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The first fossil species of *Salminus*, a conspicuous South American freshwater predatory fish (Teleostei, Characiformes), found in the Miocene of Argentina

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THE FIRST FOSSIL SPECIES OF *SALMINUS*, A CONSPICUOUS SOUTH AMERICAN
FRESHWATER PREDATORY FISH (TELEOSTEI, CHARACIFORMES), FOUND
IN THE MIOCENE OF ARGENTINA

ALBERTO LUIS CIONE*¹ and MARÍA DE LAS MERCEDES AZPÉLICUETA²

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ABSTRACT—The first fossil specimen of the characiform genus *Salminus* is described here. The material, a three-dimensionally articulated head, is very well preserved and allowed us to identify a new species. We could study both outer and inner bones. The specimen was found in the locality Toma Vieja, northeast of the city of Paraná, central eastern Argentina. The bearing horizon is the so-called ‘Conglomerado osífero,’ which is putatively included in the lowermost beds of the fluvial Ituzaingó Formation. The ‘Conglomerado osífero’ is early Tortonian (early late Miocene) in age. Recent species of *Salminus* are top-ranking pelagic predatory fishes in temperate to tropical lowland freshwaters of South America. The aquatic vertebrate fauna occurring in the bearing bed shows a similar composition to several northern South American units such as the Urumaco Formation (Venezuela, late Miocene) and La Venta Formation (Colombia, middle Miocene).

INTRODUCTION

Characiformes is one of the most diversified freshwater fish orders (1995 extant valid species; Eschmeyer and Fong, 2012). However, the fossil record is extremely poor in comparison with the present species richness (Malabarba and Malabarba, 2010). Presently, the characiforms are widely distributed throughout South America, Central America, southernmost North America, and Africa (Almirón et al., 1997; Berra, 2001) and occupy diverse ecological niches (Goulding, 1980; Lowe-McConnell, 1987).

In South America, among the most conspicuous, medium to large, open-water predator fishes are the species of the genus *Salminus*. These characiforms, known as dorados, doradas, or pirayús in Spanish-speaking countries and dourados or tarabanas in Brazil, are included in the monophyletic subfamily Salmininae as result both of morphological (Mirande, 2010) and molecular (Oliveira et al., 2011) analyses. They mainly occur in rivers and are targets of both commercial and sport fisheries (Lima and Britski, 2007). Four extant species are included in this genus (Lima and Britski, 2007). Although they are fairly common today, no fossil specimen has been reported until now.

Several Argentinian paleontologists are studying the animal and plant remains that occur in the Miocene beds cropping out in the east Paraná riverside near the city of Paraná, Entre Ríos Province, central-eastern Argentina. During surveys at the La Toma Vieja site, Jorge Ignacio Noriega found a very well preserved fish head in the base of the late Miocene freshwater Ituzaingó Formation. This material pertains to a new species of the genus *Salminus* that is described here.

Institutional Abbreviations—CAC, Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, La Plata, Argentina; CICYTTP-PV-P, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción, Diamante, Argentina; CI-FML, Fundación Miguel Lillo, San Miguel de Tucumán, Argentina; ICNMHN, Instituto de Ciencias Naturales, Museo de Historia Natural, Bogotá, Colombia; MLP, División Zoología Vertebrados, Museo de La Plata, La Plata,

Argentina; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

Anatomical Abbreviations—an, anguloarticular; ant, antorbital; ar, retroarticular; boc, basioccipital; br, branchiostegal rays; c, cap; ce, cutting edge; d, dentary; eb, epiphyseal bar; ect, ectopterygoid; epi, epiotic; ex, extrascapula; exo, exoccipital; f, frontal; h, hyomandibula; if 1–6, infraorbitals 1–6; iop, interopercle; let, lateral ethmoid; lpm, left premaxilla; m, maxilla; mbs, main basoapical sulcus; mes, mesopterygoid; mesth, mesethmoid; met, metapterygoid; na, nasal; op, opercle; q, quadrate; pa, parietal; pal, palatine; pas, parasphenoid; pf, parietal fontanelle; pm, premaxilla; pop, preopercle; pt, pterotic; pter, pterosphenoid; sbs, small basoapical sulcus; soc, supraoccipital; sor, supraorbital; sp, sphenotic; spop, suprapreopercle.

MATERIALS AND METHODS

Methods

The fossil material (CICYTTP-PV-P-1-291) was prepared mechanically with needles and abrasive jets. The comparative recent material was cleared and counterstained following Taylor and Van Dyke (1985). Dry material was also used. The detached teeth were washed with potassium hydroxide.

Comparative Material

Salminus brasiliensis (stuffed), MLP, unnumbered, 365 mm SL. *Salminus brasiliensis*, CI-FML 3784, 131.4 mm SL; CAC, several unnumbered dried skeletons. *Salminus hilarii*, MZUSP 35740, 108.9 mm SL (C&S). *Salminus affinis*, ICNMHN 16318, 255 mm SL; ICNMHN 15078, 210 mm SL.

