dentaries is convex, a character noted to be present only

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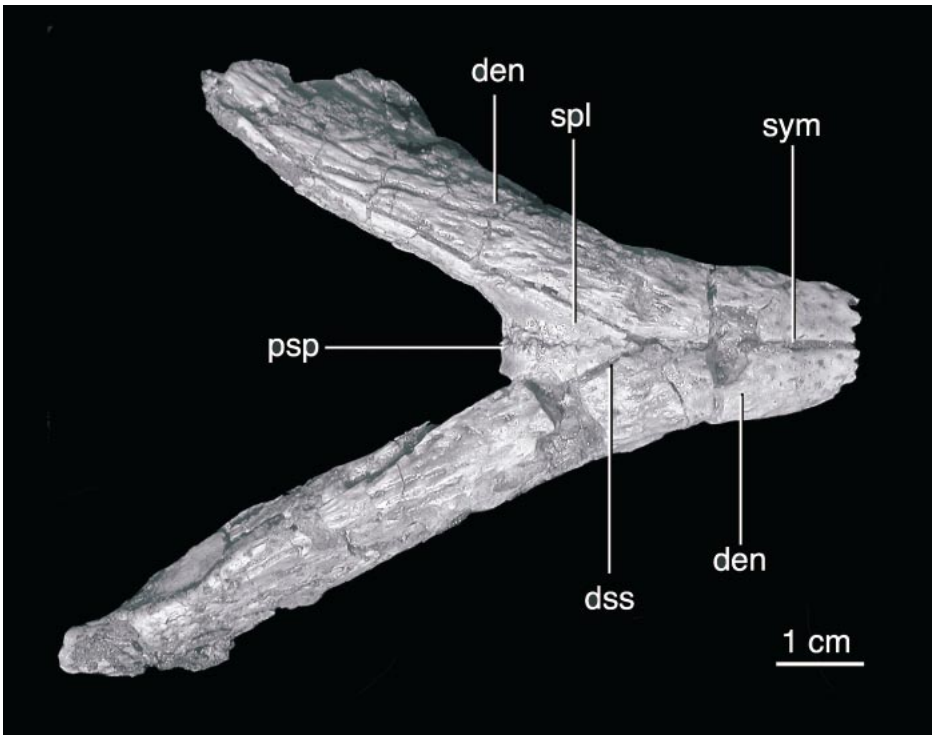

Fig. 7. Lower jaw of *Araripesuchus* sp. MPCA-PV 236 in ventral view. See appendix 4 for abbreviations.

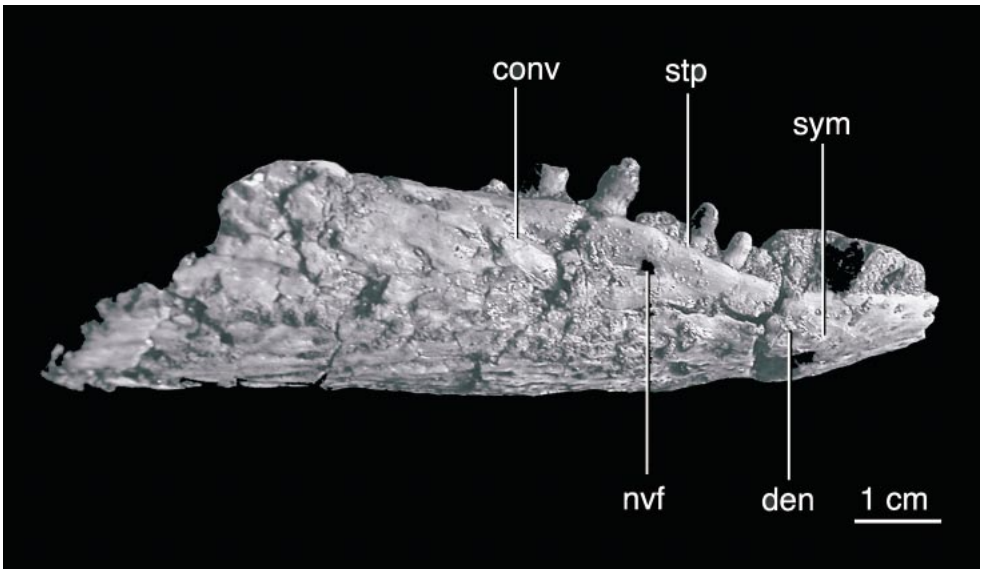

Fig. 8. Lower jaw of *Araripesuchus* sp. MPCA-PV 236 in right lateral view. See appendix 4 for abbreviations.

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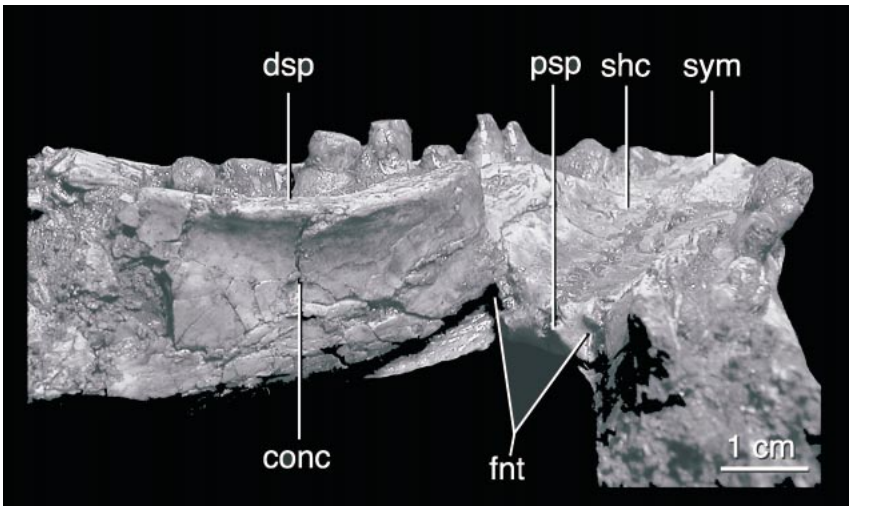

Fig. 9. Medial surface of lower jaw of *Araripesuchus* sp. MPCA-PV 236 in posteromedial view. See appendix 4 for abbreviations.

in *Araripesuchus* and neosuchians (Ortega et al., 2000).

The *splenials* are largely involved in the mandibular symphysis and contact the dentaries differentially on the ventral and dorsal surfaces. In dorsal view, the splenial-dentary suture is transversely oriented along most of its length, except for its medialmost region (at the contact between the two splenials). In this area, the splenials have an anteriorly projecting process, and the splenial-dentary suture is directed anteromedially (fig. 6). In ventral view, instead, the splenial-dentary suture is V-shaped along its entire length, contributing to one-third of the anteroposterior symphyseal length (fig. 7). The splenials have a posteriorly oriented peg on the posterior edge of the symphysis, although it is notably smaller than that of MUC-PV 235. A similar morphology is present in *A. patagonicus* (MUC-PV 269) and most notosuchians (e.g., *Uruguaysuchus aznarezi* (Rusconi, 1933; fig. 19); *Simosuchus clarki* UA 8679; *Notosuchus terrestris* MACN-RN 1037, 1040; *Comahuesuchus brachybuccalis* MOZ P 6131), but not in *A. gomesii* (AMNH 24450).

At the posterior third of the mandibular symphysis, the splenials expand dorsally, forming a vertical lamina that covers the medial surface of the dentaries. The splenial lamina is lateromedially compressed and dorsoventrally high, extending from the medial alveolar margin down to the dorsal surface of the mandibular symphysis. The medial surface of the splenials is pierced by the anterior opening of the mandibular branch of the trigeminal nerve, located lateral to the mandibular symphysis and facing posteriorly (fig. 9). A similar condition is also present in *A. gomesii* (AMNH 24450) and *Simosuchus clarki* (UA 8679), but not in derived notosuchians (e.g., *Notosuchus terrestris* MACN-RN 1037; *Comahuesuchus brachybuccalis* MOZ P 6131). As in the specimen MPCA-PV 235, the medial surface of the splenial lamina lacks a posterior opening for the mandibular branch of the trigeminal nerve.

