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THE POSTCRANIAL ANATOMY OF *YACARERANI BOLIVIENSIS* AND THE PHYLOGENETIC SIGNIFICANCE OF THE NOTOSUCHIAN POSTCRANIAL SKELETON

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ABSTRACT—In this contribution, we describe new specimens of *Yacarerani boliviensis* from the Cajones Formation (Upper Cretaceous) of Bolivia. We focus on the postcranial anatomy of *Y. boliviensis*, because this anatomical region is completely unknown in other sphagesaurid notosuchians up to the present. At least eight individuals representing almost the entire postcranial skeleton are described. Although the postcranial anatomy of *Yacarerani* resembles that of other notosuchians in many features, five autapomorphic characters were identified: pedicles of the atlas bearing a lateral bulge; absence of rounded depressions on the dorsal surface of the anterior to middle dorsal vertebrae; coracoid bearing an oblique crest on its lateral surface; lateromedially compressed anterior ungual phalanges; and femur with a shallow depression for the M. puboischiofemoralis internus 1 and M. caudifemoralis longus. Observed variation in the postcranial anatomy of basal mesoeucrocodylians was incorporated as new characters in a phylogenetic analysis, expanding the postcranial information used in current phylogenetic data sets. The phylogenetic analysis depicts *Yacarerani* forming a clade with *Adamantinasuchus*, which is positioned at the base of Sphagesauridae. This family is well nested among a clade of 'advanced notosuchians,' and *Mariliasuchus* is recovered as its sister group. The cladistic analysis recovered new postcranial synapomorphies for Notosuchia and less inclusive clades, although the fact that many taxa lack postcranial remains limits the number of unambiguous postcranial synapomorphies within Notosuchia.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Yacarerani boliviensis is a notosuchian crocodyliform described by Novas et al. (2009) from the Upper Cretaceous Cajones Formation of Santa Cruz de La Sierra, Bolivia. The material recovered is beautifully preserved and represents the first crocodyliform remains reported from the Mesozoic of Bolivia. The holotype material along with the referred material (see below) of *Yacarerani* were found in close association with unhatched eggs, which have a similar morphology to those found associated with the Brazilian notosuchian *Mariliasuchus* (Ribeiro et al., 2006). In the original contribution, *Yacarerani* was described on the basis of cranial material because the postcranium was still unprepared (Novas et al., 2009). The original description highlighted the particular craniomandibular morphology of *Yacarerani*, emphasizing the structure of the teeth, which permitted the recognition of its affinities with *Adamantinasuchus* among notosuchians. Most authors have agreed on the close affinities of these two taxa (Andrade et al., 2011; Iori and

Carvalho, 2011; Iori et al., 2013), with the sole exception of Turner and Sertich (2010), who placed it as sister to *Adamantinasuchus* plus *Armadillosuchus*. Moreover, recent studies (Monte-feltro et al., 2013; Pol et al., 2014) have recovered the clade *Yacarerani* + *Adamantinasuchus* within Sphagesauridae, a clade of notosuchian crocodyliforms with highly modified cranial and dental anatomy (Kuhn, 1968; Pol, 2003; Marinho and Carvalho, 2007; Iori et al., 2011; Pol et al., 2014), although Turner and Sertich (2010) found it to be closer to baurusuchids than to sphagesaurids.

The family Sphagesauridae was erected by Kuhn (1968) to include *Sphagesaurus huenei* Price, 1950, only represented by two teeth at that time. The peculiar morphology of those teeth, which were very different from those of all other crocodyliforms known, justified the creation of a monotypic family. Later, new material was described and referred to *Sphagesaurus huenei* (Pol, 2003), which allowed the identification of its phylogenetic affinities among derived notosuchians. Recently new taxa with sphagesaurid affinities have been reported, further increasing the diversity of this clade of notosuchians. Recent authors have disagreed on the taxonomic content of Sphagesauridae, partly due to differences in the phylogenetic results and taxon sampling (Andrade and Bertini, 2008; Iori and Carvalho, 2011; Iori et al.,

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2013). Recently, Pol et al. (2014) recognized eight taxa as members of this family, divided in three clades. A clade of derived and large-bodied forms (*Sphagesaurus huenei* Price, 1950; *Armadillosuchus arrudai* Marinho and Carvalho, 2009; *Caryonosuchus pricei* Kellner, Campos, Riff, and Andrade, 2011), the genus *Caipirasuchus* with three species (*C. montealtensis* (Andrade and Bertini, 2008; *Caipirasuchus paulistanus* Iori and Carvalho, 2011; *Caipirasuchus stenognathus* Pol et al., 2014), and a basal clade formed by *Yacarerani* and *Adamantinasuchus*. Although the sphagesaurid affinities of the clade *Yacarerani* + *Adamantinasuchus* have been disputed by previous authors (Novas et al., 2009; Turner and Sertich, 2010; Iori and Carvalho, 2011; Iori et al., 2011, 2013), these two taxa share with derived sphagesaurids features in their dentition, skull, and mandibular anatomy (Nobre and Carvalho, 2006; Marinho and Carvalho, 2007; Montefeltro et al., 2013; Pol et al., 2014). Sphagesauridae has a limited geographical and temporal distribution, given that *Yacarerani* is currently the only sphagesaurid found outside the Adamantina Formation of the Bauru Group.

Our knowledge of the anatomy of Sphagesauridae is almost exclusively from well-preserved craniomandibular remains, with only a few reported but largely undescribed postcrania of *Adamantinasuchus*, *Armadillosuchus*, and *Yacarerani*. The postcrania of *Yacarerani* described here include multiple closely associated specimens that encompass the entire postcranial skeleton. These represent the first significant postcranial remains of a sphagesaurid and one of the most complete postcrania known for a notosuchian crocodyliform.

Postcranial studies of notosuchians (and other crocodyliforms) are presently limited (Pol, 2005; Turner, 2006; Leardi and Pol, 2009; Georgi and Krause, 2010; Sertich and Groenke, 2010; Nobre and Carvalho, 2013), and only a few of them have focused on their phylogenetic information (Pol et al., 2012). The aim of this contribution is to describe in detail the postcranial anatomy of *Yacarerani boliviensis* and to evaluate the impact of this anatomical region on assessing the phylogenetic relationships of notosuchian crocodyliforms.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, U.S.A.; FMNH PR, The Field Museum, Chicago, Illinois, U.S.A.; GPIT, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Tübingen, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCF, Museo Carmen Funes, Plaza Huincul, Argentina; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.; MNK-PAL, Museo de Historia Natural Noel Kempf Mercado, Santa Cruz de la Sierra, Bolivia; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; MZSP, Museu Zoologia, Universidade de São Paulo, São Paulo, Brazil; SAM, Iziko-South African Museum, Cape Town, South Africa; UA, University of Antananarivo, Antananarivo, Madagascar; UAM, Universidad Autónoma de Madrid, Madrid, Spain; ZPAL, Instytut Paleobiologii PAN, Warszawa, Poland.

Anatomical Abbreviations—a + it + ft, insertion of the Mm. ambiens, iliotibialis 1–3, and femorotibialis; a asr, articular surface for the radius on the proximal end of the ulna; abgl, anterior bulge of the glenoid; ac, margin of the acetabulum; acp, acromion process; acra, anterior crest of the radiale; adc, apex of the deltopectoral crest; adhd, anterior distal humeral depression; ah, anterior hollow; aha, anterior heel of the axial centrum; alas, anterolateral articular surface on the astragalus; alpt, anterolateral proximal process of the tibia; alpu, anterolateral process of the ulna; als, anterolateral facing surface of the humerus; aml, anterior medial lamina; aop, anterior oblique process of the distal end of the ulna; ap, anteroventral process of the neural arch of the axis; apg, astragalar peg; api, anterior proximal process of the ischium; apu, anterior process of the ulna; ar, anterior roller;

asf, articular surface for the fibula; asfc, articular surface for the fibular condyle; astc, articular surface for the tibial condyle; asu, articular surface for the ulna; asul, articular surface for the ulnare; atl, astragalar-tarsale ligament pit; ax ns, axial neural spine; c amb, crest for the origin of the M. ambiens; c fdl, crest for the origin of the flexor digitorum longus; c scstl, crest for the attachment of the scapulosternal ligament; ch, chevron; cha, chevron articular surface; cor f, coracoid foramen; cph, crest on the posterior surface of the humerus; ct, calcaneal tuber; d ds, depression for the M. deltoideus scapularis; d ist, depression for the insertion of the M. ischiotrochantericus; d pife 2, depression for the insertion of the M. puboischiofemoralis internus 2; d tm, depression for the M. teres major; dc, deltopectoral crest; dc 2 + 3, distal carpal 2+3; dfdV, depression for the origin of the M. flexor digiti quinti pars superficialis et profundus; dfu, depression for the M. flexor ulnaris; di, diapophyses; dmpul, distomedial process of the ulnare; dpq, depression for the M. pronator quadratus; ect, ectepicondyle; ent, entepicondyle; fbf, fibular facet; fbh, fibular head; fc, fibular condyle; fdt4, facet for the distal tarsal 4; ff, fossa flexoria; fh, femoral head; fpf, femoral proximal fold; ft, fourth trochanter; gl, glenoid; gt, greater trochanter; hh, humeral head; hpc, humeral proximal crest oriented proximodistally; hy, hypapophyses; ilft, iliofibularis trochanter; isa, ischial antitrochanter; lcu, lateral crest of the proximal end of the ulna; ld, lateral depression; ld + tm, pit for the common insertion of the M. latissimus dorsi and M. teres major; lp at, lateral process of the atlantal neural arch; lpc, lateral plantar crest of the calcaneal tuber; lpr, lateral proximal process of the radius; lsc, lateral supracondylar crest; lt, lateral tubercle; ltbf, facet for the lateral condyle of the tibia; Mc I–V, metacarpals I–V; mdr, medial distal roller; mlpz, postzygapophyseal medial lamina; mpc, medial plantar crest of the calcaneal tuber; msc, medial supracondylar crest; mt, medial tuberosity; Mt I–IV, metatarsals I–IV; mtbf, facet for the medial tibial condyle; nf, nutrient foramina; ns, neural spine; oc pglp, oblique crest of the postglenoid process; ol, olecranon process; padl, paradiapophyseal lamina; para, parapophyses; pdhd, posterior distal humeral depression; piap, pit for the astragalar peg; pit, proximolateral pit of the tibia; plp Mc I, proximolateral process of the metacarpal I; plpa, proximolateral process of the astragalus; plpt, posterolateral proximal process of the tibia; pmd, proximomedial depression of the astragalus; pml, posterior medial lamina; pmpa, posteromedial process of the radiale; pmpt, posteromedial proximal process of the tibia; pmpul, proximomedial process of the ulnare; pof, postspinal fossa; polf, popliteal fossa; pop, posterior oblique process of the distal end of the ulna; poz, postzygapophyses; ppfbh, posterior projection of the fibular head; ppi, posterior proximal process of the ischium; ppra, proximal process of the radiale; prar, posterior rim of the anterior roller; prz, prezygapophyses; pxd, proximal astragalar depression; rad, radiale; rbb, rugosities for the insertion of the M. biceps brachii; rc, radial condyle; sc, supinator crest; shc, depression for the M. scapulohumeralis caudalis; spozl, spinopostzygapophyseal lamina; sprzl, spinoprezygapophyseal lamina; tal, tibial-astragalar ligament pit; tc, tibial condyle; tp, transverse processes; trc, astragalar trochlea; uc, ulnar condyle; uln, ulnare; ung, ungual phalanx; vk, ventral keel.

SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES Clark, 1986

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

NOTOSUCHIA Gasparini, 1971 (sensu Sereno et al., 2001)

SPHAGESAURIDAE Kuhn, 1968

YACARERANI BOLIVIENSIS Novas, Pais, Pol, Carvalho, Scanferla, Mones, and Suárez Riglos, 2009

Holotype—MNK-PAL5063, complete skull and mandibles.

Referred Specimens—MNK-PAL5064-A, almost complete lower jaws articulated with a partial skull (pterygoid, ectopterygoid, jugal, squamosal, and quadrate) and associated postcrania, including a partial cervicodorsal series and appendicular elements (i.e., right pectoral girdle, right humerus, right tibia); MNK-PAL5064-B, semi-articulated specimen represented by postcrania recovered from the same block as MNK-PAL5064-A including an almost complete dorsal series and elements from both fore- and hind limbs; MNK-PAL5064-C, isolated postcrania from the same block as MNK-PAL5064-A and 5064-B that cannot be associated with the articulated specimens; MNK-PAL5064-D, isolated mandibular bones (splenial and coronoid) and disarticulated postcrania including axial and appendicular elements; MNK-PAL5064-E, fragmentary crania (fragments of premaxilla, maxilla and jugal) and associated postcrania including an articulated cervical and anterior dorsal vertebrae, both humeri, ulnae, partial radius, radiale, and right ischium.

Locality and Horizon—Amboro National Park, Santa Cruz de la Sierra, Bolivia, from levels of the Cajones Formation, Upper Cretaceous. Based on previous fossil findings, the age of the formation was inferred to be Maastrichtian (López, 1975; Aguilera et al., 1989), but an older age was proposed based on the similarities of *Yacarerani* with the crocodyliform fauna from the Adamantina Formation (Novas et al., 2009).

Emended Diagnosis—Notosuchian crocodyliform characterized by the following cranial autapomorphies: nasals rostrally expanded above external nares; palatines bearing median sagittal crest; retroarticular process rounded and rostrocaudally short relative to lateromedial width of glenoid facets of articular; jugal laterally expanded, forming ornamented prong at level of postorbital bar; incisiviforms separated from molariforms by a diastema; and molariform tooth rows rostrally convergent and almost in contact at midline. Among the postcranial remains, the following diagnostic characters were identified (autapomorphies marked with an asterisk): pedicles of atlas bearing a lateral bulge*; knob-like hypapophyses present up to sixth dorsal vertebra, strong ventral keels present on cervical and anterior dorsal vertebrae; absence of rounded depressions on dorsal surface of anterior to middle dorsal vertebrae*; anteriorly expanded acromial region of scapula; coracoid bearing oblique crest on lateral surface*; single distal carpal (2+3); lateromedially compressed anterior ungual phalanges*; femur with shallow depression for M. puboischiofemoralis internus 1 (PIFI1) and M. caudifemoralis longus (CFL)*; low fourth trochanter on femur*; anterior hollow of astragalus divided into dorsal and ventral regions by strong crest; nutrient foramen on dorsal region of anterior hollow; and nutrient foramen on dorsal surface of calcaneal tuber.

MATERIALS AND METHODS

Specimens of *Yacarerani boliviensis*

The materials of *Yacarerani boliviensis* were recovered from a fine- to medium-grained red sandstone layer of the Los Cajones Formation. The specimens were found in a monospecific assemblage, including articulated, partially articulated, and disarticulated materials. Postcrania studied in this contribution were recovered by mechanical preparation of the three blocks that contained all specimens. As noted above (see Referred Specimens), more than one individual is represented in this sample. The block that contained most fossils, including the holotype (MNK-PAL5063), also contained associated unhatched eggs (Novas et al., 2009) and all of the referred material described here (MNK-PAL5064-A, 5064-B, and 5064-C).

Novas et al. (2009:1316) originally included “a complete exquisitely preserved skeleton” as the holotype specimen. Subsequent preparation of the blocks containing the materials revealed that the holotype specimen lacked postcranial remains that can be definitively associated with the skull. Thus, we here

restrict the type material (MNK-PAL5063) of *Yacarerani boliviensis* to the well-preserved skull and mandibles figured by Novas et al. (2009). The remaining material recovered from the same block is regarded as referred specimens. MNK-PAL5064-A includes articulated cranial, mandibular, and postcranial elements. In the same block, specimen MNK-PAL5064-B was found as a set of semi-articulated postcrania. Several other postcrania were found in this block and could not be confidently associated with any of the above-mentioned specimens. Therefore, all additional material retrieved from this block has been cataloged as MNK-PAL5064-C, which includes bones from at least three different individuals based on the number of duplicated appendicular elements (three left tibiae; two complete and one proximal half).

The remaining specimens were recovered from two blocks collected adjacent to the holotype block. Specimen MNK-PAL5064-D includes fragmentary mandibular bones and associated postcrania (middle to posterior dorsal vertebrae, anterior caudal vertebrae, and appendicular elements, such as a complete humerus). Finally, MNK-PAL5064-E includes disarticulated remains of at least two individuals, given the presence of two left humeri. Among the repeated elements of this block there is a considerable size difference, such that the length of the smallest humerus is 75% the length of the largest.

The entire assemblage of bones found in the three blocks indicates that there are at least eight individuals based on overlapping postcranial elements. The list of elements under each of the collection numbers is included in Supplementary Data. Catalog numbers MNK-PAL5064-C and 5064-E certainly include more than one individual (a minimum of three and two, respectively). With the exception of the two humeri of MNK-PAL5064-E (see above), all other duplicated elements have slight size variation, allowing us to infer a similar ontogenetic stage for most individuals.

Osteological and Muscular Terminology

The postcrania are described following the osteological nomenclature proposed by Mook (1921), Romer (1956), and Hoffstetter and Gasc (1969), although, in contrast to the semi-erect postures of extant crocodylians, basal crocodyliforms have been inferred to have erect postures (Parrish, 1986, 1987; Pol, 2005). In order to reflect that posture, we follow the limb bone orientation of Pol (2005), where they are oriented as if they were held in a vertical position. The inference of appendicular myology has been a common procedure in recent crocodyliform postcranial descriptions (Turner, 2006; Nascimento and Zaher, 2010; Sertich and Groenke, 2010; Pol et al., 2012). For such inferences, we followed Meers (2003) and Jasinosky et al. (2006) for the forelimb and Romer (1923) for the hind limb musculature when possible (see also Hutchinson, 2001a, 2001b; Carrano and Hutchinson, 2002).

DESCRIPTION

Here, we focus on the description of recovered postcrania, housed in the MNK-PAL collection under the number 5064 (A to E). Comparisons in the text are made with other taxa that preserve postcrania. Sources of information of those taxa are summarized in Table 1.

Axial Skeleton

The axial skeleton of *Yacarerani boliviensis* is well represented. Most regions of the vertebral column are preserved in at least one specimen. These elements include vertebral centra and neural arches, with the exception of the sacral vertebrae. All centra are amphicoelous, as in most non-eusuchian crocodyliforms, with the posterior articular surfaces anteroposteriorly deeper

TABLE 1. List of taxa used for comparisons in the text.

Taxon	Source
<i>Araripesuchus gomesii</i>	AMNH 24450
<i>Araripesuchus tsangatsangana</i>	Turner (2006)
<i>Barcosuchus gradilis</i>	MPEF-PV 3095; Leardi and Pol (2009)
<i>Baurusuchus albertoi</i>	Nascimento (2008); Nascimento and Zaher (2010)
<i>Caiman latirostris</i>	MPEF-AC 205
<i>Chimaerasuchus paradoxus</i>	IVPP V 8274
<i>Edentosuchus tienshanensis</i>	IVPP V 3236
<i>Gobiosuchus kielanae</i>	ZPAL MgR-II/67
<i>Iberosuchus macrodon</i>	Ortega (2004)
<i>Lomasuchus palpebrosus</i>	MCF-PVPH 160
<i>Mahajangasuchus insignis</i>	UA 8654
<i>Malawisuchus mwakayasyunguti</i>	Gomani (1997)
<i>Mariliasuchus amarali</i>	MZSP-PV 50; Nobre and Carvalho (2013)
<i>Notosuchus terrestris</i>	MACN-PV RN 1037, 1042, 1122, S/N; MUCPV 900; Pol (2005); Fiorelli and Calvo (2008)
<i>Orthosuchus stormbergi</i>	SAM-PK 409
<i>Protosuchus richardsoni</i>	AMNH 3024; MCZ 6727
<i>Sebecus icaeorhinus</i>	AMNH 3159; MPEF-PV 1776, 3971, 3972; Pol et al. (2012)
<i>Simosuchus clarki</i>	UA 8679; FMNH PR 2596, 2597, 2598; Georgi and Krause (2010); Sertich and Groenke (2010)
<i>Steneosaurus bollensis</i>	GPIT 1909 s.264
<i>Stratiotosuchus maxhechti</i>	Riff (2007); Riff and Kellner (2011)
<i>Uruguaysuchus aznarezi</i>	Soto et al. (2011)

than the anterior surfaces. In all specimens, the centra are not fused to the neural arches, with a clear neurocentral suture even in the posterior-most caudal vertebrae. As a consequence, many neural arches are isolated and disarticulated from their respective centra.

Cervical Vertebrae—Cervical vertebrae (C) are preserved in at least two of the specimens, MNK-PAL5064-A and 5064-E. Specimen MNK-PAL5064-E includes an isolated atlas, a series of six almost complete articulated vertebrae (axis to C7), and the anterior fourth of the penultimate cervical (C8) (Fig. 1A–F). Two isolated vertebral arches (probably C4 and C5) (Fig. 2A–E) and disarticulated fragmentary cervical neural arches were recovered from MNK-PAL5064-A.

The atlas is represented by its complete right neural arch (Fig. 1A–C). The proximal portion of the pedicle is expanded and ventromedially directed. The medial surface of the proximal end of the neural arch is rugose and is divided by a very slight oblique crest that delimits an anterodorsal surface for the articulation with the occipital condyle and a posteroventral one that represents the articular surface with the odontoid process (Fig. 1B). The proximal half of the pedicle has a well-developed lateral bulge (Fig. 1A, C) as in *Simosuchus*, a feature absent in other mesoeucrocodylians (e.g., *Notosuchus*, *Baurusuchus albertoi*, and *Caiman yacare*) in which the atlantal neural arches are known. This bulge forms an abrupt step on the lateral surface of the atlantal neural arch in both anterior and posterior views. Dorsal to the bulge, the lateral surface of the atlantal neural arch is convex. The dorsal edge of the neural arch is almost straight in lateral view, and its anterior and posterior ends are not strongly projected as in *Notosuchus*, unlike other mesoeucrocodylians (e.g., *Simosuchus*, *B. albertoi*, and *C. yacare*). As in most crocodyliforms, the prezygapophysis is located on the medial surface of the dorsal end of the arch, facing anteromedially, and the postzygapophysis is located on the posterolateral surface of the atlantal neural arch.

The axis is almost completely preserved, only lacking the odontoid process and the distal end of the spine. The axial centrum is anteroposteriorly shorter in comparison with the lengths of the postaxial cervical centra (Fig. 1D). This condition is also present in other basal mesoeucrocodylians (e.g., *Barcosuchus*, *Simosuchus*, *Mariliasuchus*, *B. albertoi*, and *Sebecus icaeorhinus*), contrasting with the condition of extant crocodylians, where the axial centrum is slightly longer than the anterior-most

postaxial centrum. As in most notosuchians (e.g., *Barcosuchus*, *Simosuchus*, *B. albertoi*, and *S. icaeorhinus*), the ventral surface of the axial centrum in *Yacarerani* has a slight central crest but lacks a projected hypapophysis (Fig. 1F), unlike the laminar axial hypapophysis of extant taxa. The anterior margin of the ventral surface of the centrum is greatly expanded ventrally, forming a strong anterior heel. In anterior view, the articular surface for the odontoid process is rugose and does not reach the ventral edge of the anterior heel of the centrum. The anterior heel probably represents the articular surface for the atlantal intercentrum. The parapophyses are located on the ventral edge of the lateral surfaces of the intercentrum. A lateral crest projects posteriorly to the parapophyseal facet, attenuating at the midpoint of the centrum length. Dorsally, the lateral surface of the axis is concave.