GEOLOGIC SETTING

The material was collected in the Paraná riverside cliffs at the Toma Vieja, a site located to the northeast of the city of Paraná, Entre Ríos Province, Argentina (Fig. 1; 31°41'S 60°28'W). The fossil-bearing bed is the ‘Conglomerado osífero’ (‘bony

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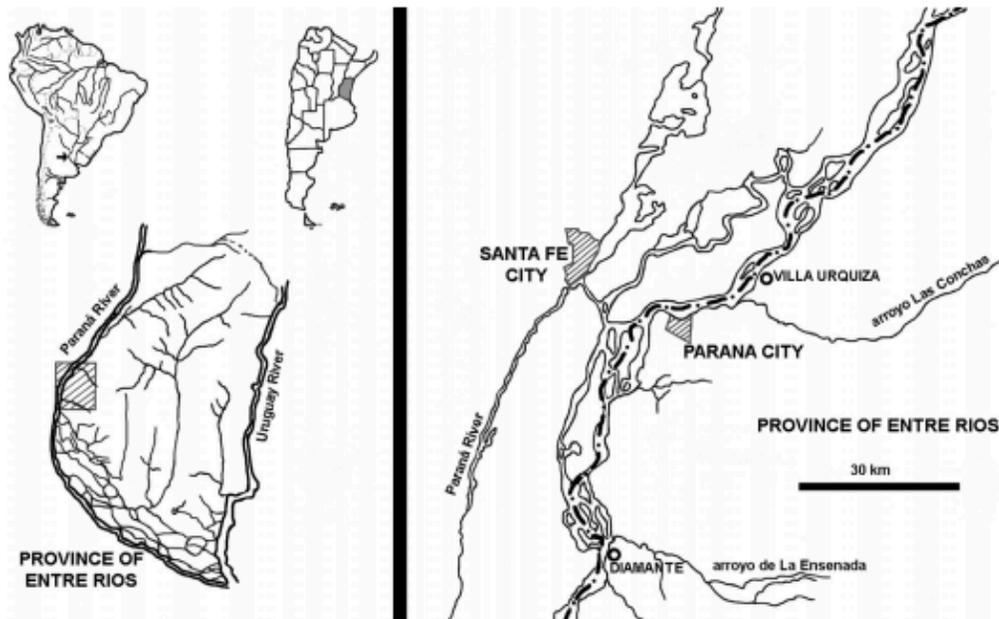


FIGURE 1. Map of collecting area.

conglomerate") located at the base of the fluvial Ituzaingó Formation, which overlays the marine beds of the Paraná Formation.

The marine and continental fossiliferous beds of southwestern Entre Ríos Province are known since the 19th century. However, the current stratigraphic scheme was proposed more recently (see Aceñolaza, 2000; Fig. 2). It involves two Miocene units: the partly marine Paraná Formation and the continental Ituzaingó Formation. The Paraná Formation is mainly composed of green mudstones and sandstones with oyster banks (Aceñolaza, 2000). The unit was deposited during the large marine encroachment that covered the Chaco-Pampean region during the middle Miocene ('Mid Transgressive Onlap Sequence'—see Uliana and Biddle, 1988; Cione et al., 2000, 2005; Uba et al., 2009). The fluvial Ituzaingó Formation is composed of a basal conglomerate ('Conglomerado osífero') with abundant vertebrate remains that is overlain by whitish to yellow-brown sandstones and green mudstones that produce few fossils. The 'Conglomerado osífero,' which occurs in paleochannels excavated in the Paraná Formation, is laterally interrupted and is rarely exposed as a result of frequent landslides (Aceñolaza, 2000).

Marine mammals occurring in the top of the Paraná Formation indicate a late Miocene age (Cione et al., 2000). Sr isotope ages obtained from the correlative Puerto Madryn Formation from Patagonia indicate a Tortonian age (Scasso et al., 2001) as well as a date from the top of the Yecua Formation of Bolivia (a U-Pb date of 7.17 ± 0.34 Ma; Uba et al., 2009). Mammals occurring at the base of the overlying Ituzaingó Formation are Huayquerian in age in the South American chronology (Cione et al., 2000; Cione and Tonni, 2005). The Huayquerian ranges from about 9 Ma to about 6 Ma, with radiometric and magnetostratigraphic calibration in western Argentina (Tortonian-Messinian, late Miocene; sea Flynn and Swisher, 1995; Cione et al., 2000). A continental Pliocene–Pleistocene (Marplatian to

Platan in the South American chronology) sequence overlies both units (Cione et al., 2000; Candela et al., 2007).

The 'Conglomerado Osífero' contains remains of elasmobranchs (reworked marine and some continental), teleosts, crocodylians, chelonians, birds, and several groups of terrestrial and aquatic mammals (Cione et al., 2000). Along with the dorado studied here, many described and undescribed teleosts occur: catfishes (doradiids, callichthyids, loriciariids, pimelodiids, ariids), characiforms (Cynodontidae indet., the Serrasalminae *Megapiranha paranensis*, the Anostominae *Leporinus scalabrinii*), and perciforms (Sciaenidae indet.) (Cione, 1978; Arratia and Cione, 1996; Cione and Casciotta, 1997; Cione et al., 2000, 2005, 2009, 2012, in press; Bogan et al., 2012).

SYSTEMATIC PALEONTOLOGY

CHARACIFORMES Fink and Fink, 1981
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SALMINUS Agassiz in Spix and Agassiz, 1829
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(Figs. 3–7)

Holotype—CICYTTP-PV-P-1-291, a well-preserved three-dimensional skull.

Etymology—Named after the paleontologist Jorge Ignacio Noriega.

Diagnosis—*Salminus* that differs from the other species of the genus in having the longest premaxilla and maxilla (the posterior margin of the maxilla surpasses the posterior margin of the infraorbital 2), the largest (and oblong) orbit, the supraorbital forming a ledge that roofs the ocular cavity, the posteroventral corner of preopercle not rounded, and the upper dorsal skull profile concave. *Salminus noriega* also differs from *S. franciscanus*