Posterior to the mandibular symphysis, the splenial lamina is further expanded dorsoventrally, covering the entire medial surfaces of the mandibular rami, being slightly exposed on the ventral surface of the mandible (fig. 9). The presence of such an extensive splenial lamina is not uncommon among crocodyliforms. However, the splenial's medial surface in MPCA-PV 236 is markedly concave instead of being flat or slightly convex (fig. 9). The dorsal margin of the splenial lamina is slightly expanded lateromedially, forming a dorsally facing flat surface slightly ornamented with grooves and ridges. This broad surface forms the medial margin of the alveolar groove (figs. 6, 9).

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There are at least four premaxillary *teeth* on the left side of MPCA-PV 236, but none of them preserves its crowns. The teeth are implanted in discrete alveoli separated by complete bony septa. The third of these elements is the largest. The anterior maxillary teeth are also poorly preserved, although the presence of a hypertrophied maxillary tooth can be observed close to the anterior edge of the left maxilla. Three posterior maxillary teeth were preserved on the right side. These elements lie in an alveolar groove, and the last one of them is bulbous and has a marked constriction between its root and crown. There are 12 dentary teeth preserved on the left dentary and they show some degree of heterodonty. The dentary likely bears 3 or 4 teeth in addition to the 12 teeth preserved in MPCA-PV 236. The anteriormost six teeth are slightly procumbent, small, and conical. Anterior procumbent teeth in the lower jaw are absent in *A. gomesii* (AMNH 24450) and *A. patagonicus* (MUC-PV 283) and were previously known to occur only in *Anatosuchus minor* (Sereno et al., 2003), *Comahuesuchus brachybuccalis* (Martinelli, 2003), *Mariliasuchus amarali* (Carvalho and Bertini, 1999), *Bretesuchus bonapartei* (PVL 4735), and *Sebecus icaeorhinus* (AMNH 3160). However, in these taxa this condition is much more developed than in MPCA-PV 236. The crowns of the last five mandibular teeth are bulbous and separated from their roots by a marked constriction, a widespread condition among mesoeucrocodylians. Unfortunately, most of the posterior crowns were not completely preserved and characters of their apical region cannot be determined.

The first preserved dentary tooth is implanted in separate alveoli, while posterior mandibular teeth are arranged on a continuous alveolar groove. Between subsequent teeth the groove is lateromedially constricted by expansions of the dentary, although these do not contact each other, forming complete alveolar septa (fig. 6). Anteriorly, the groove is lateromedially narrow but it markedly widens at the level of the five most posterior teeth. At this point, the buccal and lingual edges of the tooth groove are lateromedially wide with a flat dorsally facing surface (figs. 6, 9). Discrete alveoli were previously noted in *Araripesuchus* and neosuchians (Ortega et al., 2000). However, the type specimen of *A. gomesii* (DGM 432-R) and the specimen MPCA-PV 236 clearly show the presence of a continuous alveolar groove for the posterior mandibular teeth. Furthermore, the alveolar groove of *A. gomesii* (DGM 432-R) is remarkably similar to that of MPCA-PV 236, since the left and right toothrows are subparallel to each other along most of their length, but they markedly diverge laterally at the level of the last four teeth. In some extant crocodyliforms (e.g., alligatorids), the posterior dentary alveoli are incompletely septated in young individuals and become increasingly septated during ontogeny. However, in several notosuchian crocodyliforms the posterior mandibular teeth remain arranged on a continuous alveolar groove in presumably adult specimens (e.g., *Notosuchus terrestris* MLP 64-IV-16-13, *Malawisuchus mwakayasyunguti* MAL-49, *Libycosuchus brevirostris* BSP 1912.VIII.574, *Simosuchus clarki* UA 8679).

PHYLOGENETIC RELATIONSHIPS

Araripesuchus was traditionally considered to be related to *Notosuchus* and other forms from the Cretaceous of South America (Price, 1959; Gasparini, 1971). However, in recent cladistic analyses, *Araripesuchus* was depicted in different positions within the basal clades of Mesoeucrocodylia (Clark, 1994; Wu and Sues, 1996; Wu et al., 1997; Buckley and Brochu, 1999; Buckley et al., 2000; Ortega et al., 2000; Pol, 2003; Sereno et al., 2001, 2003; Pol and Norell, 2004a).

In order to analyze the phylogenetic affinities of these specimens, a cladistic analysis was conducted using a dataset of 230 characters scored for 50 taxa. This dataset is an extension of that used in previous studies (Pol et al., 2004; Pol and Norell, 2004b) with the addition of 1 character from Wu and Sues (1996), 3 characters from Buckley and Brochu (1999), 17 characters of Ortega et al. (2000), and 10 new characters. The sampled taxa included numerous basal mesoeucrocodylians, including the three previously described species of *Araripesuchus* and 20 other non-neosuchian crocodyliforms. This dataset was analyzed with equally weighted

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parsimony using TNT (vers. 1.0, Goloboff et al., 2003). A heuristic tree-search strategy was conducted performing 1000 replicates of random addition sequences plus TBR branch swapping (holding 10 trees per replicate), followed by a final round of TBR branch swapping. Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions (i.e., rule 1). This analysis resulted in six most parsimonious trees of 750 steps (CI = 0.373; RI = 0.679) found in all replicates.

All the most parsimonious hypotheses cluster the three previously known *Araripesuchus* species together with *A. buitreraensis* and the specimen MPCA-PV 236 (fig. 10), corroborating the monophyly of this genus and justifying the taxonomic assignment of the specimens described here.

The African *A. wegeneri* is located as the basalmost member of *Araripesuchus*, being the sister taxon of the clade composed by all South American *Araripesuchus* (fig. 10), as in a recently published analysis (Turner, 2004a). The monophyly of *Araripesuchus* (including *A. wegeneri*) is supported by the presence of two unambiguous synapomorphies regarding the morphology of the maxilla (common to all most parsimonious trees). The lateral edge of the snout of all these taxa is laterally bulged at the enlarged maxillary tooth and is markedly concave posteriorly to this point, having a sinusoidal contour (character 173–1; paralleled in some derived neosuchians). Additionally, the alveolar edge of the maxilla extends ventrally at the level of the enlarged maxillary tooth in all *Araripesuchus* taxa (character 178–1), except for *A. patagonicus*, where this condition is reversed. Both characters are also present in non-longirostrine neosuchians, and therefore they only provide support for the monophyly of this group given the phylogenetic position of the *Araripesuchus* clade as the most basal group of Notosuchia (fig. 10). Other putative synapomorphies of this clade are optimized as ambiguous due to the missing information in its basal members: (1) ascending postorbital process located on the posterior half of the jugal (character 143–2), paralleled in *Simosuchus clarki* and some basal crocodyliforms; (2) absence of ornamentation on the posteroventral region of quadratojugal (character 144–0), paralleled in several basal crocodylomorphs and baurusuchids; (3) concave, trough-shaped dorsal surface of mandibular symphysis (character 184–1). The first two characters are missing in *A. wegeneri*, *A. buitreraensis*, and MPCA-PV 236, while the third one is missing in *A. wegeneri*, *A. buitreraensis*, and *A. patagonicus*. Further study or remains of these taxa will determine if these characters are diagnostic of the entire clade of *Araripesuchus* or of a restricted subgroup.

