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ARTICLE

A NEW CAIMANINE (CROCODYLIA, ALLIGATOROIDEA) SPECIES FROM THE SOLIMÕES FORMATION OF BRAZIL AND THE PHYLOGENY OF CAIMANINAE

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ABSTRACT—The Miocene deposits of South America are notable for their diverse crocodyliform fauna, of which the giant caimanine *Purussaurus* is a well-known example. This contribution describes a new caimanine, *Acresuchus pachytemporalis*, gen. et sp. nov., based on an almost complete skull and mandible from the late Miocene Solimões Formation of the southwestern Brazilian Amazonia. This new taxon is based on a unique combination of characters, of which the presence of an upturned posterolateral margin of the squamosal throughout the entire lateral margin of the bone (a 'horn'), with a dorsoventral expansion in the posterior portion of the eminence, stands out. We conducted a phylogenetic analysis of Eusuchia, which showed the new taxon as sister to *Purussaurus*. This placement allows discussion about the evolution of gigantism in the *Acresuchus-Purussaurus* clade, which reveals several characters that may be related to gigantism. Additionally, *Acresuchus* was probably a medium-sized generalist caimanine that had an ecological niche similar to the extant *Melanosuchus niger*. Until now, crocodyliforms that had such niches were unknown from the Solimões Formation.

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

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INTRODUCTION

All living crocodylian species are nested within crown group Crocodylia Gmelin, 1789, which is divided into three main lineages: Gavialoidea Hay, 1930, Crocodyloidea Fitzinger, 1826, and Alligatoroidea Gray, 1844. This latter clade is stem based (sensu Cantino and de Queiroz, 2000), defined by Brochu (1999, 2003) as including all species of Crocodylia more closely related to *Alligator mississippiensis* (Daudin, 1802) than to *Gavialis gangeticus* (Gmelin, 1789) or *Crocodylus niloticus*. Within Alligatoroidea is the less inclusive clade Caimaninae Brochu, 1999, which is also stem based, defined as being formed of the species closer to *Caiman crocodilus* (Linnaeus, 1758) than to *Alligator mississippiensis* (sensu Brochu, 1999, following Norell et al., 1994).

The extant diversity of Caimaninae comprises three genera—*Caiman* Spix, 1825, *Melanosuchus* Gray, 1862, and *Paleosuchus* Gray, 1862, with a total of six species recognized: *C. crocodilus*, *C. latirostris* (Daudin, 1802), *C. yacare* (Daudin, 1802), *M. niger* (Spix, 1825), *P. palpebrosus* (Cuvier, 1807), and *P. trigonatus* (Schneider, 1801). All extant species exclusively occur in South America, with the exception of *Caiman crocodilus*, which is also naturally present in Central America and the Caribbean (Medem, 1983; Thorbjarnarson, 1992; Brochu, 1999). However, the fossil record of the group is much more rich and diverse (e.g., Langston, 1965; Brochu, 1999, 2010, 2011; Riff et al., 2010; Bona et al., 2013b), tracing back unequivocally to the early Paleocene of Argentina, with the species *Eocaiman palaeocenicus* Bona, 2007, *Necrosuchus ionensis* Simpson, 1937, and *Notocaiman stromeri* Rusconi, 1937 (Bona, 2007; Brochu, 2011). Additionally, there is a putative record from the Upper Cretaceous of the U.S. state of Montana (Bryant, 1989). As seen for the extant species, the fossil diversity of Caimaninae is predominantly South American, with the notable exceptions of *Orthogenysuchus olseni* Mook, 1924, and *Tsoabichi greenriverensis* Brochu, 2010, both from the Eocene of the United States (Brochu, 1999, 2010, 2011), and *Culebrasuchus mesoamericanus* Hastings, Bloch, Jaramillo, Rincon, and MacFadden, 2013, and

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Centenariosuchus gilmorei Hastings, Bloch, Jaramillo, Rincon, and MacFadden, 2013, from the early Miocene of Panama in Central America (Hastings et al., 2013, 2016).

The fossil record shows the Miocene as the period when Caimaninae reached the apex of both their diversity and their morphological disparity (Riff et al., 2010; Salas-Gismondi et al., 2015; Souza et al., 2016; Cidade et al., 2017). The middle Miocene fauna of La Venta, in Colombia (Langston, 1965; Langston and Gasparini, 1997), and the late Miocene rocks of the Ituzaingó Formation, in Argentina (Bona et al., 2013b), the Urumaco Formation, in Venezuela (Aguilera, 2004; Riff et al., 2010), and the Solimões Formation, in Brazil (Riff et al., 2010; Souza et al., 2016) stand out as yielding the richest and most diverse fossil records of the group. Specifically, the Urumaco and Solimões formations, located in the Amazon region, are regarded as having two of the richest crocodylian fossil faunas of the world (Riff et al., 2010).

Aside from the living genera *Caiman*, *Melanosuchus*, and *Paleosuchus*, the caimanine fossil record from the Miocene of South America comprises three distinctive, peculiar morphotypes: the 'duck-faced,' putative gulp-feeding *Mourasuchus* Price, 1964 (Price, 1964; Langston, 1965; Bocquentin-Villanueva, 1984; Gasparini, 1985; Bona et al., 2013a, 2013b; Cidade et al., 2017), the durophagous taxa *Balanerodus*, *Globidentosuchus*, *Gnatusuchus*, *Kuttanacaiman*, and *Caiman wannlangstoni* (Langston, 1965; Langston and Gasparini, 1997; Scheyer et al., 2013; Salas-Gismondi et al., 2015), and the giant, top predator *Purussaurus* Barbosa-Rodrigues, 1892 (Barbosa-Rodrigues, 1892; Mook, 1941; Langston, 1965; Price, 1967; Bocquentin-Villanueva et al., 1989; Aguilera et al., 2006), which could have reached as much as 12 m in total body length (Riff and Aguilera, 2008; Riff et al., 2010; Aureliano et al., 2015). The Solimões Formation has a high crocodylian diversity with eight proposed species, including four caimanines (Fortier, 2011). Occurrences of *Caiman*, *Mourasuchus*, and *Purussaurus* have been recorded from this formation, the latter being represented only by *P. brasiliensis* Barbosa-Rodrigues, 1892 (Bocquentin-Villanueva et al., 1989; Riff et al., 2010).

In this work, a new caimanine species is described from the Solimões Formation and from the *Purussaurus* lineage. This new taxon may offer meaningful insight into the diversity of the crocodylian fauna of the South American Miocene and also provide a new perspective on the evolution of gigantism in the well-known predator *Purussaurus*.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **CIAAP**, Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **MCT**, Museu de Ciências da Terra, Rio de Janeiro, Brazil; **MN**, Museu Nacional, Rio de Janeiro, Brazil; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **UFAC**, Universidade Federal do Acre, Rio Branco, Brazil.

Anatomical Abbreviations—**af**, adductor fossa; **an**, angular; **ar**, articular; **bo**, basioccipital; **bs**, basisphenoid; **cr**, coronoid; **d**, dentary; **da**, dentary alveolous; **emf**, external mandibular fenestra; **en**, external naris; **ex**, exoccipital; **f**, frontal; **fic**, foramen intermandibularis caudalis; **fm**, foramen magnum; **fv**, foramen vagus; **if**, incisive foramen; **itf**, infratemporal fenestra; **j**, jugal; **l**, lacrimal; **ls**, laterosphenoid; **m**, maxilla; **ma**, maxillary alveolous; **ms**, mandibular symphysis; **n**, nasal; **o**, orbit; **oc**, occipital condyle; **p**, parietal; **pf**, prefrontal; **pm**, premaxilla; **pma**, premaxillary alveolus; **po**, postorbital; **pt**, pterygoid; **ptf**, posttemporal fenestra; **q**, quadrate; **qj**, quadratojugal; **san**, surangular; **sfo**, supratemporal fossa; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **stf**, supratemporal fenestra.

REMARKS ON NOMENCLATURE

Prior to this work, two other species names have been proposed based on the specimen here described as the holotype (UFAC-2507): '*Caiman niteroiensis*' (Souza-Filho and Bocquentin, 1991) and '*Caiman pachytemporalis*' (Souza-Filho, 1998). These names created some confusion about the taxonomic affinities of UFAC-2507 since recent publications treated '*Caiman niteroiensis*' as valid species (e.g., Riff et al., 2010). However, because neither of these names has been proposed in an official publication, with Souza-Filho and Bocquentin (1991) being a conference abstract and Souza-Filho (1998) a Ph.D. dissertation, both violate articles from Chapter 3 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999). As such, neither is a valid species name for UFAC-2507. Therefore, the only taxonomically valid name for this taxon is the one proposed in this work: *Acresuchus pachytemporalis*.

MATERIALS AND METHODS

The phylogenetic data matrix was created with the software Mesquite, version 2.75 (Maddison and Maddison, 2011). The phylogenetic analysis was made with the software Tree Analysis Using New Technology (TNT version 1.5; Goloboff et al., 2008; Goloboff and Catalano, 2016). The analysis was performed using traditional search for RAS (random addition sequences) with a 'random seed' value of zero, 20,000 replications, and 10 cladograms saved per replication. The branch swapping algorithm used was 'Tree Bisection Reconnection' (TBR) and the existing trees were replaced in the analysis. After this first analysis, a second round of TBR with the trees in memory (RAM) from the first analyses was conducted. The trees in both analyses were collapsed after the search. The characters were unordered.

The phylogenetic analysis was performed with a modified version of the matrix of Cidade et al. (2017) that includes 93 eusuchian taxa in the ingroup and the non-eusuchian crocodyliform *Bernissartia fagesii* Dollo, 1883, as outgroup. The phylogenetic characters are listed in Appendix S1 in Supplementary Data 1. This matrix is based mainly on that of Brochu (2011), with additional input from other work (see Appendix S2 in Supplementary Data 1 for details). Of the ingroup taxa, 88 were already included in the matrix of Cidade et al. (2017). The scoring of *Necrosuchus ionensis*, *Melanosuchus fisheri* Medina, 1976, *Caiman gasparinae* Bona and Carabajal, 2013, *Purussaurus brasiliensis*, and specimen UCMP-39997 was based on other previous work (Barrios, 2011; Brochu, 2011; Bona et al., 2013b; Pinheiro et al., 2013; Salas-Gismondi et al., 2015) with complimentary scorings by the authors (see Appendix S2), whereas the scoring of *Acresuchus pachytemporalis* was made entirely by the authors. *Bernissartia fagesii* was also included in Brochu (2011) and Cidade et al. (2017). The analysis of this study included the 187 morphological characters by Cidade et al. (2017) and Brochu (2011), with one character being rephrased (Character 156) and several scorings revised (see Appendix S2). The fossil specimen UCMP-39978, from the middle Miocene of La Venta (Colombia) described by Langston (1965), was assigned to '*Caiman lutescens*' (Rovereto, 1912) in all previous analyses except Brochu (2011); consistent with this, we follow Bona et al. (2013b) in considering that this specimen cannot be assigned to *C. lutescens*. Codings for all taxa form Appendix S3 in Supplementary Data 1. A Nexus file of the matrix is available as Supplementary Data 2.

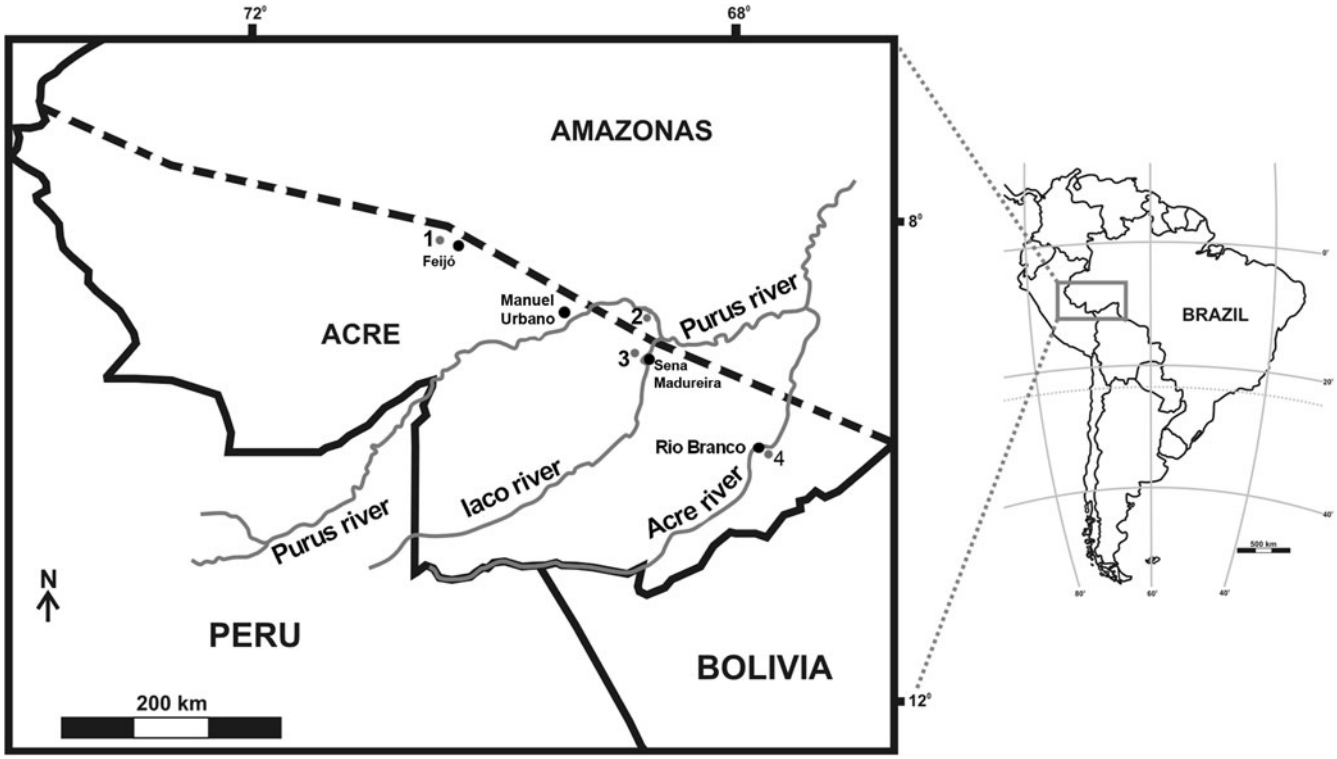

FIGURE 1. Map of the Brazilian state of Acre (modified from Hsiou, 2010) showing the localities from which the material of *Acresuchus pachytemporalis* is known. Gray dots represent the localities; black dots represent municipalities. The dashed line represents the border between Brazilian states and continuous lines represent borders between countries. **Key**: **1**, Morro do Careca; **2**, Talismã; **3**, Lula; **4**, Niteroi.

SYSTEMATIC PALEONTOLOGY

CROCODYLIA Gmelin, 1789 (sensu Benton and Clark, 1988)
ALLIGATOROIDEA Gray, 1844 (sensu Brochu, 2003, following Norell et al., 1994)
CAIMANINAE Brochu, 1999 (following Norell, 1988)
ACRESUCHUS, gen. nov.

Type Species—*Acresuchus pachytemporalis*, gen. et sp. nov.

Etymology—'Acre' from the name of the Brazilian state where the holotype was found, and 'suchus' from the ancient Greek word for 'crocodile.'

Diagnosis—Same as the type species.

ACRESUCHUS PACHYTEMPORALIS, gen. et sp. nov.

Holotype—UFAC-2507, a nearly complete skull with both hemimandibles.