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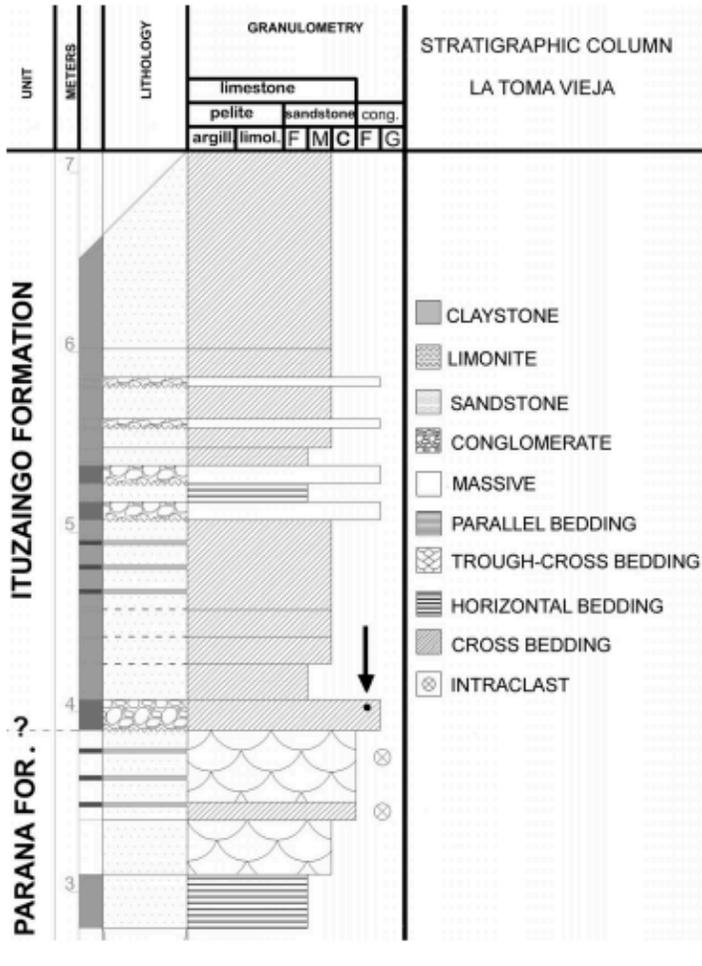


FIGURE 2. Section at the Toma Vieja locality. The arrow indicates the level from which the specimen was collected. Meters indicate the height above the normal river level.

(of all sizes) and *S. brasiliensis* (smaller than 35 cm SL) in having a second dentary tooth in the outer series of similar size than the remaining teeth (vs. larger than remaining teeth); from *S. brasiliensis* in having a narrower dentary horizontal blade, a narrower maxilla, and a larger and longer supraorbital; from *S. affinis* in having a deeper head, and a lower jaw less strongly included; and at least from *S. brasiliensis* and *S. hilarii* in the shape of mesethmoid (lateral sides concave in dorsal view).

DESCRIPTION

The material consists of a three-dimensional cranium about 90 mm long (Figs. 3–7). The right side preserves the dermal bones in position (Figs. 3, 4). In the left side of the skull many dermal bones were not preserved (Figs. 5, 6). This allowed, after mechanical preparation, the study of several internal bones of the neurocranium and suspensorium. The snout is blunt and the dorsal skull roof profile is slightly concave. The mesethmoid, infraorbitals, preopercle, premaxilla, maxilla, dentary, retroartic-

ular, and anguloarticular are ornamented with ridges that are particularly prominent on the frontal and parietal (Fig. 7). The external surface of the opercle is smooth.

Neurocranium

The mesethmoid ends in a conic process that serves as a surface for reception of the nonmovable premaxillae in the anterior part of the skull. In dorsal view, it is triangular with concave lateral margins (Fig. 7). The nasal is long and slender. The dorsal surface of the cranium is partially roofed by the two frontals. The anterior part of the frontal sutures overlies the mesethmoid. These sutures are scarcely interdigitated. Each frontal contacts the other along the anterior half of its length, a character that is common in genus *Salminus* but uncommon in other characiforms. The posterior half of the bone bounds the posterior fontanelle (Fig. 7). The epiphyseal bar is partially preserved. The parietals are short and separated in the midline by the posterior part of the fontanelle; they contact with the

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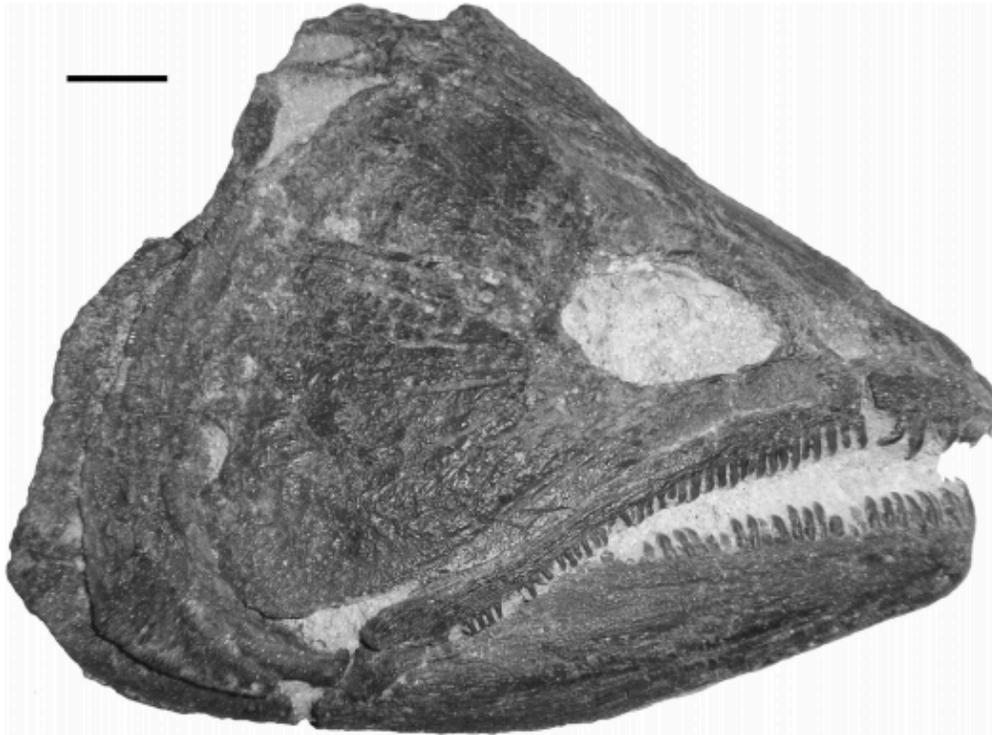


