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Uberabasuchus terrificus sp. nov., a New Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil

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Abstract

A new fairly complete and articulated skull of a Peirosauridae crocodylomorph from Bauru Basin (Late Cretaceous), Brazil, is described. The fossil is from a level of clayish sandstone within Serra do Veadinho sequence, Peirópolis, Uberaba County, Minas Gerais State. The sedimentary strata of Serra do Veadinho belong to the Marília Formation (Serra da Galga Member), Bauru Group, considered to be Campanian-Maastrichtian in age. The species – *Uberabasuchus terrificus* sp. nov. – is a peirosaurid with moderately narrow snout, large round orbits protected by supraorbital bones of triangular shape and an antorbital fenestra bounded posteriorly by a deep groove. This fossil resembles *Peirosaurus tormini* Price, 1955 in the size pattern of premaxillary teeth and by showing a similar wedge-like maxillary process in the premaxilla. It also shares some morphological features with the other species of the Peirosauridae, namely the crocodylomorph *Lomasuchus palpebrosus* Gasparini, Chiappe and Fernandez, 1991 from Argentina. Their common features comprise a moderately narrow snout and the deep lateral groove at the premaxilla and maxilla articulation for the reception of a large mandibular tooth. However, the nasal participates in the external nares and does not divide the nasal aperture, producing a "beak-like" structure at the extremity of the snout which is unique among peirosaurids. The stratigraphic setting suggests that the specimen was buried when a flash flood overflowed the shallow channels of a braided fluvial system.

Parsimony analysis of 183 morphological characters is performed for 23 crocodylomorphs. Analysis of the morphological data matrix resulted in three most parsimonious trees (374 steps, CI = 0.679; RI = 0.826). The new species is closely related to *Mahajangasuchus* and both, in addition to *Peirosaurus* and *Lomasuchus*, compose the Peirosauridae.

Key words: Crocodylomorpha, Peirosauridae, *Uberabasuchus*, Cretaceous, Brazil.

Introduction

The origin and development of the intracratonic Bauru Basin (Cretaceous) in southeastern Brazil is related to break-up of Gondwana during the South Atlantic opening. The continental rupture originated this inland basin by the process of thermo-mechanical subsidence (Fernandes and Coimbra, 1996) upon volcanic rock. The oldest sediments in this basin (despite a probable origin during Aptian times – Fulfaro, Perinotto and Barcelos, 1994) – are considered as Turonian-Santonian in age (Castro et al., 1999) comprising argillaceous siltstones and fine sandstones which point to deposition in subaquous, lacustrine environment. During the Upper Cretaceous, there was a progressive increase in aridity due to the persistence of a hot climate and topographic heights surrounding the basin, which comprised alluvial plains, braided rivers and small temporary ponds.

There was an alternation between severely hot dry and rainy seasons, and a greatly diverse fauna and flora was established in the basin. Charophyte algae, pteridophyte sporocarpes (Marsiliaceae), coniferophyte logs, ostracods, gastropods, bivalves, invertebrate and vertebrate ichnofossils as well as a diversified vertebrate fauna of fishes, amphibians, reptiles (lizards, snakes, turtles, crocodylomorphs, Dinosauria) and mammals are frequent (Barbosa, 1955; Petri, 1955; Suarez and Arruda, 1968; Arid and Vizotto, 1965, 1971; Estes and Price, 1973; Lima et al., 1986; Baez and Peri, 1989; Bertini, 1994a, b; Kischlat et al., 1994; Manzini et al., 1996; Castro et al., 1999; Senra and Silva e Silva, 1999).

The new crocodylomorph fossil was found in a palaeoenvironmental setting of fine sandstones deposited during sudden floods on alluvial plains during a dry and hot season (which produced the reported mudcracks, Fig. 2). Freshwater ponds and rivers were scarce, generally drying out during long droughts. This was a very restrictive factor and the fauna and flora of this region should be well adapted to endure these severe environmental conditions. The flash floods during rainy seasons represented a catastrophic event that allowed the fossilization of articulated animals, such as the one described herein.

The fossil was excavated in Peirópolis, municipality of Uberaba (Minas Gerais State). From this same area, two crocodylomorphs have been already described: *Itasuchus jesuinoi* Price, 1955 and *Peirosaurus tormini* Price, 1955, both coming from rocks considered Campanian-Maastrichtian. The new species is a peirosaurid that shares some features with *Peirosaurus* and the Argentinian genus *Lomasuchus* Gasparini, Chiappe and Fernandez, 1991. Aspects of the anatomy, palaeoenvironmental settings and relationships with other crocodylomorphs are discussed in this paper.

The Bauru Basin Crocodylomorphs

The crocodylomorphs from this basin comprise at least five distinct groups of "mesosuchian crocodiles". The oldest ones are the notosuchids of Adamantina/Araçatuba Formation (Carvalho and Bertini, 1998, 1999, 2000). They are found in fine quartzose sandstones and siltstones of Turonian-Santonian age (Bertini and Carvalho, 1999; Castro et al., 1999) that have been interpreted by Batezzelli et al. (1999) as deposition in subaquous, lacustrine environments. One species was defined – *Mariliasuchus amarali* Carvalho and Bertini, 1999 – from these deposits (Carvalho and Bertini, 1999). Price (1950a) described from the Marília Formation (São Paulo State) *Sphagesaurus huenei* Price, 1950, as a notosuchid but, as pointed out by Bonaparte (1978) and Gasparini et al. (1991), the dental structure and tooth replacement do not correspond to any known notosuchid.

The baurusuchids are a later group found on the upper portion of the Adamantina Formation (Campanian) and in the Marília Formation (Campanian-Maastrichtian) that probably evolved from the notosuchids (Buffetaut, 1980). There is a unique species – *Baurusuchus pachecoi* Price, 1945 – in the Marília Formation (Price, 1945). In the Adamantina Formation (São Paulo State), there is another baurusuchid with a developed lateral flange on the jugal, a marked depression of the posterodorsal surface of the frontals and inflated edges of the maxillae named *Stratiotosuchus maxhechti* (Campos et al., 2001). There are also evidences of a new species of *Baurusuchus* identified through an anterior portion of skull and mandible (Brandt Neto et al., 1991, 1992; Bertini et al., 1999).

Goniopholis paulistanus Roxo, 1936 based on isolated teeth and a tibia (Roxo, 1936), and non-articulated specimens such as ?*Brasileosaurus pachecoi* Huene, 1931 both from the Adamantina Formation (São Paulo State) reveal few diagnostic aspects, hampering their allocation in an adequate systematic position, as already pointed out by Price (1950b) and Bertini (1994a).

Some crocodiles, such as *Itasuchus jesuinoi* from the Marília Formation (Peirópolis-Uberaba, Minas Gerais State) were first attributed to the Goniopholidae (Price, 1955) and latter to Trematochampsidae (Buffetaut, 1985), although Gasparini et al. (1991) considered that the characteristics exhibited by *Itasuchus* do not allow confirmation of its affinities to those taxa previously cited. There is also an undescribed "mesosuchian" from the Adamantina Formation, São José do Rio Preto County (São Paulo State) referred to by Brandt Neto et al. (2001) and another one from the Marília Formation, Peirópolis locality (Azevedo and Campos, 1993).

The peirosaurids are represented by *Peirosaurus tormini* Price, 1955 from the Marília Formation (Peirópolis, Uberaba, Minas Gerais State). Gasparini (1982) established the family Peirosauridae including this specimen. The new species described herein is from the same locality as *Peirosaurus*.

Geology

The Bauru Basin comprises an area of 370,000 sq km, partially covering the states of São Paulo, Paraná, Mato Grosso do Sul, Minas Gerais and Goiás, in Brazil (Fig. 1). It was a depression developed during the Gondwanan rupture in the Late Cretaceous, within which at least 300 meters of a siliciclastic sequence accumulated. It overlays basalts of the Serra Geral Formation from which it is separated by a regional erosive surface (Fernandes and Coimbra, 1996, 1999).

The lithostratigraphic units of the Bauru Basin are grouped into the Caiuá and Bauru groups, although some authors (Fulfaro et al., 1999) proposed a separated pre-

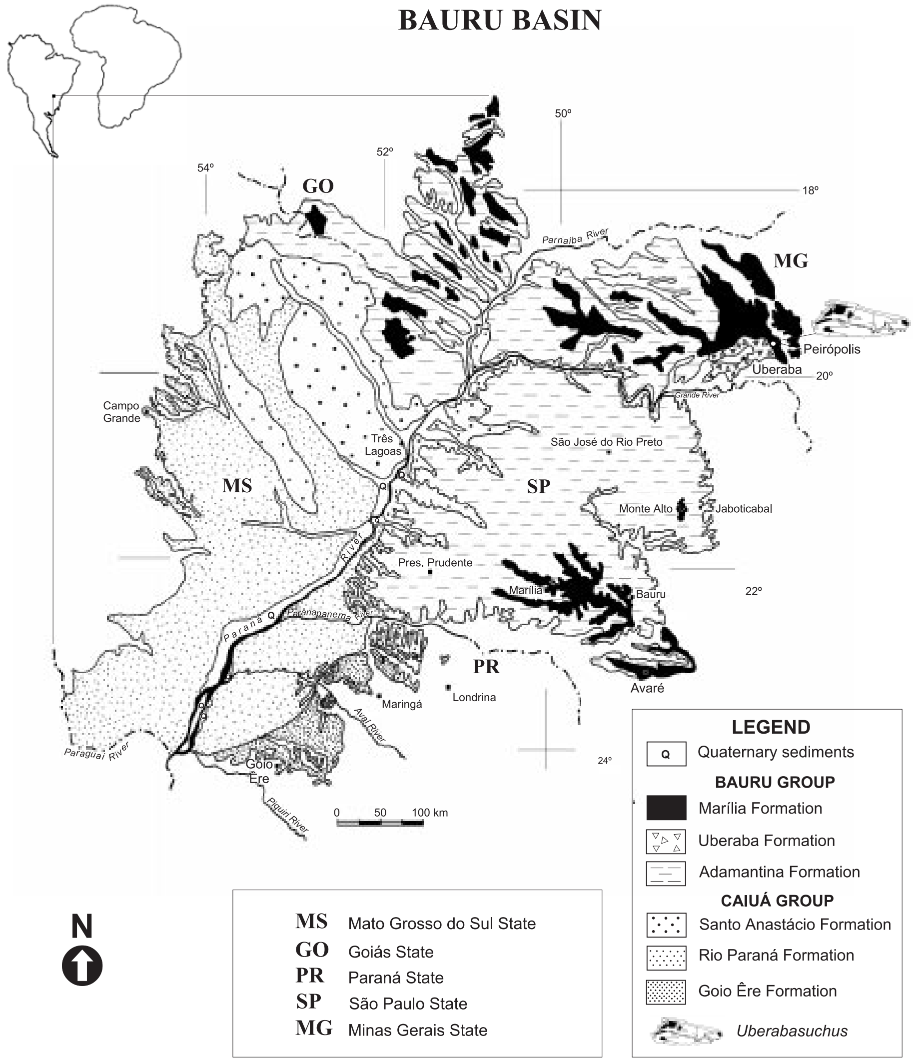

Fig. 1. Geological map of the Bauru Basin, southern Brazil in the context of Gondwana (80 Ma) (modified from Fernandes and Coimbra, 1996).

Bauru Basin of Aptian-Albian age that comprises the Caiuá Group. The age of the Bauru Basin ranges from Aptian to Maastrichtian (Fúlfaro, Perinotto and Barcelos, 1994). There are different proposals to subdivide these groups (Soares et al., 1980; Fernandes and Coimbra, 1992, 1996). The Bauru Group was divided by Fernandes and Coimbra (1996) into three formations, namely Adamantina, Uberaba and Marília. The Adamantina Formation (Turonian-Santonian age, Castro et al., 1999; Dias-Brito et al., 2001) is a sequence of fine sandstones intercalated by mudstones, siltstones and clayish sandstones. The lowermost part of this unit was redefined by Batezelli et al. (1999) as the Araçatuba Formation. The Uberaba Formation (Coniacian-Campanian, Goldberg and Garcia, 2000) is composed of fine greenish sandstones interbedded by siltstones, coarse sandstones, mudstones and volcanoclastics. The Marília Formation was formally proposed by Soares et al. (1980) as a sequence of coarse to conglomeratic sandstones, mudstones and carbonate levels. The sandstone is composed of quartz (monocrystalline > polycrystalline), feldspars (orthoclase + microcline > oligoclase), and fragments of metasedimentary (schist, phyllites and less quartzite), volcanic (trachytes, basalt) and sedimentary rocks (quartz siltstones). They are mainly classified as subfeldsarenites and feldspathic litarenites (Andreis et al., 1999). The age of these deposits based on the vertebrate fauna is considered as Campanian-Maastrichtian (Bertini, 1993; Gobbo-Rodrigues et al., 2001). Dias-Brito et al. (2001) established a Maastrichtian age on charophytes and ostracods.

In the Uberaba region (Minas Gerais State), the Marília Formation is divided in the Ponte Alta and Serra da Galga members. The Ponte Alta Member is made up of coarse sandstones, conglomerates and breccias associated with impure carbonates. Carbonate cements sometimes produce caliche levels. The Serra da Galga Member is composed of fine to coarse-grained sandstones, associated with conglomerates in fining-upwards cycles.

The Ponte Alta and Serra da Galga members of Marília

Formation can also be differentiated by their diagenetic evolution. The diagenesis includes early calcretes, silcretes and palycretes, while late barite, dolomite and dedolomitization are restricted to the Ponte Alta Member. Quartz overgrowth, pyrite and late calcite cementation occurs in the Serra da Galga Member (Alves and Ribeiro, 1999). The high content of carbonates, producing calcrete, carbonate levels and highly cemented sandstones in the Marília Formation are interpreted as an extensive carbonatization of these deposits by carbonate-rich groundwater that sometimes produces a non-pedogenic groundwater calcrete (Silva et al., 1994). Because of this widespread diagenetic process, Etchebehere et al. (1999) proposed that the Ponte Alta Member does not belong to the Marília Formation, but instead, to a calcretization event superimposed on deposits of the Uberaba Formation, through groundwater action. However, Goldberg and Garcia (2000) interpreted this richness in carbonates as resulting from palaeoenvironmental and palaeoclimatic conditions. There was an increase in aridity from the time of deposition of the Uberaba Formation to the times when the Marília Formation was deposited. These authors suggest that the Marília Formation was deposited by braided fluvial systems that had developed a wide alluvial plain with small lakes. The impure limestones and marls (Ponte Alta Member) were deposited during dry seasons in small lakes or as carbonate paleosoils. Following intense rains upstream, these deposits were reworked by ephemeral braided streams and redeposited together with other clastic materials (Serra da Galga Member).

The fossils found in the Marília Formation are charophyte gyrogonites, pteridophyte sporocarpe, coniferophyte logs, freshwater molluscs (gastropods and bivalves), conchostracans, invertebrate ichnofossils (*Skolithos* and *Arenicolithes*), dinosaur eggs, coprolites, and a variety of vertebrate remains such as fish scales, frog bones, turtles, lizards, crocodylomorphs and dinosaurs (Mezzalira, 1980; Campanha et al., 1992; Bertini, 1993; Bertini et al., 1993; Senra and Silva e Silva, 1999; Magalhães Ribeiro and Ribeiro, 1999; Magalhães Ribeiro, 2000). According to Goldberg and Garcia (2000), the fossiliferous deposits of this formation (Serra da Galga Member) in the neighborhood of Uberaba correspond to medium- to coarse-grained fluvial sandstone with reworked microcystalline calcrete fragments.