Referred Material—UFAC-1187, UFAC-1379, UFAC-1486, UFAC-3142, UFAC-4153, UFAC-4154, UFAC-4183, UFAC-4678, UFAC-5256, UFAC-6384, all posterior portions of the skull table with variable sizes and degrees of preservation.

Etymology—The specific epithet '*pachytemporalis*' alludes to the accentuated pachyostosis present in the squamosals of the holotype.

Occurrence—Solimões Formation, late Miocene (equivalent to the Huayquerian land mammal age according to Latrubesse et al., 2010, based on paleontological content [vertebrates and palynology] and facies analysis), Acre Basin, Brazil. The holotype and four referred specimens (UFAC-4153, UFAC-4154, UFAC-4183, and UFAC-4678) come from the fossiliferous locality 'Niteroi' (10°8′2.27″S, 67°48′48.84″W: Bona et al., 2013b; UTM 19L 629983E, 8879539S, datum WGS84: Kerber et al., 2017), which is located on the east bank of the Acre River (Fig. 1), between the cities of Rio Branco and Senador Guiomard, in the Brazilian state of Acre (Bona et al., 2013b). Two referred specimens (UFAC-1187, UFAC-1379) are from the 'Lula' locality, one (UFAC-5256) from the 'Morro do Careca' locality (Fig. 1), one (UFAC-6384) from an unknown locality on the margins of the BR-364 highway in the municipality of Feijó, in Acre (Fig. 1), one (UFAC-3142) from the 'Talismã' locality, located in the right margin of the Upper Purus River, in the Amazonas state (Fig. 1), and one (UFAC-1486) from an unknown locality in the upper portion of the Acre River (Fig. 1).

Diagnosis—Caimanine with a medium-sized body, teeth with smooth (non-serrated) carinae, orbits large in comparison with other caimanines, having roughly straight margins that are larger than the infratemporal fenestrae, circular external naris, posterior margin of the skull table transversely straight to slightly concave, *posterolateral margin of squamosal upturned throughout the entire dorsal lateral margin with a dorsoventral expansion in the posterior portion of the eminence (*autapomorphy within Caimaninae).

GEOLOGICAL SETTING

The sediments of the Solimões Formation, outcropping within the Acre and Solimões basins (Caputo et al., 1971; Eiras et al., 1994), are continental in origin and composed mainly of claystones, with calcareous concretions and calcite as well as gypsum veins, lying in horizontal to subhorizontal beds that can

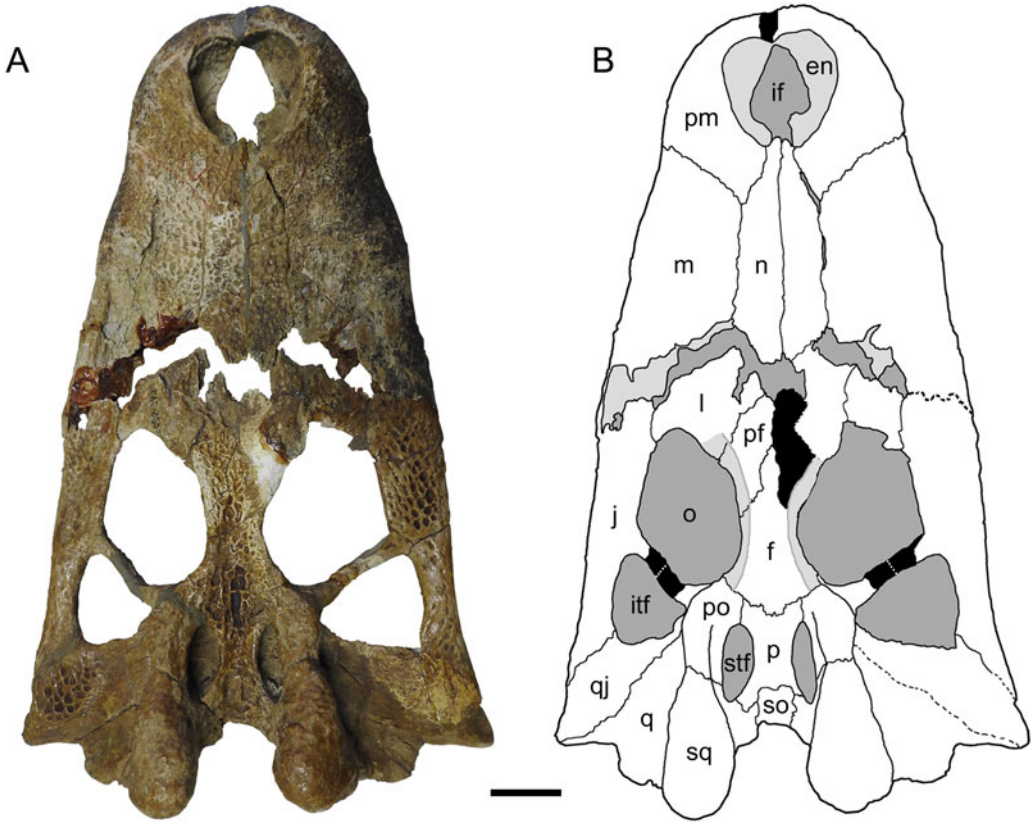

FIGURE 2. *Acresuchus pachytemporalis*, UFAC-2507, skull of the holotype. **A**, dorsal view; **B**, schematic drawing illustrating bones and sutures. Scale bar equals 5 cm.

reach thicknesses of over 1000 m (Latrubesse et al., 2010). The depositional environment of the formation is described as being predominantly floodplain-lacustrine-paludal (Latrubesse et al., 2010), having the Andes chain as the main source of the sediments (Latrubesse et al., 1997). Although previous works assign the Solimões Formation to a late Miocene—Pliocene age (e.g., Latrubesse, 1992; Latrubesse et al., 1997), recent geological, palynological, and sedimentological data (Cozzuol, 2006; Latrubesse et al., 2010) and absolute dating using radioisotopes (Bissaro-Junior et al., 2019) have indicated a late Miocene age for the Formation. (Cozzuol, 2006; Latrubesse et al., 2010), corresponding to the Huayquerian (?9–6.8 Ma) South American Land Mammal Age (SALMA; Fortier et al., 2014).

The Niteroi locality, specifically where the holotype of *Acresuchus pachytemporalis* was collected, consists of moderately consolidated claystone layers, as well as sandstones and siltstones in smaller quantities, deposited in a low-energy environment (Campbell et al., 2006; Latrubesse et al., 2007, 2010). An absolute dating via U-Pb radioisotopes dating of detrital zircon of the Niteroi locality showed an age of 8.5 ± 0.5 Ma for it, corresponding to the Tortonian stage of the late Miocene (Bissaro-Junior et al., 2019).

DESCRIPTION

General Preservation Status of the Holotype

The skull of the holotype is nearly complete, with a rupture in front of the orbits (Figs. 2–5) along the surfaces of the jugal, the maxilla, the prefrontal, and the lacrimal, separating the rostrum from the posterior portion of the skull. The skull has a total length (measured from the tip of the snout to the posterior extremity of the quadrate) of 51.5 cm. It is generally well preserved, with many portions of the skull having notable ornamentation, such as on the dorsal portion of the skull table (Fig. 6), especially on the frontal bone at its most posterior portion, the left quadratojugal, the right jugal, and the anterior portion of the dorsal surface of the left jugal. The dorsal surfaces of the nasals, the maxillae, and the premaxillae also bear relatively well-preserved ornamentation, although not as marked as those on the posterior portion of the skull.

In occipital view, the specimen is fully preserved from the dorsal margin of the supraoccipital and the highly elevated squamosals (see Squamosals, below) to the ventral margin of the basioccipital. Ventral to this, there is only a small fragment of the pterygoid (Fig. 4).

In ventral view, neither the palatines nor the prefrontal pillars are preserved (Fig. 3), whereas the basisphenoid is partially preserved, including part of the basisphenoid rostrum. Ventrally, both premaxillae are preserved, but with a wide rupture between them posterior to the incisive foramen (Fig. 3). Both maxillae are incompletely preserved, mainly due to the fact that the rupture between the two premaxillae is also present between the two maxillae (Fig. 3).

The left and right hemimandibles were preserved unsutured. The right hemimandible is almost entirely preserved (Figs. 7, 8). The main missing parts are the anterior-most portion of the splenial; the anterior-most portion of the surangular that surrounds the dentary in medial view; the medial portion of the angular, which is missing from the anterior margin of the foramen intermandibularis caudalis to the sutural connection of the angular with the articular and surangular bones; and most

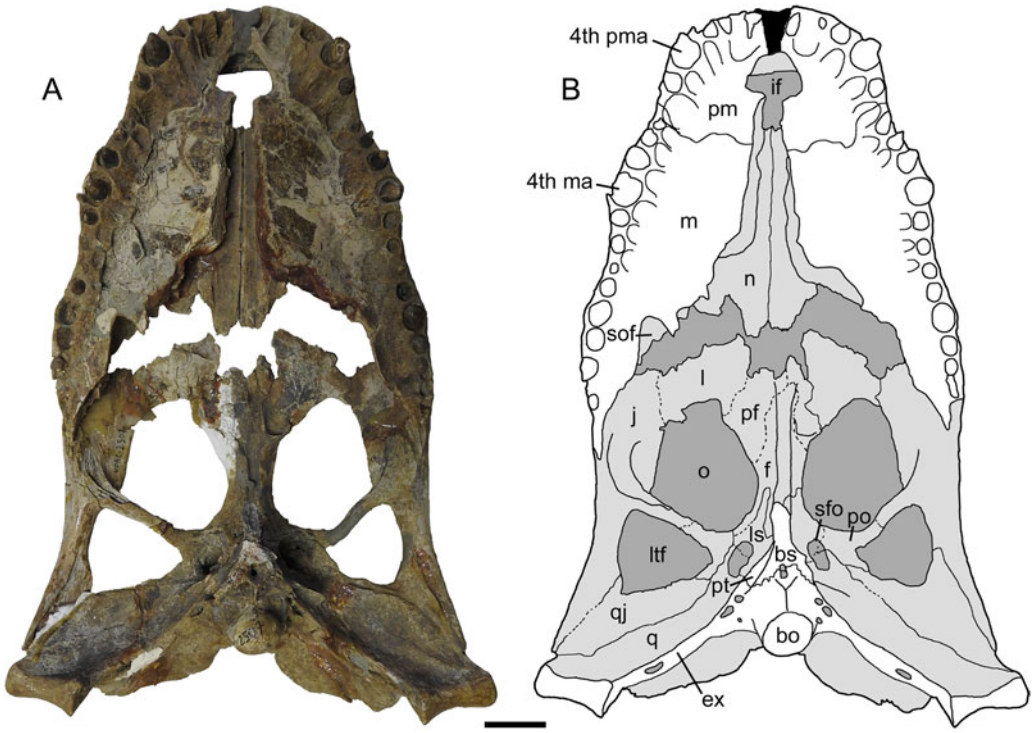

FIGURE 3. *Acresuchus pachytemporalis*, UFAC-2507, skull of the holotype. **A**, ventral view; **B**, schematic drawing illustrating bones and sutures. Scale bar equals 5 cm.

of the coronoid. The missing parts of the left hemimandible are (all in medial view; Fig. 9) the anterior extremity of the splenial and the posterior-most part of the splenial, along with the most anterior portion of the dorsal ramus of the angular, including most of the dorsal margin of the foramen intermandibularis caudalis, and there are no remains that can be identified as belonging to the coronoid.

Despite the damage observed and described in the holotype, no breakage and/or weathering was found that could have been the result of transport or long exposure (for the relation between bone weathering and transport/exposure, see Behrensmeyer, 1978). The specimen does not present any deformation, such as compression, and the outer bone surface is entirely preserved. The main rupture observed in the rostrum of the holotype most likely occurred after burial, but this hypothesis still needs to be properly assessed by future taphonomic work. This preservation may be considered good, which is congruent with the depositional environment of the Niteroi site, described as a low-energy environment in which vertebrate fossils typically exhibit good preservation due to little or no transport between the place of death and the place of burial (Campbell et al., 2006). However, it is important to note that well-preserved fossil crocodyliforms may also come from different depositional environments than low-energy ones (e.g., Syme and Salisbury, 2014), and that a proper, comprehensive taphonomic analysis of the assembly of the Niteroi locality has yet to be made.

Skull of the Holotype

Premaxillae—The premaxillae are almost completely preserved; the anterior-most portion of the medial suture between the two bones is missing, specifically from the tip of the snout to the anterior margin of the external naris. This separation was covered by resin, in both dorsal and ventral views (Figs. 2, 3), during the preparation of the holotype. In ventral view, the posterior-most portion of the suture is also separated; as described above, in ventral view, the areas between both premaxillae and both maxillae are ruptured from the posterior margin of the incisive foramen to the posterior-most extent of the preserved maxillae (Fig. 3).

Posteriorly, each premaxilla meets its corresponding maxilla and nasal bone in dorsal view, but they do not meet each other posterior to the external naris, allowing the nasal bones to reach the posterior margin of the external naris (Fig. 2). Each premaxilla also meets each corresponding maxilla in ventral view (Fig. 3).

Both premaxillae have five alveoli (Fig. 3). In both elements the fourth alveolus is the largest, followed by the third, and then by the first, with the second and the fifth being the smallest. In the right premaxilla, only the three posterior alveoli have preserved teeth. The first two are completely preserved, whereas the third one has its crown broken near the apex. Additionally, the first tooth preserved is smaller than the other two, likely being a more recently erupted tooth in its first stages of growth. In the left premaxilla, only the last two alveoli have teeth preserved. In the first, the apical crown is broken and only a basal portion of the tooth is preserved, whereas the second tooth is complete. These premaxillary teeth are conical, with a circular cross-section and with apices more robust than pointed.

Both premaxillae preserve four occlusion pits lingual to the upper tooth row ventrally (Fig. 3). The first and fourth occlusion pits are the deepest, in accordance with the fact that the first and fourth dentary teeth are largest among those that occlude with the premaxilla. Additionally, both of the last occlusion pits are situated between the sutures of each premaxilla with each maxilla. The fourth pit demonstrates that the fourth dentary tooth occludes in a pit, rather than in a notch, in *Acresuchus*.

The external naris is large (Fig. 2), with a roughly circular shape, and projects dorsally. In dorsal view, the incisive foramen may be seen in entirety through the external naris

(Fig. 2). Both nasal bones reach the external naris at its posterior margin, although not bisecting it (Fig. 2).

The premaxillary surface lateral to the external naris is smooth (i.e., without a notch), although this area shows a slight elevation (Fig. 2), mainly on the posterior margin, when compared with the remaining dorsal surface of the premaxillae. This area of the premaxillae also exhibits a roughly rugose surface—without marked ornamentation—in contrast to the marked ornamentation seen on the remaining surface of these bones. The dorsal premaxillary processes do not extend beyond the third maxillary alveoli.

Ventrally, the incisive foramen is small (i.e., less than half the greatest width of premaxillae sensu Brochu 2011, character 88-0), with a roughly 'teardrop-like' shape, i.e., with the anterior margin more lateromedially compressed than the posterior one (Fig. 3), although its posterior margin is discontinuous given the aforementioned rupture of the interpremaxillary suture seen in this specimen. Although the incisive foramen is situated far from the premaxillary tooth row at the level of the second or third alveolus, the rupture of the interpremaxillary suture in the region between the tip of the snout and the anterior margin of the incisive foramen leaves it unclear whether the foramen did or did not project between the first premaxillary teeth.

