

A NEW GIANT *PURUSSAURUS* (CROCODYLIFORMES, ALLIGATORIDAE) FROM THE UPPER MIOCENE URUMACO FORMATION, VENEZUELA

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SYNOPSIS Fossil Crocodylia are taxonomically diverse in South America, particularly in the upper Miocene Urumaco Formation (Venezuela). Among them is the giant alligatoroid *Purussaurus*, previously known from the upper Miocene Solimões Formation in Brasil (*P. brasiliensis*) and the middle Miocene of La Venta in Colombia (*P. neivensis*). New specimens of Crocodylia from the Urumaco Formation are described and a new species, *Purussaurus mirandai*, erected. This is characterised by a large, elongate and extremely flat skull, a very large narial opening comprising almost 60% of rostral length and a large incisive foramen that extends anteriorly between the fossae for the first mandibular teeth. *Purussaurus mirandai* sp. nov. was the largest predator in the swampy environments and represented the top trophic level in the Urumaco assemblage. A phylogenetic analysis of 164 characters in 68 ingroup crocodile taxa supported the association of *P. neivensis* and *P. mirandai* with five synapomorphies and confirmed the sister-group relationship of the genus with the Nettosuchidae.

KEY WORDS Urumaco, Miocene, Alligatoridae, *Purussaurus*

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INTRODUCTION

South American Alligatoridae have traditionally been considered immigrants from North America (Gasparini 1996).

They form a well-supported monophyletic group, the Caimaninae, diagnosed as a stem-group of species more closely related to *Caiman crocodylus* than to *Alligator mississippiensis* (Brochu 1999), which includes many of the Tertiary

records of Crocodyliformes from South America. The living fauna includes the large-sized *Melanosuchus niger*, from the Amazon River Basin, and smaller forms with more terrestrial habits, such as *Paleosuchus*. In addition, there are, in South America, three living caiman species: *Caiman latirostris*, *C. crocodylus* and *C. yacare* (Carvalho 1951; Thorbjarnarson 1992).

The geological record of caimans show them to have been diverse in both species and ecological adaptation. The oldest records from South America are from the Palaeocene of Rio de Janeiro State, Brasil and consist of fragments from the Itaboraí Basin (Paula-Couto 1970; Gasparini 1996). One of the oldest taxa formally described is *Necrosuchus ionensis* Simpson, 1937 from the Palaeocene Salamanca Formation of Chubut, Argentina. This species was originally placed in the North American genus *Leidyosuchus*, but more recently affinities with the Crocodylidae (Langston 1965) and, perhaps, Caimaninae (Brochu 1997) have been suggested. This and other records from Argentina are too fragmentary to provide major insights into the early evolution of the group (Langston 1965; Gasparini 1981). Perhaps the Palaeocene–Eocene *Eocaiman cavernensis* Simpson, 1933 from Chubut in Argentina and the middle Miocene of Colombia (Langston 1965; Gasparini 1996) is the most basal form of this clade (Brochu 1999, 2000, 2003).

Oligocene records are mostly fragmentary. Noteworthy is *Caiman tremembensis* Chiappe (1988), from the Tremembé Formation, São Paulo, Brasil, one of the smallest known South American alligatorids. Another Oligocene form is *Balanerodus longimus* Langston (1965), also reported from the Miocene La Victoria Formation, Honda Group of Colombia (Langston & Gasparini 1997). The phylogenetic position of this species is uncertain.

The Miocene–Pliocene has, without doubt, the richest crocodyl diversity in South America. There are several species known from three Formations: La Venta (Colombia), Solimões (Brasil) and Urumaco (Venezuela). These formations preserve mostly fluvial–lacustrine deposits (as well as marine ones in the case of Urumaco) and share most of the genera in common. From the Solimões Formation the following taxa have been reported: *Caiman brevirostris* Souza-Filho, 1987, *C. niteroiensis* Souza-Filho & Bocquentin-Villanueva, 1991, *Mourasuchus amazonensis* Price, 1964, *M. nativus* (Gasparini 1985; Bocquentin-Villanueva & Souza-Filho 1990) and *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892, as well as an indeterminate species of *Caiman* with dorsal expansions with the form of horns in the post-orbital and squamosal bones (Jonas Pereira de Souza Filho, pers. comm.). From La Venta, the following taxa have been reported: *Balanerodus longimus* (Langston & Gasparini 1997), *Caiman latirostris* (= *Caiman* cf. *lutescens* of Langston 1965; Gasparini & Baez 1975), *Purussaurus neivensis* (Mook 1941; Langston 1965); *Mourasuchus atopus* (Langston 1965) and *Eocaiman* sp. (Langston 1965; Langston & Gasparini 1997), as well as indeterminate caimans and alligatorids (Langston 1965) and several gavialids and crocodyles (Langston 1965; Gasparini 1996; Langston & Gasparini 1997).

In addition fragmentary records related to *Caiman* of Miocene–Pliocene age are known from the Entrerrios Formation, Paraná, Argentina (Rovereto 1912; Patterson 1936; Gasparini & Baez 1975; Langston & Gasparini 1997). *Mourasuchus nativus* has also been reported from this deposit

(Gasparini 1985), as well as from the Solimões Formation. The probable occurrence of *Purussaurus* in Peru (Loreto Department), close to the boundary with the State of Acre, is cited by Langston (1965) and Salas & Urbina (2003).

The Upper Miocene Urumaco Formation (Falcón State, Venezuela) has yielded an astonishingly diverse crocodylian fauna, with several representatives of alligatoroid, crocodyloid and gavialoid (Aguilera 2004). All living morphotypes (Brochu 2001), including blunt, slender and generalised-snout forms, are present together with forms having excessively broad snouts, a morphotype extinct today. The blunt-snout forms are represented by the small *Caiman brevirostris* Souza Filho, 1987 while generalised-snout forms include *Melanosuchus fischeri* Medina, 1976. The slender-snout forms, however, are the most diverse, with five gavialoid species: *Gryposuchus colombianus* (Langston, 1965); *G. jessei* Gürich, 1912; *Hesperogavialis cruxenti* Bocquentin-Villanueva & Buffetaut, 1981; *Ikanogavialis gameroi* Sill, 1970 and *Brasilosuchus mendesi* Souza Filho & Bocquentin-Villanueva, 1989. Among these slender forms, some, like *Ikanogavialis*, are considerably longirostrine. This morphotype also includes two distinct specimens traditionally referred to the tomistomid *Thecachampsia* (Aguilera 2004). Another morphotype includes the Nettosuchids, an alligatoroid group, also co-occurring in Brasil, Colombia and Argentina (Gasparini 1996), characterised by having a duck-faced skull, extremely broad, long and dorsoventrally compressed rostrum with diminute teeth and a fragile mandibular symphysis. Netosuchids are represented in the Urumaco Formation by *Mourasuchus arendsi* Bocquentin-Villanueva, 1984.

