

New remains of a gavialoid crocodilian from the late Oligocene–early Miocene of the Pirabas Formation, Brazil

HELOISA MORAES-SANTOS^{1*}, JEAN BOCQUENTIN VILLANUEVA² and PETER MANN TOLEDO³

¹*Coordenação de Ciências da Terra e Ecologia, Museu Paraense Emilio Goeldi, Av. Perimetral, 1901 66077-830, Belém, Para, Brazil*

²*LPP, Universidade Federal da Acre, Acre, Brazil*

³*CCST, Instituto Nacional de Pesquisas Espaciais, São José do Rio Preto, Brazil*

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New specimens of gavialoids collected from the Pirabas Formation, Brazil, provide additional information about the evolutionary evolution of Gavialoidea during the late Oligocene–early Miocene. We describe a specimen that has a more gracile symphyseal mandible than any other South American gavialoid. This fossil represents an unusually diverse radiation of gavialoids that were probably ecologically differentiated from each other by size and dietary specialization.

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INTRODUCTION

The Late Oligocene was a time of extensive marine invasions, probably because of a combination of tectonic subsidence and high sea level stands. Marine sediments of this age are common in North and South America and the Greater Antilles (Iturralde-Vinent & MacPhee, 1999). The Pirabas Formation, on the northern coast of Brazil (Fig. 1), was considered Oligo-Miocene in age by Ferreira (1982), based on the presence of the gastropod *Orthaulax pugnax*. According to Góes *et al.* (1990) and Rossetti (2001), distinct facies characterize the Pirabas Formation as having been deposited in an open marine environment with warm, shallow, agitated waters, including areas of lagoons, estuaries, and mangroves. Significant sea level falls were successively followed by major sea level rises and transgressions.

Remains of fossil vertebrates and invertebrates are relatively common in Neogene faunas of the

Pirabas Formation in the north-eastern Amazon region, where they have been collected for more than 120 years (White, 1887; Rossetti & Góes, 2004). A small collection of isolated and fragmentary remains of fossil Crocodyliformes has accumulated in the collections of the Museu Paraense Emilio Goeldi, Belém, Brazil, over the past 20 years (Toledo *et al.*, 1997; Rossetti, 2001; Rossetti & Góes, 2004). These specimens, collected from the late Oligocene–early Miocene Pirabas Formation, are the subject of this paper. The presence of gavialoid species in South America has often been discussed by different authors and has resulted in several controversies. Longirostrine crocodylians occur in the Cenozoic along the Atlantic coast of North America. These forms include the fossils generally referred to *Gavialosuchus* (Toula & Kail, 1885) or *Thecachampsia* (Cope, 1867) known from the Late Miocene of Florida and Middle Miocene of Virginia and Maryland (Mook, 1921a; Myrick, 2001).

Longirostrine crocodylians from South America have been known since Burmeister (1885) reported

*Corresponding author. E-mail: hmoraes@museu-goeldi.br



Figure 1. Summary map of the study region in north-east South America, showing the localities discussed in the text.

them. The best known are from the Middle Miocene of La Venta (Langston, 1965; Langston & Gasparini, 1997), the Late Miocene of the Urumaco Formation of Venezuela (Sill, 1970; Bocquentin Villanueva & Buffetaut, 1981; Aguilera, 2004; Riff & Aguilera, 2008), Peru (Kraus, 1998), and Brazil (Souza Filho & Bocquentin, 1989; Souza Filho, 1998). Brochu & Rincon (2004) described *Siquesiquesuchus venezuelensis* from a near-shore marine fauna from the Early Miocene Castillo Formation in Venezuela and recently Vélez-Juarbe, Brochu & Santos (2007) reported a new gharial from the Oligocene of Puerto Rico.

Previous descriptions of the crocodilian remains from the Pirabas Formation, deposited at the Museu Paraense Emilio Goeldi, Belém, were provided by Toledo *et al.* (1997) and Rossetti & Góes (2004). However, the poor state of preservation of the material did not permit inferences concerning intergeneric relationships. The new specimens recently collected are shown here to belong to an indeterminate gavialoid. The purpose of this paper is to discuss the phylogenetic and ecological significance of the finds.

