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FOSSIL CROCODILIANS FROM THE HIGH GUAJIRA PENINSULA OF

COLOMBIA, AND THE HISTORY OF NEOGENE CROCODILIAN DIVERSITY IN

TROPICAL SOUTH AMERICA

by

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FOSSIL CROCODILIANS FROM THE HIGH GUAJIRA PENINSULA OF

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University of Nebraska, 2014

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The greatest diversity of Cenozoic crocodilians occurred during the Miocene in equatorial South America. However, the origin of this high diversity and its relationship to environmental factors are poorly understood. Most described species come from localities assigned to Laventan (13.8-11.8 Ma) and Huayquerian (9.0-6.8 Ma) South American land mammal ages (SALMAS), whereas the record is sparse in the early to middle Miocene and after the latest Miocene and Pliocene. Field research in the Castilletes (early Miocene-Pliocene) Formation in the High Guajira Peninsula of Colombia provides new fossil data on the origin of Neotropical crocodylian diversity. The Castilletes Formation crops out most extensively in the Cocinetas Basin, and represent depositional environments consisting of deltaic and shallow marine systems in the lower Castilletes and predominately fluvial environments in the upper Castilletes. Crocodilian fossils from the Castilletes Formation include gavialoids, alligatoroids and crocodyloids. Gavialoid remains have been recovered from both terrestrial and shallow marine deposits in the lower Castilletes. Remains of the specialized caimanines *Purussaurus* and *Mourasuchus* extend the temporal range of both lineages into the early middle Miocene (15-16 Ma). These records suggest that high diversity crocodilian assemblages were already established by the early Miocene or late Oligocene.

Fossils from the upper Castilletes Formation include cranial elements identified as a non-tomistomine crocodyloid, some of them assigned to cf. *Crocodylus*. These records indicate that by the Pliocene, endemic assemblages were extinct, at least in the northern parts of the continent, allowing the establishment of *Crocodylus.* The pattern of crocodilian diversity in the Neogene of equatorial South America suggests that diversity was highly linked to hydrographic conditions. The development of high diversity assemblages developed in a time of greater connections among river drainages and mega-wetland systems. The isolation of river drainages and disappearance of mega-wetlands are correlated with the extinction of most crocodilian lineages. Aridity in peripheral drainages may have caused local extinctions outside Amazonia. The change from wetland to riverine conditions has been proposed as the cause of crocodilian extinctions in the western Amazon, but this remains to be tested.

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INTRODUCTION

The greatest diversity of crocodilians during the Cenozoic occurred during the middle and late Miocene of Equatorial South America (Fig. 1, A). Our knowledge of this diversity is based on fossil assemblages found in Peru (Fitzcarrald), Colombia (La Venta), Brasil (Acre) and Venezuela (Urumaco). In these localities at least seven species have been described (Riff, et al, 2009; Scheyer et al, 2013), whereas the highest number of extant species from the same region is four (e.g., Marioni et al, 2013). The fossil assemblages were composed of a diverse array of caimanine alligatoroids and gavialoids, together with the putative tomistomine crocodyloid *Charactosuchus* (Langston, 1965; Souza Filho, 1991; Souza Filho and Bocquentin-Villanueva 1989; Souza Filho et al, 1993). Terrestrial sebecid crocodiliforms were also present in middle Miocene localities (Langston, 1965; Busbey, 1986; Salas-Gismondi et al, 2007). Taxonomic diversity was accompanied by a high diversity of feeding ecomorphologies, including not only longirostrine, "generalized" (Brochu, 2003) and blunt-snouted forms present in modern crocodilians, but also extreme variations such as gavialoids with snouts longer than those of modern longirostrine crocodilians (Sill, 1970; Kraus, 1998; Brochu and Rincón, 2004); durophagous caimans (Scheyer et al, 2013), and *Mourasuchus*, a caiman with a broad, flat, elongated rostrum and a slender jaw (Price, 1964; Langston, 1966; Bocquentin-Villanueva, 1984). The range of size was also greater than in modern communities, with estimated lengths of 8 to 10 meters for representatives of the caiman *Purussaurus* (Langston, 1965; Bocquentin-Villanueva, 1989; Aguilera et al, 2006) and the gavialoid *Gryposuchus* (Riff and Aguilera, 2008).

In contrast with the high diversity of middle and late Miocene localities, the diversity of South American crocodilians is poorly known for the early–middle Miocene and the Pliocene. High diversity crocodilian assemblages of the middle and late Miocene are also geographically and stratigraphically disparate, and the most continuous record comes from the Urumaco sequence in Venezuela, ranging from the latest middle Miocene to the lower Pliocene (Scheyer, et al, 2013). The lack of a long, continuous, and geographically constrained record of crocodilian diversity for the Neogene of tropical South America limits the ability to infer the origins of New World crocodilian diversity, its relationship to environmental factors (climate, hydrography and faunal composition), and the timing and mode of the origin of modern crocodilian faunas.

Field research in a stratigraphic section encompassing the early Miocene through early Pliocene in the High Guajira Peninsula of Colombia (Fig. 1 B) has produced several crocodilian-bearing levels. This long and continuous record provides a unique perspective on histories of crocodilian diversity and faunal change in equatorial South America. Crocodilians representing the three living lineages (Alligatoroidea, Crocodyloidea, Gavialoidea) were collected at different levels of the sequence (Fig. 2). In this work I describe these specimens and discuss their significance in terms of the evolution of crocodilian communities during the Neogene.

Institutional abbreviations— STRI-CTPA: Center for Tropical Paleoecology and Archaeology, Smithsonian Tropical Research Institute, Panama; UCMP: University of California Museum of Paleontology.

Geological Setting— The Castilletes Formation crops out in the Alta Guajira Peninsula of Northern Colombia (Renz, 1960; Rollins, 1965; Irving, 1972). It is characterized by marly limestones, clays, calcareous and non-calcareous sandstones, and conglomerates. Toward the base of the formation, the limestones are coarse textured, marly, argillaceous, sandy fossiliferous, and fairly indurated. The clays are silty, brown to buff, gray, greenish-gray and reddish, with some sandy zones. Towards the top, the reddish-yellow sandstones and conglomeratic sandstones are more common, poorly sorted and with matrix supported in channel lenses. The unit rests conformably on the Jimol Formation and the upper contact is not exposed. The Castilletes Formation is ~340 m thick in the study area. The unit was deposited in a very shallow marine environment (Rollins, 1965) intermixed with continental facies produced by fan delta progradation and fluvial deposits. The Castilletes Formation is rich both in marine and terrestrial fossils including plants, bivalves, gastropods, crabs, fishes, turtles, crocodilians and mammals. Renz (1960) suggested an early Miocene age for the basal sediments based on the foraminiferan *Miogypsina antillea* (Cushman, 1919). Bürgl (1960) estimated a middle Miocene age based on invertebrate fossils, and Rollins (1965) proposed Miocene to Early Pliocene based upon its stratigraphic position between the middle Miocene Jimol formation and the overlaying Quaternary deposits. Additional age estimates are based on strontium isotope data taken from mollusks in the coquinas and shell beds of the Castilletes Formation. Strontium isotopes indicate an age of 17.5-10.0 Ma for the lower Castilletes, and 5-2.7 Ma for the upper Castilletes (Jaramillo et al., unpub. data).

Crocodilian fossils have been recovered from five localities representing different levels within the stratigraphic section (Fig. 2). Locality 390091 (Big Croc Locality), is approximately 8.7 km NW of Puerto Lopez. The section at this locality begins with approximately 1 m of fine grained sandstones representing the top of the Jimol Formation. The base of the Castilletes Formation is marked by a thin coquina with sandy matrix, which is overlain by grey, slightly laminated mudstone bed six meters thick that contains some trace fossils. These mudstones are overlain by a thick oyster bed, laterally grading to coquinas. On top of this layer there are four meters of highly bioturbated, massive, muddy, fine grained sandstones, overlain by a coquina that has an erosive base with horizontal trace fossils. Disarticulated vertebrate remains were found washed on top of this bed that is overlain by six meters of badly exposed grey mudstones and a coquina with sandy matrix of middle thickness. The 1.5 meters of this section overlaying the coquina are covered and overlain by another coquina and a 1 meter thick bed of medium-grained sandstone. Strontium isotopes of shells from the upper coquina yielded age estimates of 17.19 and 17.45 (Jaramillo et al., unpub. data).

Locality 390092 (Gharial Locality) is approximately 9 km NW of Puerto Lopez. At the base of this part of the section there is a coquina layer interposed between two light grey layers of sandy mudstone. Strontium isotopes of shells from this coquina yielded age estimates of 17.33 and 17.45 Ma (Jaramillo et al., unpub. data). Thin (<1 m) conglomeratic lenses are found on top of these layers, overlain by a 7 m bed of badly exposed grey mudstones. On top of these mudstones there is a set of layers made of conglomeratic, coarse grained sandstones with trough cross-bedding that contains

calcareous lenses with abundant mollusks. Cranial fragments of a gavialoid crocodilian, the only vertebrate specimen recovered from this part of the section, come from one of these lenses. The sandstone is overlain by another 7.5 m of grey mudstones. The top of the section at this locality there is a thick (approximately 1.8 m) bed of fossiliferous fine grained sandstone and coquina.

Locality 390090 (La Tienda) is approximately 8 km NW of Puerto Lopez. At this locality there is a 9 meter thick sequence of slightly laminated gray mudstones with intercalations of yellowish and reddish coquinas that can be continuous or forming lenses. The coquinas are thinner in the lower half of the section, being thicker towards the top. The thickest and uppermost coquina has calcareous concretions containing abundant portunid crabs. Shark and ray teeth are abundant in this locality, and isolated bone fragments can be also found. The concretions in the upper coquina contain more complete disarticulated bones. Strontium isotopes of shells from coquina levels yield age estimates between 16.89 and 17.51 Ma (Jaramillo et al., unpub. data).

Locality 390094 (Patajau Valley 1) is approximately 5.7 Km NW of Puerto Lopez. 15 m of yellowish and reddish mudstones comprise the lower and middle part of the section at this locality. These mudstones form the low topography at the center of the valley. Thin layers with abundant mollusk remains can be found interspersed with the mudstones higher in the section. These shell layers show lateral variation, with abundant oysters at some points and local concentrations of freshwater bivalves and gastropods. The top of the section at this locality is marked by a thick coquina with abundant mollusk remains.

Vertebrate fossils, including fish, turtles and mammals, are abundant in this locality. Both partial, disarticulated skeletons and isolated bones were found within the concentrations of fresh water mollusks. Strontium isotopes of shells from the vertebrate-bearing levels yield age estimates between 16.07 and 16.33 (Jaramillo et al., unpub. data).

Locality 390085 (Kaitamana Cemetery) is 6 Km NE of Castilletes and 1.2 km north of the Venezuelan border. In this locality, packages of reddish grey fossiliferous mudstone 2 meters thick alternate with coquinas 10-40 cm thick. The mudstones have abundant invertebrate remains and gypsum veins. Near the base of the lowermost mudstone there are elongate concretions with shells and isolated bones. A thin coquina separates this layer from the mudstone where crocodilian remains were found. The stratigraphic position relative to the contact with the Jimol Formation, marker beds, and fossil invertebrates indicate that the Kaitamana beds correlate with those in the Patajau Valley (Jaramillo et al., unpub. data).

The upper Castilletes crops out in Locality 390075 (Police Station), near the Venezuelan Border and north of Bahía Cocinetas. The lower part of this section is characterized by conglomeratic, coarse grained sandstone and conglomerates with subangular cobbles, in layers with planar and trough cross-bedding. Fish, reptile and mammal fossils, represented by disarticulated bones and teeth, occur in this part of the section. The conglomeratic layers grade into medium-grained sandstones with ripple-mark lamination and climbing ripples, and to mudstones with thin intercalations of very fine grained sandstones. The sandstones are arranged in fining-upward sequences 3 to 5 meters thick,

with erosive bases and channel geometries. Towards the top of the outcrop there is a thick, massive layer of coquina with an erosive base and ichnofossils. Strontium isotopes of shells from this coquina indicate an age of 5.0-2.7 Ma.

SYSTEMATIC PALEONTOLOGY

CROCODYLIA Gmelin, 1789

GAVIALOIDEA Hay, 1930

Gen. et sp. indet.

Materials—STRI-CTPA-16561: portions of the maxillae, nasals, frontal, prefrontals, lacrimals, jugals and palatines (Fig. 3A-B). STRI-CTPA-16567: Rostrum fragment of longirostrine crocodilian (Fig. 3 C-F). STRI-CTPA-16791: isolated axis and odontoid (Fig. 3 G-H).