The Marília Formation was deposited in alluvial fans, braided fluvial systems, alluvial plains and ephemeral lakes

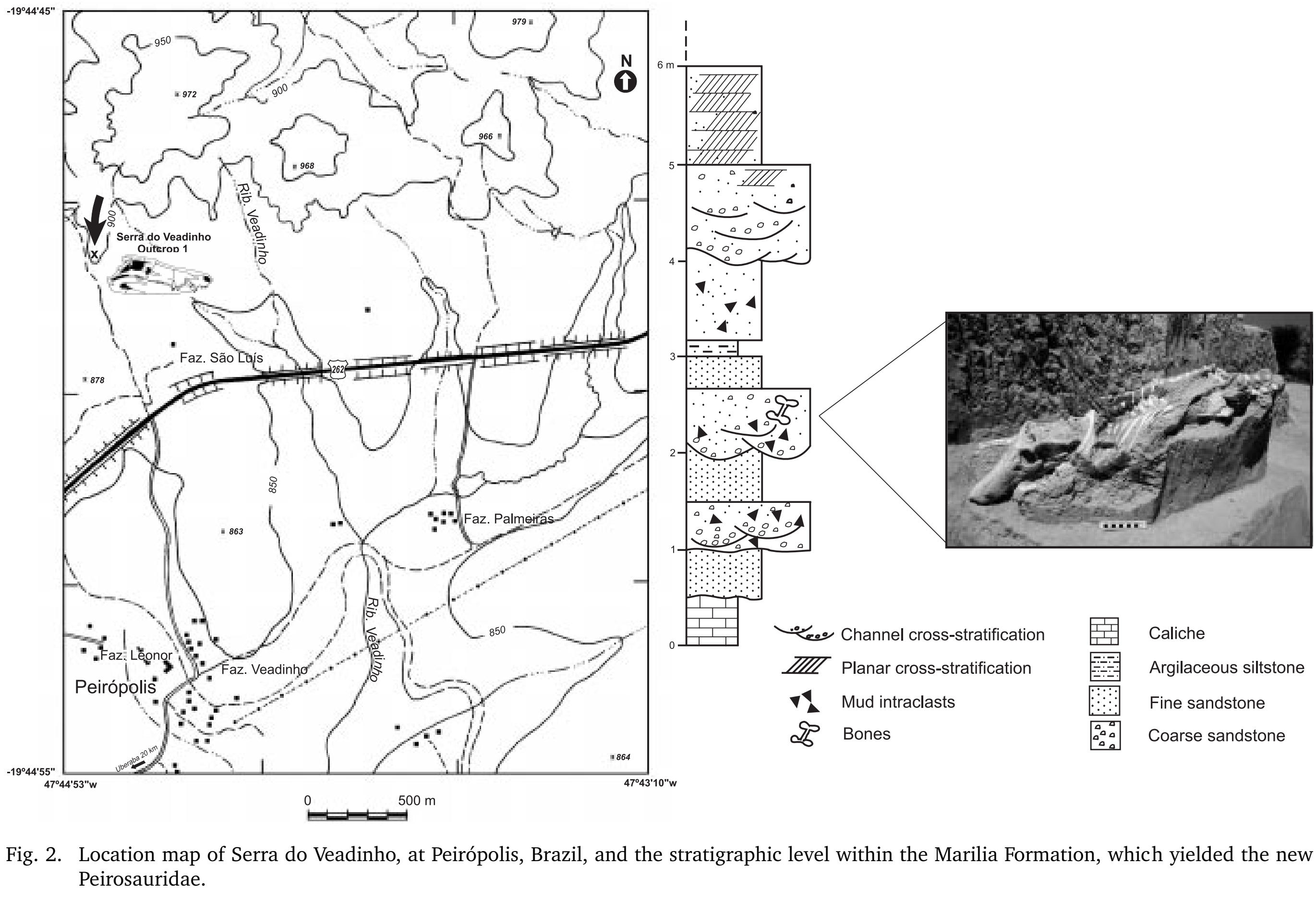

Fig. 2. Location map of Serra do Veadinho, at Peirópolis, Brazil, and the stratigraphic level within the Marilia Formation, which yielded the new Peirosauridae.

under a hot and dry climate. In the Uberaba region, Garcia et al. (1999) argued that the paleoclimatic conditions changed to become more arid during the Maastrichtian. The aridity was considered by Goldberg and Garcia (2000) to reflect the global climatic conditions and the existence of topographic heights that allowed the development of a dry microclimate in the region. The more humid climate was restricted to the surrounding mountains that acted as geographic barriers to the entry of humid winds. The climatic seasonality was marked by longer dry intervals interrupted by periods of heavy rains, when small lakes and temporary ponds, which were relatively deep during the flood periods (Senra and Silva e Silva, 1999), supported an abundant and diversified flora and fauna.

The deposits at Serra do Veadinho (Marília Formation, Serra da Galga Member), located at Peirópolis (Municipality of Uberaba), which yielded the fossil described herein are composed of carbonate-rich sandstones associated with impure limestones, overlain by coarse to conglomeratic sandstones and fine sandstones interbedded with clayish sandstones (Fig. 2). The dominant geometry of the strata is tabular, although trough cross-bedding and planar cross-stratification are also common. The lowermost carbonate rich sandstones are quartz-feldspathic sandstones, whitish in colour. They are followed upwards by clast supported conglomerates and coarse sandstones with trough cross-bedding. The clastic components of the conglomerate sandstones are pebbles of basalt, quartz, chert, quartzite, caliche fragments and clay intraclasts. There are fining-upwards cycles finished by fine quartz-rich sandstones with planar cross-stratification. Interbedded are pelites, clayish sandstones and coarse sandstones, with mud intraclasts. The new crocodylomorph species was excavated at a level of clayish sandstone.

The Serra do Veadinho sequence is positioned within the Marília Formation and should be divided into the Ponte Alta Member (carbonate rich sandstones and impure carbonates) and Serra da Galga Member (conglomerates and sandstones interbedded with pelites). However, according to Andreis et al. (1999) the petrologic analysis of this sequence around 60 meters thick in Serra do Veadinho, does not allow the division in two distinct members. The carbonate cementation and caliche levels are related to groundwater cementation (phreatic origin). The coarser succession is interpreted as a channel facies related to braided fluvial systems flowing to NW-N, while pelites are considered as abandoned channel facies.

The fossil was found almost complete, with the skull articulated with the axial and appendicular skeleton. It was positioned parallel in relation to the bedding plane, with the anterior and posterior members relatively erect as in life. The caudal vertebrae were lost. The preservation of this fossil suggests that it was buried during a flash flood. The main fossil elements found in this sequence are non-articulated bones and bone fragments that have been interpreted (Garcia et al., 1999) as the result of seasonality in the life cycles. During the dry seasons many animals died and had their remains exposed on the plains; later during the rainy season, this material was carried away together with fluvial sediments and deposited in the channels. It is also considered that after a long drought, the first rains were torrential rains, caused flash floods, producing the flooding of large areas, killing animals and rapidly burying them under large quantities of sediments. The occurrence of an articulate crocodylomorph and also an almost complete dinosaur egg (suggesting that there was a nearby nesting area) in the same stratigraphic level of clayish sandstones, reinforces the interpretation that they were buried just after death, during the floods.

Systematic Palaeontology

The classification of the new specimen was based on the comparative studies by Price (1955), Gasparini (1982) and Gasparini et al. (1991). The osteologic terminology follows Colbert (1946), Romer (1956) and Gasparini et al. (1991).

Crocodylomorpha Walker, 1970

Crocodyliformes Benton and Clark, 1988

Peirosauridae Gasparini, 1982

Uberabasuchus nov. gen.

Type-species: Uberabasuchus terrificus sp. nov.

Etymology: For the county of Uberaba, Minas Gerais State, Brazil, where the specimen was found, plus *souchos*, Greek for crocodile.

Diagnosis (skull): Moderately narrow-snouted crocodile. Tip of snout with a slender anterior process projected forwards. Deep vertical groove at the juncture of the premaxilla and maxilla for the reception of a large mandibular tooth (4th). Five premaxillary teeth circular in cross-section progressively increase in size from the anterior to posterior region of premaxilla; the first two small and close to one another, the last three larger and more widely spaced. Wedge-like maxillary process of the premaxilla is large. External nares in vertical position and protruding anteriorly. Nasals participating in the external nares and not dividing the nasal aperture. Orbit of circular shape. Antorbital fenestra present, bounded in its posterior border by a deep groove. One triangular supraorbital bone bordering each orbit. Postorbital bar not superficial. Ascending process of jugal arising from internal surface of jugal. The anterior ramus of the jugal is almost as high as the posterior ramus. The supratemporal fenestra is bordered by the parietal, frontal, postorbital and squamosal. The supratemporal fenestrae, which are elliptical, much smaller than orbits, are enclosed in a large depression on the cranial table. Splenials participating in the mandibular symphysis. Mandible high and laterally compressed. Angular making up at least two thirds the lower border of mandibular ramus. Articular with expanded concave surface. Mandibular fenestra triangular, aligned with the laterotemporal fenestra and extending anteriorly until the middle orbit. At least ten teeth on the dentary (probably ranging from 11-12 teeth). *Uberabasuchus* presents two autapomorphies that are: lateral contour of rostrum straight in dorsal view and retroarticular process without a medial shelf.

Uberabasuchus terrificus sp. nov.

(Figs. 3, 4, 5)

Holotype: CPPLIP nº 630 (Centro de Pesquisas Paleontológicas Llewellyn Ivor Price - Peirópolis, Uberaba County, Minas Gerais State, Brazil). Skull, mandible and part of the axial and appendicular skeleton.

Locality: Outcrop 1 (Fig. 2) in Serra do Veadinho, Caieira, Peirópolis, Uberaba County, Minas Gerais State - Brazil. 4 km North of Peirópolis.19° 43' 24,6" S and 47° 44' 45. 4" W

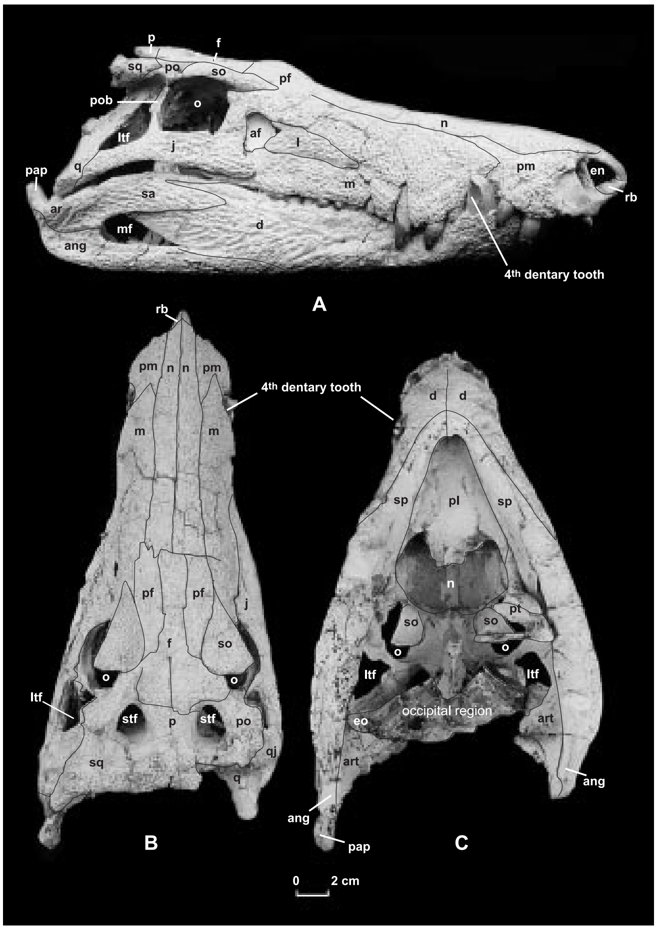

Fig. 3. *Uberabasuchus terrificus* sp. nov. specimen CPPLIP nº 630. (A) Right lateral view. (B) Dorsal view. (C) Ventral view of skull and mandible (Photographs by Mr. Carlos Alberto da Silva Silvestre).

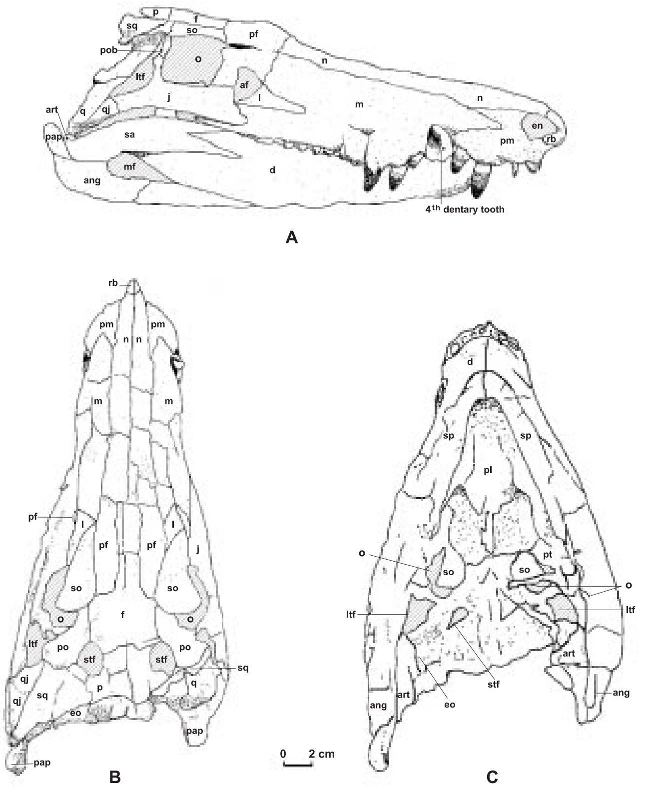

Fig. 4. Skull and mandible of *Uberabasuchus terrificus* sp. nov. (A) Right lateral view. (B) Dorsal view. (C) Ventral view of skull and mandible.

Stratigraphic context: Bauru Basin, Marília Formation (Serra da Galga Member. Upper Cretaceous: Campanian-Maastrichtian.

Species etymology: terrificus referring to a terrible, predatory animal.

Description

Skull

The skull of *Uberabasuchus* is triangular in shape, with a moderately narrow snout. The cranial table is continuous with the dorsal border of the snout, and in lateral view the tip of the snout points downward. There is a large antorbital fenestra approximately a third the size of the orbit. The round orbits are laterally positioned: each one is covered by a single supraorbital bone of triangular shape. The supratemporal fenestrae are elliptical in shape and smaller than the orbit. The cranial table and its borders are sculptured by grooves that are smaller on the supraorbital bones.