FIGURE 3. Photograph of *Salminus noriegai*, sp. nov. (CICYTTP-PV-P-1-291), in right lateral view. Scale bar equals 1 cm.

supraoccipital and posterolaterally with the pterotic. The posterior margin of parietals is strongly concave (Fig. 7). The parietal part of the supratemporal branch of the cephalic lateral line runs near to the caudal part of the parietal. The pterotic and the pterotic spine are long. The pterotic sutures anteromedially with the frontal, medially with the parietal, and posteriorly with the epiotic. The extrascapula is relatively long and laminar. It overlaps the epiotic, pterotic, and parietal. The supraoccipital contacts laterally with pterotic and lateroposteriorly with the extrascapula. The fontanelle is caudally bounded by the supraoccipital. The supraoccipital process is broken. The right epiotic articulates with the supraoccipital and pterotic. Both exoccipitals are preserved. They are robust and both show the foramina for the vagus nerve. They suture with the posterior portion of basioccipital. The strong articular condyle of the basioccipital is well preserved. A small portion of the lateral ethmoid, median portion of the parasphenoid, and dorsal part of the sphenotic are preserved. The articular area for the hyomandibula and the sphenotic spine are lost.

Orbital Series

The anteroposteriorly elongated right orbit is well preserved (Figs. 3, 4). It is surrounded by a complete series of antorbital, infraorbitals, and supraorbital. The antorbital is a strong, wide bone with an anterior pointed projection. The upper portion ar-

ticulates with the supraorbital. The infraorbital 1 is rectangular and overlaps the anterior part of maxilla (Figs. 3, 4). The infraorbital 2 is quadrangular anteriorly and has a long posterior portion. The infraorbitals 3 and 5 are fan-shaped. The infraorbital 4 is slender and as long as infraorbitals 3 and 5. The infraorbital 6 is badly preserved. The supraorbital is a very large, rhomboidal bone, forming a ledge that roofs the ocular cavity.

Jaws

The premaxilla, maxilla, and lower jaw are exposed on both sides (Figs. 3–6). The premaxilla is a stout, short bone with the ascending process longer than the dentigerous process. The dorsal articular process is longer than the lateral process. The premaxillae are almost completely separated by the mesethmoid spine (Fig. 7). The maxilla is very long and narrow, reaching the level of the posterior end of the dentary. The anterior process is visible only through both nares. The dentary constitutes the major part of the lower jaw, which is long and robust. Ventrally, it bears a horizontal, relatively narrow blade. The suture between anguloarticular and retroarticular is visible. Teeth are much better preserved in the right premaxilla, maxilla, and dentary (Figs. 3–6). There are two tooth series in the premaxilla and dentary. The outer premaxillary series has at least seven teeth; the inner series has 12 teeth. The right maxilla bears at least 39 teeth and the left dentary, 26 large teeth. Tooth shape is similar

FIGURE 3. Photograph of *Salminus noriegai*, sp. nov. (CICYTTP-PV-P-1-291), in right lateral view. Scale bar equals 1 cm.

supraoccipital and posterolaterally with the pterotic. The posterior margin of parietals is strongly concave (Fig. 7). The parietal part of the supratemporal branch of the cephalic lateral line runs near to the caudal part of the parietal. The pterotic and the pterotic spine are long. The pterotic sutures anteromedially with the frontal, medially with the parietal, and posteriorly with the epiotic. The extrascapula is relatively long and laminar. It overlaps the epiotic, pterotic, and parietal. The supraoccipital contacts laterally with pterotic and lateroposteriorly with the extrascapula. The fontanelle is caudally bounded by the supraoccipital. The supraoccipital process is broken. The right epiotic articulates with the supraoccipital and pterotic. Both exoccipitals are preserved. They are robust and both show the foramina for the vagus nerve. They suture with the posterior portion of basioccipital. The strong articular condyle of the basioccipital is well preserved. A small portion of the lateral ethmoid, median portion of the parasphenoid, and dorsal part of the sphenotic are preserved. The articular area for the hyomandibula and the sphenotic spine are lost.

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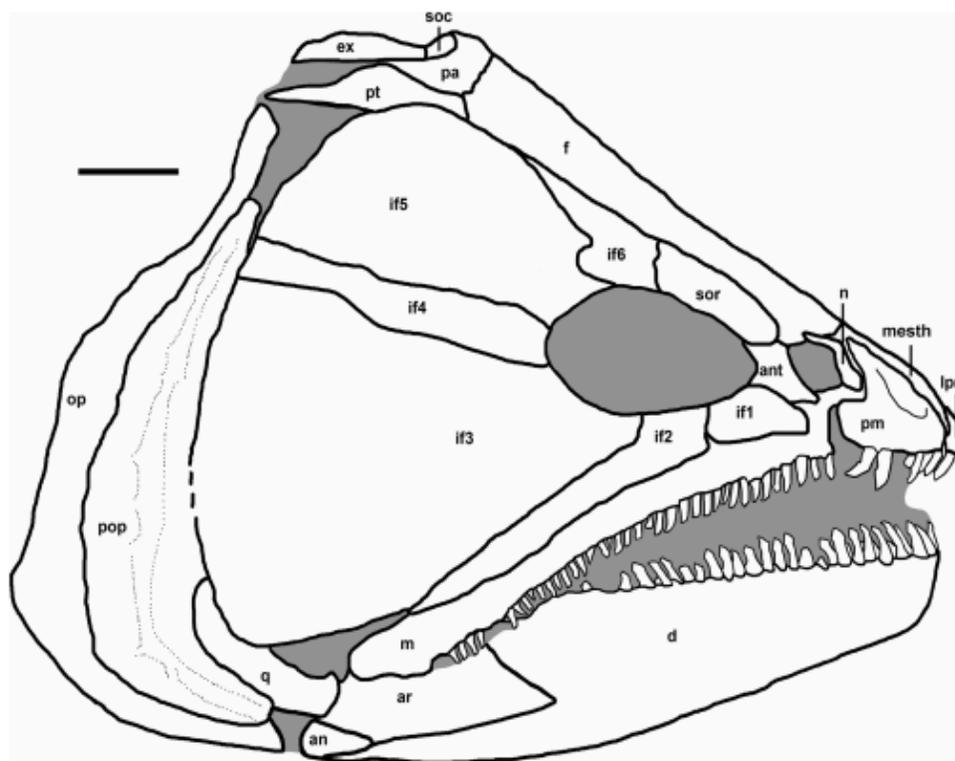