Localities and Horizons— STRI-CTPA-16561was collected in locality 390092 "Gharial Locality", approximately 9 km W of Puerto Lopez. Lower Castilletes Formation (17.4 to 16.8 Ma; Jaramillo et al., unpub. data).

Description— This specimen includes fragments of the rostrum, the interorbital space, and the region just anterior and lateral to the orbits. Two fragments correspond to parts of the anterior half of the rostrum on the left side. Another, more posterior, section of the rostrum is preserved on both sides, and the portion of the rostrum closer of the orbits is represented by three additional fragments. The preserved fragments indicate that the

rostrum was long and slender. The surface of the rostrum was smooth, without ridges or elevated portions.

Maxilla— There are eight preserved fragments of the maxillae in STRI-CTPA-16561. The maxillae formed an elongated, slender rostrum as in other gavialoids. In dorsal view, the lateral surfaces of the maxillae are festooned with the laterally protruding rims of the alveoli. This festooning is more pronounced in two fragments, suggesting they were more anterior in the rostrum. There is no festooning on the lateral surfaces of those fragments that articulate with the jugals. The suture with the nasals is anteromedially inclined in a very acute angle relative to the midline. In lateral view, the alveolar edges are higher than the palatine surface, as in other gavialoids (Singh and Bustard, 1982; Hua and Jouve, 2004; Jouve et al, 2008). In ventral view, the preserved alveoli are all of similar size, and more closely spaced in the posterior fragments.

Nasals— Three fragments of the nasals are preserved, all of them in articulation with fragments of the maxillae. In dorsal view these fragments are long and slender, indicating that the nasals had long, slender anterior processes separating the maxillae in the midline in at least the posterior portion of the rostrum.

Frontal— Part of the anterior process of the frontal is preserved in STRI-CTPA-16561. In dorsal view the preserved portion of the frontal can be seen as a subrectangular, elongated element, slightly tapering towards its anterior end. The anterior process of the frontal extended far anterior to the anterior margin of the orbit. The section corresponding

to the interorbital space is narrow as in *Ikanogavialis* (Sill, 1970), *Piscogavialis* (Kraus, 1998), and *Siquisiquesuchus*, and unlike the broad plate seen in *Gryposuchus* and *Gavialis* (Sill, 1970; Kraus, 1998; Brochu and Rincón, 2004; Langston and Gasparini, 2007).

Prefrontals— In dorsal view, the preserved portions of the prefrontals are articulating on both sides of the frontal. The prefrontals are triangular, and longer than wide in dorsal view. The sutures with the frontal are almost parallel, whereas the lateral suture with the lacrimal is strongly inclined anteromedially. The tapering anterior portion of the prefrontals indicates that they were shorter than the frontal. Part of the orbital rim can be seen as a thickened ridge on the anteroposterior border of the right prefrontal.

Lacrimal— Portions of the lacrimals are preserved lateral to both prefrontals in STRI-CTPA-16561. In dorsal view, the preserved portion of the right lacrimal is roughly trapezoidal and inclined with respect to the midline. The left lacrimal is represented by a small, square fragment in dorsal view. The preserved contact with the prefrontal on the right side indicates that the lacrimal was longer than the prefrontal.

Jugals— The jugals preserved small portions of the anterior processes, articulated with the maxillae and lacrimals in the posterior portion of the rostrum. The preserved fragments indicate that the jugals were slender in the region close to the orbits, as in other longirostrine crocodilians.

Palatines— Portions of the palatines are preserved on the posterior fragment of the rostrum of STRI-CTPA-16561. In ventral view they are rectangular, longer than wide. The palatines comprise more than half the width of the ventral surface of the rostrum at this point. The lack of a lateral suture with the maxillae suggests that the anterior border of the suborbital fenestrae was anterior to the orbits.

Rostrum fragment from La Tienda locality— This is a small fragment of a rostrum at the level of the tooth row, preserving one complete alveolus and the interalveolar spaces anterior and posterior to it (Fig. 3 C-F). The lateral surface of STRI-CTPA-16567 is flat and inclined relative to the tooth row. The fragment is elongated and roughly rectangular in external view. The lateral surface is flat and inclined, with small neurovascular foramina. The lateral margin is festooned, as the alveoli are laterally extended relative to the interalveolar spaces. In lateral view the buccal surface is elevated, indicating that the tooth rows were lower than the buccal surfaces, as in gavialoids (Singh and Bustard, 1982; Hua and Jouve, 2004; Jouve et al, 2008). In ventral view the buccal surface is curved and continuous with the surface of the interalveolar spaces. Two nutrient foramina are found on this surface, medial to the tooth row. One is on the posterior interalveolar space, and other medial to the anterior rim of the preserved alveolus. In medial view, internal portions of the alveoli can be seen. These are anterolaterally oriented. A long cylindrical cast of sediment on the medial surface, just medial to the alveoli, could represent the passage for the meckel's cartilage or the trigeminal nerve.

Isolated axis and odontoid— The axial centrum and odontoid are complete, but the neural arch only preserves small portions attached to the centrum (Fig. 3 G-H). The external surface is worn. The odontoid is fused to the axial centrum. In dorsal view the element is roughly hourglass-shaped, with a wider anterior portion formed by the odontoid diapophyses. There is an elongated foramen on the floor of the neural canal. In lateral view the centrum has a roughly rectangular outline, with anterior and posterior prominences formed by the odontoid process and the posterior end of the centrum. In lateral view the odontoid process slopes downwards, and near the dorsal margin the neurocentral suture can be seen. In ventral view the anterior portion of the centrum lacks a prominent keel formed by the hypapophysis. It has instead a shallow depression, laterally bordered by two low crests that extend by approximately half the length of the centrum. This divided, or forked hypapophysis is characteristic of both gavialoids (Brochu, 1997) and the giant caiman *Purussaurus neivensis* (Langston, 1965; Brochu, 1999). However, the hypapophyseal crests in *P. neivensis* are more projected ventrally, forming two prominent knobs on the ventral surface of the centrum. Also, the fused odontoid in STRI-CTPA-16791 suggests this is a mature individual (Brochu, 1996), and this axis is smaller (axis and odontoid length 66.04 mm) than this element is in the giant caiman *Purussaurus* (126 mm; Langston, 1965).

ALLIGATOROIDEA Gray, 1844

ALLIGATORIDAE Cuvier, 1807

Gen. et sp. indet (Fig. 4)

Materials— STRI-CTPA-17145: fragment of right maxilla (Fig. 4A-F), frontal? (Fig. 4G-H), and four incomplete vertebrae (Fig. 4I-P)

Localities and Horizons— STRI-CTPA-17145 was collected in Locality 390091, approximately 9 km NW of Puerto Lopez. Lower Castilletes Formation (approximately 7.4 Ma; Jaramillo et al., unpub. data), approximately 13 meters above the contact with the underlying Jimol Formation.

Maxilla— This element comprises part of the right posterior process. It preserves part of the lateral and palatal surfaces of the maxilla. In dorsal and ventral views this element is roughly rectangular. The dorsal surface is worn; near the posterior side there is an opening that represents the passage for the maxillary ramus of the trigeminal nerve. In lateral and medial view the maxilla fragment has a roughly square outline. The posterodorsal and anteroventral corners of the fragment are projected so that the anterior and posterior margins are oblique in lateral and medial view. The lateral surface is curved and shows several foramina for the small nerves of the Integumentary Sense Organs (e. g. Jackson, et al, 1996; Soares, 2002; Leitch and Catania, 2012). The ventral surface includes five alveolar rims, of which the first and fifth are incomplete. The alveoli are filled with sediment, closely spaced and become smaller towards the posterior end. Only the first alveolus preserves part of the original tooth. There are four nutrient foramina on the palatal surface, medial to the septa separating alveoli. The alveoli are completely surrounded by the palatal surface of the maxilla, which is wide medial to the tooth row. This maxillary shelf separating the toothrow from the ectopterygoid, is a synapomorphy

of Alligatoroidea (Brochu, 1999). The passage for the maxillary branch of the trigeminal nerve can be seen again in posterior view, as an opening on the broken surface of the maxilla, just lateral to the last alveolus.

frontal─ A partial frontal is preserved in STRI-CTPA-17145. In dorsal view it is roughly trapezoidal, with a concave margin as part of the orbital rim and a convex posterior margin that represents the suture with the parietal. This border indicates that that the frontoparietal suture was entirely on the surface of the skull table, as in alligatorids (Brochu, 1999). In ventral view this element has a shallow, elongate depression representing the groove for the olfactory tract.

Vertebrae─ Remains of four vertebral centra are preserved in STRI-CTPA-17145. All of them are worn and external surfaces are not discernible. Two of them comprise only the concave anterior end of centra, and two others are incomplete centra with portions of the neural arches. All preserved vertebrae have unfused neurocentral sutures, indicating a still inmature animal. The most complete centrum (Fig. 4I, J) is 90.35 mm long.

CAIMANINAE Brochu, 1999

Cf. *PURUSSAURUS* sp. Barbosa-Rodrigues, 1892

(Fig. 5A-Q)

Materials— STRI-CTPA-16800, tooth fragment. STRI-CTPA-16802, isolated tooth. STRI-CTPA-16803, isolated tooth. STRI-CTPA-16804, Small incomplete osteoderm. STRI-CTPA-16806, incomplete osteoderm.

Localities and Horizons— All specimens come from locality 390094, Patajau Valley, approximately 5.7 km NW of Puerto Lopez. Middle Castilletes Formation (16.3 to 15.5 Ma; Jaramillo et al., unpub. data).

Teeth— Referred teeth are thick, blunt, and their basal section is round. The basal diameter is approximately 0.8 times the crown height for STRI-CTPA-16802 and STRI-CTPA-16803. STRI-CTPA-16800 is represented only by the upper half of the crown. The preserved portions of enamel have a wrinkled surface, which is more marked near the tip of STRI-CTPA-16800. This wrinkling becomes less marked towards the base, where only a fine striation is present. There are two main carinae on the mesial and distal sides of the teeth, but the enamel on the labial and lingual surfaces is not fluted to form secondary carinae. The mesial and distal carinae have an appearance superficially similar to that seen in ziphodont teeth (Langston, 1975). However, the carinae have thin perpendicular crests rather than true denticles. These crests are anastomosed and continuous with the wrinkles on the labial and lingual surfaces. These teeth can be better described as false-ziphodont teeth (Legasa et al, 1994; Prasad and Broin, 2002; Andrade and Bertini, 2008). The overall morphology of these teeth is indistinguishable of that described for the caimanine *Purussaurus* (Langston, 1965; Aguilera et al, 2006). The teeth of *Purussaurus mirandai* have been previously described as having "denticles" on their carinae surfaces

(Aguilera et al, 2006). These structures most likely correspond as the perpendicular crests of false-ziphodont teeth, as those on the teeth of *Purussaurus neivensis*.

Osteoderms— In external view, these osteoderm fragments have flat, linear broken surfaces. The preserved outline is roughly semicircular in STRI-CTPA-16804 and trapezoidal in STRI-CTPA-16806. The external surface is smooth and has small foramina, but lacks the ornamentation pits typical of crocodilian osteoderms (Buffrenil, 1982). Both specimens are very thick compared to crocodilian osteoderms of similar size. There are no sharply defined keels, the external surface is raised in the middle and slopes to the sides in an angle of 20-25°. The ventral surface is flat in STRI-CTPA-16804, whereas there is a soft concavity in STRI-CTPA-16806.

These osteoderms are similar to those described for specimens of *Purussaurus brasiliensis*, *P. neivensis* and *P. mirandai* (Mook, 1921; Langston, 1965; Scheyer and Moreno, 2010). The lack of ornamentation pits on the external surface of these osteoderms has been interpreted by previous authors as an artifact of preservation (Mook, 1921; Langston, 1965). However, the pitting pattern is not evident in a thin section of a *P. mirandai* osteoderm (Scheyer and Moreno-Bernal, 2010), indicating that thick, unornamented osteoderms are diagnostic for the genus *Purussaurus*.

Cf. *MOURASUCHUS* sp. Price, 1964.

(Fig. 5R-W)

Materials— STRI-CTPA-16558: maxillary fragment and associated lacrimal.

Localities and Horizons— This specimen comes from locality 390085 (Kaitamana), 4.5 Km west of Castilletes and 1.2 km north of the Venezuelan border. Middle Castilletes Formation (16 Ma; Jaramillo et al., unpub. data).

Description— This specimen comprises a small fragment of a maxillary and a lacrimal; both found less than 5 cm away from each other.

