A NEW NEOSUCHIAN CROCODYLOMORPH (CROCODYLIFORMES, MESOEUCROCODYLIA) FROM THE EARLY CRETACEOUS OF NORTH-EAST BRAZIL

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Abstract: A new neosuchian crocodylomorph, *Susisuchus jaguaribensis* sp. nov., is described based on fragmentary but diagnostic material. It was found in fluvial-braided sediments of the Lima Campos Basin, north-eastern Brazil, 115 km from where *Susisuchus anatoceps* was found, in rocks of the Crato Formation, Araripe Basin. *S. jaguaribensis* and *S. anatoceps* share a squamosal–parietal contact in the posterior wall of the supratemporal fenestra. A phylogenetic analysis places the genus *Susisuchus* as the sister group to Eusuchia, confirming earlier studies. Because of its position, we recovered the family name Susisuchidae, but with a new definition, being node-based group including the last common ancestor of *Susisuchus anatoceps* and *Susisuchus jaguaribensis* and all of its descendents. This new species corroborates the idea that the origin of eusuchians was a complex evolutionary event and that the fossil record is still very incomplete.

Key words: Crocodyliformes, Mesoeucrocodylia, Neosuchia, *Susisuchus*, new species, Early Cretaceous, north-east Brazil.

BRAZILIAN crocodylomorphs form a very expressive record of Mesozoic vertebrates, with more than twenty species described up to now. They are representatives of many groups of mesoeucrocodylians: notosuchians (*sensu* Sereno *et al.* 2001), baurusuchids, peirosaurids and neosuchians (Bertini *et al.* 1993; Salisbury *et al.* 2003, Carvalho *et al.* 2004, 2005, 2007). The only known Triassic crocodylomorph is the sphenosuchian *Barberenasuchus brasiliensis* from the Ladinian of Santa Maria formation, Paraná Basin (Mattar 1987), and it is the oldest of this group. However, Kischlat (2001), studying basal archosaurs, has questioned the taxonomic status of this species as a basal crocodylomorph and suggested that *Barberenasuchus brasiliensis* is indeed a rauisuchian archosaur.

The Lower Cretaceous species are the notosuchian *Araripesuchus gomesi* (Price, 1959), the neosuchians *Caririsuchus camposi* (Kellner, 1987) and *Susisuchus anatoceps* (Salisbury *et al.,* 2003), all from the Aptian–Albian of Araripe Basin; the neosuchian *Sarcosuchus hartii* (Marsh, 1869) and the gavialoid *Thoracosaurus bahiensis* (Marsh, 1869) from the Aptian of the Recôncavo Basin, but the later one still has a questionable taxonomic status (Buffetaut and Taquet 1977); and the notosuchian *Candidodon itapecuruense* (Carvalho and Campos, 1988) from the Aptian–Albian of the Parnaiba basin.

The Upper Cretaceous species are mainly the notosuchians, baurusuchids and peirosaurids from the Turonian–Maastrichtian of Bauru basin: *Adamantinasuchus navae* (Nobre and Carvalho, 2006), *Baurusuchus pachecoi* (Price, 1945), *Baurusuchus salgadoensis* (Carvalho *et al.*, 2005), *Itasuchus jesuinoi* (Price, 1955), *Mariliasuchus amarali* (Carvalho and Bertini, 1999), *Mariliasuchus robustus* (Nobre *et al.,* 2007), *Montealtosuchus arrudacamposi* (Carvalho *et al.,* 2007), *Peirosaurus tormini* (Price, 1955), *Sphagesaurus huenei* (Price, 1950), *Sphagesaurus montealtensis* (Andrade and Bertini, 2008), *Stratiotosuhus maxhechtii* (Campos *et al.,* 2001), *Uberabasuchus terrificus* (Carvalho *et al.,* 2004), and three taxa with questionable taxonomic status as a result of a few diagnostic characters, *Brasileosaurus pachecoi* (Huene, 1931), *Goniopholis paulistanus* (Roxo, 1936) and *Pholidosaurus milwardi* (Roxo, 1929). Completing the list of Upper Cretaceous species, there are the dyrosaurid *Hyposaurus derbianus* (Cope, 1886), from the Maastrichtian of the Pernambuco–Paraíba basin.

Besides the formally described species, there are fossil remains of Cretaceous crocodylomorphs for other Brazilian basins, being basically isolated teeth an osteoderms (Carvalho 1994; Carvalho and Nobre 2001; Elias *et al.* 2004).
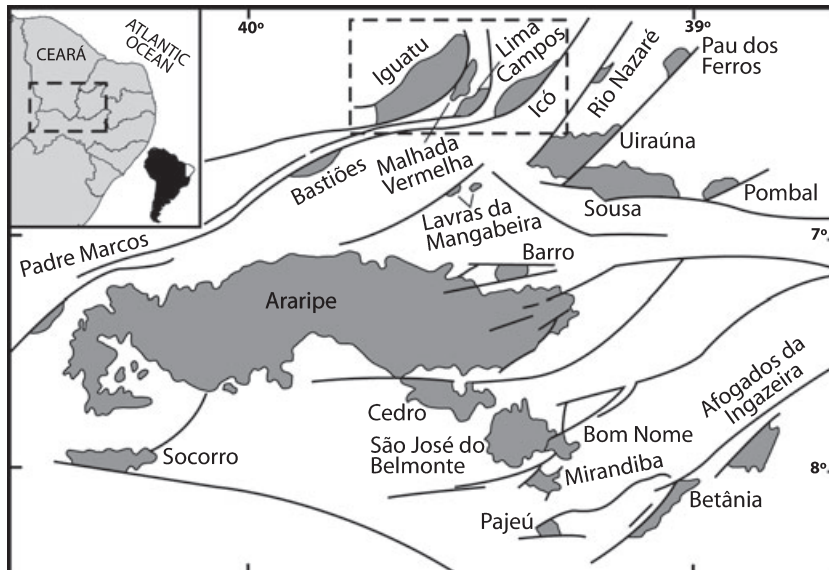
In this work, we describe a new neosuchian crocodylomorph, *Susisuchus jaguaribensis* sp. nov., from the Berriasian–Barremian (Early Cretaceous) of Lima Campos basin, north-eastern Brazil, based on a partial skull.
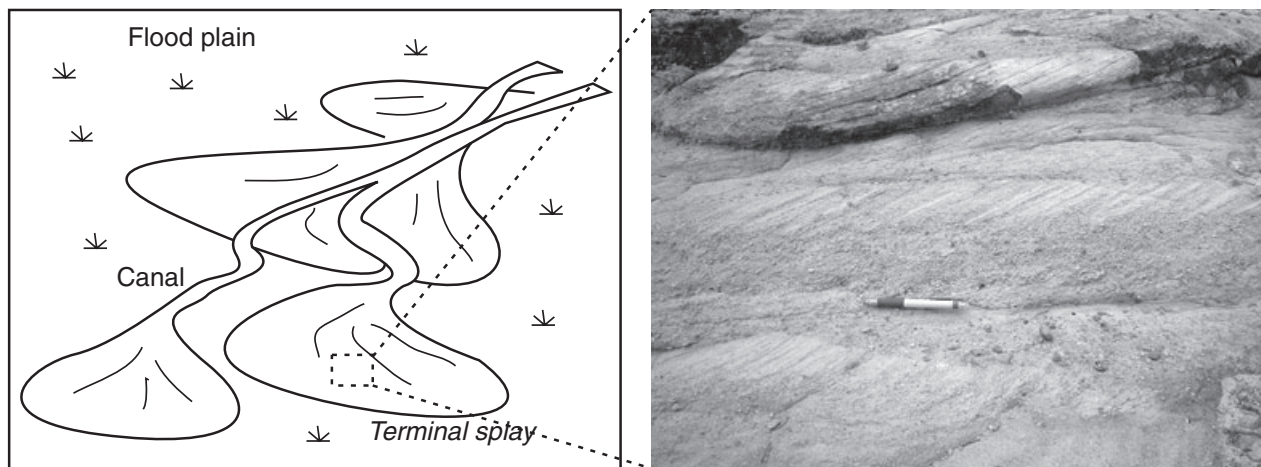
GEOLOGICAL SETTING

The Lima Campos Basin is one of the four small basins from north-eastern Brazil that are usually grouped as 'Iguatu Basins': Icó, Iguatu, Lima Campos and Malhada Vermelha (Text-fig. 1). The Iguatu Group, including the sedimentary deposits of the four basins as a whole, is divided traditionally into three formations, from base to top: Icó, Malhada Vermelha and Lima Campos. Its sediments were deposited in a continental environment, mainly represented by fluvial systems (Beurlen and Mabesoone 1969; Matos 1987; Ponte *et al.* 1990), and reproduce the incomplete record of the rifting process of Gondwana and consequent Proto-Atlantic Ocean formation in the most landwards located rift basins of Brazil during Late Jurassic and Cretaceous (Arima 2007). The age of the Iguatu Group is Berriasian–Barremian (Early Cretaceous), based on ostracodes and conchostracans (Ghignone 1972; Mabesoone and Campanha 1974). Ichnofossils, plant fragments, 'reptiles' and fish fragments, pollens and spores have been reported (Lima 1990; Ponte *et al.* 1990; Carvalho 2000).