The Urumaco assemblage, together with the late Miocene Solimões Formation in Brasil and the middle Miocene of La Venta in Colombia, are notable for their high diversity and disparity of crocodylian forms. Usually the number of sympatric forms are much fewer (Brochu 2001). In this paper we describe a new form that represents yet another morphotype for Urumaco, increasing the extraordinary ecomorphological diversity of this fauna.

This form was initially reported by Bocquentin-Villanueva *et al.* (1989), who recorded it as a large *Purussaurus* skull and associated mandible but left it in open nomenclature, because too little was known about it at that time. We recently had the opportunity to examine these specimens along with a nearly complete skull with associated mandible and several post-cranial remains of *Purussaurus* that had recently been collected. Comparisons of these additional fossils with *P. brasiliensis* Barbosa-Rodrigues, 1892 from the upper Miocene Solimões Formation in Brasil and *P. neivensis* (Mook, 1941) from the middle Miocene of La Venta in Colombia, show that the Urumaco *Purussaurus* is taxonomically distinct from both previously described species.

MATERIALS AND METHODS

The institutional abbreviations used in this paper are as follows: **AMU-CURS**, Alcaldía del Municipio Urumaco, Venezuela; **DGM**, Divisão de Geologia e Mineralogia do Departamento Nacional de Produção Mineral, Rio de Janeiro, Brasil; **INGEOMINAS**, Instituto de Geología y Minería, Bogotá, Colombia; **MCC**, Museo de Ciencias Naturales

Table 1 Measurements of the giant South American fossils alligatorids.

Measurements (mm)	<i>Purussaurus mirandai</i> sp. nov.		<i>Purussaurus brasiliensis</i>				<i>Purussaurus neivensis</i>	
	UNEFM-CIAAP	AMU-CURS	UFAC	UFAC	UFAC	DGM	UCMP	INGEOMINAS
	1369	1260	1118	1403	4770	527-R	39704	DHL-45
Maximal skull length	1260			1400			801	
Basal skull length	1170	1030		1300			857	418
Snout length	770			910			558	256
Interorbital width (anterior)	595			740	610		444	232
Maximal skull width	685	680		820			535	233
Orbital length	170			195			148	88
Orbital width	130							
Infratemporal fenestrae length	160							
Infratemporal fenestrae width	90							
Supratemporal fossae length	86							
Supratemporal fossae width	55							
Supratemporal fenestrae length	37							
Supratemporal fenestrae width	33							
Interorbital length	145			170			83	33
Skull table width	280			345			201	120
Occipital condyle width	55			90			58	38
Parietal to basioccipital height	174			210				
Palatine fenestra	320			330			227	111
Width between palatine fenestra	148			220				56
Maximal mandible length	1450	1260	1595			1750		
Mandible symphysis length	210	170	200			270		
Mandibular symphysis width	120	80	130					
Height of mandible at angular level		290						
External mandibular fenestra length		210						
External mandibular fenestra height		98						
Humero total length	470							
Femur total length	510							

de Caracas, Venezuela; **MCZ**, Museum of Comparative Zoology, Harvard University, USA; **UFAC**, Universidade Federal do Estado de Acre, Rio Branco, Brasil; **PUC-MG**, Pontificia Universidade Católica de Minas Gerais, Belo Horizonte, Brasil; **UCV**, Universidad Central de Venezuela; **UNEFM-CIAAP**, Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela.

Specimens were collected during several expeditions to the Urumaco Formation between 1958 and 2003 by teams from the MCZ (B. Patterson), UCV (J. Royo-Gómez), UNEFM (O. Aguilera), UFAC (J. Bocquetin-Villanueva) and AMU (R. Sánchez). The fossils are a three-dimensional articulated skull and mandibles and disarticulated and usually broken postcranial bones obtained individually from surface exposures in the field. Preservation ranges from near perfect to badly abraded or broken, normally covered with a hard gypsite layer. Matrix surrounding Urumaco specimens varies from fine, loose sand to grey or brown often limey claystones, which were removed during excavation with shovel, hammer and brushes. Adhesive sediments required softening with water and manual cleaning with fine-tipped dental tools. Some broken but clearly associated specimens were reconstructed.

Comparative materials that were studied included *Purussaurus brasiliensis* (UFAC 1118 (mandible), UFAC 1403 (complete skull), UFAC 1773 (left and right premaxilla), UFAC 4770 (incomplete skull) and DGM 527-R (mandible)) and *P. neivensis* deposited in INGEOMINAS (DHL-45 (nearly complete skull)). Measurements were made on overall specimen size and, as preservation allowed, landmark-based linear dimensions for proportional (shape) com-



Figure 1 Location of the sampling sites of El Mamón, Tío Gregorio, Corralito, El Hatillo and El Picache, all north of the town of Urumaco, Falcón State, northwestern Venezuela.

parisons among species. Measurements were taken with vernier calipers and dividers, rounded to nearest mm (Table 1).

GEOLOGICAL SETTING

The sample area (Fig. 1) includes the following named localities: El Mamón, Tío Gregorio, Corralito and El Hatillo,

all north of the town of Urumaco, Falcón State, northwestern Venezuela. Specimens were obtained from the middle and upper members of the Urumaco Formation.

The middle member of the Urumaco Formation consists mostly of claystone and sand. The grey claystone yields microfossils and the brown claystone contains vertebrate remains such as reptiles, mammals, marine and freshwater fish, as well as coprolites and wood (Díaz de Gamero & Linares 1989; Aguilera 2004). The sandy beds range from shelly sandstones to consolidated coquina limestone. In the lower half of this middle member there is an abundant and diverse marine fish and mollusc fauna in a sandy matrix. The palaeoenvironments are interpreted as inner sub-littoral and coastal lagoon with riverine and estuarine influence (Díaz de Gamero 1996; Aguilera 2004).

The upper member of the Urumaco Formation also comprises grey to brown, often limey claystones with thin intercalated and locally shelly sandstones. The uppermost layer is referred to as the 'capa de tortugas' because of its abundant remains of *Bairdemys* turtles (Díaz de Gamero & Linares 1989). Several localities and levels have concentrations of vertebrate fossils. The vertebrate fauna includes marine, estuarine and freshwater fishes, terrestrial, freshwater and marine turtles and crocodylians and terrestrial and aquatic/semiaquatic mammals (Sánchez-Villagra *et al.* 2003; Aguilera 2004). The palaeoenvironments were tropical near-shore marine to low coastal savannas with freshwater rivers.

For additional information about these geological units see Ministerio de Energía y Minas (1997). A complete list of the fossil fauna from the Urumaco Formation has been recently summarised in Sánchez-Villagra *et al.* (2003) and Aguilera (2004). A late Miocene age for the Urumaco Formation is indicated by foraminiferans, while the mammals suggest a South American land mammal age between Chasicocoan and Huayquerian (Díaz de Gamero & Linares 1989), or approximately 9 Ma (Marshall & Sempere 1993).

SYSTEMATIC PALAEOLOGY

CROCODYLIFORMES (Benton & Clark, 1988)

ALLIGATORIDAE Gray, 1844

PURUSSAURUS Barbosa-Rodrigues, 1892

TYPE SPECIES. *Purussaurus brasiliensis* Barbosa-Rodrigues 1892.