The pedicles of the neural arch of the axis are longer than the centrum, projecting anteriorly beyond the anterior end of the axial centrum (Fig. 1D). The anteroventral region of the pedicles has two rounded, anteroventrally exposed facets for the articulation of the unpreserved odontoid process. At the anteroventral region of the pedicles, but on their lateral surface, the diapophyses are preserved. These are anteroposteriorly elongated, poorly expanded laterally, and located just dorsal to the neurocentral suture. The axial neural spine is anteroposteriorly short and quadrangular in cross-section, located on the posterior half of the neural arch, leaving a shallow prespinal fossa divided by an anterior medial lamina of the spine (Fig. 1E). This axial neural spine morphology is also present in other notosuchians (e.g., *Simosuchus*, *Mariliasuchus*, *Notosuchus*, *B. albertoi*), contrasting with the anteroposteriorly elongated spine of basal crocodylomorphs (e.g., *Hesperosuchus*), basal crocodyliforms (e.g., *Orthosuchus*), and neosuchians (e.g., *Caiman*, *Dyrosaurus*, *Theriosuchus*, *Steneosaurus*). The prezygapophyses are located on the lateral surface of the pedicles and project anteriorly, leaving a ventral notch for the passage of the C1 spinal nerve. The prezygapophyses are exposed laterally as in *B. albertoi*, contrasting with the dorsolaterally exposed prezygapophyses of *Simosuchus* and extant crocodylians. The postzygapophyses are more dorsally positioned than the prezygapophyses, as in most crocodyliforms, and bear weakly developed spinopostzygapophyseal laminae. The axial postzygapophyses meet the prezygapophyses of the C3 at an angle of approximately 75° with respect to the dorsoventral plane.

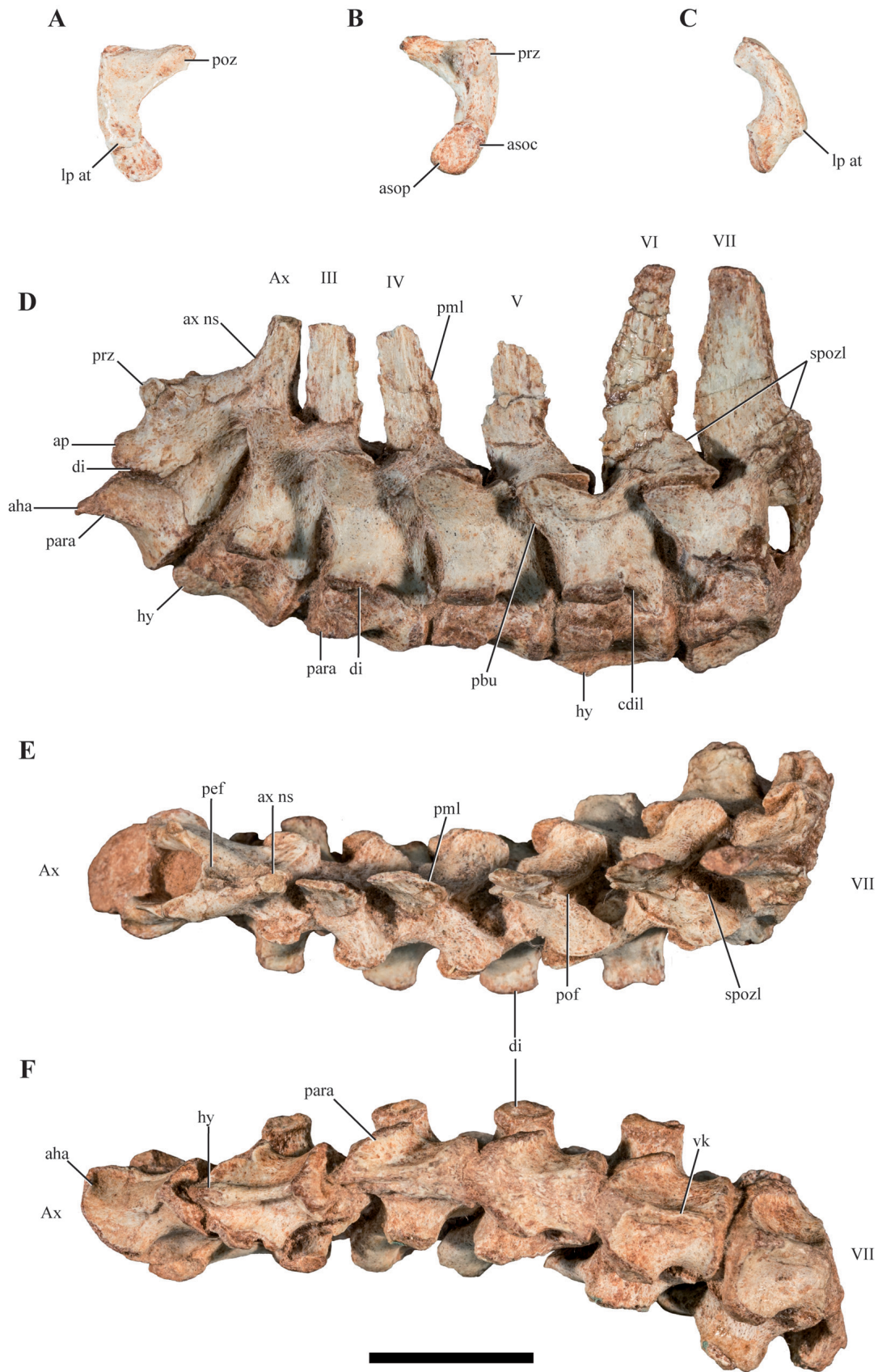


FIGURE 1. Left neural arch of the atlas of *Yacarerani boliviensis* (MNK-PAL5064-E) in **A**, lateral, **B**, medial, and **C**, anterior views. Articulated cervical vertebrae (axis to C7) of *Yacarerani boliviensis* (MNK-PAL5064-E) in **D**, lateral, **E**, dorsal, and **F**, ventral views. Roman numerals indicate the number of each cervical vertebra; **Ax**, axis. Scale bar equals 1 cm.

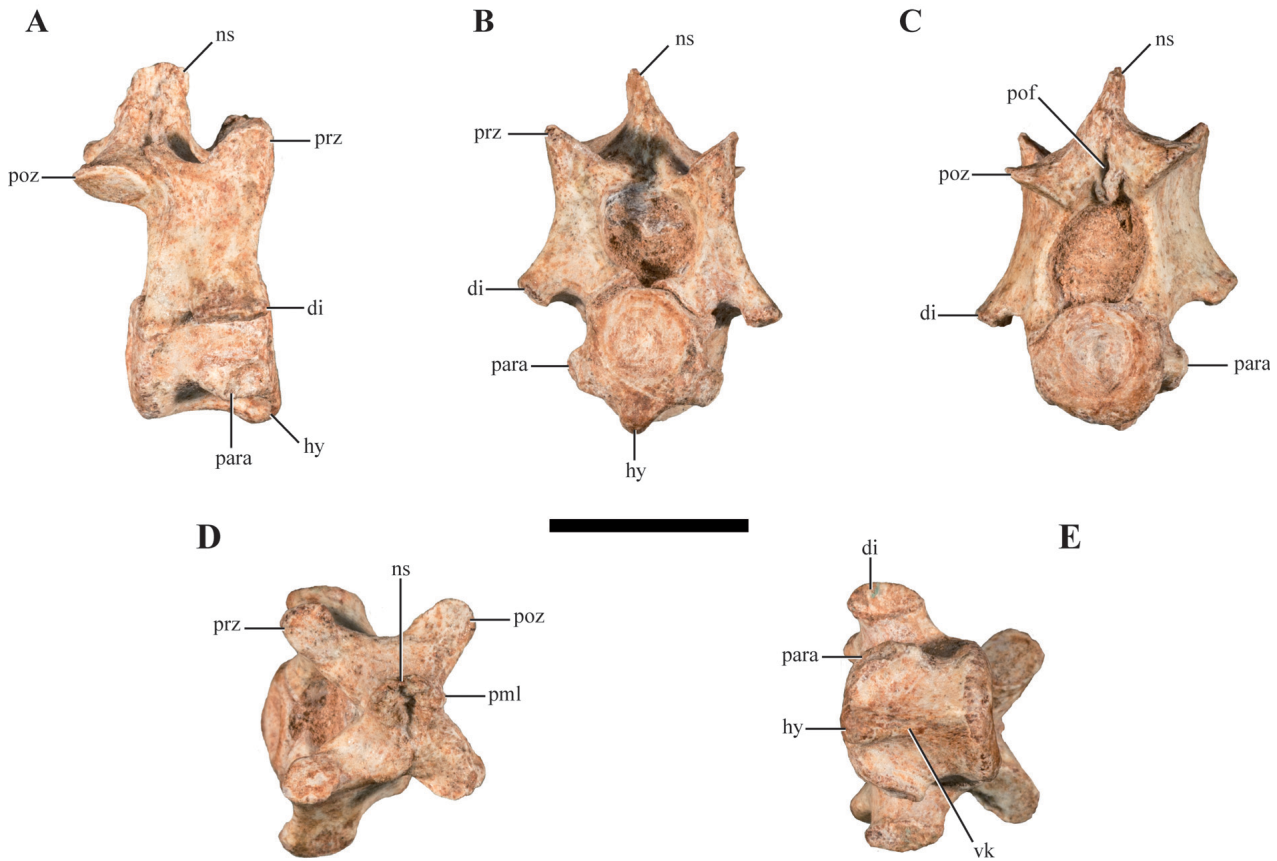


FIGURE 2. Middle cervical vertebra (C4/C5) of *Yacarerani boliviensis* (MNK-PAL5064-B) in **A**, lateral, **B**, anterior, **C**, posterior, **D**, dorsal, and **E**, ventral views. Scale bar equals 1 cm.

The postaxial cervical centra of *Yacarerani* are anteroposteriorly longer than tall (Figs. 1D, 2A), as in most crocodyliforms (e.g., *Protosuchus richardsoni*, *Orthosuchus*, *Araripesuchus tsangatsangana*, *Araripesuchus gomesii*, *Simosuchus*, *Barcinosuchus*, *B. albertoi*, *Marillasuchus*, *Notosuchus*, and *S. icaeorhinus*) but contrasting with the proportionately short and high cervical centra of *Mahajangasuchus*. The centra are subequal in length along the cervical series. All postaxial cervical centra have well-developed hypapophyses on the anterior margins of their ventral surfaces, although they are well preserved only in C3 and C7 (Figs. 1F, 2A, B, E). The hypapophysis of C3 is laminar and more ventrally projected than the blunt ('knob-like' sensu Leardi and Pol, 2009) hypapophysis of C6. Low hypapophyses on the posterior cervicals are also present in *Mahajangasuchus*, *Simosuchus*, and *Barcinosuchus*, contrasting with the more distally projected laminar hypapophyses of *S. icaeorhinus* and extant crocodylians. The hypapophyses continue posteriorly as strong ventral keels that reach the posterior articular surface of the centra (Figs. 1F, 2E), as in *Barcinosuchus*, *Simosuchus*, and *Notosuchus*. In *Mahajangasuchus* and *S. icaeorhinus*, these crests are less developed and do not reach the posterior articular surface. The parapophyses are located on the lateral surfaces of the centra, starting on the anteroventral edge of the centrum in C3 and rising gradually to a position slightly dorsal to the mid-height of the centrum in C7, well ventral to the neurocentral suture. The facets for the tubercles of the cervical ribs are anteroposteriorly elongated, constituting half of the total length of the centra (Fig. 1D). The parapophyses project posteriorly as strong crests that do not reach the posterior articular surface of the centra (Fig. 2A). Dorsal to the parapophyses, the lateral surfaces of the

centra have strong concavities, limited dorsally by the neurocentral suture.

The neural arches are tall and slightly anterodorsally slanted. The diapophyses are located on the anterolateral surfaces of the arches (Fig. 1D). In C3, the diapophyses originate on the ventral half of each arch and are restricted to the anterior half of each arch, and the facets for the tubercle of the ribs are anteroposteriorly short and ventrolaterally oriented. Along the cervical series, the diapophyses rise dorsally, become more elongated, and change the orientation of their rib facets (facing more laterally). Thus, on C7, the diapophyses originate at the dorsoventral midpoint of the lateral surfaces of the neural arch and occupy most of the lateral surfaces of the neural arch, and their rib facets face laterally. This gradual rise of the diapophyses is common among crocodyliforms, but not their gradual anteroposterior elongation. This condition is only shared with *Notosuchus*, whereas other basal mesoeucrocodylians (*Mahajangasuchus*, *Simosuchus*, *B. albertoi*, *S. icaeorhinus*) have quadrangular distal ends of the diapophyses in the posterior cervicals. Accessory laminae originating from the diapophyses (anterior and posterior centrodiapophyseal laminae) are weakly developed on C3 but are more strongly developed in more posterior cervical vertebrae. These laminae enclose a triangular depression ventral to the diapophyses that is most developed in C4–C6. Lateral depressions limited by centrodiapophyseal laminae are not observed in other crocodyliforms.

The postaxial cervical neural spines of *Yacarerani* are more elongated than the neural spine of the axis (Fig. 1E). The neural spines are also displaced posteriorly on the dorsal surface of the neural arch, but they lack a large prespinal fossa and instead have

an anteroposteriorly short slit-like notch (Fig. 2B). In contrast, the cervical vertebrae of *Mahajangasuchus*, *B. albertoi*, *Iberosuchus*, and *S. icaeorhinus* bear well-developed prespinal fossae. The neural spines of C3 and C4 are anteriorly slanted, whereas those of C5–C7 are almost vertical. Anteriorly slanted cervical neural spines are also present in other notosuchians (e.g., *A. gomesii*, *Simosuchus*, *Mariliasuchus*, *B. albertoi*, *Notosuchus*, and *S. icaeorhinus*), contrasting with the more vertically oriented spines of *Mahajangasuchus* and extant crocodylians. Among notosuchians, the vertical orientation of the neural spines is present in C5 in *Yacararani* and *Notosuchus*, whereas in *Simosuchus* it appears in C6, and in *B. albertoi* in C7. The posterior surfaces of the cervical neural spines bear well-developed posterior medial laminae that attenuate at the bases of the neural spines. Ventral to the posterior medial laminae and between the postzygapophyses, a deep, triangular, and posteriorly exposed postspinal fossa is present (Fig. 2C). This fossa has a bony lamina that limits its ventral margin, as in most basal mesoeucrocodylians (e.g., *Mahajangasuchus*, *Simosuchus*, *Notosuchus*, and *B. albertoi*) but unlike in *S. icaeorhinus*, in which this lamina is absent.

The prezygapophyses are dorsally projecting and strongly recurved, with their articular surface facing mostly medially (Fig. 2B) in the anterior cervical vertebrae (C3–C4), as in other notosuchians (Pol et al., 2012). The prezygapophyses from the middle to posterior cervicals (C5–C7) are anterodorsally projecting and face anteromedially. The anterior cervicals bear slight ridges on their anterior surface. This ridge forms a slight bulge on the anterior surface of the prezygapophyses (Fig. 1D), as in sebecosuchians, *Mahajangasuchus*, and *A. tsangatsangana* but not in *Notosuchus*, *A. gomesii*, *Uruguaysuchus*, *Simosuchus*, or *Mariliasuchus* (Pol et al., 2012). The articulation between the anterior cervicals precludes determining the presence of the medial triangular depression, which is present in other taxa that have this distinct bulge on the prezygapophyses. The postzygapophyses originate more dorsally than the prezygapophyses, and their articular surface are oriented posterolaterally. The spinopostzygapophyseal laminae are absent or weakly developed on the anterior and middle cervicals, but are prominent in C6. Well-developed spinopostzygapophyseal laminae are present in several basal ziphosuchians (e.g., *Malawisuchus*, *Notosuchus*, *Mariliasuchus*, and *Simosuchus*; Pol, 2005; Georgi and Krause, 2010; Pol et al., 2012) and in *Uberabasuchus*.

Dorsal Vertebrae—Dorsal vertebrae (D) are preserved in specimens MNK-PAL5064-A, 5064-B, and 5064-E. Of these, MNK-PAL5064-B includes an articulated series representing D3 to D7 (Fig. 3A–C) and two isolated anterior dorsal vertebrae (D1? and D2) (Fig. 4A–E). Specimen MNK-PAL5064-A includes portions of the centra and the neural arches of an articulated series ranging from D3 to D5 and also several middle to posterior dorsal vertebrae, represented either by complete elements or isolated neural arches, while MNK-PAL5064-E includes an isolated D4, an articulated series of anterior dorsal vertebrae (D5–D7), and an isolated middle dorsal. Dorsal vertebrae will be described here in three regions: anterior, middle, and posterior.

The anterior dorsal vertebrae are well represented in the *Yacararani* specimens. Relative position of the anterior dorsal vertebrae in the dorsal series is based mainly on the position of parapophyses relative to the neurocentral suture. The migration of the parapophyses onto the neural arch where they merge with the diapophyses is abrupt: the parapophyses are located on the neurocentral suture in the anterior-most dorsal vertebrae and abruptly ascend and merge with the diapophyses in D5 (Fig. 3A). This abrupt migration is widely distributed among notosuchian crocodylians, with the exception of *Notosuchus* and *S. icaeorhinus* (in which the parapophyses gradually rise along the dorsal series; Pol et al., 2012). The abrupt migration of the parapophysis can be reflected in the number of dorsal vertebrae where this process is located between the level of the base and the roof of the

neural canal. Most crocodylians lack a vertebra (*Sarcosuchus*, *Terminonaris*) or have one vertebra (*Orthosuchus*, *A. gomesii*, *Mahajangasuchus*, *Simosuchus*, *C. yacare*) in which the parapophyses are located at the level of the neural canal. However, there are at least three vertebrae in *Notosuchus* and four in *S. icaeorhinus* that are placed at this level.

In *Yacararani* (MNK-PAL5064-B), the two vertebrae with their parapophyses contacting the neurocentral suture are identified as D3 and D4 (Fig. 3A). Two isolated anterior dorsal vertebrae also have their parapophyses at the level of the neurocentral suture, but on these the parapophyses are slightly more ventrally positioned, allowing us to identify these as more anterior elements. Given that these two elements differ in the position of their parapophyses, we can identify them as D1 and D2. The parapophyses of D1 are more ventrally positioned than the neurocentral suture, whereas in D2 the parapophyses slightly contact the neurocentral suture dorsally. Thus, in *Yacararani boliviensis*, the parapophyses of D2–D4 are at the level of the neurocentral suture. The parapophyses contact the neurocentral suture up to D4 also in *Notosuchus* and *Mariliasuchus*; in *Orthosuchus*, *A. gomesii*, and *Mahajangasuchus*, this contact is present up to D3; and in *Simosuchus* and *B. albertoi*, the last vertebra has its parapophyses contacting the neurocentral suture is D2, as in extant crocodylians (Hoffstetter and Gasc, 1969) and basal crocodylomorphs (e.g., *Terrestriusuchus*; Crush, 1984). Unlike modern crocodylians, the parapophyses of the anterior-most dorsal vertebrae (up to D4) in *Yacararani boliviensis* are dorsoventrally oriented (Figs. 3A, 4B) as in other notosuchians (e.g., *A. tsangatsangana*, *A. gomesii*, *Barcinosuchus*, *Mahajangasuchus*, *Simosuchus*, *B. albertoi*, and *S. icaeorhinus*), contrasting with the obliquely oriented parapophyses of the anterior dorsals of the neosuchians.

The anterior dorsal vertebral centra are broader than those of the posterior cervicals. All the anterior dorsal centra bear knob-like hypapophyses, being reduced to a very faint knob in D7 (Fig. 4B, C, E). This condition contrasts with that of extant crocodylians and *Simosuchus*, where the hypapophyses are restricted to D4. In contrast, derived ziphosuchians (*S. icaeorhinus* and *B. albertoi*) have hypapophyses up to D6, as in *Yacararani boliviensis*. The hypapophyses project posteriorly, forming strong crests on the ventral surface of the centra that reach the posterior articular surface of the vertebrae, except for D7, which lacks this ventral crest. These crests are absent in extant crocodylians but are present and are restricted to the anterior-most dorsals in *Protosuchus richardsoni*, *Orthosuchus*, *Mahajangasuchus*, *Notosuchus*, *Barcinosuchus*, *A. gomesii*, *Simosuchus*, and *Malawisuchus*. In *Yacararani*, the lateral surfaces of the dorsal centra (up to D6) are markedly concave when the ventral crests are present (Fig. 3A, C), given that the lateral depressions are less pronounced in more posterior dorsals.

The anterior dorsal neural arches are vertical or slightly posteriorly slanted (Fig. 4B), unlike the anteriorly slanted neural arches of the cervical vertebrae. The development of accessory laminae (centrodiapophyseal laminae) on the lateral surface of centra is weak. As previously mentioned, the parapophysis is connected to the diapophysis in D5 through a well-developed parapodiapophyseal lamina (Fig. 3A), as in *Orthosuchus*, *Notosuchus*, *B. albertoi*, *S. icaeorhinus*, *Mahajangasuchus*, and *Lomasuchus*. This lamina is absent or weakly developed in non-crocodyliiform crocodylomorphs (i.e., *Terrestriusuchus* [Crush, 1984] and *Dibothrosuchus* [IVPP V 7907; Wu and Chatterjee, 1993]), neosuchian crocodylians, and *Simosuchus*. The migration of the parapophyses to become aligned with the diapophyses is gradual, with the former still ventral to the latter in D7 (as in the above-mentioned notosuchians). In contrast, the dorsal migration in *Simosuchus* is very abrupt, with the parapophyses and diapophyses completely aligned on D5.