The premaxillary bones are dorsally separated by the paired nasals that are enlarged and extend anteriorly where they meet a rostral bone. Jointly they produce a snout "beak" (Fig. 5). In the upper portion, the articulation with the nasals are not clearly defined. The external nares are bordered by the nasals, rostral bone and the premaxilla. They are in a vertical position and are slightly longer than high. There are smooth depressions on both sides of the premaxillary bones, around the external nares. The premaxilla bears five premaxillary teeth, conical and circular in cross-section. These teeth become progressively bigger from the anterior to posterior region of premaxilla; the first three are small and closely set, and the last two are larger and more evenly spaced. The size pattern of these teeth is similar to *Peirosaurus*, i.e., the first tooth is the smaller, the second a little bigger; the third and fifth are bigger than the first and second ones. The fourth tooth is the largest of the series. A serrated posterior edge on the first premaxillary tooth, as present in *Peirosaurus*, was not observed. The second to fifth premaxillary teeth have finely serrated keels.

The maxilla is triangular in lateral view. It is higher posteriorly, with an anterior, wedge-like process tapering downwards into the premaxilla. The lower border has a depression for the mandibular tusk. The nearly vertical posterior border contacts the lacrimal, prefrontal and jugal. The nasal contacts the medial border of the maxilla through almost all its length. It is ornamented by small grooves on the surface. Ventrally, the maxilla is elongated (part of it is missing). The two posteriormost teeth of the maxilla are placed anterior to the preorbital fenestra as in *Lomasuchus*. The maxillary wedge-like anterior process, is larger than the one in *Lomasuchus* and has the same proportions as in *Peirosaurus*. There are at least 12 maxillary teeth, showing some degree of heterodonty. The first three teeth are moderately compressed, progressively bigger, with the lingual side slightly flattened and the labial is convex. Their posterior edges are finely serrated. The third maxillary tooth is the largest on the toothrow. The remaining nine teeth are smaller, subequal and subcircular. The crowns are spatulate and/or globe-shaped, with fine serrations at the crowns. The smaller teeth are located posteriorly in the maxilla. The maxilla has a sinuous outline. In profile the first four maxillary teeth are located in a pronounced convexity and the following ones are distributed in a more straight line.

The nasals are long and elongated and reach the anterior region of the rostrum. They participate in the projection similar to a beak that protects the external nares. The elongation of nasals projects them far forwards from the anterior limits of the premaxillae. It is bordered by the maxilla, prefrontal and frontal. The posterior half is almost flat, while the anterior one has a slight dorsal convexity. The nasals become progressively narrow, becoming wedge-shaped in their anterior extremity. They participate in the margins of the external nares, but there is not an internarial wall dividing the narial aperture or any kind of septum inside the nares. Posteriorly their contacts are not clearly defined. They may be limited to the anterior end of prefrontals, with a straight border between them and the frontal.

The rectangular prefrontals are limited by the nasal, maxilla, lacrimal, supraorbital and frontal. Their anterior margins are relatively straight and the caudal margins are slightly curved. The internal prefrontal wall contributes to the anterior wall of the orbit. A possible contact with the palatines is not preserved.

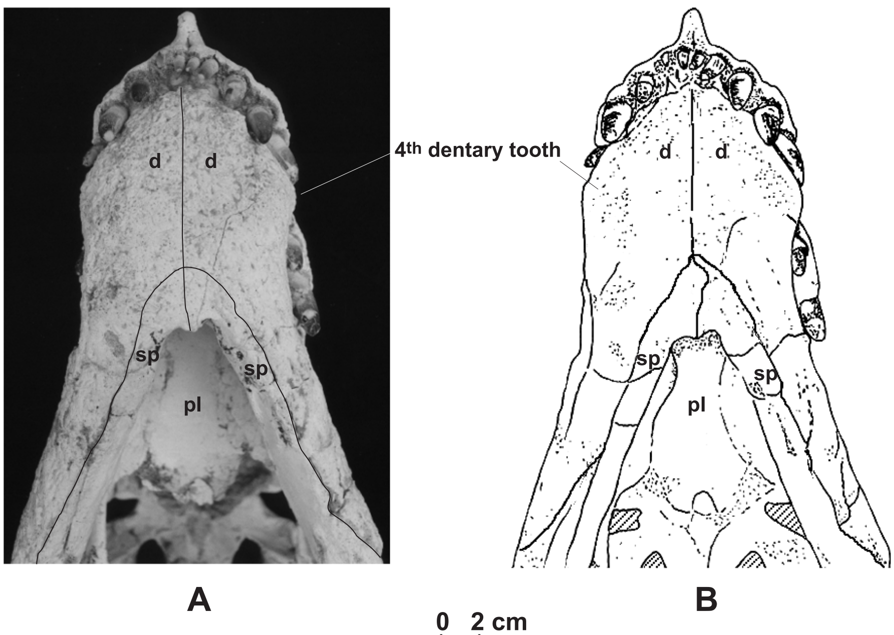

Fig. 5. Detail of the anteriormost region of the ventral view of skull and mandible. Note a short projection at the tip of snout producing a "beak", probably a rostral bone (rb). Photograph by Mr. Carlos Alberto da Silva Silvestre.

The lacrimals are triangular-shaped, elongated, and enclose a large triangular antorbital fenestra. This fenestra is bounded in its posterior border by a deep groove. The unusual position of this fenestra is possibly an anatomical feature unique to these kind of Crocodylomorphs (Ralph Molnar, pers. comm.). The lacrimals contact the maxilla, prefrontal and supraorbital.

The supraorbital is a single bone of triangular shape projected outwards from the orbital foramen notch. They are large and cover 2/3 of the upper border of the orbital region. Their surfaces are deeply sculptured by small grooves, and they present a gentle convexity on the external margins that protects the orbits.

The jugal contacts the maxilla at the middle point of the antorbital fenestra. It presents a small projection that abuts the maxilla. The jugal portion that constitutes the lower margin of the orbit is slightly concave. Posteriorly to the postorbital bar it presents almost the same height as anteriorly.

The frontal is an elongated bone bordering the nasals and the prefrontals. Its posterior area is enlarged, neighbouring the supraorbital, postorbital and delimiting part of the supratemporal fenestra. It passed from a flattened surface anteriorly to a slightly depressed area on the cranial table.

The parietal forms a three-branched element (the right branch is not completely preserved) and it is in contact with the frontal, squamosal and postorbital. Its posterior border is slightly convex. The parietal is flattened centrally. The supratemporal fenestrae are much smaller than the orbits, and enclosed in a large depression on the cranial table. They are located on a straight line with the laterotemporal fenestrae.

The postorbital contacts the frontal along a straight line. In dorsal view it bends gently to meet the supraorbital and follows the curvature of the orbits, where it shows a concave shape. At its opposite border the postorbital also follows the curvature of the supratemporal fenestra, becoming narrower in its middle part. The upper (postorbital) portion of the postorbital bar is more steeply inclined than the lower (jugal) portion (Fig. 3A). The postorbital bone is concave. It presents a posterior flattened wedge that contributes to the irregular shape of the postorbital bar at the connection with the ascending process of the jugal. This ascending process comes from the medial side of the jugal.

The squamosal is quadrangular in shape and borders the postorbital, parietal and the supratemporal fenestra. Its outer borders are straight; the contact with the supratemporal fenestra produces a wide curvature. The central area of the squamosal is depressed.

The quadratojugal is an elongated bone, strongly curved, projecting the posterior region of the skull downward and delimiting the posterior margin of the triangular-shaped laterotemporal fenestra. The quadrate contacts with the articular surface of the mandible.

The palatines are only partially preserved, as well as the occipital region and the basisphenoid: this element is as broad as long and meets a large pterygoid (only the left one is preserved) at a right angle. In the occipital region, a broad exoccipital bone (left side) is preserved.

Mandible

The mandible, still articulated with the skull, is sculptured by vermiform grooves. It was preserved complete, with the dentary, splenial, angular, surangular and articular. The anterior end of the mandible is projected upward; its middle part is straight, the posterior region (the surangular) being elevated.

The anteriormost part of dentary is flattened and bears four conical teeth. The first three are of the same size. The fourth, the largest one of this series, also conical, although on the right mandibular ramus this tooth shows an upward curved wear surface in its anterior portion, while the posterior region of the tooth is convex. The fourth dentary tooth has a thecodontian-like alveolar collar, projecting it upward into a notch between the last premaxillary and the first maxillary tooth. No serrations were observed on these teeth. Posterior to this flattened part, the dentary border becomes more vertical and shows two external grooves where two maxillary teeth fit. Then the dentary becomes thin and compressed, and in lateral view presents almost the same height as its length. Along the upper edge of the dentary there are at least six smaller teeth whose distribution is medial to the upper maxillary toothrow. The teeth throughout are subequal in size and subcircular, with a constriction in the base of the crown. Similarly to the upper teeth, the crowns are spatulated and globe-shaped, with fine serrations. This series of dentary teeth is arranged in a straight line to match the opposing border of the maxillary teeth. The dentary extends as far as the mandibular fenestra, where it forms part of the anterior border. The lower surface of the dentary presents a long symphysis, which extends as far as the position of the third maxillary tooth. The splenials participate in the symphysis.

The splenials are thin and high, covering the inner surface of the mandibular ramus from the alveolar border to the lower edge of the dentaries. Their posterior borders extend up the position of the pterygoids.

The angular extends posteriorly from the dentary as a very thin projection to the back of the mandible. It forms the lower border of the mandibular ramus for at least two thirds of its length, owing to a thin and long process, which extends beneath the dentary and splenial. It borders the mandibular fenestrae and rises posteriorly to form the postarticular process.

The surangular is located above the angular, extending up to the posterior end of the antorbital fenestra. The surangular borders the upper margin of a large triangular mandibular fenestra, whose rear limit is aligned with posterior margin of the laterotemporal fenestra. Anteriorly it is aligned with the orbit.

The right articular is still articulated with the quadrate, making for an expanded concave surface in this area. In posterior view its junction with a middle convex border limiting the articulation surface is slightly sinuous.

The Peirosauridae: Comparative Insights among the Species

The Peirosauridae was defined by Gasparini (1982) on the basis of tooth morphology, the number of premaxillary teeth, the extension of the maxillary tooth row in relation to the antorbital fenestra, and the rostral development and festooning. Later reviewed by Gasparini et al. (1991) the peirosaurids were defined as "moderately high-snouted crocodyles in which monophyly is supported by several derived features such as: prominent maxillary wedge-like process penetrating dorsally the premaxilla; very short premaxilla in ventral view; 14-15 maxillary teeth with tooth differentiation, the posterior ones being low and globular with a clear neck; elongated central crest and strong lateral knobs on the basioccipital". These authors also considered that this clade should be diagnosed as having a "deep maxillary notch, subcircular to moderately compressed teeth with finely serrated anterior and posterior edges; antero-lateral external nares, separated by nasals; long and uniformily wide nasals; lacrimal-nasal contact absent; supraoccipital not participating in the cranial table; maxillary tooth row continues with two or three teeth posterior to the anterior margin of the suborbital fenestra; broad and incompletely divided internal nares, placed between the palatines and pterygoids; broad and anteriorly inclined basisphenoid, only exposed in occipital view; large paired supraorbital bones; deeply sculptured skull and jaws."

Only two peirosaurids from South America have been described so far. The first was *Peirosaurus tormini* Price, 1955 from Bauru Basin (Peirópolis, Uberaba County). It comes from the Upper Cretaceous rocks of the Marília Formation. Price (1955) defined this species based on the skull and some elements of the axial skeleton such as the slightly amphicoelous vertebrae and the thin dermal plates, sculptured by pitting and with a low longitudinal keel (distinguished by the abdominal ones that are smaller plates without keel). The skull was diagnosed as having a "premaxilla with five conical teeth; maxillary and posterior teeth of the mandible with short spatulated crowns and finely serrated keels. A shallow lateral groove at the juncture of the premaxilla and maxilla for the reception of a large mandibular tooth. Premaxilla with a slender anterior process, inclined forward. Nasals participating in the naris and probably with thin projections dividing the narial aperture. External nares in vertical position, turned slightly forward, and protruding anteriorly. Anterior and subnarial surface of premaxilla smooth, unsculptured, and continuous with the smooth surface of the internal nasal passage. Postnarial surface of the premaxilla sculptured by shallow vermiform grooves. Maxillae wedging forward, on the palatal plane, reaching the incisive foramen. At least one large palpebral bone, the anterior". Price (1955) associated *Peirosaurus tormini* to the sebecosuchians based on the high laterally compressed rostrum and the serrated teeth. Lately, Gasparini et al. (1991) also discovered this species in the Argentinian locality of Loma de La Lata, Department of Confluencia, Neuquén Province. In the same region another high-snouted crocodile named *Lomasuchus palpebrosus* was collected and both were grouped in the Peirosauridae. These fossils came from the Río Colorado Formation, Neuquén Group (Upper Cretaceous, probably Campanian-Maastrichtian or Coniacian-Santonian).

Lomasuchus palpebrosus described by Gasparini et al. (1991) "has a moderately narrow snout. The maxillary wedge-like process in the premaxilla is also narrower. The last maxillary tooth does not reach the rostral margin of the internal nares. Teeth more compressed than *Peirosaurus*. An antorbital fenestra is present. The supraorbital bones join each other and cover the entire dorsal margin of the orbit. The lateral margin of the squamosal is sharply downturned towards the quadrate, producing an internally concave overhang. Orbit of rectangular shape. Robust posteroventral end of quadratojugal."

Uberabasuchus terrificus sp. nov. can also be ascribed to this family despite the antero-lateral external nares are not separated by nasals, nor are the nasals long and uniformly wide as proposed to the family diagnosis of Gasparini et al. (1991). This probably is due to the poor preservation conditions of the fossils described by these authors and Price (1955), were there was some degree of inference concerning the existence of an internarial wall. This structure is not present in *Uberabasuchus*. Another distinguishing aspect is that some teeth of this species do not have serrated keels. Some teeth, as the first premaxillary do not have a posterior serrated edge (only the anterior edge), and there are no serrated edges on the first four dentary teeth. Despite this, the size pattern of these teeth is similar to *Peirosaurus* – five premaxillary teeth circular in cross-section, progressively greater from the anterior to posterior region of premaxilla, the first two small and confluent, the last three larger and more evenly spaced. As the premaxilla of *Lomasuchus* is poorly preserved it is unknown if this pattern also occurs in this genus. Another common aspect with *Peirosaurus* is the maxillary wedge-like process in the premaxilla that is larger than in *Lomasuchus*. *Uberabasuchus* and *Lomasuchus* share some common skull characteristics such as the moderately narrow snout, a deep lateral groove at the juncture of the premaxilla and maxilla for the reception of a large mandibular tooth (4th), the sharply downturned lateral margin of the squamosal toward the quadrate, producing an internally concave overhang and a robust posteroventral end of the quadratojugal. Although both present an antorbital fenestra, there is a deep groove surrounding the posterior border of the one of *Uberabasuchus* while there is no fossa or depression surrounding the antorbital fenestra of *Lomasuchus*. *Peirosaurus* presents a broad snout, a shallow groove at the juncture of the premaxilla and maxilla for the reception of the large mandibular tooth (4th) and there is no antorbital fenestra. Its parietal, squamosal and quadratojugal were not preserved.