All South American members of *Araripesuchus* in this analysis form a monophyletic group supported by three unambiguous synapomorphies. The posterior maxillary and dentary teeth are not compressed lateromedially at their base (character 140–0) in the South American species of *Araripesuchus* but are lateromedially compressed in *A. wegeneri*, most basal notosuchians (e.g., *Uruguaysuchus aznarezi*, *Simosuchus clarki*), and in several basal crocodyliforms (e.g., *Hsisosuchus chungkingensis*, the Fruita form). The lateral surface of the dentaries lacks a well-developed longitudinal ridge (character 188–0); this ridge divides the lateral surface of the dentaries in a dorsal region exposed laterodorsally and a vertical ventral region in most basal crocodyliforms and notosuchians (except for sebecosuchians). These two characters are paralleled in neosuchians and therefore provide support for this South American clade only when *Araripesuchus* is depicted as related to notosuchians. The third synapomorphic character is the presence of a straight dorsal edge of the dentary with an abrupt dorsal outgrowth (character 156–1) described above for the specimen MPCA-PV 236. As noted above, this morphology is also present in *A. gomesii* and is moderately developed in *A. buitreraensis*, but is currently unknown in *A. patagonicus*. Two additional putative synapomorphies from the morphology of the choana are ambiguously optimized and might also diagnose this clade: presence of a T-shaped choanal septum (character 186–1) that completely divides the internal nares opening (character 70–2). These two characters are missing in *A. wegeneri* and are also present in *Simosuchus clarki*. Further material of the African taxon and successive outgroups

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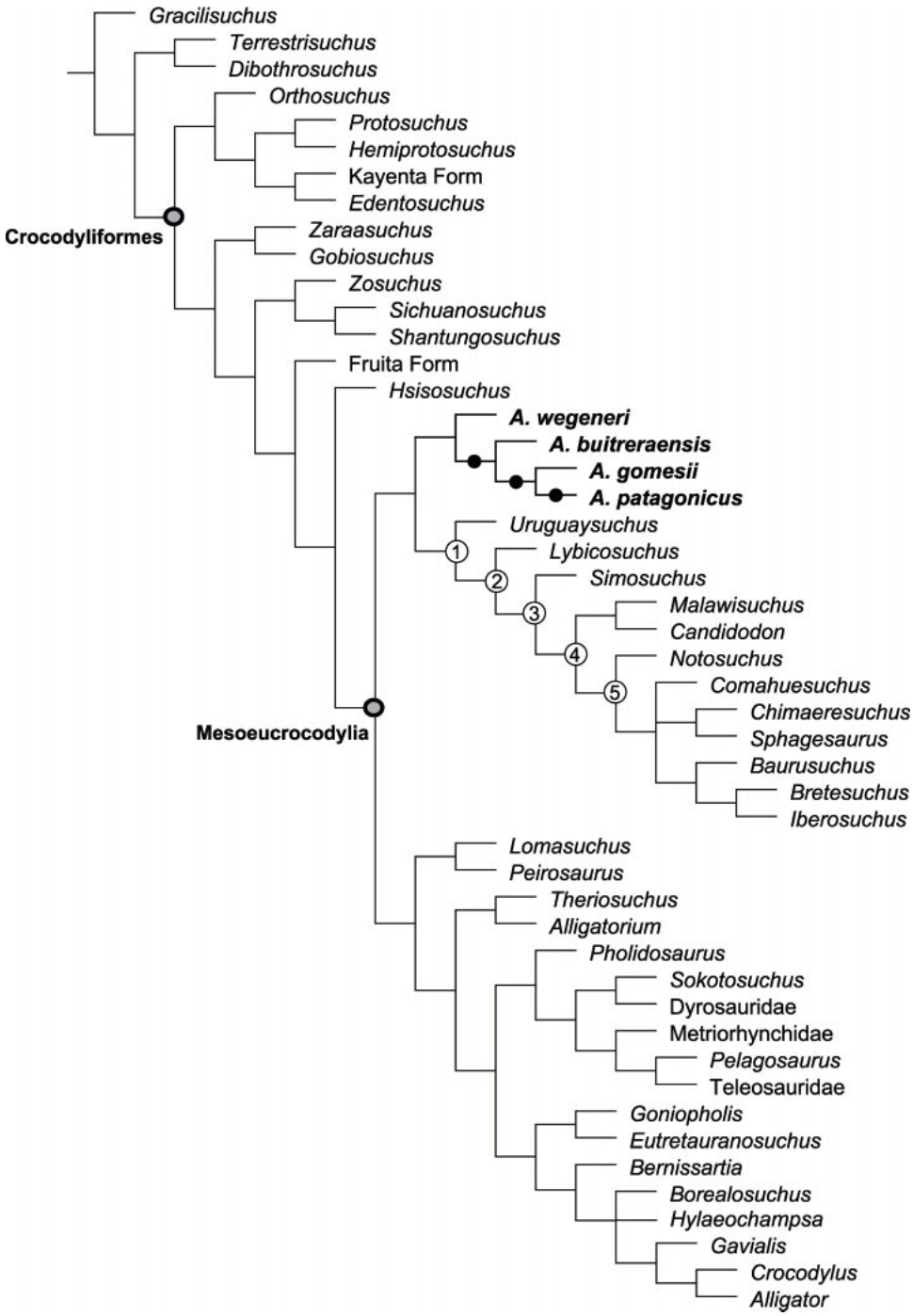

Fig. 10. Reduced strict consensus of the six most parsimonious trees obtained in the cladistic analysis using TNT (Goloboff et al., 2003). The specimen MPCA-PV 236 is excluded from the consensus (small solid circles show its alternative positions within the *Araripesuchus* clade).

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would help to determine if this character is synapomorphic of the South American *Araripesuchus* or if it diagnoses a larger group of taxa.

In the strict consensus of this analysis the South American *Araripesuchus* subclade lacks internal resolution; however, these taxa are collapsed due to the alternative positions of the specimen MPCA-PV 236 within that clade (fig. 10). Disregarding the alternative positions of MPCA-PV 236, all the most parsimonious trees agree in displaying *A. buitreraensis* as the sister taxon of the clade formed by *A. gomesii* and *A. patagonicus* (fig. 10). These two taxa share five characters to the exclusion of *A. buitreraensis*. The lateral margins of the nasals are markedly concave along their suture with the premaxillae (character 127–0) instead of being straight as in *A. buitreraensis* and *A. wegeneri*. The caudal edges of nasals are transversely oriented (character 162–1) instead of being caudally separated by an acute anterior process of the frontal as in *A. buitreraensis*. The postorbital process of the jugal is posteriorly inset from the lateral surface of the jugal (character 164–1). The pterygoid flanges are thin and laminar (character 193–0), lacking the dorsoventrally thick flanges with pneumatic spaces present in *A. buitreraensis*. Finally, the T-shaped choanal septum of *A. gomesii* and *A. patagonicus* tapers anteriorly (character 220–1), in contrast to anteriorly broad septum of *A. buitreraensis* and *Simosuchus clarki*.

Araripesuchus is consistently depicted as the most basal group of a large clade that is congruent with the traditional taxonomic content of Notosuchia (Gasparini, 1971) with the addition of sebecosuchians (depicted here nested within notosuchians; fig. 10). This phylogenetic position contrasts with the results of some previous cladistic analyses (e.g., Clark, 1994; Buckley and Brochu, 1999; Buckley et al., 2000; Ortega et al., 2000; Turner, 2004a), where *Araripesuchus* was depicted as more closely related to neosuchians than to notosuchians. However, the results presented here agree with the hypotheses proposed by other authors (Wu and Sues, 1996; Sereno et al., 2001, 2003; Pol 1999b; Pol and Norell, 2004a) in which *Araripesuchus* was depicted as closer to *Notosuchus* than to neosuchians. Sereno et al. (2001) recognized a clade composed by a subset of the taxa included here and defined the taxon Notosuchia as all crocodyliforms more closely related to *Notosuchus* than to *Crocodylus*.

In our dataset, the *Araripesuchus* clade is supported in this position by 10 synapomorphies present in all most parsimonious trees. The alveolar edge of the premaxilla-maxilla contact lacks a large notch or fenestra (character 9–0). The lateral surface of the maxilla is pierced by several large neurovascular foramina aligned above the alveolar margin (character 138–1), being paralleled in some basal crocodyliforms (e.g., *Protosuchus richardsoni*, *Sichuanosuchus shuhanensis*). The distal body of the quadrate (ventral to the triple contact between this element, the exoccipital, and the squamosal) is directed ventrally (character 149–1) rather than posteroventrally. The splenials bear the previously described peg located posteriorly on the ventral surface of the mandibular symphysis (character 181–1; reversed in *A. gomesii*). The dentary lacks a posteroventral process extending beneath the mandibular fenestra (character 70–1). The retroarticular process of these forms is formed by a broad rounded surface projected posteroventrally and facing dorsomedially (character 71–2). In some notosuchians this surface is slightly concave (e.g., *Notosuchus terrestris*) while in others it is flat or barely concave (e.g., *A. gomesii*). The area of insertion of the m. pterygoideus extends onto the lateral surface of the angular (character 76–1), a character paralleled in crocodylians. The cervical vertebrae have anteroposteriorly narrow, rodlike neural spines (character 90–1) and bear moderately developed hypapophyseal keels on their ventral surface (character 91–1). The sacrum is composed by three elements (character 115–1), the last two of which are fused in some taxa (Pol, 2005). Additionally, several other synapomorphies may diagnose Notosuchia, but they are ambiguously optimized due to lack of information on notosuchian outgroups. Some of the most conspicuous characters are the presence of a small foramen located on the lateral surface of the snout, at the premaxilla-maxilla suture (character 135–1), the presence of a vertical ridge

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on the posterior surface of the distal body of the quadrate (character 150–1), the absence of a posterior buttress in the glenoid facet of the articular (character 182–1), and the absence of an anterolateral process in the dorsal osteoderms (character 96–0; paralleled in derived neosuchians).