Maxila— This fragment comprises a small section of the tooth row region preserving a complete alveolus and a small portion of a second. The lateral and medial surfaces can be distinguished, whereas the orientation of the fragment along the anterior-posterior axis is uncertain. In dorsal view, the fragment is elongated and roughly rectangular with one concave end formed by the rim of the incomplete alveolus. The complete alveolus is straight and vertically oriented. Lateral to this alveolus there is a narrow groove that represents the passage for a neurovascular foramen. The lateral surface is trapezoidal, vertically parallel to the alveoli and ornamented with tiny foramina. The interalveolar spaces are elevated with respect to the level of alveolar rims. In medial view the fragment has a roughly triangular shape. The surface medial to the tooth row is less vertical than the lateral surface. In medial view the space between the two preserved alveoli is elevated only on the lateral side, the medial portion of the interalveolar space being lower than the alveolar rims. In ventral view the fragment has the same roughly rectangular outline as in dorsal view. The complete alveolus is 5 mm wide and 6 mm long and interalveolar space

is 5 mm long, almost as long as the preserved alveolus. The alveoli are vertically oriented

unlike the oblique, overlapping alveoli of some longirostrine crocodilians, making

impossible to distinguish the anteroposterior orientation of the fragment. There is a

shallow semicircular pit in the interalveolar space. This pit is more medially placed than

both alveoli; its lateral rim is thicker and higher than the medial one.

Lacrimal— The lacrimal preserves most of the dorsal surface, including parts of the

orbital rim and the lateral contact with the maxilla and jugal. The anterior process and the

medial contact with the nasal and prefrontal are broken. Most of the ventral surface is

lacking in this element. In dorsal view the lacrimal is triangular, with a posterior concave

margin formed by the orbital rim. The dorsal surface has a thick longitudinal canthus on

its medial portion. This canthus lays entirely on the Lacrimal, as the surface medial to it is

flat, and is posteriorly continuous with the raised orbital margin. The lateral portion of the

dorsal surface has a C-shaped, laterally open concavity bordered by the canthus and the

orbital margin. The dorsal surface is ornamented with pits that are rounder and smaller on

the canthus and the orbital rim, becoming bigger and more oval in the low surfaces.

In lateral view the lacrimal has a roughly triangular outline. The dorsal margin is almost

flat near the orbital margin, and becomes steeper anteriorly. The orbital margin is higher

medially and slopes laterally and posteriorly. The ventral margin is horizontal in lateral

view. The lateral contact with the maxilla and jugal is a thin horizontal slit that is

internally divided by a thin, diagonal posterior crest. This crest may represent the site

where the maxilla and jugal meet on the lateral margin of the lacrimal. The thin lamina

ventral to the slit is broken. This broken lamina likely represents the lateral portion of the Lacrimal that is overlapped by the maxilla and jugal in crocodilians (Busbey 1997). In medial view the dorsal and ventral margins of the lacrimal are posteriorly parallel, converging anteriorly as the dorsal margin slopes down. The surface of the canthus is almost vertical, and the broken surface of the lamina medial to it is horizontal.

In anterior view this element is roughly triangular, with a broad base and a flattened upper angle. The orbital rim is elevated, and slopes laterally, unlike gavialoids, in which the lateral portion of the lacrimal orbital rim is raised. In anterior view the broken surface of the anterior process and the lateral contact of the lacrimal meet on the ventral margin. There is a ventral concavity that represents the anterior opening of the nasolacrimal duct. In posterior view the outline is also triangular as in anterior view. The posterior opening of the nasolacrimal duct can be seen on the internal surface of the orbit. There are three smaller foramina on the internal surface of the orbit. Two of these foramina lay dorsal to the nasolacrimal duct opening, and one lateral to it. Part of the articulation with the prefrontal can be seen as a notch on the medial portion of the ventral margin.

In ventral view the lacrimal is roughly triangular with a concave posterior margin, as it is in dorsal view. The ventral surface is broken, exposing part of the nasolacrimal duct, which is tear-shaped, with straight, anteriorly converging lateral margins and a rounded, convex posterior margin. Part of the contact with the maxilla and jugal can be seen on the lateral margin of the ventral surface. Medial to the nasolacrimal duct the ventral surface is

transversely concave, lateral to it the surface is broken anteriorly. Part of the articulation with the prefrontal can be seen on the posteromedial portion of the lateral surface.

CROCODYLIDAE Cuvier, 1807

Gen et sp. indet

(Fig. 6)

Materials— STRI-CTPA-12939: partial premaxila (Fig. 6A-C). STRI-CTPA-16180, skull and mandible fragments including portions of the frontal, parietal, supraoccipital, right postorbital, right squamosal, left jugal, left dentary, left angular, left surangular, and four partial osteoderms (Fig. 6D-R).

Localities and Horizons— Both specimens come from Locality 390075, near the border with Venezuela. They were collected in fluvial sandstones of the Upper Castilletes Formation. Early Pliocene (5 to 2.7 Ma; Jaramillo et al., unpub. data).

Partial premaxilla— STRI-CTPA-12939 comprises part of a right premaxilla preserving part of the narial rim and parts of the third, fourth and fifth alveoli. The anterior, medial and posterior portions of the premaxilla are lacking, as well as most of the palatal surface medial to the alveoli. In dorsal view, this element is roughly semicircular, with a truncated anterior margin. The lateral border is curved and convex, with a short but deep posterior concavity that represents a notch for the fourth mandibular tooth. The medial margin of the dorsal surface is concave in the first two thirds of the element, following the narial

opening rim. The narial rim is flush with the dorsal surface of the premaxilla. Part of the palatal process of the premaxilla can be seen projecting medially inside the narial opening. Posterior to the narial rim the premaxilla is broken. The dorsal surface of the premaxilla is worn and ornamentation pits are not discernable on the surface.

In lateral view the dorsal margin is linear on the anterior portion of the narial rim, becoming higher posterior to it. The ventral border is convex and undulated in most of the element, becoming strongly upturned near the posterior end, where the notch for the fourth mandibular tooth is placed. Above this notch, only a small part of the premaxilla is preserved. The lateral surface is marked by a row some neurovascular foramina close to the alveolar margin. In medial view the premaxilla the internal surfaces of the fourth alveolus and the narial opening. A deep cylindrical cavity, projects anterodorsally from the rim of fourth alveolus and may represent the internal cavities of both the third and fourth alveolus. The internal cavity of the narial opening can be seen in medial view as concave surface, with an anteriorly truncated margin. The preserved narial cavity is bounded dorsally by the narial rim, ventrally by the palatal process and posteriorly by the broken base of the ascending process. Ventral to the narial cavity, the palatal process of the premaxilla slopes lateroventrally.

The palatal surface medial to the tooth row is broken and the incisive foramen rim is not preserved. A small cavity portion preserved on the anterolateral portion of the element may represent either the posterlateral rim of the third alveolus or an occlusal pit. Posterior to this cavity, the fourth alveolus preserves the lateral, posterior and most of the medial

rim. The fifth alveolus is complete. Between the fourth and fifth alveolus there is a deep occlusion pit that is placed very close to the lateral margin of the premaxilla, indicating that tooth occlusion was interdigitating. The lateral margin is broken and worn immediately posterior to the fifth alveolus, on the anterior side of the notch for the fourth mandibular tooth. The palatal surface preserved medial to the alveoli is broken and does not extend to the midline. The palatal surface is smooth, with some nutrient foramina medial to the alveoli.

Fragments of skull and mandible— STRI-CTPA-16180 is comprised of several associated fragments with ornamentation patterns consistent with skull or mandibular fragments. It includes portions portions of the frontal, parietal, supraoccipital, right postorbital, right squamosal, left dentary, left angular, left surangular, two osteoderm fragments and five indeterminate fragments.

 Frontal— The frontal is almost complete, lacking the tip of the anterior process and part of the ventral processes. In dorsal view, the preserved portion of the anterior process is narrow with subparallel margins, and the portion between the orbital rims is expanded and roughly trapezoidal. The suture with the prefrontals is convex and marks the transition between the anterior process and the interorbital plate. The frontal is wider than long between the orbital rims. The posterior suture with the postorbitals and parietal is concave. The dorsal surface of the frontal is gently concave and covered by ornamentation pits, which are larger towards the midline. There is a short sagittal crest, bordered by aligned ornamentation pits, between the orbit rims. The orbital rims have a

smooth surface but they are not particularly thickened. In ventral view there is a groove for the olfactory tract.

Jugal— A portion of the left jugal is preserved in STRI-CTPA-16180. The preserved portion represents part of the infraorbital arcade. Part of the lateral surface is broken, together with the ventral, anterior and posterior margins. All the remaining surfaces are worn. In dorsal view the jugal fragment has an hourglass-like outline. Part of the orbital rim is preserved as a longitudinal crest that becomes wider posteriorly. The orbital rim separates a flat lateral surface and a concave medial surface. This crest represents the orbital rim is wider near the posterior end of the jugal.

Postorbital— A fragment of the dorsal plate, posterior to the right postorbital bar is preserved. The preserved portion of the postorbital has a roughly square outline in dorsal view. The lateral border is worn and sinuous. The smooth, concave medial border represents the lateral rim of the supratemporal fenestra. The anterior margin is truncated and the posterior border is convex. The dorsal surface is ornamented with pits that become more elongated posteriorly. In lateral view the dorsal surface of the postorbital is flat. The postorbital ventral margin is anteriorly convex and posteriorly concave. In medial view the rim of the supratemporal fenestra can be distinguished as a smooth vertical surface. In anterior view the broken surface is anteriorly inclined and the ventral margin is convex. The posterior surface of the postorbital has a series of intercalating grooves and crests representing part of the contact with the squamosal.

Parietal— The preserved portion of this element comprises the dorsal surface of the posterior plate, and a short portion of the interfenestral bar. The anterior process is not preserved. The ventral surface is partially worn, and details such as the passage for the temporoorbital artery are not visible. In dorsal view the posterior plate of the parietal is roughly square. The posteriomedial rim of both supratemporal fenestrae is preserved. The rims are not very thickened; they rise above the surface of the parietal. The supratemporal fenestrae rims are curved and do not show the overgrowth typical of caimans (Brochu, 1999). The parietal plates are anteroposteriorly broad posterior to the supratemporal fenestrae, indicating that the posterior edges of the fenestrae were thick (Jouve, 2004). The posterior margin of the parietal is curved and posteriorly convex, with a triangular notch in the midline where the supraoccipital is articulated. The dorsal surface of the parietal has large ornamentation pits, separated by slender crests. In ventral view, the parietal is worn, exposing the internal structure. Near the posterior border there is a small ovoid cavity, likely representing the mastoid atrium. This cavity does not continue anteriorly into an expanded parietal sinus as in alligatorids and gavialoids (Brochu, 1997).

Squamosal— The dorsal surface of the right squamosal is preserved. In dorsal view the anterior portion of the squamosal is a roughly rectangular, with a triangular posterolateral projection formed by the squamosal prong. On the anteromedial corner a smooth, concave internal surface represents the lateral rim of the supraoccipital fenestra. The lateral margin of the squamosal is laterally bowed, indicating that the skull table was posteriorly wide. The posterior margin, medial to the squamosal prong, is concave. The squamosal is ornamented with deep pits in most of the dorsal surface. Near the margins

the surface is smooth, particularly on the lateral margin, which is thickened and dorsally convex.

Supraoccipital— A fragment of the dorsal process of the supraoccipital is wedged on the posterior margin of the parietal. In dorsal view the supraoccipital is small and roughly triangular. The supraoccipital does not exclude the parietal from the posterior border of the skull table.

Dentary— Part of the posterolateral surface of the left dentary is preserved. The fragment is anteroposteriorly elongated, with broken margins. The dorsal margin has an anterior elevation that includes the lateral border of an enlarged alveolus (probably the eleventh alveolus). Posterior to this alveolus, the dorsal margin of the dentary slopes upwards. The margins of other alveoli are not preserved as the dorsal margin is worn. The lateral surface of the dentary is vertically oriented and laterally convex. The lateral surface of the dentary has several neurovascular foramina of different sizes that open on the worn internal surface. Foramina on the posterior portion of the lateral surface have their posterior margin expanded into a groove. There are some elongated ornamentation pits near the posteroventral portion of this element.

Surangular— A fragment of the lateral surface of the left surangular, comprising part of the rim around the glenoid fossa and the lateral surface ventral to it, is preserved in STRI-CTPA-16180. In dorsal view, the surangular fragment is long and narrow, with an irregular outline. The dorsal surface slopes laterally, becoming higher posteriorly where

part of the dorsal process of the surangular is preserved. A shallow longitudinal groove, with a row of ornamentation pits on its bottom, lies just lateral and anterior to the dorsal process. Some foramina also lie on the bottom of this groove. The dorsal surface of the surangular is smooth, excepting for the foramina and pits on the lateral groove.