Maxillae—In ventral view, the maxillae have their most medial portion preserved until the level of the sixth maxillary alveolus. In both maxillae, the missing portion of the bones increases in a mediolateral direction until the most lateral portion of both bones reaches approximately the level of the 12th maxillary alveolus, a point after which both bones are no longer preserved (Fig. 3). Because the most posterior portions of the tooth rows of both maxillae are not preserved, the total number of maxillary alveoli was probably more than 12, but the exact number cannot be known.

In dorsal view, there is no rupture between the premaxillae and the maxillae as there is in ventral view. Posteriorly, however, the rupture between the maxillae and the rest of the skull comprises practically the same region as that visible in ventral view. The maxillae contact the premaxillae anteriorly and the nasals medially. Due to this fracture, none of the sutures of the maxillae with the bones they contact posteriorly are preserved (Fig. 2).

The maxillae of *Acresuchus pachytemporalis* form most of the snout, whereas their ventral (palatal) portions constitute a considerable part of the secondary palate, as in all living Crocodylia (Fig. 2). There is no sign of a possible ventral exposure of the vomer between the premaxillae and the maxillae in the holotype. Even though the area where the vomer could be exposed is fragmented, the visible arrangement of the bones in the area does not indicate a possible ventral exposure of the vomer between them.

The teeth (and alveoli) of both maxillae and dentaries are circular in cross-section (Figs. 3, 8). Occlusion pits of the dentary teeth located in the maxillae show that all dentary teeth occluded lingual to the maxillary teeth (Fig. 3). The fourth alveolus is the largest in the maxillary tooth row.

Dorsally in the maxillae, there are no signs of preorbital ridges. Very prominent 'canthi rostralli' are also absent in the new taxon. In the most posterior portions of both maxillae, in the area that would contact the lacrimals, there are several small depressions. The poor preservation of the area, however, leaves some doubt about whether these are real anatomical structures or simply fractures left on the dorsal area of the maxillae.

Nasals—The nasals of *Acresuchus pachytemporalis* are anteroposteriorly short and relatively wide mediolaterally (Fig. 2), similar to the morphology described for these bones in alligatorids by Iordansky (1973). The nasals are not completely preserved: the posterior-most portions of both nasals, which would contact the prefrontals and possibly the lacrimals, are missing due to the transverse rupture present in the skull. Anteriorly, each nasal contacts each corresponding premaxilla anterolaterally. Posterior to this, each nasal contacts the ipsilateral maxilla in all the area in which they are preserved (Fig. 2). In ventral view, when viewing dorsally through the rupture between the two maxillae, it is possible to see the internal dorsal roof of the narial passage, which is preserved until the level of the 14th alveolus of both maxillae (Fig. 3).

Prefrontals—Neither element is completely preserved, and their most anterior portions are missing due to the fracture present in the skull (Fig. 2). The descending processes of the prefrontals (the prefrontal pillars) are not preserved complete in the holotype of *Acresuchus pachytemporalis* (see Fig. 3). Whereas the left prefrontal preserves most of its original ornamentation of the dorsal surface, the right prefrontal has its dorsal surface mostly damaged, with nothing of the original ornamentation preserved. The prefrontals meet medially (Fig. 2).

In the prefrontals, or in their contacts with the lacrimals, there is no sign of prominent preorbital ridges. The prefrontal surface adjacent to the orbital rim, as well as the orbital rim as a whole, is smooth, with no presence of knob-like processes. The orbital rims of *Acresuchus* are upturned.

Lacrimals—The lacrimals are only partially preserved; their most anterior portions are lacking, just as with the surfaces of the prefrontals (Fig. 2). Therefore, although it is possible that the lacrimals of the holotype contacted the nasals medially, this cannot be demonstrated.

Frontal—The frontal is completely preserved (Fig. 2), forming the roof of the anterior part of the braincase as in all living Crocodylia (Iordansky, 1973). Its dorsal surface is well preserved, conserving most of the ornamentation of the bone (see Fig. 6) except in the area adjacent to the right prefrontal. Ventrally, the frontal preserves the cristae cranii frontales, a pair of descending crests that protect the olfactory tract in living Crocodylia (Iordansky, 1973; Fig. 3).

As described for the prefrontals, the lateral margins of the frontal are upturned, forming the dorsal edges of the orbits. Dorsally, the frontal contacts both prefrontals anteriorly through an acute anterior process projected between them (Fig. 2). Posteriorly, the frontal contacts each postorbital laterally, and the parietal posteriorly. The frontoparietal suture is located entirely on the skull table, not contacting the supratemporal fenestrae, and is concavoconvex sensu Brochu (1997, character 139-0; equivalent to Brochu's [2011] character 151-0). Posteroventrally, the frontal also contacts the laterosphenoid.

Postorbitals—The postorbitals are completely preserved, with both conserving their dorsal flat plates, which form the anterolateral corners of the cranial roof (Figs. 2, 6), as well as their descending processes, which constitute the dorsal portion of the postorbital bars (Fig. 3). Dorsally, all the sutures of both postorbitals are visible: with the frontal anteriorly, with the parietal medially, and with each corresponding squamosal posteriorly. The dorsal surfaces of the postorbital plates are dorsoventrally elevated, except in their most lateral portions. These surfaces are continuous with the elevation present in both squamosal bones, and this constitutes an important diagnostic feature of *Acresuchus pachytemporalis*, as described below.

The descending processes of the postorbitals articulate ventrally with ascending processes of each corresponding jugal to form the postorbital bar (Fig. 3). It is also possible that the descending processes of the postorbitals of this species articulated with ascending processes of each

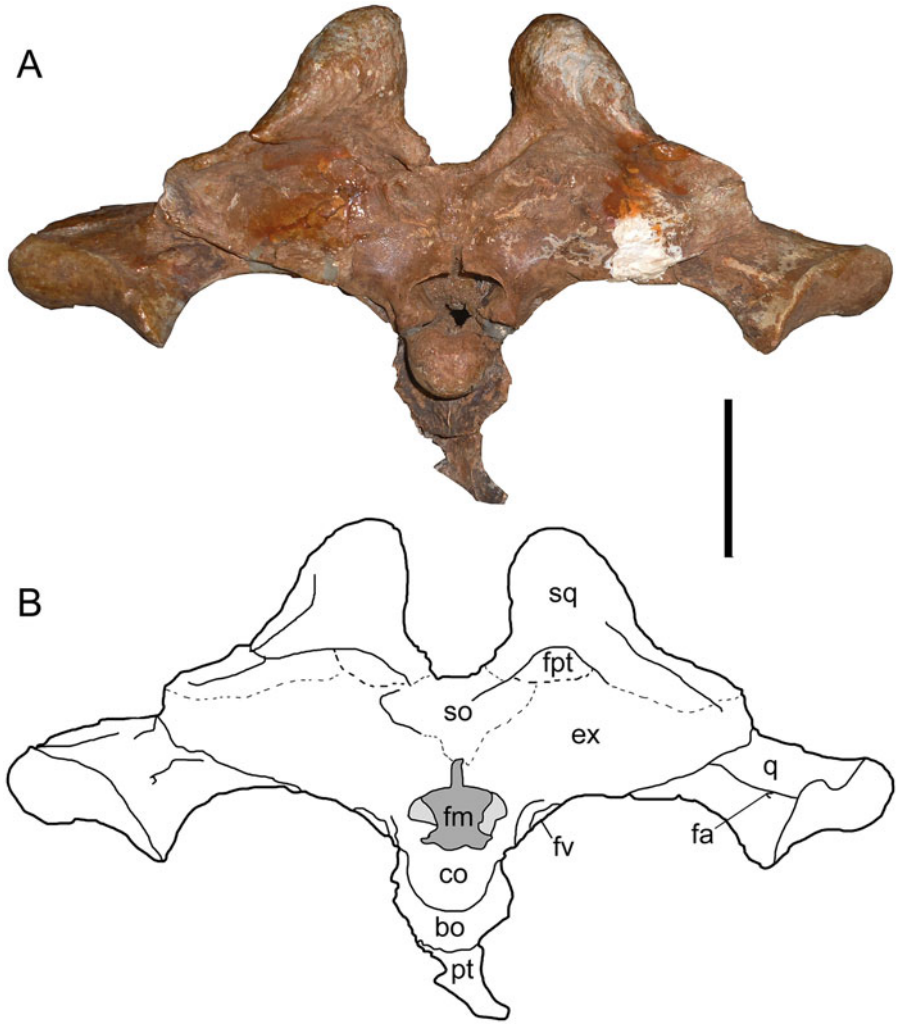

FIGURE 4. *Acresuchus pachytemporalis*, UFAC-2507, skull of the holotype. **A**, occipital view; **B**, schematic drawing illustrating bones and sutures. Scale bar equals 5 cm.

ectopterygoid as well. The ectopterygoids are not preserved in *Acresuchus pachytemporalis*, but in the lateral portion of, and also in the area immediately anterior to, each postorbital bar, there is a concavity that may correspond, at least partially, to the place where the ectpterygoids were situated (Fig. 3). If this interpretation is correct, then it is probable that the postorbitals indeed articulated with the ectopterygoids ventrolaterally at the postorbital bar, even though the possible sutural contacts between these two bones are also not discernible in the holotype. The postorbital bar is slender and bears a short, anteriorly directed process in its dorsal portion while also being inset from the anterolateral edge of the skull table.

Parietal—The parietal is completely preserved, constituting most of the roof of the braincase, as in all Crocodylia (Iordansky, 1973), as well as the medial margins of the supratemporal fenestrae, which in *Acresuchus* are of large size and roughly oval in shape (Figs. 2, 6). The parietal preserves most of the original ornamentation on its dorsal surface (Fig. 6). Anteriorly, the parietal contacts the frontal; laterally, on each side, the parietal contacts the postorbital anteriorly and the squamosal posteriorly. Posteriorly, the parietal contacts the supraoccipital and the squamosals and does not contact the posterior margin of the skull table (Figs. 2, 6).

Squamosal—Both elements are nearly completely preserved (Figs. 2, 4, 5, 10). In dorsal view, each squamosal contacts each corresponding postorbital anteriorly, and both meet anteromedially with the parietal and medially with the supraoccipital (Fig. 2). In occipital view, each squamosal meets each corresponding exoccipital ventrally and the supraoccipital medioventrally (Fig. 4). In lateral view, the squamosal contacts the postorbital anteroventrally and the quadrate ventrally; the squamosal and the quadrate constitute the margins of the otic apertures, each of which has a bowed posterior margin (Fig. 10). The dorsal and ventral rims of the squamosal groove are parallel (Fig. 10).

The most striking feature of this bone in *Acresuchus pachytemporalis* is the large eminence present in its lateral and posterior portions, which forms a 'horn' in the posterior portion of the skull table (Figs. 6, 10). Although most of the squamosal is elevated (except for the most medial portion of the bone, adjacent to the supraoccipital), the eminence is markedly larger posteriorly than anteriorly, surpassing significantly the level of the posterior margin of the skull table (Fig. 6).

Jugals—Both jugals are nearly completely preserved; most of the anterior portion of the left jugal is absent due to the transverse fracture present in the region anterior to the orbits; the anterior portion of the right jugal is preserved, but eroded (due to the same transverse fracture), preventing the limit with the maxilla from being properly distinguished (Fig. 2). Posterior to the fracture, the jugals are almost completely preserved dorsally and ventrally, aside from some erosion, in the ventral portion of both jugals, of the region immediately posterior to the fracture (Fig. 3). The right jugal is better

FIGURE 5. *Acresuchus pachytemporalis*, UFAC-2507, skull of the holotype in **A**, right and **B**, left lateral views. Scale bar equals 5 cm.

preserved, both in dorsal and ventral views, exhibiting some of the original ornamentation of its dorsal surface, whereas the left jugal exhibits a rather rough, slightly eroded surface in both dorsal and ventral views (Figs. 2, 3). The jugals are lateromedially slender and dorsoventrally low.

Anteriorly, the ascending process of the jugal contacts the ventrally descending process of the postorbital and, as such, constitutes the ventral portion of the postorbital bar (Fig. 3), which is ventrally inset to the jugal as is typical in Brevirostres (Brochu, 1997). As mentioned previously, the ectopterygoids are not preserved, but there are concavities in the areas close to the ventral portion of each postorbital bar that may, at least partially, correspond to the areas where the ectopterygoids would be positioned. If this interpretation is correct, that would mean that the jugals of *Acresuchus pachytemporalis* would contact each corresponding ectopterygoid ventromedially, as is common in Crocodylia (see Iordansky, 1973). Posteriorly, both jugals contact each corresponding quadratojugal, both dorsally and ventrally (Figs. 2, 3).

The jugal forms the lateral margin of the orbits and infratemporal fenestrae (Fig. 2). The medial jugal foramen is small (Brochu, 2011, character 102-0), as in most eusuchians (Brochu, 1997). In lateral view, the portion that forms the lateral margins of the orbits presents its dorsal margin as linear and more elevated than the dorsal margin of the jugal portion that forms the lateral margins of the infratemporal fenestrae. These latter margins are concave on their dorsal surfaces, giving a rounded aspect to the triangular shape of the infratemporal fenestrae.

Quadratojugals—Both elements are nearly completely preserved. In dorsal view, the left quadratojugal still preserves most of its original ornamentation (Fig. 2). The right quadratojugal, however, has a rather rough, slightly damaged surface (Fig. 3). The quadratojugals contact the jugal anterolaterally, projecting a long anterior process along the lower temporal bar (Fig. 2). Posteriorly, the quadratojugal contacts the quadrate (Figs. 2, 3).

FIGURE 6. *Acresuchus pachytemporalis*, UFAC-2507, dorsal surface of the skull table. Scale bar equals 5 cm.

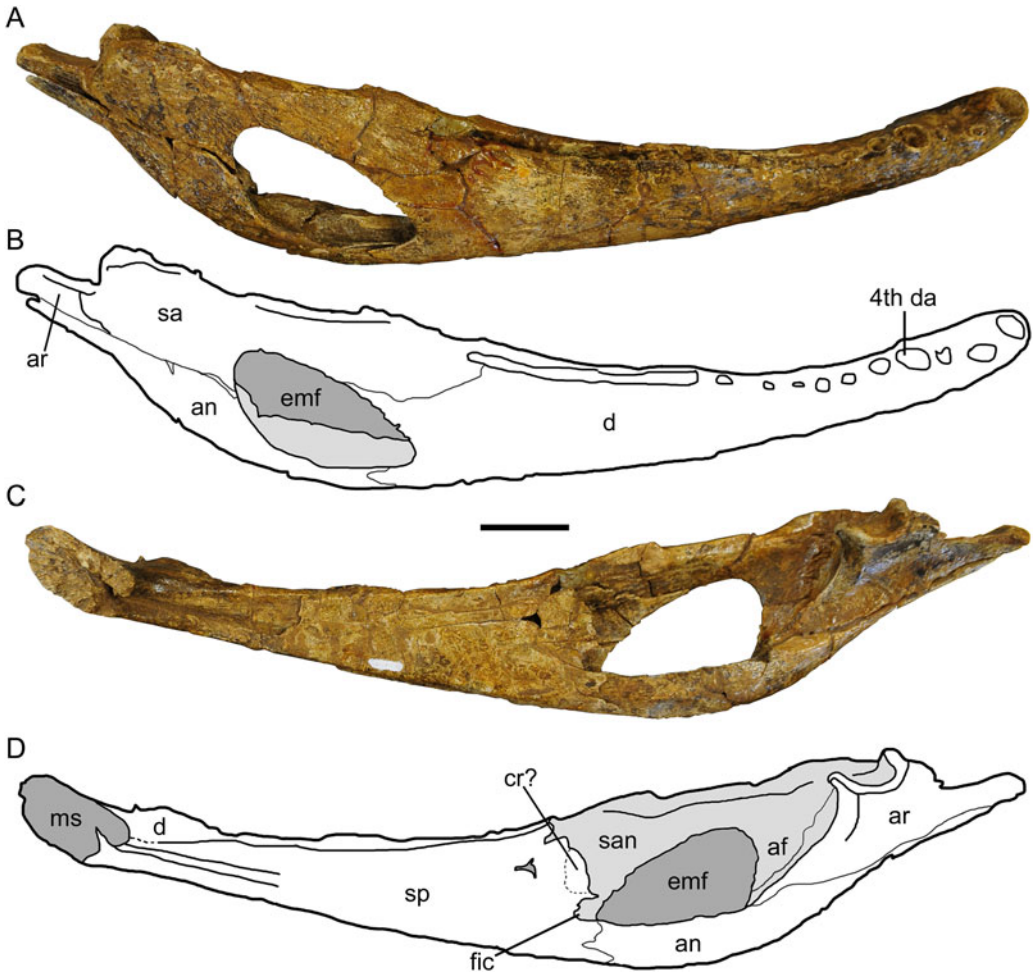

FIGURE 7. *Acresuchus pachytemporalis*, UFAC-2507, right mandibular ramus, photographs and schematic drawing illustrating bones and sutures in **A**, **B**, lateral and **C**, **D**, medial views. Scale bar equals 5 cm.