FIGURE 4. Interpretative drawing of *Salminus noriegai*, sp. nov. (CICYTTP-PV-P-1-291), in right lateral view. Scale bar equals 1 cm.

in all dentigerous bones excepting the posterior teeth of the inner row of the dentary, which are very small and conical and have a rounded base. Each tooth peduncle is rectangular and labiolingually elongated and has four well-delimited faces. We detached a tooth from a Recent specimen for comparison (Fig. 8). There are two deep main basoapical sulci in the symphyseal and commissural faces and smaller sulci on all the root faces. The large symphyseal and commissural sulci separate the peduncle into two sectors, which gives it the appearance of a figure '8.' The tooth cap is lanceolate and covered by enameloid. The labial face is convex and the lingual is rather concave. Consequently, the cap is lingually curved. There are well-formed symphyseal and commissural cutting edges.

Suspensorium

The robust quadrate resembles that of other characids. The hyomandibula is large and deep with a slender ventral part and a fan-shaped dorsal portion (Figs. 5, 6). It is ventrally displaced, exposing the posterodorsal portion of the articulation with neurocranium. The metapterygoid is laminar and quadrangular. It bounds a large fenestra along with the quadrate. The ectopterygoid possesses a slender posterior portion. The mesopterygoid is fragmentary. The palatine is mesially displaced and quadrangular in shape.

Opercular Bones and Branchiostegals

The left opercle is displaced but rather well preserved; only the anterior portion of the right opercle is present (Figs. 3–6). The opercle is deep and wide. The wide right interopercle is almost complete. The line of contact with the opercle is slightly diagonal. The 'L'-shaped left preopercle has a squared-off posteroventral corner and a deep vertical arm. The sensory canal runs in the middle part in both the vertical and horizontal arms. There are three exits of the sensory canal in the vertical arm and two in the horizontal arm. The quadrate is firmly articulated with the preopercle. Below and behind the left interopercle there are three fragmentary branchiostegals.

DISCUSSION

Several phylogenetic analyses of the order Characiformes or some of its families have been performed using molecular (Ortí and Meyer, 1997; Calcagnotto et al., 2005; Oliveira et al., 2011) and morphological (Lucena, 1993; Buckup, 1998; Miranda, 2010) data. The most recent phylogenetic analyses using each methodology gave different definitions of the family Characidae. The morphological analysis of Miranda (2010), which had a more inclusive concept of the family, included the genus *Salminus*. The molecular analysis of Oliveira et al. (2011), which included some morphological data, diagnosed the family with two morphological characters in addition to molecular data. Those morphological

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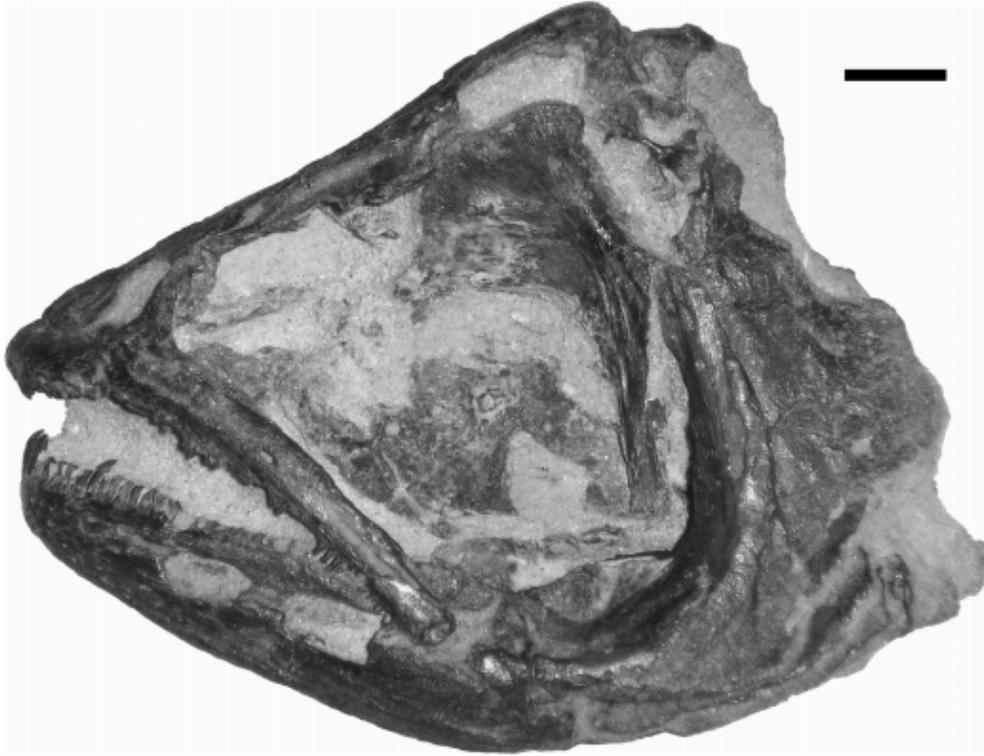


FIGURE 5. Photograph of *Salminus noriegai*, sp. nov. (CICYTTP-PV-P-1-291), in left lateral view. Scale bar equals 1 cm.

characters are the absence of supraorbital and the emergence of the hyoid artery from the anterior ceratohyal proximate to the articulation of that bone with the posterior ceratohyal. This analysis does not include the genus *Salminus* in Characidae; it was assigned to the family Bryconidae. Unfortunately, Oliveira et al. (2011) did not use morphological data for clades outside their Characidae. Consequently, we use the morphological analysis of Miranda as a basis for discussing our systematic assignation.