The specimen described here was collected in sediments of the Lima Campos basin, near BR-404 roadway in the extreme south of the Lima Campos dam (east of the basin), in the municipality of Icó, State of Ceará. The outcrop (Text-fig. 2), informally named IG-150 (Arima 2007), is composed of conglomeratic coarse-grained sandstone with tubular and through cross-bedded stratification and intercalated by fine-to-middle–grained sandstone, deposited in a fluvial-braided system.

TEXT-FIG. 1. North-eastern Brazil sedimentary basins. Dashed box encompasses Iguatu basins. Modified from Carvalho (2000).

TEXT-FIG. 2. Outcroup IG-150 from the Lima Campos basin. (Picture by Naoki Arima (Petrobras)).

Arima (2007), in a general study of Iguatu basins, including the Lima Campos Basin, recognized eleven lithofacies that grouped together constitute four architectural elements: canal, gravel bar, crevasse splay and floodplain (Text-fig. 2). The architectural element associations allowed the recognition of proximal, median and distal portions of a fluvial distributary system (Nichols & Fisher 2006). The IG-150 outcrop has sediments from the distal portion of this fluvial system.

The fossil here presented was collected from middle-grained sandstone, at the top of IG-150 outcrop sequence.
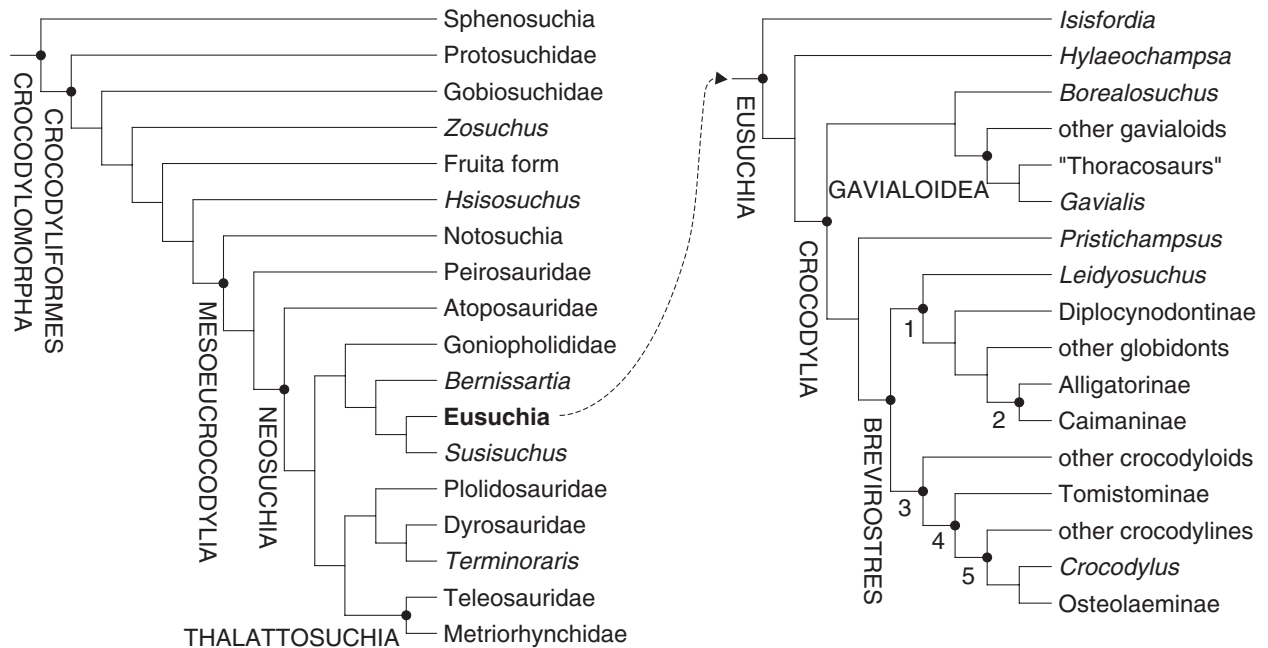
MATERIALS AND METHODS

The fossil described here (UFRGS-PV0001K) is housed in the collection of the Laboratory of Vertebrate Palaeontology, at Universidade Federal do Rio Grande do (UFRGS), Porto Alegre. It was collected during a geological expedition to north-east Brazil (Ceará and other states), lead by Dr Michael Holz (UFRGS), in January 2006. The main objective of that expedition was to study the stratigraphy of the poorly known Iguatu basins.

A dental drill was used to remove the hard rocky matrix and needles to remove the free sediment. Paraloid B72 was applied on the fossil surface to prevent bone cracking.

TAXONOMIC BACKGROUND

The taxonomic classification of crocodylomorphs follows mainly Clark (1994) and Brochu (1999), with Neosuchia and Notosuchia definitions of Sereno et al. (2001). Peirosauridae was removed from Neosuchia, as in Gasparini et al. (2006). Thalattosuchia is included inside Neosuchia, as a member of 'Metasuchia' (Clark 1994; Buckley and Brochu 1999; Ortega et al. 2000; Wu et al. 2001b; Brochu et al. 2002; Pol and Norell 2004a, b; Pol and Apesteguía 2005) and not its sister group (Benton and Clark 1988; Buckley et al. 2000; Sereno et al. 2001, 2003; Turner and Calvo 2005; Turner 2006; Larsson and Sues 2007). Eusuchia was applied according to the apomorphy-based definition of Salisbury et al. (2006), because the phylogenetic relationships of some basal eusuchians, like Aegyptosuchus (Stromer, 1933) and Dolichochampsa (Gasparini & Buffetaut, 1980), are not resolved to allow a node-based definition. Text-figure 3 shows the crocodylomorph classification modified from Clark (1994), Brochu (1999), Pol and Apesteguía (2005), Gasparini et al. (2006) and Salisbury et al. (2006). Although weakly supported, the sister group relationship between Borealosuchus and Gavialoidea (Salisbury et al. 2006) was maintained.

Anatomical and taxonomic characterization was based mainly on Iordansky (1973), Brochu (1999) and Salisbury et al. (2003, 2006). The anatomical nomenclature and abbreviation follow Iordansky (1973) and Brochu (1999,

TEXT-FIG. 3. Taxonomic classification of crocodylomorphs, based on Clark (1994), Brochu (1999), Pol and Apesteguía (2005), Salisbury et al. (2006) and Gasparini et al. (2006). Numerated clades: 1-Alligatoroidea, 2-Alligatoridae, 3-Crocodyloidea, 4-Crocodylidae, 5-Crocodylinae.

2007). The systematic analysis used the data matrix of Delfino *et al.* (2008*a*), which was based on Salisbury *et al.*'s (2006) dataset and Turner and Buckley (2008) for the basic phylogenetic methods to recover the most parsimonious trees.

SYSTEMATIC PALAEONTOLOGY

CROCODYLOMORPHA Walker, 1968
CROCODYLIFORMES Benton and Clark, 1988
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
NEOSUCHIA Benton and Clark, 1988

SUSISUCHIDAE Salisbury *et al.,* 2003

New definition. A node-based group including the last common ancestors of *Susisuchus anatoceps*, *Susisuchus jaguaribensis* and all of its descendents.

Unambiguous synapomorphy. The parietal and the squamosal meet along the caudal wall of the supratemporal fenestra (character 131-2).

Ambiguous synapomorphies. The nuchal shield is differentiated from the dorsal shield into more than four nuchal osteoderms in two parallel rows (character 38-3); the prootic is largely obscured externally by the quadrate and the laterosphenoid (character 74-1); the dentary tooth 4 occludes in a pit between the premaxilla and the maxilla, and no presence of notch early in ontogeny (character 77-1); the maxillary alveoli #4 and #5 are homodont (character 89-3); the maxilla sends a caudal process between the lacrymal and the prefrontal (character 93-2); the dorsal process of the jugal is flush with the lateral surface of the jugal (character 146-0); the height of the peduncle of the neural arch on the caudal cervical vertebrae is considerably greater than that of the peduncle on neural arch of each of the thoracic, sacral and cranialmost caudal vertebrae (character 169-1); the caudal vertebrae are all amphicoelous (character 171-0).

Discussion. The clade including *Susisuchus anatoceps* and *S. jaguaribensis* can be diagnosed on the basis of a parietal–squamosal contact along the caudal wall of the supratemporal fenestra. This feature is unique among non-eusuchian neosuchians and supports the monophyly of Susisuchidae. Among eusuchians, this characteristic convergently evolved in alligatoroids (a synapomorphy according to Delfino *et al.* 2008*b*), like *Diplocynodon muelleri* (Kälin 1936; Piras and Buscalioni 2006), *D. tormis* (Buscalioni *et al.* 1992; Piras and Buscalioni 2006) and globidontans, except for *Brachychampsa montana* (Gilmore 1911; Norell *et al.* 1994; Brochu 1999). Support of this group is weak, largely because of the incompleteness of *S. jaguaribensis*. The great number of ambiguous synapomorphies is actually autapomorphies of *S. Anato-*

ceps in an analysis excluding *S. jaguaribensis*. Those characters could not be coded for the latter taxon. We expect that more materials could solve the ambiguousness of some characters.