INSTITUTIONAL ABBREVIATIONS

IGM, Geological Survey of Colombia INGEOMINAS; MBLUZ-P, Museo de Biología de la Universidad del Zulia, Maracaibo, Venezuela; MPEG, Museu Paraense Emilio Goeldi, Belém, Brazil; UFAC, Universidade Federal de Acre, Rio Branco, Brazil.

MATERIAL AND PROVENANCE

All material cited below is from the Pirabas Formation.

MPEG 1130-V, partial portion of mandibular symphysis from Capanema, Pará; MPEG 1010-V, right lateral portion of mandibular symphysis from Capanema, Pará; MPEG 609-V, incomplete cervical vertebra; MPEG 116-V and MPEG 1129-V, two isolated teeth; MPEG 608-V, region articular of left mandible from Salinópolis, Pará (material studied by Rossetti & Góes, 2004); MPEG 227-V, incomplete left angular (studied by Toledo *et al.*, 1997); MPEG 228 V, isolated vertebral centrum from São João de Pirabas, Pará (briefly cited by Toledo *et al.*, 1997).

SYSTEMATICS

Crocodyliformes (Benton & Clark, 1988)

Eusuchia Huxley, 1875

Crocodylia Gmelin, 1789 (*sensu* Benton & Clark, 1988)

Gavialoidea Hay, 1930

DESCRIPTION

New material

MPEG 1130-V, partial portion of mandibular symphysis (Fig. 2): The specimen is a short portion of slender and dorsoventrally flattened mandibular symphysis lacking the posterior end. All the teeth are missing. The splenials are very long and together form both a conspicuous portion of the specimen, badly damaged anteriorly. The lateral margins converge slightly anteriorly. The mandibular symphysis would have originally been long and narrow (Figs 2, 3). The dorsoventrally flattened preserved portion is slightly less than 125 mm long, 40.7 mm in maximum width, dorsoventral diameter 13.7 mm at the posterior end and 10.4 mm at the anterior end. The posterior part of the symphysis is not preserved but the portion studied is posteriorly expanded and probably extended near the posterior end of the splenial symphysis. Approaching this region, the mandible is deeper and this is emphasized by the depth of the ventral part in this area. The specimen has a firmly fused mandibular symphysis marked by a medial groove dorsally and ventrally. No teeth are present, so inferences about the nature of the dentition are derived from the empty dental alveoli that remain. The fragment bears four essentially complete alveoli on the left side, five on the right. The alveoli are subcircular in cross section and project posteroventrally. All of the teeth have been dislodged but portion of the root of a tooth is lodged in the most posterior alveolus in the right ramus. The collars formed by the alveolar margins are moderate but there are significant notches between adjacent rounded alveoli. As the collars are present in the posterior part of the symphysis, this condition differs from that of *Piscogavialis*, where similar collars are