Araripesuchus is depicted as the most basal group of Notosuchia due to the absence of the following derived characters that diagnose the different notosuchian nodes: dorsal parasagittal osteoderms rounded or ovate (character 95–1; node 1 [a similarly composed group (including sebecosuchians and most notosuchians with the exception of *Araripesuchus*) was referred to as Ziphosuchia by Ortega et al., 2000]); quadrate-articular joint located ventral to the level of the toothrow (character 105–2; node 1); absence of an enlarged maxillary tooth (character 79–0; node 2); presence of a distinctly smooth surface above the alveolar margin on the lateral surface of the maxilla (character 107–1; node 2); extensive perinarial fossa with a rounded concave surface facing anteriorly (character 221–1; node 2); external surface of skull roof ornamented with grooves and ridges (character 1–1; node 3); dorsal surface of frontal with a sagittal ridge (character 22–1; node 3); dorsal edge of surangular markedly bowed (character 74–1; node 3); seven (or less) maxillary teeth (character 108–1; node 4); posterior end of choanal groove (at internal nares) wider than nasopharyngeal passage at the palatine bar (character 42–1; node 5); presence of posterolateral rodlike palatine bar (character 227–1; node 5); ectopterygoid extending medially on ventral surface of pterygoid flanges, approximately covering the ventral half of them (character 230–1; node 5).

As is evident above from the number of convergences and parallelisms, the character distribution among basal mesoeucrocodylians is rather conflictive, and homoplasy levels are remarkably high. In addition to this, the presence of fragmentary or poorly known forms in the analysis results in minimal Bremer support values for most of these nodes. The phylogenetic position of the *Araripesuchus* clade is also minimally supported, showing that new data can overturn this hypothesis. In particular, several authors have proposed *Araripesuchus* to be more closely related to neosuchians than to notosuchians (Clark, 1994; Ortega et al., 2000; Buckley and Brochu, 1999; Buckley et al., 2000; Turner, 2004a). However, in the dataset presented here, trees supporting neosuchian affinities for *Araripesuchus* are markedly suboptimal. The most parsimonious tree that depicts *Araripesuchus* in that position requires six extra steps.

DISCUSSION

As mentioned above, the phylogenetic position of *Araripesuchus* has been repeatedly debated in the recent literature. Most of previous studies have exclusively considered the information provided by the type species of this group, *A. gomesii* (but see Ortega et al., 2000 and Turner, 2004a). This taxon, known from the Romualdo Member of the Santana Formation (Middle–Late Albian), has a conflictive combination of characters that alternatively suggests neosuchian and notosuchian affinities (see diagnoses above). The remains found in the Candeleros Formation (Cenomanian–Turonian) of Patagonia (including the specimens described here and *A. patagonicus*) provide novel and interesting phylogenetic information. These remains (in particular *A. buitreraensis* and *A. patagonicus*) add an additional set of derived similarities with notosuchians that are absent in *A. gomesii* (e.g., posterior peg in splenial symphysis), demonstrating their relevance for understanding the phylogenetic relationships of this group.

Araripesuchus has been the focus of several studies due to its distribution in Cretaceous beds of both Brazil and Continental Africa at the time of the South Atlantic opening (Buffetaut, 1981; Kellner, 1994). Recently, the generic assignment of *A. wegeneri* was questioned (Ortega et al., 2000; Prasad and Lapparent de Broin, 2002). Under the phylogenetic hypotheses proposed by these authors, the biogeographic informativeness of the *Araripesuchus* clade would be notably diminished. In contrast, the phylogenetic analysis presented here depicts this fragmentary African taxon as the most basal member of the *Araripesuchus* clade, indicating its potential relevance for biogeographical studies

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as originally proposed (Buffetaut, 1981; see also Turner, 2004a). It must be noted, however, that the position of *A. wegeneri* is extremely poorly supported, and biogeographical scenarios made upon these results should be taken cautiously. The poorly supported position of the Early Cretaceous *A. wegeneri* is partially caused by the fragmentary nature of its type specimen but also by the presence of some conflict in its character distribution. Further studies and additional material on this taxon are extremely relevant for understanding the early evolution of *Araripesuchus* and its biogeographical implications. Furthermore, the study of recently reported materials preliminarily referred to this clade from the Late Cretaceous of Madagascar and Niger (Buckley et al., 1997; Sereno et al., 2004; Turner, 2004b), as well as from Coniacian–Santonian beds of Patagonia (S.A., in prep), will provide critical information to test the alternative biogeographical hypotheses for the Cretaceous of Gondwana (Krause et al., 1997; Turner, 2004a; Sereno et al., 2004).

Diversity and Taxonomy of Patagonian *Araripesuchus*

The two specimens described here were found in the same horizon of the Candeleros Formation (Cenomanian–Turonian) and both show phylogenetic affinities with the *Araripesuchus* clade (see above). These, however, differ from each other in several characters, suggesting that they may belong to different taxa (e.g., ornamentation pattern of the ventral surface of the lower jaw, development of the dorsal outgrowth on the dentary alveolar margin, presence of a longitudinal groove on the lateral surface of the dentaries, convexity and ornamentation of the lateral surface below the alveolar margin of the dentaries, development of a posterior symphyseal peg, medial surface of splenials markedly concave, enlarged anterior dentary tooth [opposed to premaxilla-maxilla contact] producing a lateral bulge in the dentary). Some of these differences could be affected by ontogenetic variation, although neither of the two specimens is significantly smaller than the other. The incomplete nature of MPCA-PV 236 and the lack of knowledge of ontogenetic and individual variation among these basal mesoeucrocodylians preclude a formal taxonomic distinction between these specimens.

Interestingly, the previously known *Araripesuchus* taxon from Patagonia, *A. patagonicus*, was found in a ferruginous sandstone horizon from the Lower level of the Candeleros Formation (interpreted to be Albian in age; Calvo, 1991). The stratigraphic correlation of this level with those outcropping at La Buitrera is not fully understood, although the faunal composition seems to differ markedly between them. The type specimen of *A. buitreraensis* (MPCA-PV 235), however, differs from all known specimens of *A. patagonicus* in the presence of seven characters (i.e., long and acute anterior process of frontals extending anteriorly between the nasals, frontals extending into supratemporal fenestra, narrow parietal dorsal surface between supratemporal fossa, anterior palpebral remarkably broad on its anterior end, internal nares septum tapering posteriorly, pterygoid flanges pneumatic and poorly expanded at their lateral ends, transversely elongated depression on ventral surface of pterygoid flanges located close to the posterior margin of suborbital fenestra).

Some of these differences could be explained by ontogenetic variation (e.g., narrow parietal between supratemporal openings), since some characters suggest that the known specimens of *A. patagonicus* might be juveniles or subadults (e.g., poorly developed ornamentation, relatively large orbits and short rostrum). The extension of the frontal into the supratemporal fossa also shows ontogenetic variation in some members of Crocodylia. For example, the frontal does not enter the supratemporal fossa in young individuals of some taxa, but it may intersect its rim in larger specimens (e.g., basal globidontans, *Gavialis gangeticus*; Brochu, 1999; C.A. Brochu, personal commun.). This only causes a moderate decrease in the extension of the parietal-postorbital suture within the supratemporal fossa. The difference between the condition of MPCA-PV 235 and the known specimens of *A. patagonicus* is considerably larger. In *A. patagonicus* the frontal does not extend into the supratemporal fossa, and the parietal and postorbital contact extensively within this

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opening. In the specimen MPCA-PV 235, however, the frontal extends widely into the supratemporal fossa, reaching the margin of the supratemporal fenestra and precluding the parietal and postorbital to contact each other. Despite the possible ontogenetic explanation for these two differences, it is not clear how the remaining five characters of those noted above could be explained by ontogenetic change. Therefore, these differences are considered here as characters distinguishing *A. patagonicus* and *A. buitreraensis*.