DIAGNOSIS. Giant alligatorids with enlarged and wide skull; snout tip rounded and ornamented with coarse reticulating ridges and pits; long and wide narial aperture surrounded by a large narial fossa formed by developed rostral canthi that extend posteriorly to the prefrontal–frontal contact; oval incisive foramen entirely surrounded by the premaxillae; nasal and lacrymal bones not in contact; large supratemporal fenestra; squamosal high and long posteriorly; nasal and frontal bones separated by the prefrontal bones; posterior dorsal margin of the skull table (squamosal and supraoccipital) strongly concave.

REMARKS. This genus was erected by Barbosa-Rodrigues (1892), with type species *Purussaurus brasiliensis*, on the basis of a fragmented mandible from the Amazon Purus river in Brasil. However, his holotype was subsequently lost

(Price 1967). Gervais (1876) had earlier described the species *Dinosuchus terror* based on a large vertebra collected from the Amazon. Mook (1921) subsequently described a large Colombian alligatorid mandible as *Dinosuchus neivensis* and a deformed Amazon symphysis toothed mandible (Langston 1965; Price 1967) as *Brachygnathosuchus brasiliensis*. Nopcsa (1924), however, recognised that the three taxa (*Brachygnathosuchus brasiliensis*, *Purussaurus brasiliensis* and *Dinosuchus neivensis*) were synonymous, keeping *Purussaurus* as the senior synonym by date priority. Langston (1965) reviewed the Colombian specimens and concluded that *Dinosuchus terror* is a *nomen vanum* and renamed the Colombian species *Caiman neivensis*. Patterson (1936, 1943) recognised *Purussaurus* as a synonym of *Caiman*. More recently, Bocquentin-Villanueva *et al.* (1989) compared an additional skull and associated mandible from the Urumaco Formation (Venezuela) and the Solimões Formation (Brasil) and re-erected the genus *Purussaurus* with the two species *P. brasiliensis* Barbosa-Rodrigues, 1892 and *P. neivensis* (Mook, 1941).

Purussaurus mirandai sp. nov. (Figs 2–4, 7 A–C)

1989 *Purussaurus* sp. Bocquentin-Villanueva *et al.*: 427–438, figs 1, 2.

2003 *Purussaurus* sp. Sánchez-Villagra *et al.*: 15.

2004 *Purussaurus* sp. Aguilera: 90–92.

ETYMOLOGY. After Francisco de Miranda, from whom the University in Coro is named, in recognition of his historical contributions to the Hispano American independence.

TYPE SPECIMENS. Holotype: UNEFM-CIAAP-1369, a complete skull with associated mandibles, femur and ischium, collected in 1987 by J. Bocquentin-Villanueva at El Hatillo. Paratypes: AMU-CURS-135 (a skull with associated mandibles), El Hatillo; MCC URU-115-72V (premaxilla and maxilla), El Picache; MCC URU-157-72V (dentary), Tío Gregorio; UNEFM-CIAAP-1445, (right mandible), El Hatillo.

OTHER MATERIAL EXAMINED. AMU-CURS-33 (isolated posterior tooth), Tío Gregorio; AMU-CURS-57 (mandible), Tío Gregorio; MCC URU-76-72V (mandible), 0.5 km north of quebrada El Picache and 50 m east of Chiguaje fault; UNEFM-CIAAP-1363 (pubis), UNEFM-CIAAP-1367 (scapula, coracoid and ilium), UNEFM-CIAAP-1370 (humerus), El Hatillo.

OCCURRENCE. All specimens come from the upper Miocene Urumaco Formation, Falcón State, northwestern Venezuela.

DIAGNOSIS. Skull large, elongated and much flatter than in *P. brasiliensis* and *P. neivensis*. Snout with an elongated median depression, wider than in *P. brasiliensis* and *P. neivensis*, and with very large narial opening, almost 60% of rostral length. Premaxilla and maxilla suture extend posteriorly on the ventral skull surface, with premaxillary bones extending posteriorly to the fourth maxillary alveolus, while the inverted 'V' suture shape on the palatal face reaches the fifth maxillary tooth level. On the dorsal skull surface, premaxillae extend up to the lateral margins of the narial depression. Premaxillae bear a large incisive foramen that extends anteriorly between the occlusive fossae for the first mandibular teeth, not so further



Figure 2 *Purussaurus mirandai* sp. nov., holotype, UNEFM-CIAAP-1369, El Hatillo, upper Miocene Urumaco Formation, Urumaco, Venezuela. Skull with associated mandibles in dorsal (A), ventral (B), lateral (C) and occipital view (D); mandible in occlusal view (E). Scale bars = 200 mm.

anteriorly extended in *P. neivensis* and *P. brasiliensis*. Concave posterior dorsal margin of the skull table (squamosal and supraoccipital), with a linear contour, being rounded in *P. neivensis* and *P. brasiliensis*. The lacrymal and prefrontal are elongated and nearly of the same length. Occipital condyle more massive than in other *Purussaurus*. The dental formula consists of 5 premaxillary, 14 maxillary and 21 mandibular teeth.

DESCRIPTION. Enlarged, wide and robust skull, much flatter than that of *P. brasiliensis* and *P. neivensis*, with typical rounded and robust alligatorid snout tip with large anterior

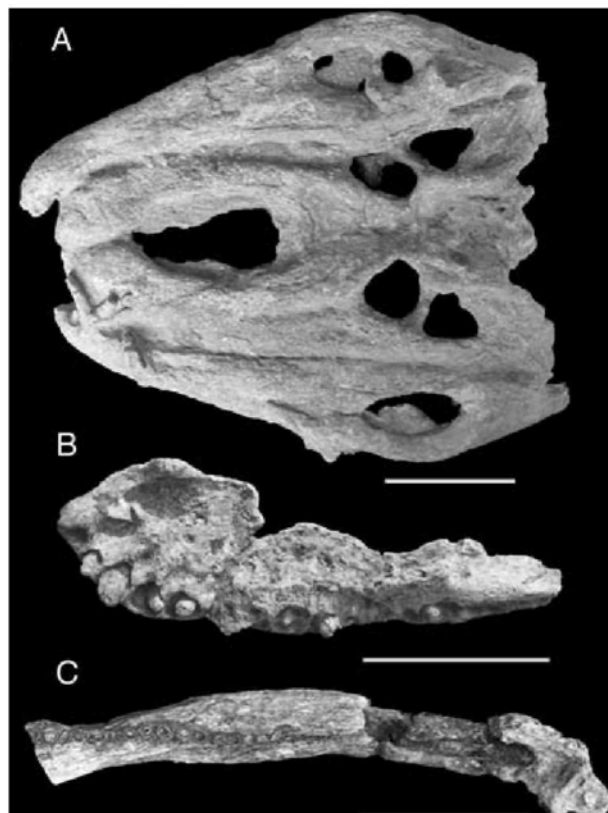


Figure 3 *Purussaurus mirandai* sp. nov. A, Paratype, AMU-CURS-1353 (a skull with associated mandibles in dorsal view), El Hatillo. B, Paratype, MCC URU-115-72V (premaxilla and maxilla in palatal view), 3.5 km northwest of El Picache. C, Paratype, UNEFM-CIAAP-1445, (right mandible in occlusal view), El Hatillo. Scale bars = 300 mm.

premaxillary teeth. The total skull length is 1260 mm. The maxilla height reaches 135 mm at the level of the first maxillary alveolus and forms a lateral wall. The narial aperture is a wide, elongated and deep longitudinal fossa, with parallel margins that reach 390 mm in length and 205 mm in transverse diameter. Behind the narial opening, the rostral surface is transversally concave and is surrounded by the prefrontal, lacrymal and maxillary longitudinal elevations (rostral canthi).