The morphology and spatial arrangement of skull bones of the Paraná Formation fossil presents several synapomorphies of the unnamed clade defined in the node 176 that groups the subfamilies Salmininae + (Agoniatinae + (Cynodontinae + Acetrorhynchinae)) (see figure 126 of Miranda, 2010). These synapomorphies are: articulation between second and third infraorbitals posteroventrally angled (state 2 of character 62), quadrate with anterodorsal portion equal or longer than ventral region (state 1 of character 150), articulation between quadrate and anguloarticular posterior to middle eye (state 1 of character 154), and probable articulation between ventral margin of metapterygoid and posterodorsal margin of quadrate present (state 1 of character 155).

The skull most resembles that of the basal monogeneric subfamily Salmininae (see Eigenmann, 1917, 1922; Fuster de Plaza, 1950; Roberts, 1969; Miranda, 2010). Notwithstanding the fact that *Salminus* is known since the first part of 19th century (Spix and Agassiz, 1829) and that it is a conspicuous fish of the South

American ichthyofauna, the intrageneric relationships have been scarcely studied (Lima, 2006; Lima and Britski, 2007). The genus is usually considered, on morphological grounds, a basal characid (Géry, 1977; Malabarba and Weitzman, 2003), but see Oliveira et al. (2011). Several phylogenetic analyses using molecular data have suggested *Salminus* to be the sister taxon of *Brycon* (Ort and Meyer, 1997; Calcagnotto et al., 2005; Oliveira et al., 2011), another supposed basal characid, a view contradicted by morphology (Lima, 2006; Lima and Britski, 2007; Miranda, 2010).

Lima (2006) made the first general morphological and phylogenetic analysis for the species of *Salminus*. He proposed several autapomorphies for the genus. In the fossil we observed only one: fourth infraorbital narrow and long (state 1 of character 2). Additionally, Lima (2006) suggested that other characters were probable synapomorphies of *Salminus*, although they were not exclusive for the genus. We found some of these characters in the fossil: internal process of the premaxilla where the anterior portion of maxilla lies (state 1 of character 8), inner tooth series of dentary complete (state 2 of character 13), anterior process of hyomandibula reaching ectopterygoid (state 1 of character 18), temporal fossa present (state 1 of character 27), and frontoparietal fontanelle small (state 2 of character 32).

Lima (2006:16) also proposed that the peculiar tooth shape ("dentes pedunculados, de base cilíndrica e coroa aproximadamente triangular") was a synapomorphy for *Salminus*. Although agreeing with that, we herein include other characters in this

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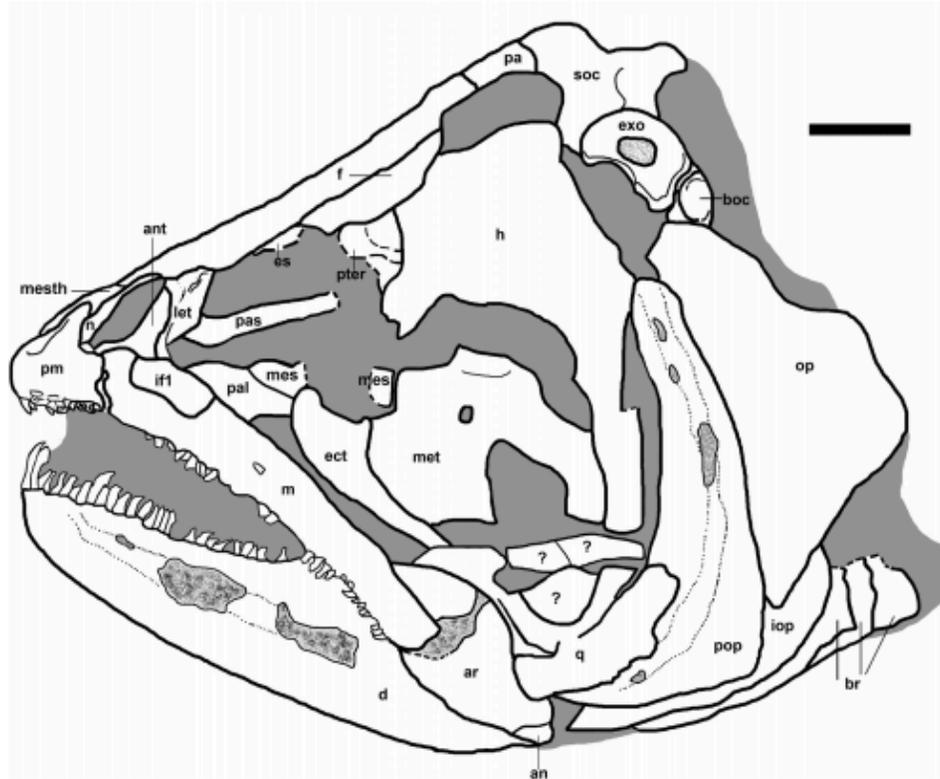


FIGURE 6. Interpretative drawing of *Salminus noriegai*, sp. nov. (CICYTTP-PV-P-1-291), in left lateral view. Scale bar equals 1 cm.