Thus, the taxonomic assignment proposed here depicts at least two distinct *Araripesuchus* species from Los Candeleros Formation (and potentially a third one represented by MPCA-PV 236). The rather high number of closely related species from the same formation is certainly unusual but is supported by the character distribution among the known specimens. Furthermore, additional undescribed crocodyliforms collected at the same locality, not closely related to Araripesuchus, show a surprisingly high diversity of crocodyliforms (Carignano et al., 2002). New individuals from Los Candeleros Formation (especially those representing different ontogenetic stages of *Araripesuchus*) would be critical to further test the taxonomic assignments proposed here.

CONCLUSIONS

The two crocodyliform specimens described here from the Early Late Cretaceous of Patagonia are closely related to previously described species of *Araripesuchus* (Price, 1959; Ortega et al., 2000). These specimens add relevant phylogenetic information for understanding the evolutionary history of this clade as well as its diversity during the Cretaceous in southern South America.

The set of most parsimonious trees found in the phylogenetic analysis presented here is congruent with some aspects of the two previous phylogenetic analyses of this genus (Ortega et al., 2000; Turner, 2004a), depicting *Araripesuchus* as a basal mesoeucrocodylian clade within which the South American taxa are more closely related to each other than to *A. wegeneri* (from the Early Cretaceous of Africa). However, the new information provided by the specimens described here and the new character data considered in this phylogenetic analysis suggest that the *Araripesuchus* clade is the most basal member of Notosuchia, the largest and most diverse clade of Cretaceous Gondwanan crocodyliforms.

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APPENDIX 1

Character List Corresponding to Data Matrix Used in Phylogenetic Analysis

Character definitions 1–101 are from Clark (1994) and have the same numeration as in the original publication. Character 5 was excluded from the analysis (due to its dependence 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 sources are 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, 104, 105, 106, 108, 126, 143, 149, 164, 177, 192, and 221 were set as ordered characters [marked with a plus sign (+) in this list].

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

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

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

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

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

Character 6 (modified from Clark, 1994: char. 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: char. 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: char. 8). Premaxilla-maxilla contact: *premaxilla loosely overlies maxilla (0), or sutured together along a butt joint (1).*

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

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

Character 11 (Clark, 1994: char. 11). Nasal contacts lacrimal (0), or does not contact (1).

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

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

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Character 14 (Clark, 1994: char. 14). Nasal-premaxilla contact: *present (0), or absent (1).*

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

Character 16 (Clark, 1994: char. 16). Postorbital-jugal contact: *postorbital anterior to jugal (0), or postorbital medial to jugal (1), or postorbital lateral to jugal (2).*

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

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

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

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

Character 21 (Clark, 1994: char. 21). Frontals: *paired (0), unpaired (1).*

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

Character 23 (modified from Clark, 1994: char. 23 by Buckley and Brochu, 1999: char. 81). (+) Parieto-postorbital suture: *absent from dorsal surface of skull roof and supratemporal fossa (0), 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: char. 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: char. 25). Postorbital bar: *sculpted (if skull sculpted) (0), or unsculpted (1).*

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

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

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

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

Character 30 (Clark, 1994: char. 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: char. 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: char. 32). Parietal: *with broad occipital portion (0), or without broad occipital portion (1).*

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

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

Character 35 (Clark, 1994: char. 35). Posterodorsal corner of the squamosal: *squared off, lacking extra ''lobe'' (0), or with unsculpted ''lobe'' (1).*

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

Character 37 (Clark, 1994: char. 37). (+) Palatines: *do not meet on palate below the narial passage (0), 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: char. 38). Pterygoid: *restricted to palate and suspensorium, joints with quadrate and basisphenoid overlapping (0), or 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: char. 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: char. 40). Palatal surface of pterygoids: *smooth (0), or sculpted (1).*

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

Character 42 (modified from Clark, 1994: char. 42 by Ortega et al., 2000: char. 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).*

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

Character 44 (modified from Clark, 1994: char. 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: char. 45). (+) Quadrate: *without fenestrae (0), with single fenestrae (1), or with three or more fenestrae on dorsal and posteromedial surfaces (2).*

Character 46 (Clark, 1994: char. 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: char. 47). Dorsal, primary head of quadrate articulates with: *squamosal, otoccipital, and prootic (0), or with prootic and laterosphenoid (1).*

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

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

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

Character 51 (Clark, 1994: char. 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: char. 52). Eustachian tubes: *not enclosed between basioccipital and basisphenoid (0), or entirely enclosed (1).*

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

Character 54 (Clark, 1994: char. 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: char. 55 by Ortega et al., 2000: char. 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: char. 56). Basisphenoid: *exposed on ventral surface of braincase (0), or virtually excluded from ventral surface by pterygoid and basioccipital (1).*

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

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

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

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

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

Character 62 (Clark, 1994: char. 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: char. 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: char. 64). Posterior surface of supraoccipital: *nearly flat (0), or with bilateral posterior prominences (1).*

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

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

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

Character 68 (modified from Clark, 1994: char. 68 by Ortega et al., 2000: char. 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: char. 69). (+) Choanal groove: *undivided (0), partially septated (1), or completely septated (2).*

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

Character 71 (modified from Clark, 1994: char. 71). Retroarticular process: *absent or extremely reduced (0), very short, broad, and robust (1), with an extensive rounded, wide, and flat (or slightly concave) surface projected posteroventrally and facing dorsomedially (2), posteriorly*

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elongated, triangular-shaped and facing dorsally (3), or posteroventrally projecting and paddle-shaped (4).

Character 72 (Clark, 1994: char. 72). Prearticular: *present (0), or absent (1).*

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

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

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

Character 76 (Clark, 1994: char. 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: char. 77). (+) Splenial involvement in symphysis in ventral view: *not involved (0), involved slightly in symphysis (1), or extensively involved (2).*

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

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

Character 80 (Clark, 1994: char. 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: char. 81). Dentary teeth posterior to tooth opposite premaxilla-maxilla contact: *equal in size (0), or enlarged dentary teeth opposite to smaller teeth in maxillary toothrow (1).*

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

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

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

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

Character 86 (Clark, 1994: char. 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: char. 87). Distal end of femur: *with large lateral facet for the fibula (0), or with very small facet (1).*

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

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

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

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

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

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

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

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

Character 96 (modified from Clark, 1994: char. 96, and Brochu, 1997a: char. 40). (+) Dorsal osteoderms: *without articular anterior process (0), 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: char. 97 by Ortega et al., 2000: chars. 107, 108). (+) Rows of dorsal osteoderms: *two parallel rows (0), more than two (1), or more than four with accessory ranges of osteoderms (sensu Frey, 1988) (2).*

Character 98 (Clark, 1994: char. 98). Osteoderms: *some or all imbricated (0), or sutured to one another (1).*

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

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

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

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

Character 103 (modified from Wu and Sues, 1996: char. 17). Mandibular symphysis in lateral view: *shallow and tapering anteriorly (0), deep and tapering anteriorly (1), deep and anteriorly convex (2), or shallow and anteriorly convex (3).*

Character 104 (modified from Wu and Sues, 1996: char. 23). (+) Articular facet for quadrate condyle: *equal in length to the quadrate condyles (0), slightly longer (1), or close to three times the length of the quadrate condyles (2).*

Character 105 (modified from Wu and Sues, 1996: char. 24 and Wu et al., 1997: char. 124). (+) Jaw joint: *placed at level with basioccipital condyle (0), below basioccipital condyle about above level of lower toothrow (1), or below level of toothrow (2).*