In lateral view this element has an irregular outline, with broken ventral, anterior and posterior margins. The dorsal margin becomes progressively elevated in the two anterior thirds. On the posterior third of the dorsal margin a shallow depression separates the anterior elevation from a higher one that represents the beginning of the dorsal process of the surangular. The ventral portion of this element is a flat plate heavily ornamented with pits of different sizes. In medial view, the surface of the surangular is rough and marked by neurovascular foramina that open externally on the dorsal groove. This configuration is similar to that seen in Neotropical species of *Crocodylus*, and almost identical to the same region in STRI-CTPA-16211.

Angular— A small piece of bone is interpreted here as a fragment of the lateral surface of a left angular. This element has a roughly ovate outline, with broken, festooned margins. Approximately one third of its surface is covered by ornamentation pits of different sizes; the rest of the element is smooth. The ornamented and smooth surface slope in opposite directions and meet at a very open angle. This configuration is similar to that on the lateral surface of the angular, where a diagonal ridge separates an ornamented anterior surface of a posterior smooth surface in some crocodilians (e. g., Iordansky, 1976).

Osteoderms— STRI-CTPA-16180 preserves four osteoderms, they are broken and their surfaces are worn. Their preserved borders indicate that these elements were subrectangular and had well defined keels. On the external surfaces of two of them there are circular ornamentation pits between 5 and 10 mm.

Discussion— STRI-CTPA-16180 lacks the parietal sinus found in alligatoroids and gavialoids. This feature is a synapomorphy of Crocodyloidea (Brochu, 1997). Other features, even though not diagnostic, are consistent with those found in crocodyloids. The supratemporal fenestrae have well defined rims, unlike most caimans, in which the supratemporal fenestrae are closed by the overgrowth of skull table bones (Brochu, 1999). The dorsal exposure of the supraoccipital is very small, unlike the large element seen in caimans (Brochu, 1999). The parietal plates are anteroposteriorly broad posterior to the supratemporal fenestrae, unlike those of South American gavialoids and *Gavialis* (Jouve, 2004). The robusticity of the dentary fragment relative to other elements of STRI-CTPA-16180 indicates that STRI-CTPA-16180 does not represent a longirostrine form.

Cf. *CROCODYLUS* sp. Laurenti, 1769

(Fig. 7)

Materials— STRI-CTPA-17702: posterior fragment of a right mandibular ramus (Fig. 7).

Localities and Horizons— This specimen comes from Locality 390075, near the border with Venezuela. It was collected in fluvial sandstones of the Upper Castilletes Formation. Early Pliocene (5 to 2.7 Ma; Jaramillo et al., unpub. data).

Description— STRI-CTPA-17702 is the posterior portion of a right mandibular ramus, posterior to the mandibular external fenestra, and including the tip of the retroarticular process. It comprises portions of the articular, surangular and angular.

Surangular— The surangular is incomplete posterior to the external mandibular fenestra. In lateral view, the surangular is elongated, with parallel dorsal and ventral margins, lateral to the glenoid fossa. The surangular tapers posterior to the glenoid fossa, sending a slender process that extends almost to the end of the retroarticular process. The dorsal process of the surangular in STRI-CTPA-17702 is truncated, and a portion of the articular can be seen laterally, as in *Crocodylus* and *Voay robustus* (Brochu, 2000, 2007). In dorsal view, the surangular-articular suture is strongly bowed laterally within the glenoid fossa, as in other crocodyloids. The lingual foramen for the articular artery and alveolar nerve is located on the suture between articular and surangular, as seen in *Alligator*, *Crocodylus* and *Osteolaemus*, and unlike the condition seen in the Caimaninae or *Gavialis* (Brochu, 1999).

Articular— This element is almost complete, missing only part of the anterior process and the medial flange of the retroarticular process, and part of the glenoid fosa posterior rim. The dorsal surface of the glenoid fossa is divided by a diagonal elevation into two hemifossae, of which the lateral one is larger. The foramen aerum is located in the medial margin or the articular, just posterior to the glenoid fossa, in contrast to the dorsally shifted position seen in all alligatoroid crocodilians (Brochu, 1999). The retroarticular

process of STRI-CTPA-17702 is posterodorsally projected and higher than the posterior edge of the articular fossa. The anteroposterior crest on the dorsal surface of the retroarticular process is not as tall and sharp as it is in *Gavialis* (Langston and Gasparini, 1997; Brochu and Rincón, 2004). In lateral view, a portion of the articular, posterior to the glenoid fossa, can be seen above the truncated dorsal process of the surangular. In medial view, the ventral tip of the articular is broken. The medial surface of the articular is extended dorsally to the lingual foramen for the articular artery, as in osteolamines and *Crocodylus* (Aoki, 1992; Brochu, 1997).

Angular— In lateral view, the ventral margin of the angular is broadly convex. Posterior to the glenoid fossa, a tapering process extends onto the retroarticular process. The lateral surface of the angular is rugose anteriorly and smooth on the retroarticular process. In medial view, the articular is a pointed, thin exposure wedged ventral to the articular. This

 medial surface of the angular is narrow and does not extend to the tip of the retroarticular process. The angular is slender ventral to the articular in medial view, unlike the dorsoventrally high exposure seen in alligatorids (Mead, et al 2005).

Discussion— STRI-CTPA-17702 has several characters found in Crocodyloidea. The surangular-articular suture laterally bowed on the glenoid fossa is a crocodyloid character, and a process dorsal to the lingual foramen for the articular artery and alveolar nerve is found both in *Crocodylus* and osteolamines. The position of the lingual foramen on the surangular-articular suture is also shared by *Alligator*. However, the foramen aerum in

STRI-CTPA-17702 is located in the medial margin or the articular, and not dorsally shifted as in all alligatoroids (Brochu, 1999). The dorsal process of the surangular in *Osteolaemus* is not truncated and the articular is not visible in lateral view, thus discarding the assignment to this last genus. The combination of characters of STRI-CTPA-17702 is also found in *Voay robustus* (Brochu, 1999). However, the retroarticular process in STRI-CTPA-17702 is more curved and higher than the edge of the articular fossa in lateral view. This is unlike the condition in *V. robustus*, where the retroarticular process is shorter, less curved, and lower than the posterior edge of the articular fossa (Brochu, 2007).

EUSUCHIA Huxley, 1875

Incertae Sedis

(Fig. 8)

Vertebrae— Ten isolated postaxial vertebrae have been recovered from different levels of the Castilletes Formation (Fig. 8). six vertebrae are dorsals, three are cervicals, one is a caudal and two are represented only by centra. All vertebrae have strongly procoelus centra and represent eusuchian crocodilians. A posterior cervical (STRI-CTPA-16422) from locality 390085 and an anterior dorsal (STRI-CTPA-16789) from locality 390094, both of similar size (centrum length: 35.89 and 37.41 mm, respectively) have completely fused neurocentral sutures. Fusion of neurocentral sutures in crocodilians is a reliable indicator of maturity (Brochu, 1996), and its presence in vertebrae from the anterior portion of the body of relatively small crocodilians indicates the presence of small, still

unidentified taxa. A larger vertebral centrum (STRI-CTPA-16788) collected in locality

390094 has an open, rugose sutural surface (Fig. 8 W-X).

Most crocodilian vertebrae from locality 390075 are cervicals (STRI-CTPA-16167,

16296) or anterior dorsals (STRI-CTPA-16203). All of them have completely fused

neurocentral sutures. Three anterior dorsals (STRI-CTPA-17704) were found articulated.

A smaller dorsal vertebra (STRI-CTPA-16320) has unfused neurocentral sutures. The

largest vertebra from locality 390075 has a long transversal process (STRI-CTPA-19554),

and may represent a posterior dorsal or a lumbar element.

Cf. EUSUCHIA Huxley, 1875

Gen et sp. indet.

(Figs. 9-10)

Indeterminate skull fragments— A rostrum fragment (STRI-CTPA-16334), including

the external half of an alveolus, was found in locality 390085 (Fig. 9A-C). This fragment

is narrow and elongate; the anterior and posterior ends are truncated by oblique fractures.

In dorsal view the lateral margin is straight, without festooning. In lateral view the

external surface is ornamented with pits and foramina. In medial view the alveolar cavity

is strongly inclined in anterolateral direction. In ventral view there is a shallow depression

laying slightly lateral to the alveolar rim. This depression likely represents an occlusion

pit. This rostrum fragment most likely represents a longirostrine crocodilian.

Additional skull fragments representing crocodilians of several sizes, were collected in the early Pliocene Police Station locality (Fig. 9). An isolated fragment (STRI-CTPA-13109) includes portions of the left lacrimal and jugal (Fig. 9 D-F). In dorsal view this fragment is of irregular outline and preserves a short curved portion of the orbital rim near its posteromedial margin. The suture between the lacrimal and the jugal is straight. In ventral view the lacrimal surface is marked by an elongated depression corresponding to the nasolacrimal duct. A small fragment (STRI-CTPA-16352) likely represents the posterolateral corner of the right squamosal, including a small portion of the dorsal plate, the fossa for the ear flap and the squamosal prong (Fig. 9G). An irregular, elongated fragment (STRI-CTPA-16240) has a very ornamented and convex external surface. It represents the lateral surface of the rostrum either on the maxilla or the infraorbital arcade of the jugal (Fig. 9H).

Teeth— Crocodilian teeth from different levels of the Castilletes Formation are similar in size and shape to those of modern crocodilians. These include both broad and more slender, pointed forms (Fig. 9K-Y). An isolated tooth (STRI-CTPA-17158) from locality 390094 is distinct from the blunt teeth collected in the same level and described here as cf. *Purussaurus*. This tooth is very slender and curved, with a rounded basal section. Its basal diameter (7 mm) is approximately a fifth of its length (36 mm). The carinae on the mesial and distal sides of the tooth are sharp, with smooth surfaces devoid of serrations or striations. The enamel on the labial and lingual surfaces is flutted, which forms thin secondary carinae. These carinae are parallel and regularly spaced at approximately 1 mm of each other, and 2 mm from the mesial and distal carinae. This tooth likely belongs to a

longirostrine crocodilian. Similar teeth have been described for South American gavialoids such as *Gryposuchus* (Langston and Gasparini, 1997) and *Piscogavialis* (Kraus, 1998). A small, isolated tooth (STRI-CTPA-16554) from locality 390085 is also of the slender and pointed type (Fig. 9O-P). However, the secondary carinae on this tooth are very marked and almost as prominent as the main carinae. Similar teeth are found in specimens of the alligatorid *Mourasuchus atopus* (UCMP 3812; UCMP 40177).

Most teeth from the Upper Castilletes locality 390075 are broad and pointed, with labial and lingual surfaces strongly fluted (Fig. 9Q-S). This fluting produces secondary carinae that are more separated near the base of teeth, converging near the tip of the tooth. The enamel surface in these teeth has fine microscopic wrinkles. Teeth with this ornamentation have varying width/length proportions, suggesting different positions in the jaw. Other teeth from the same locality have smooth enamel and less marked secondary carinae (Fig. 9T-Y). This ornamentation pattern is present only in teeth that are more slender and curved, suggesting that these teeth may come from a more homodont, perhaps longirostrine form.

Coracoid— A partial crocodilian coracoid (STRI-CTPA-16189) was collected in locality 390075 (Fig. 10 A-B). This element preserves the glenoid process, most of the shaft, and the posterior portion of the blade. In lateral view, this element is relatively wide compared to other crocodilians. The contact with the scapula is not preserved and it is not possible to discern if a scapulocoracoid synchondrosis was present (Brochu, 1995).

Ilium— A small isolated left ilium (STRI-CTPA-16781) was collected in locality 390094 (Fig. 10C-D). The lateral surface and its borders are well preserved, only a little part of the border between the ischiadic articular processes, and a section below the posterior process, are broken. The internal surface is worn near the dorsal edge, and the anterior and posterior sacral articular surfaces are broken. In lateral view, the anterior ischiadic process is dorsoventrally wide. The ischiadic articular surface is ventrally, rather than anteroventrally oriented. The anterior edge of the iliac blade is almost vertical above the ischiadic process, lacking the anterior process found in gavialoids (Brochu, 1997). The supraacetabular crest is dorsoventrally thin. The dorsal edge of the ilium is convex and has a modest indentation on its posterior portion. The posterior process is shorter than in other eusuchians, comprising less than a third of the ilium. The ventral surfaces of anterior and posterior ischiadic surfaces are both horizontal and lie on almost the same level.