Premaxilla low, the external rounded surface is ornamented with coarse reticulating ridges and pits, the maximal high reaching 105 mm at the snout tip. The premaxillae do not show the anterior elevation that characterises *P. neivensis*. Premaxilla bones extend posterior to the fourth maxillary alveolus and the inverted 'V' suture shape on the palatal face reaches the fifth maxillary tooth level. On the dorsal skull surface the dorsal process of the premaxilla extends along the lateral margins of the narial depression to its mid-length and contacts the nasals. On the right premaxilla, five elliptical alveoli are preserved but on the left premaxilla only four are preserved. The first alveolus is the smallest, ranging from 24–30 mm in antero–posterior diameter and 27–29 mm in labio–lingual diameter. The largest alveolus is the fourth, ranging from 44–60 mm in antero–posterior diameter and 38–60 mm in labio–lingual diameter. The second alveolus is a little smaller than the first and the third and fifth is a little smaller than the fourth. Behind the first premaxillary

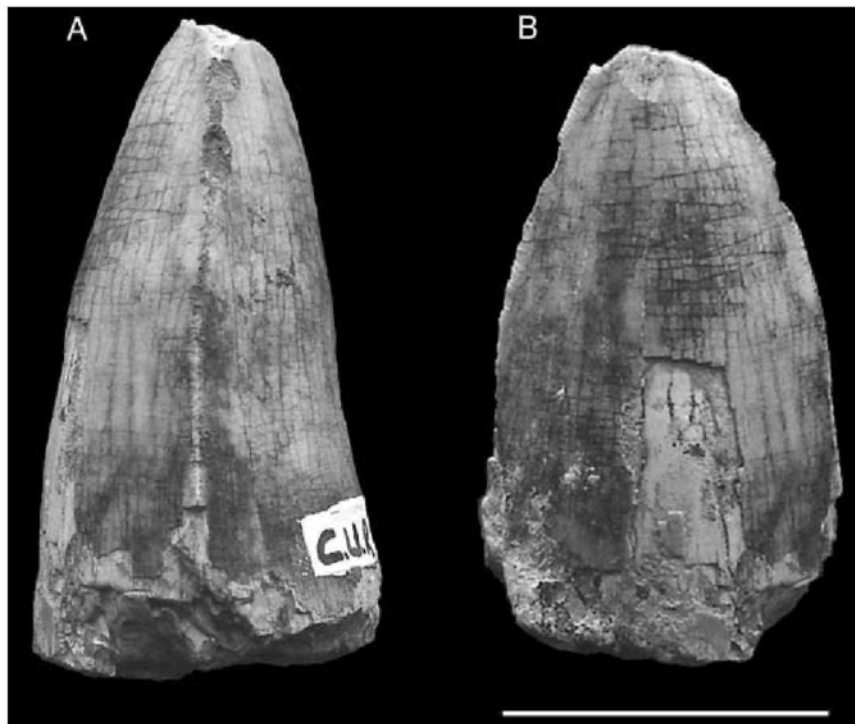


Figure 4 *Purussaurus mirandai* sp. nov., AMU-CURS-33 Tío Gregorio, upper Miocene Urumaco Formation, Urumaco, Venezuela. Isolated posterior tooth in frontal (A) and lateral (B) views. Scale bar = 30 mm.

tooth a deeper fossa (anteriorly extended up to the alveolus of the third premaxillary tooth) received the first enlarged teeth from the mandible. Behind the interalveolar space of teeth 3–4 and 4–5 there are two other occlusive fossae, smaller in size. The interalveolar diastema decreases from first to last alveoli, being 8 mm between first and second alveoli and 3 mm between fourth and fifth. Between the last premaxillary tooth and the first maxillary tooth there is a diastema of 13 mm. The maxilla are, apparently, trapezoid-shaped in dorsal view and contain 14 alveoli, varying from 44–55 mm in antero–posterior diameter and 32–48 mm in labio–lingual diameter, the fourth alveolus being the largest. The second and third teeth are just a little smaller, followed by the first and finally the fifth. The maxillary alveolar diastema is relatively uniform, ranging from 8–10 mm. Ventrally, the palatine process of the maxilla form the anterior border of the palatine fenestra and its lateral border extends up to the 10–11 interalveolar space. A deep notch on the posterior edge of the palatine fenestra can be observed.

The nasal is W-shaped in dorsal view, with a long lateral processes bordering the narial aperture that contacts the dorsal process of the pre-maxilla and the maxilla on the narial lateral margin, isolating it from the narial border. This bone forms a deep medial and longitudinal depression and, apparently, the nasal spine retains a short, massive prolongation that does not contact the premaxilla. The nasal and lacrymal are also apparently separated by the prefrontal anterior extension, with the nasal and frontal separated by the prefrontal. However, the interpretations of the nasal, prefrontal and frontal bones are tentative and require confirmation based on new, better preserved, material. The lacrymal is widely sutured with the prefrontal and forms the anterior margin of the orbit. Anteriorly, the lacrymal joins with the

maxilla in a transverse suture that continues with the jugal suture.

The suture between the prefrontal and frontal starts on the anteromedial orbital edge and joins at the middle line to form a characteristic wedge on the wider interorbital depression. Posteriorly, the frontal sutures with the parietal and postorbital. The postorbital is massive, forming one-third of the lateral table skull, part of the supratemporal fenestra and orbital margins.

The jugal is a very elongated and robust bone, anteriorly extended to the ninth maxillary tooth. Dorsally it contacts the lacrymal and maxilla in a marked groove that extends anteriorly in the maxilla up to the seventh tooth. Medially the jugal contacts the maxilla and ectopterygoid, principally the latter. A short and robust ascendant process extends from the inferior concave border of the orbits and contacts the descendent process of the postorbital posteriorly. In the infratemporal portion its surface has only a weak ornamentation and its infratemporal border is markedly less concave than its infraorbital one. Posteriorly the jugal contacts the quadratojugal in a suture orientated around 40° to the palate plane. The quadratojugal extends dorsally to the ventral surface of the postorbital and no remains of the quadratojugal spine are noted. The infratemporal fenestrae are greater than the supratemporal fenestrae and of similar size and form to the orbits.