The quadratojugal constitutes the entire posterior angle of the infratemporal fenestra, preventing any participation of the jugal (Fig. 2). The quadratojugal spine is absent.

Quadrates—Both quadrates are completely preserved (Figs. 2, 3). The quadrate contacts the quadratojugal anterolaterally and the squamosal dorsomedially. In the anterior region of the braincase, the quadrate contacts the laterosphenoid and the pterygoid anteriorly and the postorbital dorsally.

In occipital view, the quadrate has a medial oblique contact with the exoccipital (Fig. 4). The foramen aereum is small and situated in a notch on the dorsal surface of the bone. On the ventral surface of the quadrate, crests for insertion of tendons and aponeuroses of the mandibular adductor muscles are present (Iordansky, 1973). On the left quadrate, crests that may correspond to crests 'A' and 'D' of Iordansky (1973) are remarkably evident.

The contact facet of the quadrate with the articular bone is a wide, convex, and smooth surface. The surface is slightly posteromedially displaced, with the small medial hemicondyle displaced in a more posteroventral direction (Fig. 4).

Supraoccipital—The supraoccipital is nearly completely preserved. In dorsal view, the bone has a large exposure on the skull table, contacting the parietal anteriorly (Fig. 2). The supraoccipital also contacts the squamosals laterally (in both dorsal and occipital views; Figs. 2, 4) and the exoccipitals laterally and ventrally (in occipital view only; Fig. 4).

Both posttemporal fenestrae are preserved. These structures are delimited dorsally and laterally by the squamosals, ventrolaterally by the exoccipitals, and ventromedially by the supraoccipital (Fig. 4). The dorsal, ventral, and medial borders of the fenestrae are surrounded by bony crests, which are absent in the lateral portion of the fenestrae.

Exoccipitals—The exoccipitals of *Acresuchus pachytemporalis* are nearly completely preserved, forming most of the occipital surface of the skull table. They contact the squamosals dorsally, the supraoccipital dorsomedially, and the quadrates laterally (Fig. 4) through a rather oblique contact in which the cranioquadrate canal exit is situated, as is common in Crocodylia (Iordansky, 1973). The cranioquadrate canal extends to the middle ear cavity, providing passage for the main branch of the facial nerve (cranial nerve VII), the orbitotemporal artery, and the lateral cephalic vein (Iordansky, 1973). The exoccipitals also meet each other medially (even though the area in which they meet is fractured) and dorsally at the foramen magnum, thus preventing the supraoccipital from contacting this foramen (Fig. 4) as is common in Crocodylia (Iordansky, 1973).

Ventrally, the exoccipital is not very well preserved lateral to the foramen magnum and occipital condyle. As a result, it is

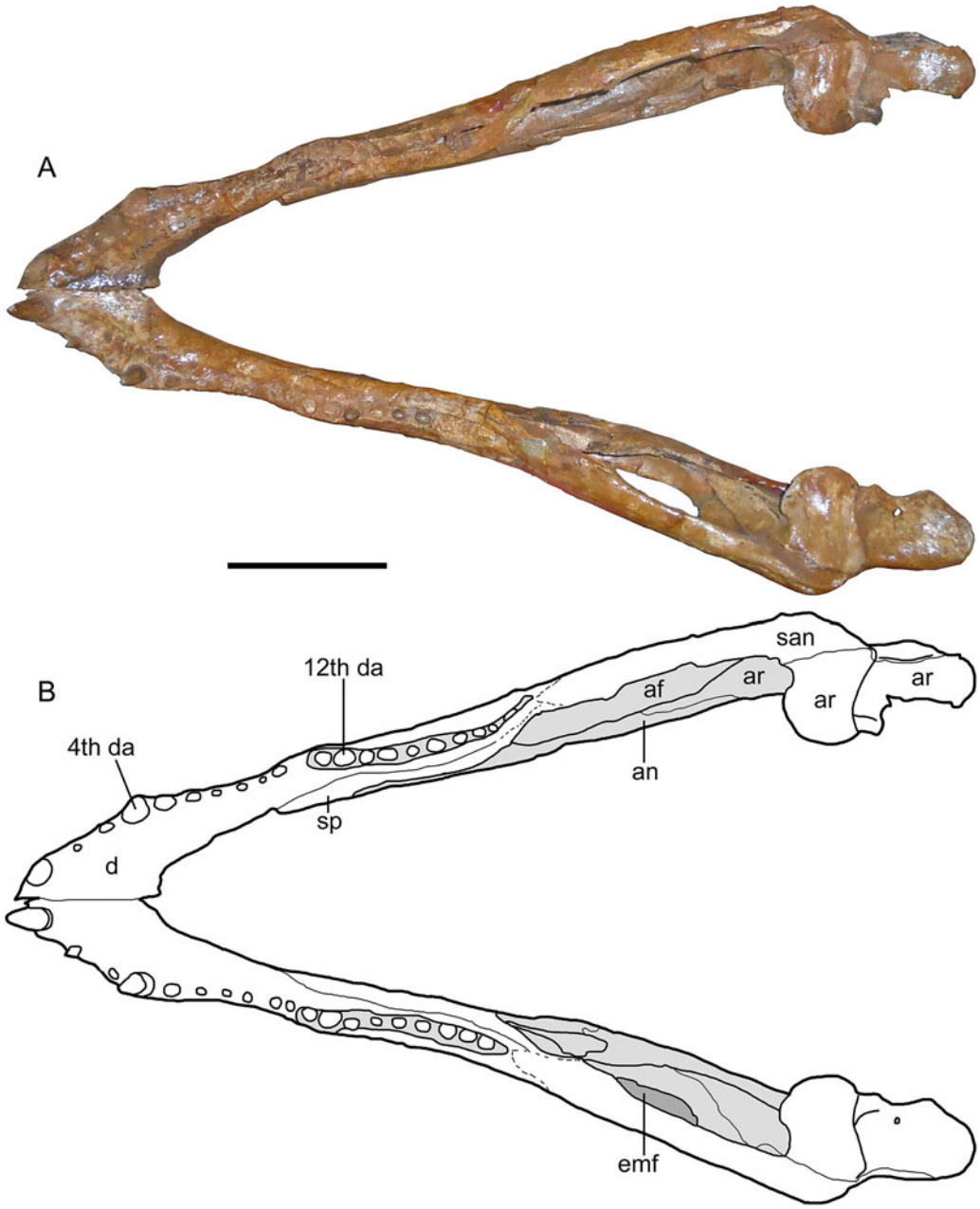

FIGURE 8. *Acresuchus pachytemporalis*, UFAC-2507, holotype, right (upper) and left (lower) mandibular rami. **A**, dorsal view; **B**, schematic drawing illustrating bones and sutures. Scale bar equals 10 cm.

not possible to assess whether the ventral processes of the exoccipitals lateral to the basioccipital were slender or robust (Brochu, 2011, character 176). Dorsal to this area, there are three circular openings. The ventral opening is here interpreted as the carotid foramen, for the passage of the internal carotid artery (Bona and Desojo, 2011; = foramen caroticum posterius of Iordansky, 1973). Dorsal to this, there are two openings: the medial one, smaller, is here interpreted as an opening for cranial nerve XII, following Iordansky (1973). The lateral, larger, one is here interpreted as being the foramen vagus, which contains cranial nerves IX and X, as well as the ramus communicans that connects cranial nerves VII and IX (Iordansky, 1973).

Basioccipital—The basioccipital is nearly completely preserved. The occipital condyle is complete (Fig. 4), formed exclusively by the basioccipital, as in all Crocodylia (Iordansky, 1973). Ventral to the condyle, the basioccipital plate (sensu Iordansky, 1973) is nearly complete (Figs. 4, 11) and is oriented posteriorly sensu Brochu (2011, character 170-1). The ventral and lateral margins of the plate, which form the basioccipital tubera (see Brochu, 1997, character 162, and the equivalent of Brochu's [2011] character 176) are slightly eroded, although the general morphology of the plate is preserved. The basioccipital tubera of *Acresuchus pachytemporalis* are not very developed. The medial crest of the basioccipital is preserved (Fig. 4). In living crocodylians, the tubera and the medial crest serve

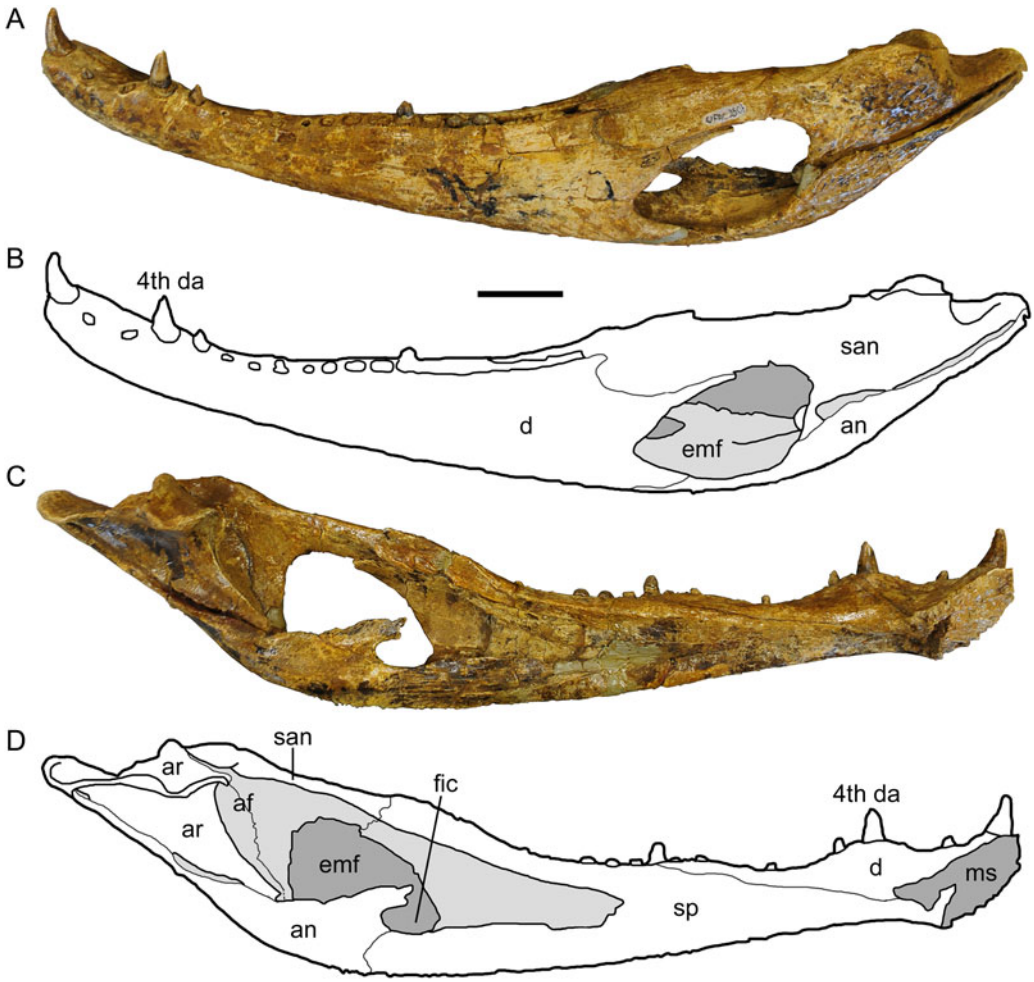

FIGURE 9. *Acresuchus pachytemporalis*, UFAC-2507, holotype, left mandibular ramus, photographs and schematic drawings illustrating bones and sutures in **A**, **B**, lateral and **C**, **D**, medial views. Scale bar equals 5 cm.

as attachments for the tendons of the muscles basioccipitovertebralis and occipitotransversalis profundus (Iordansky, 1973).

Basisphenoid—The basisphenoid is partially preserved (Fig. 11). It is possible to observe that the basisphenoid forms the anterior wall of the medial eustachian canal, because it contacts the basioccipital plate posteriorly. Only a proximal portion of the basisphenoid rostrum is preserved (Fig. 11).

Pterygoids—Only part of the pterygoids are preserved. In anterior view of the basicranium, the pterygoids contact the laterosphenoids dorsally and the basisphenoid anteromedially (Fig. 11). Ventral to the basisphenoid and the basioccipital, a small fragment of the pterygoids is preserved (Fig. 3), composed mostly of the right posteromedial ascending process of the bone (sensu Iordansky, 1973). No other portions of the pterygoids are preserved.

Laterosphenoid—Both bones are nearly completely preserved, forming the anterior parts of the lateral walls of the braincase and surrounding the foramen ovale, as is common in Crocodylia (Iordansky, 1973). It also extends dorsally to form the anteroventral area of the medial wall of the supratemporal fenestrae (Fig. 11), as described for *Caiman latirostris* by Bona and Desojo (2011). The laterosphenoid contacts the frontal and the postorbital dorsally, the quadrate posteriorly, and the basisphenoid and the pterygoid ventrally (Fig. 11). The laterosphenoids also contact each other medially through their anterodorsal portions. They, along with frontal bone dorsally, form the circular foramen for the olfactory tract of the forebrain.

Mandible of the Holotype

Dentary—Both dentaries of *Acresuchus pachytemporalis* are almost completely preserved, with some wear on their surfaces (Figs. 7–9). The dentaries form the greatest portion of the mandibular ramus, as in Crocodylia (Iordansky, 1973), specifically in lateral and dorsal view. The dentary contacts the splenial posteromedially and both the surangular and angular posteriorly, while also forming the anterior margin of the external mandibular fenestra. The dentary-surangular suture contacts the external mandibular fenestra anterior to the posterodorsal corner (Figs. 7, 9).

The mandibular symphysis of *Acresuchus* extends to the level of the fifth alveolus (character 49-0; Fig. 8). The anterior teeth project anterodorsally. The teeth and alveoli of the dentary, as well as those of the maxillae, are circular in cross-section. The first and fourth dentary teeth (only preserved in the left dentary) are noticeably the largest. The fourth alveolus is separated from—and larger than—the third. Between the fourth and the 10th alveoli, the dentary is 'gently curved'

FIGURE 10. *Acresuchus pachytemporalis*, UFAC-2507, skull table of the holotype in **A**, right and **B**, left lateral views. Scale bar equals 3 cm.