Genus SUSISUCHUS Salisbury *et al.,* 2003

Type species. Susisuchus anatoceps (Salisbury *et al.*, 2003), from the Aptian of Crato formation, Araripe basin, State of Ceará, Brazil.

Emended differential diagnosis. Small neosuchian that is distinguished from other advanced neosuchian genera by the possession of the following combination of features: massive postorbital bar (character 70-0), quadratojugal forming the caudal angle of the infratemporal fenestra (character 75-0), quadrate jugal extends to the superior angle of infratemporal fenestra (character 80-0), linear frontoparietal suture (character 86-0), supratemporal fenestra with fossa (character 87-0), rostromedial corner of supratemporal fenestra smooth (character 92-1), margin of orbit flush with skull surface (character 103-0), quadrate bearing a small, ventrally reflected medial hemicondyle (112-0), parietal and squamosal meet along caudal wall of the supratemporal foramen (131-2), exoccipital with small or no boss medial to the paroccipital process, long process lateral to the caudal aperture of the cranioquadrate canal (character 141-1), and postorbital inset from the lateral edge of the dorsal part of the postorbital (character 175-1). All these features are present in both *Susisuchus anatoceps* and *S. jaguaribensis*, and represent the main features to differentiate them from other advanced neosuchians.

Susisuchus anatoceps Salisbury *et al.,* 2003

Type specimen. SMNK 3804 PAL (Staatliches Museum für Naturkunde Karlsruhe), an incomplete and partially articulated skeleton.

Type locality. Nova Olinda member, Crato Formation (Aptian), Araripe basin. The calcareous slab lacks provenance information, but was probably collected between the cities of Nova Olinda and Santana do Cariri, both from State of Ceará (Salisbury *et al.,* 2003).

Emended diagnosis. Susisuchus anatoceps is distinguished from the new species by the following combination of features: quadratojugal spine greatly reduced or absent at maturity (character 69-1); postorbital contacting quadratojugal, but not quadrate, medially (character 76-1); frontoparietal suture deeply within supratemporal

fenestra; the frontal prevents broad contact between the postorbital and the parietal (character 81-0); large supra-occipital exposure on dorsal skull table (character 82-2); skull table with broad lateral curvature; and short caudo-lateral process of the squamosal (character 140-0).

Susisuchus jaguaribensis sp. nov.

Derivation of name. After Jaguaribe, the name of an important perennial river that provides water for the Iguatu region.

Holotype. UFRGS-PV0001K, posterior portion of skull (Pl. 1, figs 1–4).

Type locality, horizon and age. South of Lima Campos dam, at the municipality of Icó (Ceará State), north-east Brazil, in a middle-grained sandstone with calcite cementation, regarded as Berriasian–Barremian (local age Rio da Serra-Aratu, Early Creta-ceous) based on chonchostracan and ostracode biostratigraphy (Ponte *et al.,* 1990). Geographic coordinates: 6°24′32.557′S and 38°57′57.173′W. The distance between the localities where *S. anatoceps* and *S. jaguaribensis* were found is ∼ 115 km.

Diagnosis. Susisuchus jaguaribensis is differentiated by the presence of the following combination of features: qua-dratojugal spine prominent at maturity (character 69-0); postorbital contacts quadrate and quadratojugal at dorsal angle of intratemporal fenestra (character 76-2); frontopa-rietal suture entirely on skull table (character 81-2); small or absent supraoccipital exposure on dorsal skull table (character 82-01); skull table with nearly horizontal sides; significant caudolateral process of the squamosal (140-1).

Remarks. Comparing with phylogenetically closely related crocodylomorphs, i.e. *Susisuchus anatoceps* and *Isisfordia duncani, S. jaguaribensis* would have ∼ 10 cm of skull length and 65 cm of body length. It is bigger than *S. anat-oceps* (described as a juvenile specimen with ∼ 50 cm), but almost half size of *I. duncani* (described as an adult specimen with ∼ 110 cm). Although being small, the specimen described here cannot be attributed to a juve-nile, but at least to a young adult, because of its advanced fusion status of cranial sutures, mainly those from neu-rocranium, and the size of the quadratojugal spine (see details below). Using the skull and body length into the regression formulae of Farlow *et al.* (2005), we can esti-mate the body weight of *S. jaguaribensis* to be between 0.6 and 1 kg.

Description

The preserved bones in the specimen are quadrates, quadratoju-gals, squamosals, postorbitals, parietal, frontal, exoccipitals, basioccipital, basisphenoid and laterosphenoid. The dorsal bones, exoccipitals and basioccipital are well preserved, but the margins of the bones of the basicranium are difficult to distinguish.

General features. The skull table is planar with a rectangular out-line in dorsal view, with nearly horizontal sides (characters 123-1 and 140-1) and outer surface of dermal bones heavily orna-mented with deep pits and grooves. The flat and extended skull roof surrounds the relatively anteroposteriorly short supratem-poral fenestra. Its length is shorter than the orbital length, and the dermal bones of skull roof do not overhang its rim (charac-ter 87-0). The anteromedial corner of the supratemporal fenestra is smooth (character 92-0). The margin of the orbit is flush with the skull surface (character 103-0). The occipital surface ventral to the basioccipital condyle slopes rostroventrally (character 174-0). The bar between the orbit and the supratemporal fenestra is broad and solid, with broadly sculpted dorsal surface. The jaw joint (quadrate position) is level with the basioccipital condyle. The anterior aperture of the post-temporal canal in dorsal view is hidden and overlapped by the squamosal rim of the supratem-poral fenestra. Although the supraoccipital is not preserved, its suture with the exoccipitals and the posteriorized parietal could be determined, allowing us infer that the supraoccipital exposure on the dorsal skull table is small or absent, but not large in pro-portion to the size of the cranial table, as occurs in *Susisuchus anatoceps* (Salisbury *et al.,* 2003).

Frontal. The T-shaped frontal is almost complete, lacking the anterior portion that contacts the prefrontal and the nasal (both not preserved). It contacts the postorbital posterolaterally and the parietal posteriorly. The suture between the frontal and these bones, dorsally, is limited to the skull table and does not enter the supratemporal fenestra. Therefore, there is no frontal partici-pation in the supratemporal fenestra (character 81-2). Among mesoeucrocodylians, this character is seen in notosuchians and brevirostrine eusuchians. In thalattosuchians and many neosu-chians, like dyrosaurids (Buffetaut 1978, 1979) and *Sarcosuchus imperator* (Sereno *et al.,* 2001), the frontoparietal suture enters supratemporal fenestra. The frontal is a singular bone, and no interfrontal suture is visible as occurs at maturity in most mes-oeucrocodylians. In primitive crocodylomorphs, like the sphe-nosuchid *Dromicosuchus grallator* Sues *et al.,* 2003 and the protosuchid *Protosuchus richardsoni* (Colbert and Mook, 1951), there are two frontals divided by a median suture. Paired fron-tals are found in the thalattosuchian *Pelagosaurus typus* (Pierce and Benton 2006). In *S. jaguaribensis,* the serrated frontoparietal suture is linear (character 86-0) and not concavoconvex. The first condition is plesiomorphic for crocodylomorphs, whereas the second condition is found in eusuchians. The dorsal surface of the two bones is flat, a typical condition of crocodylomorphs. However, some mesoeucrocodylians, such as some dyrosaurids and the notosuchians *Simosuchus clarki* (Buckley *et al.,* 2000) and *Comahuesuchus brachybuccalis* (Bonaparte, 1991), have a sagittal crest along the midline suture. As in most croco-dylomorphs, the frontal width between the orbits is narrow, when compared with some other crocodylomorphs, like the tha-lattosuchian *Pelagosaurus typus* (Pierce and Benton, 2006) and

the extant eusuchian *Gavialis gangeticus* Gmelin, 1789, which have a very broad frontal (Brochu 1999).

Parietal. The parietal is almost complete, lacking the posterior portion that contacts supraoccipital. Therefore, the contact between the parietal and the exoccipital could not be determined. The parietal contacts the squamosal laterally, the postorbital anterolaterally, the frontal anteriorly and the latherosphenoid ventrolaterally inside the supratemporal fenestra. The parietal roof between supratemporal fenestrae is flat. The serrated frontoparietal suture is linear (character 86-0). There is no small foramen in the medial parietal wall of supratemporal fenestra (character 104-0). The parietal and the squamosal meet along the caudal wall of the supratemporal foramen (character 131-2). This feature is found in alligatoroids, like *Diplocynodon muelleri* (Kälin, 1936; Piras and Buscalioni, 2006), *D. tormis* (Buscalioni *et al.,* 1992; Piras and Buscalioni 2006) and globidontans, except for *Brachychampsa montana* (Gilmore, 1911; Norell *et al.* 1994; Brochu 1999). This feature is also found outside the alligatoroids, as for the non-eusuchian neosuchian *Susisuchus anatoceps*, and a few mesoeucrocodylians, such as *Araripesuchus gomesi* (Price, 1959; Hetch 1991) and dyrosaurids (Brochu *et al.* 2002; Jouve 2005; Jouve *et al.* 2005, 2006*b*), as stated in Salisbury *et al.* (2006).