The orbit of *Uberabasuchus* is circular while the one of *Lomasuchus* is rectangular; it was not preserved in *Peirosaurus*. One supraorbital bone protects the orbit of *Peirosaurus* and *Uberabasuchus* distinctly from *Lomasuchus* where the protection was done by two supraorbital bones fused to each other. The postorbital bar in *Lomasuchus* is almost superficial, with the ascending process of jugal coming from the external surface of jugal. In *Uberabasuchus* this structure is not superficial, and the ascending process of jugal comes from the internal surface of jugal that presents almost the same height posterior to the postorbital bar. In *Lomasuchus* the jugal posterior to postorbital bar clearly decreases in height. Another skull difference between *Uberabasuchus* and *Lomasuchus* concerns the posterior border of parietal. It is slightly convex and presents a flattened central area in *Uberabasuchus* while it is slightly concave and its central area is depressed in *Lomasuchus*.

The splenials participate in the mandibular symphysis of *Uberabasuchus* and *Peirosaurus*. This could not be observed in *Lomasuchus* as the anteriormost region of mandible was not preserved. *Peirosaurus* lacks the middle and almost all the posteriormost region of mandible, while it is high and laterally compressed in *Uberabasuchus* and *Lomasuchus*. In *Peirosaurus* the last maxillary tooth reaches the rostral margin of the internal nares, while in *Uberabasuchus* and *Lomasuchus* this is not the case. These latter genera also share two maxillary teeth placed posteriorly to the front margin of the antorbital fenestra.

Price (1955) described a Goniopholidae – *Itasuchus jesuinoi* – whose general tooth pattern shows some similarities with the Peirosauridae. Despite this, the comparison with *Uberabasuchus* indicates striking differences. *Itasuchus* has at least 16 teeth in the dentary and the splenial symphisis extends as far as the 10th tooth. *Uberabasuchus* probably possess 11-12 dentary teeth and the symphisis is limited to the 5th tooth. The outline of the mandible is also distinct. The two halfs of the dentary are joined in a V-shaped pattern in *Itasuchus* due a strong lateral divergence of the dentary rami posterior to the symphisis. In *Uberabasuchus*, there is no such strong lateral divergence, the mandible presents an U-shaped pattern. Also, as observed by Ralph Molnar (pers. com., 2003) *Itasuchus* has a larger laterotemporal fenestra and the dentary is more gracile than that of *Uberabasuchus*. Although not preserved, the snout of *Itasuchus* was probably narrower than that of *Uberabasuchus*.

Phylogeny of the Peirosauridae and its Relationships within the Terrestrial Gondwana Crocodylomorpha

Previous studies

The first phylogenetic analysis concerning the peirosaurids was presented by Gasparini et al. (1991). Their resulting topology showed that Peirosauridae form a natural group defined by the following characters: presence of wedge-like process of the maxilla extending into the premaxilla; premaxilla very short in palatal view; 14-15 maxillary teeth; and strong lateral knobs on the basioccipital. Until now this family is known in South America, Madagascar (Buckley and Brochu, 1999), and continental Africa (Larsson and Gado, 2000).

There are different suggestions concerning the phylogeny of terrestrial crocodylomorphs from Gondwana. Hecht and Tarsitano (1983) based on the structure of the quadrate and its pneumatic system postulated that Notosuchia and Protosuchia have a close affinity as sister-group or ancestor-descendent relationship. Benton and Clark (1988) erected the name Metasuchia for a group comprising non-thalatosuchian mesoeucrocodilians such as the "notosuchians" and the sebecosuchians. These authors suggested that *Notosuchus* is more advanced than an unnamed crocodylomorph, "the Fruita Form", but it is the most primitive of the paraphyletic "notosuchians". Other species, such as *Libycosuchus*, *Sebecus*, *Baurusuchus*, and *Araripesuchus* have uncertain relationships with *Notosuchus*, which are obscured by a puzzling pattern of character distributions. Gomani (1997) discussed the relationships of *Malawisuchus* with the primitive metasuchians *Notosuchus*, *Uruguaysuchus*, *Araripesuchus*, *Sebecus*, *Baurusuchus*, *Libycosuchus*, the "Fruita Form", *Candidodon*, and *Chimaerasuchus*. The cladistic analysis showed that *Malawisuchus*, *Candidodon*, *Chimaerasuchus*, and *Notosuchus* form a clade supported by multicusped posterior teeth. This has reinforced the proposal of Gasparini et al. (1991) that *Baurusuchus* and *Sebecus* form a clade, while *Malawisuchus*, *Candidodon* and *Chimaerasuchus* compose another. The cladistic analysis of Benton and Clark (1988) also presented this pattern. It was considered that if the derived similarities between *Baurusuchus* and *Sebecus* indicate a valid natural group, then *Araripesuchus* would be more closely related to the Neosuchia (which includes eusuchians). This idea was also postulated by Hecht and Tarsitano (1983) based on the posterior position of squamosal contacts with the dorsal surface of the quadrate. This was also interpreted as evidence of the close relationship betweeen *Araripesuchus* and more advanced crocodyliforms.

Outside Gondwanan context, *Chimaerasuchus*, from the Lower Cretaceous of China, was interpreted as a sister-group of *Notosuchus* and *Malawisuchus* by Wu et al. (1995) and Wu and Sues (1996). Based on these data, these authors cast doubts on the endemic distribution of the Notosuchidae in Gondwana during the Cretaceous. Pol (1999), in his phylogenetic study of basal mesoeucrocodylians, considered that the monophyly of Notosuchia should be rejected and pointed out a clade that includes *Baurusuchus*. This author considered that *Baurusuchus* has all the notosuchian synapomorphies that can be scored, and additionally, shares several derived characters that define its position nested within Notosuchia. Ortega et al. (2000) studied the phylogenetic context of *Araripesuchus* considering that it does not constitute a clade within Notosuchia but is rather a sister-group of Neosuchia. Furthermore, the derived conditions of the characters that diagnose *Araripesuchus* + Neosuchia are not shared by any of the other basal mesoeucrocodylians (*Baurusuchus*, *Sebecus*, *Bretesuchus*, *Libycosuchus*, and *Iberosuchus*). Buckley et al. (2000) described *Simosuchus*, a Late Cretaceous crocodyliform from Madagascar, which they included in a clade consisting of several other small-bodied, short-snouted Gondwanan crocodyliforms, including *Notosuchus*, *Libycosuchus*, *Uruguaysuchus*, and *Malawisuchus*. The Malagasy *Simosuchus* and the South American *Uruguaysuchus* are linked by two unambiguous synapomorphies: internal nares divided by a septum and strongly spatulated posterior teeth. Buckley and Brochu (1999) analysed the mesoeucrocodylian *Mahajangasuchus* from the Upper Cretaceous of Madagascar and considered it as the closest relative of Peirosauridae, sharing a single synapomorphy – a splenial that is mediolaterally thick dorsally. The peirosaurids have also been recognized in continental Africa. Larsson and Gado (2000) described from Elrhaz Formation (Aptian, Niger) the crocodyliform *Stolokrosuchus lapparenti*. They considered that it is nested between goniopholidids and the *Bernissartia* + Crocodylia clade. Accordingly to Larsson and Gado (2000), *Stolokrosuchus lapparenti* has a non-resolved sister-taxon relationship with *Peirosaurus* and *Lomasuchus*, supporting both the monophyly of Peirosauridae and the inclusion of *Stolokrosuchus* within this family.

Cladistic analysis

To analyse the phylogenetic position of the taxon *Uberabasuchus* with other peirosaurids and to some terrestrial Gondwanan crocodylomorphs, we used the characters and character states proposed by Ortega et al. (2000), as well as a new character - the palpebral ossification. The cladistic analysis was based on the genera that have adequate descriptions and a significant occurrence, especially from continents that were part of Gondwana. The selected taxa for the outgroup were the same as Ortega et al. (2000), whereas we used baurusuchids, sebecosuchids, araripesuchids, notosuchids, and peirosaurids as ingroup. The characters were reassessed from Ortega et al. (2000), Bonaparte (1991), Buckley and Brochu (1996, 1997, 1999), Buckley et al. (2000), Campos et al. (2001), Carvalho and Bertini (1999), Clark et al. (1989), Gasparini (1982), Gasparini et al. (1991), Gomani (1997), Larsson and Gado (2000), Nobre (2000), Nobre and Carvalho (2001), Price (1955), Wu and Sues (1996) and Wu et al. (1995). Additional data was obtained by examining the holotype of *Itasuchus*, *Candidodon*, and *Mariliasuchus*.

The data matrix comprises four outgroup taxa (*Postosuchus*, *Sphenosuchus*, *Dibothrosuchus*, and *Protosuchus*), and 19 ingroup crocodyliform taxa (Table 1). Data concerning *Araripesuchus* and *Itasuchus* were based on *Araripesuchus gomesii* Price, 1959 and *Itasuchus jesuinoi* Price, 1955, respectively. The taxon Baurusuchidae comprises merged information on *Baurusuchus* – taken from Ortega et al. (2000) – and *Stratiotosuchus* (Campos et al., 2001). The matrix was processed using PAUP 3.1.1 for Macintosh (Swofford and Begle, 1993), and after a previous heuristic search, we reweighted characters based on rescaled values of each character. The cladogram resulted from a strict consensus tree (Fig. 7) of three possible topologies after a strict parsimony analysis through a heuristic search with 100 replicantes. The three resulting topologies only differ on the position within the outgroup taxa. The relationships within the ingroup are the same on the different resulting trees. In order to test clades support of the resulted topologies, we conducted a bootstrap analysis using 700 replicates, and Bremer's support analysis using TreeRot program (Sorenson, 1999). The tree has a length of 374 steps, the consistency index

Table 1. The data matrix (modified from Ortega et al., 2000) contains all of the data used for the cladistic analysis. See table 2 for character descriptions and character states. Supplementary data from Bonaparte (1991), Buckley and Brochu (1996, 1997, 1999), Buckley et al. (2000), Campos et al. (2001), Carvalho and Bertini (1999), Clark et al. (1989), Gasparini (1982), Gasparini et al. (1991), Gomani (1997), Larsson and Gado (2000), Nobre (2000), Nobre and Carvalho (2001), Price (1955), Wu and Sues (1996) and Wu et al. (1995). *Araripesuchus* characters refer to *Araripesuchus gomesii*. *Itasuchus* characters refer to *Itasuchus jesuinoi*. The genera *Baurusuchus* and *Stratiotosuchus* were merged in Baurusuchidae.

Postosuchus
0000000000??000000000000000000?0000000000000000000000000000000?
00??0?00000000?000000000?0000000?000?00000000????????0??0
00000???00000??000000?0000??????00000??00?00000??0?000?????????

Sphenosuchus
000000000000110000000000000010?1000?000000000000000000000000000
00?00?011000000100000000000000001010100000000000000000100000
000000010000?00000000000??000000000??00?00010001000?0000000?0?

Dibothrosuchus
000000000100000000000000001101000000100000000000000000000000000
??0?01100000?100000000?0000001?10000000000000000000000100000
000000010000?000000000000?000000000??00?00010??1?00??????????

Protosuchus
011001100010011001000000001010?1000001101101110000110010010
000010000101101000010100100000000?001?10?000000?00000?100
01000101000000100 0?0100000?00000?000?000000000?000?10?2?0000
0000?0?00

Uberabasuchus
1?001111?0?101000?0100001111??1000??1?111000?101?100?????????0??
????010001?????0100110?11??010001?110?00?10??11?????0?0???
???????001000?10??00??0?1???01110110???1?01???????0?????????0

Lomasuchus
1000101100??1?00000100001101??1000??1111101111?0010????011111?
110?1001100?02?110100110?????0?100???0?000?1??????????????
??????????01???0?011?00?0?????????01?000??001???2?1011?0??????2

Peirosaurus
10001?1?00??1100000100001??1??1????????10?1?????????????????1??????001
110?????1??10?010?0??????0????10000?1????1?11??0????????????
1010??00???1??????????1???01?0???0001?????????10??????0

Mahajangasuchus
??
0??00001111?100?100?1?110?00??00??1?11?10?0???1?1?01?10??0?????
?1???????100?1????????11?0???1?0??????????01??

Notosuchus
0010001000100010011000001111101000??1011101011000110110011011111
1010001100002011000101001001101 0?100101001 10???01?10101?1110000
1010001010000001000010 10?100100000000001001 12?000001100000?

Araripesuchus
10100010?0010000000110001101111001??1011101011000100?100111111110?
0001100002?1101010?0?100000101100100011100001101010101 1100?0??111110
10001110000 0101?1101010000?00000?1200000110000??1

Malawisuchus
10100011?00111000?0100001101??1001??1?111010?11101?00????1?1?011??
1001100????110?01?10010????1?1110011?0110???0?1???0?????0?
?????0011?0????0?00?????1?1??10110??10111??????0?001??????0

Candidodon
10000010000?000000000100110 1???0011?1011001111000 1?0110001?111????0?
011001???110001000?0??????0????01110?1????1?????0???????????1001
1?1?1000?00?01??0?1??1011????0110?01?1?0001?10?01?0

Mariliasuchus
0000011?0111010?10000001111??1001111011000111000100010011?1110?0?
00111000?2?110101000100?00110?1?110000?1??????????0??11?000?001
101110?10?0?00101?0011???00001?10?10?11?1?10?1?00?01?0

Uruguaysuchus
1100001 0?00???0000000100 1111??1000??10010010 10111??001001111?1010
?0001100002?1100010000100000101100110101100?00?01?1000?11000000
10001110000010000??00110010101001000100120000000100000?

Comahuesuchus
0?101010000???0001100000 0110??100??????1111010111111010??????
1010???1110000??1?0001010???0???0101?01000110????????????????????????
0101?1??????1000?????1???011100?01110??0?0100?1???????

Chimaerasuchus
0???011100?111100?001001??2??
011??????1?0?000???00???11??0??001?1?1????0?00?10??1120?000??10110?
?????1??00?01?10?1?00?????0011?0120?1?0???0?00??

Simosuchus
111011110?100000110101001101??10010?10110010?0011??0?1?00000
10110?01011000???11000?010?0????11001?10010001?????????????????????????
0010??101?0?0??0??????0???001?????001???2??000?1???????1

Baurusuchidae
000(01)0(01)110(01)1?01(01)(01)(01)10(01)00011(01)(01)(01)1010(01)
0001(01)1111101100010011001111111110?0011100102?110001011?11101010
11000000000??????????0?????????1?100010(01)0100110101 10??11101
011000?001(01)0??2?1011011??????

Sebecus
0000001?011?1101010000?1101??10000111011111110?01000110?11
111110?1011100002?110000000?1?00???011010000000???????????????????
????0001?00000110010?????111101?0???00000????10110???????0

Libycosuchus
00100?1??00110100110000?11?1??1000?011111110110001001 10?11?
1111?0?1011100002?110001000?1?0??000?1?0?????0??????????????????
??????0??0010?0?110?0000???11010000?0?000?0??2?101001???????

Stolokrosuchus
0?010110000?00001000000011010?10000?00010010?0100100010000?
1100?1?1011100????11?????????????????????????0?1?????????????????
?????0?00?0?00???1????????????10011????000???2??1?1?0???????