The neural spines are posteriorly inclined and anteroposteriorly shorter in the anterior dorsals (D2–D4) than in the

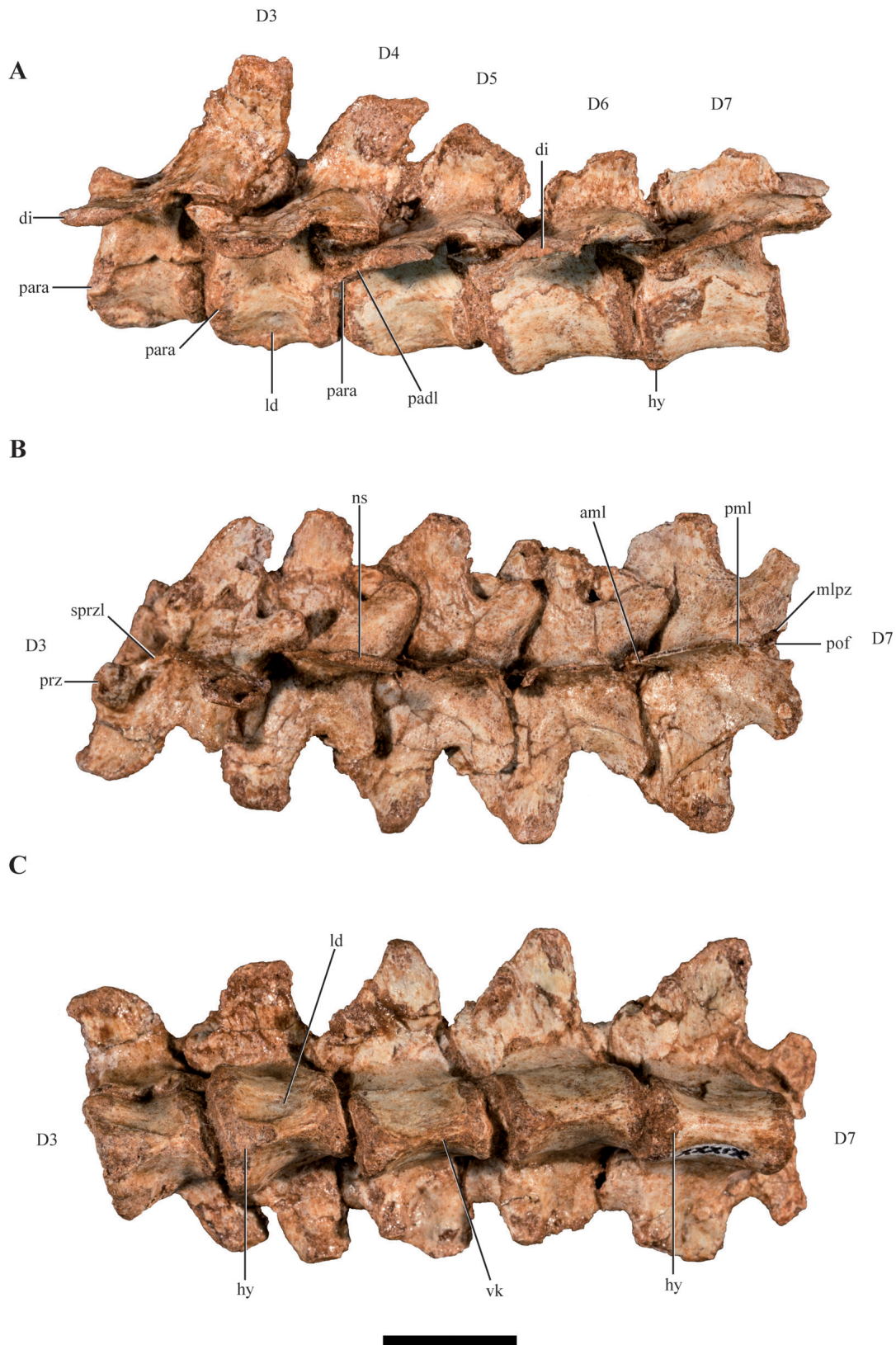


FIGURE 3. Articulated anterior and middle dorsal vertebrae (D3–D7) of *Yacarerani boliviensis* (MNK-PAL5064-E) in **A**, lateral, **B**, dorsal, and **C**, ventral views. Scale bar equals 1 cm.

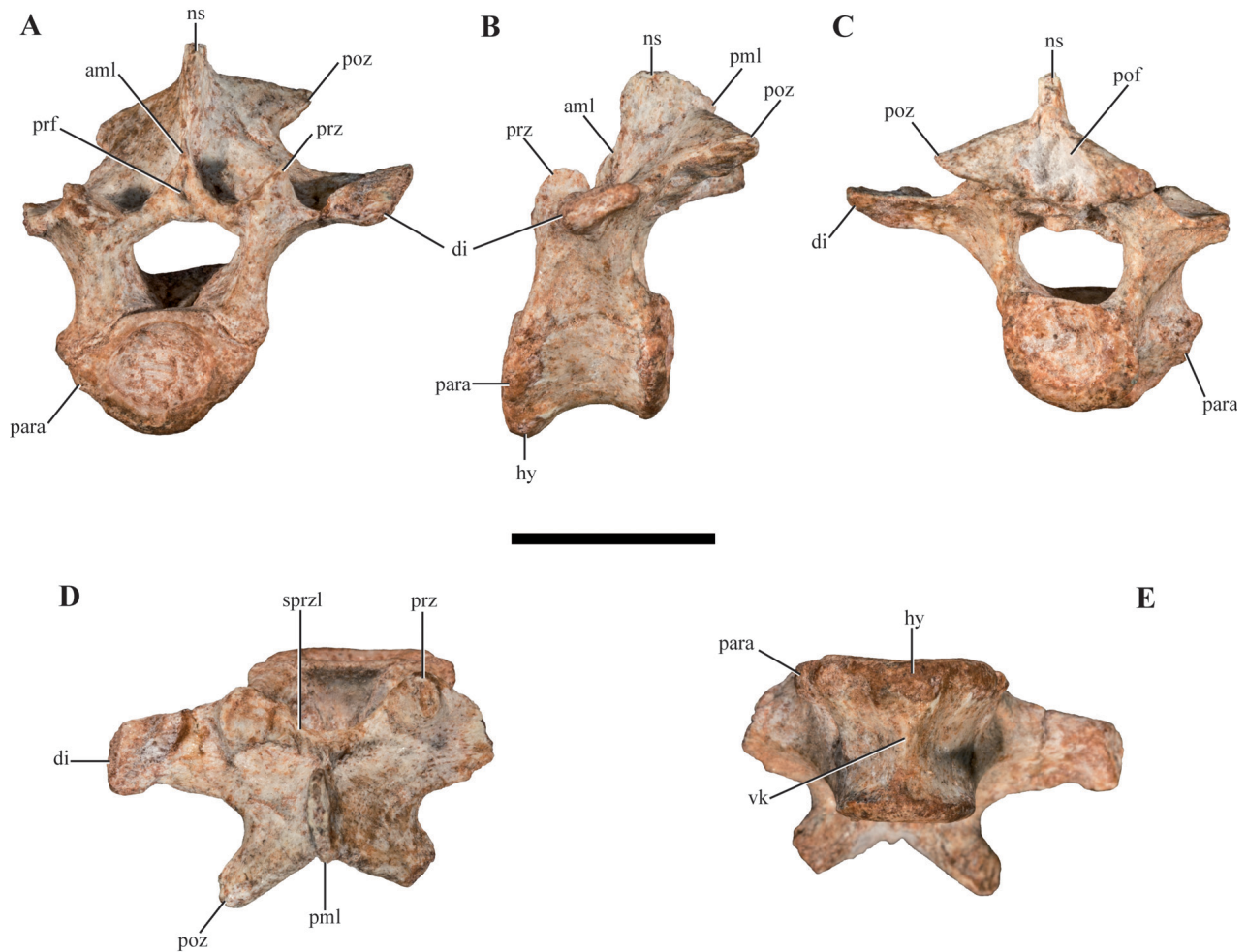


FIGURE 4. Anterior dorsal vertebra (D1/D2) of *Yacarerani boliviensis* (MNK-PAL5064-B) in **A**, lateral, **B**, anterior, **C**, posterior, **D**, dorsal, and **E**, ventral views. Scale bar equals 1 cm.

posterior cervical vertebrae (Fig. 4D), because they do not occupy the entire dorsal surface of the neural arch. The spines are longer on the more posterior vertebrae (D5–D7) and occupy most of the dorsal surface of the neural arches (Fig. 3B). The anterior and posterior medial laminae of the neural spines are well developed in the dorsal vertebrae, especially posterior to D4. The anterior medial laminae bifurcate just anterior to the anterior margin of the neural arch, forming moderately developed spinoprezygapophyseal laminae (Fig. 4A). The spinoprezygapophyseal laminae enclose a shallow and anteriorly exposed triangular prespinal fossa. The presence of this fossa is difficult to determine in other basal mesoeucrocodylians, because it requires well-preserved and completely prepared anterior dorsal vertebrae. *Mahajangasuchus* has a prespinal fossa bounded by spinoprezygapophyseal laminae in the anterior dorsal vertebrae, but these are deeper and are not anteriorly oriented as in *Yacarerani*. Well-developed prespinal fossae on the anterior dorsal vertebrae are also present in sebecosuchians (*B. albertoi*, *S. icaeorhinus*, and *Iberosuchus*). Unlike in most notosuchians (Pol et al., 2012), the anterior dorsal vertebrae of *Yacarerani* lack the well-developed, rounded depressions located between the base of the neural spines and the dorsal surfaces of the postzygapophyseal process. The posterior medial lamina is also well developed on the anterior dorsals of *Yacarerani* and a deep triangular postspinal fossa is present, bounded by a thin lamina between the postzygapophyses (Fig. 4C). A similar structure is present in

the anterior-most dorsal vertebrae of *Yacarerani*, *Mahajangasuchus*, and *B. albertoi*, but is absent in *S. icaeorhinus*. The distal ends of the neural spines are not distinctly expanded, resembling those of other basal mesoeucrocodylians (e.g., *A. tsangatsangana*, *Mahajangasuchus*, *Simosuchus*, and *B. albertoi*) but contrasting with the expanded distal ends of these spines in crocodylians and *Sarcosuchus*. The articular surfaces of the prezygapophyses are more dorsally oriented than in the cervicals (Figs. 3B, 4D). The postzygapophyses are almost horizontal and lack the development of the sharp spinopostzygapophyseal laminae described for the posterior cervicals.

The middle dorsal vertebrae have more mediolaterally compressed centra than the anterior dorsals (Fig. 5E). In spite of this mediolateral compression, the lateral surfaces of the centra are not significantly excavated as in the anterior dorsals or the cervicals. The neural arches of the middle dorsal vertebrae are vertically oriented. The parapophyses are almost level with the diapophyses (Fig. 5B). The neural spines are centered on the dorsal surface of the neural arch and occupy most of this surface (Fig. 5D). The anterior and posterior medial laminae of the neural spines are more extensive in these vertebrae than in the preceding dorsals and the prespinal fossa is absent in the middle dorsal vertebrae (Fig. 5A). The postspinal fossa, in contrast, is much more developed, being bounded ventrally by a medial lamina that extends between the postzygapophyses. This medial lamina

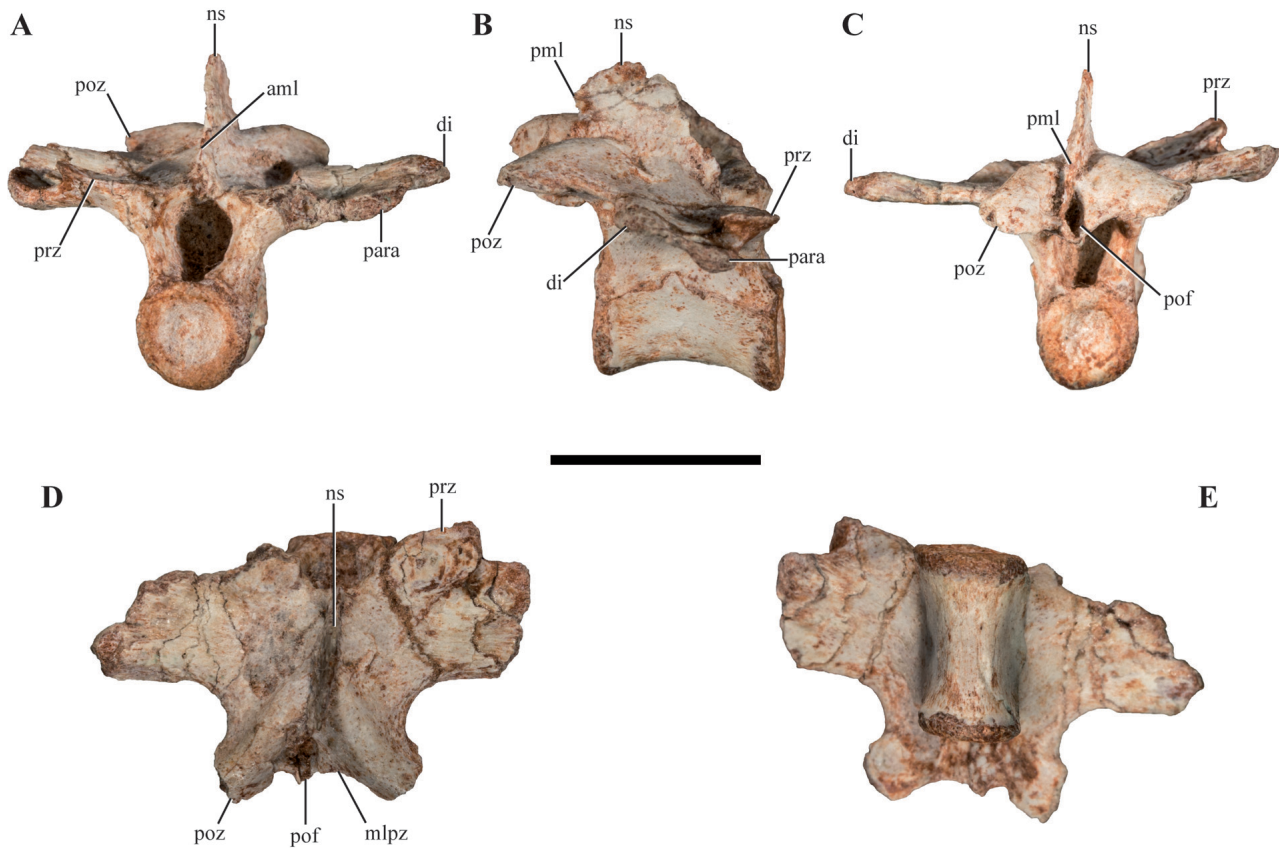


FIGURE 5. Middle dorsal vertebra of *Yacarerani boliviensis* (MNK-PAL5064-E) in **A**, lateral, **B**, anterior, **C**, posterior, **D**, dorsal, and **E**, ventral views. Scale bar equals 1 cm.

of the postzygapophyses is almost at the same plane as the postzygapophyses (Fig. 5C), as in *A. tsangatsangana*, contrasting with the more ventrally projected laminae of *Mahajangasuchus*, *B. albertoi*, and *S. icaeorhinus*. The pre- and postzygapophyses are located almost at the same dorsoventral level. Unlike the anterior dorsals, the prezygapophyses and the postzygapophyses are almost horizontal.

The posterior dorsal vertebrae are similar to the middle dorsals, but are generally more robust (Fig. 6A, C) due to the lower dorsoventral height of the centra. The neural arches are also dorsoventrally shorter and have proportionately larger pre- and postzygapophyses. The neural spines are subvertical and have well-developed medial laminae (Fig. 6B).

Sacral/Proximal Caudal Vertebrae—Two isolated centra were recovered from MNK-PAL5064-D and one isolated centrum was recovered from MNK-PAL5064-C. The sacral centra are markedly wider and lower than those of presacral vertebrae. This difference is especially marked in one of the centra of MNK-PAL5064-D and the centrum of MNK-PAL5064-C, because they are subquadrangular in ventral view. The articular surfaces of the centra are weakly concave, and their dorsal surfaces are pierced by two nutrient foramina. The remaining sacral centrum of MNK-PAL5064-D is dorsoventrally higher and has more concave articular surfaces. The ventral surface of this centrum bears two weak longitudinal ridges.

The lack of preserved neural arches in the sacral vertebrae precludes an accurate identification of these centra, because both sacral centra and proximal caudal centra are usually wide in some crocodylians (e.g., *A. tsangatsangana* and *A. gomesii*). Nonetheless, broad proximal caudal vertebrae are not present in all mesoeucrocodylians: the proximal caudals of

Mariliasuchus, *B. albertoi*, and extant crocodylians are longer than wide.

Caudal Vertebrae—An articulated series of at least six proximal caudals are identified in MNK-PAL5064-D (Fig. 7A–C). All the caudal centra are unfused and disarticulated from their neural arches. The first caudal centrum is wide, low, and bears two weak ridges on its ventral surface. The remaining caudal centra are elongated and have their lateral surfaces excavated (Fig. 7A). As in the proximal caudal vertebra, the rest of the caudals have two longitudinal ridges on their ventral surfaces, but in the more posterior centra, these ridges are much more strongly developed than in the proximal elements (Fig. 7C). These ridges expand posteriorly to form the processes for the articulation of the hemal arches.

The pedicles of caudal neural arches are dorsoventrally low, and the transverse processes are located ventral to the pre- and postzygapophyses (Fig. 7A). The prezygapophyses are anterodorsally projecting, with their articular surfaces dorsomedially oriented. The postzygapophyses have their articular surfaces exposed ventrolaterally. The neural spines are anteroposteriorly short and occupy only part of the dorsal surface of the neural arch (Fig. 7B). The neural spine of the first caudal vertebra is slightly different: it is anteroposteriorly expanded and tapers markedly at its distal end. The hemal arches are ‘Y’-shaped as in all crocodylians.

Ribs—Most ribs were preserved disarticulated from the vertebrae. Two cervical ribs were recovered: one isolated and the other in articulation with an anterior cervical centrum, both from MNK-PAL5064-B. These cervical ribs are anteroposteriorly elongated and have anterior and posterior processes for articulation with the preceding and succeeding vertebrae,

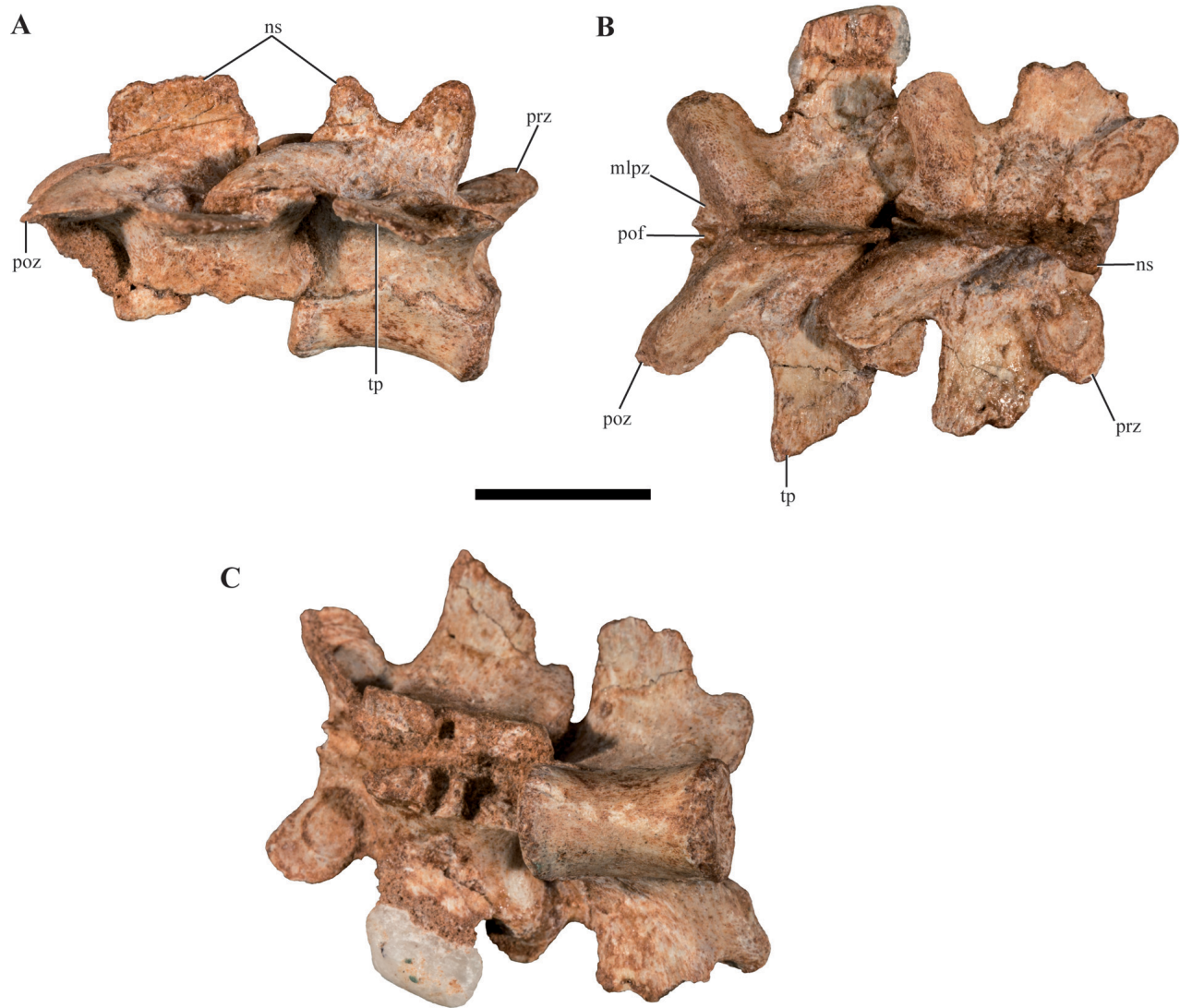


FIGURE 6. Posterior dorsal vertebrae of *Yacarerani boliviensis* (MNK-PAL5064-B) in **A**, lateral, **B**, dorsal, and **C**, ventral views. Scale bar equals 1 cm.

as in all crocodyliforms. The posterior process lacks the postero-dorsally projected spine that is present in *Mahajangasuchus*, *Araripesuchus* (e.g., *A. gomesii*, *A. tsangatsangana*, and *A. patagonicus*), and *Simosuchus*.

The postcervical ribs are preserved disarticulated from their centra. The articular processes of the more anterior ones are widely separated, and their distal ends are more robust in comparison with the more posterior ribs. Some ribs preserve laminar uncinate processes on their anterior margins.

Pectoral Girdle

The pectoral girdle is represented in three different individuals: MNK-PAL5064-A includes a right scapula and coracoid; MNK-PAL5064-C includes a left coracoid; and MNK-PAL5064-E includes a right scapula, the proximal end of the left scapula, and the left coracoid.

Scapula—Two right scapulae are completely preserved. The proximal end of the scapula is subrectangular in lateral view, with its anterior margin strongly expanded and forming a sub-quadrangular anterior expansion, which has a rounded anterior margin that forms an abrupt step with the acromial region of the scapula (Fig. 8A). This abrupt anterior expansion is also present in *Simosuchus* but contrasts with the poorly expanded anterior margins of the proximal ends of the scapulae of *A. gomesii*, *Anatosuchus*, *Notosuchus*, and *Mahajangasuchus*. The articular surface for the coracoid is triangular in proximal view and does not reach the anterior end of the proximal expansion of the scapula. No crest for the scapular head of the *M. triceps brachii* is present on the posterolateral surface of the proximal expansion of the scapula. The glenoid facet of the scapula is directed ventrally, forming a dorsal roof to the glenoid facet of the coracoid as in other basal mesoeucrocodylians (e.g., *Mahajangasuchus*, *Simosuchus*, *Notosuchus*, *Mariliasuchus*, *B. albertoi*, and

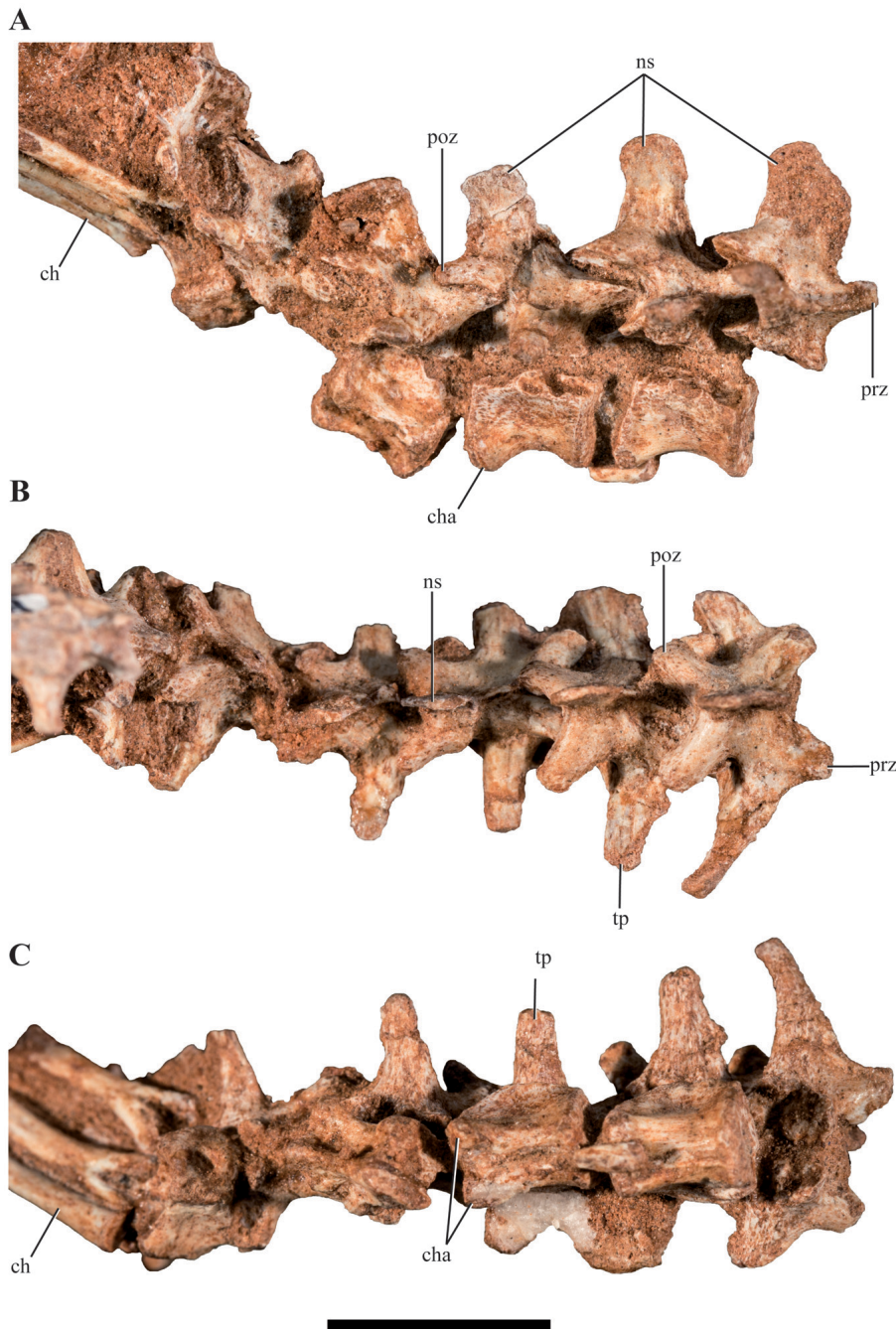


FIGURE 7. Anterior caudal vertebrae of *Yacararani boliviensis* (MNK-PAL5064-D) in **A**, lateral, **B**, dorsal, and **C**, ventral views. Scale bar equals 1 cm.