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complex shape (Fig. 8): tooth peduncle with four well-delimited faces, two deep basoapical sulci, and other smaller in the symphyseal and commissural peduncle faces; peduncle rectangular and labiolingually expanded; large symphyseal and commissural sulci separating the base into two sectors, giving it the appearance of a figure 8 in basal view; and the cap of teeth lanceolate, tooth cap labial face convex and lingual rather concave, and cap covered by enameloid with the lateral carenae forming cutting edges.

Currently, four species of *Salminus* are recognized: *Salminus affinis* Steindachner, 1880, *Salminus brasiliensis* (Cuvier, 1816), *Salminus franciscanus* Lima and Britski, 2007, and *Salminus hilarii* Valenciennes in Cuvier and Valenciennes, 1850.

Salminus noriegai can be distinguished from all other *Salminus* species in having (1) a long premaxilla and a very long maxilla whose posterior margin surpasses the posterior margin of the infraorbital 2; (2) an oblong and proportionally very large orbit; (3) the supraorbital forming a ledge that roofs the ocular cavity; and (4) dorsally, the profile is concave whereas it is convex in *S. brasiliensis*, *S. affinis*, and *S. hilarii* and straight in *S. franciscanus*. *Salminus noriegai* differs from *S. franciscanus* (of all sizes) and *S. brasiliensis* (smaller than 35 cm SL) in having a second dentary tooth in the outer series of similar size to that of the remaining teeth (rather than larger than the remaining teeth) (see Lima and Britski, 2007). *Salminus noriegai* differs from *S. brasiliensis* in that

the preopercle is 'L'-shaped rather than curved; a narrower horizontal blade of the dentary; a narrow maxilla; a larger and longer supraorbital; and both lateral sides of the mesethmoid concave in dorsal view instead of straight. *Salminus noriegai* possesses two of the 14 autapomorphies of *S. brasiliensis* (used as representative of *Salminus*) listed by Miranda (2010): posttemporal fossa well developed and inner tooth row of premaxillary comprising eight or more teeth (12 teeth in the fossil); and the remaining 12 characters are not observable in the fossil. *Salminus noriegai* differs from *S. affinis* in having a deeper head and a relatively longer lower jaw. In *S. affinis* the depth of the head at the level of posterior margin of infraorbitals is much smaller than the distance between the snout tip and the posterior margin of infraorbitals in comparison with the other species including *S. noriegai*. *Salminus noriegai* differs from *S. brasiliensis* and *S. hilarii* in the shape of mesethmoid (lateral sides concave in dorsal view).

Biogeography

The Neotropical region was divided into two major ichthyogeographic units—the Austral and Brazilian subregions—by Ringuélet (1975; see also Almirón et al., 1997; Arratia, 1997; Casciotta et al., 1999). Characiformes are almost exclusively limited to the Brazilian subregion, where most of the diversity is

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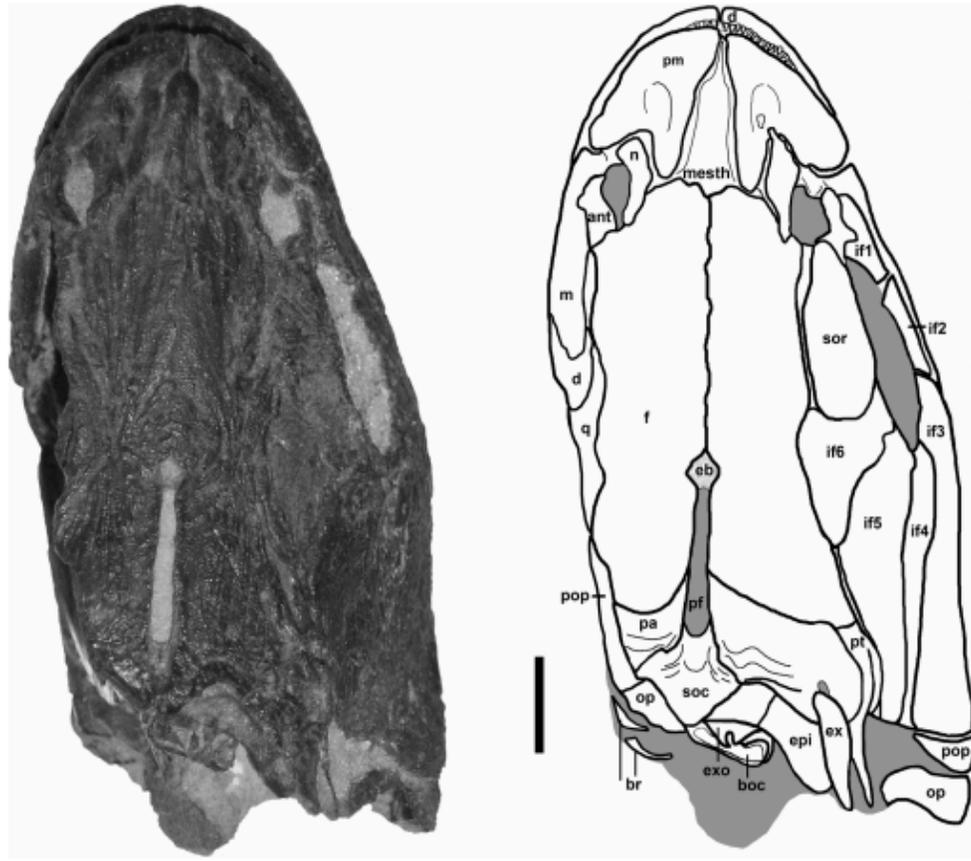


FIGURE 7. Photograph and interpretative drawing of *Salminus noriegai*, sp. nov. (CICYTTP-PV-P-1-291), in dorsal view. Scale bar equals 1 cm.