Postorbital. The right postorbital is completely preserved, while the left one lacks the posterolateral portion. The postorbital contacts the squamosal posteriorly, the parietal and frontal medially and the jugal ventrally at the end of the descending process (postorbital bar). The postorbital contacts the quadrate and the quadratojugal at the dorsal angle of the infratemporal fenestra (character 76-2). This feature is shared among some neosuchians, like the atoposaurid *Theriosuchus guimarotae* (Schwarz and Salisbury, 2005), and globidont alligatoroids (Brochu 1999). The parieto-postorbital suture is present within the supratemporal fenestra and on the dorsal surface of the skull roof (character 81-2). This is not a common feature of non-eusuchian crocodylomorphs, being present in the protosuchid *Protosuchus richardsoni* (Colbert and Mook, 1951), the notosuchian *Comahuesuchus brachybuccalis* (Bonaparte, 1991) and many crocodylians, like the gavialoid *Piscogavialis jugaliperforatus* (Kraus, 1998; Jouve *et al.* 2006*a*) and the osteolaemine *Voay robustus* (Brochu, 2007). The postorbital participates in the infratemporal fenestra, bordering it. This is a widespread feature among mesoeucrocodylians (Pol and Apesteguía 2005). The postorbital bar is subcylindrical in cross-section and massiveness (character 70-0) when compared to its length. These features are

found together in some mesoeucrocodylians, like the baurusuchid *Stratiotosuchus maxhechti* (Campos *et al.,* 2001), the advanced neosuchian *Bernissartia fagesii* (Buscalioni and Sanz, 1990), the basal eusuchian *Hylaeochampsa vectiana* (Delfino *et al.,* 2008*a*), gavialoids (Pol and Apesteguía 2005; Vélez-Juarbe *et al.,* 2007) and the basal globidontan *Acynodon* (Delfino *et al.,* 2008*b*). The postorbital bar is unsculpted, a mesoeucrocodylian feature, except for the teleosaurids (Eudes-Deslongchamps 1863; Buffetaut 1982). The dorsal part of the postorbital bar is constricted, distinct from the dorsal part of the postorbital, inset from the lateral edge of the dorsal part (character 175-1). This is a crocodyliform feature, except for thalattosuchians (Gasparini and Diaz 1977; Gasparini *et al.* 2006). There is no foramen in the dorsal surface of the postorbital bar. This mainly crocodylian characteristic is found in a few basal mesoeucrocodylians, like the notosuchian *Araripesuchus gomesii* (Price 1959; Hetch 1991), the atoposaurid *Theriosuchus guimarotae* (Schwarz and Salisbury, 2005) and the goniopholidid *Sunosuchus junggarensis* (Wu *et al.,* 1996). The anterolateral process of the postorbital is absent. This process can be found in *Dyrosaurus* (Buffetaut, 1978), *Sokotosuchus ianwilsoni* (Halstead, 1975; Buffetaut 1979), *Terminonaris robusta* (Wu *et al.,* 2001*b*) and *Sarcosuchus imperator* Broin and Taquet 1966 (Sereno *et al.* 2001). The dorsal part of the postorbital has anterior and lateral edges only. This is the basal condition for crocodylomorphs, differing to an anterolaterally facing edge in *Hsisosuchus chungkingensis* (Young and Chow, 1953; Li *et al.* 1994; Wu *et al.* 1994), notosuchians (Pol and Apesteguía 2005) and the peirosaurid *Lomasuchus palpebrosus* (Gasparini *et al.* 1991). The bar between the orbit and the supratemporal fenestra (mainly postorbital) is broad, solid and sculpted dorsally. This is a widespread feature among crocodylomorphs, differing from the narrow bar (with less sculpted surface) of the protosuchid *Zosuchus davidsoni* (Pol and Norell, 2004*a*), the notosuchian *Araripesuchus patagonicus* (Ortega *et al.,* 2000) and atoposaurids (Wellnhofer 1971; Schwarz and Salisbury 2005).
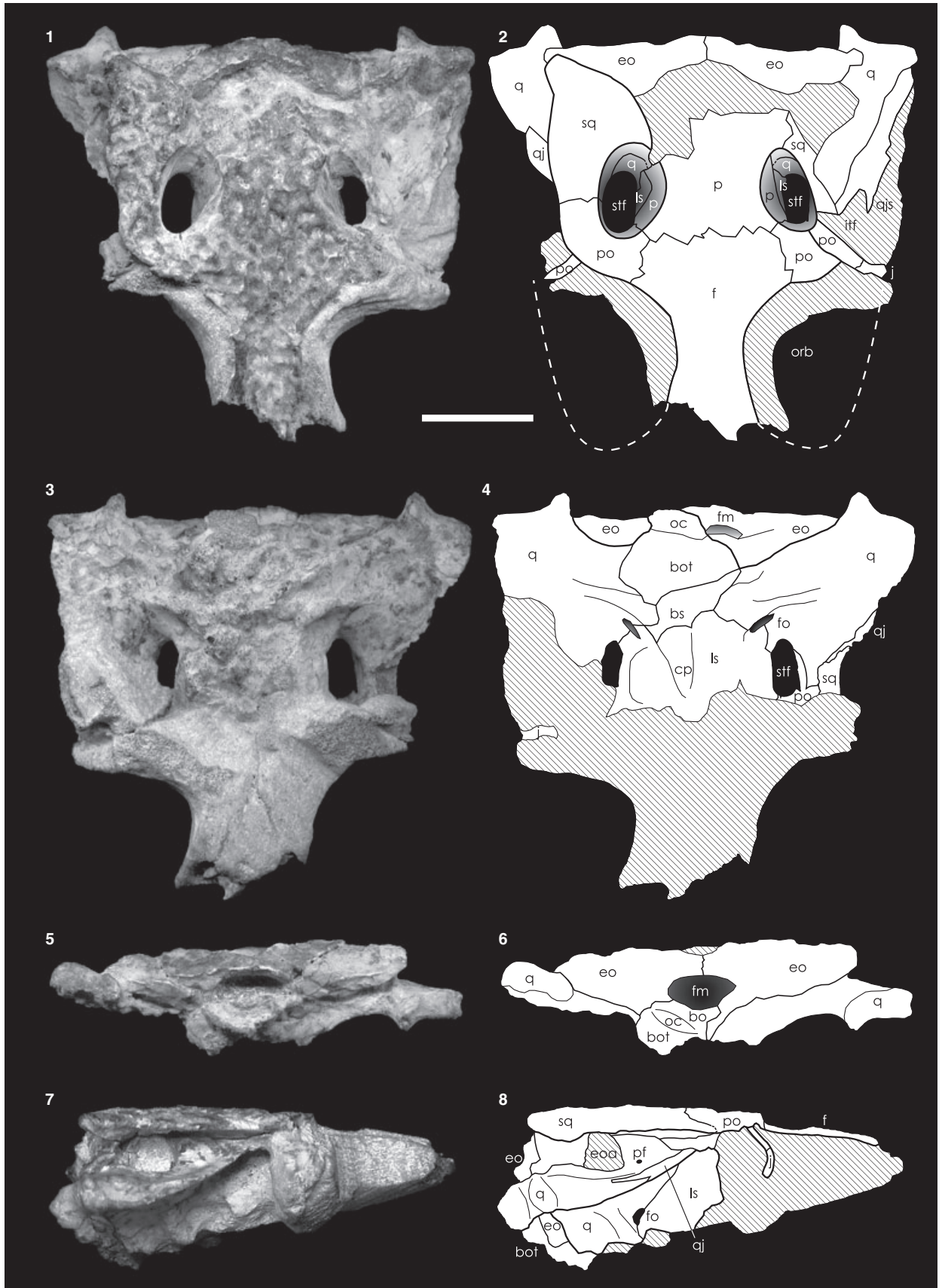
Squamosal. The right squamosal is completely preserved, while the left one has only the region that encircles the supratemporal fenestra. Dorsally, it is flat and triangular shaped. The caudolateral corner of the squamosal forms a distinct prong (preserved with some erosion), which is dorsal to the paroccipital process of the exoccipital (character 140-1) and very similar to that of crocodylians. The squamosal contacts the portorbital anteriorly and the parietal medially. Posteroventrally it contacts the exoccipital, and ventromedially the quadrate. The parietal and the squamosal meet along the caudal wall of the supratemporal fenestra (character 131-2). The quadratosquamosal suture

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EXPLANATION OF PLATE 1

Figs 1–4. Skull of *Susisuchus jaguaribensis* gen. et sp. nov.; holotype. (UFRGS-PV0001K). 1, dorsal, 2, ventral, 3, occipital and 4, right lateral views.