Itasuchus
??????????????????01??????????????0?????????????????????????????????
??????0???????001010?1???????????011100?1???????????0?????????????
01?????????????????????1???????????0?0???????????????????

0.679, and retention index 0.826. The rescaled consistency index is 0.640. We recognized 20 clades within the 19 ingroup crocodyliform specimens, of which 13 are new taxa (see next section for a detailed description of each clade). To test the hypothesis proposed by Larsson and Gado (2000), *Stolokrosuchus* as a Peirosauridae, we have manipulated the resulted topologies in MacClade program version 3 (Maddison and Maddison, 1992). The manipulated tree is 40 steps longer compared to our results, which suggests that *Stolokrosuchus* is not a Peirosauridae.

Definitons and diagnoses of taxa

In this section we provide diagnoses for the major taxa included in selected crocodylomorphs. The following taxa and their contents are diagnosed here: Gondwanasuchia (new taxon), Chimaerasuchidae (new taxon), Notosuchimorpha (new taxon), Notosuchiformes (new taxon), Uruguaysuchidae Gasparini, 1971, Terriasuchia (new taxon), Notosuchia Gasparini, 1971 (new combination), Peirosaurimorpha (new taxon), Candidodontidae (new taxon), Peirosauriformes (new taxon), Peirosauroidea (new taxon), Itasuchidae (new taxon), Peirosauridae Gasparini, 1982 (new combination), Lomasuchinae (new taxon), Mahajangasuchini (new taxon), Ziphosuchia Ortega, Gasparini, Buscalioni and Calvo, 2000, Notosuchidae Dollo, 1914, Baurusuchoidea (new taxon), Baurusuchidae Price, 1945, and Sebecidae Colbert, 1946.

Characters are referred to in the following discussions according to their numbered order as given in table 1 and 2, and nodes described are those presented in figure 7. Notations in brackets indicate the direction of character transformation. Unambiguous characters are marked in bold font.

Gondwanasuchia, new taxon

Definition: The most recent common ancestor of Chimaerasuchidae and Notosuchimorpha
Etymology: *Souchus*, Greek for crocodyle; Gondwana referring to a paleogeographic configuration.
Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (*Bootstrap*: 96; Bremer: 2).
12. Naso-oral fenestrae formed by maxilla and premaxilla. [0-1]
25. Frontals fused. [0-1]
38. Quadratojugal visible beneath jugal. [1-0]
48. Quadratojugal contacts postorbital at point, or there is no contact at all. [0-1]
49. No contact between quadratojugal and postorbital. [0-1]

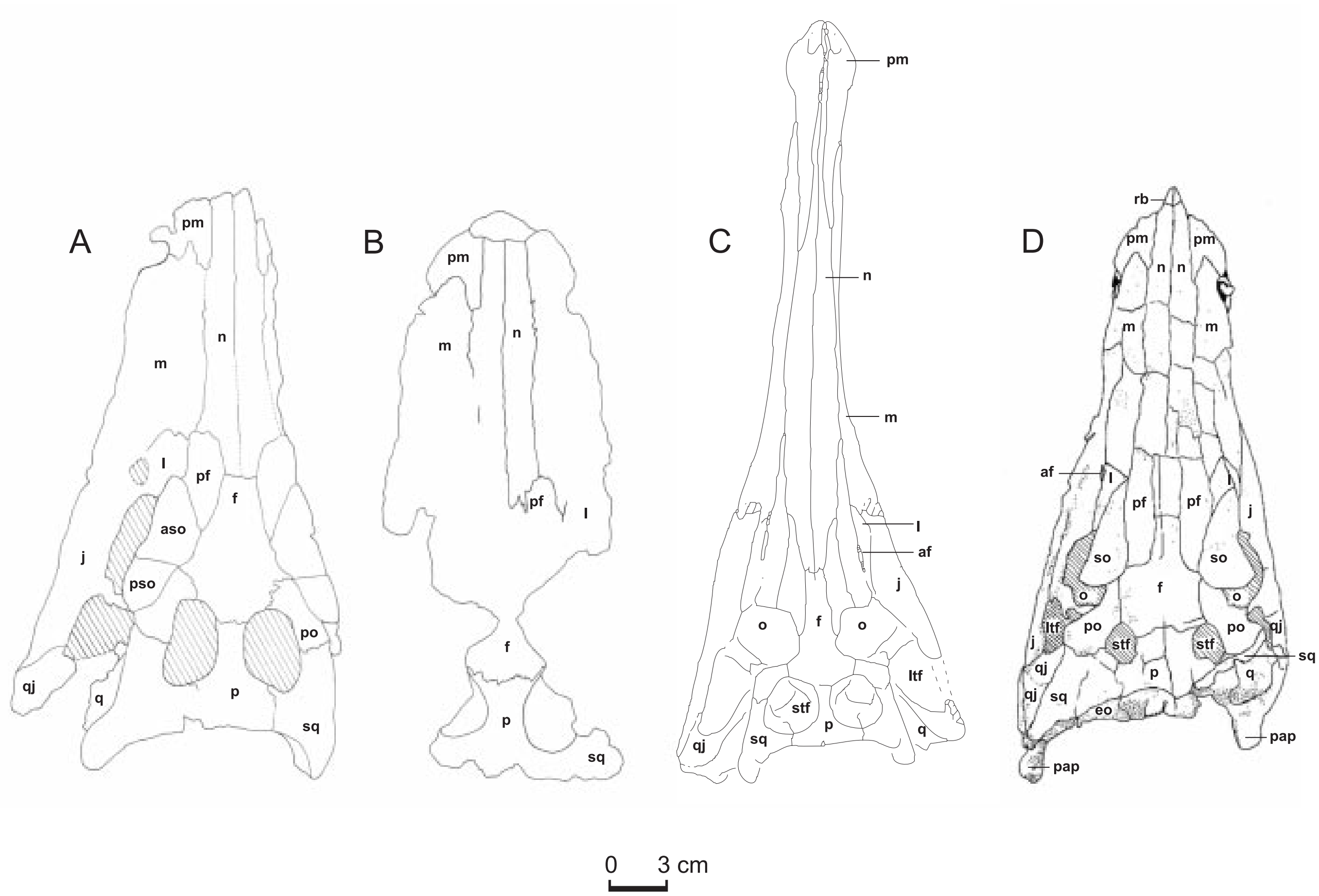

Fig. 6. Skull morphology of peirosaurids. (A) *Lomasuchus*. (B) *Peirosaurus*. (D) *Uberabasuchus* (A and B modified from Gasparini et al., 1991) and (C) the supposed peirosaurid *Stolokrosuchus* (modified from Larsson and Gado, 2000).

61. Ectopterygoid makes contact with maxillary palatal branch. [0-1]
64. Occipital foraminae for cranial nerve IX in a separate passage. [0-1]
66. Cranial projection of iliac blade reduced to a tuberosity. [0-1]
76. Cranio-quadrate canal closed by a thick lamina formed by squamosal, quadrate and exoccipital. [0-2]
79. Palatines or pterygoids participating on caudal opening of naso-pharyngeal duct (internal nares). [0-1]
85. Post-caniniform dentary teeth with waves of size variation (heterodont). [0-1]
97. Absence of prearticular. [0-1]
106. Tip of maxillary tooth crown ventrally directed and dentary tooth crown dorsally directed, and both lingually curved. [0-1]
121. Scapula as long as coracoid. [0-1]
146. Ectopterygoidean medial descendent branch distally forked. [0-1]
150. Proximal head of radial wider than distal one. [0-1]
154. Dorsal surface of caudal branch of quadrate without depression. [0-1]
157. Skull roof square or rectangular shaped and with a longitudinal dominant axis. [0-1]
158. Squamosal showing a smooth lobe differentiated from the skull by a caudolateral groove. [0-1]
177. Primary pterygoidean palate with deep parasagittal depressions on the external face of the palate. [0-1]

Chimaerasuchidae, new taxon

Definition: The most recent common ancestor of *Chimaerasuchus* and *Simosuchus* and all of their descendants.
Etymology: referring to *Chimaerasuchus*-like groups.
Diagnosis: The members of this taxon possess the following synapomorphies
(*Bootstrap*: 66; Bremer: 1).
8. Premaxillo-maxillary suture zigzag-shaped in lateral view. [0-1]
34. Jugal portion of postorbital bar medially displaced and a ridge separates postorbital bar from lateral surface of jugal. [0-1]
39. Quadratojugal extends anteriorly forming part of dorsal edge of infratemporal bar. [0-1]
66. Cranial projection of iliac blade absent. [1-2]
83. Dentary extends caudally up to end of tooth row. [1-0]
93. Caudal edge of angular ascends and surpasses the articular glenoid cavity. [0-1]
96. Anterior projection of surangular unique and acute in lateral view. [1-0]

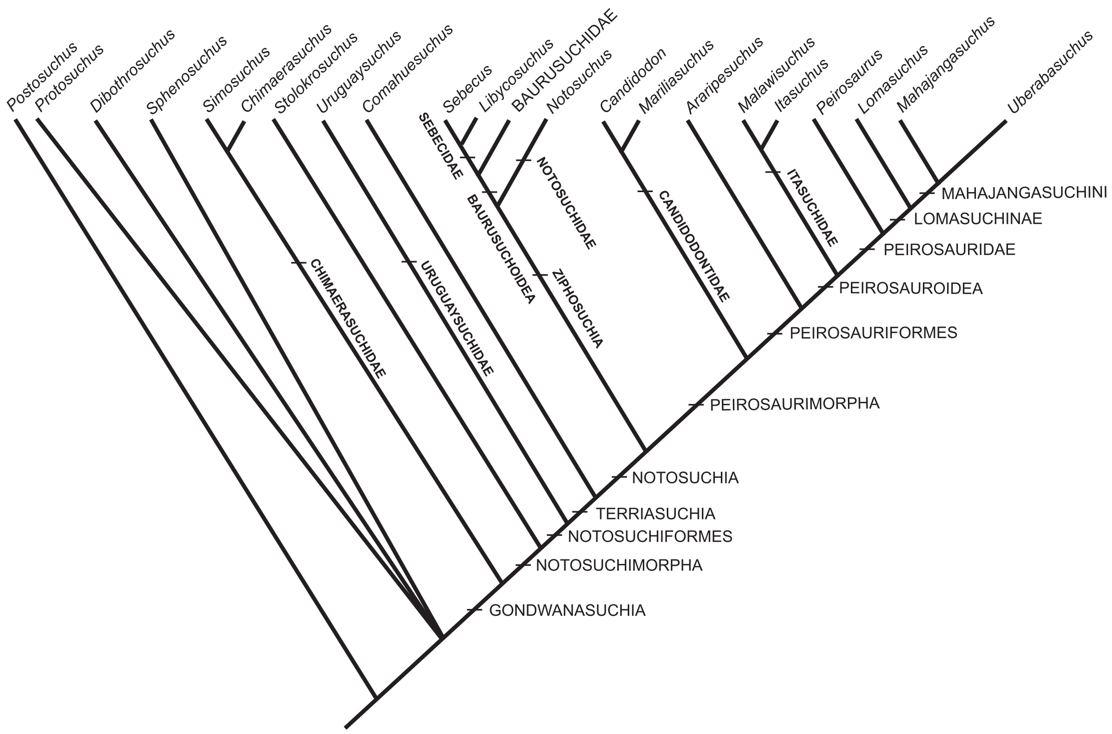

Fig. 7. Consensus tree of three possible topologies after a strict parsimony analysis of a matrix with 4 outgroup and 19 ingroup crocodyliform taxa. Tree with 374 steps, consistency index of 0.679, and retention index of 0.826.

Table 2. Characters and character states of the main terrestrial crocodylomorphs found in the Gondwanian context (modified from Ortega et al., 2000) employed in the cladistic analysis.

1. Ornamentation of external surface of cranial dermal bones
0 - smooth or formed by grooves and ridges; 1 - with circular or subpolygonal pits
2. Sculpturing of palatal surface
0 - maxillary palatal surface smooth; 1 - maxillary palatal surface ornamented with ridges
3. Rostral length
0 - distance from anterior orbital edge to anterior contour of rostrum equal or longer than distance from anterior orbital edge to posterior parietal contour; 1 - distance from anterior orbital edge to anterior contour of rostrum shorter than distance from anterior orbital edge to posterior parietal contour
4. Rostral length
0 - distance from anterior orbital edge to anterior contour of rostrum shorter, equal or slightly longer than distance from anterior orbital edge to posterior parietal contour; 1 - distance from anterior orbital edge to anterior contour of rostrum at least twice than distance from anterior orbital edge to posterior parietal contour
5. Rostral section
0 - tubular, almost as deep as wide; 1 - wider than deep
6. Premaxillo-maxillary suture in lateral view
0 - vertical; 1 - caudodorsally directed
7. Premaxillo-maxillary joint
0 - premaxilla overlapping maxilla; 1 - premaxilla and maxilla sutured
8. Premaxillo-maxillary suture in lateral view
0 - straight; 1 - zigzag shaped
9. Direction of premaxillo-maxillary suture in palatal view
0 - cranially directed; 1 - caudally directed
Direction of suture is evaluated with respect to a theoretical line that passes between the lateral contact of bones
10. Ventral edge of premaxilla with respect to ventral edge of maxilla in lateral view
0 - placed almost at same height; 1 - deeper, and anterior dorsal contour of dentary is also strongly concave
11. Oral cavity communicates with nasal cavity through palatal perforations (naso-oral fenestrae), besides internal nares
0 - no; 1 - yes
12. Naso-oral fenestrae formed by
0 - maxilla and premaxilla; 1 - premaxilla
13. Foramen at premaxillo-maxillary suture in lateral view
0 - present; 1 - absent
14. Premaxillo-maxillary notch
0 - absent; 1 - present
15. Last premaxillary alveolus the largest of premaxillary tooth row
0 - no; 1 - yes
16. External nares
0 - facing frontal, laterofrontal or frontodorsally; 1 - facing dorsally
17. Position of external nares with respect to anterior rostral contour in dorsal view
0 - concealed; 1 - a premaxillary bar separates external nares and anterior rostral contour
18. Relative position of last maxillary tooth with anterior edge of palatine fenestra
0 - last maxillary tooth caudal to anterior edge of palatine fenestra; 1 - last maxillary tooth cranial to anterior edge of palatine fenestra
19. Dental implantation
0 - teeth set in isolated alveoli; 1 - teeth set disposed in a groove
20. Size of maxillary teeth
0 - all maxillary teeth similar in size or with largest alveolus placed at middle of maxillary row; 1 - tooth row with waves of size variation
21. Ventral edge of maxilla in lateral view
0 - straight or convex; 1 - sinusoidal
22. Rostral tip of nasals
0 - nasals reach the caudal edge of external nares; 1 - nasals do not reach the caudal edge of external nares
23. Rostral tip of nasals
0 - nasals reach premaxillae; 1 - nasals do not reach premaxillae
24. Caudal tip of nasals
0 - caudally nasals converge at sagittal plane; 1 - nasals caudally separated by an anterior sagittal projection of frontal
25. Frontals
0 - separated; 1 - fused
26. Dorsal fronto-parietal surface
0 - reduced to a narrow bar; 1 - wide
27. Parieto-postorbital suture
0 - absent on dorsal surface of skull roof; 1 - present on dorsal surface of skull roof
28. Parietals
0 - separated; 1 - fused
29. Prefrontal pillars
0 - do not reach palate; 1 - reach palate and solid fused
30. Prefrontal pillars when integrated in palate
0 - pilllars transversely expanded; 1 - transversely expanded in their dorsal half and columnar ventrally; 2 - pillars longitudinally expanded in their dorsal part and columnar ventrally
31. Postfrontals
0 - present; 1 - absent
32. Antero-lateral spine of postorbital
0 - absent; 1 - postorbitals project a short and sharp spine
33. Relative length between postorbital and squamosal
0 - squamosal is longer; 1 - postorbital is longer
34. Jugal portion of postorbital bar
0 - flushes with lateral surface of jugal; 1 - medially displaced and a ridge separates postorbital bar from lateral surface of jugal
35. Caudal tip of ectopterygoid-jugal contact
0 - placed cranial to post-orbital bar; 1 - placed caudal and surpassing postorbital bar
36. Ectopterygoid-postorbital suture
0 - ectopterygoid does not contact postorbital; 1 - ectopterygoid contacts postorbital on medial side of postorbital bar
37. Postorbital and jugal forming postorbital bar in lateral view
0 - jugal sets caudal to postorbital; 1 - postorbital is medial or caudal to jugal
38. Jugal and quadratojugal in lateral view
0 - quadratojugal visible beneath jugal; 1 - quadratojugal is not exposed
39. Corner of infratemporal fenestra in lateral view
0 - jugal-quadratojugal suture lies at posteroventral corner; 1 - quatratojugal extends anteriorly forming part of dorsal edge of infratemporal bar
40. Skull roof
0 - not developed, postorbito-squamosal dorsal surface on a lower plane than fronto - parietal dorsal surface; 1 - developed postorbito-squamosal and fronto-parietal surfaces are on the same plane
41. Supratemporal fenestrae
0 - relatively large, covering most of surface of skull roof; 1 - relatively short, fenestrae surrounded by a flat and extended skull roof
42. Outer surface of squamosal
0 - laterodorsally oriented; 1 - dorsally oriented
43. Contour of squamosal in dorsal view
0 - curved; 1 - L-shaped