concentrated in the continent (Ringuet, 1975; Arratia, 1997). The family Characidae sensu Miranda (2010) is one of the most diversified families in the order, with more than 138 genera and 700 species (Berra, 2001), and is largely responsible, along with loricariid catfishes and cichlid perciforms, for the remarkable diversity of the subregion. Even when the more restricted

concept of the family of Oliveira et al. (2011) is accepted, the clade is remarkably diverse. The Austral ichthyofauna is more closely related to West Gondwanan faunas (e.g., Australia and New Zealand; Ringuet, 1975) and the Brazilian ichthyofauna to African faunas (Patterson, 1975). Characiformes are mostly confined to tropical and subtropical climates (Vari and Malabarba, 1998). Their diversity dramatically diminishes southward. *Salminus* occurs in most of the area where characiforms are distributed, but it is absent in the southern part of the continent and in the western side of the Andes south of Ecuador (Fig. 9). The southernmost range of the genus is the Rfo de la Plata estuary (*S. brasiliensis*; Ringuet, 1975; M.M.A., pers. observ.). The fossil species *Salminus noriegai* was found within the southern area of the present distribution of the genus, about 400 km north of its southernmost boundary.

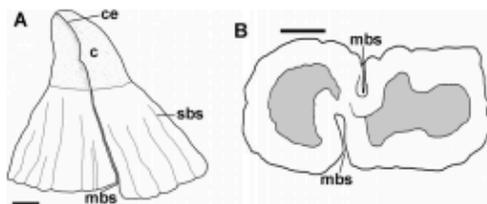


FIGURE 8. Tooth of *Salminus brasiliensis*. A, lateral view; B, transversal basal section. Scale bar equals 1 mm.

Minimum Age of the Clade

In most groups of Neotropical fishes, paleontological and biogeographic evidence suggest that adaptive diversification takes a long time and requires a lot of space (Albert et al., 2010;

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FIGURE 9. Geographic distribution of the different species of *Salminus*. 1, *Salminus affinis*; 2, *S. brasiliensis*; 3, *S. franciscanus*; 4, *S. hilarii*. The black circle indicates the type locality (La Toma Vieja) of *S. noriegai*.

Lundberg et al., 2010). According to the phylogenetic analysis of Mirande (2010) based on morphology, the monogeneric subfamily Salmininae is the sister group of the clade formed by the Agoniatinae, Cynodontinae, and Acestrorhynchinae. The Cynodontinae are known in La Venta Formation of the Magdalena valley in Colombia, which is dated at about 15 Ma (Mora et al., 2010). Consequently, the minimum age of genus *Salminus* might be middle Miocene and the discovery of *S. noriegai* in sediments of 9 Ma or less does not alter this minimal age. Cynodontines also occur in the 'Conglomerado osífero,' along with *S. noriegai* (Cione and Casciotta, 1997; Cione et al., 2005, 2012). Agoniatines and acestrorhynchines do not have fossil records.

According to the molecular phylogenetic analysis of Oliveira et al. (2010), *Salminus* is the sister group of *Brycon*. *Brycon* was identified in late Oligocene–early Miocene beds at Tremembé in Brazil (Malabarba, 1998). Consequently, following this cladistic scheme, the minimum age of *Salminus* should be extended to that age.

The occurrence of genus *Salminus* in the early Tortonian (and in the older beds by indirect evidence as well) corroborates the finding that many recent fish genera were present in the Miocene. More precisely, the Miocene Brazilian fish fauna (sensu Ringuelet, 1975) of the Neotropics has strong similarities with the Recent one (Lundberg et al., 2010). However, the record shows that many Miocene genera and species became extinct and are not present today (Cione et al., in press). *Salminus noriegai* is one of these extinct species.

ACKNOWLEDGMENTS

We thank the following institutions and individuals: Consejo Nacional de Investigaciones Científicas y Técnicas, Agencia Nacional de Promoción Científica y Tecnológica, and Universidad Nacional de La Plata for permanent financial support; staff of the Centro de Investigaciones Científicas y de Transferencia de Tecnología a la Producción for assistance in the field; J. Noriega for loaning of the holotype; J. H. Laza for preparing the material; J. I. Mojica, G. A. Ballen, and J. A. Anyelo Vanegas-Ríos for valuable information about *S. affinis*; A. Carlini and H. Britski for loaning recent material; and M. Mirande and an anonymous reviewer for valuable comments on the manuscript.

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franciscanus; 4, *S. hi-larii*. The black circle indicates the type locality (La Toma Vieja) of *S. noriegai*.

Lundberg et al., 2010). According to the phylogenetic analysis of Mirande (2010) based on morphology, the monogeneric subfamily Salmininae is the sister group of the clade formed by the Agoniatinae, Cynodontinae, and Acestrorhynchinae. The Cynodontinae are known in La Venta Formation of the Magdalena valley in Colombia, which is dated at about 15 Ma (Mora et al., 2010). Consequently, the minimum age of genus *Salminus* might be middle Miocene and the discovery of *S. noriegai* in sediments of 9 Ma or less does not alter this minimal age. Cynodontines also occur in the 'Conglomerado osífero,' along with *S. noriegai* (Cione and Casciotta, 1997; Cione et al., 2005, 2012). Agoniatines and acestrorhynchines do not have fossil records.

According to the molecular phylogenetic analysis of Oliveira et al. (2010), *Salminus* is the sister group of *Brycon*. *Brycon* was identified in late Oligocene–early Miocene beds at Tremembé in Brazil (Malabarba, 1998). Consequently, following this cladistic scheme, the minimum age of *Salminus* should be extended to that age.

The occurrence of genus *Salminus* in the early Tortonian (and in the older beds by indirect evidence as well) corroborates the finding that many recent fish genera were present in the Miocene. More precisely, the Miocene Brazilian fish fauna (sensu Ringuelet, 1975) of the Neotropics has strong similarities with the Recent one (Lundberg et al., 2010). However, the record shows that many Miocene genera and species became extinct and are not present today (Cione et al., in press). *Salminus noriegai* is one of these extinct species.

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