(sensu Brochu, 2011, character 50-0; see Fig. 8). The 12th alveolus is the largest of those situated posterior to the fourth (character 51-2).

Splenial—Both elements are nearly completely preserved (Figs. 7, 9), each forming a considerable part of the medial portion of the mandible. The left splenial is missing the posterior-most portion of its dorsal region (Fig. 9). The right splenial is also missing a portion in a similar area, although to a lesser degree than the left splenial. Additionally, the right splenial is also missing its anterior-most portion, which contacts the dentary dorsally and anteriorly, medially exposing the anterior portion of the Meckelian canal (Fig. 7). The splenial contacts the dentary dorsally and anteriorly, the surangular posterodorsally, and the angular and the coronoid, which are only preserved posteriorly on the right side (Fig. 7, 9). The splenial of *Acresuchus pachytemporalis* does not participate in the mandibular symphysis (Figs. 7, 9), with its anterior tip passing dorsal to the Meckelian groove.

Coronoid—Only a medial part of the most medial portion of the right coronoid is possibly preserved (Fig. 7), with the most dorsal and ventral parts of the medial portion being absent. This tentative portion of the coronoid is situated dorsal to the anterior margin of the incompletely preserved foramen intermandibularis caudalis (Fig. 7).

Surangular—Both surangulars of *Acresuchus pachytemporalis* are nearly completely preserved. The surangular forms the dorsal region of the adductor fossa in medial view, as well as the posterior portion of the dorsal margin and the dorsal portion of the posterior margin of the external mandibular fenestra in lateral view. It contacts the dentary anteriorly and anterolaterally, the splenial anteromedially, the articular posteriorly and medially, and the angular ventromedially and posteroventrally (Figs. 7–9).

Medially, the surangular-angular suture meets the articular dorsal to the latter's ventral tip. Additionally, in this view the surangular contacts the articular continuously, without a sulcus; it 'flushes' against the articular, sensu Brochu (2011, character 74-1).

Dorsally, the surangular continues to the dorsal tip of the lateral wall of the glenoid fossa, as in most eusuchians, whereas the surangular-articular suture is orientated anteroposteriorly within the fossa. Posterior to this, the left surangular extends to the posterior end of the retroarticular process, whereas the right surangular is broken at its posterior-most extent.

The external mandibular fenestra is present and is very large in the new taxon (Fig. 7, 9), allowing most of the foramen intermandibularis caudalis to be visible in lateral view (Brochu, 2011, character 63-2). Even though this foramen is not entirely

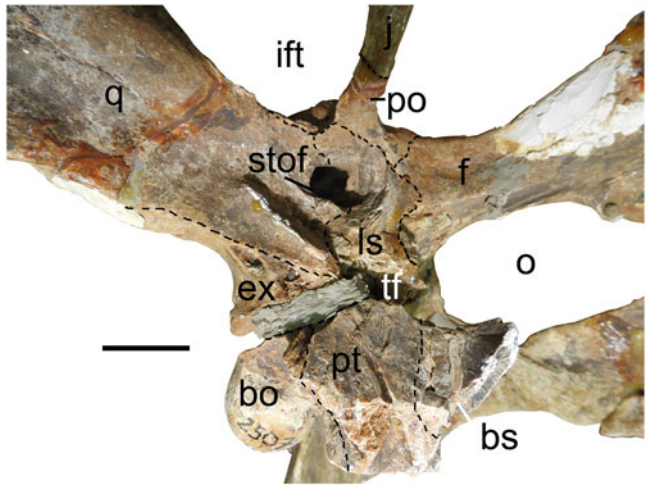

FIGURE 11. *Acresuchus pachytemporalis*, UFAC-2507, holotype, posterior portion of the skull in anterolateral view. Scale bar equals 5 cm.

preserved on either side, the position of this opening can be seen in the left mandibular ramus (Fig. 9). The angular-surangular suture passes broadly along the ventral margin of the external mandibular fenestra (Brochu, 2011, character 60-1; Figs. 7, 9).

Angular—The angulars are nearly completely preserved (Figs. 7–9). Both lack the dorsal part of their anterior-most portion in medial view, which would constitute the dorsal portion of the foramen intermandibularis caudalis (Figs. 7, 9). The right angular lacks this region completely (Fig. 7), implying that the posterior margin and most of the dorsal margin of the foramen intermandibularis caudalis are not preserved. Meanwhile, the left angular preserves only its posterior portion, in such a way that at least the posterior margin of the foramen is preserved, as well as the most posterior portion of the dorsal margin of the foramen (Fig. 9). In medial view, the bone contacts the splenial anteriorly, the coronoid dorsally, and the articular posterodorsally; in lateral view, it contacts the dentary anteriorly and the surangular dorsally (Figs. 7, 9). In dorsal view, the angular also has lateral contacts with the surangular anteriorly and the articular posteriorly (Fig. 8).

Articular—The articulars are completely preserved, including the retroarticular processes, the glenoid fossae, and the

descending processes of both (Figs. 7–9). The only considerable damage is a circular hole near the medial margin of the retroarticular process of the left articular (Fig. 8). The glenoid fossa serves as the articular surface with the hemicondyles of the quadrate, as in all Crocodylia (Iordansky, 1973). The articular surface of the glenoid fossa is smooth, with the medial portion slightly more ventrally displaced than the lateral one. The retroarticular process projects posterodorsally. The articular contacts the surangular ventrolaterally (through its descending process) and dorsolaterally (through the glenoid fossa and the retroarticular process) and the angular ventromedially (through its descending process) and ventrally, in medial view (Figs. 7–9).

Teeth

The teeth of *Acresuchus pachytemporalis* have well-marked, non-serrated carinae, and the enamel presents some longitudinal lines parallel to the carinae.

Referred Specimens

The 10 referred specimens of *Acresuchus pachytemporalis* all consist of isolated skull tables with variable sizes and degrees of preservation (Fig. 12). All of the specimens preserve the parietal, both postorbitals (except UFAC-6384, which only preserves the right postorbital), the supraoccipital, and the most posterior portion of the frontals; three of these specimens preserve a larger part of the most posterior portion that the others (Fig. 12). Six of the specimens (UFAC-1486, UFAC-3142, UFAC-4153, UFAC-4154, UFAC-4183, and UFAC-4678) also preserve the squamosals and part of the quadrates and of the exoccipitals. Two specimens (UFAC-1187 and UFAC-5256) also preserve only part of the squamosals, the quadrates, and the exoccipitals. Specimen UFAC-1379 preserves the left squamosal and part of the right squamosal and the exoccipitals, and UFAC-6384 also preserves the right squamosal and part of the right exoccipital.

Seven of the referred specimens (UFAC-1486, UFAC-3142, UFAC-4153, UFAC-4154, UFAC-4183, UFAC-4678, and UFAC-6384) can be assigned to the new taxon because they exhibit the upturning on the posterolateral margin of the squamosal bone throughout the entire lateral margin, with a dorsoventral expansion of the posterior portion of the eminence that is an autapomorphy of *Acresuchus pachytemporalis* within Caimaninae. The other three (UFAC-1187, UFAC-1379, and UFAC-5256) have the posterior portions of their squamosals (the portion in which the eminence is larger in *A. pachytemporalis*) incomplete, except for the right squamosal of UFAC-1379, which is more complete and exhibits the eminence (Fig. 12I). However, the postorbitals and the anterior portions of the squamosals in these specimens are not elevated as in the other referred specimens and in the holotype (see Figs. 2, 4–6, 12). Nevertheless, the three specimens can be assigned to the new species for exhibiting supratemporal fenestrae that are large, significantly longer than wide, with an oval shape (which is a unique synapomorphy of the *Acresuchus* + *Purussaurus* clade) and for exhibiting a straight posterior margin of the skull table, which is present in *A. pachytemporalis* (Fig. 6) but absent in *Purussaurus* (Cidade et al., 2017). The differences observed between UFAC-1187, UFAC-1379, UFAC-5256, the holotype, and the other specimens referred to *A. pachytemporalis* raise the possibility that either the size of the eminence is intraspecifically variable or that the specimens may belong to another species of *Acresuchus*. Additionally, however, the three specimens have a relative small size when compared with the other referred specimens and the holotype (Figs. 2, 12). This in turn raises the possibility that the smaller size of the eminence may be related to a difference in ontogenetic development, which is observed in extant crocodylians (as it is in *Crocodylus niloticus* and other species of *Crocodylus* according to Brochu et al., 2010). Another possibility is that the difference is due to sexual dimorphism; the possibility that the eminences could be used in courtship or mating displays is examined in the discussion.

COMPARISONS

Skull

Premaxillae—The premaxillae of *Acresuchus pachytemporalis* exhibit the same general morphology as those of nearly all brevirostrine crocodylians (Fig. 2), including all caimanines except for *Mourasuchus*, which exhibits dorsoventrally flattened premaxillae that follow the overall aspect of the rostrum in this group (see Price, 1964; Bocquentin-Villanueva, 1984). The presence of five alveoli in each of the premaxillae is the morphology in all alligatoroids except for *Paleosuchus*, which has four alveoli (Brochu, 1999). The presence of tooth occlusal surfaces between the sutures of each premaxilla with each maxilla, on both sides, is considered a common feature among alligatorids by Iordansky (1973). The fourth dentary tooth occluding in a pit rather than in a notch in *Acresuchus* is a well-known feature of most alligatoroids, with exception of *Leidyosuchus canadensis* Lambe, 1907, and *Diplocynodon remensis* Smith, De Lapparent, and Delfino, 2014, which have the fourth and fifth dentary teeth occluding in a notch (Brochu, 1999, 2011; Wu et al., 2001; Smith et al., 2014).

The large, roughly circular shape of the external naris of *Acresuchus pachytemporalis* (Fig. 2) is a morphology shared with most Eusuchia, with the exceptions of *Mourasuchus amazonensis* Price, 1964, *M. pattersoni* Cidade, Solórzano, Rincón, Riff, and Hsiou, 2017, *Purussaurus mirandai* Aguilera, Riff, and Bocquentin-Villanueva, and *P. brasiliensis* (Price, 1964; Bocquentin-Villanueva et al., 1989; Aguilera et al., 2006; Cidade et al., 2017). The dorsal projection of the external naris in *Acresuchus* is also present in all caimanines except *Tsoabichi greenriverensis* and *Caiman wannlangstoni* Salas-Gismondi, Flynn, Baby, Tejada-Lara, Wesselingh, and Antoine, 2015 (Brochu, 2010; Salas-Gismondi et al., 2015). The nasal bones reaching the external naris in its posterior margin but not bisecting the naris is a feature observed in all caimanines except *Mourasuchus* (Price, 1964; Bocquentin-Villanueva, 1984), *Caiman gasparinae* (Bona and Carabajal, 2013), and *Globidentosuchus* Scheyer, Aguilera, Delfino, Fortier, Carlini, Sánchez, Carrillo-Briceño, Quiroz, and Sánchez-Villagra, 2013 (Scheyer et al., 2013), in which the nasals are excluded from the external naris, at least externally.

The smooth premaxillary surface lateral to the external naris, without the presence of a notch, is a feature shared with all caimanines except *Gnatusuchus* Salas-Gismondi, Flynn, Baby, Tejada-Lara, Wesselingh, and Antoine, 2015, *Mourasuchus atopus* (Langston, 1965), and *M. arendsi* Bocquentin-Villanueva, 1984. The presence of a slight elevation mainly in the posterior margin of the premaxillary surface lateral to the external naris, and its more rugose surface, is also seen in some specimens of caimanine taxa analyzed for this study, such as *Caiman crocodilus* (AMNH 43291), *Melanosuchus niger* (AMNH R-58130), and *Paleosuchus palpebrosus* (AMNH 93812). This elevation may correspond to the 'posterolateral ridge' that Bona and Desojo (2011) referred to as being present in *Caiman latirostris*. It is noteworthy that, although elevated, the lateral surface of the external naris in *Acresuchus* is not considered here to be similar to the thin crest reported in *Tsoabichi greenriverensis*

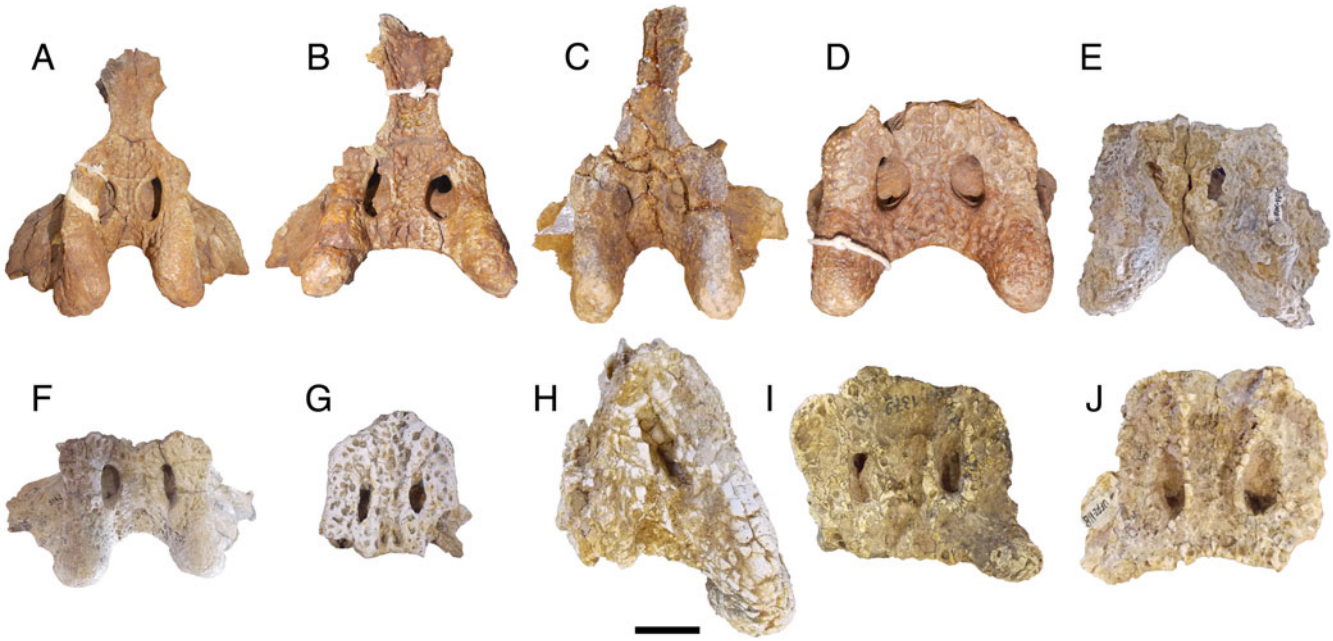

FIGURE 12. *Acresuchus pachytemporalis*, referred specimens in dorsal view. **A**, UFAC-4678; **B**, UFAC-4154; **C**, UFAC-4183; **D**, UFAC-4153; **E**, UFAC-1486; **F**, UFAC-3142; **G**, UFAC-5256; **H**, UFAC-6384; **I**, UFAC-1379; **J**, UFAC-1187. Scale bar equals 1 cm.

by Brochu (2010), while also being different from the marked knob seen around the external naris in *Mourasuchus arendsi* (Cidade et al., 2017). The condition of the dorsal premaxillary processes not extending beyond the third maxillary alveolus seen in *Acresuchus* is also the condition in all caimanines except *Mourasuchus* (Price, 1964; Bocquentin-Villanueva, 1984) and *Caiman brevirostris* Souza-Filho, 1987 (Fortier et al., 2014).