Table 2. *Contd.*

44. Quadrate inclination with respect to a horizontal plane including the cranial roof
0 - craniocaudal axis of quadrate inclined more than 45 degrees; 1 - craniocaudal axis of quadrate inclined less than 45 degrees
45. Longitudinal groove on dorsolateral surface of squamosal
0 - absent; 1 - present
46. Infratemporal fenestrae
0 - facing laterally; 1 - facing laterodorsally
47. Quadratojugal spine at caudal margin of infratemporal fenestrae
0 - absent; 1 - present
48. Quadratojugal contacts postorbital
0 - widely; 1 - at point, quadratojugal is dorsally acute, or there is no contact at all
49. Quadratojugal contacts postorbital
0 - yes; 1 - no
50. Quadrate fenestrated
0 - quadrate lacking fenestrae; 1 - quadrate fenestrated even if it possesses one fenestra which in such case is placed on dorsal surface of the cranial ascendent process of quadrate
51. Quadrate fenestrated
0 - with more than one fenestra; 1 - with just one fenestra
52. Relative position of cranio-mandibular joint
0 - beneath basioccipital ventral edge; 1 - aligned with basioccipital
53. Quadrate condyles
0 - almost aligned; 1 - medial condyle expands ventrally
54. Dorsocaudal edge of quadrate
0 - straight or smoothly curved; 1 - forming otic notch
55. Dorsal surface of caudal branch of quadrate
0 - concave or flat and smooth; 1 - with a longitudinal ridge from base of paraoccipital process to articular end
56. Pterygoidean secondary palate
0 - pterygoids of primary palate exposed and they do not contact each other secondarily on midline; 1 - pterygoids meet on midline forming a secondary palate
57. Basipterygoid processes
0 - expanded; 1 - reduced to a narrow crista or absent
58. Pterygoids
0 - caudally separated; 1 - caudally fused
59. Vomer
0 - exposed on palate between premaxillae and maxillae; 1 - hidden by palatal branch of maxillae
60. Palatal secondary palate
0 - palatines of primary palate exposed and they do not contact each other secondarily on midline; 1 - palatines meet on midline forming a secondary palate
61. Ectopterygoid-maxilla contact
0 - ectopterygoid does not connect to palatal ramus of maxilla; 1 - ectopterygoid makes contact with maxillary palatal ramus
62. Supraoccipital exposure on cranial roof
0 - no, parietals contact on occiput avoiding dorsal exposition of supraoccipital; 1 - supraoccipital connects parietal at posterior edge of skull roof or is clearly exposed in dorsal surface of cranial roof
63. Bones bounding foramen magnum
0 - exoccipitals and supraoccipital; 1 - exoccipitals
64. Occipital foramina for cranial nerves IX, X, and XI
0 - all passing through a common foramen; 1 - metoptic foramen (IX) in a separate passage
65. Basioccipital surface under foramen magnum
0 - caudoventrally oriented; 1 - vertical and occipitally oriented
66. Cranial projection of iliac blade
0 - present and as long as the caudal projection; 1 - reduced to a tuberosity; 2 – absent
67. Basisphenoid in ventral view
0 - widely exposed; 1 - almost excluded from ventral view and hidden by pterygoid and basioccipital
68. Relative length of basisphenoid and basiooccipital
0 - basisphenoid shorter or equal than basioccipital; 1 - basisphenoid longer and transversely wider than basioccipital
69. Antorbital fenestra
0 - present; 1 - absent or reduced to a tiny foramen
70. Nasal participation in antorbital fenestra
0 - yes; 1 - no
71. Jugal participation in antorbital fenestra
0 - yes; 1 - no
72. Supratemporal fenestra
0 - present; 1 - absent
73. Infratemporal fenestra
0 - wide; 1 - forming a vertical slot
74. Infratemporal fenestra
0 - shorter than it is deep or at least as long as deep; 1 - much longer than deep
75. Anterior opening in the temporo-orbital region
0 - exposed in dorsal view; 1 - hidden in dorsal view, and overlapped by squamosal rim of supra-temporal fossa
76. Cranio-quadrate canal
0 - laterally open; 1 - closed off by a thin lamina formed by squamosal, quadrate and exoccipital; 2 - closed off by a thick lamina formed by squamosal, quadrate and exoccipital
77. Iliac blad
0 - with posterior lamina as high as anterior one; 1 - with posterior lamina higher than anterior one
78. Maxilla forms part of secondary palate
0 - no; 1 - yes
79. Palatines or pterygoids participating on caudal opening of naso-pharyngeal duct (internal nares)
0 - no; 1 - yes
80. External mandibular fenestra
0 - present as a wide foramen; 1 - present but very reduced; 2 - absent
81. Mandibular compression
0 - dentary compressed, formed by almost vertical lateral and medial laminae; 1 - dentary transversely expanded, almost as wide as high, and with convex lateroventral surface
82. Suture between dentaries
0 - separated mandibular symphysis; 1 - dentaries fused, at least ventrally in the mandibular symphysis
83. Dorsocaudal branch of dentary
0 - dentary extends caudally up to end of tooth row; 1 - dentary extends beyond tooth row and with a dorsal ascending projection
84. Lateral contour of dentary in dorsal view
0 - straight; 1 - sigmoidal
85. Post-caniniform dentary teeth
0 - almost homodont in size; 1 - with waves of size variation
86. Outline of dentary tooth row in dorsal view
0 - straight; 1 - sigmoidal
87. Proximal articular head of tibia
0 - with two concavities separated by a crest; 1 -with one concave articulating area
88. Splenial symphysis
0 - splenial not involved in mandibular symphysis, splenials just touch or do not contact each other; 1 - splenials form a significant part of symphysis
89. Splenials behind symphysis
0 - thin and lateromedially compressed; 1 - broad and robust
90. Foramen intramandibularis oralis
0 - small or absent; 1 - big slot-like foramen

Table 2. *Contd.*

91. Emergence of the mandibular branch of trigeminus nerve in the medial side of mandible
0 - caudal to symphysis; 1 - enclosed within symphysis
92. Transversal section of splenial
0 - plane; 1 - convex
93. Caudal edge of angular
0 - does not ascend to the articular glenoid cavity; 1 - ascend, surpassing the articular glenoid cavity
94. Caudal edge of surangular
0 - slopes ventrally; 1 - slopes dorsally
95. Rear portion of dentary in dorsal view
0 - does not expand medial to tooth row; 1 - medially expanded to tooth row
96. Anterior projection of surangular in lateral view
0 - unique and acute; 1 - forked
97. Prearticular
0 - present; 1 - absent
98. Coronoid size
0 - short; 1 - long, anteriorly extended
99. Surangular and quadratojugal taking part in craniomandibular joint
0 - no; 1 - yes
100. Mesial and distal margin of tooth crowns
0 - with denticulate carinae (denticles are isolated units, distinctly shaped and sized); 1 - without carinae or with carinae smooth or crenulated (crenulation is made of enamel wrinkles)
101. Root of maxillary and dentary teeth
0 - as wide or narrower than its crowns; 1 - inflated roots, wider than its crowns
102. Shape of tooth crowns in bucal view
0 - triangular; 1 - trapezoidal
103. Lingual side of maxillary and dentary teeth
0 - without a longitudinal depression; 1 - with a longitudinal depression affecting roots and crowns
104. Maxillary and dentary teeth transverse section
0 - labiolingually compressed; 1 - subcircular
105. Glenoid fossa of articular
0 - craniocaudally similar to articular surface of quadrate; 1 - craniocaudally longer than articular surface of quadrate
106. Tip of maxillary and dentary tooth crowns
0 - caudally curved; 1 - dorsal directed or lingually curved
107. Number of longitudinal rows of osteoderms forming presacral dorsal armor
0 - two; 1 - four
108. Presence of accessory ranges of osteoderms, that is, more than four longitudinal rows of osteoderms forming presacral dorsal armour or four longitudinal rows in which the parasagitals must show two longitudinal keels
0 - no; 1 - yes
109. Continuity of dorsal armour
0 - dorsal armour continues from neck to tail; 1 - dorsal armour shows a narrowing or gap at cervico-thoracic juncture
110. Presacral dorsal osteoderms
0 - lateroventrally deflected; 1 - flat
111. Ornamentation of presacral dorsal osteoderms
0 - smooth or made of ridges and grooves; 1 - with a pitted surface
112. Dorsal paravertebral osteoderms constituting a hemiplastron
0 - hemiband is narrower than its craniocaudal length; 1 - hemiband is wider than its craniocaudal length
113. Imbrication of osteoderms
0 - osteoderms of presacral dorsal armour with an anterior peg that articulates into a socket of anterior one; 1 - osteoderms without anterior projection
114. Imbrication of osteoderms
0 - osteoderms of presacral dorsal armour with a short caudal salient peg; 1 - osteoderms with a straight caudal edge
115. Number of keels on transverse bands of presacral dorsal armour
0 - two; 1 - more than two
116. Coracoid shaft
0 - short; 1 - long shaft extending ventrally
117. Cervical and dorsal centra
0 - amphicoelous; 1 - procoelous
118. Styliform process of coracoid
0 - present; 1 - absent
119. Centrum of first caudal vertebra
0 - amphicoelous; 1 - procoelous
120. Contour of scapular blade
0 - dorsally broad and with concave cranial and caudal edges; 1 - dorsally broad and with a concave cranial edge but straight or convex caudal one; 2 - dorsally narrow, straight cranial and caudal edges
121. Relative length of coracoid and scapula
0 - scapula is at least one third longer than coracoid; 1 - scapula as long as coracoid
122. Glenoid surface of coracoid
0 - extended on a subhorizontal plane; 1 - extended on a vertical plane; 2 - extended on a oblique plane, and the glenoid lip facing outwards and posteroventrally
123. Humeral proximal head
0 - facing backwards (posterodorsally); 1 - facing dorsally, and with a lateromedial major axis
124. Inner tuberosity of proximal head of humerus
0 - developed and with articular facet bending ventrally or obliquely; 1 - not developed and with articular surface facing dorsally
125. Ligamental depression on anterior surface of humerus
0 - immediately lateral to inner tuberosity and below humeral head; 1 - displaced laterally towards the border of the shaft and located lateral to humeral head
126. Lateral profile of deltopectoral crest
0 - convex; 1 - concave
127. Radiale
0 - longer than wide; 1 - as long as wide (considering its proximal width as reference)
128. Relative length of radius and ulna
0 - radius as long as ulna; 1 - radius longer, at least 1/3 of ulnar length
129. Proximal carpals
0 - short, almost spherical; 1 - radial and ulnar elongated
130. Lateral contour of rostrum in dorsal view
0 - straight; 1 - with constrictions and with a sinusoidal aspect
131. Mesio-distal length of tooth crowns
0 - decreasing towards the rear of tooth row; 1 - increasing towards the rear of tooth row
132. Heterodonty of maxilla and dentary
0 - homodont; 1 - with different dental morphologies (heterodont)
133. Number of premaxillary teeth
0 - five; 1 - less than five
134. Exposition of posterior part of angular in ventral view
0 - angular surface (where pterygoidean muscle is attached) ventrally exposed; 1 - angular laterally displaced and overlapping articular, with surface for pterygoidean muscle attachment facing laterally
135. Caudal branch of quadrate
0 - at least as long as broad; 1 - shorter than broad
136. Palatal maxillary platform
0 - absent; 1 - present, avoiding contact between ectopterygoid and maxillary alveoli