Osteoderms— four small osteoderms (STRI-CTPA-16336, 16424, 16415, 16426) were recovered from locality 390085. They are roughly rectangular, being longer than wide (Fig. 10E-H) and flat to slightly convex. Two of these osteoderms have low, thin keels on the posterior half of the dorsal surface. Lateral surfaces have irregular projections, suggesting that they were articulating with other elements.

Osteoderms collected in locality 390075 are similar to those of large size (>3 m) living crocodilians (Fig. 10 I-O). They are flat to slightly convex, with a sharply defined keel running through most of the length of the osteoderm. These elements are ornamented with

circular and oval pits in a radiating pattern from the keel. Some of these osteoderms (STRI-CTPA-16240, 17136, 20337, 20432) are wider than long, roughly square or with a straight medial and convex lateral margins (Fig. 10 I-M). These probably represent elements of the dorsal shield. Other osteoderms (STRI-CTPA-16215, 19620) have a rounded outline with irregular margins, and can be interpreted as lateral elements (Fig. 10 N-O).

DISCUSSION

Miocene faunas of the lower and middle Castilletes Formation— The number of described South American crocodilians is higher for the Miocene than for any other epoch of the Cenozoic (Riff, et al, 2009); however, most species come from four high diversity assemblages assigned to the middle Miocene Laventan (13.8-11.8 Ma) and the late Miocene Huayquerian (9.0-6.8 Ma) South American Land Mammal ages (SALMAS) (Fig. 11A). Older crocodilian records such as those from the Parangula Formation (Paolillo and Linares, 2007) or the Castillo Formation (Brochu and Rincón, 2004) are less well known, each with only one described species (Fig. 11A). An additional monospecific record is that of *Piscogavialis*, from the latest Miocene of Pisco in Peru (Kraus, 1998). Among high diversity assemblages, those from La Venta and Fiztcarrald are Laventan (Guerrero, 1997; Antoine, et al, 2007), whereas the Acre fauna is considered Huayquerian (Cozzuol, 2006). In the Urumaco sequence both SALMAs are represented by the Laventan Socorro Formation and the Huayquerian Urumaco Formation (Linares, 2004; Quiroz and Jaramillo; 2010; Scheyer et al, 2013.). There are similarities between

Laventan and Huayquerian assemblages. For example, species of the gavialoid *Gryposuchus* and the specialized caimanines *Purussaurus* and *Mourasuchus* are present in all four localities, whereas the putative tomistomine *Charactosuchus* has been reported in La Venta, Urumaco, and Acre (Riff et al, 2009). The presence of these taxa in geographically disparate localities of Laventan and Huayquerian age indicates that these lineages persisted for at least seven million years, and occupied a wide geographic range. The gavialoid *Ikanogavialis*, present in both the Socorro and Urumaco formations (Sill, 1970; Scheyer, et al, 2013), represents another long lived taxon, although one with a more geographically restricted record.

Localities in the early Miocene portion of the Castilletes Formation are also characterized by both gavialoids and caimanine alligatoroids. Gavialoid remains from localities 390090 (La Tienda) and 390091(Gharial Locality) were found in shallow marine deposits, which is consistent with the evolutionary history of the group. The oldest gavialoids come from marine deposits, suggesting that they lived in coastal and estuarine environments (e. g. Troxell, 1925, Delfino et al 2005, Brochu, 2004, 2006a, 2006b; Hua and Jouve, 2004; Jouve et al, 2006, 2008). The oldest records of Neotropical gavialoids are latest Oligocene or earliest Miocene in age. These records come from marginal marine deposits in Antillean, Atlantic and Caribbean localities (Velez-Juarbe et al, 2006; Brochu and Rincón, 2004; Moraes-Santos et al, 2011). All these records, together with the presence of the gavialoid *Piscogavialis* in latest Miocene Pacific coastal deposits of Peru indicate that, even though living *Gavialis* is a freshwater species, gavialoids have been occupying marine habitats for most of their history.

Fossil caimans from the Paleogene are small, comparable in size to living species of *Caiman* and *Paleosuchus* (e. g. Brochu, 2010, 2011; Bona, 2007; Pinheiro et al, 2012), and small species are present through the whole history of caimaninae (e g, Patterson, 1936; Sousa-Filho, 1987; Sousa Filho and Bocquentin-Villanueva, 1991). Larger forms, some of them exceeding the maximum size of modern species were known only from the middle and late Miocene. The size of alligatorid remains from locality 390092 indicates that large caimanine taxa were already present by the early Miocene.

Remains of the caiman *Purussaurus* from Patajau Valley locality and *Mourasuchus* from the Kaitamana Cemetery locality represent taxa already known for Laventan and Huayquerian Faunas. However, these localities are at least two million years older than the earliest records of Fitzcarrald, La Venta, and the Socorro Formation in the Urumaco Sequence (Langston, 1965; Salas-Gismondi et al, 2007; Scheyer et al, 2013). These records extend the temporal range of two specialized lineages into the early middle Miocene. The presence of gavialoids in the same locality as *Purussaurus* remains indicates further similarities with Laventan and Huayquerian faunas, suggesting an early Miocene or Oligocene establishment of diverse gavialoid-caimanine assemblages. In this scenario, early middle Miocene records are also expected for other middle-late Miocene lineages, such as the gavialoids *Gryposuchus* and *Ikanogavialis*.

Crocodilians from the upper Castilletes— Fossils of *Crocodylus* in the Neotropics are scarce and restricted to the Plio-Pleistocene. A complete skull from the state of Rondonia,

Brazil (Fortier et al 2007), and remains of *Crocodylus rhombifer* from the late Quaternary of the Antilles (Morgan and Albury, 2013) indicate that in the recent past the genus had a greater distribution within the Neotropics. Unequivocal fossils of *Crocodylus* have been reported from the Plio-Pleistocene in Costa Rica (Mead et al, 2006). A jaw from the late Pliocene of Mexico, attributed to *Crocodylus morelet*i (Miller, 1980), is based on more ambiguous material. The oldest Neotropical representative of the genus is *Crocodylus falconensis* from the Pliocene San Gregorio Formation of Venezuela (Scheyer, et al, 2013). This taxon is based on an almost complete skull, and a phylogenetic analysis places it as the sister taxon of all living new world *Crocodylus* (Scheyer, et al, 2013). Some crocodilian specimens from the upper Castilletes formation can be identified a non-tomistomine crocodyloid taxon, likely representing an early record of neotropical *Crocodylus*. The ocurrence of cf. *Crocodylus* from the upper Castilletes Formation is an additional record of the lineage in the Pliocene of South America, expanding the geographical range of the genus in the continent.

Both morphological and recent molecular analyses provide support for a monophyletic clade of New World *Crocodylus*, closely related to the African lineage (Brochu, 2000, 2003; Meredith et al, 2011; Oaks, 2011; Hekkala et al, 2011). The relationships of African fossil *Crocodylus* are still greatly unresolved, however, because of poor morphological support for clades within *Crocodylus* (Brochu, 2000), and insufficient character data for some taxa (Brochu and Storrs, 2012). The only character that unites all known Neotropical *Crocodylus* is the presence of a medial elongated boss on the rostrum (Brochu, 2000). This medial boss is also seen in *C. falconensis* from Venezuela and

Crocodylus checchiai, from the Miocene of East Africa, (Maccagno, 1947; Delfino, 2008, Scheyer et al, 2013). Molecular analyses place the divergence time of African and New World *Crocodylus* near the Miocene-Pliocene boundary (Hekkala et al, 2011; Oaks, 2011). *C. falconensis* was collected in the San Gregorio Formation of the Urumaco sequence, which is middle to late Pliocene in age (Hambalek et al, 1994; Rey 1997), and younger than the proposed divergence time of African and New World *Crocodylus*. The age of the upper Castilletes where cf. *Crocodylus* remains were collected is still not well constrained. Some mammals from the same deposits, currently under study, suggest affinities with the latest Miocene-earliest Pliocene Montehermosan SALMA (6.8 – 4.0 Ma). If a Montehermosan age is confirmed for the upper Castilletes, specimens described here would represent a record even closer to the divergence time of African and New World *Crocodylus*.

Crocodilian faunas and environmental change— The Neogene was a time of great climatic and hydrographic change in equatorial South America (Fig. 11B). Many of these changes are related to the isolation of drainage basins caused by Andean uplift (Wesselingh et al, 2009). Prior to the late Miocene, the western Amazon basin had restricted connections to the Caribbean Sea through the Orinoco basin, but was isolated from the eastern Amazon basin by the Purus Arch. Peripheral drainages such as those in the Magdalena and Maracaibo basins had extensive connections with the Amazon and Orinoco (Lundberg, et al 1998). These connections explain the presence of shared taxa among Miocene crocodilian assemblages in equatorial South America. The presence in the Lower Castilletes Formation of two caimanine taxa (*Purussaurus* and *Mourasuchus*)

shared with other Miocene assemblages suggests that drainage connections extended to the northernmost portion of the continent. In the early late Miocene, (11-7 Ma) the uplift of the Vaupes arch isolated the Orinoco and Amazon basins, closing the main connection between the Amazon and the Caribbean (Hoorn et al. 1995; Diaz de Gamero 1996; Mora et al, 2009). Contemporaneous Huayquerian crocodilian assemblages include those from Acre in the Amazon basin and Urumaco in the northern South America. The presence of taxa common to both assemblages indicate that, despite the isolation of the Orinoco and Amazon, connections with the Caribbean were still present, perhaps through the Magdalena basin.

During the latest Miocene and Pliocene (7.0-2.5 Ma), the accelerated uplift of the northern Andes led to the separation of the Orinoco and Amazon systems and the complete isolation of peripheral drainages (Magdalena, Maracaibo, and coastal Venezuela) previously connected to Amazonia (Lundberg et al, 1998). In some of these new basins, aridity increased by the generation of rain shadows (Mora et al, 2009; Bookhagen and Streecker, 2009), leading to the disappearing of rain forests and the local extirpation of several groups of fishes (Lundberg, et al, 2009). The extinction of many lineages typical of Laventan and Huayquerian faunas has been attributed to these climatic and hydrographic changes (Riff, et al, 2009; Scheyer, et al, 2013). In the Urumaco sequence, for example, crocodilians are absent in the Late Miocene-Early Pliocene Codore Formation, when climates become more arid and rain forests disappeared in the region. The presence of fossil mammals and birds in this interval indicates that the

absence of crocodilians is a result of local extinction, rather than preservational bias (Scheyer et al, 2010).

From the Late Miocene onwards, there was a marked decrease in global crocodilian diversity, coincident with high latitude cooling and aridification of continental interiors (Markwick, 1998). It is during the late Miocene and Pliocene when *Crocodylus* disperses into several continents, filling the voids left by local extinctions (Brochu, 2003; Oaks, 2011). The occurrence of cf. *Crocodylus* in the upper Castilletes Formation and *Crocodylus falconensis* in the San Gregorio Formation of the Urumaco Sequence indicates that the extinction of endemic crocodilian lineages had left vacant habitats for the establishment of immigrant taxa by the Pliocene, at least in the northern part of the continent.

Increasing aridity may explain local extinction of crocodilian taxa in peripheral drainages. However, the wet Amazonian climates basin have been present since the late Oligocene-early Miocene (Salati & Vose, 1984; Vonhof & Kaandorp, 2009; Sepulchre et al, 2009), and most of Amazonia remained wet and forested during the ice ages of the Quaternary (Colinvaux & Oliveira, 2000; Maslin, et al 2012). This leads to wonder why most lineages got extinct also in the Amazon drainage, where climatic conditions have not experienced drastic change. During the late Oligocene-early Miocene (24-11 Ma), an extensive mega-wetland system (Pebas System) was established in the Andean foreland basin (Wesselingh and Salo, 2006; Wesselingh et al, 2006 a, 2006b, 2009). Mega-wetland conditions remained through most of the Miocene, first as a "Pebas system" with

restricted connections to the Caribbean, and later as an "Acre system" in which the connection with the Caribbean was lost, and transcontinental drainage that connected it to the Atlantic Ocean. During the latest Miocene and Pliocene (7.0-2.5 Ma), Andean uplift increased, and the filling of the eastern foreland basins resulted in the establishment of a fully developed Amazon River drainage. Mega-wetlands have been interpreted as the extensive, long term environment that allowed the development of high diversity crocodilian assemblages (Salas-Gismondi, et al 2007). The shift from wetland to riverine conditions has also been suggested as a cause for crocodilian extinctions in Amazonia (Riff et al, 2009). High crocodilian diversity in some localities; however, also occurs in localities with riverine deposits (La Venta) or coastal habitats (Urumaco), and the effect of mega-wetlands in crocodilian diversity remains as a potential, still untested hypothesis.