Figs 5–8. Schematic drawings with osteological interpretation. 5, dorsal, 6, ventral, 7, occipital and 8, right lateral views.

Abbreviations: bo, basioccipital; bot, basioccipital tubera; bs, basisphenoid; cp, capitate process of laterosphenoid; eoa, external otic aperture; eo, exoccipital; fm, foramen magnum; f, frontal; fo, foramen ovale; itf, infratemporal fenestra; j, jugal; ls, laterosphenoid; oc, occipital condyle; orb, orbit; p, parietal; pf, pneumatic foramen; po, postorbital; q, quadrate; qj, quadratojugal; qjs; quadratojugal spine; sq, squamosal; stf, supratemporal fenestra. Scale bar represents 1 cm.

PLATE 1

FORTIER and SCHULTZ, *Susisuchus*

extends dorsally along the caudal margin of the external auditory meatus (character 132-0). In lateral aspect, the postorbitosquamosal suture is oriented ventrally (character 163-0), differing from the condition in brevirostrine crocodylians, in which this suture passes medially, ventral to the skull table. The squamosal does not extend ventrally to the lateral extent of exoccipital and quadrate (character 150-0), a well-known condition for mesoeucrocodylians, except for osteolaemine crocodylians (Brochu 2007). The dorsal and the ventral rims of the squamosal groove for the external ear valve mulculature are nearly parallel (84-0), a mesoeucrocodylian feature. This condition is different for the gavialoids and many tomistomines, for which the squamosal groove flares rostrally (Brochu 1999, 2007). Atoposaurids have an unsculpted extra lobe in the posterodorsal corner of the squamosal, but the basal feature in crocodylomorphs, including *Susisuchus jaguaribensis*, is a squared off posterodorsal corner lacking a lobe (Wellnhofer 1971; Ortega *et al.* 2000). The posterolateral process of the squamosal is poorly developed and projects horizontally at the same level of the skull table. This feature is shared only by a few basal crocodylomorphs (Pol and Apesteguía 2005), like the sphenosuchid *Dibothrosuchus elaphros* (Simmons, 1965; Wu and Chatterjee 1993) and the protosuchid *Edentosuchus tienshanensis* (Young, 1973; Pol *et al.* 2004), and neosuchians, except for dyrosaurids (Buffetaut 1978, 1979). Other crocodylomorphs have an elongated process, directed posteriorly or posterolaterally (Pol and Apesteguía 2005). The squamosal length is longer than the postorbital. This is the plesiomorphic feature of crocodyliforms, except for the thalattosuchians, which have the opposite condition (Gasparini *et al.* 2006). The outer surface of the squamosal is laterodorsally oriented and reduced and unsculpted, a feature present only within the neosuchians. The dorsal surface of the posterolateral region of the squamosal does not have ridges. Among crocodylomorphs, only *Gobiosuchus kielanae* (Osmolska, 1972; Osmolska *et al.* 1997) and *Zaraasuchus shepardi* (Pol and Norell, 2004b) have three curved ridges oriented longitudinally. The squamosal has a descending process, as in others crocodyliforms.

Jugal. Only the dorsal ascending process of both jugals are preserved, forming the inferior part of the postorbital bar, positioned laterally to the postorbital like in most mesoeucrocodylians, except for *Simosuchus clarki* (Buckley *et al.* 2000), whose jugal is posterior to postorbital, and thalattosuchians, in which the jugal is medial to postorbital (Gasparini *et al.* 2006). The position of the jugo-quadratojugal suture indicates that the posterior process of the jugal extends posterior to the infratemporal fenestra. This feature is widespread among crocodylomorphs, differing from some notosuchians, like *Sphagesaurus huenei* (Pol, 2003), the thalattosuchian *Pelagosaurus typus* Bronn 1841 (Pierce and Benton 2006) and the neosuchian genus *Goniopholis* (Mook, 1942; Salisbury *et al.* 1999). The jugal part of postorbital bar is directed posterodorsally. This is common for mesoeucrocodylians, except for some brevirostrine crocodylians (Brochu 1999, 2007) and notosuchians, like *Notosuchus terrestris* Woodward, 1896 (Gasparini 1971) and *Uruguaysuchus aznarezi* (Rusconi, 1933).

Quadratojugal. Both of the quadratojugals are preserved, but they are incomplete. The right one has only the medial part, along the medioventral quadratojugal suture. The left one has the medial part and the quadratojugal spine. The suture with the jugal is not preserved. The quadratojugal contacts the quadrate medially and the postorbital anteriorly. The quadratojugal is ornamented laterally, a homoplastic characteristic that appears in a few crocodylomophs. In neosuchians, only thalattosuchians have an unornamented quadratojugal (Gasparini and Diaz 1977; Pol and Apesteguía 2005; Gasparini *et al.* 2006). The quadratojugal spine is high, sharp and situated between the caudal and the superior angles of intratemporal fenestra (characters 69-0 and 114-1). A quadratojugal spine appears only among some neosuchians, such as *Bernissartia fagesii* (Buscalioni and Sanz, 1990) and *Terminonaris robusta* (Mook, 1934; Wu *et al.* 2001b). Among eusuchians, the basal taxon *Ihakurtosuchus makadii* (Ösi *et al.* 2007; Ösi 2008) and alligatoroids have a reduced or even an absent quadratojugal spine (Norell 1989; Brochu 1999). *Piscogavialis jugaliperforatus* Kraus, 1998 is the only gavialoid that has a reduced or even an absent quadratojugal spine (Delfino *et al.* 2005). The dorsal ramus of quadratojugal is dorsally tapered with a narrow postorbital contact. This is a basal condition of crocodylomorphs, differing only for many basal crocodyliforms, like the protosuchid *Protosuchus richardsoni* (Colbert and Mook, 1951) and the gobiosuchid *Zosuchus davidsoni* Pol and Norell, 2004a, and a few notosuchians, like *Baurusuchus pachecoi* (Price, 1945) and *Simosuchus clarki* (Buckley *et al.*, 2000). The quadratojugal forms the caudal angle of the infratemporal fenestra (character 75-0) and extends to the superior angle of this fenestra (character 80-0). These features are shared among the majority of crocodyliforms, except for many crocodylines, in which the jugal forms the caudal angle of the infratemporal fenestra, and the quadratojugal does not extend to the superior angle of this fenestra, permitting the participation of the quadrate in this fenestra (Brochu 1999, 2007). Mesoeucrocodylians have no ridge along the dorsal section of the quadrato-quadratojugal contact, as do some protosuchids and gobiosuchids (Colbert and Mook 1951; Pol and Norell 2004a, b). The posteroventral corner of quadratojugal reaches the quadrate condyles, a feature characteristic of non-thalattosuchian neosuchians (Gasparini *et al.* 2006) and for many basal crocodylomorphs, like *Protosuchys richarsoni* (Colbert and Mook, 1951), and notosuchians, like *Araripesuchus gomesi* (Price, 1959; Hetch 1991) and *Simosuchus clarki* (Buckley *et al.*, 2000). The posterolateral end of quadratojugal is sharp, tightly overlapping the quadrate. This feature is widespread among crocodylomorphs, differing only for a few basal crocodyliforms, like *Zosuchus davidsoni* (Pol and Norell, 2004a) and *Sichuanosuchus shuhanensis* (Wu *et al.*, 1997).

Quadrate. Both quadrates are preserved. But only the right one is near *in vivo* position; the left one is elevated in the posterior end, to almost the height of the skull table. Dorsally, the quadrate articulates with the exoccipital medially, the quadratojugal laterally (in a lateroventral contact), the squamosal anterolaterally (inside the external otic aperture) and postorbital in the anterolateral edge. The quadrate participates of the lateral wall of the supratemporal fenestra, contacting the squamosal ventromedially and the laterosphenoid laterally. There is no evidence for a quadrato-parietal contact within the supratemporal