Table 2. *Contd.*

137. Septated internal nares
0 - yes; 1 - no
138. Pterygoidean flanges
0 - laminar; 1 - bar-like
139. Depression on primary pterygoidean palate posterior to internal nares
0 - depression wider than palatine bar; 1 - narrower than palatine bar between palatal fenestrae
140. Postmaxillary internal nares
0 - present; 1 - absent
141. Retroarticular process
0 - without a medial shelf; 1 - with a medial shelf
142. Internal nares
0 - far from caudal contour of skull; 1 - close to caudal contour of skull
143. Caudal edge of internal nares
0 - cranial to rear edge of palatine fenestra; 1 - caudal to the rear edge of palatine fenestra
144. Ventral edge of external mandibular fenestra
0 - smooth; 1 - with a depression surrounding the edge
145. Lateral surface of anterior branch of jugal
0 - smooth, plane or concave; 1 - with a pronounced triangular depression
146. Ectopterygoid medial descending branch
0 - single; 1 - distally forked
147. Medial shelf of retroarticular process
0 - vertical and facing medially; 1 - facing dorsally
148. Coracoid shaft
0 - blade-like; 1 - rod-like
149. Femoral shaft
0 - slightly twisted, proximal and distal articular facets are twisted each other about 30 degrees; 1 - strongly twisted, proximal and distal articular facets are twisted each other about 60 degrees
150. Proximal and distal ends of radiale
0 - almost equally expanded; 1 - proximal head wider than distal one
151. Mandibular symphysis
0 - short; 1 - long, dentary symphysis prolongs caudal to 4^{th} alveoli
152. Craniocaudal length of retroarticular process
0 - less than craniocaudal length of articular glenoid fossa; 1 - much longer than craniocaudal length of articular glenoid fossa
153. Dorsal surface of retroarticular process
0 - facing craniocaudally; 1 - facing dorsal or craniodorsally
154. Dorsal surface of caudal branch of quadrate
0 - with a triangular depression; 1 - without depression
155. Dorsal contour of rostrum in lateral view
0 - straight or convex; 1 - concave
156. Teeth at anterior part of maxilla
0 - no prominent tooth; 1 - second or third alveoli enlarged; 2 - fourth or fifth alveoli enlarged
157. Skull roof
0 - rectangular and with a major transverse axis; 1 - square or rectangular and with a longitudinal dominant axis
158. Caudolateral lobe of squamosal
0 - not differentiated; 1 - squamosal showing a smooth lobe differentiated from the skull by a caudolateral groove
159. Anterior opening of cranio-quadrate passage in otic area (when cranio-quadrate canal is closed off)
0 - not expanded; 1 - opening expanded forming a caudal notch
160. Ventral border of exoccipital
0 - straight, and leaving posterior opening of cranio-quadrate passage visible in occipital view; 1 - convex and ventrally overhanging and obscuring posterior opening of cranio-quadrate passage from occipital view
161. Length from proximal articular facet of femur to distal end of fourth trocanter
0 - more than one third of total femoral length; 1 - one third or less of total femoral length
162. Largest mandibular teeth
0 - unique; 1 - double, generally third and fourth
163. Premaxillo-maxillar suture in palatal view
0 - acute; 1 - straight and orthogonal with the sagittal plane
164. Number of maxillary teeth
0 - ten or more;1 - less than ten
165. Naso-lachrymal suture
0 - nasal extensively contacts lachryma1; 1 - nasal and lachrymal do not contact or with a short contact
166. Articulation of medial process of articular and otoccipital
0 - absent; 1 - present
167. Internal edge of proximal ulna head
0 - concave; 1 - straight
168. Section of ulna shaft
0 - circular; 1 - compressed at least at distal end
169. Prefronto-frontal joint
0 - prefrontal overlaps frontal; 1 - frontal overlaps prefrontal; 2 - frontal and prefrontal with a interdigitate suture
170. Distal lateral condyle of humerus in posterior view
0 - projecting a sharp ridge towards shaft and delimiting a flat lateral plane; 1 - smooth
171. Lachrymal descending lateral process
0 - columnar; 1 - laminar
172. Lachrymal orbital contour
0 - facing laterally; 1 - facing laterodorsally
173. Cranial jugal branch
0 - as deep or slightly deeper than caudal branch; 1 - much deeper than caudal branch
174. Lateral surface of jugal in ventral view
0 - exposed lateral to maxilla, jugal outwardly bowed; 1 - not visible in ventral view, jugal straight
175. Palatal surface
0 - concave; 1 - plane
176. Occipital condyle
0 - caudally directed; 1 - ventrocaudally directed
177. Primary pterygoidean palate
0 - without parasagittal depressions; 1 - with deep parasagittal depressions on the external face of the palate
178. Deltopectoral crest of humerus
0 - partially visible in caudal view; 1 - hidden in caudal view
179. Ligamental pit below humeral head on posterior surface
0 - delimiting a ridge on its medial border; 1 - pit displaced laterally between humeral head and lateral tuberosity
180. Humeral shaft
0 - straight; 1 - sigmoidal, with a pronounced posterior curvature of shaft on proximal area of humerus
181. Proximal and distal head of humerus
0 - each twisted more than 30 degrees; 1 - each twisted less than 30 degrees
182. Inner distal condyle of humerus
0 - with a vertical extension of trochlea; 1 - transversely expanded
183. Palpebral ossification
0 - one; 1 - two; 2 - two fused

99. Neither surangular nor quadratojugal taking part in craniomandibular joint. [0-1]
102. Tooth crowns trapezoidal in buccal view. [0-1]
122. Glenoid surface of coracoid extended on a oblique plane, and the glenoid lip facing outwards and posteroventrally. [1-2]
132. Heterodonty of maxillary and dentary teeth. [0-1]
136. Palatal maxillary platform present, preventing contact between ectopterygoid and maxillary alveoli. [0-1]
138. Pterygoidean flanges bar-like. [0-1]
148. Rod-like coracoid shaft. [0-1]
153. Dorsal surface of retroarticular process facing dorsally or craniodorsally. [0-1]
176. Occipital condyle ventrocaudally directed. [0-1]
183. Two palpebral ossifications. [0-1]

Notosuchimorpha, new taxon

Definition: The most recent common ancestor of *Stolokrosuchus* and Notosuchiformes and all of their descendants.
Etymology: Greek, *morphe*, form; Notosuchia, referring to notosuchian-like groups.
Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (*Bootstrap*: 81; Bremer: 1).
3. Distance from anterior orbital edge to anterior contour of rostrum equal or longer than distance from anterior orbital edge to posterior parietal contour. [1-0]
11. Communication between oral and nasal cavities only by internal nares. [1-0]
18. Last maxillary tooth caudal to anterior edge of palatine fenestra. [1-0]
47. Quadratojugal spine at caudal margin of infratemporal fenestra. [0-1]
59. Vomer hidden by palatal branch of maxillae. [0-1]
60. Palatines meet on midline forming a secondary palate. [0-1]
63. Exoccipitals bounding foramen magnum. [1-0]
68. Basisphenoid shorter or equal to basioccipital. [1-0]
83. Dentary extends beyond tooth row and with a dorsal ascending projection. [0-1]
88. Splenials form a significant part of mandibular symphysis. [0-1]
100. Mesial and distal margin of tooth crowns without carinae or with carinae smooth or crenulated. [0-1]
105. Glenoid fossa of articular craniocaudally longer than articular surface of quadrate. [0-1]
114. Osteoderms with straight caudal edge. [0-1]
151. Mandibular symphysis long; dentary prolongs caudally to fourth alveoli. [0-1]

Notosuchiformes, new taxon

Definition: The most recent common ancestor of Uruguaysuchidae and Notosuchia and all of their descendants.
Etymology: Latin, *forma*, form, referring to notosuchian-like groups.
Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (*Bootstrap*: 83; Bremer: 2).
6. Premaxillo-maxillary suture vertical in lateral view. [1-0]
27. Parieto-postorbital suture present on dorsal surface of skull roof. [0-1]
29. Prefrontal pillars being solidly integrated, reaching palate. [0-1]
57. Basipterygoid processes absent or reduced to a narrow crista. [0-1]
58. Pterygoids caudally fused. [0-1]
62. Supraoccipital connects parietal at posterior edge of skull roof or is clearly exposed in dorsal surface of cranial roof. [0-1]
133. Less than five premaxillary teeth. [0-1]
156. Second or third maxillary alveoli enlarged. [0-1]
157. Skull roof is rectangular with a major transverse axis. [1-0]

Uruguaysuchidae Gasparini, 1971

Definition: The most recent common ancestor of *Uruguaysuchus* and all of its descendants.
Diagnosis: The members of this taxon possess the following synapomorphies (*Bootstrap*: $\leq$ 50; Bremer: 1).
1. Ornamentation of external surface of cranial dermal bones with circular or subpolygonal pits. [0-1]
22. Nasals do not reach the caudal edge of external nares. [0-1]
85. Post-caniniform dentary teeth almost homodont in size. [1-0]
101. Inflated roots of maxillary and dentary teeth, wider than in crowns. [0-1]
103. Ligual side of maxillary and dentary teeth with longitudinal depression affecting roots and crowns. [0-1]
134. Angular laterally displaced and overlapping articular, with surface for pterygoid muscle attachment facing laterally in ventral view. [0-1]

Terriasuchia new taxon

Definition: The most recent common ancestor of Notosuchia and *Comahuesuchus* and all of their descendants.
Etymology: Latin, *terrian*, referred to terrestrial habits; plus *souchos*, Greek for crocodile.
Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (*Bootstrap*: $\leq$ 50; Bremer: 1).
2. Smooth maxillary palatal surface. [1-0]
3. Distance from anterior orbital edge to anterior contour of rostrum shorter than distance from anterior orbital edge to posterior parietal contour [0-1]

18. Last maxillary tooth cranial to anterior edge of palatine fenestra. [0-1]
39. Quadratojugal extends anteriorly forming part of dorsal edge of infratemporal bar. [0-1]
41. Supratemporal fenestra relatively short surrounded by a flat and extended skull roof. [0-1]
118. Styliform process of coracoid absent. [0-1]
152. Craniocaudal length of retroarticular process much longer than craniocaudal length of articular glenoid fossa. [0-1]
164. Less than ten maxillary teeth. [0-1]
167. Internal edge of proximal ulna head straight. [0-1]
176. Occipital condyle ventrocaudally directed. [0-1]

Notosuchia Gasparini, 1971

Definition: The most recent common ancestor of Ziphosuchia and Peirosaurimorpha and all of their descendants.
Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (*Bootstrap*: 68; Bremer: 1).
27. Parieto-postorbital suture absent on dorsal surface of skull roof. [1-0]
46. Infratemporal fenestrae facing laterodorsally. [0-1]
47. Absence of quadratojugal spine at caudal margin of infratemporal fenestrae. [1-0]
48. Quadratojugal contacts postorbital widely. [1-0]
49. Quadratojugal contacts postorbital. [1-0]
63. Exoccipitals are the only bones surrounding foramen magnum. [0-1]
158. Caudolateral lobe of squamosal is not differentiated. [1-0]
165. Nasal extensively contacts lachrymal. [1-0]

Peirosaurimorpha, new taxon

Definition: The most recent common ancestor of Candidodontidae and Peirosauriformes and all of their descendants.
Etymology: Greek, *morphe*, form, referring to peirosaurid-like groups.
Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (*Bootstrap*: 71; Bremer: 1).
1. Ornamentation of external surface of cranial dermal bones with circular or subpolygonal pits. [0-1]
18. Last maxillary tooth caudal to anterior edge of palatine fenestra.[1-0]
30. Prefrontal pillars when integrated in palate transversally expanded in their dorsal half and columnar ventrally. [0-1]
34. Jugal portion of postorbital bar medially displaced and a ridge separates postorbital bar from lateral surface of jugal. [0-1]
35. Caudal tip of ectopterygoidean-jugal caudally placed and surpassing postorbital bar. [0-1]
36. Ectopterygoid contacts postorbital on medial side of postorbital bar. [0-1]
81. Dentary transverselly expanded, almost as wide as high, and with convex lateroventral surface. [0-1]
87. Proximal articular head of tibia with one concave articulating area. [0-1]
93. Caudal edge of angular ascends surpassing the articular glenoid cavity. [0-1]
111. Dorsal osteoderms with a pitted surface. [0-1]
130. Lateral contour of rostrum with constrictions and with a sinusoidal aspect in dorsal view. [0-1]
132. Heterodonty of maxillary and dentary teeth. [0-1]
147. Medial shelf of retroarticular process facing dorsally. [0-1]
175. Plane palatal surface. [0-1]
177. Primary pterygoid palate without parasagittal depressions. [1-0]
181. Proximal and distal ends of humerus each turned less than 30 degrees. [0-1]

Candidodontidae, new taxon

Definition: The most recent common ancestor of *Candidodon* and *Mariliasuchus* and all of their descendants.
Etymology: Referring to *Candidodon*-like groups.
Diagnosis: The members of this taxon possess the following synapomorphies (*Bootstrap*: 85; Bremer: 2).
3. Rostral length distance from anterior orbital edge to anterior contour of rostrum equal or longer than distance from anterior orbital edge to posterior parietal contour. [1-0]
41. Supratemporal fenestrae relatively large, covering most of surface of skull roof. [1-0]
44. Craniocaudal axis of quadrate inclined less than 45 degrees to the horizontal. [0-1]
63. Exoccipitals and supraoccipital bounding foramen magnum. [1-0]
85. Postcaniniform dentary teeth almost homodont in size. [1-0]
88. Splenial not involved in mandibular symphysis, splenials just touch or do not contact each other. [1-0]
99. Surangular and quadratojugal taking part in craniomandibular joint. [0-1]
134. Angular laterally displaced and overlapping articular, with surface for pterygoid muscle attachment facing laterally in ventral view. [0-1]
137. No septated internal nares. [0-1]
144. Ventral edge of external mandibular fenestra with a depression bounding this edge. [0-1]
159. Anterior opening of cranio-quadrate passage expanded, forming a caudal notch. [0-1]

163. Premaxillo-maxillary suture straight and orthogonal with the sagittal plane in palatal view. [0-1]
170. Distal lateral condyle of humerus smooth in posterior view. [0-1]

Peirosauriformes, new taxon

Definition: The most recent common ancestor of *Araripesuchus* and Peirosauroidea and all of their descendants.
Etymology: Latin, *forma*, form, referring to peirosaurid-like groups.
Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (*Bootstrap*: 64; Bremer: 1).
20. Size of teeth with waves of size variation along maxillary toothrow. [0-1]
125. Ligamental depression on anterior surface of humerus displaced laterally toward the border of the shaft and located lateral to humeral head. [0-1]
128. Radius longer, at least 1/3 of ulnar length [0-1]
139. Depression on primary pterygoid palate posterior to internal nares narrower than palatine bar between palatal fenestrae. [0-1]
140. Postmaxillary internal nares absent. [0-1]
146. Single ectopterygoidean medial descendent branch. [0-1]
149. The femoral shaft is twisted so that the proximal and distal articular faces are inclined at about 60º to each other. [0-1]
150. Proximal and distal ends of radius almost equally expanded. [1-0]
164. Ten or more maxillary teeth. [1-0]

Peirosauroidea, new taxon

Definition: The most recent common ancestor of Itasuchidae and Peirosauridae and all of their descendants.
Etymology: Greek, *iedes*, like, referring to peirosaurid-like groups.
Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (*Bootstrap*: 51; Bremer: 1).
8. Premaxillo-maxillary suture zigzag-shaped in lateral view. [0-1]
13. Absence of a foramen at premaxillo-maxillary suture in lateral view. [0-1]
14. Premaxillo-maxillary notch present. [0-1]
38. Quadratojugal is not exposed in lateral view. [0-1]
48. Quadratojugal contacts postorbital at a point, quadratojugal is dorsally acute, or there is no contact at all. [0-1]
62. No supraoccipital exposure on cranial roof, parietals contact on occiput avoiding dorsal exposure of supraoccipital. [1-0]
67. Basisphenoid almost hidden from ventral view and covered by pterygoid and basioccipital in ventral view. [0-1]
74. Infratemporal fenestra much longer than deep. [0-1]
98. Coronoid long, anteriorly extended. [0-1]
110. Presacral dorsal osteoderms flat. [0-1]
113. Osteoderms without anterior projection. [0-1]
135. Posterior branch of quadrate at least as long as broad. [1-0]
153. Dorsal surface of retroarticular process facing dorsal or craniodorsally. [0-1]
157. Skull roof square or rectangular and with a longitudinal dominant axis. [0-1]
165. Nasal and lachrymal do not contact or with a short contact. [0-1]
171. Lachrymal lateral descending process with a laminar aspect. [0-1]