The skull table is large and wide. The posterior dorsal margin of the skull table (squamosal and supraoccipital) is strongly concave with a linear contour, like a half-hexahedron. This concavity also occurs in *Mourasuchus* and in *Caiman neivensis* (Rovereto 1912; Price 1964; Brochu 1999), but is much deeper in all *Purussaurus* species and curvilinear in all forms above. The lateral border is formed by an enlarged and elevated squamosal, extending posterolaterally

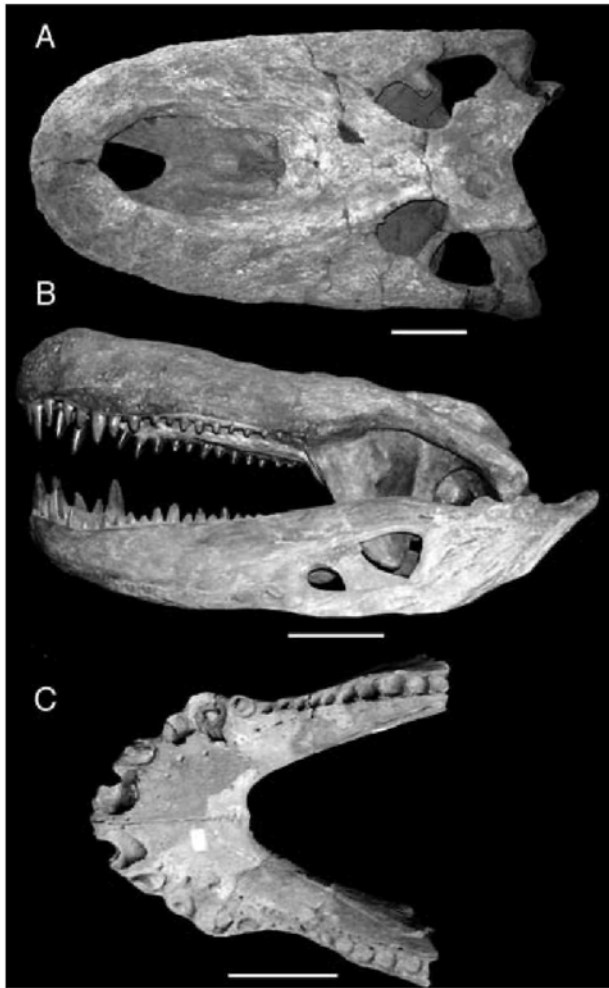


Figure 5 *Purussaurus brasiliensis*, upper Miocene Solimões Formation in Acre, Brasil. **A**, UFAC 1118, skull in dorsal view. **B**, PUC-MG, cast from the reconstructed skull with associated mandibles in lateral view. **C**, DGM 527-R, mandible in occlusal view. Scale bars = 200 mm.

along occipital prolongations. The parietal forms the area between the largest supratemporal fenestra and sutures posteriorly with the small supraoccipital. The supratemporal fenestra are small, closely positioned (25 mm apart) and circumscribed by shallow fossae along the anterior, posterior and medial margins, with a small bone projection only along its lateral margins. Their main axes are antero–posteriorly oriented and their lateral borders are parallel.

The occipital surface is mostly vertical. The foramen magnum is reduced by diagenetic alteration in all available specimens. The basioccipital and occipital condyles are massive, the latter being 60 mm in width. The occipital condyle is disproportionately robust and larger than in *P. brasiliensis*. Apparently, the descendent process of the exoccipital extends ventrally to the mid-height of the basioccipital tubera. These tubera are robust and trapezoidal in form.

The quadrate has two distinct condyles, the lateral one being almost one-third greater than the medial one.

The palatines extend anteriorly between the fifth and sixth maxillary alveoli, with a concave–convex suture. The palatine–pterygoid suture lies a little anterior to the posterior apex of the palatine fenestra, formed totally by the pterygoids.

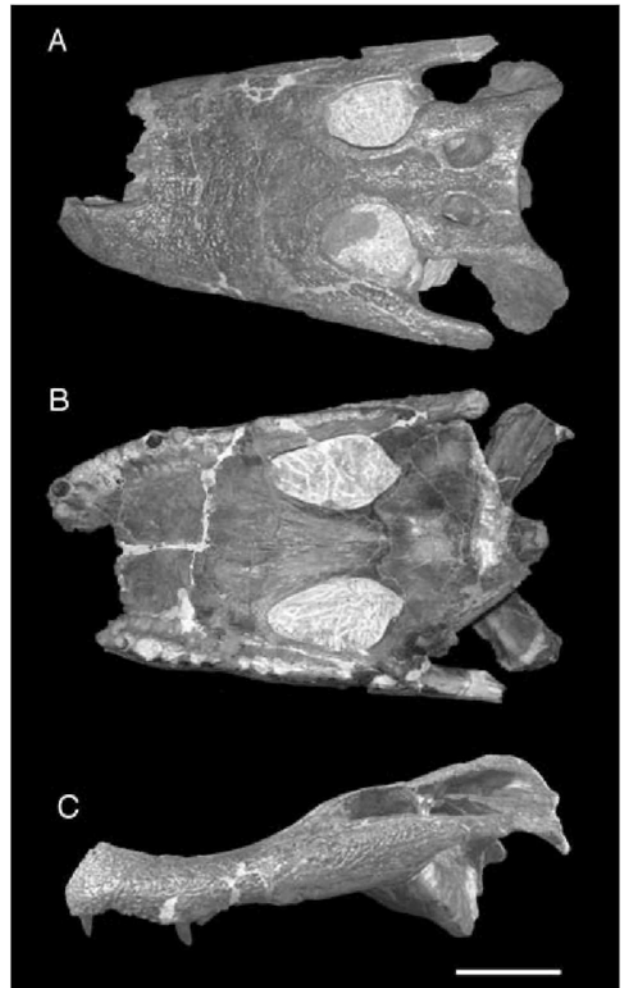


Figure 6 *Purussaurus neivensis*, INGEOMINAS DHL-45, middle Miocene La Venta fauna of Colombia. Nearly complete skull in dorsal (**A**), ventral (**B**) and lateral (**C**) views. Scale bars = 100 mm.

The medial margins of the palatine fenestra are bowed. The ectopterygoids extend anteriorly up to the twelfth maxillary tooth and apparently do not form its alveolar wall. Their ascendant process lies principally over the maxilla.

Behind the choanes, the pterygoids form a deep notch between two ventral, post-choanal, robust projections arranged in parallel. This condition is recurrent among the living caimaninae (Brochu 1999). *Purussaurus neivensis* shows these projections, but they are strongly divergent (Langston 1965). Behind these projections the basisphenoid is visible, projecting ventrally almost to the ventral border of the basioccipital tubera. The choanal aperture is close to the posterior edge of the pterygoids and anterior to the Eustacian foramen. It is divided by a bony septum and is wider than it is long (36 × 15 mm).