Character 106 (modified from Wu and Sues, 1996: char. 27 and Ortega et al., 2000: char. 133). (+) Premaxillary teeth: *five (0), four (1), three (2), or two (3).*

Character 107 (modified from Wu and Sues, 1996: char. 29). Unsculptured region along alveolar margin on lateral surface of maxilla: *absent (0), or present (1).*

Character 108 (Wu and Sues, 1996: char. 30). (+) Maxilla: *with eight or more teeth (0), seven (1), six (2), five (3), or four teeth (1).*

Character 109 (Wu and Sues, 1996: char. 33). Coracoid: *without posteromedial or ventromedial process (0), with elongate posteromedial process (1), or distally expanded ventromedial process (2).*

Character 110 (Wu and Sues, 1996: char. 40). Radiale and ulnare: *short and massive (0), or elongate (1).*

Character 111 (modified from Gomani, 1997: char. 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: char. 32). Basioccipital and ventral part of otoccipital: *facing posteriorly (0), or posteroventrally (1).*

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

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

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

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

Character 117 (Buscalioni and Sanz, 1988: char. 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: char. 5). Lateral surface of the dentary: *without a longitudinal depression (0), or with a longitudinal depression (1).*

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

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

Character 121 (modified from Pol, 1999a: char. 133 and Ortega et al., 2000: char. 145). 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: char. 134). Jugal: *does not exceed the anterior margin of orbit (0), or exceeds margin (1).*

Character 123 (Pol, 1999a: char. 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: char. 136). Dorsal border of external nares: *formed mostly by the nasals (0), or by both the nasals and premaxilla (1).*

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

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

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

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

Character 129 (Pol, 1999a: char. 143). Palatine anteromedial margin: *exceeding the anterior margin of the palatal fenestrae extending anteriorly*

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between the maxillae (0), or not exceeding the anterior margin of palatal fenestrae (1).

Character 130 (Pol, 1999a: char. 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: char. 145). Maxilla-lacrimal contact: *partly included in antorbital fossa (0), or completely included (1).*

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

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

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

Character 135 (Pol, 1999a: char. 149 and Ortega et al., 2000: char. 13). 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: char. 150). Jugal posterior process: *exceeding posteriorly the infratemporal fenestrae (0), or not (1).*

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

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

Character 139 (modified from Pol, 1999a: char. 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: char. 154 and Ortega et al., 2000: char. 104). Maxillary teeth: *not compressed laterally (0), or compressed laterally (1).*

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

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

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

Character 144 (Pol, 1999a: char. 158 and Ortega et al., 2000: char. 36). Postorbital-ectopterygoid contact: *present (0), or absent (1).*

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

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

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

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

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

Character 150 (Pol, 1999a: char. 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: char. 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: char. 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: char. 170). Postzygapophyses of axis: *well developed, curved laterally (0), or poorly developed (1).*

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

Character 155 (Pol, 1999b: char. 213). Unsculpted region in the dentary below the toothrow: *absent (0), or present (1).*

Character 156 (modified from Ortega et al., 1995: char. 1 and Buckley and Brochu, 1999: char. 107). Dorsal edge of dentary: *slightly concave or straight and subparallel to the longitudinal axis of skull (0), straight with an abrupt dorsal expansion, being straight posteriorly (1), with a single dorsal expansion and concave posterior to this (2), or sinusoidal, with two concave waves (3).*

Character 157 (modified from Ortega et al., 1995: char. 2 and Buckley and Brochu, 1999: char. 108). Dentary compression and lateroventral surface anterior to mandibular fenestra: *compressed and vertical (0), or not compressed and convex (1).*

Character 158 (Ortega et al., 1996: char. 7 and

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Buckley and Brochu, 1999: char. 110). Splenial: *thin posterior to symphysis (0), or splenial robust dorsally posterior to symphysis (1).*

Character 159 (Ortega et al., 1996: char. 13 and Buckley et al., 2000: char. 117). Cheek teeth: *not constricted at base of crown (0), or constricted (1).*

Character 160 (Ortega et al., 2000: char. 10). Ventral edge of premaxilla located: *at the same height as ventral edge of maxilla (0), or located deeper, with the dorsal contour of anterior part of dentary strongly concave (1).*

Character 161 (modified from Ortega et al., 2000: char. 19). Maxillary dental implantation: *teeth in isolated alveoli (0), or located on a dental groove (1).*

Character 162 (Ortega et al., 2000: char. 24). Caudal tip of nasals: *converge at sagittal plane (0), or caudally separated by anterior sagittal projection of frontals (1).*

Character 163 (Ortega et al., 2000: char. 33). Relative length between squamosal and postorbital: *squamosal is longer (0), or postorbital is longer (1).*

Character 164 (modified from Ortega et al., 2000: char. 34). (+) Jugal portion of postorbital bar: *flushes with lateral surface of jugal (0), anteriorly continuous but posteriorly inset (1), or medially displaced and a ridge separates postorbital bar from lateral surface of jugal (2).*

Character 165 (Ortega et al., 2000: char. 42). Outer surface of squamosal laterodorsally oriented: *extensive (0), or reduced and sculpted (1), or reduced and unsculpted (2).*

Character 166 (Ortega et al., 2000: char. 47). Quadratojugal spine at caudal margin of infratemporal fenestra: *absent (0), or present (1).*

Character 167 (Ortega et al., 2000: char. 53). Quadrate condyles *almost aligned (0), or medial condyle expands ventrally (1).*

Character 168 (Ortega et al., 2000: char. 62). Exposure of supraoccipital in skull roof: *absent (0), or present (1).*

Character 169 (Ortega et al., 2000: char. 75). Anterior opening of temporo-orbital in dorsal view: *exposed (0), or hidden in dorsal view and overlapped by squamosal rim of supratemporal fossa (1).*

Character 170 (Ortega et al., 2000: char. 90). Foramen intramandibularis oralis: *small or absent (0), or big and slotlike (1).*

Character 171 (Ortega et al., 2000: char. 101). Width of root of teeth with respect to crown: *narrower or equal (0), or wider (1).*

Character 172 (Ortega et al., 2000: char. 109). Gap in cervico-thoracic dorsal armor: *absent (0), or present (1).*

Character 173 (Ortega et al., 2000: char. 130). Lateral contour of snout in dorsal view: *straight (0), or sinusoidal (1).*

Character 174 (Ortega et al., 2000: char. 138). Pterygoidean flanges: *laminar and expanded (0), or barlike (1).*

Character 175 (Ortega et al., 2000: char. 146). Ectopterygoid medial process: *single (0), or forked (1).*

Character 176 (modified from Ortega et al., 2000: char. 157). Skull roof: *rectangular-shaped in dorsal view (0), or trapezoidal in shape (1).*

Character 177 (Ortega et al., 2000: char. 30). (+) Prefrontal pillars when integrated in palate: *pillars transversely expanded (0), transversely expanded in their dorsal part and columnar ventrally (1), or longitudinally expanded in their dorsal part and columnar ventrally (2).*

Character 178 (Ortega et al., 2000: char. 21). Ventral edge of maxilla in lateral view: *straight or convex (0), or sinusoidal (1).*

Character 179 (modified from Ortega et al., 2000: char. 156). Position of first enlarged maxillary teeth: *second or third alveoli (0), or fourth or fifth (1).*

Character 180: Splenial-dentary suture at symphysis on ventral surface: *V-shaped (0), or transversal (1).*

Character 181: Posterior peg at symphysis: *absent (0), or present (1).*

Character 182: Posterior ridge on glenoid fossa of articular: *present (0), or absent (1).*

Character 183 (modified from Gomani, 1997: char. 46 and Buckley et al., 2000: char. 113). Cusps of teeth: *unique cusp (0), one main cusp with smaller cusps arranged in one row (1), one main cusp with smaller cusps arranged in more than one row (2), several cusps of equal size arranged in more than one row (3), or multiple small cusps along edges of occlusal surface (4).*

Character 184: Dorsal surface of mandibular symphysis: *flat or slightly concave (0), or strongly concave and narrow, trough-shaped (1).*

Character 185: Medial surface of splenials posterior to symphysis: *flat or slightly convex (0), or markedly concave (1).*

Character 186: Choanal septum shape: *narrow vertical bony sheet (0), or T-shaped bar expanded ventrally (1).*

Character 187 (Pol and Norell, 2004a: char. 164). Cross section of distal end of quadrate: *mediolaterally wide and anteroposteriorly thin (0), or subquadrangular (1).*

Character 188. Lateral surface of dentaries below alveolar margin, at middle to posterior region of toothrow: *vertically oriented, continuous with rest of lateral surface of the dentaries (0), or flat surface exposed laterodorsally, divided by a ridge*

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from rest of the lateral surface of the dentaries (1).