Stratiotosuchus). There is a slight, lateral bulge on the anterior margin of the glenoid facet on the scapula (Fig. 8A). On the region where this lateral bulge is present, there is a slight ventrally projected process, as in other notosuchians (e.g., *Mahajangasuchus*, *Simosuchus*, and *Notosuchus*) but contrasting with extant forms (e.g., *Caiman yacare*) and basal crocodyliforms (e.g., *Orthosuchus*) that lack this process.

The scapular blade is greatly expanded distally, having its minimum anteroposterior length just dorsal to the anterior expansion of the proximal end. *Yacararani* lacks a well-developed posterior flange for the attachment of the medial scapulosternal ligament (Fig. 8A), which is present in other notosuchians (e.g., *Mahajangasuchus*, *A. tsangatsangana*, *A. gomesii*, *Simosuchus*, *Mariliasuchus*, and *B. albertoi*). *Yacararani* also lacks proximodistally oriented crests on the lateral

surface of the scapula, as in *Notosuchus*, *Mariliasuchus*, *Stratiotosuchus*, and *B. albertoi*. In *A. tsangatsangana*, *A. gomesii*, *Mahajangasuchus*, and *Simosuchus*, there is a proximodistally oriented ridge on the posterior half of the scapular blade, separating the origin of the M. teres major and M. deltoideus scapularis (Turner, 2006; Sertich and Groenke, 2010). *Araripesuchus tsangatsangana* and *Simosuchus* also have an additional crest with the same orientation on the anterior half of the scapular blade (sr3 of Turner, 2006), interpreted as separating the origin of the M. deltoideus scapularis from the insertion of the M. trapezius (Sertich and Groenke, 2010). *Yacararani* bears a divided depression on the distal half of the scapular blade that does not reach the distal end of the blade. The anterior division of this depression corresponds topographically with the origin of the M. deltoideus scapularis, and the posterior one with the origin

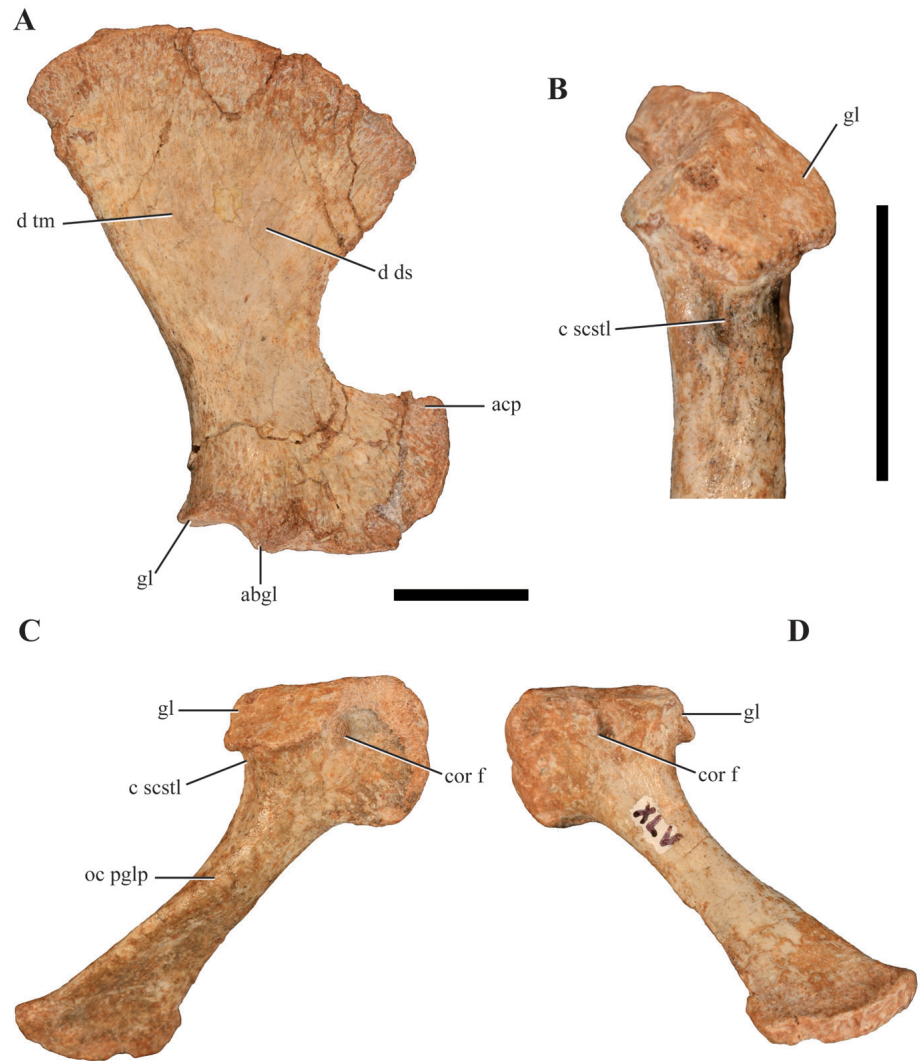


FIGURE 8. Pectoral girdle elements of *Yacarerani boliviensis* (MNK-PAL5064-A). Right scapula in **A**, lateral view. Right coracoid, detail of the proximal region in **B**, posterior, **C**, lateral, and **D**, ventral views. All scale bars equal 1 cm.

of the *M. teres major*. The distal end of the scapula is anteroposteriorly more than twice as long as the proximal end (Buckley and Brochu, 1999), as in most notosuchians (e.g., *Mahajangasuchus*, *Notosuchus*, *Simosuchus*, *Stratiotosuchus*, and *B. albertoi*). The distal end of the scapular blade has an asymmetrical profile in lateral view, with the anterior end more projected and proximally placed than the posterior end.

Coracoid—The right coracoid of MNK-PAL5064-A is the best preserved of these elements (Fig. 8B–D). The proximal end of the coracoid is subrectangular in lateral view, due to the presence of a subquadrangular anterior expansion, as in most crocodyliforms (Fig. 8C). The articular surface for the scapula is ‘L’-shaped in proximal view, contrasting with the subtriangular proximal surface of *S. icaeorhinus* and the subrectangular surface of *Protosuchus*, *Lomasuchus*, *Notosuchus*, and baurusuchids. In lateral view, the coracoid foramen opens proximal to the distal margin of the glenoid facet on the coracoid, whereas it opens more proximally and very near the articular surface in medial view (Fig. 8D). This condition is shared with other notosuchians (e.g., *Notosuchus*, *A. tsangatsangana*, *Stratiotosuchus*) and contrasts with the more distally placed coracoid foramen on the medial surface of *S. icaeorhinus* and extant forms. The glenoid facet of the coracoid is directed posterolaterally, but the lateral component is strongly developed, unlike most crocodyliforms. This facet is anteroposteriorly wide, occupying almost half of the

width of the proximal end of the coracoid in lateral view (Fig. 8C), as in *Notosuchus* (MACN-PV RN 1024b), *Marillasuchus*, *Stratiotosuchus*, and *B. albertoi*. Ventral to the glenoid and displaced medially, a slightly developed crest is present (Fig. 8B), which is interpreted as the coracoidal attachment of the medial scapulosternal ligament. Some notosuchians (e.g., *A. tsangatsangana*, *Simosuchus*, and *B. albertoi*) have a lateral groove associated with this crest, which further demarcates this structure. Unlike these taxa, *Yacarerani* has a crest ventral to the glenoid facet of the coracoid without having a pendent glenoid process.

The postglenoid (or ventral) process is elongated and distally expanded as in all crocodyliforms. The shaft of this process is elongated anteroposteriorly with respect to its lateromedial width, unlike the rod-like shaft of *S. icaeorhinus*. The proximal portion of the postglenoid process is divided from the distal one by a slight oblique crest (Fig. 8C), which is interpreted as separating the origin of the *M. coracobrachialis ventralis* from the more proximal origin of the *M. biceps brachii* and *M. supracoracoideus brevis*. This oblique crest is also present in *Protosuchus richardsoni*, but is absent in other mesoeucrocodylians except for *Chimaerasuchus*. As in *Notosuchus*, the distal end of the postglenoid process is rounded and does not bear acute anterior and posterior processes, differing from the condition of *A. tsangatsangana*, *Simosuchus*, *Stratiotosuchus*, *Baurusuchus*, and extant crocodylians. The distal end of the

coracoid of *Yacarerani* is strongly medially deflected and twisted 45° counterclockwise with respect to the proximal end.

Forelimb

As with the pectoral girdle, the forelimb elements are represented in multiple individuals (in this case at least three) and all elements are present in the recovered remains.

Humerus—Five humeri have been preserved, two right elements in MNK-PAL5064-A and 5064-B; a left humerus in MNK-PAL5064-C; and two left elements (a larger and a smaller one) in MNK-PAL5064-E. The humerus of *Yacarerani* is robust (Fig. 9A–D), having a robusticity index (Turner, 2006) above 0.1 (ranging between 0.11 and 0.12), resembling the ratio of other forms with robust humeri (e.g., extant crocodilians, 0.12–0.14; *Simosuchus*, 0.12; *Notosuchus*, 0.14). The proximal end is greatly

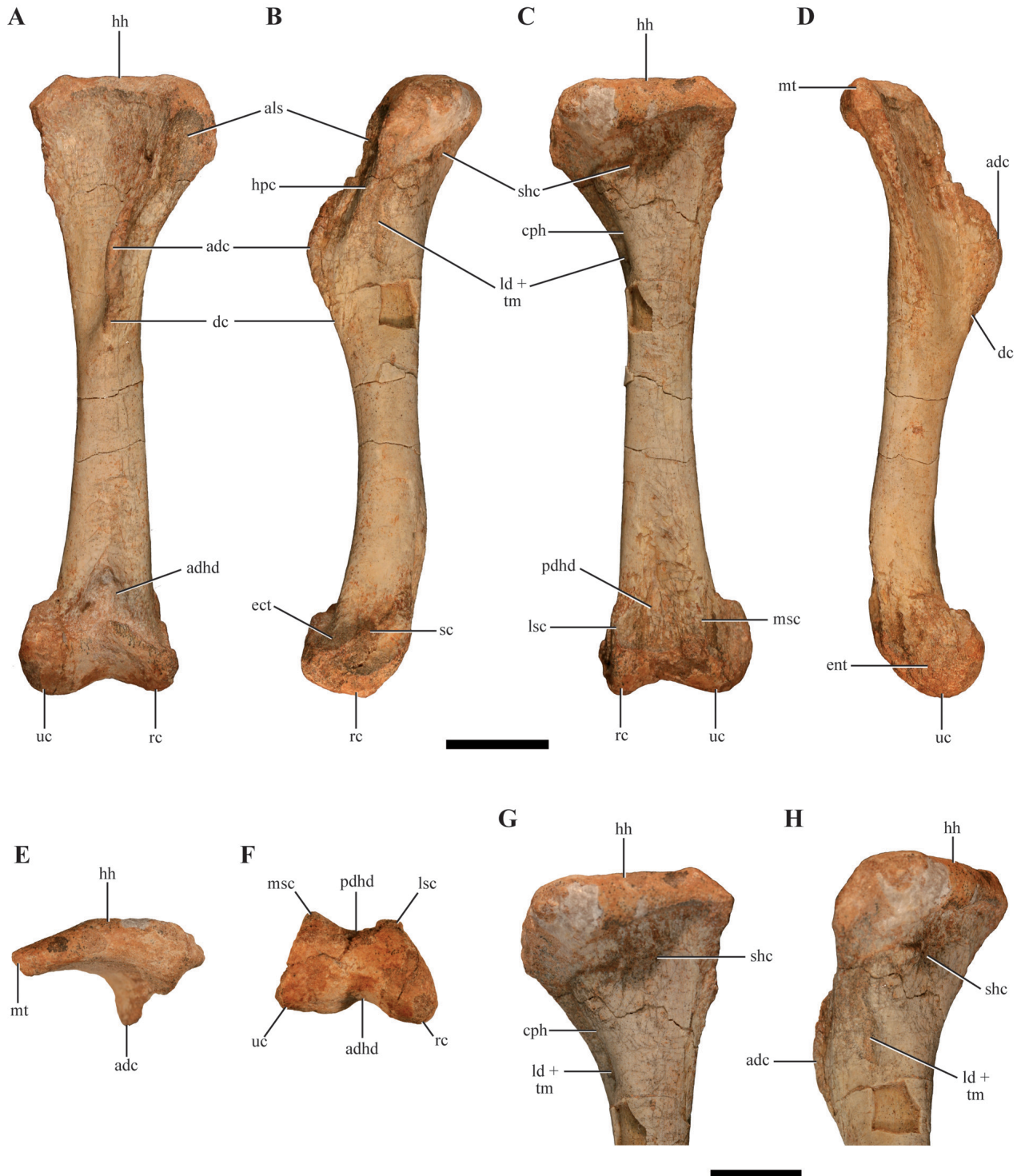


FIGURE 9. Left humerus of *Yacarerani boliviensis* (MNK-PAL5064-E) in **A**, anterior, **B**, lateral, **C**, posterior, **D**, medial, **E** proximal, and **F**, distal views. Detail of the proximal end of the humerus (MNK-PAL5064A) in **G**, posterior and **H**, posterolateral views. All scale bars equal 1 cm.

expanded, and its lateromedial development is greater than that of the distal end (Fig. 9A, C). The humeral head is mediolaterally broad and crescent-shaped in proximal view, having its maximum anteroposterior length at its central area (Fig. 9E). This central thickening corresponds to the presence of a dorsal lip of the articular surface at the posterior surface of the proximal end of the humerus. Ventral to the dorsal lip there is a subcircular depression (Fig. 9C, G–H) that is correlated with the insertion of the M. scapulohumeralis caudalis, as in most notosuchians (e.g., *A. tsangatsangana*, *A. gomesii*, *Mahajangasuchus*, *Simosuchus*, *Notosuchus*, *Mariliasuchus*, *Stratiosuchus*, *B. albertoi*, *Iberosuchus*, and *S. icaeorhinus*). The internal tuberosity is slightly projected medially and leaves a non-articular surface exposed proximomedially, as in most crocodyliforms except for *Chimaerasuchus*, *S. icaeorhinus*, *Iberosuchus*, and baurusuchids (e.g., *Stratiosuchus* and *B. albertoi*), which have the internal tuberosity exposed medially.

The deltopectoral crest is displaced medially and leaves an anterolaterally facing surface (Fig. 9A), as in most ziphosuchians. This surface has been correlated with an anterior displacement of several glenohumeral stabilizers (Pol et al., 2012). The deltopectoral crest reaches more than one-third of the total humeral length, but its apex is in a more proximal position. There is a proximodistally elongated tubercle for the insertion of the supracoracoideus complex on the apex of the deltopectoral crest, as in most crocodyliforms (Fig. 9A, B, D). This well-developed apex is directed slightly medially and gives the deltopectoral crest a triangular profile in lateral view. Such a profile is present in most crocodyliforms except for *Notosuchus*, *Simosuchus*, *S. icaeorhinus*, and baurusuchids (e.g., *Stratiosuchus* and *B. albertoi*), which lack this significantly developed apex. The distal end of the deltopectoral crest is medially displaced as in *A. tsangatsangana*, *Iberosuchus*, and sebecosuchians, but differs from the latter because it fails to reach the mediolateral midpoint of the humeral shaft (Fig. 9A). At the same level as the apex of the deltopectoral crest, but on the posterior surface of the humerus, a rounded depression is present (Fig. 9B, G, H). Some individual variation is present in this feature among the available humeri of *Yacarerani*: this depression is preserved as a deep pit on the right humerus of MNK-PAL5064-A and the large left humerus of MNK-PAL5064-E, whereas it is a shallower depression on the left humerus of MNK-PAL5064-B. It corresponds topographically with the common insertion of the M. latissimus dorsi and M. teres major. This scar is absent in *Notosuchus*, weakly developed in *Stratiosuchus*, *B. albertoi*, and *S. icaeorhinus*, and is clearly present in other mesoeucrocodylians (e.g., *A. tsangatsangana*, *A. gomesii*, *Mahajangasuchus*, *Mariliasuchus*, *Iberosuchus*, *Theriosuchus*, and *Caiman*) and basal crocodyliforms (e.g., *Protosuchus richardsoni*). In crocodylians and *Iberosuchus*, this deep depression is placed just distal to a crest that runs proximodistally on the posterior surface of the humerus. This crest is present in *Mahajangasuchus*, *A. gomesii*, *S. icaeorhinus*, *Simosuchus*, *Mariliasuchus*, *Yacarerani*, and *Theriosuchus*, but is placed lateral to the muscle scar.

The distal end has less lateromedial development than the proximal end (Fig. 9A, C). The distal condyles are slightly projected anteriorly (Fig. 9B), but they do not form a dorsal shelf as in *Sebecus* and *Iberosuchus* (Pol et al., 2012). On its anterior and posterior surfaces, the distal end of the humerus bears deep depressions located proximal to the distal condyles. The anterior triangular distal depression has some variation among the available humeri (from moderately depressed in MNK-PAL5064-B to very deep in MNK-PAL5064-A and 5064-E). This difference might be attributable to preservation of the different humeri because there are signs of crushing in this region in some elements. Deep depressions on the anterior and posterior surfaces of the distal end of the humerus are also present

in *Lomasuchus*, *A. gomesii*, *Simosuchus*, *Stratiosuchus*, and *S. icaeorhinus*, but in extant crocodylians, *Mariliasuchus*, and *Notosuchus*, the depressions are shallow. The anterior and posterior depressions of the distal end of the humerus are limited laterally and medially by well-developed supracondylar ridges. In *Yacarerani*, the lateral supracondylar ridge of the anterior surface and the medial supracondylar crest of the posterior surface of the distal end of the humerus are the most prominent of these crests. This condition is shared with *Uruguaysuchus* (Rusconi, 1933), *Araripesuchus*, *Notosuchus*, and *Simosuchus*. The lateral and medial distal surfaces are flat (Fig. 9B, D) as in other notosuchians (e.g., *Mahajangasuchus*, *A. tsangatsangana*, *A. gomesii*, *Simosuchus*, *Notosuchus*, *Mariliasuchus*, *S. icaeorhinus*, and baurusuchids). The ectepicondyle bears a weak oblique supinator crest (Fig. 9B) and the entepicondyle is concave (Fig. 9D), marking the origins of the M. pronator teres and the M. flexor digitorum longus. In distal view, the trochlea is deep and the radial and ulnar condyles have similar lateromedial development, but the ulnar condyle is more anteriorly projected and the radial condyle is more posteriorly projected (Fig. 9F).

Ulna—Two complete left ulnae are preserved (MNK-PAL5064-B and 5064-E) as well as the proximal half of another left ulna (MNK-PAL5064-E). The ulna is sigmoidal in lateral view with the distal end exposed posterodistally (Fig. 10A), as in most crocodyliforms. The proximal end of the ulna is triangular in proximal view (Fig. 10C), with the medial margin being weakly concave as in *Notosuchus* (MACN-PV RN 1024b) and *Simosuchus*. The medial margins of the proximal end of the ulna of *Stratiosuchus* and *S. icaeorhinus*, in contrast, bear a well-developed fossa. The proximal end of *Yacarerani* is poorly expanded lateromedially, unlike the condition present in most crocodyliforms (e.g., *Simosuchus*, *Caiman yacare*, *S. icaeorhinus*, *Mahajangasuchus*, and *Stratiosuchus*) that have broad proximal ends. The olecranon process is ossified in *Yacarerani*, as in *Simosuchus*, *Mariliasuchus*, and *S. icaeorhinus*, but is not separated from the articular surface for the ulnar condyle of the humerus. The anterior edge of the ulna bears two processes in proximal view, an anterior and an anterolateral process, as in other ziphosuchians (e.g., *Notosuchus*, *Simosuchus*, *S. icaeorhinus*, *Stratiosuchus*, and *B. albertoi*). These limit the radial articular surface on the ulna. The morphology of the ulnar articular processes for the radius contrasts with that of extant crocodylians and *Mahajangasuchus*, in which the anterolateral proximal process is displaced anteriorly, leaving the articular surface for the radius exposed mainly anteriorly. The anterolateral process projects distally as a short proximodistal crest that separates the lateral depression for the insertion of the M. flexor ulnaris and the origin of the M. extensor carpi radialis brevis from the ulnar origin of the M. pronator quadratus. The medial surface of the proximal end is slightly concave (Fig. 10B).

The ulnar shaft is anteroposteriorly elongated, with its anterior margin straight and posterior margin rounded. The distal end is curved medially and is slightly rotated, forming an angle of approximately 15° with the major axis of the proximal end. It is anteroposteriorly elongated and is anteroposteriorly shorter than the proximal end. In distal view, the ulna does not have strongly marked oblique processes (anterior and posterior) and anterolateral bulge, thus differing from those of *Mahajangasuchus*, *Simosuchus*, *Notosuchus*, and *S. icaeorhinus*. The distal condyle is arched laterally, with the posterior end of the distal surface more medially projecting than the anterior one (Fig. 10D).