Conclusions — The age of crocodilian fossils from the lower Castilletes Formation is early to early middle Miocene, whereas crocodilians from the upper Castilletes Formation come from Pliocene deposits. These new records provide new data on poorly known intervals of crocodilian evolution in equatorial South America. Both gavialoids and caimanines were present in the early Miocene. The occurrence of *Purussaurus* and *Mourasuchus* in the early middle Miocene Patajau and Kaitamana beds represent early records for lineages previously known from younger Laventan and Huayquerian faunas. These records expand the temporal range of high diversity gavialoid-caimanine assemblages into the early middle Miocene. The Castilletes Formation record also expands the geographic range of Miocene endemic crocodilian faunas to latitudes equivalent to those of Central America.

Crocodilian diversity during the Neogene in equatorial South was highly linked to hydrographic conditions. The connections between hydrographic basins and the development of mega-wetland systems in equatorial South America allowed the long persistence of several lineages over an extensive geographical range. The extinction of gavialoids and specialized caimanines in equatorial South America was likely caused by the isolation and aridification of peripheral basins, together with the disappearance of mega-wetlands. The presence of cf. *Crocodylus* in the upper Castilletes Formation extends the geographical range of Neotropical *Crocodylus* in the Pliocene, and represents an immigrant taxon that occupied the hydrographical basins after the extinction of Miocene assemblages.

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FIGURE CAPTIONS

Figure 1. **A**, Map of equatorial South America showing the geographical position of Neogene and Quaternary crocodilian localities; **B**, Geographical position of the Cosinetas basin in the Guajira Peninsula of Colombia. **Abreviations**: **1**, late Oligocene-early Miocene Castillo Ftion, Falcón State, Venezuela; **2**, Middle Miocene Parángula Formation, Barinas State, Venezuela; **3**, Middle Miocene Fitzcarrald Fauna, Ipururo Formation, Madre de Dios Department, Peru; **4**, Middle Miocene La Venta Fauna, Honda Group, Huila Department, Colombia; **5**, Acre Fauna, late Miocene Solimões Formation, Acre State, Brazil; **6**, middle Miocene-Pliocene Faunas in the Urumaco sequence, Falcón State, Venezuela; **7**, Miocene-Pliocene Castilletes Formation, Guajira Department, Colombia; **8**, late Pliocene Pisco Formation Montemar level, Arequipa Department, Peru; **9**, Pleistocene Mesa Formation, Breal de Orocual, Monagas State, Venezuela; **10**, Late Pleistocene Rio Madeira Formation, Rondonia State, Brasil.

Figure 2. Stratigraphic Section for the Castilletes Formation in the Cosinetas basin (Jaramillo et al., in prep.), showing the stratigraphic position of crocodilian samples.

Figure 3. Gavialoids from the lower Castilletes Formation. **A** and **B**, STRI-CTPA-16561, portions of the maxillae, nasals, frontal, prefrontals, lacrimals, jugals and palatines in dorsal and ventral views. **C**-**E**, STRI-CTPA-16567 Rostrum fragment of longirostrine crocodilian in Lateral, medial, anterior and posterior views. **F** and **G**, STRI-CTPA-16791, partial axis in lateral and ventral views. **Abreviations**: **al**, alveolus; **f**, frontal; **hy**, axial

hypapophyses; **j**, jugal; **l**, lacrimal; **mx**, maxilla; **n**, nasal; **pal**, palatine; **trig?**, possible passage for the trigeminal nerve.

Figure 4. Alligatoroidea gen et sp indet, STRI-CTPA-17145. **A-F**, fragment of posterior left maxilla in ventral (**A**), dorsal (**B**), medial (**C**), lateral (**D**), posterior (**E**), and anterior (**F**) views. **G-H**, partial frontal in dorsal (G) and ventral (H) views. **I-P** Partial vertebrae in anterior (**I**, **K**, **M**, **O**) and lateral (**J**, **L**, **N**, **P**) views. **Abreviations**: **al1**, anterior alveolus; al5, posterior alveolus; **ec-mx**, suture with the ectopterygoid; **ncs**, neurocentrum suture; **olf**, groove for the olfactory tract; **trig**, passage for the trigeminal nerve. Scale = 50 mm.

Figure 5. Caimanine alligatoroids from the lower Castilletes Formation. **A-I**, cf. *Purussaurus*, isolated tooth in labial; lingual; and lateral views: STRI-CTPA-16800 (**A-C**); STRI-CTPA-16802 (**D-F**); STRI-CTPA-16803(**G-I**). Scale = 10 mm. **J**, detail of teeth in STRI-CTPA-16800 in lateral view, showing the wrinkled ornamentation of the enamel. Scale = 5 mm. **K**, *Purussaurus neivensis*, UCMP , detail of teeth in labial view, showing the wrinkled enamel surface. **L-Q**, cf. *Purussaurus*, incomplete osteoderms in dorsal, lateral and ventral views: STRI-CTPA-16806 (**L-M**); STRI-CTPA-16804 (**O-Q**). Scale = 5 mm. **R-W**, cf. *Mourasuchus*, STRI-CTPA 16558. **R-U**, lacrimal in ventral (**R**); dorsal (**S**); lateral (**T**); and posterior (**U**) views. **V-W,** maxilla fragment in dorsal (**V**) and ventral (**W**) views. **Abbreviations**: **1acd**, lacrimal duct; **lacf**, lacrimal foramen; **preo**, preorbital canthus; **ocp**, oclussal pit. Scale = 10 mm.

Figure 6. Crocodyloids from the upper Castilletes Formation. **A-C**, STRI-CTPA Partial premaxila in dorsal (**A**); ventral (**B**); and lateral (**C**) views. **D-O**, STRI-CTPA , fragments of skull, mandible, and osteoderms. **D**, frontal in dorsal view; **E**, frontal in ventral view; **F-G**, Parietal and supraoccipital in dorsal (**F**) and ventral (**G**) views. **H**, partial right squamosal. **I-J**, partial right postorbital in dorsal (**I**) and ventral (**J**) views. **K**, partial left jugal. **L-O**, partial osteoderms in dorsal view. **P**, fragment of right dentary in lateral view. **Q**, fragment of right surangular in lateral view. **R**, angular fragment in lateral view. Abbreviations: **al**, external rim of eleventh? alveolus; **nar**, narial rim; **not**, notch for the fourth mandibular tooth; **ocp**, occlusal pit; **olf**, groove for the olfactory tract; **orb**, orbital rim; **so**, supraoccipital; **stf**, supratemporal fenestrae rim. Scale = 50 mm.

Figure 7. cf. *Crocodylus* from the upper Castilletes Formation. **A-C**, STRI-CTPA-17702, posterior fragment of right mandibular ramus in dorsal (**A**); lateral (**B**); and medial (**C**) views. D, detail of glenoid fossa in dorsal view. E, detail of surangular-articular suture in medial view. Abbreviations: **an**, angular; **ar**, articular; **faan**, foramen for articular artery and alveolar nerve; **fae**, foramen aerum; **sa**, surangular.

Figure 8. Eusuchian vertebrae from the Castilletes Formation. All in anterior and right lateral views, unless otherwise stated. **A-B**, STRI-CTPA-16422, posterior cervical vertebra from the locality 390085 (Cemetery). **C-I**, vertebrae from locality 390094 (Patajau Valley). **C-D**, STRI-CTPA-16789, anterior dorsal vertebra. **E-G**, STRI-CTPA-16788 isolated centrum in anterior (**E**), dorsal (**F**), and right lateral (**G**) views. **H-I**, STRI-CTPA-1 caudal centrum. **J-X**, vertebrae from locality 390075 (Police Station). **J-K**,

STRI-CTPA-16167, cervical vertebra. **L-N**, STRI-CTPA-16203, anterior dorsal in anterior (**L**), lateral right (**M**), and lateral left (**N**) views. **Q-R**, STRI-CTPA-16296, cervical vertebra. **S-V**, articulated series of 3 vertebrae, the posterior element (**S-T**) was detached from the other two (**U-V**) during collection. **W-X**, dorsal or lumbar vertebra. Scale = 50 cm.

Figure 9. Crocodilian skull fragments and teeth from the Castilletes formation. **A-C**, STRI-CTPA-16334, rostrum fragment from locality 390090 (La tienda) in medial (**A**), lateral (**B**), and occlusal (**C**) views. Scale = 10 mm. **D-J**, skull fragments from the upper Castilletes Formation, locality 390075 (Police Station). **D-F**, STRI-CTPA13109, articulated lacrimal and jugal fragments in dorsal (**D**) and ventral (**E**) views, and undetermined skull fragment (**F**). Scale = 50 mm. **G**, STRI-CTPA-16352, partial squamosal in dorsal view. Scale = 10 mm**. H-J**, STRI-CTPA-16240, partial jugal or maxilla in lateral view (**H**) and indeterminate skull fragments (**I**, **J**). Scale = 50 mm. **K-Y**, crocodilian teeth from the Castilletes Formation. **K-M**, STRI-CTPA-17158, slender, sharp tooth from locality 390094 (Patajau Valley) in labial (**K**), lingual (**L**), and lateral (**M**) views. **N**, detail of STRI-CTPA-17158, showing thin, parallel secunday carinae. **O-P**, STRI-CTPA-16554, slender tooth from locality 390085 (Kaitamana) in internal (**O**) and lateral (**P**) views. Q-S, STRI-CTPA-****, tooth from locality 390075 (Police Station) in labial (**Q**), lingual (**R**), and lateral (**S**) views. **T-Y**, STRI-CTPA-16277 (**T-V**) and STRI-CTPA-16278 (**W-Y**), slender teeth from locality 390075 (Police Station) in labial (**Q**), lingual (**R**), and lateral (**S**) views.

Figure 10. Crocodilian poscranials and osteoderms from the Castilletes Formation. **A-B**, STRI-CTPA-16189, partial coracoid from locality 390075 (Police Station) in lateral (**A**) and medial (**B**) views. Scale = 50 mm. **C-D**, STRI-CTPA-16781, ilium from locality 390094 (Patajau Valley) in lateral (**C**) and medial (**D**) views. Scale = 50 mm. **E-H**, osteoderms from locality 390085 (Kaitamana): STRI-CTPA-16336 (**E**), STRI-CTPA-16424 (**F**), STRI-CTPA-16415 (**G**), STRI-CTPA-16426 (**H**). Scale = 10 mm. I-O, dorsal and lateral osteoderms from locality 390075 (Police Station). **I-J**, STRI-CTPA-20432, complete dorsal osteoderm in dorsal (**I**) and posterior (**J**) views. Scale = 50 mm. **K-M**, incomplete dorsal osteoderms: STRI-CTPA-16240 (**K**), STRI-CTPA-17136 (**L**), STRI-CTPA-20337 (**M**). Scale = 50 mm. **N-O**, lateral osteoderms: STRI-CTPA-19620 (**N**), STRI-CTPA-16215 (**O**). Scale = 50 mm.