fenestra. The quadrate bears a small pneumatic foramen on the dorsal surface, lying anteriorly to the external otic aperture. Among neosuchians, this condition is found in eusuchians, like *Borealosuchus formidabilis* (Erickson, 1976; Brochu 1997) and *Diplocynodon hantoniensis* (Turner and Buckley, 2008), and in derived neosuchians, like *Theriosuchus pusillus* (Clark, 1994; Ortega *et al.* 2000) and *Sunosuchus* (Turner and Buckley, 2008). The quadrate does not participate in the infratemporal fenestra (character 80-0). It has a small ventrally reflected medial hemicondyle (character 112-0). This feature is shared among many advanced neosuchians, but differs from the condition found in crocodylians (Brochu 1999). Alligatoroids have a small medial hemicondyle (Brochu 2004), and the gavialoid *Eosuchus* and crocodyloids have an expanded medial hemicondyle (Brochu 2007). The quadrate has a significant ventral process on lateral braincase wall (character 127-0), and the suture with the squamosal extends dorsally along caudal margin of the external auditory meatus (character 132-0). The posterior edge, dorsal to exoccipital contact, is narrow and strongly concave. The primary head of the quadrate articulates with the prootic and the laterosphenoid. These features are widely distributed in mesoeucrocodylians, except in thalattosuchians (Gasparini *et al.* 2006). The ventrolateral contact of the exoccipital with the quadrate is broad, like in all crocodylomorphs, except to the very narrow condition of many protosuchians. The exoccipital, squamosal and quadrate meet broadly lateral to the cranioquadrate passage. This feature is widely distributed in crocodyliforms, except for basal protosuchians, like *Protosuchus richardsoni* Brown, 1933 (Colbert and Mook 1951), whose bones do not meet to enclose the passage, and for thalattosuchians and *Simosuchus clarki* Buckley *et al.,* 2000, in which passage is enclosed near the lateral edge of the skull. The pterygoid ramus of the quadrate has a flat ventral edge, and the ventromedial part of quadrate does not contact the exoccipital. These two features are common in crocodyliformes. The jaw joint, inferred from the position of quadrate articular condyles, is placed at level with the basioccipital condyle. This condition is found in derived neosuchians, like *Bernissartia fagesii* Dollo, 1883 (Buscalioni and Sanz 1990) and *Susisuchus anatoceps*, and eusuchians. The quadrate main axis is directed posteroventrally, the distal end has only one plane facing posteriorly, and the condyles are closely aligned horizontally. All these features are common to Crocodylomorpha, but differ from those found in notosuchians, like *Baurusuchus pachecoi* and *Sphagesaurus huenei* (Pol and Apesteguía 2005). In cross-section, the distal end of quadrate is mesolaterally wide and anteroposteriorly thin, a widely distributed feature among crocodyliforms, except for *Araripesuchus* (Price, 1959; Hetch 1991) and *Simosuchus clarki* (Buckley *et al.,* 2000), in which this region is subquadrangular in cross-section. The development of the distal quadrate body to the exoccipital–quadrate contact is distinct, like in derived neosuchians, eusuchians and many notosuchians (Pol and Apesteguía 2005). There is no ridge along the dorsal section of quadrato-quadratojugal contact, a widespread feature among mesoeucrocodylians. The presence of a ventrolateral orientation of quadrate body distal to quadrato-exoccipital contact in posterior view is shared among eusuchians, neosuchians, dyrosaurids, thalattosuchians and two notosuchians, *Libycosuchus brevirostris* (Stromer, 1914) and

Iberosuchus macrodon (Antunes, 1975; Buffetaut, 1982; Pol and Apesteguía 2005). The prootics are largely obscured by the quadrate and laterosphenoid externally (character 74-1). This is an interesting feature that appears in *S. jaguaribensis*, many alligatorids, like *Brachychampsa montana* (Gilmore, 1911; Brochu 1999; Sullivan and Lucas, 2003), and advanced crocodylids, like *Voay robustus* (Brochu, 2007).

Laterosphenoid. The laterosphenoid forms the anterior part of the lateral wall of the braincase in front of the foramen ovale. Dorsally, it contacts the parietal and the quadrate in the posteromedial wall of the supratemporal fenestra. There is no evidence for a contact between the squamosal and the laterosphenoid within the supratemporal fenestra. Ventrally, it contacts the basisphenoid medially, the quadrate posterolaterally and the postorbital laterally. The laterosphenoid articulates with the primary head of quadrate. Ventrally, the laterosphenoid forms the medial margin of the supratemporal fenestra and the anterolateral margin of the foramen ovale, where it obscures the prootic (character 74-1), as occurs in the South American gavialoids (Brochu 2006), alligatorids (Brochu 1999) and almost all crocodylines (Brochu 2007). The capitate process of laterosphenoid is oriented rostrocaudally (character 130-1). This feature is shared probably with the atoposaurid *Pachycheilosuchus trinquei* (Rogers 2003) and eusuchians, except for many gavialoids (Brochu 1999, 2006) and *Allodaposuchus precedens* (Delfino *et al.,* 2008*a*).

Basisphenoid. This bone forms the ventral wall of the braincase. It contacts the basioccipital posteriorly, the quadrate posterolaterally and the latherosphenoid anterolaterally. The basisphenoid can be seen in the ventral view because of the loss of the pterygoids. It is mostly covered by the pterygoid and basioccipital, with virtually no ventral exposure, as in neosuchians, except for atoposaurids and thalattosuchians, and the sebecosuchians *Bretesuchus bonapartei* (Gasparini *et al.,* 1993) and *Iberosuchus macrodon* (Antunes, 1975). The basisphenoid forms a thin sheet shorter than the basioccipital (character 113-1), like in *Bernissartia fagessi* (Buscalioni and Sanz, 1990) and the majority of eusuchians, except for the basal form *Iharkutosuchus makadii* (Ösi *et al.,* 2007; Ösi 2008), some gavialoids (Brochu 1999, 2006) and the basal globidontan *Acynodon iberoccitanus* (Delfino *et al.,* 2008*a*). The basisphenoid is not exposed extensively on the braincase wall anterior to the foramen ovale (character 129-0), a common feature in dyrosaurids (Buffetaut 1978) and neosuchians (Pol and Apesteguía 2005), except for derived crocodylids (Brochu 2007). The mesoeucrocodylians (including *Susisuchus jaguaribensis*) have no paired ridges located medially on the ventral surface of basisphenoid, as do *Notosuchus terrestris* (Gasparini *et al.* 2006), teleosaurids and baurusuchids (Price 1945; Buffetaut 1982; Carvalho *et al.,* 2005).

Basioccipital. This bone is completely preserved, but distorted, dislocated to the left side of the skull, covering the left ventrolateral portion of the basisphenoid. The occipital condyle is dorsoventrally flattened, and the small basioccipital tubera is distorted anteroventrally. Among crocodyliforms, this condition differs only in thalattosuchians (Gasparini *et al.* 2006) and dyrosaurids (Buffetaut 1978). The basioccipital contacts exoccipitals and qua-

drates laterally and basisphenoid anteriorly, and it forms the ventral margin of the foramen magnum. There are no well-developed bilateral tuberosities, like in gavialoids, dyrosaurids, thalattosuchians and the sebecosuchian *Bretesuchus bonapartei* Gasparini *et al.,* 2003 (Buffetaut 1978; Brochu 2006; Gasparini *et al.* 2006). The occipital condyle faces posteriorly, as in peirosaurid (Gasparini *et al.* 1991; Carvalho *et al.* 2007) and neosuchian mesoeucrododylians (Pol and Apesteguía 2005).

Exoccipital. Both exoccipitals are preserved, but distorted and broken. The dorsal portion of both is broken and slopes posteroventrally, allowing a great exposition in the dorsal view. The exoccipital contacts the squamosal and the supraoccipital (no preserved), the quadrate lateroventrally and the basioccipital ventrally. The exoccipitals broadly meet dorsally to the foramen magnum, separating the supraoccipital from the foramen. In occipital view, the exoccipital has laterally a long and thick parocipital process, between the quadrate and the squamosal. The caudal margin for the otic aperture is smooth and continuous with the paroccipital process (character 102-0). The paroccipital process has no prominent medial boss, and the process lateral to the caudal aperture of the cranioquadrate canal is long (character 141-1). In mesoeucrocodylians, this feature is shared among thalattosuchians, the derived neosuchian genus *Susisuchus*, *Isisfordia duncani* and crocodylians. Only the basal eusuchians *Hylaeochampsa vectiana* (Owen, 1874), *Iharkutosuchus makadii* (Ösi *et al.,* 2007; Ösi 2008) and *Allodaposuchus precedens* (Nopcsa, 1928; Buscalioni *et al.,* 2001) lack this feature (Brochu 1999; Gasparini *et al.* 2006; Salisbury *et al.* 2006). The exoccipital terminates dorsal to the basioccipital tubera (character 151-0), a basal feature of mesoeucrodylians, differing from the slender or robust process of non-'thoracosaurs' gavialoids and caimanines (Brochu 1999, 2006). The ventrolateral contact of the exoccipital with the quadrate is broad. The exoccipital, squamosal and quadrate meet broadly lateral to the cranioquadrate passage. The ventromedial part of the quadrate does not contact the exoccipital. These three features are shared among almost all mesoeucrocodylians (Pol and Apesteguía 2005; Gasparini *et al.* 2006).