Radius—A complete right radius (MNK-PAL5064-A) and the proximal half of a left radius (MNK-PAL5064-B) have been recovered (Fig. 10E–H). The complete radius is slightly damaged in comparison with other forelimb elements, being broken and displaced at the level of its midshaft. The radius is not as

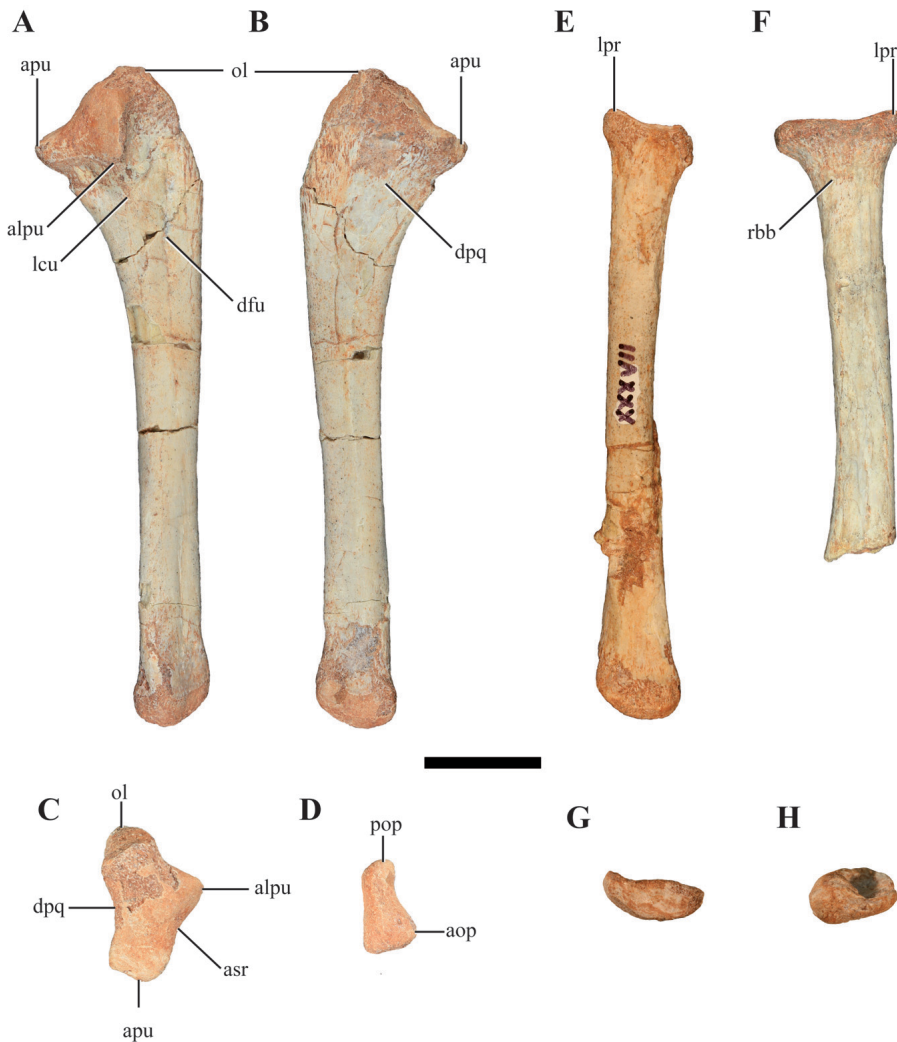


FIGURE 10. Anterior zeugopodium of *Yacarerani boliviensis*. Left ulna (MNK-PAL5064-E) in **A**, lateral, **B**, medial, **C**, proximal, and **D**, distal views. Right radius (MNK-PAL5064A) in **E**, anterior, **G**, proximal, and **H**, distal views. Left partial radius (MNK-PAL5064D) in **F**, posterior view. Scale bar equals 1 cm.

gracile as the radius of uruguaysuchids (e.g., *A. tsangatsangana*, *A. gomesii*), and the shaft is slightly curved laterally (Fig. 10E).

The proximal end is similar in its anteroposterior development to the distal end. The proximal end bears a lateral process that is more proximally projected than the medial edge (Fig. 10E). In proximal view, the articular surface for the radial condyle of the humerus is lateromedially compressed and crescent-shaped, being concave posteriorly and convex anteriorly (Fig. 10G) as in *Simosuchus*, *Notosuchus*, and *Stratiotosuchus*. This differs from the elliptical proximal end of the radius of extant crocodylians. The proximomedial region of the complete radius is damaged, and the presence of a humeroradialis tubercle cannot be determined. Slight rugosities that topographically correspond with the insertion of the *M. biceps brachii* are present in the proximal half of the left radius of MNK-PAL5064-E (Fig. 10F), and are similar to those of the radius of *A. tsangatsangana*, *Simosuchus*, and *Stratiotosuchus* (as well as extant crocodylians).

The radial shaft is elliptical in cross-section and lacks a longitudinal crest. The distal end is asymmetrical, projecting further medially and with its maximum anteroposterior length at its medial edge. The anterior surface of the radius is rounded in distal view (Fig. 10H), unlike that of most crocodylians (e.g., *Simosuchus*, *Notosuchus*, *Stratiotosuchus*, and *Caiman yacare*), which have straight anterior radial surfaces in distal view.

Radiale—The radiale is represented by four specimens, a left radiale articulated with the manus (MNK-PAL5064-B), an

isolated proximal half of a left radiale and complete right radiale from MNK-PAL5064-D, and a right radiale (MNK-PAL5064-E). The radiale is elongated as in all crocodylomorphs and is the largest element of the carpus, both wider and longer than the ulnare (Fig. 11A–F). The proximal end is wider than the distal end, mainly due to the development of a posterolateral process. The proximal surface is concave and crescent-shaped, with the convex margin oriented anteromedially (Fig. 11E). Along the posteromedial edge of the radiale, an elongated distally projecting process is present. The posteromedial process is separated from the proximal surface by a proximally projecting process, as in most basal mesoeucrocodylians (e.g., *A. tsangatsangana*, *Simosuchus*, *Notosuchus*, *Stratiotosuchus*, and *B. albertoi*). This proximal process is weakly developed in extant crocodylians and *S. icaeorhinus*. The posterolateral process extends along the proximal third of the radiale, but its distal end projects posteriorly (Fig. 11C). This allows recognition of two different articular surfaces on this process, a posterolateral surface for articulation with the ulna and an additional surface (posteriorly displaced) for the articulation with the medial process of the proximal end of the ulnare. This surface for the medial process of the ulnare is only present in ziphosuchians and uruguaysuchids. A distinct articular surface for the ulnare is also present in *Mahajangasuchus*, but the facet for the ulnare in *Yacarerani* is located on the ventral border of the posterior process for articulation with the ulna. Medial to the posterolateral process, the posterior surface

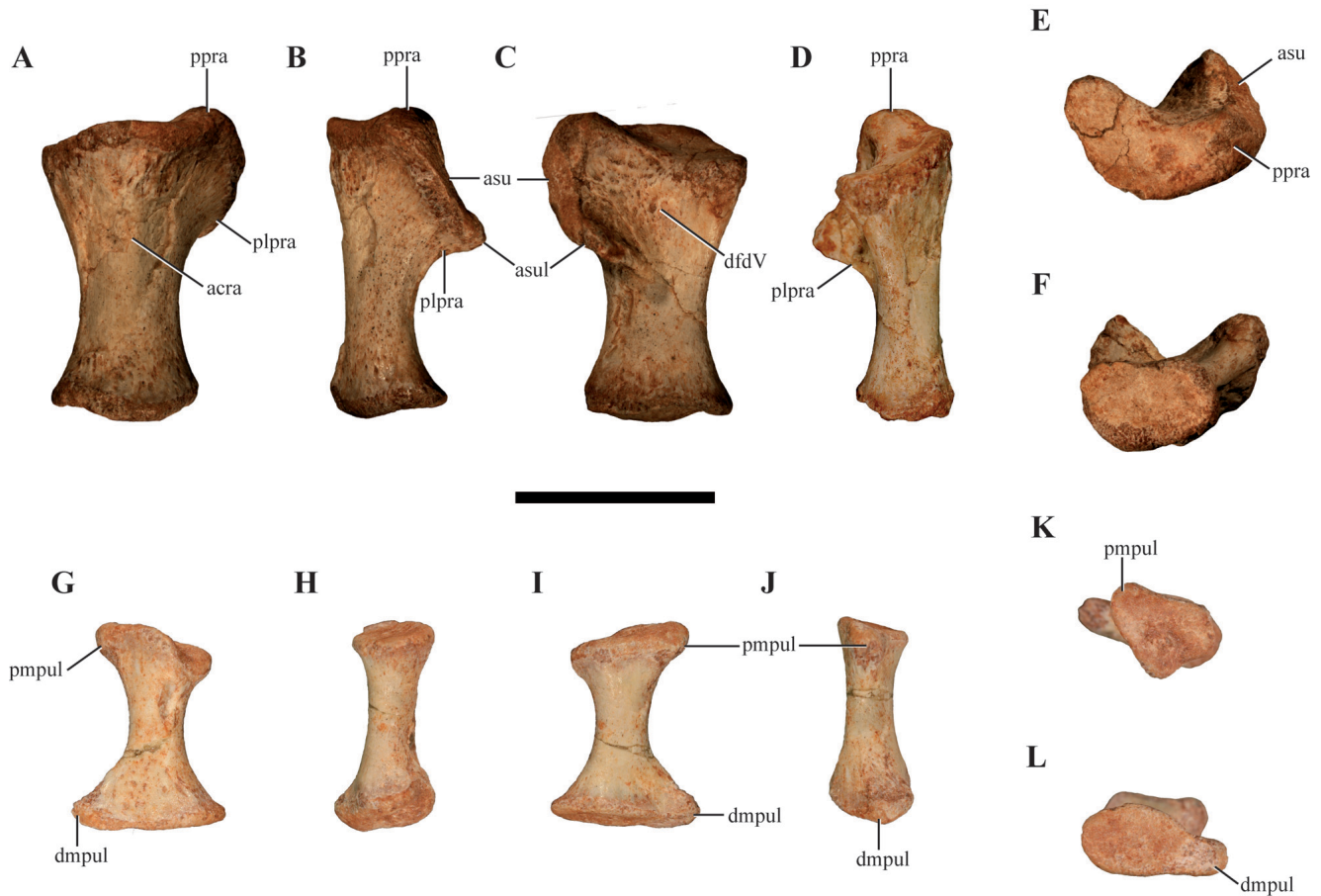


FIGURE 11. Proximal carpals of *Yacarerani boliviensis*. Right radiale (MNK-PAL5064-E) in **A**, anterior, **B**, medial, **C**, posterior, **D**, lateral, **E**, proximal, and **F**, distal views. Left ulnare (MNK-PAL5064-D) in **G**, anterior, **H**, lateral, **I**, posterior, **J**, medial, **K**, proximal, and **L**, distal views. Scale bar equals 1 cm.

of the radiale is concave and rugose, which corresponds topographically with the origin of the *M. flexor digiti quinti pars superficialis et profundus*.

The anterior surface of the radiale bears a longitudinal crest that attenuates along the proximal third of the shaft (Fig. 11A). This crest is interpreted as the origin of the *M. extensor digiti II superficialis* and *M. extensor pollicis superficialis et indicis proprius*. It is present in ziphosuchians (e.g., *Notosuchus*, *Sebecus*, *Stratiotosuchus*, *Simosuchus*) and is variably present on the left and right radiale of the holotype of *Mahajangasuchus*. The shaft of the radiale attains its minimum width at approximately half its length and expands distally. The distal end is subrectangular and concave in distal view (Fig. 11F) for the articulation with metacarpal I and a distal carpal.

Ulnare—Three ulnaria have been preserved in the referred material of *Yacarerani*: a left element articulated with the manus (MNK-PAL5064-B), an isolated left ulnare (MNK-PAL5064-D), and an isolated right ulnare (MNK-PAL5064-E). The ulnare is elongated, but proximodistally shorter than the radiale (Fig. 11G–L). The proximal end is lateromedially narrower than the distal end (Fig. 11G, I). The distal half is greatly expanded mediolaterally, being much wider than the proximal end as in all ziphosuchians and *Mahajangasuchus*. The articular surface for the ulna bears a median groove and is triangular in proximal view, with the medial apex more projecting than the others (Fig. 11K). The proximomedial margin forms a medial process that articulates with the posteromedial articular surface on the posterolateral process of the radiale (Figs. 11I, J, L;

12A–D). The distolateral edge of the ulnare has a facet for the articulation with the radiale. As in *Simosuchus* and *Mahajangasuchus*, but not more derived ziphosuchians (e.g., *Notosuchus*, *Stratiotosuchus*, and *B. albertoi*), the distomedial edge is not more distally projecting than the rest of the distal end of the ulnare (Fig. 11G).

Distal Carpal—As in *Simosuchus* (Sertich and Groenke, 2010) and *Baurusuchus pachecoi* (Nascimento and Zaher, 2010), a single distal carpal is preserved (Fig. 12A). The distal carpal of *Yacarerani* is ovoid in dorsal view and has straight proximal and rounded distal surfaces. The presence of two ossified distal carpals is a widespread condition among crocodyliforms: two distal carpals are present in Crocodylia, *Notosuchus*, *Chimaerasuchus* (Wu and Sues, 1996), *Stratiotosuchus* (Riff, 2007), and *Orthosuchus*. The homology of these carpals has been debated, but most authors have accepted that the medial element represents distal carpal 2+3 and the lateral element distal carpal 4+5 (Muller and Alberch, 1990; Buscalioni et al., 1997). However, unlike *Simosuchus* and *Baurusuchus*, the preserved element of *Yacarerani* likely contacted the radiale and ulnare proximally, and metacarpals I and II distally (Fig. 12). Based on its position with respect to the metacarpus, we interpret the distal carpal of *Simosuchus* and *Baurusuchus* as distal carpal 4+5, and the distal carpal preserved in *Yacarerani* as distal carpal 2+3.

Manus—The articulated manus of MNK-PAL5064-E preserves at least partial remains of all digits (Fig. 12A–F). Metacarpal (Mc) I is the stoutest in the manus, having a strongly expanded proximal end, as in most mesoeucrocodylians and

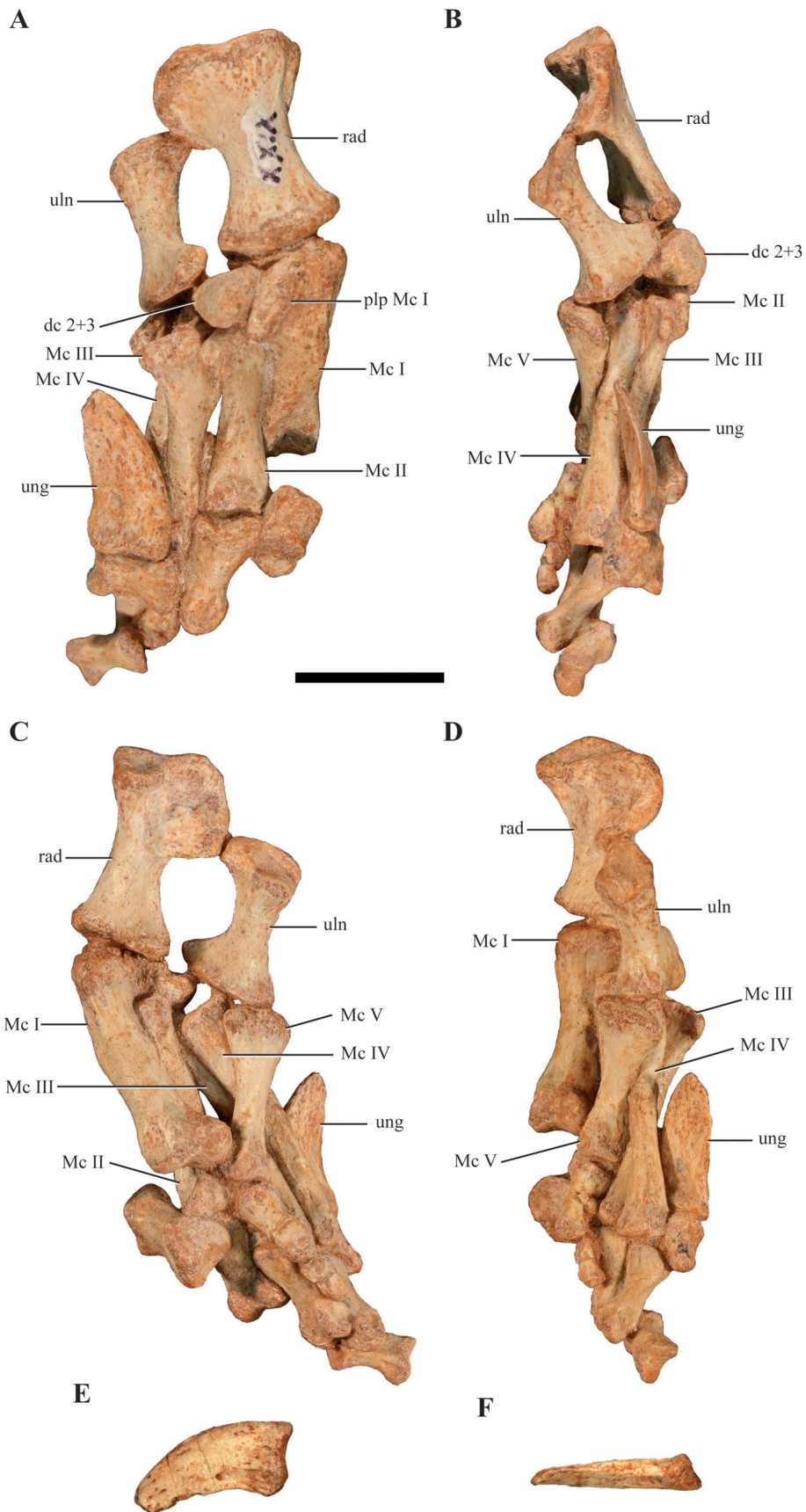


FIGURE 12. Right articulated manus of *Yacarerani boliviensis* (MNK-PAL5064-B) in **A**, anterior, **B**, lateral, **C**, posterior, and **D**, medial views. Isolated ungual phalanx of *Yacarerani boliviensis* (MNK-PAL5064-C) in **E**, lateral and **F**, ventral views. Scale bar equals 1 cm.

Orthosuchus. The proximal end of this metacarpal is strongly asymmetrical, with a lateral process exposed proximolaterally that articulates with the distal carpal and covers the medial proximal end of Mc II (Fig. 12A). A slight lateral process is also present in *Simosuchus*, but is not as strongly developed as in *Yacarerani*. This morphology has not been reported previously in any other crocodyliform and might represent an autapomorphy of *Yacarerani* (or a derived feature of sphagesaurids). The longest metacarpal is Mc III or IV, followed by Mc II, I, and V, in that order. Metacarpals II and III bear proximomedial processes that cover the adjacent metacarpal laterally. Although the manus of *Yacarerani* is slightly crushed and the degree of overlap could have been taphonomically exaggerated, each metacarpal bears a medially directed proximomedial process. These proximomedial processes are also present in other basal mesoeucrocodylians such as *A. tsangatsangana*, *Simosuchus*, *B. pachecoi*, *Stratiosuchus*, and extant crocodylians, but are not as medially projecting as in *Yacarerani*. The proximal ends of the metacarpals are rotated 40–45° relative to their distal ends.

All the manual phalanges of *Yacarerani* are more elongated proximodistally than lateromedially (Fig. 12A, C, D), as in most crocodyliforms but contrasting with the blocky manual phalanges of *Simosuchus*. The preserved phalangeal formula for each digit is 1-3-2-1-2, although phalanges from all digits with the exception of digit II are lacking when compared with the most widespread phalangeal formula among crocodylomorphs (2-3-4-4-3). The presence of more than four phalanges on digit IV remains as an autapomorphy of *Anatosuchus* (Sereno and Larsson, 2009), because the fourth digit has four phalanges in other known notosuchians (*A. wegneri* [Sereno and Larsson, 2008]; *B. albertoi*) or the total number of phalanges is unknown due to lack of preservation in known specimens (e.g., *Simosuchus*, *Yacarerani*, *Stratiosuchus*). The proximal ends of the phalanges bear weak extensor processes and their proximal surfaces have a weakly developed proximal crest, dividing the articular surface for the articulation with the metacarpals or the distal surface of more proximal phalanges. The distal surfaces bear two distal condyles with a well-developed intercondylar groove, a feature especially marked in the more distal phalanges. The only preserved ungual phalanx is that of the first digit. This phalanx is strongly compressed mediolaterally, but is not significantly curved and does not bear well-developed flexor tubercles (Fig. 12 E, F). Strong mediolateral compression of the ungual phalanx has not been reported in any other crocodyliform and might represent an autapomorphy of *Yacarerani* (or a derived feature of a group within sphagesaurids).

Pelvic Girdle

The pelvic girdle is partially known, because no remains of the ilium were recovered and some of the other elements are incomplete.

Pubis—The pubis is represented by three elements from two different individuals: a complete left pubis from MNK-PAL5064-C and an almost complete left pubis and the distal blade of a right element from MNK-PAL5064-D. The pubis has, as in most crocodylomorphs, a pubic shaft that expands distally, forming a subtriangular blade in lateral view (Fig. 13A, B). The articular surface for the ischium is compressed lateromedially, being anteroposteriorly longer than lateromedially wide. The proximodorsal end of the shaft has a short rugose crest that corresponds topographically with the origin of the *M. ambiens* (Fig. 13A). The shaft is moderately developed as in most mesoeucrocodylians, and similar in length to the total length of the distal blade. This condition contrasts with the morphology of *Protosuchus richardsoni* (AMNH FARB 3024), where the pubis has a very long shaft with a poorly expanded distal blade that is less proximodistally developed than the pubic shaft. *Stratiosuchus* has a similar condition, but unlike *Protosuchus*, the distal end of the pubis is slightly more dorsoventrally expanded than the shaft. Additionally, as in other basal mesoeucrocodylians (e.g., *A. tsangatsangana*, *Simosuchus*, and *Mahajangasuchus*), the pubic blade is not significantly rotated with respect to the proximal end of the pubic shaft, such that the internal surface of the blade faces dorsomedially rather than dorsally as in extant crocodylians. The medial surface of the pubis is concave and, as in extant forms, is the origin of the *M. puboischiofemoralis internus* 1. The lateral surface of the distal end of the pubis does not bear any particular scar, but is inferred to be the origin of the *M. puboischiofemoralis internus* 2.

Ischium—This element is known from three incomplete elements: a left ischium with the anterodistal margin damaged (MNK-PAL5064-C), a right element with the distal part missing (MNK-PAL5064-D), and a right ischium lacking its distal end (MNK-PAL5064-E). The proximal end of the ischium has well-developed anterior and posterior processes separated by a notch that forms the posteroventral margin of the acetabulum (Fig. 13C, D). Thus, the acetabulum of *Yacarerani* is perforated at least on its posteroventral region, as in *Protosuchus*, other basal mesoeucrocodylians (e.g., *Mahajangasuchus*, *Sebecus*, and *Chimaerasuchus*), and extant crocodylians (*Caiman latirostris*).