Maxillae—The absence of an exposure of the vomer between the premaxillae and the maxillae in *Acresuchus* is shared with most eusuchians, because such exposure occurs only and consistently in both species of *Melanosuchus* (Brochu, 1997, 1999).

The teeth and alveoli of both maxillae and dentaries being circular in cross-section differs from the laterally compressed posterior teeth seen in *Kuttanacaiman* Salas-Gismondi, Flynn, Baby, Tejada-Lara, Wesselingh, and Antoine, 2015, *Paleosuchus*, and *Mourasuchus*. All dentary teeth occluding lingually to the maxillary teeth is a morphology also seen in living alligatorids (Brochu, 1997). The fourth alveolus as the largest of the maxillary tooth row is a feature shared with all caimanines except *Culebrasuchus*, *Gnatusuchus*, and *Globidentosuchus*.

The absence of preorbital ridges seen in *Acresuchus* is a morphology shared with all alligatoroids (see Brochu, 1997), whereas the absence of very prominent 'canthi rostralli' is the same morphology present in most caimanines except *Purussaurus mirandai*, *Melanosuchus*, *Caiman latirostris*, *C. brevirostris*, and *C. wannlangstoni*. The tentative small depressions present in the most posterior portions of both maxillae may be homologous to the similar shallow depressions present in *P. neivensis* (Mook, 1941) and to the accentuated depressions of *P. mirandai* and *P. brasiliensis*. The presence of the accentuated depressions in *P. mirandai* and *P. brasiliensis* has been associated with the biting performance of these forms (Aureliano et al., 2015), as will be discussed below.

Nasals—The nasals of this taxon are longer than the remarkably short nasals present in *Purussaurus neivensis* and *Purussaurus brasiliensis* (Bocquentin-Villanueva et al., 1989; Aguilera et al., 2006). The reduction of the nasals in these two *Purussaurus* species, however, is evidently related to the accentuated increase in the size of the external naris present in both, which is not so accentuated in *P. neivensis* (see Aguilera et al., 2006) or *Acresuchus.* These differences in the size of the external naris may be related to the evolution of gigantism in the *Purussaurus* lineage, as will be discussed later.

Prefrontals—The medial contact between the prefrontals is also present in many taxa within Caimaninae, such as *Purussaurus*, *Mourasuchus*, *Kuttanacaiman*, *Globidentosuchus*, *Melanosuchus fisheri*, *Caiman yacare*, *C. wannlangstoni*, and some individuals of *C. crocodilus* (Brochu, 1999, 2013; Cidade et al., 2017).

The absence of prominent preorbital ridges in *Acresuchus pachytemporalis* is a common feature among neosuchians (Brochu, 1997). The absence of knob-like processes in the prefrontal surface adjacent to the orbital rim is similar to the morphology of most eusuchians and all caimanines except for *Mourasuchus*, which has a marked knob in the anteromedial region of the orbits (Bona et al., 2013b). The upturning of the orbital rims is a morphology shared by all caimanines except *Gnatusuchus*, *Kuttanacaiman*, *Globidentosuchus*, and *Culebrasuchus* (Fig. 2).

Frontal—The placement of the frontoparietal suture entirely on the skull table is a morphology shared with all caimanines. The concavoconvex shape of the frontoparietal suture is a character shared with many caimanines, such as *Purussaurus*, *Gnatusuchus*, *Globidentosuchus*, *Caiman crocodilus*, *C. yacare*, *C. wannlangstoni*, and *C. brevirostris*.

Postorbitals—A slender postorbital bar inset from the anterolateral edge of the skull table with a short, not prominent, process is a set of a characters shared between *Acresuchus pachytemporalis* and most eusuchians (see Brochu, 1997).

Parietal—The parietal not contacting the posterior margin of the skull table is a feature common to all caimanines for which this part of the skull is known, except *Tsoabichi*, *Paleosuchus*,

and what is described for *Purussaurus mirandai* (see Aguilera et al., 2006:fig. 7).

The large, roughly oval, supratemporal fenestrae of *Acresuchus pachytemporalis* are similar to the supratemporal fenestrae of the species of *Purussaurus* (see Aguilera et al., 2006; Aureliano et al., 2015). However, in all other eusuchians, the supratemporal fenestrae have a different morphology. In most non-caimanine eusuchians, these fenestrae are not overhung by the dermal bones delimiting it, exhibiting a 'fossa' in its surroundings (Brochu, 2011, character 152-0). Within Caimaninae, most fossil and extant species exhibit small fenestrae, of which most are rounded in shape, although some taxa exhibit oval supratemporal fenestrae, such as *Tsoabichi greenriverensis* (Brochu, 2010), *Caiman lutescens* (Bona et al., 2013b), and at least some specimens of *Melanosuchus niger* (AMNH R-58130, MN-3174, MCT-286-RR). These are strikingly smaller than those of *Acresuchus* and *Purussaurus* relative to the size of the skull table. Moreover, in *Paleosuchus*, the fenestrae close during ontogeny in most individuals (Brochu, 1997). The large size of the supratemporal fenestrae in *Acresuchus* and *Purussaurus* may be related to an increase of the insertion area of the M. adductor mandibulae externus profundus (Iordansky, 1973; Holliday and Witmer, 2007; = M. pseudotemporalis of Schumacher, 1973) or to a thermoregulation function of the brain, both of which may be related to increasing size in the *Acresuchus* + *Purussaurus* lineage, as will be discussed later.

Squamosal—The bowed posterior margin of the otic apertures is a morphology shared with most taxa of the clades Alligatoroidea and Crocodyloidea (see Brochu, 2011). The parallel dorsal and ventral rims of the squamosal groove are also present in most eusuchians (Brochu, 1997).

The most striking feature of this bone in *Acresuchus pachytemporalis* is the large eminence present in its lateral and posterior portions, which forms a 'horn' in the posterior portion of the skull table (Figs. 6, 10). Although most of the squamosal is elevated (except for the most medial portion of the bones, adjacent to the supraoccipital), the eminence is markedly larger posteriorly than anteriorly, surpassing significantly the dorsal level of the posterior margin of the skull table (Figs. 6, 10).

These highly hypertrophied, posterolaterally positioned 'horns' of *Acresuchus pachytemporalis* are also seen in the alligatorid *Ceratosuchus burdoshi* Schmidt, 1938 (Fig. 13C), from the Paleocene of the U.S.A. (Schmidt, 1938; Bartels, 1984). The morphology of these two taxa led to the creation of a new state for Character 156 that concerns this feature (see Appendix S1 in Supplementary Data 1). Within Caimaninae, both *Purussaurus neivensis* and *P. mirandai* have the lateral margins of the squamosals upturned, but not to the degree seen in the new taxon. Additionally, the lateral margins of the squamosals of *P. neivensis* and *P. mirandai* are uniformly elevated, without the distinct 'second' elevation that occurs from the posterior portion of the supratemporal fenestrae in *Acresuchus pachytemporalis*. The species *Mourasuchus arendsi* also has hypertrophied squamosals (Gasparini, 1985; Bona et al., 2013a; Cidade et al., 2018; Scheyer and Delfino, 2016; Fig. 13B), but these differ from those of *Acresuchus pachytemporalis* by having the entire dorsal surface elevated, not only the lateral portion.

Outside Caimaninae, other crocodylians also exhibit hypertrophied squamosals. The extinct *Aldabrachampsus dilophus* Brochu, 2006, the extant *Crocodylus siamensis* Schneider, 1801 (Brochu et al., 2010) and *Crocodylus rhombifer* Cuvier, 1807 (Brochu, 2000; Fig. 13A), and some large individuals of most extant species of *Crocodylus* Laurenti, 1768, such as *C. niloticus* (Brochu et al., 2010; G.M.C., pers. observ.), have their lateral margins of the squamosals elevated, but not as prominently as in *Acresuchus pachytemporalis*. The extinct *Voay robustus* (Grandidier and Vaillant, 1872) has its squamosals more hypertrophied in the posterior portion of the bones (see Brochu, 2007), like in the new taxon, but differs from the latter by presenting a lateromedial expansion (Fig. 13D). This last morphology has also led to the creation of another new state for Character 156 (see Appendix S1). The extinct *Crocodylus anthropophagus* Brochu, Njau, Blumenschine, and Densmore, 2010, also has hypertrophied squamosals (Brochu et al., 2010), but the holotype material is too fragmented to allow a thorough comparison between the morphology of the squamosal, as a whole, and the squamosal of other species.

As such, the hypertrophied squamosals of *Acresuchus pachytemporalis*—with an eminence larger in the posterior portion of the lateral margins of the squamosals in which there is not a lateromedial expansion—may be seen as an unique feature of this species within Caimaninae and hence as a diagnostic feature of the new taxon, being shared only with the alligatorine *Ceratosuchus burdoshi*. Moreover, the evolution of these squamosal horns in the *Acresuchus* + *Purussaurus* clade may be related to the evolution of gigantism in this lineage, as will be detailed in Discussion, below.

Jugals—The mediolaterally slender and dorsoventrally low jugals of *Acresuchus pachytemporalis* are similar to those present in most eusuchians and all caimanines except *Mourasuchus amazonensis* and *M. pattersoni* (Cidade et al., 2017).

Quadratojugals—The long anterior process of the quadratojugal along the lower temporal bar (Brochu, 2011, character 144-0) observed in *Acresuchus pachytemporalis* is also present in most eusuchians and all alligatoroids for which the character is known (Brochu, 2011). The posterior angle of the infratemporal fenestra being composed entirely of the quadratojugal, preventing any participation of the jugal, is a morphology shared with most eusuchians and with all alligatoroids for which this character is known (Brochu, 2011; Fig. 2). The absence of the quadratojugal spine is shared with most alligatoroids (Brochu, 2011).

Quadrates—The small size of the foramen aereum is a morphology shared with most eusuchians, whereas its location on the dorsal surface and in a notch (Brochu, 2011, character 181-1) are features shared with most alligatoroids (Brochu, 2011).

Supraoccipital—The posttemporal fenestrae of *Acresuchus pachytemporalis*, which are delimited ventromedially by the supraoccipital, are not proportionally as large in this taxon as in *Purussaurus* and not as anteroposteriorly deep as in *Mourasuchus* (see Bona et al., 2013a, 2013b), resembling more those of living caimanines.

Basioccipital—The poor development of the basioccipital tubera observed in *Acresuchus pachytemporalis* is also present in most eusuchians except for some longirostrine forms such as *Gavialis* Oppel, 1811, and *Thoracosaurus* Leidy, 1852 (Brochu, 1997).

Mandible

Dentary—The dentary-surangular suture contacting the external mandibular fenestra anterior to the posterodorsal corner seen in *Acresuchus pachytemporalis* is a morphology shared with most eusuchians (see Brochu, 2011). The extension of the mandibular symphysis to the level of the fifth alveolus is a feature also present in most caimanines except *Mourasuchus*, *Eocaiman* Simpson, 1933, *Globidentosuchus*, and *Gnatusuchus*. The anterodorsal projection of the anterior teeth is shared with all alligatoroids except *Eocaiman cavernensis* Simpson, 1933, *E. itaboraiensis* Pinheiro, Fortier, Pol, Campos, and Bergqvist,

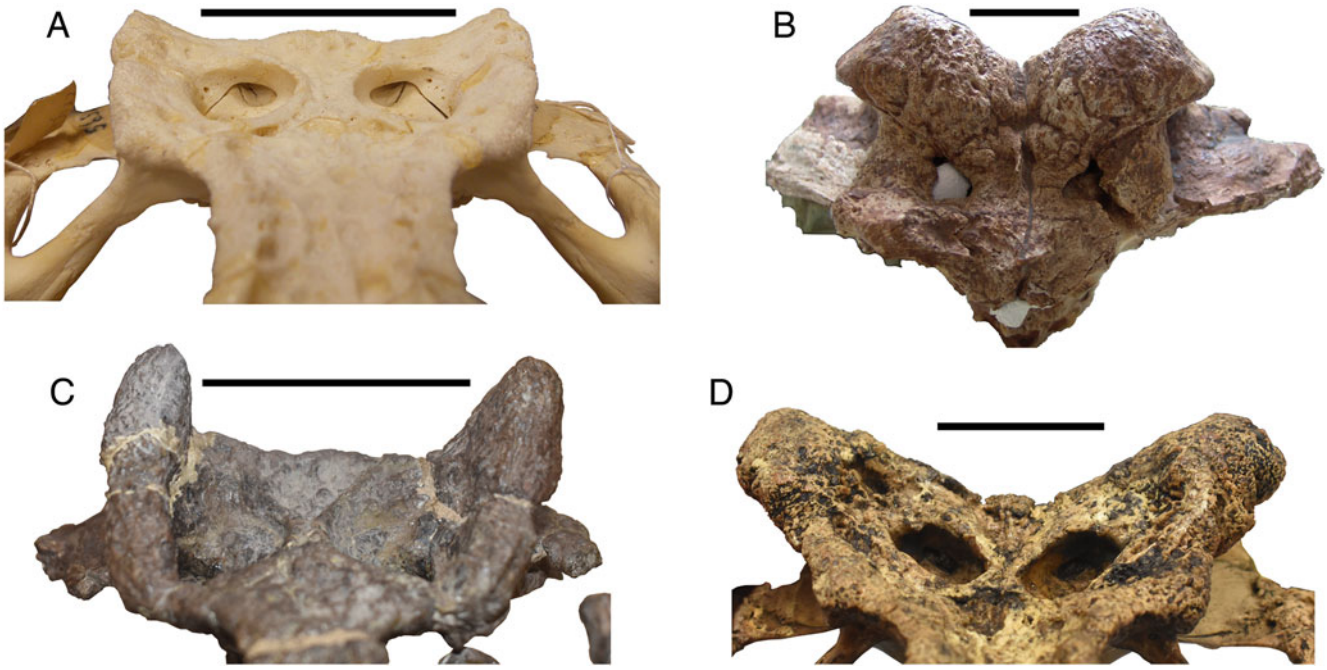

FIGURE 13. Crocodylian skull tables in anterodorsal view exhibiting the diversity in morphology of squamosal eminences. **A**, *Crocodylus rhombifer*, AMNH R-6178; **B**, *Mourasuchus arendsi*, UFAC-1431; **C**, *Ceratosuchus burdoshi*, FMNH P15576, holotype; **D**, *Voay robustus*, AMNH 3101. Scale bars equal 5 cm.

2013, and *Gnatusuchus* (Brochu, 2011; Pinheiro et al., 2013; Salas-Gismondi et al., 2015). The fourth alveolus separated from the third alveolus, while also being the larger of the two, is a character also observed in all alligatorids except *Gnatusuchus*, in which these alveoli are separated but nearly of the same size (Salas-Gimsondi et al., 2015), and *Leidyosuchus* and *Diplocynodon*, in which the two alveoli are confluent and nearly of the same size (Brochu, 2011). The 'gently curved' morphology of the dentary between the fourth and the 10th alveoli (sensu Brochu, 2011, character 50-0) is shared with all caimanines except *Mourasuchus* (see Langston, 1965; Bona et al., 2013b) and *Culebrasuchus mesoamericanus* (Hastings et al., 2013), in which it is linear. The 12th alveolus as the largest of those situated posterior to the fourth is a feature shared with all caimanines in which this character is known, except *Mourasuchus* and *Globidentosuchus.*

Splenial—The splenial of *Acresuchus pachytemporalis* not reaching the mandibular symphysis (Figs. 7, 9), with its anterior tip passing dorsal to the Meckelian groove, is a character shared with all caimanines except *Globidentosuchus* and *Gnatusuchus* (Scheyer et al., 2013; Salas-Gismondi et al., 2015).