Discussion. Despite the incompleteness of the skull presented here, it possesses clear diagnostic features. A great number of cranial characteristics could be identified and studied comparatively with other crocodylomorphs. The main characteristics could be seen in the dorsal view as a result of a better preservation of this part. The sutures are partly fused, but most of them could be delimited.
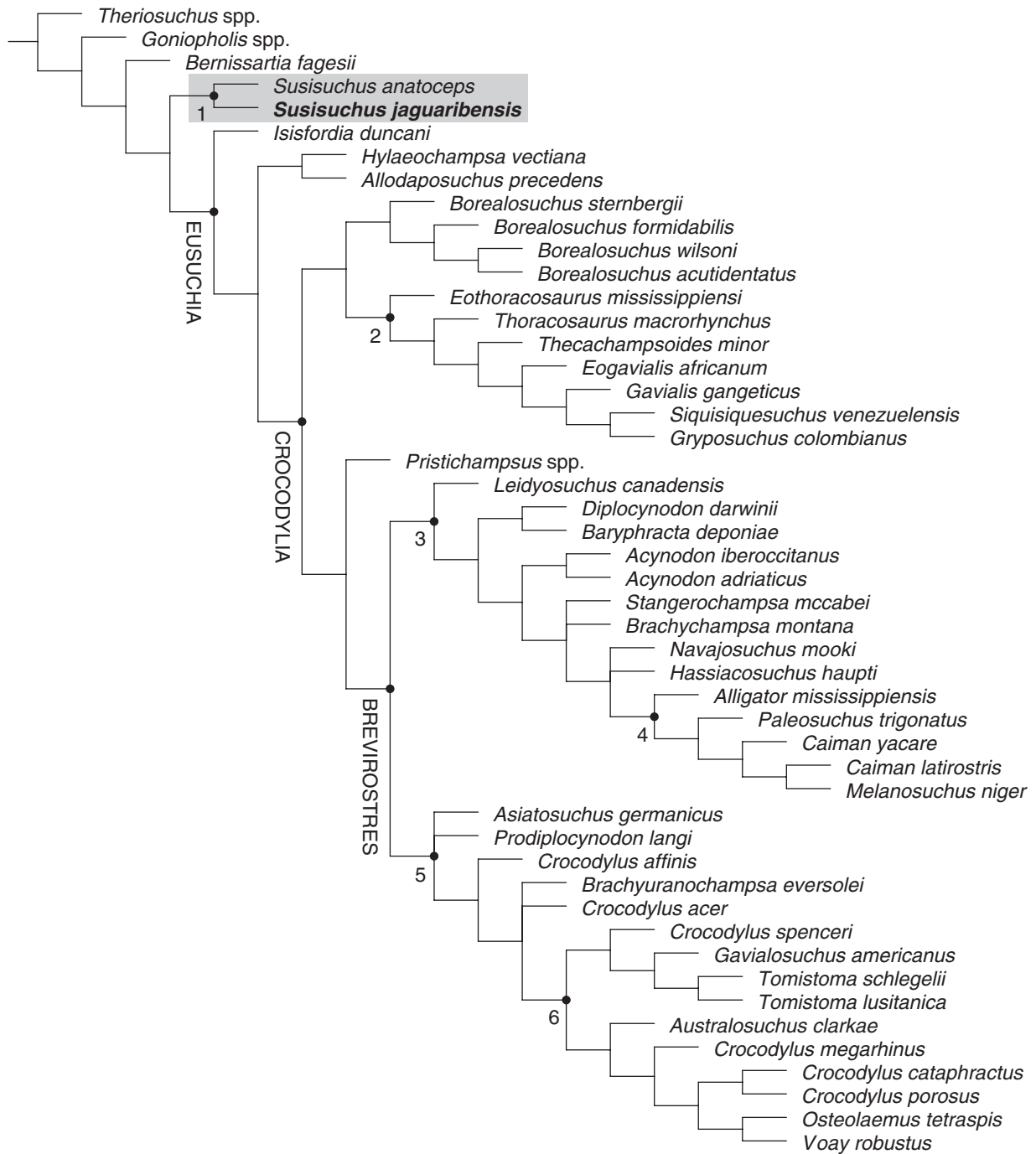
The heavy ornamentation differs from the pattern shown in thalattosuchians, dyrosaurids and some notosuchians, like baurusuchids and *Sphagesaurus huenei* (Pol, 2003). *Susisuchus jaguaribensis* differs from thalattosuchians and dyrosaurids by the possession of small supratratemporal fenestrae, shorter than the orbits. Smooth anteromedial corner of supratemporal fenestra is shared by *Susisuchus anatoceps*, *S. jaguaribensis* and the majority of eusuchians (Brochu 1999). The skull table with nearly horizontal sides is found in some neosuchians and the majority of eusuchians. However, *S. jaguaribensis* differs from the former group because of the verticalized basicranium, typical of eusuchians (Tarsitano 1985). The jaw joint position and the temp-

oro-orbital anterior opening of *S. jaguaribensis* are found in many neosuchians and eusuchians, like *S. anatoceps* and *Isisfordia duncani* (Salisbury *et al.,* 2006), even though the temporo-orbital anterior opening condition is found also in the protosuchid *Zosuchus davidsoni* (Pol and Norell, 2004a).

Susisuchus jaguaribensis denotes a great affinity with the neosuchians, because of a set of features shown only in this group of mesoeucrocodylians: (1) dorsal part of the postorbital with anterior and lateral edges only; (2) posterolateral process of the squamosal not elongated and projected horizontally at the same level of the skull; (3) reduced and unsculpted outer surface of squamosal oriented laterodorsally; (4) basisphenoid practically excluded from ventral surface; (5) basioccipital with large pendulous tubera; (6) jaw joint placed at the same level with basioccipital condyle; (7) basioccipital and ventral part of exoccipital facing posteriorly; (8) quadratojugal ornamentation; (9) presence of a spine-shaped quadratrojugal spine; (10) quadrate distal end with only one place facing posteriorly (occurs in *Simosuchus clarki* too); and (11) the absence of a quadrate fenestra.

Among neosuchians, *Susisuchus anatoceps* is the taxon that shares more features with *Susisuchus jaguaribensis* (characters 70, 75, 80, 84, 86, 87, 92, 103, 104, 112, 123, 131, 141, 150, 174, 175). Among advanced neosuchians, only these two taxa have the contact of squamosal and parietal at the posterior margin of the supratemporal fenestra (character 131-2), a feature widely distributed among globidontans (Delfino *et al.* 2008b) and in a number of remotely related mesoeucrocodylians, such as *Araripesuchus* and dyrosaurids (Salisbury *et al.* 2006). *Susisuchus jaguaribensis* has other characteristics shared with eusuchians, indicating their close relationship: (1) participation limited or absent of the frontal within the supratemporal fenestra; (2) parieto-postorbital suture present within supratemporal fenestra and on dorsal surface of skull roof; (3) postorbital contacts quadratojugal with significant descending process; (4) prootic largely obscured by quadrate and laterosphenoid externally; (5) frontoparietal suture on skull table entirely; (6) anteromedial corner of supratemporal fenestra smooth (also present in *Susisuchus anatoceps*); (7) capitate process of laterosphenoid oriented anteroposteriorly towards the midline; (8) skull table with nearly horizontal sides; (9) postorbital bar inset from the lateral edge of the dorsal part of the postorbital (also present in *Bernissartia fagesii* and *S. anatoceps*); (10) exoccipital with small or no boss medial to the paroccipital process and (11) long process lateral to the caudal aperture of the cranioquadrate canal; last two features shared with *S. anatoceps*. Some of these features have evolved homoplastically between *S. jaguaribensis* and eusuchians.

The large quadratojugal spine arises from the midpoint of the posterior border of the infratemporal fenestra, as in many neosuchians. Accordingly to Wu *et al.* (2001a), the quadratojugal spine displays an ontogenetic variation, becoming larger in larger specimens of *Leidyosuchus canadensis* and in extant crocodylians (Norell 1989; Brochu 1999). Using this principle and considering that this structure is relatively bigger in the holotype of *S. jaguaribensis* than in that of *S. anatoceps*, it is suggested that the former specimen is relatively older. Furthermore, the advanced fusion status of cranial sutures, mainly those from neurocranium, suggests that this specimen is at least a young adult or even an adult.

Theriosuchus spp.
Goniopholis spp.
Bernissartia fagesii
Susisuchus anatoceps
Susisuchus jaguaribensis
Isisfordia duncani
Hylaeochampsa vectiana
Allodaposuchus precedens
Borealosuchus sternbergii
Borealosuchus formidabilis
Borealosuchus wilsoni
Borealosuchus acutidentatus
Eothoracosaurus mississippiensi
Thoracosaurus macrorhynchus
Thecachampsoides minor
Eogavialis africanum
Gavialis gangeticus
Siquisiquesuchus venezuelensis
Gryposuchus colombianus
Pristichampsus spp.
Leidyosuchus canadensis
Diplocynodon darwinii
Baryphracta deponiae
Acynodon iberoccitanus
Acynodon adriaticus
Stangerochampsa mccabei
Brachychampsa montana
Navajosuchus mooki
Hassiacosuchus haupti
Alligator mississippiensis
Paleosuchus trigonatus
Caiman yacare
Caiman latirostris
Melanosuchus niger
Asiatosuchus germanicus
Prodiplocynodon langi
Crocodylus affinis
Brachyuranochampsa eversolei
Crocodylus acer
Crocodylus spenceri
Gavialosuchus americanus
Tomistoma schlegelii
Tomistoma lusitanica
Australosuchus clarkae
Crocodylus megarhinus
Crocodylus cataphractus
Crocodylus porosus
Osteolaemus tetraspis
Voay robustus

EUSUCHIA
CROCODYLIA
BREVIROSTRES

1
2
3
4
5
6

TEXT-FIG. 4. Strict consensus of six equally optimal trees, each one with 524 steps, CI = 0.44 and RI = 0.75. The genus *Susisuchus* was positioned as a monophyletic group, forming the clade 1, Susisuchidae. Clade names: 2-Gavialoidea, 3-Alligatoroidea, 4-Alligatoridae, 5-Crocodyloidea, 6-Crocodylidae. To a stratigraphical and geographical context, see Salisbury *et al.* (2006).