Figure 11. Crocodilian faunas and hydrographic change in equatorial South America during the Neogene and Quaternary. **A**, crocodilian assemblages through time. Individual taxa names from Riff, et al (2009) and Scheyer et al (2013). Locality numbers are as in figure 1. **B**, history of hydrographic systems during the Neogene of South America. The upper bar represents different hydrographic systems (Pebas, Acre, Amazon) in the western Amazonian basin. Shorter bars indicate the approximate establishment of separate peripheral basins (Orinoco, Magdalena, Maracaibo) after isolation from the western amazon. **Abbreviations 1**. *Siquisiquesuchus venezuelensis*; **2**, *Barinasuchus arveloi*; **3**, *Purussaurus sp*; **4**, *Mourasuchus sp.*; **5**, *Caiman sp.*; **6**, *Paleosuchus sp.*; **7**, *Gryposuchus sp.*; **8**, Sebecidae gen et sp indet.; **9**, *Purussaurus neivensis*; **10**, *Mourasuchus atopus*, **11**, *Eocaiman* sp; **12**; *Caiman* cf. *lutescens*; **13**, *Gryposuchus*

colombianus; **14**, *Charactoschus fieldsi*; **15**, *Langstonia huilensis*; 16, *Purussaurus brasiliensis*; **17**, *Mourasuchus amazonicus*, *M. nativus*, and *M. arendsi*; **18**, *Caiman niteroiensis*; **19**, *Caiman brevirostris*; **20**, *Gryposuchus jessei*; **21**, *Hesperogavialis* sp.; **22**, *Charactosuchus mendesi*; **23**, *Ikanogavialis gameroi*; **24**, cf. *Thecachampsa*; **25**, *Purussaurus mirandai*; **26**, *Mourasuchus arendsi* and *M. nativus*; **27**, *Melanosuchus fisheri*; **28**, *Globidentosuchus brachyrostris*; **29**, *Gryposuchus arendsi*; **30**, *Hesperogavialis cruxenti*; **31**, *Charactosuchus mendesi* and *C. sansoai*; **32**, *Crocodylus falconensis*; **33**, Alligatoridae gen et sp indet; **34** Gavialoidea gen et sp indet; **35**, cf. *Crocodylus*; **36**, *Piscogavialis jugaliperforatus*; **37**, *Caiman venezuelensis*; **38** *Crocodylus* sp.
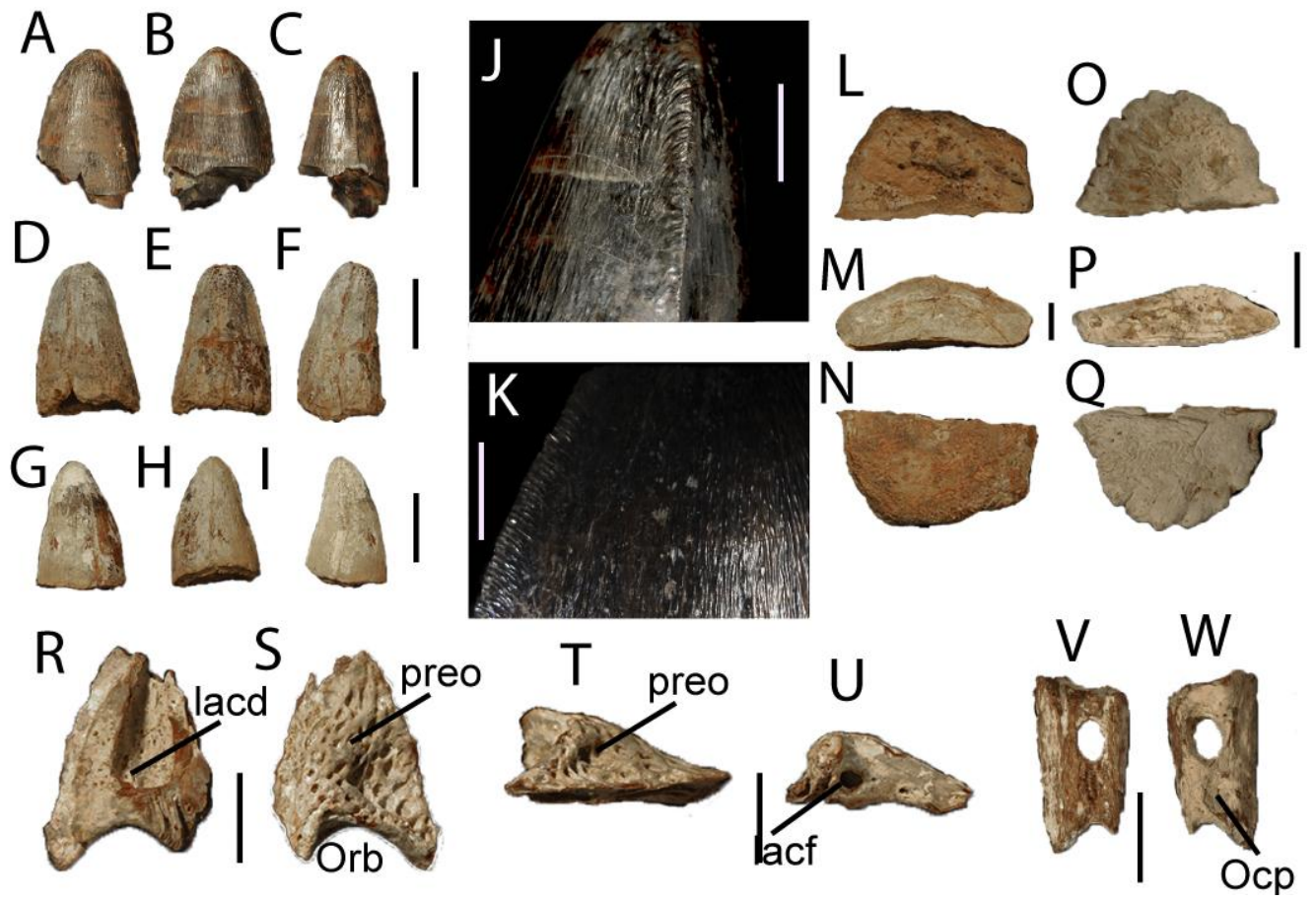
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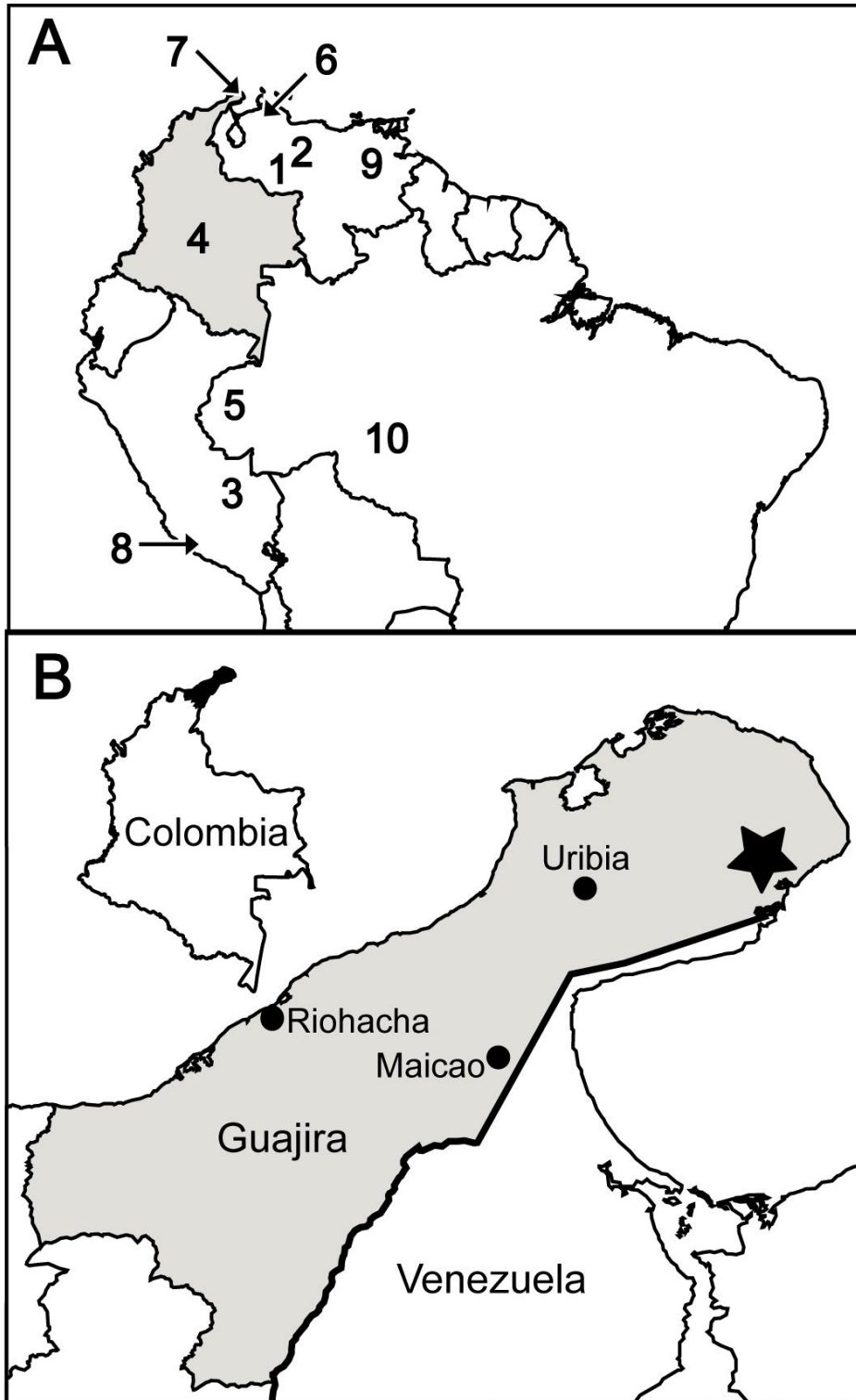
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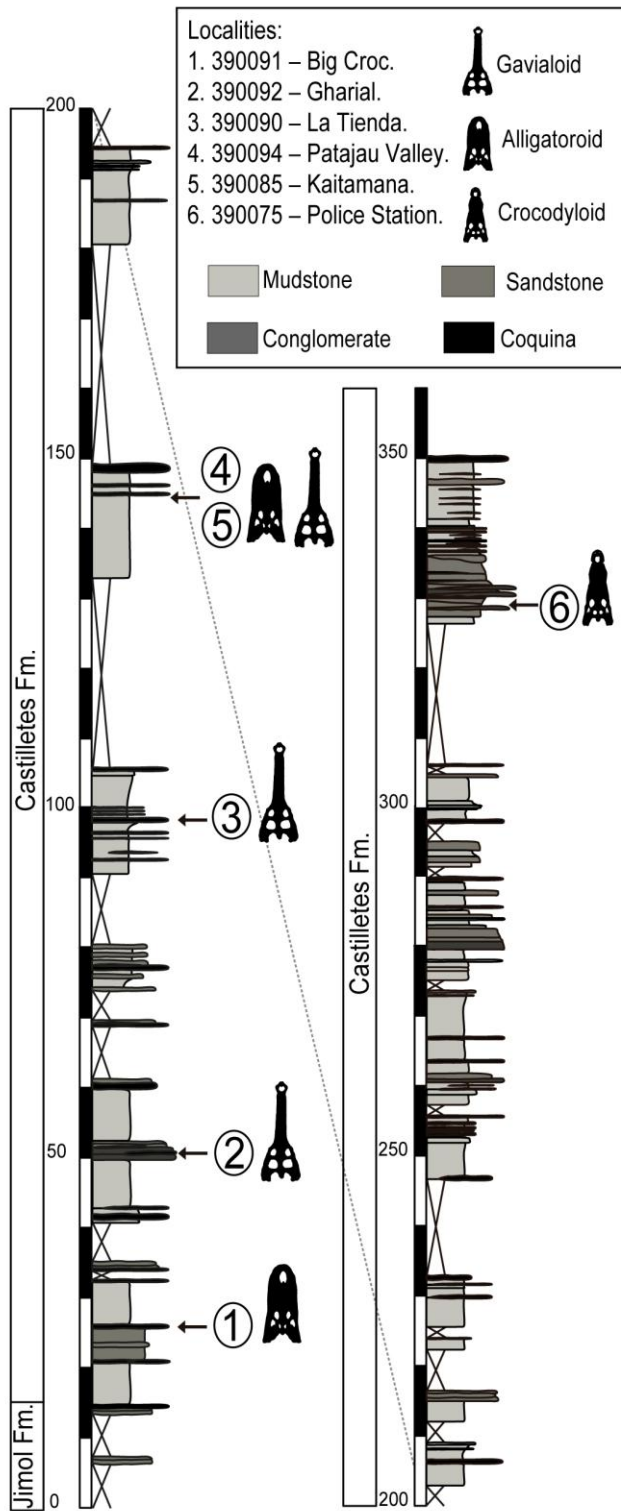
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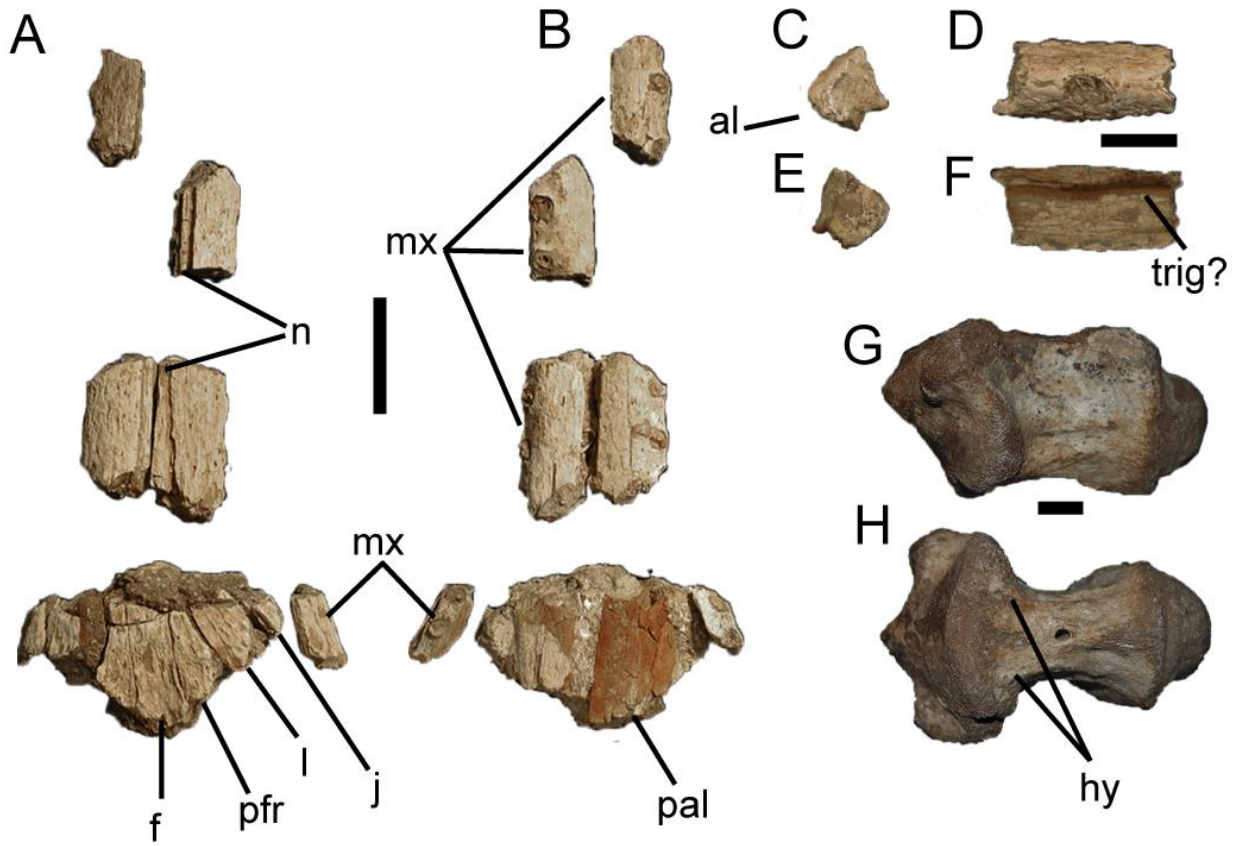
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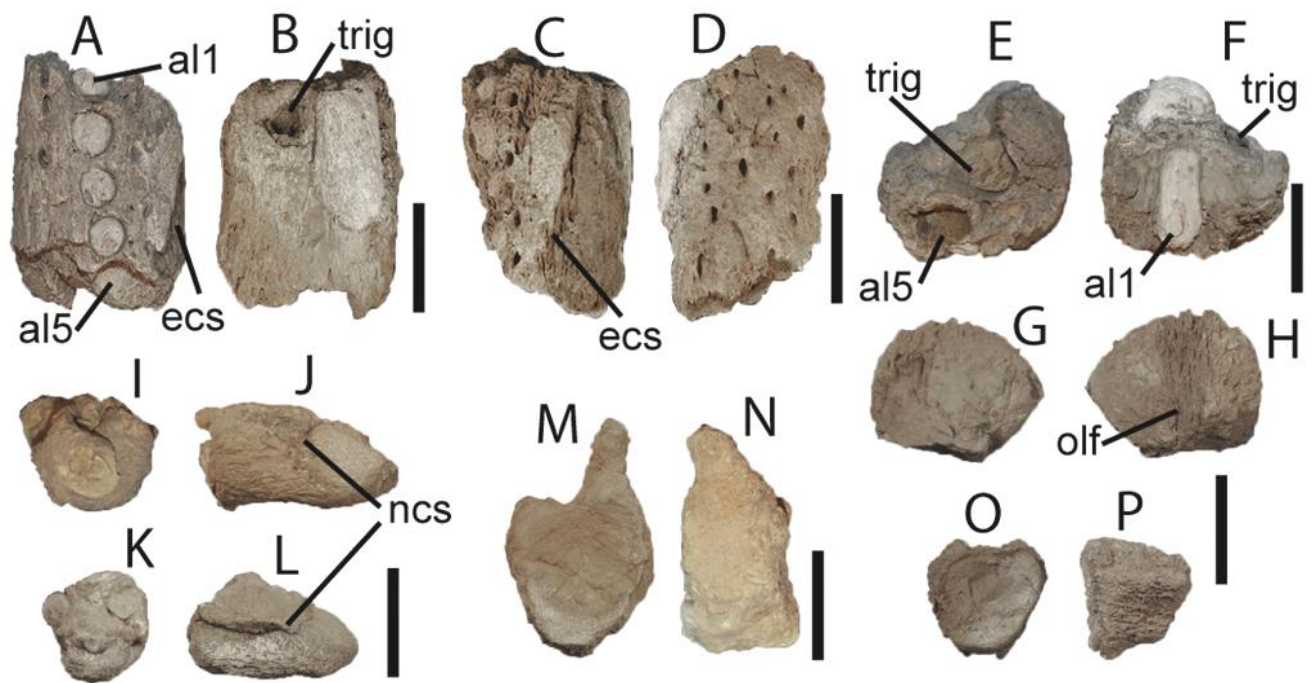
FIGURE 5