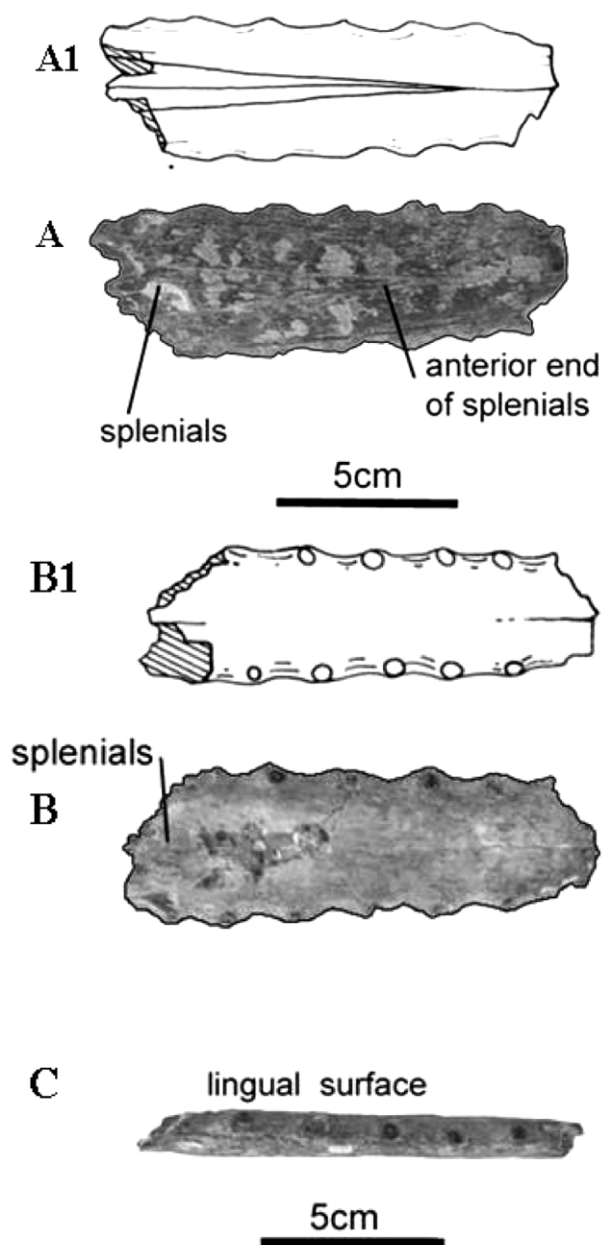


Figure 2. Gavialoid indet., partial symphyseal portion of mandible, MPEG 1130-V: A, ventral view and A1, schematic ventral view; B, lingual view and B1 schematic ventral view; C, right lateral view.

restricted to the anterior part of the rostrum. Alveolar salients are not strongly developed but the condition of the deep interalveolar notches can be viewed in *Ikanogavialis*. The teeth were implanted irregularly opposite one another, and were separated by relatively wide and depressed intervals from the preceding and succeeding teeth. Distances between alveoli vary from 10 to 15 mm. The spacing shows no obvious correlation of left and right tooth row.

The outer face of each ramus is slightly indented between the alveoli, suggesting that the opposite teeth on the rostrum bite between the mandibular teeth. The alveoli are 5 to 5.7 mm in maximum diameter but the size of the alveoli varies only slightly and the dentition can be described as homodont. The transversal distance between opposite alveoli at the first pair counting backward from the anterior extremity is 30.6 mm and at the fifth pair 32 mm. The alveolar tooth row is laterally placed on the dentary but crosses the dentary from the labial edge onto the dorsal side. The ventral portion of the symphysis is composed of dense bone, whose convex surface is faintly striated. In ventral view, the splenials meet along the symphysis with an accentuated posterior constriction and an acute anterior termination.

The lingual surface of the symphysis is essentially flat transversely. In lingual (oral) view, the sutural contact between the dentaries and the splenials is not readily seen. The surface of the longitudinal median region is badly abraded and the sutures are not well preserved. However, the very flattened symphyseal portion is sufficiently informative to rule out any confusion with a rostral fragment.

Right lateral portion of symphyseal mandible MPEG 1010-V (Fig. 4): Three subcircular alveoli with prominent borders are preserved in the fragmentary portion of symphyseal mandible (anteroposterior length 54 mm). This specimen is consistent in size and morphology with the small portion studied above and may represent a single individual. The diameter of the largest alveoli, at the middle part of the fragment, is 6 mm.

Isolated teeth: Only two specimens of single teeth are preserved. They are divided into asymmetrical surfaces by well-developed anterior and posterior carinae that divide the tooth subequally. Striae are present on all surfaces and extend from near the apex to the basis of the crown. The enamel is fine. Compared to the teeth of *Gryposuchus* (Langston & Gasparini, 1997), those of the specimens differ in having smaller diameters.

MPEG 116-V (Fig. 5): This slender tooth is in a state of excellent preservation. It is made up of slightly built simple cones, subcircular in cross section. The length of the crown is 18.5 mm, the diameter 6.3 mm.

MPEG 1129-V (Fig. 5): The crown is flattened from side to side, slightly recurved toward apex. The length is 21 mm, the diameter between the carinae 6.2 mm.