The mandible is robust with 21 alveoli. The left lower jaw length is 1490 mm. The symphysis is oval and maintains this form and proportion in a juvenile specimen, AMU-CURS-57. It reaches the fifth left alveolus in the holotype, but reaches only the fourth tooth in MCC URU 76-72V and in the juvenile specimen. The splenial does not reach the symphysis, extending only to the eighth tooth and it

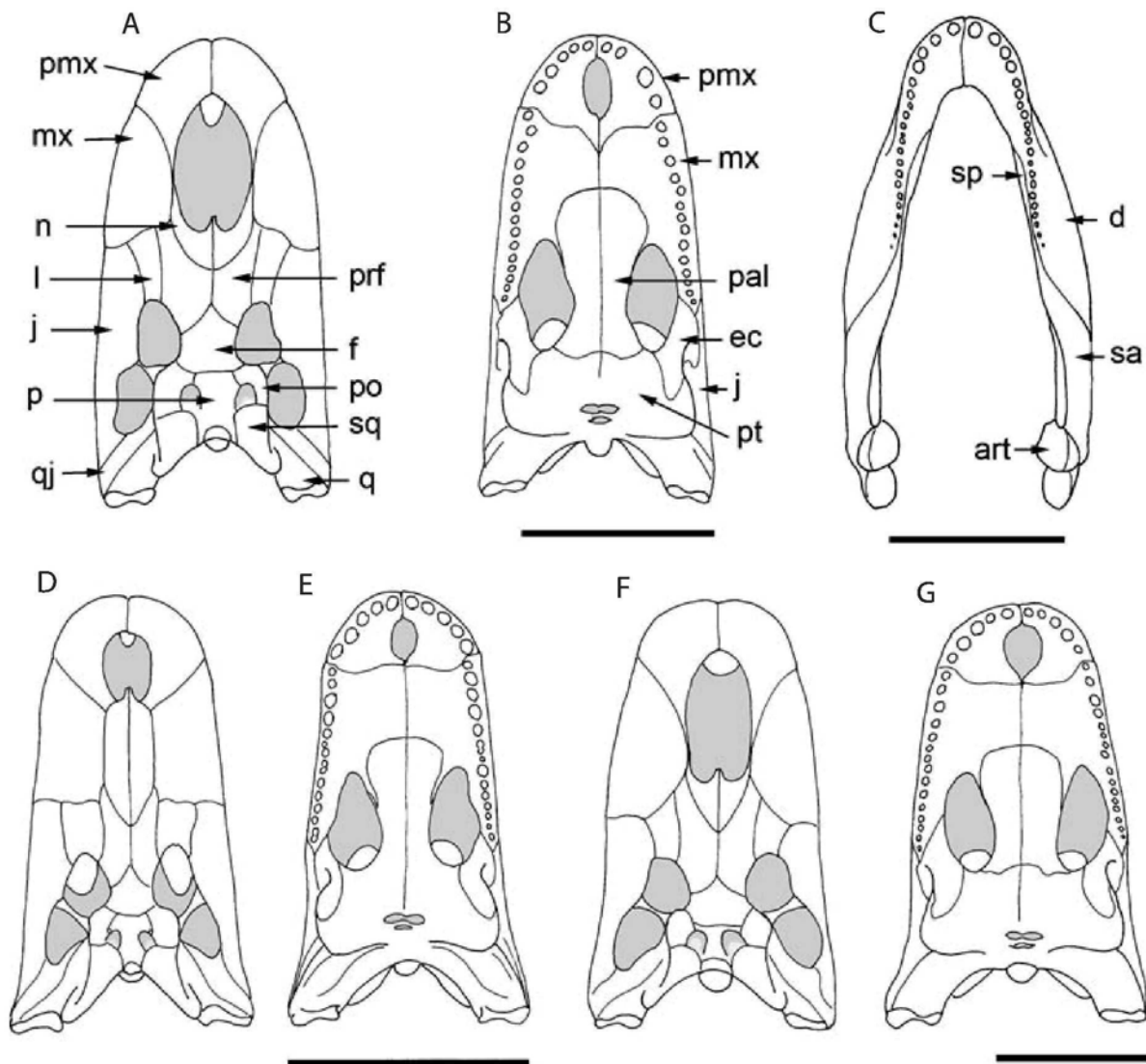


Figure 7 Schematic drawings of skulls of *Purussaurus*. **A–C**, *P. mirandai* sp. nov., UNEFM-CIAAP-1369; **A**, dorsal view; **B**, palatal view; **C**, mandible. **D–E**, *P. neivensis* UCMF 39704; **D**, dorsal view; **E**, palatal view. **F, G**, *P. brasiliensis*, UFAC 1118; **F**, dorsal view; **G**, palatal view. Abbreviations: **art**, articular; **d**, dentary; **ec**, ectopterygoid; **f**, frontal; **j**, jugal; **l**, lacrymal; **mx**, maxilla; **n**, nasal; **p**, parietal; **pal**, palatine; **po**, postorbital; **prf**, prefrontal; **pt**, pterygoid; **pmx**, premaxilla; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sp**, splenial, **sq**, squamosal. Scale bars = 500 mm.

forms the internal border of alveoli 16–21. The angular is long and extends anteriorly up to the twentieth mandibular tooth, being only a little bent dorsally. Only the inferior half of the coronoid is preserved. Between the coronoid, angular and splenial there is a deep groove, probably representing the foramen intramandibularis caudalis, with a taphonomically altered shape. This groove is visible laterally through the external mandibular fenestrae. The surangular is wedged between the dentary and splenial, extending anteriorly close to the last mandibular alveolus. The glenoid fossae have two short but robust transverse crests, the posterior being the more developed. These crests exclude fore–aft movements of the mandible. The posterior crest is formed principally by the articular, but has a lateral contribution of the surangular. Laterally, the glenoid fossae have a longitudinal crest formed by the surangular. This bone is extended posteriorly to the posterior transverse crest of the glenoid fossae

and does not contribute to the retroarticular process. The angular makes a great contribution to the retroarticular process, extending lateroventrally near the posterior apex of this process. The retroarticular process is short and robust, extends well below the glenoid fossae and is not dorsally inclined but rather longitudinally concave. In the ventral border of the external mandibular fenestrae, the articular has a medial crest extending anteriorly close to a similar crest in the dorsal surface of the angular. Between these crests there is a postero-medially orientated groove. The external mandibular fenestra is long and tall (210 × 98 mm) and is formed anteriorly by the dentary, while its dorsal border is formed almost exclusively by the surangular, although the dentary also forms a small part. The angular–surangular suture passes along the posterior border of the mandibular fenestra, as in modern caimans. The more vertical festooned portion of the mandible lies in the region of alveoli 1–5, the largest of the series. The