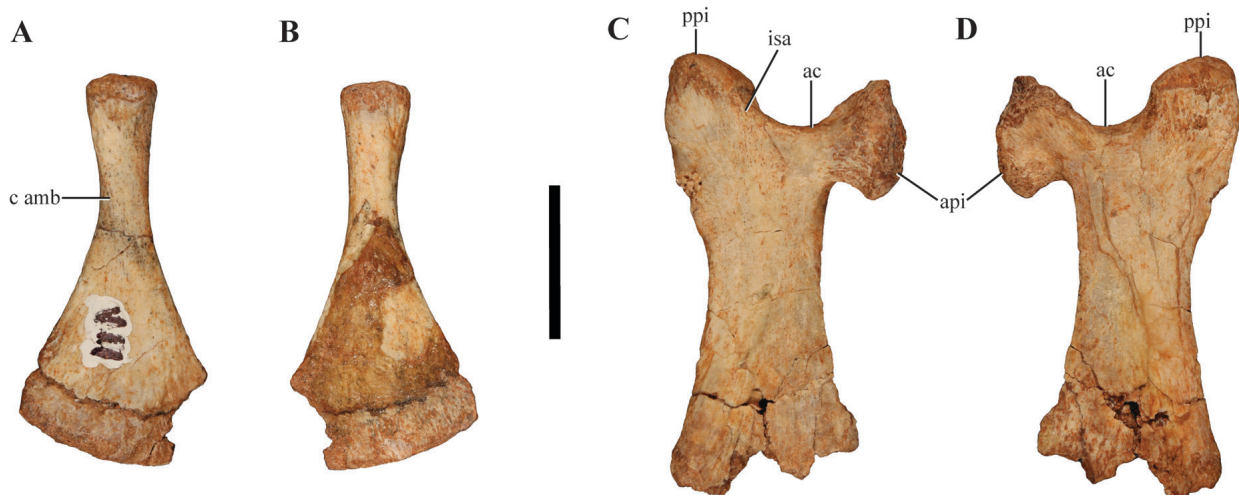


FIGURE 13. Pelvic girdle elements of *Yacarerani boliviensis*. Left pubis (MNK-PAL5064-B) in **A**, lateral and **B**, medial views. Right ischium (MNK-PAL5064-E) in **C**, lateral and **D**, medial views. Scale bar equals 1 cm.

The posterior process is dorsally directed and bears a triangular, anterolaterally exposed ischial antitrochanter. As in other basal mesoeucrocodylians (e.g., *Mahajangasuchus*, *A. gomesii*, and *Chimaerasuchus*), the ischial antitrochanter is restricted to the dorsal region of the posterior process of the ilium and its lateral exposure is also restricted, contrasting with the widely exposed antitrochanter that extends along the entire dorsal surface in extant crocodylians. The articular facet for the pubis is elongated and located on the dorsal surface of the posterior process. The anterior proximal process of the ischium is anteriorly expanded in lateral view, as in *Mahajangasuchus*, *Araripesuchus*, and *Caiman latirostris* but contrasting with the long, acute anterior process of basal crocodylians (e.g., *Protosuchus* AMNH FARB 3024, *Orthosuchus* SAM-PK-409). In proximal view, the anterior process has two distinct articular surfaces: a proximodistally elongated ventral articular surface for the pubis and a triangular lateromedially elongated surface for the ilium. Thus, the ischium excludes the pubis from articulation with the ilium as in all mesoeucrocodylians.

The ischial blade is distally incomplete. The proximal region of the blade is markedly wide and bears a very slight oblique crest that runs posterodistally. This crest encloses a triangular depression on the anteroventral part of the ischium, the inferred surface of origin of the M. puboischiofemoralis internus 3 and M. adductor 1. Posterodorsal to this surface, separated by the oblique crest, the M. adductor 2 originates from the posterior edge of the pubis. The medial surface of the ischium bears a deep triangular depression with its apex oriented distally, which corresponds topographically with the origin of the M. ischiotrochantericus.

Hind Limb

The hind limb of *Yacarerani boliviensis* is represented by a complete left femur and the distal end of a right femur from MNK-PAL5064-B. The zeugopodium is known from two complete zeugopodia from MNK-PAL5064-B, and from multiple additional elements that are either partial or complete (see Referred Specimens). The tarsus is represented by three right astragali (one from MNK-PAL5064-C and two from MNK-PAL5064-D), as well as a right (MNK-PAL5064-D) and a left (MNK-PAL5064-C) calcaneum. Finally, the rest of the pes is known from metatarsals, some of which have been preserved in articulation (MNK-PAL5064-D). The elements from MNK-PAL5064-B are the best preserved and most complete.

Femur—The femur has a slight sigmoid profile in lateral and medial views (Fig. 14B, D). The curvature of the femur is weak, as in *S. icaeorhinus* and extant crocodylians, mainly due to its almost straight anteromedial margin. The proximal end of the femur lacks a distinctive neck and is wide and flat to slightly concave in anterior and posterior views. The femoral head is elongated in proximal view, and its major axis is oriented anteromedially, forming an angle of approximately 45° with respect to the transverse axis of the distal end (Fig. 14E). The femoral head has its maximum width at its anteromedial margin and narrows posterolaterally. The posterolateral surface of the proximal end is narrow and flat and is identified here as the greater trochanter, the main insertion site of the M. puboischiofemoralis externus. The greater trochanter is limited laterally and medially by two well-developed crests that extend along the proximal fourth of the femoral length, reaching distally to the level of the fourth trochanter (Fig. 14A, C). The medial crest that bounds the greater trochanter is more distally projected, as in most basal mesoeucrocodylians and extant crocodylians except for *S. icaeorhinus* (Pol et al., 2012). A distally extensive greater trochanter that reaches the level of the fourth trochanter is also present in most crocodylians (e.g., *P. richardsoni*, *A. gomesii*, *A. tsangatsangana*, *Simosuchus*, *Notosuchus*, *Mariliasuchus*, and *Stratiosuchus*), with the exception of *S. icaeorhinus*,

Mahajangasuchus, and *Iberosuchus*. Just anterior to the lateral crest of the greater trochanter, the lateral surface of the femur has an ovoid depression bounded posteriorly by muscle scars. This depression is interpreted as the insertion for the posterior head of the puboischiofemoralis internus 2 (Fig. 14C). Proximal to this ovoid depression, a smaller and shallower subcircular one is present on the posterior edge of the proximal surface of the femur, which corresponds topographically with the insertion of the M. ischiotrochantericus. On the anterior edge of the femoral head, a distinct proximal condylar fold (Brochu, 1992) is present. This fold originates at the anteromedial edge of the femoral head and crosses the anterior edge of the proximal end to reach the anterior margin of the lateral surface of the femur, as in extant crocodylians.

The fourth trochanter is reduced to a low bump on the medial surface of the femur (Fig. 14D), extending distally up to approximately 30% of the total length of the femur (from the proximal end). This low fourth trochanter lacks a strongly marked proximodistal crest separating the insertion of the M. caudofemoralis brevis anterior from the posterior insertion of the M. caudofemoralis longus. The absence of such crest has also been noted in *S. icaeorhinus*, but contrasts with its presence in other notosuchians (e.g., *A. tsangatsangana*, *Simosuchus*, *Mariliasuchus*, *B. albertoi*, *Stratiosuchus*, and *Mahajangasuchus*) and extant crocodylians. *Yacarerani* lacks the development of an anterior flange to the fourth trochanter, which has been inferred as serving for the insertion of the first head of the puboischiofemoralis internus (Turner, 2006). This flange is also absent in *S. icaeorhinus* and extant forms, but is present in most other notosuchians (e.g., *A. tsangatsangana*, *Simosuchus*, *Notosuchus*, *Uruguaysuchus*, *Baurusuchus*, and *Stratiosuchus*).

The shaft is elliptical in cross-section and lacks identifiable muscle scars except for a faintly developed linea intermuscularis caudalis (Hutchinson, 2001a). The distal end of the femur is similar in width to the proximal end (Fig. 14F). The fibular condyle is more distally projecting than the tibial condyle, and as in most notosuchians these condyles form an angle of 120°. This condition contrasts with that of extant crocodylians, where the fibular condyle is less distally projecting. In posterior view, the distal condyles have well-developed supracondylar ridges that limit a deep and elongated popliteal fossa. The anterior surface is damaged in the complete femur, but on the distal end of MNK-PAL5064-A a strong medial supracondylar crest is present. This crest together with the medial supracondylar crest of the posterior surface of the distal end defines an almost flat medial surface of the distal end. The distal condyles are subequal in distal view (Fig. 14F), with a well-defined trochlea, unlike *S. icaeorhinus* and *B. albertoi*, in which the fibular condyle is more posteriorly projecting than the tibial condyle. The fibular condyle bears a lateral facet for the contact with the fibula, as in most crocodylians.

Tibia—The best-preserved tibiae are the left elements of MNK-PAL5064A. The tibia of *Yacarerani* is a relatively slender element that is arched posteriorly (Fig. 15A–E), as in most basal mesoeucrocodylians (but to a lesser extent than in *A. tsangatsangana*).

The proximal end of the tibia is roughly rhomboidal in proximal view (Fig. 15D). This particular shape is due to the presence of three processes that can be seen in this view: the anterolateral, posteromedial, and posterolateral processes. The anterolateral and posterolateral processes are separated by a laterally facing surface on the lateral aspect of the tibia. The anterior part of this surface serves for the proximal articulation with the fibula. Just posterior to this surface there is a shallow pit (Fig. 15B), which in *Sebecus* and extant crocodylians is a groove. In crocodylians, *A. tsangatsangana*, and *Simosuchus*, this groove reaches the proximal surface, forming a notch in proximal view, but this notch is absent or poorly developed in *Mahajangasuchus*,

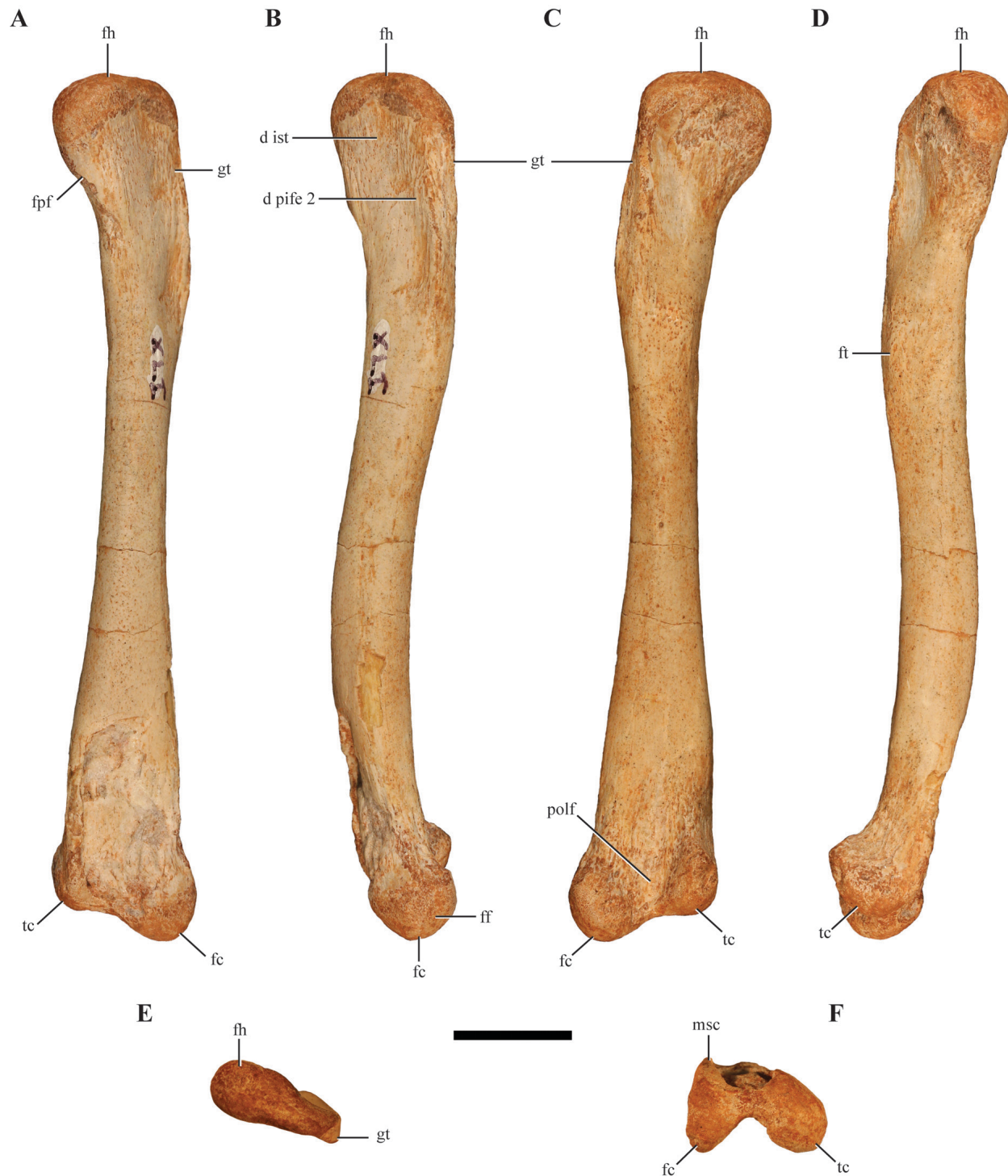


FIGURE 14. Left femur of *Yacarerani boliviensis* (MNK-PAL5064-B) in **A**, anterior, **B**, lateral, **C**, posterior, **D**, medial, **E**, proximal, **F**, distal views. Scale bar equals 1 cm.

Yacarerani, and *S. icaeorhinus*. The proximal surface is subdivided by an oblique groove that delineates two oblique antero-medially oriented facets for articulation of the distal condyles of the femur. The proximal region has very well developed muscle scars (Fig. 15A–B). The anteromedial edge of the proximal tibia has well-developed striations, interpreted as the insertion of the Mm. ambiens, iliotibialis 1–3, and femorotibialis. The fossa flexoria on the proximal end of the tibia, the site of insertion of the M.

femorotibialis externus, is exposed posteriorly as in modern crocodylians, *Mahajangasuchus*, and *S. icaeorhinus* (Fig. 15D). Medial to the fossa flexoria there are rugosities that can be associated with the insertions of the Mm. femorotibialis internus and the puboischiotibialis.

The shaft is slightly arched laterally as in most basal mesoeucrocodylians, contrasting with *Simosuchus*, basal crocodyli-forms (e.g., *Protosuchus* and *Orthosuchus*), and extant

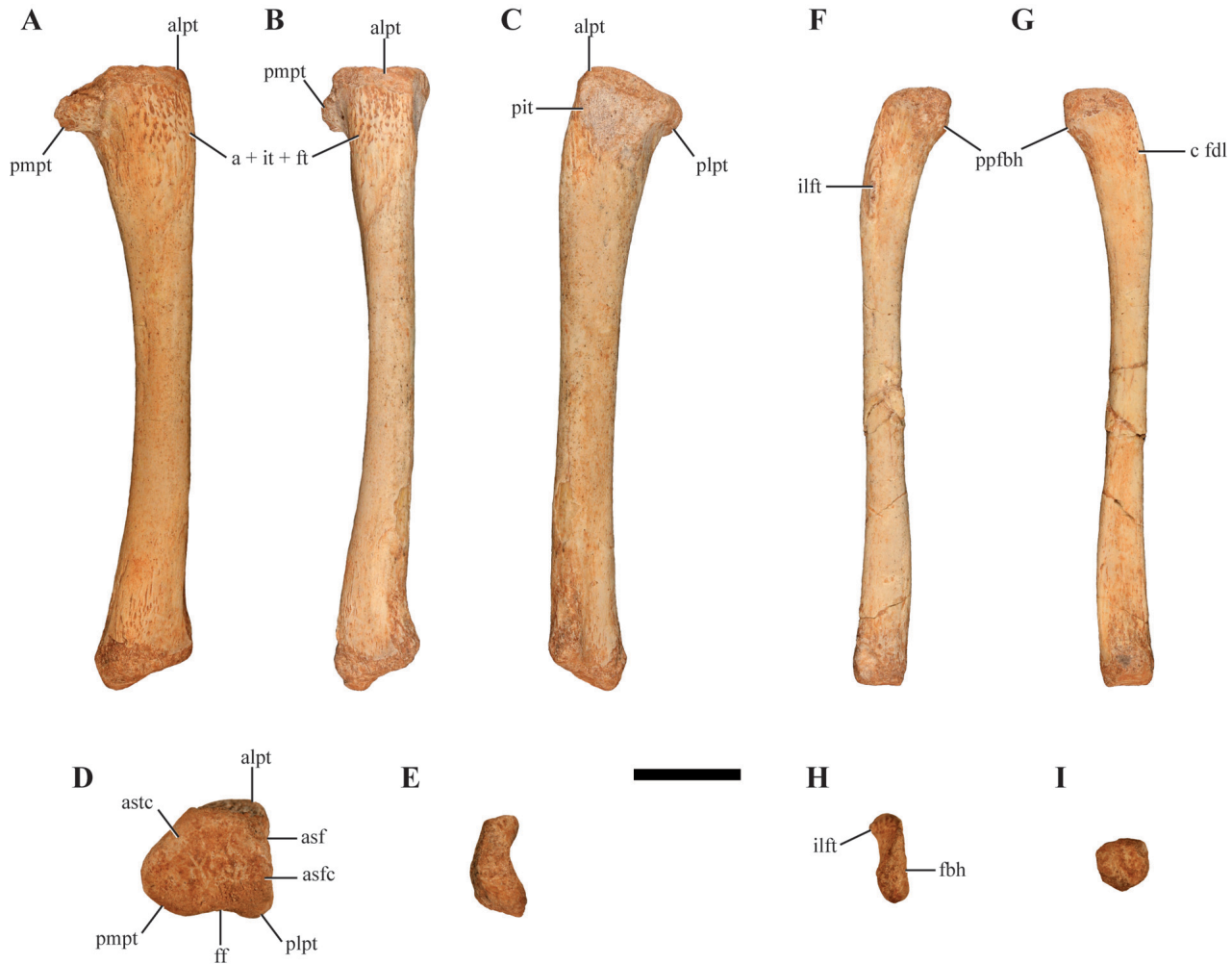


FIGURE 15. Posterior zeugopodium of *Yacarerani boliviensis* (MNK-PAL5064-B). Right tibia in **A**, lateral, **B**, anterior, **C**, posterior, **D**, proximal, and **E**, distal views. Left fibula in **F**, lateral, **G**, medial, **H**, proximal, and **I**, distal views. Scale bar equals 1 cm.

crocodilians, which have a rather straight tibial shaft. The distal end of the tibia is almost aligned with the proximal end (Fig. 15A–C), as in other basal mesoeucrocodylians (e.g., *Mahajangasuchus*, *A. tsangatsangana*, *Simosuchus*, *Stratiotosuchus*, and *S. icaeorhinus*) but contrasting with the higher degree of rotation present in crocodylians. In the latter group, the major axis of the distal end of the tibia is oriented anteroposteriorly, whereas in basal mesoeucrocodylians it is obliquely oriented. The distal condyle is arched anteromedially, attaining its major width medially (Fig. 15E).

Fibula—The fibula is a long, slender bone that is slightly shorter than the tibia (Fig. 15F, G). The proximal end is medio-laterally wider than the distal end and bears a posteriorly projecting fibular head (Fig. 15F–H). The posterior projection is weak, contrasting with the condition in *A. tsangatsangana*, in which it is almost equal to the anteroposterior development of the distal end of the fibula. The fibular head is strongly bent with respect to the anterior surface of the fibula, but lacks the anteroproximally exposed area on its proximal surface (described for *Araripesuchus*; strongly bent proximal head in Turner [2006], and also noted in *Uruguaysuchus* by Rusconi [1933]). On the anterolateral edge of the proximal end of the fibula, there is a strong crest associated with rugosities on the anterior surface (Fig. 15F). This crest is for the insertion of the *M. iliofibularis* and, as in other basal mesoeucrocodylians (e.g., *A. tsangatsangana*,

Mahajangasuchus, *B. albertoi*, and *Stratiotosuchus*), is located at approximately 15% of the total fibular length. In modern crocodylians, this crest is placed at 25% of total fibular length. On the medial surface of the proximal end, the fibula has a subtle anterior oblique crest with rugosities, which originates on the anterior surface and turns medially towards the fibular shaft (Fig. 15G). This crest corresponds topographically with the origin of the *M. flexor digitorum longus*. The lateral surface of the fibula has rugosities posterior to the iliofibularis trochanter that correspond to the insertion of a long lateral ligament (Brochu, 1992; Turner, 2006).

The shaft is smooth except for a subtle crest that runs proximodistally along the anterolateral margin of the fibula. This crest is a continuation of the iliofibularis trochanter and limits the origin of the *Mm. fibularis brevis* and *longus* anteriorly (Hutchinson, 2002). It is better developed distally and encloses a flat surface together with a posterior crest. This flat surface marks the origin of the *M. extensor hallucis longus* and the site of insertion of the stabilizer ligaments of the ankle (Schaeffer, 1941; Brinkman, 1980; Riff, 2008). The distal end of the fibula is rounded and, as in most notosuchians (e.g., *A. tsangatsangana*, *A. gomesii*, *Mahajangasuchus*, and *Stratiotosuchus*), lacks the distal medial hook present in extant crocodylians (Fig. 15I).

Astragalus—All the preserved astragali are from the right side. The astragalus of *Yacarerani* is proximodistally low and

wide in anterior view (Fig. 16A), as in *Simosuchus*, probably due to its low proximolateral process and laterally expanded medial distal roller.

In proximal view, the tibial facet on the astragalus is divided in two regions, as in most crocodyliforms (Fig. 16B, E). The facet for the lateral condyle of the tibia is located on the proximal surface of the proximolateral process. This surface is trapezoidal in proximal view, attaining its major anteroposterior development on the lateral margin and gradually narrowing medially. The anterior margin of this surface is gently curved because of the lack of a well-developed anterolateral notch on the proximal surface of the astragalus. This notch is only present in *S. icaeorhinus*, *Lomasuchus*, and *Stratiotosuchus* (Pol et al., 2012). The articular surface for the medial condyle of the tibia is crescent-shaped, with the convex side oriented medially. This surface is separated from the articular surface for the lateral condyle of the tibia by a change in the slope of the articular surface, as in *S. icaeorhinus*. In *Simosuchus* and extant crocodylians, the change in slope is not as strong as in *Yacarerani* or *S. icaeorhinus*. The posterolateral margin of the medial articular surface for the tibia is abrupt, as in *Simosuchus*, *Lomasuchus*, and extant crocodylians, and encloses a deep posteromedial pit (the astragal fossa

sensu Sertich and Groenke, 2010). This condition contrasts with that of *S. icaeorhinus*, where the posterolateral margin is not abrupt, and as a result only a very shallow depression is present (proximal astragal depression; Pol et al., 2012).