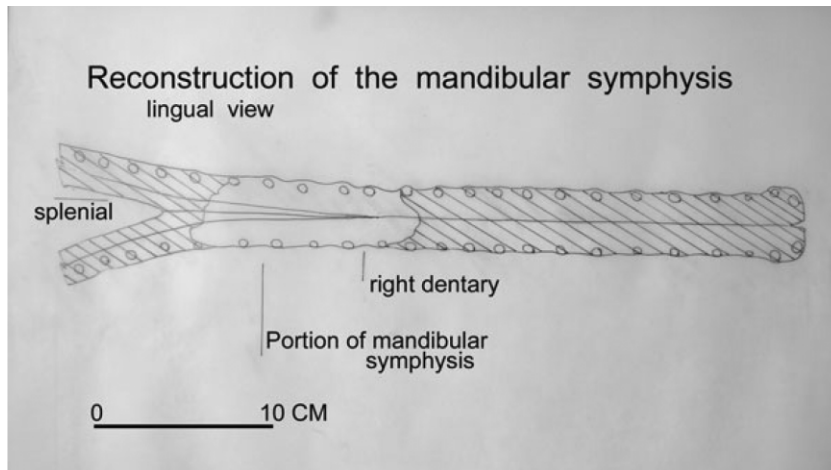


Figure 3. Reconstruction of the mandibular symphysis of *Gavialoid* indet., MPEG 1130-V.



Figure 4. *Gavialoid* indet., right lateral portion of mandible, MPEG 1010-V, in lateral view.

Angular MPEG 227-V: The maximum length of this fragmentary angular, studied by Toledo *et al.* (1997), is 95 mm. From figure 1 of these authors, the length of the mandible that corresponds to this angular is approximately 300 mm. From table 8.3 of Langston & Gasparini (1997) the mandible of the specimen IGM 184696 of *Gryposuchus* is much longer (1170 mm).

Cervical vertebra MPEG 609-V (Fig. 5): Incomplete fifth cervical vertebra lacking the neural arch. The maximum anteroposterior length is 39.5 mm. This length is greatly less than the corresponding measurement in the specimen N°7139 of *Crocodilus americanus* of the American Museum (66 mm) described by Mook (1921b).

DISCUSSION

According to Riff & Aguilera (2008), the long splenials of *Gryposuchus croizati* contribute almost one third of the symphyseal length. The length of the splenial of the specimen MPEG 1130-V is approximately 100 mm. Thus, we estimate that the original symphyseal length of the holotype specimen was approximately 300 cm. The symphyseal length of the type specimen of *Eogavialis africanum* from the Middle Eocene of Egypt is 495 mm (Andrews, 1906: 272) and the symphyseal length of the *Gryposuchus* specimen IGM 184696 is 610 mm (Langston & Gasparini, 1997: table 8.3). This latest measurement is twice as long as the estimated length of the rostrum of MPEG 1130-V. The specimen from the Pirabas Formation is much smaller than in other gavialoids. The vertebra MPEG 609-V lacks the neural arch and can be considered as being from an immature individual but the measurements of the articular MPEG 608-V (see below), and the angular MPEG 227-V confirm the important differences in size with *Gryposuchus* and suggest that the new specimens from the Pirabas Formation represent a small taxon.

The fragmentary nature of our material provides only a limited basis for taxonomic comparisons. According to Kälin (1933) the teeth of *Tomistoma* are almost vertically implanted. The mandible of *Hesperogavialis* is unknown but the teeth of the rostrum are very close together (Souza Filho, 1998). Contrary to these respective arrangements of the teeth, the alveoli of the dentaries of the specimen MPEG 1129-V are orientated posteroventrally, largely separate, and compare more favourably to the South American gavialoids *Eogavialis* and *Gavialis*. The alveoli are more laterally placed on the dentaries than in *Gryposuchus*. The pattern of the V-shaped splenial suture in the