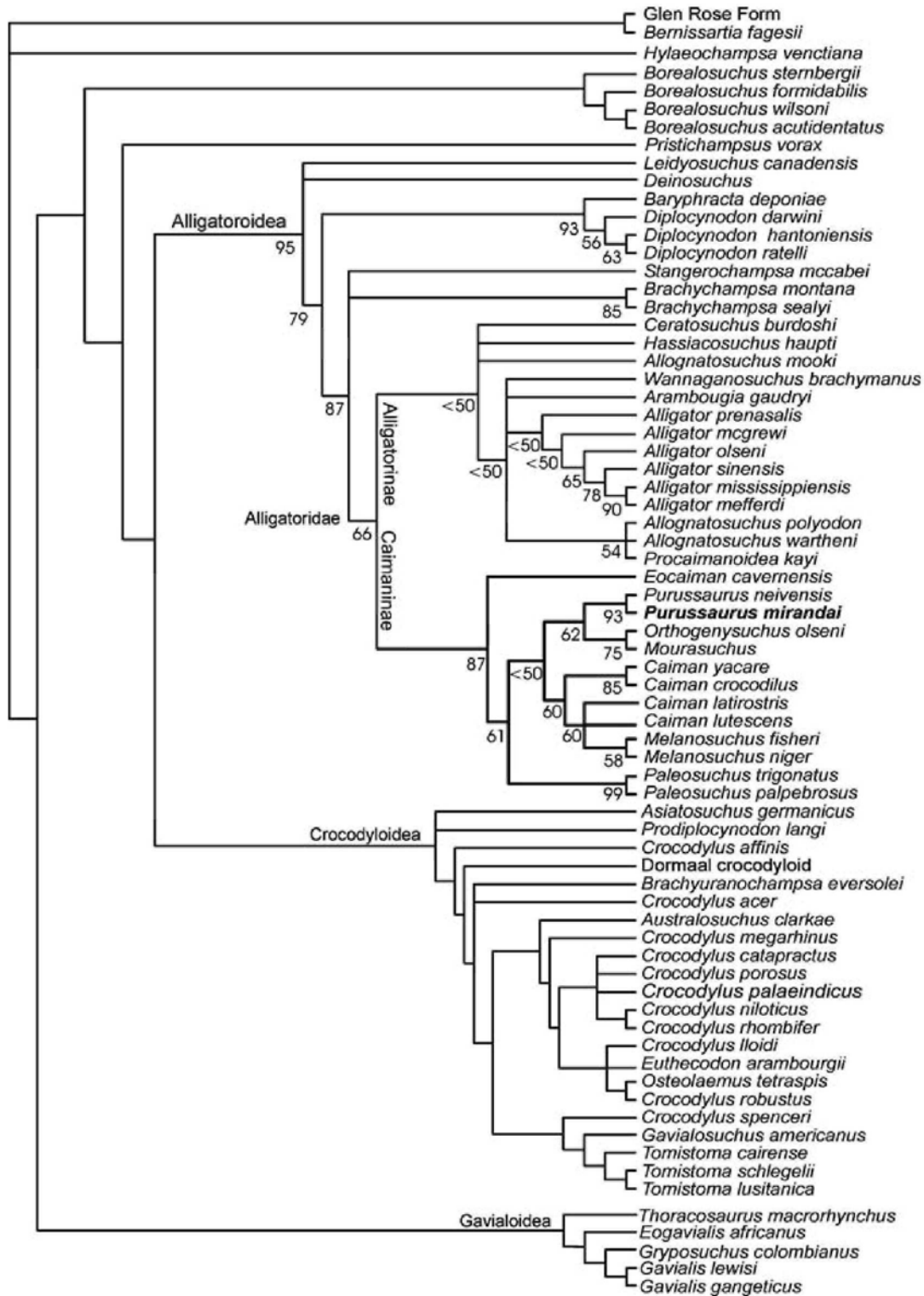


Figure 8 Strict consensus of 96 196 equally optimal trees (length = 503; Consistency Index, excluding autapomorphies = 0.413; Retention Index = 0.825). Numbers at nodes indicate bootstrap support.

posterior portion is not festooned. Horizontally, the mandible is more festooned than in *P. brasiliensis* and *P. neivensis*. The more convex portion occurs at alveoli 2–5 and is greatest at the fourth alveolus. Posterior to this, there is a weak concavity, coinciding with alveoli 6–15. Posteriorly, the alveoli are disposed in a linear series up to the twenty-second alveolus.

This linear series is in the same projected plane as the lateral border of the second alveolus. The dental series (725 mm in length) occupies the middle length of the mandible. The first five alveoli are the largest of the series and the first is the most developed, being 53–62 mm in antero–posterior diameter and 40–55 mm in labio–lingual diameter. This series

is laterally compressed. Alveoli 3 and 4 are not confluent. Alveoli 6 to the end range from 11 to 33 mm in antero–posterior and labio–lingual diameter, all being almost round. Of this series, the largest alveolus is number 12, which is 33×33 mm in diameter.

Few teeth are preserved *in situ*. The premaxillary teeth are tall, sharp, relatively compressed and bent antero–posteriorly and labio–lingually, with an antero–posterior diameter of 19–39 mm and a labio–lingual diameter of 15–30 mm. Tooth 3 is the largest (39×30 mm) and tooth 2 the smallest (19×15 mm). No anterior maxillary teeth are preserved *in situ* but some posterior ones are preserved in AMU-CURS-135. These teeth are blunted and rounded in diameter. The mandibular series are similarly arranged, with the largest anterior teeth being compressed, tall, sharp and bent, while the posterior are blunted.

Only in AMU-CURS-135 are any mandibular teeth preserved *in situ*. Mandibular teeth 3–6 are preserved, but only tooth 4 has a complete crown. This tooth is 35 mm in fore–aft basal length, 22 mm in basal width and 99 mm in crown height. The other teeth are almost 10 mm smaller in all measurements. The teeth have fore and aft carinas, but only a few are well enough preserved to show a fine striation. The third premaxillary teeth of MCC URU-115-72V and some isolated teeth associated with AMU-CURS-135 show a denticle density of 3 per 5 mm, projecting perpendicular to the carina and being 1.5 mm in height. The enamel preserved in these isolated teeth is smooth, but with longitudinal and transverse lines along the crown.

REMARKS. Specimen MCC URU-112-72V from El Picache has a relatively short skull, wide narial aperture, highly separated supratemporal fenestra and relatively large orbital and infratemporal fenestrae. These features appear to be artifacts created during reconstruction at the Museum of Comparative Zoology in Harvard, probably because the morphotype of *Purussaurus neivensis* (Mook 1941) was used as a guide. Because this specimen was incorrectly reconstructed we cannot use it for measurement or for morphological description.

A juvenile skull associated by Langston (1965) to *Purussaurus neivensis* (INGEOMINAS, DHL-45) is much smaller than the rest, but shows all the synapomorphies of *Purussaurus*. Only the weak development of the rostral canthi in this specimen is not a strictly proportional difference. The low lateral crest in its rostrum produces an abrupt division between the dorsal surface of the rostrum and the skull table. This also occurs in the other (adult) specimens of all three *Purussaurus* species. However, the strong development of those crests in the large specimens obscures this difference and the transition appears to be more gradual. The weak development of the rostral canthi associated with the aperture of many cranial sutures (Monteiro *et al.* 1997) shows that the relatively small INGEOMINAS, DHL-45 is probably a juvenile.