In *Yacarerani*, the anterior hollow is wide and deep, occupying the proximolateral region of the anterior surface of the astragalus (Fig. 16A). The anterior hollow is bounded by three crests: proximomedial, lateral, and distal. This condition is shared with *Simosuchus* and extant crocodylians. In contrast, the anterior hollow of *Lomasuchus* lacks a distal crest, whereas *S. icaeorhinus* and *Stratiotosuchus* lack both the distal and the lateral crests. Between the astragal peg and the distal roller a deep rugose pit is present on the anterior hollow, interpreted as the astragal-tarsale ligament pit. This is a well-delimited pit anteriorly in *Yacarerani* and in all known notosuchians (e.g., *A. gomesii*, *Lomasuchus*, *Simosuchus*, *S. icaeorhinus*, and *Stratiotosuchus*), but in extant crocodylians its presence is variable (absent in *C. yacare* and present in *C. latirostris*). The astragal-tarsal ligament pit is limited dorsally by a strong crest, which separates this pit from the dorsal region of the anterior hollow. This crest is also present in other basal notosuchians (e.g., *A. gomesii*, *Lomasuchus*, and

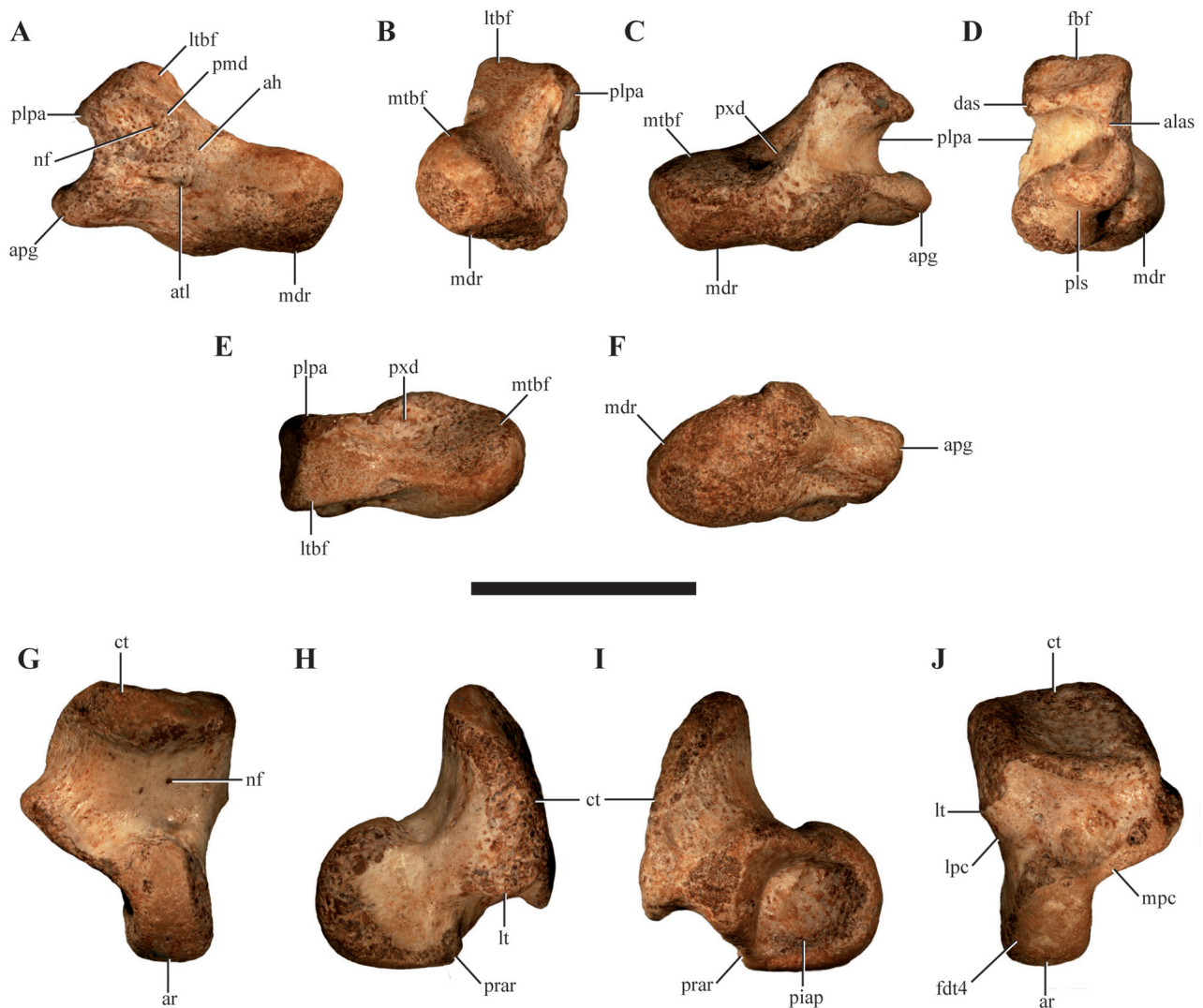


FIGURE 16. Proximal tarsals of *Yacarerani boliviensis* (MNK-PAL5064-C). Astragalus in **A**, anterior, **B**, medial, **C**, posterior, **D**, lateral, **E**, proximal, and **F**, distal views. Calcaneum in **G**, dorsal, **H**, lateral, **I**, medial, and **J**, plantar views. Scale bar equals 1 cm.

Simosuchus), but is absent in sebecosuchians (e.g., *S. icaeorhinus*, *B. albertoi*, and *Stratitosuchus*), basal crocodylians (e.g., *P. richardsoni* and *Orthosuchus*), and extant crocodylians (which have a distinct astragalar-tarsal ligament pit; e.g., *Caiman latirostris*). The dorsal region of the anterior hollow of *Yacarerani* bears a small nutrient foramen (better preserved in MNK-PAL5064-D), which is also present in *A. gomesii* and, as a larger structure, in *Simosuchus*. This nutrient foramen on the dorsal region of the anterior hollow is absent in other basal mesoeucrocodylians. *Yacarerani* does not bear a notch on the distolateral margin of the anterior hollow separating the distal articular surface for the third distal tarsal and the planar calcaneal facet. *Stratitosuchus* and extant crocodylians also lack this notch, whereas *A. gomesii*, *Lomasuchus*, *S. icaeorhinus*, and *B. albertoi* have it.

The proximolateral process is directed proximolaterally (Fig. 16A–E). The articular surface for the fibula on the astragalus is trapezoidal in lateral view, having its maximum width posteriorly and narrowing anteriorly (Fig. 16E). The fibular facet is symmetric as in most mesoeucrocodylians, whereas *S. icaeorhinus* has an asymmetric fibular facet with the posterodistal end projecting further distally.

The posterior surface of the astragalus is subdivided by a strong median crest that is oriented proximodistally (Fig. 16C). This crest starts as a short lateral distal ridge and connects with the posteromedial edge of the proximolateral process of the astragalus, as in other notosuchians (e.g., *A. gomesii*, *Simosuchus*, *B. albertoi*, and *Stratitosuchus*) except for *S. icaeorhinus* and crocodylians. In *Yacarerani*, the distal edge of the posterior surface bears two short ridges, lateral and medial. These ridges are weakly developed in *Yacarerani* and fail to form a strong posterodistal groove, which is visible in distal view in other basal mesoeucrocodylians (e.g., *Simosuchus*, *Stratitosuchus*, and *S. icaeorhinus*) and extant crocodylians.

The astragalus has three surfaces for articulation with the calcaneum: a dorsal one located on the proximolateral process, an anterolateral one located on the anterior surface of the astragalar peg, and a planar surface located on the distal surface of the astragalar peg (Fig. 16D). The dorsal surface is weakly developed in *Yacarerani* and other basal mesoeucrocodylians (e.g., *Simosuchus*, *B. albertoi*, *S. icaeorhinus*, and *Lomasuchus*), being represented by a proximal facet on the proximodorsal process that continues distally as a thin crest. This condition contrasts with the broad laterodistal facet on the proximolateral process in extant crocodylians. The distal roller is less spherical than in other crocodylians and articulates with metatarsals I and II (Fig. 16F).

Calcaneum—Two calcanea were recovered: a right element from MNK-PAL5064C and a left element from MNK-PAL5064B. The calcaneum of *Yacarerani* is typical of most crocodylians, presenting a rounded, lateromedially compressed anterior roller and a well-developed posterolaterally projecting calcaneal tuber (Fig. 16G–J). The anteroposterior length of these structures is similar in dorsal view to that of most crocodylians (Fig. 15G), unlike the robust calcaneum of *Simosuchus* (in which the anterior roller is anteroposteriorly longer in proximal view than the calcaneal tuber). In *Yacarerani*, the tuber expands distally and has its minimum lateromedial width at its mid-length. The dorsal surface is concave and has a small nutrient foramen at its mid-length. This condition is shared with *A. gomesii* and *Simosuchus*, but is absent in other mesoeucrocodylians (e.g., *Mahajangasuchus*, *Stratitosuchus*, *B. albertoi*, and *Caiman yacare*).

The anterior roller is semicircular in lateral view, with an anterodorsally rounded edge and a flat plantar margin (Fig. 15H) for the articulation with the distal tarsal 4. In plantar view, the posterior edge of this facet ends in a right angle, as in other basal mesoeucrocodylians (Fig. 16J), contrasting with the oblique

posterior margin of the facet for the distal tarsal 4 of crocodylians (Pol et al., 2012). The posterior margin of the distal surface of the anterior roller has a distinct posterior rim, creating a posteriorly exposed surface. The posteroventral margin of the lateral surface of the tuber has a well-defined tubercle. This feature is also present in *Simosuchus*, *Mariliasuchus*, *S. icaeorhinus*, *B. albertoi*, and *Stratitosuchus*, but not in crocodylians. The posteroventral tubercle on the lateral surface of the calcaneal tuber continues anteriorly as a ridge as in *Simosuchus*, *S. icaeorhinus*, *B. albertoi*, and *Stratitosuchus*. The plantar surface of the tuber has a deep fossa limited by a medial crest that connects with the expanded posterior surface of the calcaneal tuber, and a lateral ridge that fails to reach this posterior surface. The medial crest is present in most mesoeucrocodylians, but the lateral one is only present in *Yacarerani*. The posterior surface of the calcaneal tuber has an oblique groove oriented dorsolaterally to ventromedially for the passage of the M. gastrocnemius.

The astragalus articulates with the calcaneum via the astragalar peg and the anterior roller. The anterior roller articulates with the distolateral surface of the proximolateral process of the astragalus (Fig. 16I). The astragalar peg articulates with the medial surface of the anterior roller via the anterolateral facet on the peg, and with the anterior surface of the calcaneal tuber that bears a posteromedially directed process (posterior astragalar facet; Pol et al., 2012) via the astragalar trochlea. The pit for the astragalar peg is located at the junction of the medial surface of the anterior roller and the anterior surface of the calcaneal tuber.

Metatarsals—Four articulated left metatarsals (Mts) were preserved in MNK-PAL5064-C (Fig. 17A, B), and several disarticulated elements were also preserved in this specimen. The articulated metatarsals were found in close association with a left hind limb. These elements are identified as Mts I–IV, and all of them are complete except for Mt II, which only preserves its proximal half. The metatarsals are proximally imbricated at their proximal ends, with the medial metatarsal covering the proximal end of the adjacent lateral metatarsal. Except for Mt III, the proximal ends of all the elements are symmetric in dorsal view. The Mt I is the shortest and most robust metatarsal, whereas Mt III is the longest and Mt IV is the most gracile. The distal ends bear collateral depressions that are deeper on Mt I. The distal ends are

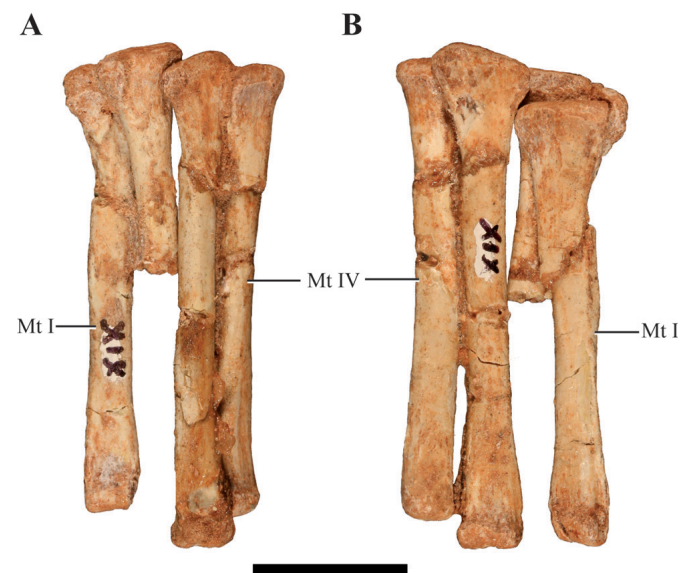


FIGURE 17. Left metatarsals of *Yacarerani boliviensis* (MNK-PAL5064-B) in **A**, dorsal and **B**, plantar views. Scale bar equals 1 cm.

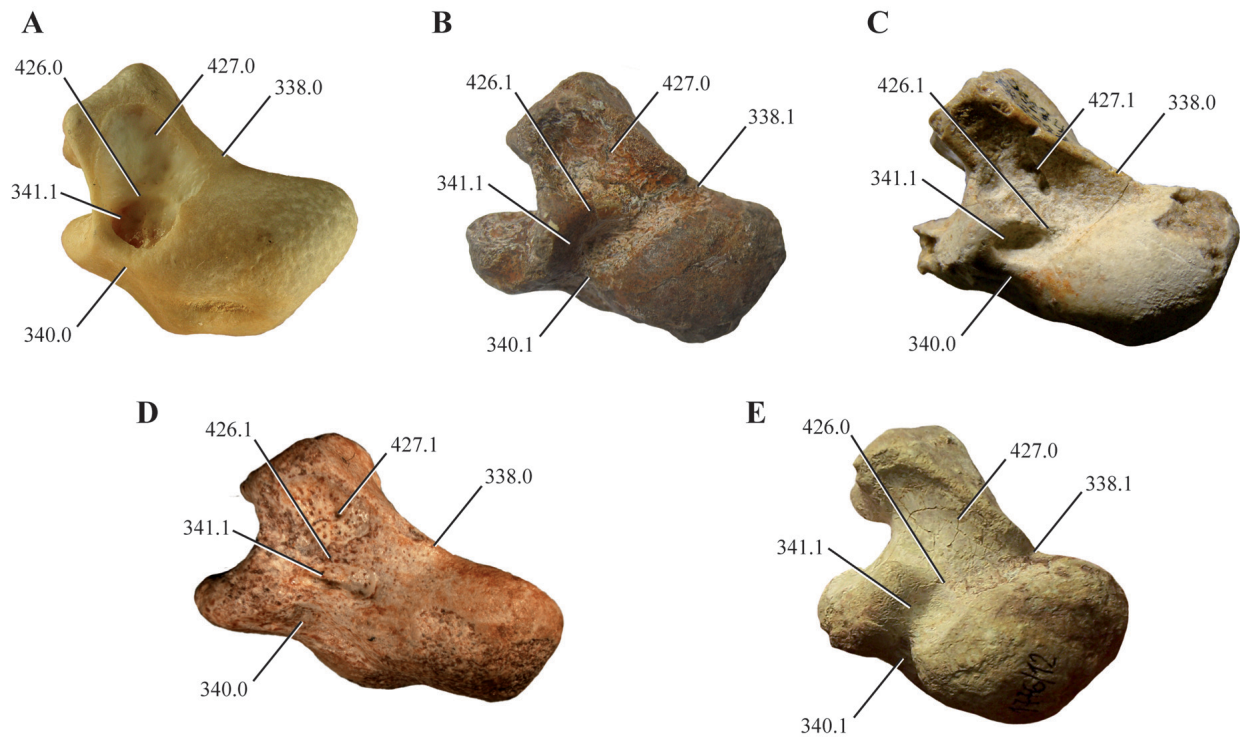


FIGURE 18. Astragali in anterior view of **A**, *Caiman latirostris* (MPEF-AC 205), **B**, *Lomasuchus palpebrosus* (MCF-PVPH 16), **C**, *Simosuchus clarki* (FMNH 2596), **D**, *Yacarerani boliviensis* (MNK-PAL5064-C), and **E**, *Sebecus icaeorhinus* (MPEF-PV 1776). Selected characters are marked (see Supplementary Data).

almost flat, except for Mt III, which has elliptical depressions on its dorsal and plantar surfaces. The distal ends are subquadrangular in distal view and bear a slightly developed trochlea.

PHYLOGENETIC RELATIONSHIPS

The new information obtained from the postcranial anatomy of *Yacarerani boliviensis* was incorporated into a phylogenetic data set. This data set represents an extended version of Pol

et al. (2014), which in turn was modified from Pol et al. (2012) through the addition of new craniomandibular characters. Here, we have increased the character sampling of postcranial information in the matrix (Figs. 18–22), adding 25 new postcranial characters and modifying three previously published characters (chars. 299, 341, and 348; see Supplementary Data). The resulting data matrix includes 437 characters and 109 taxa (see Supplementary Data). In the new data set, the proportion of postcranial characters has risen from 22.5% to 27.5% of the total character set.

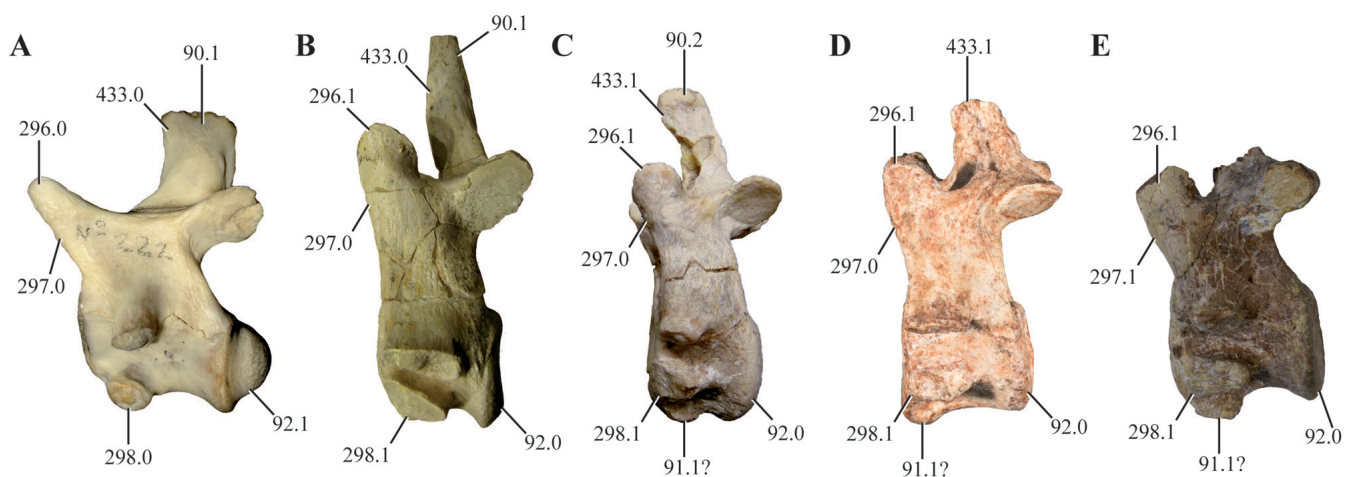


FIGURE 19. Cervical vertebrae in lateral view of **A**, *Caiman latirostris* (MPEF-AC 205), **B**, *Mahajangasuchus insignis* (UA 8654), **C**, *Simosuchus clarki* (UA 8679), **D**, *Yacarerani boliviensis* (MNK-PAL5064-B), and **E**, *Sebecus icaeorhinus* (MPEF-PV 1776). Selected characters are marked.

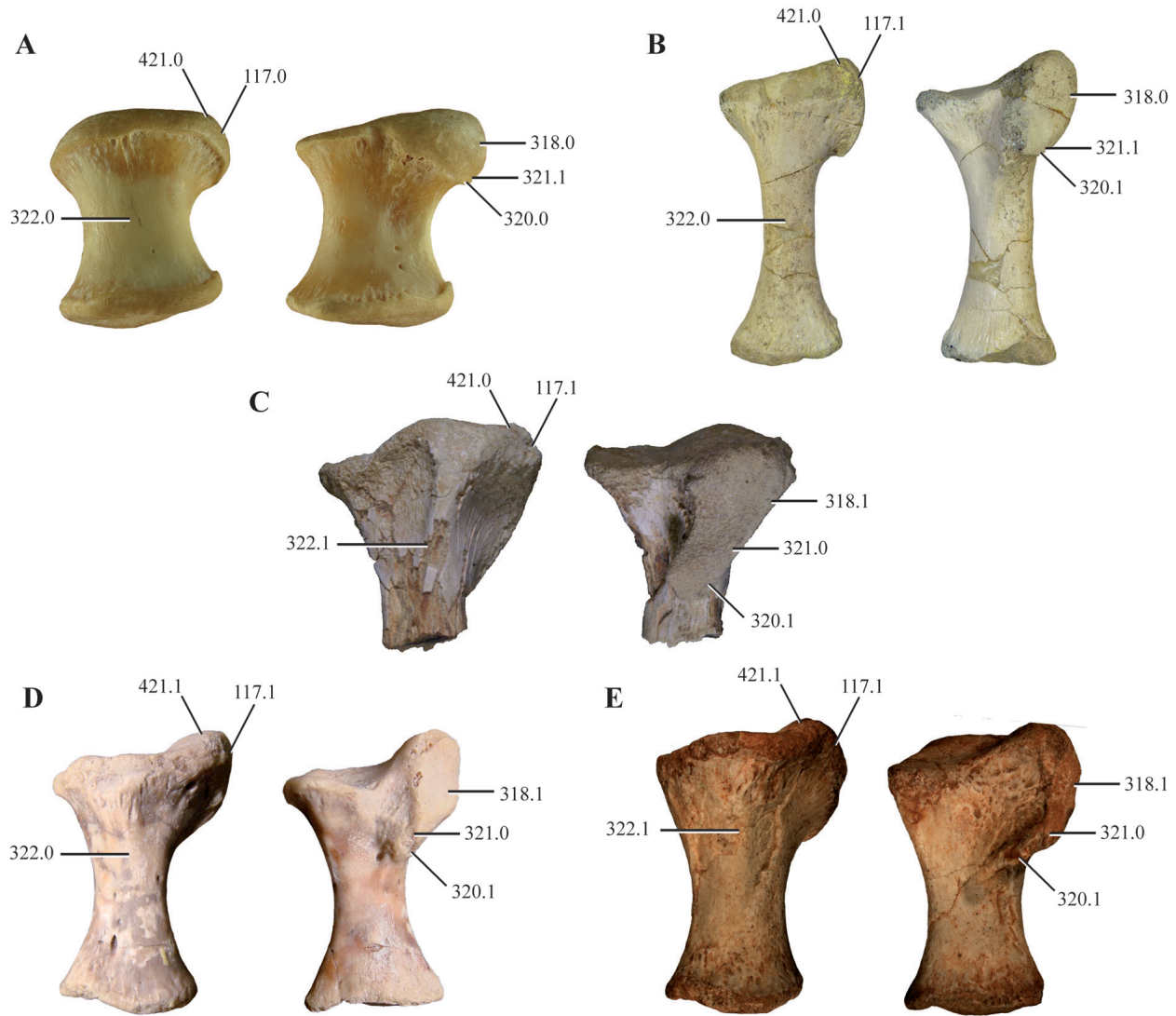


FIGURE 20. Radiale in anterior and posterior views of **A**, *Caiman latirostris* (MPEF-AC 205), **B**, *Mahajangasuchus insignis* (UA 8654), **C**, *Sebecus icaeorhinus* (MPEF-PV 1776), **D**, *Simosuchus clarki* (UA 8679), and **E**, *Yacarerani boliviensis* (MNK-PAL5064-E). Selected characters are marked (see Supplementary Data).

The data matrix was analyzed under equally weighted parsimony using TNT version 1.1 (Goloboff et al., 2008a, 2008b). A total of 9720 most parsimonious trees (MTPs) were obtained (tree length = 1675; consistency index [CI] = 0.312; retention index [RI] = 0.742) through a heuristic tree search (see Supplementary Data). The strict consensus is well resolved, but has large polytomies at the base of Sebecosuchia and the clade of advanced notosuchians (sensu Pol et al., 2014). These polytomies are caused by the unstable behavior of a few very incomplete taxa (*Coringasuchus*, *Pehuenchesuchus*, and *Pabwehshi*), and when their alternative positions are ignored, the reduced strict consensus topology shows these two clades resolved (Fig. 23; see Supplementary Data). Support measures (Bremer, Bootstrap, and Jackknife) are also affected by the presence of these (and other) fragmentary taxa, and when the support results are summarized through a reduced consensus, high nodal support is retrieved for some relevant nodes (see Supplementary Data).