Itasuchidae new taxon

Definition: The most recent common ancestor of *Itasuchus* and *Malawisuchus* and all of their descendants.
Etymology: referring to *Itasuchus*-like groups.
Diagnosis: The members of this taxon possess the following synapomorphies (*Bootstrap*: 57; Bremer: 1).
47. Quadratojugal spine at caudal margin of infratemporal fenestra. [0-1]
81. Dentary compressed, formed by almost vertical lateral and medial laminae. [1-0]
87. Proximal articular head of tibia with two concavities separated by a crest. [1-0]
101. Roots of maxillary and dentary teeth inflated, wider than crowns. [0-1]
102. Trapezoidal shape of tooth crowns in buccal view. [0-1]
111. Presacral dorsal osteoderms smooth or made of ridges and grooves. [1-0]
130. Straight lateral contour of rostrum in dorsal view. [1-0]
140. Postmaxillary internal nares. [1-0]
163. Premaxillo-maxillary suture straight and orthogonal with the sagittal plane in palatal view. [0-1]
175. Concave palatal surface. [1-0]

Peirosauridae Gasparini, 1982

Definition: The most recent common ancestor of *Peirosaurus* and Lomasuchinae and all of their descendants.
Etymology: referring to *Peirosaurus*-like groups.
Diagnosis: The members of this taxon possess the following synapomorphies (*Bootstrap*: 69; Bremer: 1).
3. Distance from anterior orbital edge to anterior contour of rostrum equal to or longer than distance from anterior

orbital edge to posterior parietal contour. [1-0]
5. Rostral section wider than deep. [0-1]
83. Dentary extends caudally up to end of tooth row. [1-0]
89. Splenials behind symphysis broad and robust. [0-1]
96. Anterior projection of surangular unique and acute in lateral view. [0-1]
99. No surangular and quadratojugal taking part in craniomandibular joint. [0-1]
133. Five premaxillary teeth. [1-0]
174. Lateral surface of jugal not visible in ventral view, jugal straight. [0-1]
176. Occipital condyle caudally directed. [1-0]

Lomasuchinae, new taxon

Definition: The most recent common ancestor of *Lomasuchus* and Mahajangasuchini and all of their descendants.
Etymology: referring to *Lomasuchus*-like groups.
Diagnosis: The members of this taxon possess the following synapomorphies (*Bootstrap*: 74; Bremer: 1).
84. Lateral contour of dentary sigmoidal in dorsal view. [0-1]
137. No septated internal nares. [0-1]
151. Mandibular symphysis short. [1-0]
162. Largest mandibular teeth double, generally the third and the fourth. [0-1]

Mahajangasuchini, new taxon

Definition: The most recent common ancestor of *Mahajangasuchus* and *Uberabasuchus* and all of their descendants.
Etymology: Referring to *Mahajangasuchus*-like groups.
Diagnosis: The members of this taxon possess the following synapomorphies (*Bootstrap*: 78; Bremer: 1).
6. Premaxillo-maxillary suture caudodorsally directed in lateral view. [0-1]
13. Presence of a foramen at premaxillo-maxillary suture in lateral view. [1-0]
27. Parieto-postorbital suture present on dorsal surface of skull roof. [0-1]
43. Contour of squamosal curved in dorsal view. [1-0]
71. Jugal participation in antorbital fenestra. [1-0]
94. Caudal edge of surangular slopes ventrally. [1-0]

Ziphosuchia Ortega, Gasparini, Buscalioni and Calvo, 2000

Definition: The most recent common ancestor of *Notosuchus*, *Libycosuchus*, and Baurusuchoidea and all of their descendants.
Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (*Bootstrap*: 69; Bremer: 1).
11. Oral cavity communicates with nasal cavity through palatal perforations (naso-oral fenestrae), besides internal nares. [0-1]
15. Last premaxillary alveolus is the largest of the premaxillary tooth row. [0-1]
53. Medial quadrate condyle expands ventrally. [0-1]
92. Transversal section of splenial convex. [0-1]
127. Radius as long as wide (considering its proximal width as reference). [0-1]
148. Coracoid shaft rod-like. [0-1]
161. Length from proximal articular facet of femur to distal end of fourth trocanter more than one third of total femoral length. [1-0]

Notosuchidae Dollo, 1914

Definition: The most recent common ancestor of *Notosuchus* and all of their descendants.
Diagnosis: Monophyly of this taxon is supported by the following synapomorphies.
12. Naso-oral fenestra formed by premaxilla. [1-0]
19. Teeth set disposed in a groove. [0-1]
27. Parieto-postorbital suture present on dorsal surface of skull roof. [0-1]
51. One quadrate fenestra. [0-1]
59. Vomer exposed on palate between premaxillae and maxillae. [1-0]
91. Emergence of the mandibular branch of trigeminus nerve in the medial side of mandible enclosed within symphysis. [0-1]
102. Tooth crown trapezoidal in buccal view. [0-1]
152. Craniocaudal length of retroarticular process less than craniocaudal length of articular glenoid fossa. [1-0]
156. No prominent teeth at anterior part of maxilla. [1-0]

Baurusuchoidea, new taxon

Definition: The most recent common ancestor of Baurusuchidae and Sebecidae and all of their descendants.
Etymology: Greek, *iedes*, like, referring to baurusuchid-like groups.
Diagnosis: Monophyly of this taxon is supported by the following synapomorphies (*Bootstrap*: 96; Bremer: 1).
3. Distance from anterior orbital edge to anterior contour of rostrum at least twice than distance from anterior orbital edge to posterior parietal contour. [1-0]
8. Premaxillo-maxillary suture zigzag shaped in lateral view. [0-1]
14. Presence of a premaxillo-maxillary notch. [0-1]
24. Nasals caudally separated by an anterior sagittal projection of frontal. [0-1]
38. Quadratojugal not exposed in lateral view. [0-1]
42. Outer surface of squamosal dorsally oriented. [0-1]

69. Antorbital fenestra absent or reduced to a tiny foramina. [0-1]
89. Splenials broad and robust behind symphysis. [0-1]
100. Mesial and distal margin of tooth crowns with denticulate carinae. [1-0]
105. Glenoid fossa of articular craniocaudally similar to articular surface of quadrate. [1-0]
106. Tip of maxillary and dentary tooth crowns caudally curved. [1-0]
140. Postmaxillary internal nares absent. [0-1]
171. Lachrymal descending lateral process laminar. [0-1]
173. Cranial jugal branch much deeper than caudal one. [0-1]
174. Lateral surface of jugal not visible in ventral view, jugal straight. [0-1]

Baurusuchidae Price, 1945

Definition: The most recent common ancestor of *Baurusuchus* and *Stratiotosuchus* and all of their descendants.
Diagnosis: The members of this taxon possess the following synapomorphies.
74. Infratemporal fenestrae much longer than deep. [0-1]
86. Sigmoidal outline of dentary tooth row in dorsal view. [0-1]
90. Big slot-like foramen intramandibularis oralis [0-1]
137. Internal nares not septated. [0-1]
143. Caudal edge of internal nares caudal to the rear edge of palatine fenestra. [0-1]
145. Lateral surface of anterior branch of jugal with a pronounced triangular depression. [0-1]
157. Skull roof square or rectangular shaped and with a longitudinal dominant axis. [0-1]

Sebecidae Colbert, 1946

Definition: The most recent common ancestor of *Sebecus* and *Libycosuchus* and all of their descendants.
Diagnosis: The members of this taxon possess the following synapomorphies (*Bootstrap*: 53; Bremer: 1).
13. Foramen at premaxillo-maxillary suture absent in lateral view. [0-1]
67. Basisphenoid in ventral view almost excluded and hidden by pterygoid and basioccipital. [0-1]
85. Post-caniniform dentary teeth almost homodont in size. [1-0]
94. Caudal edge of surangular slopes ventrally. [1-0]
146. Single ectopterygoid descending branch. [1-0]
164. Ten or more maxillary teeth. [1-0]

Palaeoecology and Palaeobiogeography of the Peirosauridae

The cranial similarities shown by recent and fossil crocodilians were considered by Iordansky (1973) to be due primarily to convergence in the feeding mode. Analysing recent crocodiles he suggested that the undulation of the jaw margin (festooning) and the pseudoheterodonty belong to a functional category that allows the crocodile to hold the captured prey more firmly between the jaws. Similarly, *Uberabasuchus* presents an undulation on the jaw margin, a true heterodonty and crenulated teeth. These features are related to the mode of capturing large prey. The morphology of jaw and teeth suggests that it could be related to the ability to grab firmly relatively large animals (Fig. 8). The lateral compression of its rostrum could be interpreted, as suggested by Buffetaut (1982) for the Baurusuchidae, as a mechanism to increase skull resistance during biting. The pointed teeth, compressed with crenulated borders could be used to perforate and to carve the prey.

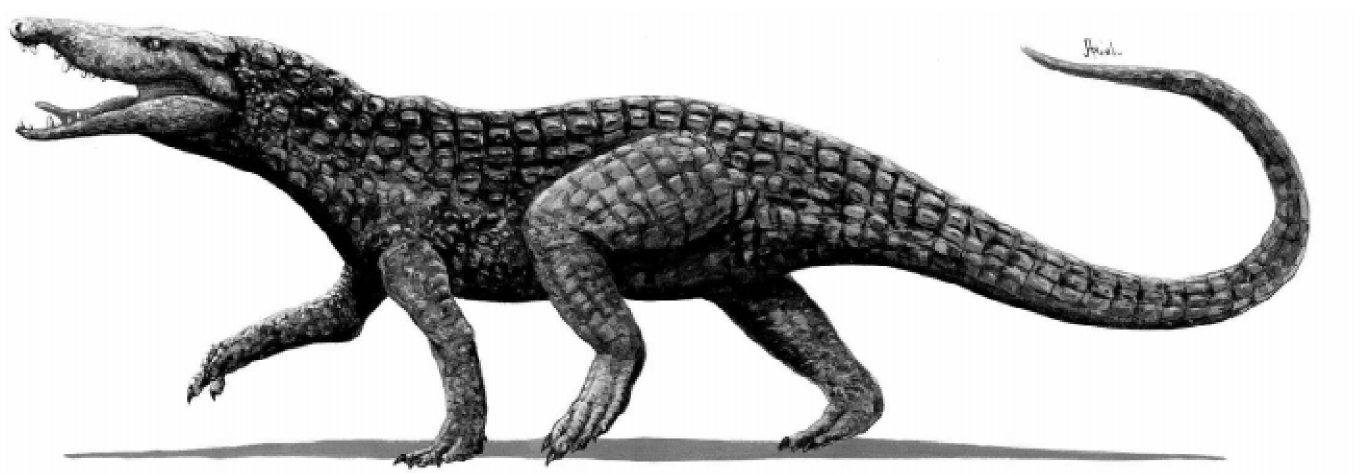

Fig. 8. Restoration of *Uberabasuchus terrificus* gen. et sp. nov. (art by Ariel Milani Martine).

The similarities of the vertebrate faunas of Gondwana led to the assumption of a South American-African connection until the Aptian (Buffetaut, 1981, 1982; Buffetaut and Taquet, 1979). A land bridge may have existed at least up to the Albian-Cenomanian (Calvo and Salgado, 1996). Notwithstanding the opening of the South Atlantic, Buffetaut (1982) also considered valid the possibility of intermittent faunal interchange after the Albian, through a chain of islands between Africa and South America or even a connection through Antarctica and Australia.

However, biogeographic studies concerning the distribution of terrestrial crocodylomorphs have showed conflicting results. Ortega et al. (2000), through the analysis of araripesuchids, considered that phylogenetically related taxa do not necessarily presuppose the existence of a continental nexus by the Aptian, and the archosaurian fauna could have been previously isolated in each continent. These authors postulated that the distribution of the notosuchids and araripesuchids does not support the hypothesis of terrestrial connections between South America and Africa after the Albian. Nevertheless, the mesoeucrocodylian *Mahajangasuchus* described by Buckley and Brochu (1999) from the Late Cretaceous of Maevarano Formation of Madagascar indicates close affinity with peirosaurids. This was considered evidence that Madagascar and South America were connected via Antarctica well into the Late Cretaceous, but were isolated from Africa by the Mozambique Channel and a widening southern Atlantic Seaway by that time. This idea that Madagascar and South America were physically and biotically linked, perhaps through Antarctica, until the Late Cretaceous, was reinforced by the phylogenetic analysis of the Malagasy crocodyliform *Simosuchus*, a possible sister-group of *Uruguaysuchus* (Buckley et al., 2000).

Buffetaut (1982) claimed that the evolution and radiation of these terrestrial groups in South America was established during the Late Jurassic and Early Cretaceous in ecological niches free of mammal-like reptiles and first mammals. The separation of South America and Africa through a marine barrier allowed the post-Aptian development, in each continent, of different families of Notosuchia, all of them derived from primitive Lower Cretaceous Uruguaysuchidae. The marine barrier was probably a very restrictive factor to the dispersal of the terrestrial Notosuchia and allowed the evolution of specialized crocodylomorphs such as the sebecosuchians and peirosaurids.

It has been postulated that the Bauru crocodylomorphs make up a diversified and endemic fauna (Bertini, 1993). Musacchio (2000) based on charophyte distribution, proposed that there was a break-down of the biogeographic isolation between the southern and northern regions of South America during the Aptian. This can be considered as the result of the breakup and separation of South America from Africa. The drainage history of South America as shown by Potter (1997) was subject to tectonic control first by regional uplifts and associated aulacogens and later (100 Ma) by colliding plates, which reversed paleoslopes on much of the South American platform. During the Lower Cretaceous, the drainage in Patagonia (including Magallanes and Neuquén basins) was towards the paleoPacific and sediment source areas were to the East and North. A compressional tectonic event, related to the South America-Africa drifting, reversed the slope to the southeast, allowing a distinct connection of the fluvial network. The connections of the drainage system of southern Argentina and central South America (e.g., Bauru Basin) from the Aptian to the Late Cretaceous probably allowed the interchange of the crocodiles and the occurrence of a common species of Peirosauridae (*Peirosaurus tormini*) both in Argentina and Brazil. *Uberabasuchus terrificus* and *Lomasuchus palpebrosus* could be species established previous to this faunal interchange. The peirosaurids probably show a wide distribution, also occurring in the Late Cretaceous of Madagascar (Buckley and Brochu, 1996, 1997, 1999); they may represent migrants through a dispersal route that supposedly involved Antarctica and Australia. Consequently, it seems to be premature to consider the Bauru crocodylomorphs as endemic. This issue should be reviewed when a better understanding of the faunal distribution among South America and Africa during the Late Cretaceous is achieved.

Legend

af - antorbital fenestra
ang -angular
art – articular
aso – anterior supraorbital
bs - basisphenoid
d - dentary
en - external nares
ex - exoccipital
f - frontal
j - jugal
l - lacrimal
ltf - laterotemporal fenestra
m - maxilla
mf - mandibular fenestra
n - nasal
o - orbit
p - parietal
pf - prefrontal
pl - palatine

pm - premaxilla
po - postorbital
pt - pterygoid
pap - postarticular process
pob - postorbital bar
pso – posterior supraorbital
q - quadrate
qj – quadratojugal
rb – rostral
sa - surangular
so - supraorbital
sp - splenial
sq - squamosal
stf - supratemporal fenestra

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