PHYLOGENETIC ANALYSIS

To determine the phylogenetic position of *Purussaurus mirandai* sp. nov. and to test the monophyly of *Purussaurus*, we used the complete matrix of 164 characters of Brochu (1999), including 68 ingroup taxa, 35 of them being non-alligatoroid. Following Brochu, *Bernissartia fagesii* and an undescribed

taxon from the Lower Cretaceous Glen Rose Formation in Texas were used as successive outgroups to root the tree. The character matrix was revised after the restudy of the holotype of *Mourasuchus arendsi* (skull and post-cranial remains, UNEFM-CIAAP-1297), consideration of information in Price (1964) and Langston (1965) for *Mourasuchus atopus* and *M. amazonensis* and the study of a juvenile skull of *Purussaurus neivensis* (INGEOMINAS, DHL-45), with 25 characters from the original matrix of Brochu (1999) being recoded and with the addition of a third state to his character 93 (prefrontal extended anterior process that separates nasal from lacrymal; see Appendix). Postcranial characters for *P. mirandai* sp. nov. are coded on the basis of material housed at UNEFM (scapula, coracoid and ilium, UNEFM-CIAAP-1367; femur and ischium, UNEFM-CIAAP-1369; humerus, UNEFM-CIAAP-1370; pubis, UNEFM-CIAAP-1363). We performed 10 separate heuristic searches with 1000 replications using PAUP* 4.0 beta for Windows (Swofford 1998), with the order of ingroup taxa being randomised in each iteration and a tree-bisection-reconnection algorithm being used for branch swapping of the trees. No differential weighting was applied and all multistate characters were left unordered. The searches found 96 196 equally optimal trees, with a length of 503; a Consistency Index (CI) of 0.413; a CI excluding autapomorphies of 0.408 and a Retention Index (RI) of 0.825. The strict consensus tree is well resolved and equivalent to that found by Brochu (1999). Bootstrap support was obtained, reducing the number of non-alligatoroid taxa to 11 (*Hylaeochampsa venticiana*, *Borealosuchus sternbergii*, *Gavialis gangeticus*, *Thoracosaurus macrorhynchus*, *Pristichampsus vorax*, *Crocodylus rhombifer*, *Osteolaemus tetraspis*, *Tomistoma schlegelii*, 'Dormaal crocodyloid', *Crocodylus affinis* and *Asiatosuchus germanicus*), to reduce computation time. This was generated after 1000 replicates in 10 simple iterations using the tree-bisection-reconnection algorithm.

The results of this analysis robustly supported the monophyly of *Purussaurus* and confirmed its position as sister-group of the Nettosuchidae, previously reported by Brochu (1999). The clade formed by *Purussaurus* plus Nettosuchidae is supported by seven unambiguous synapomorphies: dorsal margin of atlantal ribs with a modest dorsal process (reversion among Caimaninae, unknown in *P. mirandai* sp. nov.); axial hypapophysis without a deep fork (unknown in *P. mirandai* sp. nov.); axial rib tuberculum wide, with broad dorsal tip (reversion among Alligatoroidea, unknown in *P. mirandai* sp. nov.); scapulocoracoid facet anterior to glenoid fossa uniformly narrow (reversion among the Alligatoridae); prefrontals meet medially (occurring also in *Caiman yacare*); prefrontal longer than lacrymal (parallelism with *Alligator*; with nearly the same extension in *P. mirandai* sp. nov.) and the presence of preorbital ridges very prominent at maturity (parallelism with some Crocodylinae, such as *Crocodylus porosus* and *Euthecodon arambourgii*). Four ambiguous synapomorphies also support this clade: quadratojugal extends to superior angle of infratemporal fenestra; prefrontal sends anterior process that isolates lacrymal from nasal; incisive foramen large, more than half the greatest width of premaxillae; the squamosal extends ventrolaterally to lateral extend of exoccipital and quadrate.

Purussaurus (here represented by *P. neivensis* and *P. mirandai* sp. nov.) show five unambiguous synapomorphies: the retroarticular process projecting posteriorly and not

posterodorsally (reversion among the Crocodylia); the surangular is pinched off anterior to tip of retroarticular process (a reversion among the Caimaninae); the external mandibular fenestra is large, with the *foramen intermandibularis caudalis* visible laterally; the supraoccipital is large, but does not exclude the parietal from the posterior edge of the skull table (an unambiguous synapomorphy, found also in the *Paleosuchus* clade); the presence of a fossa around the supratemporal fenestra (a reversion among the Caimaninae). Furthermore, *Purussaurus* shows five ambiguous synapomorphies: the axis neural arch has a lateral process (unknown in *P. mirandai* sp. nov.); the deltoid crest of the scapula is very wide, with a broad margin; the supra-acetabular crest is broad; the splenial possessed an anterior perforation for the mandibular ramus of cranial nerve V; the frontoparietal suture is concavoconvex.

Purussaurus mirandai shows the following five autapomorphies: a shallow fossa at the anteromedial corner of the supratemporal fenestra; the lacrymal and prefrontal elongated and nearly of the same length; very prominent canthi rostralii; ectopterygoid extends to posterior tip of the lateral pterygoid flange at maturity (a reversion among alligatoroids); the incisive foramen abuts the premaxillary tooth-row. Only this last is ambiguously distributed.

Unfortunately, it was not possible to include *P. brasiliensis* in this analysis, but the presence in this form of a developed rostral canthii (less developed in *P. neivensis*, adult or juvenile), a shallow fossa at the anteromedial corner of the supratemporal fenestra (absent in *P. neivensis*) and, about all, the sharing of a huge developed external naris, with a retraction of the mid-point of the nasals, suggest that *P. mirandai* sp. nov. is more closely related to *P. brasiliensis* than to *P. neivensis*. This is compatible with the view that the crocodylian diversity of Urumaco is more similar to that of the Solimões Formation than to the La Venta fauna.

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APPENDIX Character scores of *Purussaurus minandai* sp. nov. following the character list of Brochu (1999).

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????? ????? ????? ?1?? ?1100 1?1?? ?1011 ????? 0?20? ?1?10
111?1 ???11 11?10 11101 110?0 21010 220?0 00121 10301 ?00?1
011?0 01001 ?10?? 1201? ???110 0???? ?1?10 ???01 10110 1??01
211?? ????? 001?

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Original characters are from the matrix published by Brochu (1999), which have been recoded in this work. The original coding is given in brackets, below.

Purussaurus neivensis

Character 4: 1(0); Character 11: 1(0); Character 15: 1(?); Character 20: 0(1); Character 50: 1(0); Character 51: 1(0); Character 53: 1(?); Character 80: 0(1); Character 82: 2(?); Character 87: 0(1); Character 91: 0(1); Character 93 (with new coding): 3(1); Character 108: 0(1); Character 144: 1(0); Character 150: 1(0); Character 153: 0(1).

Mourasuchus

Character 6: 1(?); Character 14: 0(?); Character 15: 1(?); Character 19: 1(?); Character 20: 0(1); Character 22: 1(?); Character 70: 0(1); Character 93 (with new coding): 3(0); Character 109: 0(?).