Character 189 (Pol and Norell, 2004a: char. 165). Palatine-pterygoid contact on palate: *palatines overlie pterygoids (0), or palatines firmly sutured to pterygoids (1).*

Character 190 (Pol et al., 2004: char. 164). Ectopterygoid main axis oriented: *laterally or slightly anterorlaterally (0), or anteriorly, subparallel to the skull longitudinal axis (1).*

Character 191 (Wu et al., 1997: char. 103). Squamosal descending process: *absent (0), or present (1).*

Character 192 (modified from Wu et al., 1997: char. 105). (+) Development of distal quadrate body ventral to otoccipital-quadrate contact: *distinct (0), incipiently distinct (1), or indistinct (2).*

Character 193 (Wu et al., 1997: char. 106). Pterygoid flanges: *thin and laminar (0), or dorsoventrally thick, with pneumatic spaces (1).*

Character 194 (Wu et al., 1997: char. 108). Postorbital participation in infratemporal fenestra: *almost or entirely excluded (0), or bordering infratemporal fenestra (1).*

Character 195 (Wu et al., 1997: char. 109). Palatines: *form margin of suborbital fenestra (0), or excluded from margin of suborbital fenestra (1).*

Character 196 (Wu et al., 1997: char. 110). Angular posterior to mandibular fenestra: *widely exposed on lateral surface of mandible (0), or shifted to the ventral surface of mandible (1).*

Character 197 (Wu et al., 1997: char. 112). Posteroventral edge of mandibular ramus: *straight or convex (0), or markedly deflected (1).*

Character 198 (modified from Wu et al., 1997: char. 119). Quadrate ramus of pterygoid in ventral view: *narrow (0), or broad (1).*

Character 199 (Wu et al., 1997: char. 121). Pterygoids: *not in contact anterior to basisphenoid on palate (0), or pterygoids in contact (1).*

Character 200 (Wu et al., 1997: char. 122). Olecranon: *well developed (0), or absent (1).*

Character 201 (Wu et al., 1997: char. 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 202 (Wu et al., 1997: char. 127). Depression on posterolateral surface of maxilla: *absent (0), or present (1).*

Character 203 (Wu et al., 1997: char. 128). Anterior palatal fenestra: *absent (0), or present (1).*

Character 204 (Pol and Norell, 2004a: char. 179). Paired ridges located medially on ventral surface of basisphenoid: *absent (0), or present (1).*

Character 205 (Pol et al., 2004a: char. 179). Ventral margin of infratemporal bar of jugal: *straight (0), or dorsally arched (1).*

Character 206 (Pol and Norell, 2004a: char. 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 207 (Pol and Norell, 2004a; char. 181). Orientation of quadrate body distal to otoccipital-quadrate contact in posterior view: *ventrally (0), or ventrolaterally (1).*

Character 208 (Gasparini et al., 1993: char. 3). Wedgelike process of the maxilla in lateral surface of premaxilla-maxilla suture: *absent (0), or present (1).*

Character 209 (Pol and Norell, 2004b: char. 181) Palpebrals: *separated from the lateral edge of the frontals (0), or extensively sutured to each other and to the lateral margin of the frontals (1).*

Character 210 (Pol and Norell, 2004b: char. 182) External surface of ascending process of jugal: *exposed laterally (0), or exposed posterolaterally (1).*

Character 211 (Pol and Norell, 2004b: char. 183) Longitudinal ridge on lateral surface of jugal below infratemporal fenestra: *absent (0), or present (1).*

Character 212 (Pol and Norell, 2004b: char. 184) Dorsal surface of posterolateral region of squamosal: *without ridges (0), or with three curved ridges oriented longitudinally (1).*

Character 213 (Pol and Norell, 2004b: char. 185) Ridge along dorsal section of quadrate-quadratojugal contact: *absent (0), or present (1).*

Character 214 (Pol and Norell, 2004b: char. 186) Sharp ridge along the ventral surface of angular: *absent (0), or present (1).*

Character 215 (Pol and Norell, 2004b: char. 187) Longitudinal ridge along the dorsolateral surface of surangular: *absent (0), or present (1).*

Character 216 (Pol and Norell, 2004b: char. 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 217 (Pol and Norell, 2004b: char. 189). Cervical region surrounded by lateral and ventral osteoderms sutured to the dorsal elements: *absent (0), or present (1).*

Character 218 (Pol and Norell, 2004b: char. 190). Appendicular osteoderms: *absent (0), or present (1).*

Character 219 (Ortega et al., 2000: char. 72). Supratemporal fenestra: *present (0), or absent (1).*

Character 220: Flat ventral surface of internal nares septum: *anteriorly broad (0), or tapering anteriorly (1).*

Character 221: (+) Perinarial fossa: *restricted extension (0), extensive, with a distinctly concave*

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surface facing anteriorly (1), or large concave surface facing anteriorly, projecting anteroventrally from the external nares opening toward the alveolar margin (2).

Character 222 (modified from Sereno et al., 2001: char. 67). Premaxillary palate circular paramedian depressions: *absent (0), present located anteriorly on the premaxilla (1), or present located at the premaxilla-maxilla suture (2).*

Character 223. Posterolateral region of nasals: *flat surface facing dorsally (0), or lateral region deflected ventrally, forming part of the lateral surface of the snout (1).*

Character 224 (Zaher et al., unpubl. data: char. 193). Ventral half of the lacrymal: *extending ventroposteriorly widely contacting the jugal (0), or tapering ventroposteriorly, does not contact or contacts the jugal only slightly (1).*

Character 225 (Zaher et al., unpubl. data: char. 194). Large foramen on the lateral surface of jugal, near its anterior margin: *absent (0), or present (1).*

Character 226 (Zaher et al., unpubl. data: char. 195). Procumbent premaxillary and anterior dentary alveoli *absent (0), or present (1).*

Character 227 (modified from Martinelli, 2003: char. 36 by Zaher et al., unpubl. data: char. 196). Rodlike posterolateral palatine bar: *absent (0), or present (1).*

Character 228 (Zaher et al., unpubl. data: char. 197). Participation of ectopterygoid in palatine bar: *no (0), or yes (1).*

Character 229 (Pol and Norell, 2004a: char. 183). Choanal opening: *opened posteriorly and continuous with pterygoid surface (0), or closed posteriorly by an elevated wall formed by the pterygoids (1).*

Character 230 (Zaher et al., unpubl. data: char. 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 2

Data Matrix Used in Phylogenetic Analysis

Character states enclosed between brackets represent conditions found to be variable within a terminal taxon (i.e., polymorphic scorings). Multiple states enclosed in braces indicate uncertainty or ambiguity in the condition of a terminal taxon (among these states, but not among the remaining character states). An electronic version of this dataset can be downloaded from http://research.amnh.org/users/dpol/crocs/araripesuchus.