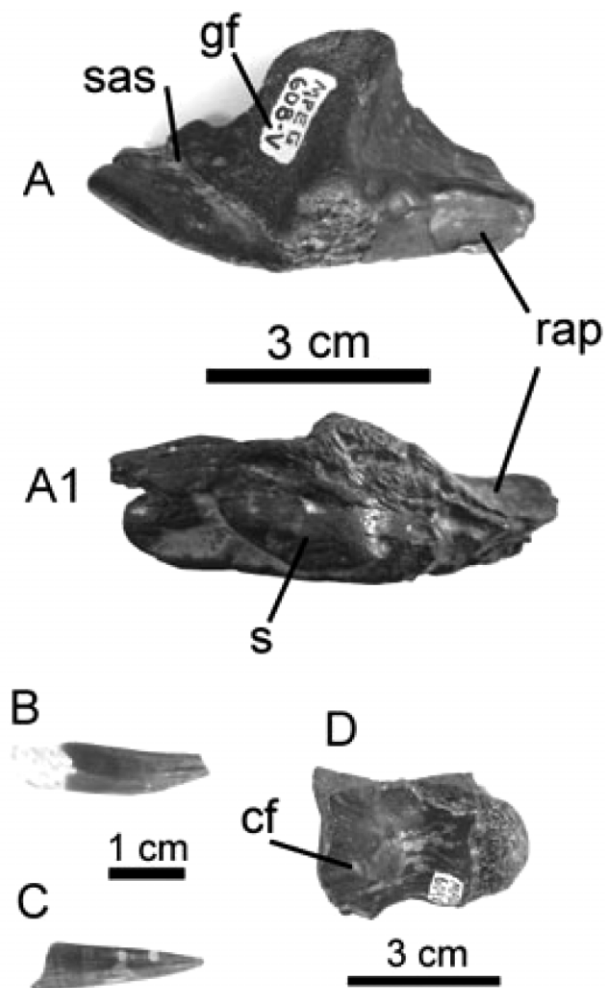


Figure 5. Gaviroid indet., MPEG 608-V. Anterior and lateroventral view (A, A1, respectively) of the articular region of a left mandible; isolated tooth, MPEG 116-V (B); isolated tooth, MPEG 1129-V (C). MPEG 609-V; right lateral view of incomplete fifth cervical vertebra, MPEG 609-V (D). Abbreviations: gf, fossa glenoid; s, surangular; sas, surangular-articular suture; rap, retroarticular process.

symphysis of MPEG 1129-V is very similar to that in *S. venezuelensis*. This character provides support for a possible synapomorphy for a clade of South American gharials as suggested by Brochu & Rincon (2004). Amongst the differences with the South American gaviroids *Gryposuchus* and *Piscogavialis* are the deep notches between mandibular teeth, the variable inter-alveolar spaces larger than alveolar diameters, and the very flattened and gracile symphysis.

MPEG 608-V, the articular region of a left mandible (Fig. 5), was studied by Rossetti & Góes (2004: fig. 13), but the fragmentary nature of the specimen did not allow an assignment to a particular genus or

species and the material was previously considered as an undetermined crocodilian. However, several features distinguish this articular from tomistomines and our new comparative analysis supports the affinities with the South American gaviroids. As in *Gryposuchus colombianus*, the posterior transverse crest formed by the articular and the supra-articular is low and the dorsal edge of the surangular that limits the fossa laterally is less pronounced than in *Tomistoma* and *Gavialis* (Langston & Gasparini, 1997). As in *S. venezuelensis*, the surangular-articular suture within the glenoid fossa lacks deep lateral indentation and appears to have been a simple lineation in the glenoid fossa.

The fossa is shallow and relatively flat. A medial prominence divides the fossa into lateral and medial concavities corresponding to the convexities of the quadratic condyle. A distinct lamina, transversely flattened, expands from the elevated posterior wall of the lateral hemifossa toward the tip of the retroarticular process. This tall crest is similar to that described in *Gr. colombianus* by Langston & Gasparini (1997) and *S. venezuelensis* figured by Brochu & Rincon (2004: text-fig. 8). The posterior end of the retroarticular process and the angular of MPEG 608-V are not preserved but the surangular is posteriorly truncated and appears distinctly pinched off by the articular and the angular (Fig. 4A). This peculiar condition is also found in *Alligator* and *Gavialis* (Brochu, 1999).

The articular MPEG 608-V differs from other gaviroids in its small size: the greatest width of the articular 608-V (34.5 mm) equals about one-half of that of the holotype of *S. venezuelensis* (approximately 70 mm from fig. 8 of Brochu & Rincon, 2004) and the width of the articular of *Gr. colombianus* IGM 184696 is approximately 100 mm (measurement from fig. 8.13 of Langston & Gasparini, 1997).