Surangular—The surangular-angular suture meeting the articular dorsal to the latter's ventral tip in medial view as observed in *Acresuchus pachytemporalis* is a feature shared with all caimanines except *Gnatusuchus*. The surangular 'flushing' against the articular (sensu Brochu, 2011, character 74-1) is shared with most alligatoroids and all caimanines, except *Mourasuchus atopus*.

The surangular continuing dorsally to the dorsal tip of the lateral wall of the glenoid fossa is a morphology shared with most eusuchians, whereas the surangular-articular suture being orientated anteroposteriorly within the fossa is shared with all alligatoroids except *Globidentosuchus* (Scheyer et al., 2013). Additionally, the surangular extending until the posterior end of the retroarticular process is shared with all caimanines for which this character is known except *Globidentosuchus* (Scheyer et al., 2013).

The external mandibular fenestra being large to the point of allowing most of the foramen intermandibularis caudalis to be visible in lateral view is shared only with *Purussaurus* among Caimaninae. The angular-surangular suture passing broadly along the ventral margin of the external mandibular fenestra is a morphology also observed in most taxa within crown-group caimans, except *Mourasuchus*.

Articular—The posterodorsal projection of the retroarticular process observed in the new taxon is shared with most eusuchians.

Teeth

The teeth of *Acresuchus pachytemporalis* (with well-marked, non-serrated carinae and enamel with longitudinal lines parallel to the carinae) are similar to the typical morphology observed in most extant crocodylians (see Prasad and de Broin, 2002). The lack of serrations in the carinae distinguishes the teeth of this taxon from the marked pseudoziphodont serrations seen in *Purussaurus* (see Aureliano et al., 2015; Souza et al., 2016).

PHYLOGENETIC ANALYSIS

A strict consensus of 16,800 cladograms was constructed (Fig. 14; Fig. S1 in Supplementary Data 1), with a best score of 641 steps (ensemble consistency index = 0.387; ensemble retention index = 0.811). It shows *Acresuchus pachytemporalis* as the sister taxon of *Purussaurus*. This clade is supported by the following three synapomorphies: (1) external mandibular fenestra present and very large, with most of the foramen intermandibularis caudalis visible in lateral view (character 63-2), shared with *Boverisuchus magnifrons* Kuhn, 1938, and all the

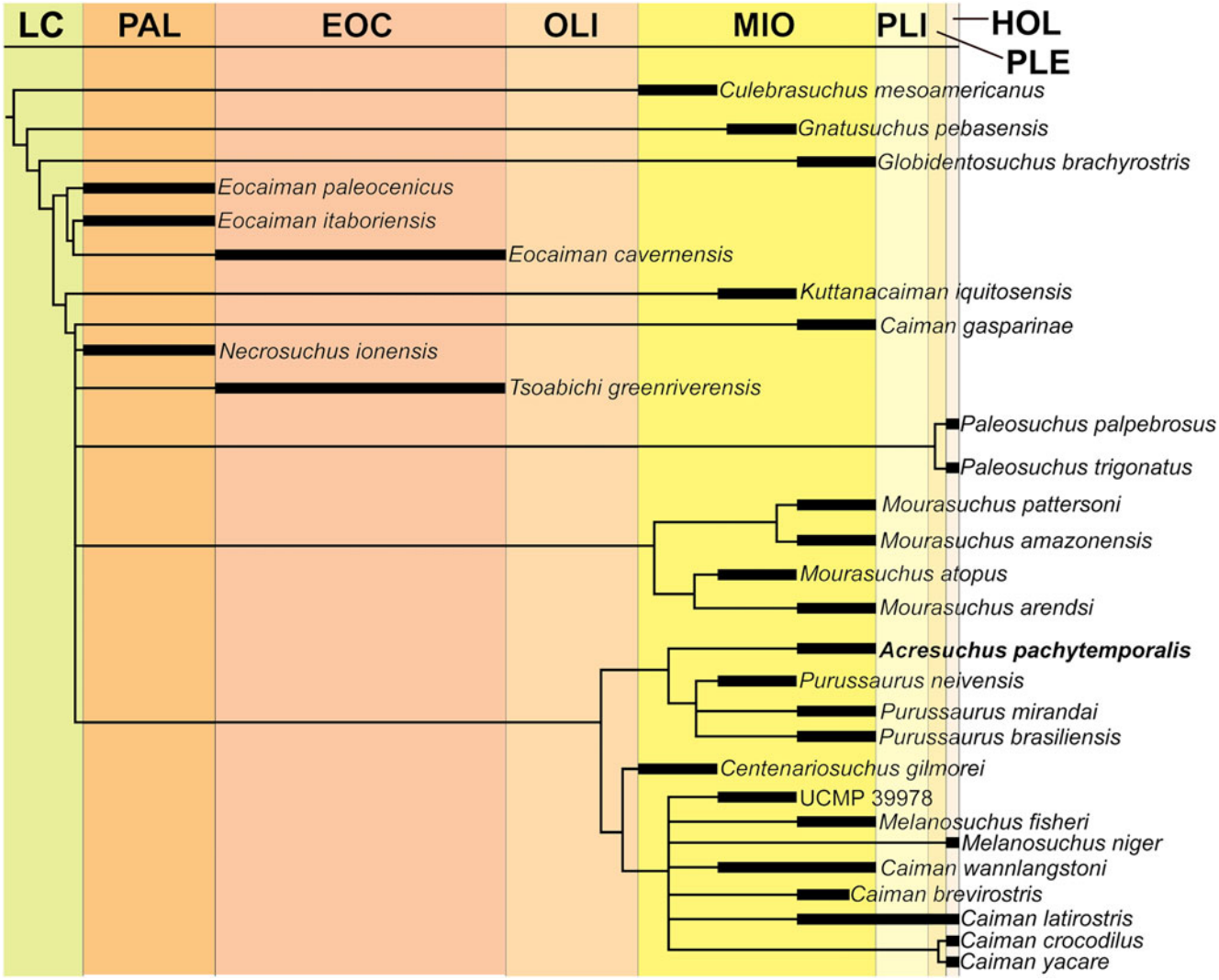

FIGURE 14. Detailed phylogeny of Caimaninae obtained in this study, highlighting the placement of *Acresuchus pachytemporalis* as the sister taxon to *Purussaurus*.

species of *Alligator* Cuvier, 1807, included in the analysis except *A. prenasalis* (Loomis, 1904) and *A. mcgrewi* Schmidt, 1941; (2) anterior tip of frontal forming simple acute point (character 130-0), a reversal within Alligatoroidea that is shared with *Kuttanacaiman*; and (3) dermal bones of the skull roof overhanging the rims of the supratemporal fenestrae near maturity, with the fenestrae large, significantly longer than wide and with an oval shape (character 151-3), which is a synapomorphy unique to this clade. *Purussaurus* is supported as a clade also by three synapomorphies: (1) external naris longer than wide (character 83-2), which is a unique synapomorphy; (2) orbits equal or subequal in size to the infratemporal fenestrae (character 181-0), a character shared convergently with *Acynodon iberoccitanus* Buscalioni, Ortega, and Vasse, 1997, *Kambara implexidens* Salisbury and Willis, 1996, *Brachychampsa montana* Gilmore, 1911, *Diplocynodon darwini* (Ludwig, 1877), *D. hantoniensis* (Wood, 1846), and *D. ratelii* Pomel, 1847; and (3) posterior margin of the skull deeply concave (character 185-1), a character shared with *Thecachampsa americana* (Sellards, 1915). The placement of *Acresuchus* relative to *Purussaurus* offers a previously unavailable opportunity to assess the evolution of *Purussaurus*, as will be discussed below.

The topology obtained for the basal caimanines does not differ from that of Cidade et al. (2017) upon recovering *Culebraushcus*, *Gnatusuchus*, *Globidentosuchus*, *Eocaiman*, as successive sister taxa to the remaining caimanines. The topology among the three species of *Eocaiman* is also similar to the previous works that included them (Pinheiro et al., 2013; Cidade et al., 2017). The placement of *Kuttanacaiman* as the sister taxon to crown-group caimanines (following Brochu, 1999) is different from that of Salas-Gismondi et al. (2015), which recovered it as the sister taxon of a two-lineage clade formed by crown-group caimans and a clade composed of *Purussaurus* and *Mourasuchus*, and from Cidade et al. (2017), which recovered it as the sister taxon of a clade formed by *Tsoabichi* and *Paleosuchus*.

The topology within crown-group caimanines presents itself as a polytomy, different from the more defined arrangement of Cidade et al. (2017). This is explained by the inclusion of two

very fragmented taxa from Argentina, *Necrosuchus ionensis* from the Paleocene and *Caiman gasparinae* from the Miocene, which were not included in the analysis of those authors. These taxa represent two of the six lineages of the polytomy, the other four being *Tsoabichi*, *Paleosuchus*, *Mourasuchus*, and a more derived clade including *Acresuchus*, *Purussaurus*, *Centenariosuchus*, and Jacarea (sensu Brochu, 1999). *Tsoabichi* appears as the sister taxon of both extant species of *Paleosuchus* in many previous analyses (e.g., in the Adams consensus of Brochu, 2010, and in the strict consensus of Scheyer et al., 2013; Fortier et al., 2014; Salas-Gismondi et al., 2015; Cidade et al., 2017), but such an arrangement was not recovered in this work. Further studies of *Necrosuchus*, *Caiman gasparinae*, and *Tsoabichi* shall address these phylogenetic issues, but these are beyond the scope of the present contribution. *Mourasuchus* is recovered as a monophyletic group, as in previous analyses (Bona et al., 2013b; Salas-Gismondi et al., 2015; Cidade et al., 2017).

The topology among the species of *Mourasuchus* is similar to that recovered by Cidade et al. (2017). The placement of the *Acresuchus* + *Purussaurus* clade as the sister taxon of a clade formed by *Centenariosuchus* and Jacarea also differs from most previous analyses by showing *Purussaurus* as not closely related to *Mourasuchus*. Most previous phylogenies had recovered *Purussaurus* as the sister taxon of a clade composed of *Mourasuchus* and the North American Eocene taxon *Orthogenysuchus olseni* (Brochu, 1999; Aguilera et al., 2006; Bona, 2007; Bona et al., 2013b; Scheyer et al., 2013; Fortier et al., 2014) or as the sister taxon of *Mourasuchus* only (Salas-Gismondi et al., 2015; Cidade et al., 2017). Ongoing preparation of the holotype of *Orthogenysuchus* revealed significant changes in the scoring of the characters for this taxon that have not yet been published. As a result, previous works have excluded this taxon from their phylogenetic analyses (Salas-Gismondi et al., 2015; Cidade et al., 2017).

Centenariosuchus gilmorei is recovered as the sister taxon of the clade Jacarea, as in Salas-Gismondi et al. (2015), but different from Hastings et al. (2013), in which this taxon is not more closely related to Jacarea than *Purussaurus neivensis* or the clade formed by *Orthogenysuchus* and *Mourasuchus*, and from Cidade et al. (2017), in which it appears as the sister taxon to a clade formed by *Purussaurus* and *Mourasuchus*. The resolution within Jacarea is a seven-branch polytomy formed by *Caiman crocodilus* and *C. yacare* and each of the following units as an independent lineage: *Caiman latirostris*, *Caiman brevirostris*, *C. wannlangstoni*, *Melanosuchus fisheri*, *M. niger*, and UCMP-39978. This is the same topology recovered by Salas-Gismondi et al. (2015).

The placement of *Caiman brevirostris* differs from Fortier et al. (2014), which recovered it as the sister taxon of the clade formed by *Caiman latirostris*, UCMP-39978, and both species of *Melanosuchus*, and from Cidade et al. (2017), which placed it only as the sister taxon of a clade formed by *C. latirostris* and *M. niger*. Cidade et al. (2017) also recovered *C. wannlangstoni* in a much more basal position within the crown-group caimanines than Salas-Gismondi et al. (2015) and the present contribution. The placement of *C. crocodilus* and *C. yacare* as a monophyletic group closer to each other than to all other jacareans recovered by this work is a basic arrangement of Jacarea exhibited in many previous analyses (e.g., Brochu, 1999, 2010, 2011; Aguilera et al., 2006; Bona, 2007; Hastings et al., 2013; Scheyer et al., 2013; Fortier et al., 2014; Cidade et al., 2017). In-depth discussion regarding the phylogenetic relationships within Jacarea is beyond the scope of this work, but the main possible reasons for the lack of definition within this clade are the incompleteness of the remains of some operational taxonomic units, such as the specimen UCMP-39978 and *Caiman brevirostris*, as well as the lack of phylogenetic characters relative to the morphological differences and similarities of the taxa within Jacarea in the current phylogenetic data sets for Crocodylia (Brochu, 2011; Salas-Gismondi et al., 2015; Cidade et al., 2017; this paper). Future works must address these issues with a specific and thorough approach.

The topology of non-caimanine alligatoroids recovered in the analysis of this paper also shows some significant differences in comparison with previous analyses. The placement of *Leidyosuchus canadensis* as the basal-most alligatoroid is also seen in most of the phylogenetic analyses performed on Alligatoroidea to date (Brochu, 1999, 2004, 2010, 2011; Bona et al., 2013b; Pinheiro et al., 2013; Scheyer et al., 2013; Fortier et al., 2014; Martin et al., 2014; Skutschas et al., 2014; Salas-Gismondi et al., 2015; Hastings et al., 2016; Wang et al., 2016; Cidade et al., 2017). *Diplocynodon* as the second most basal clade, after *Leidyosuchus*, is also recovered by most of these analyses (Brochu, 1999, 2004, 2010, 2011; Bona et al., 2013b; Pinheiro et al., 2013; Fortier et al., 2014; Skutschas et al., 2014; Salas-Gismondi et al., 2015; Wang et al., 2016; Cidade et al., 2017), except for the analyses that include *Deinosuchus*, from the Upper Cretaceous of North America, which consistently appears as a basal alligatoroid (Aguilera et al., 2006; Scheyer et al., 2013; Martin et al., 2014; Hastings et al., 2016). The analysis of this paper did not obtain any resolution within the *Diplocynodon* clade, similar to Wang et al. (2016) and Cidade et al. (2017), but differently from several previous analyses that obtained resolutions between the taxa that constitute the clade (Brochu, 1999, 2004, 2010, 2011; Aguilera et al., 2006; Hill and Lucas, 2006; Scheyer et al., 2013; Martin et al., 2014; Skutschas et al., 2014; Salas-Gismondi et al., 2015; Hastings et al., 2016). Future comprehensive analyses of basal alligatoroids shall address the issue of the placement of *Deinosuchus* and review the phylogeny of the species of *Diplocynodon*.