Gracilisuchus
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Terrestrisuchus
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Hemiprotosuchus
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Orthosuchus
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Edentosuchus
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Zaraasuchus
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Shantungosuchus
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Hsisosuchus
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?0?00000?000??0??00???0??0

Notosuchus
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Comahuesuchus
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?11?1?????????????????131??????0?10101??????
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Uruguaysuchus
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Chimaeresuchus
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Malawisuchus
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Candidodon
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Simosuchus
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1011001{01}1?1000100000000100000001000000
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Sphagesaurus
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Iberosuchus
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Lybicosuchus
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Araripesuchus gomesii
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1010001111 2011?10000?0?110201121210001 10
1{01}{01}1{01}11111?1{234}00010001001011
1002101001010100100100100000010011000210
000110?00110?101002{01}00100001000110001
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Araripesuchus patagonicus
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Araripesuchus buitreraensis
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10??01?1?0?0????00?0?????00??0??00?10

MPCA-PV 236
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Araripesuchus wegeneri
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Lomasuchus
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Peirosaurus
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Theriosuchus
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00{01}02000?000?10001110{01}?0??0?0101?01
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Alligatorium
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Goniopholis
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Eutretauranosuchus
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Pelagosaurus
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101000000110111100 1001?10001200?30000020
000110111?000000120001 11?01?00??10???????
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110000000000000?0????0?000010120100001100
00001?0000000???0???0??00?10

Teleosauridae
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002101111?0000?12000101?011?0??10??010011
01??101100001100001010 0?0??0000??10010000
110000000000?00?0???0000?00101?010?011100
010010000000000000?000??00?10

Metriorhynchidae
[02]02?121101001112010 11000?0000000110021
?0?000?0011011110010 11?1?001200?300010200
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Sokotosuchus
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Dyrosauridae
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Pholidosaurus
212?111101??11?11101100111?00100010?211?1
00001112111?101??10?100?1311?300???2?0???
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Bernissartia
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Hylaeochampsa
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Borealosuchus
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111111111113111?110?00?300000210?100100?1
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110000010000000000000?000???0?10

Gavialis
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101101112011110110101110{01}131003100012
000001111110131112111100?300000210?10010
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Crocodylus
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310?0010221011001100021 1??00000001010010
000111000010000000000000?0000000?10

Alligator
203112?101?000111000102111100 1000?002110
101111112011110100101110{01}031203100010
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0010000111000001000000000000?0000000?10

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APPENDIX 3

Fossil Taxa Used in Phylogenetic Analysis

Collection numbers of the specimens that were revised firsthand by the authors are added after the bibliographic reference.

Gracilisuchus stipanicicorum (Romer, 1972; PVL 4597, 4612)
Terrestrisuchus gracilis (Crush, 1984)
Dibothrosuchus elpahros (Wu and Chatterjee, 1993; IVPP V 7907)
Protosuchus richardsoni (Colbert and Mook, 1951; AMNH 3024, MCZ 6727, UCMP 130860, 131827)
Hemiprotosuchus leali (Bonaparte, 1971; PVL 3829)
Kayenta Form (Clark, 1986; UCMP 97638, 125359, 125871)
Edentosuchus tienshanensis (Young, 1973; IVPP V 3236; GMPKU-P 200101)
Orthosuchus stormbergi (Nash, 1975; SAM-K 409)
Gobiosuchus kielanae (Osmólska, 1972; ZPAL MgR-II/67–71)
Zaraasuchus shepardi (Pol and Norell, 2004b; IGM 100/1321)
Shantungosuchus hangjinensis (Wu et al., 1994b)
Sichuanosuchus shuhanensis (Wu et al., 1997; IVPP V 10594)
Zosuchus davidsoni (Pol and Norell, 2004a; IGM 100/1304–1308)
Fruita Form (Clark, 1985, 1994; LACM 120455a)
Hsisosuchus chungkingensis (Young and Chow, 1953; Li et al., 1994; Wu et al., 1994a; cast of CNM V 1090)
Notosuchus terrestris (Gasparini, 1971; MACN-RN 1037–1041)
Comahuesuchus brachybuccalis (Bonaparte, 1991; MUC-PV 202, MACN-N 30, 31, MOZ P 6131)
Uruguaysuchus aznarezi (Rusconi, 1933)
Chimaeresuchus paradoxus (Wu and Sues, 1996; IVPP V8274)
Malawisuchus mwakayasyunguti (Clark et al., 1989; Gomani, 1997; MAL 45, 49)
Candidodon itapecurense (Carvalho, 1994)
Simosuchus clarki (Buckley et al., 2000; UA 8679)
Libycosuchus brevirostris (Stromer, 1914; BSP 1912.VIII.574)
Araripesuchus wegeneri (Buffetaut, 1981; MNHN-GDF 700)
Araripesuchus gomesii (Price, 1959; AMNH 24450)
Araripesuchus patagonicus (Ortega et al., 2000; MUC-PV 269, 270, 283)
Araripesuchus buitreraensis MPCA-PV 235
Araripesuchus sp. MPCA-PV 236
Sphagesaurus huenei (Price, 1950; Pol, 2003; RCL 100)
Baurusuchus pachecoi (Price, 1945; DGM 299-R)
Bretesuchus bonapartei (Gasparini et al., 1993; PVL 4735)
Iberosuchus macrodon (Antunes, 1975; Ortega et al., 2000; UAM)
Lomasuchus palpebrosus (Gasparini et al., 1991; MOZ 4084 PV)
Peirosaurus tormini (Price, 1955; Gasparini et al., 1991; MOZ 1750 PV)
Theriosuchus pusillus (Owen, 1879; Clark, 1986, 1994; Ortega et al., 2000)
Alligatorium (Wellnhofer, 1971; Clark, 1986, 1994)
Eutretauranosuchus delfsi (Mook, 1967; Clark, 1986, 1994; AMNH 570)
Goniopholis (Mook, 1942; Clark, 1986, 1994; Salisbury et al., 1999; AMNH 5782)
Pholidosaurus decipiens (Owen, 1878; Clark, 1986, 1994)
Dyrosauridae (Buffetaut, 1978; Clark, 1986, 1994; CNRST-SUNY 190)
Sokotosuchus ianwilsoni (Halstead 1975; Buffetaut, 1979; Clark, 1986, 1994)
Pelagosaurus typus (EudesDeslongchamps, 1863; BSP 1890.I.5)
Teleosauridae (Buffetaut, 1982; Clark 1986, 1994; AMNH 5138, BSP 1945.XV.1, GPIT Auer-1909-f.22, MB 1921.12)
Metriorhynchidae (Gasparini and Diaz, 1977; AMNH 997, BSP AS.I.504, MACN-N 95, SMNS 10116)
Hylaeochampsa vectiana (Clark and Norell, 1992; Ortega et al., 2000)
Bernissartia fagessi (Buscalioni and Sanz, 1990; Norell and Clark, 1990)
Borealosuchus formidabilis (Erickson, 1976; Brochu, 1997b)
Gavialis gangeticus (Clark, 1994; Brochu, 1997a; FMNH 82681, 98864)
Crocodylus niloticus (Clark, 1994; Brochu, 1997a; FMNH 17157, 217153)
Alligator mississippiensis (Clark, 1994; Brochu, 1997a; FMNH 8201)

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APPENDIX 4

Anatomical Abbreviations

alg	alveolar groove
ap	alanterior palpebral
apf	anterior process of frontal
apj	ascending process of jugal
aps	anterior process of splenials
boc	basioccipital
bud	bulged lateral surface of dentary
chg	choanal groove
chs	choanal septum
conc	concave medial surface of splenials
conv	convex lateral surface of dentaries
den	dentary
dg	dentary groove
dpo	descending process of postorbital
dsp	dorsal surface of splenials
dss	dentary-splenial suture
ect	ectopterygoid
edt	enlarged dentary tooth
emt	enlarged maxillary tooth
eoc	exoccipital
fnt	anterior foramen for mandibular branch of nerve V
fpos	frontal-postorbital suture
fps	fronto-parietal suture
fr	frontal
ias	incipient alveolar septum
itf	infratemporal fenestra
j	jugal
mx	maxilla
nas	nasal
nvf	neurovascular foramen
otn	otic notch
pal	palatine
par	parietal
pmx	premaxilla
pms	premaxilla-maxilla suture
pns	pneumatic space
po	postorbital
pop	anterolateral postorbital process
ppn	posterior pterygoid notch
prf	prefrontal
psp	posterior splenial peg
pt	pterygoid
ptw	pterygoid wing
qj	quadratojugal
qpt	quadrate process of pterygoid
sang	surangular
shc	shallow concave dorsal surface of symphysis
sq	squamosal
stf	supratemporal fenestra
sfo	supratemporal fossa
stp	step on dorsal margin of dentaries
sop	suborbital opening
sph	siphonial foramen
spl	splenial
sym	mandibular symphysis
trd	transverse depression of pterygoid wing

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