Considering the nature of the sediments in which *S. Jaguaribensis* was found (Ponte *et al.* 1990) and some skull features, like the dorsal orientation of the orbits and the posteriorly oriented occipital condyle, we interpret *Susisuchus jaguaribensis* as a freshwater crocodylormorph, similar to *Isisfordia duncani* (Salisbury *et al.*, 2006) and *Susisuchus anatoceps* (Salisbury *et al.*, 2003). Analysing the associate fauna in Lima Campos basin (and Iguatu basins as a whole, Fortier and Schultz 2006a, b), *S. jaguaribensis* could feed on small fishes and molluscs, like gastropods and lamellibranchians.

PHYLOGENETIC RELATIONSHIPS

Methods. To analyse the phylogenetic affinities of *Susisuchus jaguaribensis*, a cladistic analysis was accomplished. The analysis used the data matrix of Delfino *et al.* (2008*a*), which was based on Salisbury *et al.*'s (2006) dataset that included for the first time *S. anatoceps* in a phylogenetic analysis. Two more taxa were added to this analysis, *Acynodon adriaticus* and *A. iberoccitanus*, according to the character codings from Delfino *et al.* 2008*b*, also based on Salisbury *et al.*'s (2006) dataset. A total of 49 taxa and 176 characters (some multistate and ordered) were analysed. Although fragmentary, *S. jaguaribensis* was coded for 31 characters (18%). The cladistic analysis was performed using the software TNT (ver. 1.1, Goloboff *et al.* 2003) to recover the most parsimonious trees, using the heuristic search and performing 1000 replicates (TBR branch swapping), holding 10 trees per replicate. To determinate the ACCTRANS and DELTRANS optimizations, the software Winclada (Nixon 2002) was used. The optimization was accomplished based on the strict consensus tree. See Appendix for *S. jaguaribensis* codings and the list of node reconstruction (apomorphy list).

Results. The analysis resulted in six most parsimonious trees (Text-fig. 4), each one of 524 steps (CI = 0.44, RI = 0.75). Both species within the genus *Susisuchus* were placed together as a monophyletic group and as the sister group of the Eusuchia. As a result of a new member of the genus *Susisuchus*, and the phylogenetic position of the genus, we recover a previously described family group, Susisuchidae, with a new definition, to nominate the clade that represents the sister group of Eusuchia.
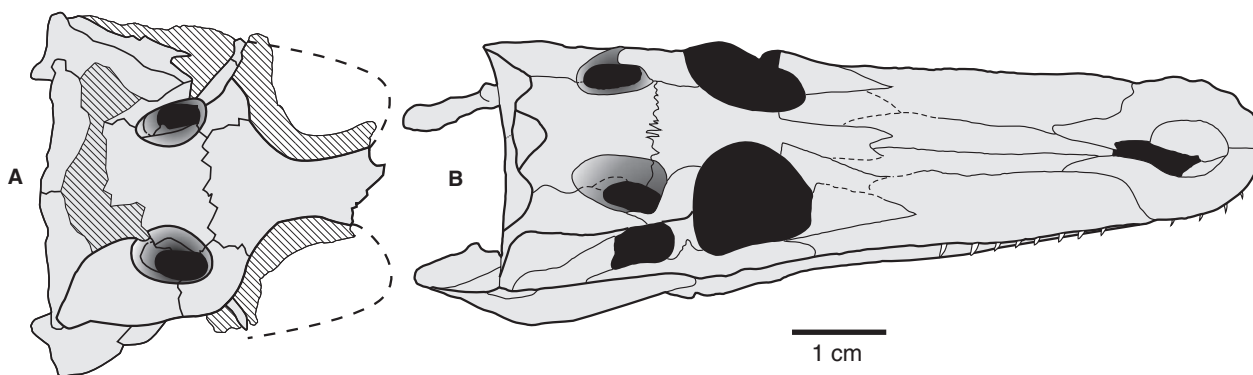
Discussion. The family name Susisuchidae is recovered to have a node-based clade definition, instead of its original description based on the apomorphies of the type species, *Susisuchus anatoceps*. Unfortunately, the synapomorphies are based only on cranial characters, because of the frag-

mentary condition of *Susisuchus jaguaribensis*. Nevertheless, the clade has important features to be diagnosticable among advanced neosuchians. The main one is the contact of the squamosal and parietal at the posterior margin of supratemporal fenestra. This feature appeared a few times in mesoeucrocodylian evolution. It is a synapomorphy of alligatoroids (Delfino *et al.* 2008*b*), and it is also found in the notosuchian *Araripesuchus gomesi* and among dyrosaurids, as stated by Salisbury *et al.* (2006). Furthermore, the accelerated transformations include a great set of features that are ambiguous because of the incomplete condition of *S. jaguaribensis*. However, the same characters were unambiguous synapomorphies of *Susisuchus* in Salisbury *et al.*'s (2006) phylogenetic analysis. Therefore, the new ACCTRAN set is not unexpected, especially given that these features are not shown for *S. jaguaribensis*. Nevertheless, the unique unambiguous synapomorphy of Susisuchidae is sufficient to support this clade formed by two species of genus *Susisuchus* (Text-fig. 5), because the parietal–squamosal contact within supratemporal fenestra has appeared a few times in mesoeucrocodylian evolution.

CONCLUSIONS

UFRGS-PV0001K has diagnostic features that allowed the recognition of a new species, *Susisuchus jaguaribensis*. This species has several affinities with *Susisuchus anatoceps*, the type species of this genus. The synapomorphy that supports the genus is the contact of squamosal and parietal in the posterior wall of supratemporal fenestra. A new emended differential diagnosis is proposed for the genus as well as for the type species, based in cranial characteristics, as a result of the incompleteness of the new species.

A cladistic analysis was performed to determinate the phylogenetic position of *Susisuchus jaguaribensis*. It showed that the genus *Susisuchus* is monophyletic and represents the sister group of Eusuchia. The family group

TEXT-FIG. 5. Susisuchid crocodyliforms. A, *Susisuchus jaguaribensis* gen. et sp. nov. B, *Susisuchus anatoceps* Salisbury *et al.*, 2006.

name Susisuchidae was recovered with a new definition, as the node-based group including the last common ancestor of *Susisuchus anatoceps* and *Susisuchus jaguaribensis* and all of its descendent. This clade is formed by a group of advanced neosuchians close to the origin of Eusuchia, sharing with this group many features. This new species corroborates the idea that the origin of eusuchians was a complex evolutionary event and that the fossil record recording it is still very incomplete.

Considering that *Barberenasuchus brasiliensis* is not a true crocodylomorph, but indeed a rauisuchian archosaur, and that the age of the sediments of Lima Campos basin is Berriasian–Barremian, *Susisuchus jaguaribensis* represents the oldest record of a Brazilian fossil crocodylomorph.

The recent collecting effort at Lima Campos basin shows that its fossil record could be much more expressive than is known up to now. Because of the importance of the new taxon and the future perspectives of fossil vertebrates of Brazilian Early Cretaceous, new field works must be realized to a better knowledge of the Iguatu basins and its fossil biocenoses.

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APPENDIX

Character coding of *Susisuchus jaguaribensis*, following the character list of Salisbury *et al.*, (2006) and modifications of Delfino *et al.*, (2008*a*).

??00???102???02[01]?0?00????1????????100??????010???????1???0?0121?????
?11???????00?????????0?????????01?

Node reconstruction (apomorphy list) that differs from the original list of Salisbury *et al.*, (2006) and Delfino *et al.* (2008*a*, *b*) and includes *Susisuchus jaguaribensis*. The tree used is identical to the one shown in Text-figure 5. Unambiguous synapomorphies underlined, ACCTRANS optimization in **bold** and DELTRANS optimization in *italic*.

SUSISUCHIDAE + EUSUCHIA

28(1), **29(1)**, 36(2), **38(1)**, 50(1), **52(1)**, **71(1)**, **77(1)**, *92(1)*, *130(1)*, 141(1), **149(1)**

SUSISUCHIDAE

38(3), **74(1)**, **79(1)**, **89(3)**, **93(2)**, **95(2)**, 131(2), **146(0)**, **169(1)**, **171(0)**

Susisuchus anatoceps

38(3), 69(1), *77(1)*, *79(1)*, 82(2), *89(3)*, *93(2)*, *95(1)*, *146(0)*, *169(1)*, *171(0)*

Susisuchus jaguaribensis

74(1), 76(2), 81(2), 140(1)