The placement of *Brachychampsa*, *Stangerochampsa*, and *Albertochampsa* as successive sister taxa to Alligatoridae is also seen in Brochu (2004) and Cidade et al. (2017). This topology differs from that of Brochu (2010), in which the three genera appear basal to Alligatoridae but in a polytomy, and from Brochu (2011, 2013), in which they appear within Alligatoridae but not forming a single clade. Additionally, Skutschas et al. (2014) recovered the three genera forming a single clade within Alligatoridae, whereas Salas-Gismondi et al. (2015) also recovered the three genera in a single clade that is the basal-most lineage of Caimaninae. These different placements of *Brachychampsa*, *Stangerochampsa*, and *Albertochampsa* indicate that an in-depth review of these three genera must be thoroughly addressed in other works. *Allognatosuchus*, *Procaimanoidea*, and *Arambourgia* forming a single clade in Alligatorinae is a topology also recovered by Brochu (2010, 2011), Scheyer et al. (2013), and Cidade et al. (2017). In Hastings et al. (2016), these three genera form a clade in Alligatoridae, but not in Alligatorinae, whereas in other analyses the genera were not recovered in a single clade.

Wannaganosuchus, *Hassiacosuchus*, *Navajosuchus*, and *Ceratosuchus* were all recovered in Alligatorinae, but as independent lineages, not forming part of any clade within that group. This topology is similar to that of Cidade et al. (2017), but different from most analyses, which recovered *Wannaganosuchus* as the sister taxon of *Alligator* (Brochu, 1999, 2004, 2010, 2011; Aguilera et al., 2006; Hastings et al., 2013; Scheyer et al., 2013; Skutschas et al., 2014; Salas-Gismondi et al., 2015; Wang et al., 2016; Whiting et al., 2016; Cidade et al., 2017). *Ceratosuchus*, *Hassiacosuchus*, and *Navajosuchus* also appear in Alligatorinae as independent lineages in many previous analyses (Brochu, 1999, 2010; Aguilera et al., 2006; Hastings et al., 2013; Whiting et al., 2016), whereas

Brochu (2004) recovered the three taxa forming a single clade within Alligatorinae. Other analyses recovered these three genera as independent lineages in Alligatoridae, but not in Alligatorinae (Brochu, 2011; Scheyer et al., 2013; Skutschas et al., 2014; Hastings et al., 2016; Wang et al., 2016). These differences in the topology of these taxa also hint at the necessity of a comprehensive phylogenetic revision of these four genera.

Alligator appears as a clade without any immediate sister taxon within Alligatorinae. This absence of an immediate sister taxon is a topology similar to that in many analyses (Brochu, 1999; Aguilera et al., 2006; Hastings et al., 2013; Whiting et al., 2016; Cidade et al., 2017), but different from those in analyses that recovered *Wannaganosuchus* as the sister taxon of *Alligator* (Brochu, 1999, 2004, 2010, 2011; Aguilera et al., 2006; Hastings et al., 2013; Scheyer et al., 2013; Skutschas et al., 2014; Wang et al., 2016; Whiting et al., 2016; Cidade et al., 2017) and in other analyses that recovered the species *Allognatosuchus polyodon* as the immediate sister taxon of *Alligator* (Pinheiro et al., 2013; Fortier et al., 2014) or recovered *Procaimanoidea kayi* and *Wannaganosuchus* as successive sister taxa (Bona et al., 2013b). The topology among the species of *Alligator* is the same as in most analyses that included the same species (Brochu, 2011; Scheyer et al., 2013; Wang et al., 2016; Cidade et al., 2017), except for Skutschas et al. (2014), which recovered *A. mefferdi* as the sister taxon of the most derived clade formed by *A. mississippiensis* and *A. thomsoni*, Hastings et al. (2016), which only recovered *A. mefferdi*, *A. mississippiensis*, and *A. thomsoni* as a clade, and Salas-Gismondi et al. (2015), which recovered *Culebrasuchus mesomaericanus* (which appears in the analysis of this paper as the basal-most caimanine) within the species of *Alligator*, as the sister taxon of the clade formed by *A. mefferdi*, *A. mississippiensis*, and *A. thomsoni* in a polytomy. This polytomy also appears in the analysis of this paper. These perspectives suggest that the phylogenetic hypotheses between the species of *Alligator* have been relatively stable over time, although more comprehensive analysis involving the placement of *C. mesoamericanus* and the resolution of the polytomy involving *A. mefferdi*, *A. mississippiensis*, and *A. thomsoni* are perspectives to be explored in future analyses.

DISCUSSION

Acresuchus and the Evolution of Gigantism in *Purussaurus*

The skull length of the holotype of *Acresuchus pachytemporalis* is significantly smaller than those of the *Purussaurus* species. The skull of the holotype of *A. pachytemporalis* has an estimated snout-to-quadrate length of 51.5 cm; the same measurement in the species of *Purussaurus* according to Aguilera et al. (2006) are 80.1 cm in *P. neivensis* (UCMP-39704), 126.0 cm in *P. mirandai* (CIAAP-1369, holotype), and 140.0 cm in *P. brasiliensis* (UFAC-1403). As such, the phylogenetic placement of *Acresuchus pachytemporalis* as the sister taxon of *Purussaurus* raises the possibility that the new taxon can be seen as an evolutionary 'transitional form' between a 'medium-sized, generalized caimanine' and the giant, highly derived *Purussaurus*. This evolutionary perspective may have as its expression some characters that differentiate the two taxa as well as characters that are shared between them. For example, *Acresuchus* lacks an anteroposteriorly enlarged external naris (see Fig. 2) present in *Purussaurus* (see Langston, 1965; Bocquentin-Villanueva et al., 1989; Aguilera et al., 2006; Aureliano et al., 2015). This feature has been proposed to have either a thermoregulatory function in large-bodied crocodiles (Moreno-Bernal, 2007) or a stress-dissipating function associated with the bite force in *Purussaurus* (Aureliano et al., 2015), which in turn is also associated with the presence of deep dorsoventral depressions between the lacrimal and maxillary bones in *Purussaurus mirandai* and *P. brasiliensis* (see Aguilera et al., 2006; Aureliano et al., 2015). As mentioned previously, the holotype of *Acresuchus* exhibits small depressions in the posterior portions of the maxillae that could be homologous to the deep depressions of *Purussaurus*. If this interpretation is correct, the evolutionary increase in size of the external naris and of the dorsoventral depression could thus be correlated to the evolution of gigantism in the *Acresuchus-Purussaurus* clade.

Simultaneously, *Acresuchus pachytemporalis* exhibits some cranial characters that are also present in *Purussaurus* and might be adaptations for large size of both the skull and the body as a whole: the medial contact between the prefrontals (Fig. 2) allows either an anterior displacement of the nasals or a posterior displacement of the frontal when compared with other, non-gigantic caimanines, although some of these present prefrontals that meet medially, such as *Caiman yacare* (Brochu, 1999) or *Caiman crocodilus* (Medem, 1981; Brochu, 2013). Both *Acresuchus* (Figs. 2, 6) and *Purussaurus* exhibit larger supratemporal fenestrae compared with other caimanines; in the supratemporal fenestrae of extant crocodylians, there is an insertion area for the M. adductor mandibulae externus profundus (Iordansky, 1973; Holliday and Witmer, 2007; = M. pseudotemporalis of Schumacher, 1973). In longirostrine, this muscle is enlarged when compared with non-longirostrine ones (Schumacher, 1973; Holliday and Witmer, 2007), which is considered an adaptation for quick seizing of prey (Schumacher, 1973). Because longirostrine crocodylians also have larger supratemporal fenestrae as compared with non-longirostrine taxa (Iordansky, 1973; Langston, 1973; Holliday and Witmer, 2007), the enlargement of these fenestrae in the *Acresuchus-Purussaurus* clade may be related to an increase in the speed, efficiency, or strength of prey capture. Additionally, the supratemporal fenestrae are the exits for vascular vessels (the temporoorbital vessels) of the basicranium (see Holiday and Gardner, 2012; Bona et al., 2013a), and the enlargement of these structures may also be related to an increase of the vascularity of the area. Such increase may be related to a thermoregulatory function, as proposed for the other fossil crocodyliforms, *Aegisuchus* Holliday and Gardner, 2012 and *Mourasuchus* (e.g., Holliday and Gardner, 2012; Bona et al., 2013a). This thermoregulatory function would be especially interesting because gigantism in crocodylians implies higher and more stable body temperatures with the risk of overheating (Moreno-Bernal, 2007); thus, a greater capacity for thermoregulation could have contributed to the achievement of gigantism in the evolution of the *Acresuchus-Purussaurus* clade (see Aureliano et al., 2015). However, more detailed studies about this feature and this taxon need to be made to evaluate these last two concepts.

A squamosal 'horn' is also present, albeit with a significantly smaller size, in the two smaller species of the giant genus *Purussaurus*: *Purussaurus neivensis* and *P. mirandai*. In the largest species (*P. brasiliensis*), however, this structure is absent. The difference in sizes of these 'horns' in *Acresuchus* and *Purussaurus* indicates that they could have evolved in inverse proportion with respect to the increase in size that occurred in the evolution of the clade. Extant crocodylians that possess squamosal eminences, such as *Crocodylus rhombifer* and *C. siamensis*, have been observed to perform social displays in which the head is elevated in such a way that the squamosal 'horns' form the pinnacle of the angle (K. Vliet, pers. comm.). These displays are performed to attract the attention of other individuals and are most frequently performed by males; thus, males may attract females to courtship

and mating through this behavior, but such displays are not a courtship/mating behavior per se (K. Vliet, pers. comm.). As such, these structures may serve to accentuate visual elements of those displays in these extant crocodylians, and a similar behavior could be performed by fossil crocodylians that present squamosal eminences, especially if these are large, like those of *Acresuchus*.

The false-ziphodont teeth observed in *Purussaurus* (Souza et al., 2016) and absent in *Acresuchus* could be a consequence of differences in enamel deposition during tooth development associated with increase in the size of the prey that could be captured by *Purussaurus* in comparison with the medium-sized *Acresuchus*. *Purussaurus* has also been suggested to perform the prey-capturing behavior known as 'death roll' (Blanco et al., 2015), and the false-ziphodont teeth may also have aided in making this specific behavior more efficient. This feature was possibly positively selected due to an increase in the predatory role of *Purussaurus* by facilitating the tearing or cutting of prey items, especially flesh.

Paleoecology of *Acresuchus*

The Solimões Formation possesses a remarkable diversity of crocodylian taxa, morphotypes, and feeding habits (see Riff et al., 2010, for a review). Such diversity consists of the giant, top predator *Purussaurus* (Barbosa-Rodrigues, 1892; Bocquentin-Villanueva et al., 1989; Aureliano et al., 2015); the 'duck'-snouted, putative gulp-feeding *Mourasuchus* (Cidade et al., 2017); the longirostrine piscivorous gavialoids *Gryposuchus* Gurich, 1912 and *Hesperogavialis* Bocquentin-Villanueva and Buffetaut, 1981; the longirostrine piscivorous crocodyloid *Charactosuchus* Langston, 1965 (Riff et al., 2010); and of medium-sized, generalist predators such as *Caiman* cf. C. *yacare* (Fortier et al., 2009, 2014) and *Caiman brevirostris*, a medium-sized, generalist predator that may have had an inclination toward durophagy, similar to the extant *Caiman latirostris* (Fortier et al., 2014).

It was not possible to assess whether the holotype of *Acresuchus pachytemporalis* was close to adult body size or even morphologically mature due to the absence of vertebrae (see Brochu, 1996), or osteoderms (Buffrénil, 1980) and long bones (Ikejiri, 2012) from which age estimates based on histology could be made. However, because all teeth present a rounded apex, we propose that this specimen had grown enough to change from the juvenile niche, with acute apex teeth, to the adult niche, with rounded apex teeth (see Erickson et al., 2003). Accordingly, if we assume that the skull is from a mature individual, its size implies that *Acresuchus* is a medium-sized caimanine (as compared with the giants *Purussaurus* and *Mourasuchus*), yet still larger than most other caimanines, including the extant species.

The skull length of a sample of 52 individuals of the largest extant caimanine, *Melanosuchus niger* (data available in Foth et al., 2013) had an average of ca. 31.5 cm; among these, the single largest skull had a length of 52.5 cm. As such, given the skull length of *Acresuchus pachytempralis*, this taxon may be considered as being at least as large as an extant *Melanosuchus*. Whether *Acresuchus* could reach even larger sizes must be addressed in future works, especially based on more complete specimens. The maxillary and mandibular dentitions of *Acresuchus* and *Melanosuchus* exhibit very similar morphologies, with most of the teeth being pointed except for the posterior-most teeth, which are blunt. In this scenario, based on the size and the morphological features already discussed, *Acresuchus* may be considered as having a diet similar to that of extant *Melanosuchus*, which consists of small invertebrates (insects, crustaceans, gastropods) for the juvenile (Silveira and Magnusson, 1999; Foth et al., 2013) and of fish and small- to medium-sized mammals for the adult (Foth et al., 2013).

Although generalist crocodylians have been known from the Solimões Formation, none have reached the size of *Acresuchus*, implying that it formed its own ecological niche, previously unknown for its environment. A similar ecological niche may have been held by different taxa in other Miocene units, such as *Melanosuchus fisheri* in the Urumaco Formation (Medina, 1976), *Caiman gasparinae* in the Ituzaingó Formation (Bona and Carabajal, 2013), and the taxon represented by the specimen UCMP-39978, formerly attributed to *Caiman* cf. *C. lutescens*, for the Honda Group (Langston, 1965; Bona et al., 2013b). The posterior-most blunt teeth of *Acresuchus* are similar to those of extant caimanines and several fossil taxa (see Fortier et al., 2014; Salas-Gismondi et al., 2015), the presence of which is a character that has been associated with both facultative and largely durophagous feeding habit, with the last being more associated specifically with the predominance of hard-shelled mollusks (see Harlan, 1824; Brochu, 2004; Salas-Gismondi et al., 2015) or turtles (Erickson, 1984; Ross and Garnett, 1989; Blanco et al., 2015). However, a largely durophagous habit for *Acresuchus* is considered unlikely. This species lacks other specific adaptations for a predominant durophagy, such as a large mandibular symphysis, extending at least beyond the level of the sixth alveolous, rostrum short relative to the total length of the skull, and posterior teeth globular (sensu Salas-Gismondi et al., 2015, character 198-1 and -2), that are present in *Globidentosuchus*, *Gnatusuchus*, *Kuttanacaiman*, and *Caiman wannlangstoni* (see Scheyer et al., 2013; Salas-Gismondi et al., 2015). It also lacks the 'shovel-like' mandible seen in *Gnatusuchus* (Salas-Gismondi et al., 2015). However, the presence of those teeth indicates that *Acresuchus* could have been a facultative durophage, performing some sort of processing of hard-shelled prey, as in the extant *C. latirostris* (Ősi and Barrett, 2011).

CONCLUSIONS

This work described *Acresuchus pachytemporalis* from the late Miocene Solimões Formation of the Acre Basin, Brazil, a new species that increases the already large crocodylomorph diversity of the Miocene of South America. This new species is diagnosed in particular by the presence of squamosal 'horns,' in which the squamosal has an upturned posterolateral margin throughout its entire lateral surface and a dorsoventral expansion toward the posterior end. This characteristic is not present in any other caimanine taxa, although it is present in the alligatorid *Ceratosuchus burdoshi*. However, *Acresuchus* differs from *Ceratosuchus* in other characteristics. The new taxon is phylogenetically placed as the sister taxon of *Purussaurus*, and some inferences about the morphological evolution of this clade are presented in this work. Some characters may be associated with the evolution of gigantism in *Purussaurus*, such as the size of the external naris and supratemporal fenestrae, although these perspectives have to be thoroughly assessed in detailed studies. Paleoecologically, *Acresuchus pachytemporalis* is proposed as a medium-sized generalist caimanine that had an ecological niche similar to the extant *Melanosuchus niger*.

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