PALAEOECOLOGY AND PALAEOGEOGRAPHY

During late Oligocene/middle Miocene highstands, water circulation patterns were substantially altered by palaeogeographical changes. The seaway between the Pacific and northern Atlantic persisted and the Orinoco River still drained into the Caribbean Sea (Hoorn *et al.*, 1995). Warm water derived from the Equatorial Atlantic would have been more widely distributed by the Circum Tropical Current (Iturralde-Vinent & MacPhee, 1999). The prevailing high sea level corresponded to a period of marine transgressions and led to deposition on several units at a continental scale in South America (Rossetti, 2001). The Pirabas Formation, in north-eastern Brazil, is characterized by diverse faunal associations in freshwater (swamps and rivers), brackish (estua-

rine), and marine (coastal lagoon, saltmarsh, and sandy littoral) environments. It has recently yielded material of three genera of dugongid sirenians: *Dioplotherium*, *Rytiodus*, and *Metaxytherium* (Toledo & Domning, 1989). The new discoveries of small and large sirenians from the Early Miocene of Puerto Rico and Cuba show that Early Miocene diversity on the Atlantic coast of South America was comparable to that which existed contemporaneously in North America (Domning & Aguilera, 2008). The gavialoid specimens from the Pirabas Formation and *S. venezuelensis* from the Early Miocene of the Castillo Formation of Venezuela were all collected from units deposited in marginal marine settings. The recent report of an indeterminate sirenian from the Castillo Formation by Domning & Aguilera (2008) is consistent with a similar palaeoenvironment in these two formations.

The phylogenetic position of Gavialoidea and its exact position with Tomistominae are still debated (Brochu & Gingerich, 2000; Harshman *et al.*, 2003; Hua & Jouve, 2004; Janke *et al.*, 2005; Salisbury *et al.*, 2006; Fortier & Schultz, 2009) but the origin of the South American gavials is doubtless to be found amongst the primitive Gavialoidea of the Eocene and Oligocene of Africa. The recently described *Ocepesuchus* from the late Maastrichtian of Morocco (Jouve *et al.*, 2008), the Palaeocene *Argochampsia* and the Middle Eocene *Eogavialis* of Egypt confirm the presence of gavialoids in Africa (Hua & Jouve, 2004; Jouve *et al.*, 2006). Presence of this group later, in South America with the recently described *Aktiogavialis puertoricensis* from the Oligocene of Puerto Rico and the specimens from the late Oligocene–early Miocene from the Pirabas Formation of Brazil, suggests more significantly that gavialoid dispersal might have taken place during the Palaeocene, across the Atlantic and Indian Oceans, with marine-adapted forms. Gavialoids must have crossed the Atlantic at the end of the Eocene or the beginning of the Oligocene, when it was narrower than today (Buffetaut, 1982; Hua & Jouve, 2004; Jouve *et al.*, 2006, 2008). According to Brochu (2004), the Palaeocene North American thoracosaurids are usually found in marginal marine sediments. This supports the contention that the earliest gavialoids were marine or coastal animals.

The new material from the Lower Palaeocene of Oulad Abdoun Basin, Morocco (Jouve *et al.*, 2008) suggests that the South American gavialoids may not be monophyletic. This is particularly important, as the polyphyly may be the result of more exchanges between Africa and South America than was previously supposed by Sill (1970), Bocquentin Villanueva & Buffetaut (1981), Buffetaut (1982), and Langston & Gasparini (1997).

CONCLUSION

The geographical distribution of fossil gavialoids implies that marine barriers were breached and some basal lineages passed through a marine phase prior to establishing themselves in nonmarine settings (Vélez-Juarbe *et al.*, 2007; Jouve *et al.*, 2008). The specimens MPEG 1010-V, 227-V, 449-V, and 227-V appear to represent a gavialoid smaller than previously known South American gavialoids. Despite obvious morphological affinities with the South American gavialoids, the fragmentary state of the specimens described does not allow any more precise identification than indeterminate gavialoid. The discovery of the new specimens in the Neotropical region makes it possible to relate the new material collected with the gavialids from Puerto Rico. However, a direct relationship cannot be established. The few remains of this small predator *Gavialoidea* associated with invertebrates, fish, sea cows, and plants characterize the near-shore marine vertebrate fauna of the Pirabas Formation in north-eastern Brazil.

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