The topology of the reduced strict consensus tree in our phylogenetic analysis is identical to that of Pol et al. (2014), recovering a monophyletic Notosuchia that is composed of two large clades: (1) Uruguaysuchidae + peirosaurids + mahajangasuchids and

(2) *Candidodon* + Ziphosuchia (Fig. 23). Within Ziphosuchia, two main clades are recovered: *Chimaerasuchus* + *Comahuesuchus* + Sebecosuchia and a clade informally named 'advanced notosuchians,' which includes Sphagesauridae, *Marillasuchus*, *Notosuchus*, and several fragmentary notosuchians from Brazil (*Labidosuchus*, *Morrinosuchus*, *Coringasuchus*).

Yacarerani is retrieved as the sister group of *Adamantinasuchus*, taking a basal position within the monophyletic Sphagesauridae, with *Marillasuchus* and *Labidosuchus* as the advanced notosuchians most closely related to sphagesaurids. Most of the synapomorphies of these clades (including Sphagesauridae and its internal nodes) are based on craniodental characters and have been discussed by Pol et al. (2014). Here, we will focus on the information provided by the postcranial characters within the context of the new data set.

Postcranial Changes in the Evolution of Notosuchia

Postcranial remains and descriptions are generally scarce among crocodyliiforms, including notosuchians. This lack of information is reflected in our data set, because more than half

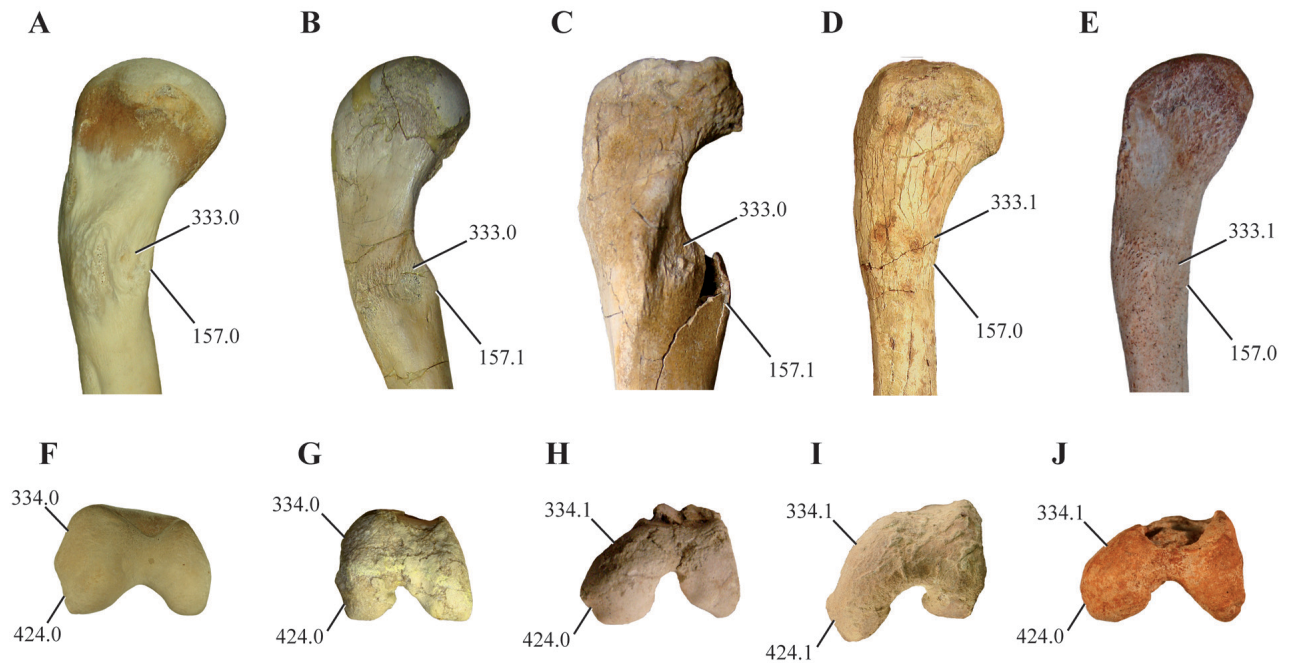


FIGURE 21. Proximal femora in posteromedial view of **A**, *Caiman latirostris* (MPEF-AC 205), **B**, *Mahajangasuchus insignis* (UA 8654), **C**, *Simosuchus clarki* (FMNH 2596), **D**, *Sebecus icaeorhinus* (MPEF-PV 1776), and **E**, *Yacarerani boliviensis* (MNK-PAL5064-B). Distal femora in distal view of **F**, *Caiman latirostris* (MPEF-AC 205), **G**, *Mahajangasuchus insignis* (UA 8654), **H**, *Simosuchus clarki* (FMNH 2596), **I**, *Sebecus icaeorhinus* (MPEF 1776), and **J**, *Yacarerani boliviensis* (MNK-PAL5064-B). Selected characters are marked (see Supplementary Data).

of the included notosuchian taxa (28 taxa, or 57%) lack informative postcranial material. For the following assessment of postcranial character optimization, all taxa lacking postcranial material were pruned from the MPTs so that their missing entries would not create ambiguous optimizations of postcranial

characters. These pruned trees were used to identify those notosuchian clades in which postcranial characters are known to change (Fig. 24).

As noted by Pol et al. (2012), Notosuchia is diagnosed by several unambiguous postcranial synapomorphies. Among the new

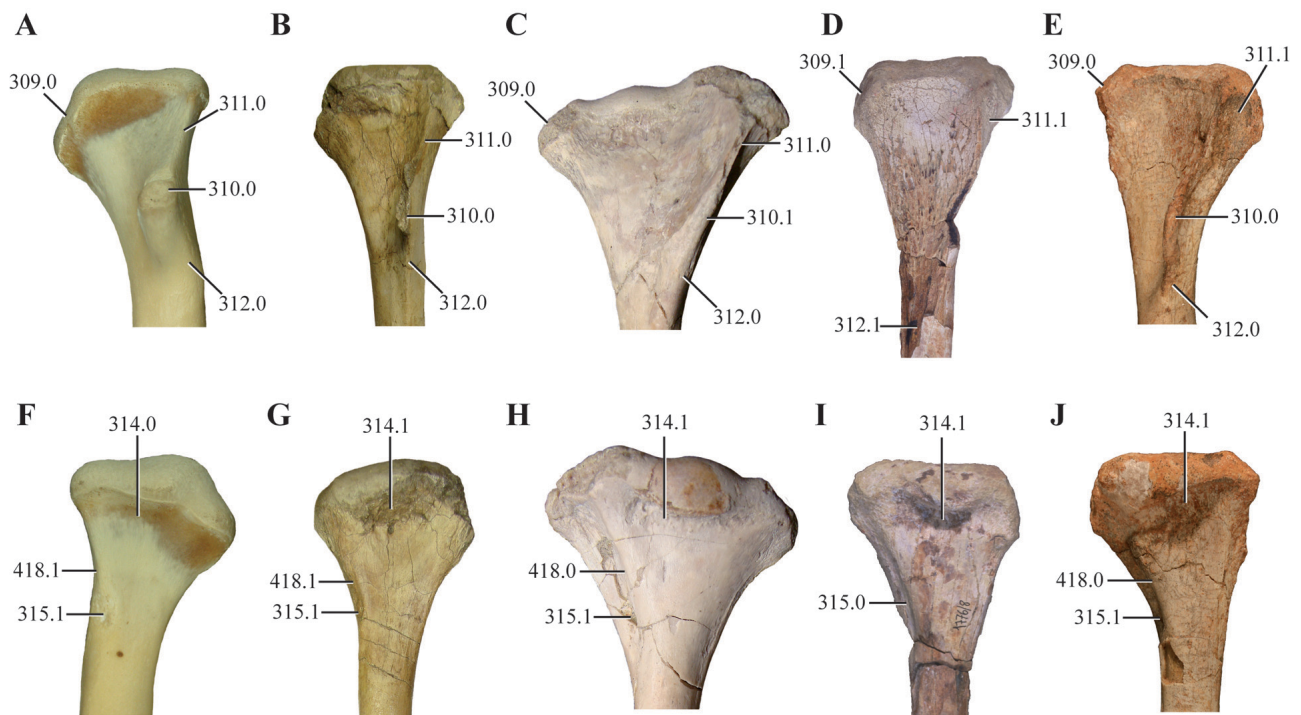


FIGURE 22. Proximal humeri in anterior and posterior views of **A** and **F**, *Caiman latirostris* (MPEF-AC 205), **B** and **G**, *Mahajangasuchus insignis* (UA 8654), **C** and **H**, *Simosuchus clarki* (FMNH 2596), **D** and **I**, *Sebecus icaeorhinus* (MPEF-PV 1776), and **E** and **J**, *Yacarerani boliviensis* (MNK-PAL5064-E). Selected characters are marked (see Supplementary Data).

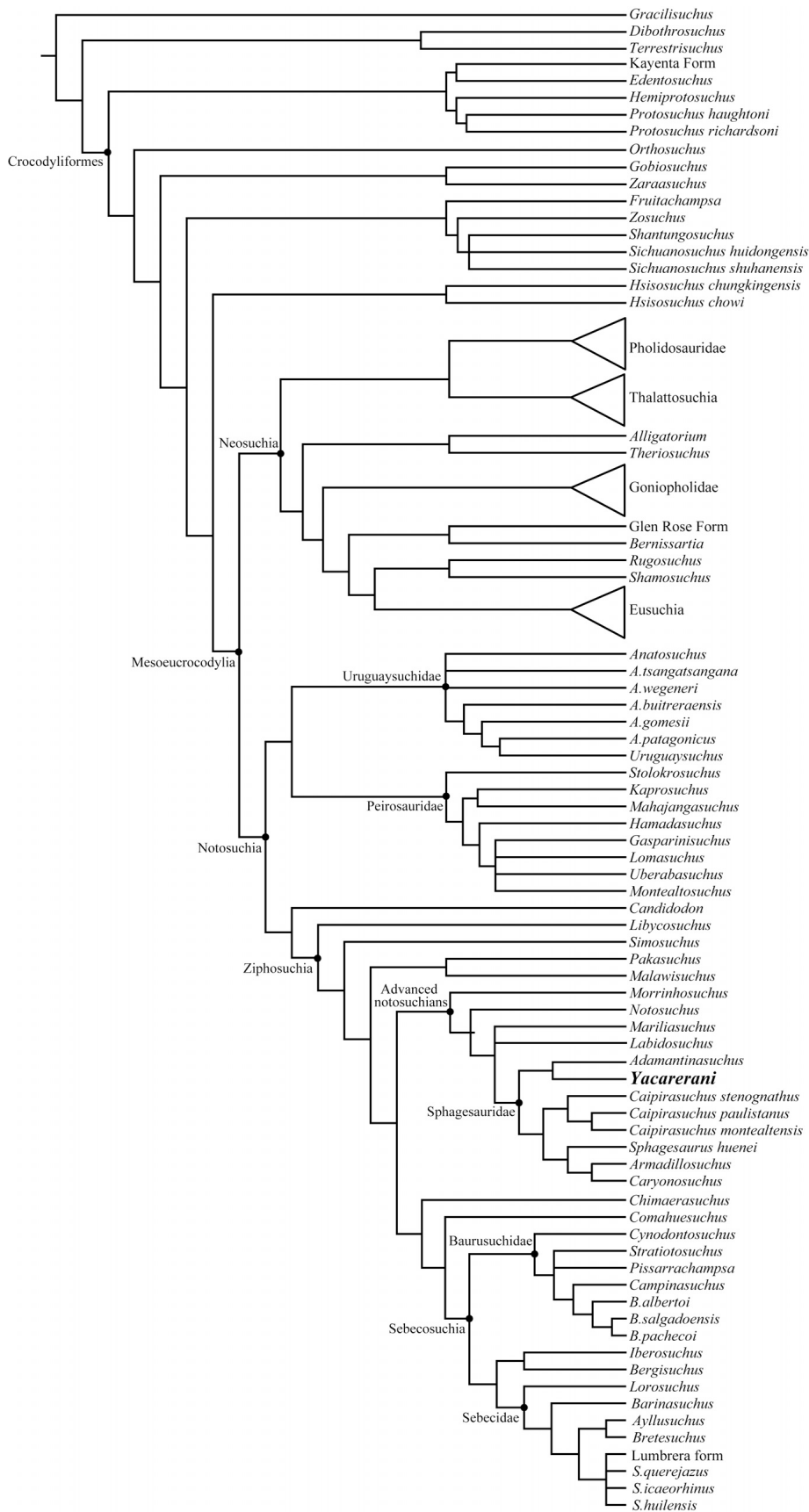


FIGURE 23. Reduced strict consensus of 9720 MTPs retrieved from the parsimony analysis ignoring the alternative positions of the *Coringasuchus*, *Pabwehshi*, and *Pehuenchesuchus*.

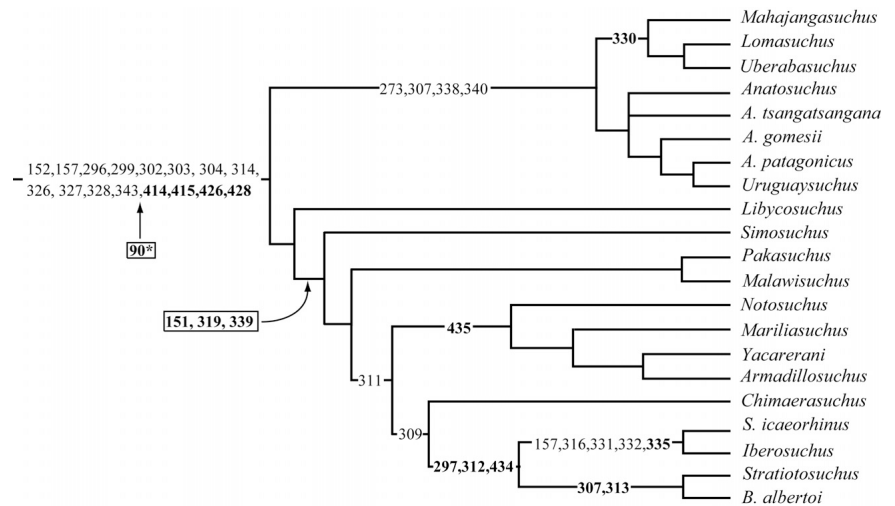


FIGURE 24. Reduced strict consensus of 9720 MTPs focusing on notosuchian interrelationships. Taxa lacking any postcranial information were pruned. Synapomorphies are marked on the consensus: in regular typography those recovered in the original reduced consensus, in bold those recovered in the pruned consensus, and inside a box those recovered after pruning *Libycosuchus*. See Postcranial Changes in the Evolution of Notosuchia for further information.

characters added to the analysis, four are optimized as synapomorphies of Notosuchia: glenoid facet of the scapula exposed proximally, being concave in lateral view, forming a dorsal roof to the glenoid facet of the coracoid (char. 414.1); the presence of an anterior bulge on the anterior margin of the glenoid facet of the scapula (char. 415.1); a strong crest separating the dorsal region of the anterior hollow of the astragalus from the astragalar-tarsale ligament pit (char. 426.1; Fig. 18); and a strong median crest oriented proximodistally on the posterior surface of the astragalus connecting the distal roller with the posteromedial edge of the proximolateral process of the astragalus (char. 428.1). A character previously recovered as a synapomorphy of Notosuchia (Pol et al., 2012) is rejected in this contribution: the proximal portion of the fibula strongly projected posteriorly (char. 272.1; Turner, 2006). *Yacarerani* has the plesiomorphic condition (char. 272.0) and introduces conflict in the distribution of this character that needs to be resolved with information from other notosuchian taxa, for which this feature is currently unknown.

Four previously proposed postcranial characters are interpreted as synapomorphies of one of the two major clades of Notosuchia, formed by Uruguaysuchidae + peirosaurids + mahajangasuchids: a posterodorsally projected spine on the posterior process of the cervical rib shaft (char. 273.1; Turner, 2006); a deep recess ventral to the glenoid facet of the coracoid (char. 307.1; Pol et al., 2012); a notch separating the tibial facet on the astragalus from the articular surface of MTs I–II on the distal roller (char. 338.1; Fig. 18; Pol et al., 2012); and a distal notch on the anterodistal surface of the astragalus, separating the articular surfaces of the planar facet of the astragalus of the distal articular surface for MTs I–II (char. 340.1; Fig. 18; Pol et al., 2012). The latter two characters, however, are interpreted as convergently acquired in some baurusuchids or sebecids, so that further scorings within Notosuchia are needed for a more thorough test of their phylogenetic information. One of the new postcranial characters included in this contribution is also recovered as synapomorphy of this clade: the third dorsal vertebra is the most posterior one in which the parapophyses are in contact with the neurocentral suture (char. 437.1).

Within this large clade of notosuchians, one postcranial character provides evidence for clustering peirosaurids and mahajangasuchids: the anterior and posterior articular surfaces of the anterior peduncle of the ilium separated by a deep notch and forming an acute angle between them (char. 330.1; Pol et al., 2012), present in *Mahajangasuchus* and *Lomasuchus*.

No postcranial synapomorphies are recovered for Ziphosuchia, but this is largely due to the scarce postcranial material of the two basal-most ziphosuchians (*Libycosuchus* and *Candidodon*). If these taxa are ignored, six characters are optimized as changing to the apomorphic condition in ziphosuchians: rod-like neural spines in all cervical vertebrae (char. 90.2; Fig. 19; modified from Clark, 1994); an anteroposteriorly short neural spine of the axis (char. 151.1; Pol, 1999); a proximodistally elongated articular surface for the ulna on the radiale (char. 319.1; Fig. 20; Pol et al., 2012); absence of a well-developed lateral supracondylar crest of the femur, with the anterior surface of the femur being continuous with the lateral one (char. 334.1; Fig. 21; Pol et al., 2012); separated planar and proximal articular surfaces for the calcaneum on the astragalus (char. 339.1; Pol et al., 2012); and anteriorly slanted neural spines of the cervical vertebrae (char. 433.1; Fig. 19; new character). Derived ziphosuchians share a single postcranial synapomorphy that is absent in two basal forms of this clade (*Simosuchus*, *Malawisuchus*): a medially displaced proximal third of the deltopectoral crest, leaving an anteriorly facing surface on the lateral margin of the anterior surface of the humerus (char. 311.1; Fig. 22; Pol et al., 2012).

The clade of advanced notosuchians that clusters *Notosuchus*, *Mariliasuchus*, and sphagesaurids is diagnosed by a single postcranial character, the presence of well-defined ventral keels on the anterior dorsal vertebrae (char. 435.1; new character). The internal nodes of this clade lack synapomorphies from the postcranial skeleton, partly because many of these taxa lack postcrania (especially sphagesaurids). New discoveries and descriptions of sphagesaurid postcrania may reveal that some characters, currently known only in *Yacarerani*, are synapomorphies of this clade (e.g., the absence of well-developed, rounded depressions located between the base of the neural spines and the postzygapophyseal process, oblique crest on the postglenoid process of the coracoid, lateromedially compressed ungual phalanges, and low fourth trochanter).

Finally, our analysis revealed two postcranial synapomorphies of Sebecosuchia that were not recovered by Pol et al. (2012): a distinct bulge present at the midpoint of the prezygapophyseal process in lateral view (char. 297.1; Fig. 19; Pol et al., 2012) and the absence of ventral keels on the cervical vertebrae (char. 434.1; new character). Furthermore, unlike other notosuchians, several sebecosuchian taxa (*B. albertoi*, *S. icaeorhinus*, *Iberosuchus*) bear well-developed prespinal fossae on the dorsal surface of the neural arch, just anterior to the base of the neural spine (char. 432.1; Fig. 19; new character), but the unknown condition

in *Chimaerasuchus*, *Comahuesuchus*, and *Pehuenchesuchus* precludes interpreting this character as an unambiguous synapomorphy of Sebecosuchia or a more inclusive clade. Pol et al. (2012) also mentioned that the vertical orientation of the area for the *M. subscapularis* (char. 309.1) was a synapomorphy of Sebecosuchia (Fig. 22), but its presence in *Chimaerasuchus* shows that this feature has a wider distribution among ziphosuchians and is recovered as a synapomorphy of *Chimaerasuchus* + *Comahuesuchus* + Sebecosuchia. The clade formed by *Sebecus* (the only representative of Sebecidae with currently described postcranium) and *Iberosuchus* is supported by five postcranial synapomorphies, two of which were not recovered by Pol et al. (2012): the lack of a distinct flange anterior to the insertion of the PIF11 and CFL (char. 157.0; Fig. 21; Buckley and Brochu, 1999) and the distal half of the tibial shaft markedly bowed in anterior view (char. 335.1; Pol et al., 2012).

CONCLUSIONS

Detailed description of the postcranium of *Yacarerani boliviensis* allows comparison of this taxon with other mesoeucrocodylian crocodyliforms and also provides the first insight into the postcranial anatomy of sphagesaurid notosuchians. *Yacarerani* has many postcranial traits in common with other notosuchians (e.g., an anteroposteriorly short axial neural spine, a wide scapular blade, a complex radiale-ulnare articulation, and modifications of the facets on the calcaneum), which in many cases differ markedly from the condition in eusuchians. This difference is even more pronounced when Ziphosuchia (a less inclusive clade that includes *Yacarerani*) is considered, although the postcranial anatomy of the basal most taxa (i.e., *Candidodon*, *Libycosuchus*) is poorly known due to the lack of well-preserved postcranial remains.

The morphological variation observed among basal mesoeucrocodylians reveals new phylogenetically informative characters, which permit the evaluation of the contribution of postcranial characters to resolving the relationships of basal mesoeucrocodylians. Although homoplasies are present, the inclusion of the new characters proposed in this contribution and the incorporation of new postcranial data on other mesoeucrocodylians support a monophyletic Notosuchia, including two main clades: a clade formed by Peirosauridae + Mahajangasuchidae + Uruguaysuchidae (*Araripesuchus* + *Anatosuchus* + *Uruguaysuchus*) and *Candidodon* + Ziphosuchia, a large group that includes some basal forms (i.e., *Libycosuchus*, *Simosuchus*, *Pakasuchus*, *Malawisuchus*) and two derived clades, advanced notosuchians and Sebecosuchia. This topology was recently proposed in the study of Pol et al. (2014) but is here further reinforced by the postcranial characters, with higher support measures for most of the clades recovered (see Supplementary Data). This shows, in agreement with recent studies (Pol, 2005; Turner, 2006; Sertich and Groenke, 2010; Pol et al., 2012), that the postcranial skeleton provides valuable phylogenetic information on the evolution of basal mesoeucrocodylians.

Sphagesauridae was recovered as a well-supported clade nested within advanced notosuchians, as the sister group of *Mariliasuchus amarali*. A closer relationship of *Mariliasuchus* with Sphagesauridae (rather than with *Notosuchus terrestris*) has one of the highest support values recovered within Notosuchia. No unambiguous postcranial synapomorphies diagnose Sphagesauridae in our analysis, given that *Yacarerani boliviensis* is the only sphagesaurid with well-preserved postcranial remains described to date. New finds and description of known material (such as *Armadillosuchus*) may be of great relevance, because some of the postcranial characters recognized as autapomorphies of *Yacarerani* might be optimized as synapomorphies of the clade *Yacarerani* + *Adamantinasuchus* or the entire sphagesaurid clade.

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