FIGURE 6

FIGURE 7

A

B

C

D

E

medially located fae

bowed sa-ar suture

truncated sa
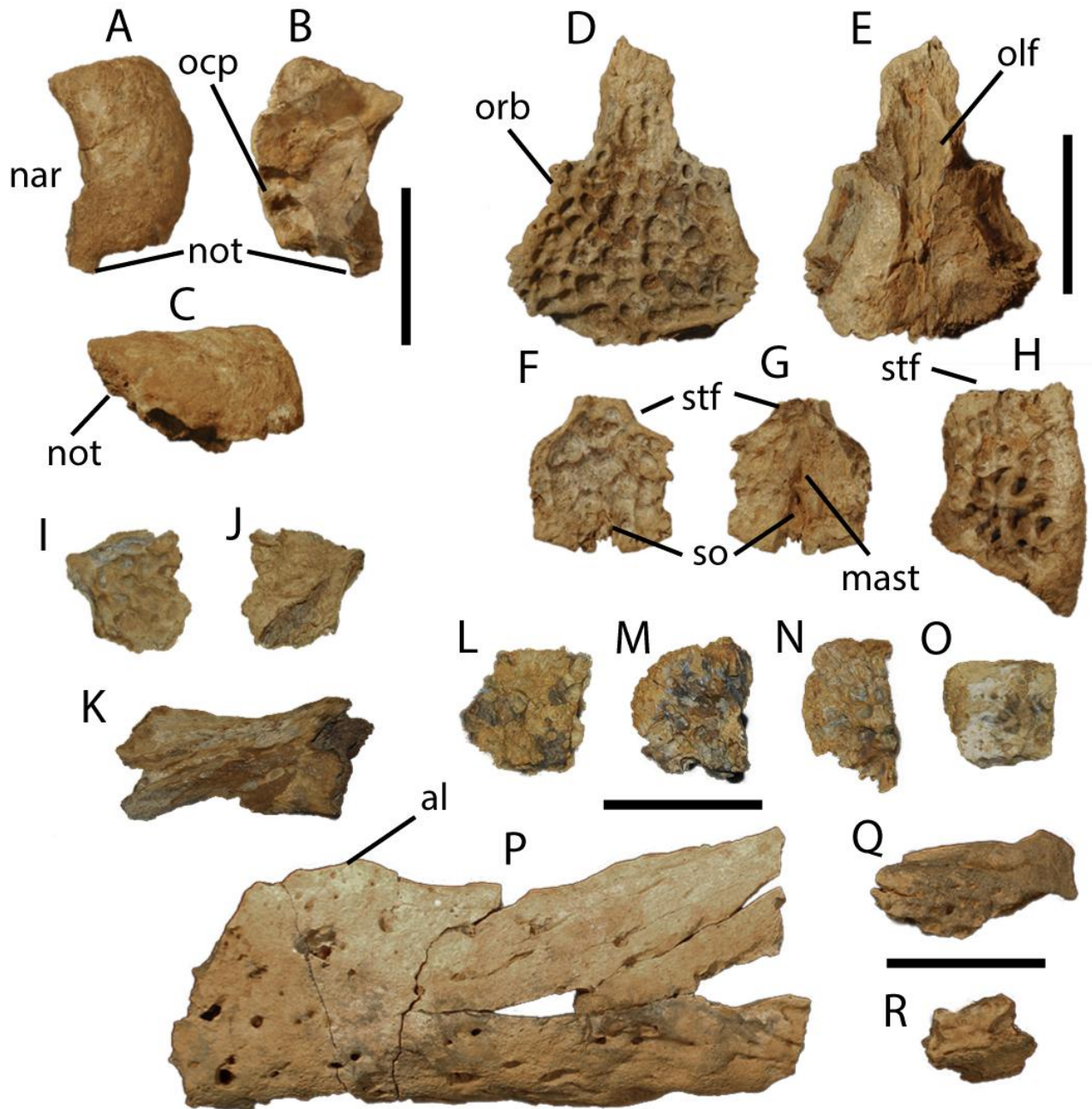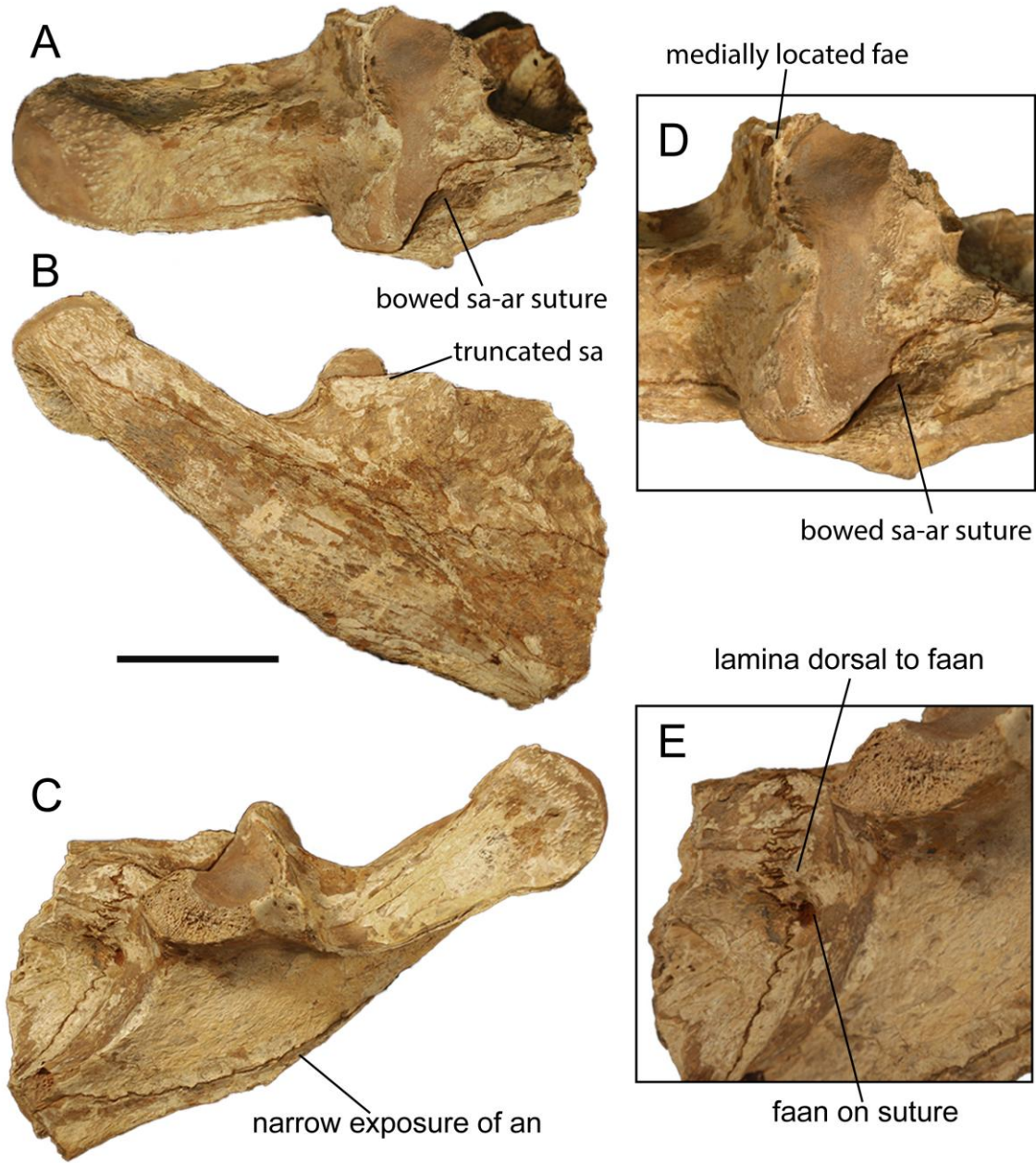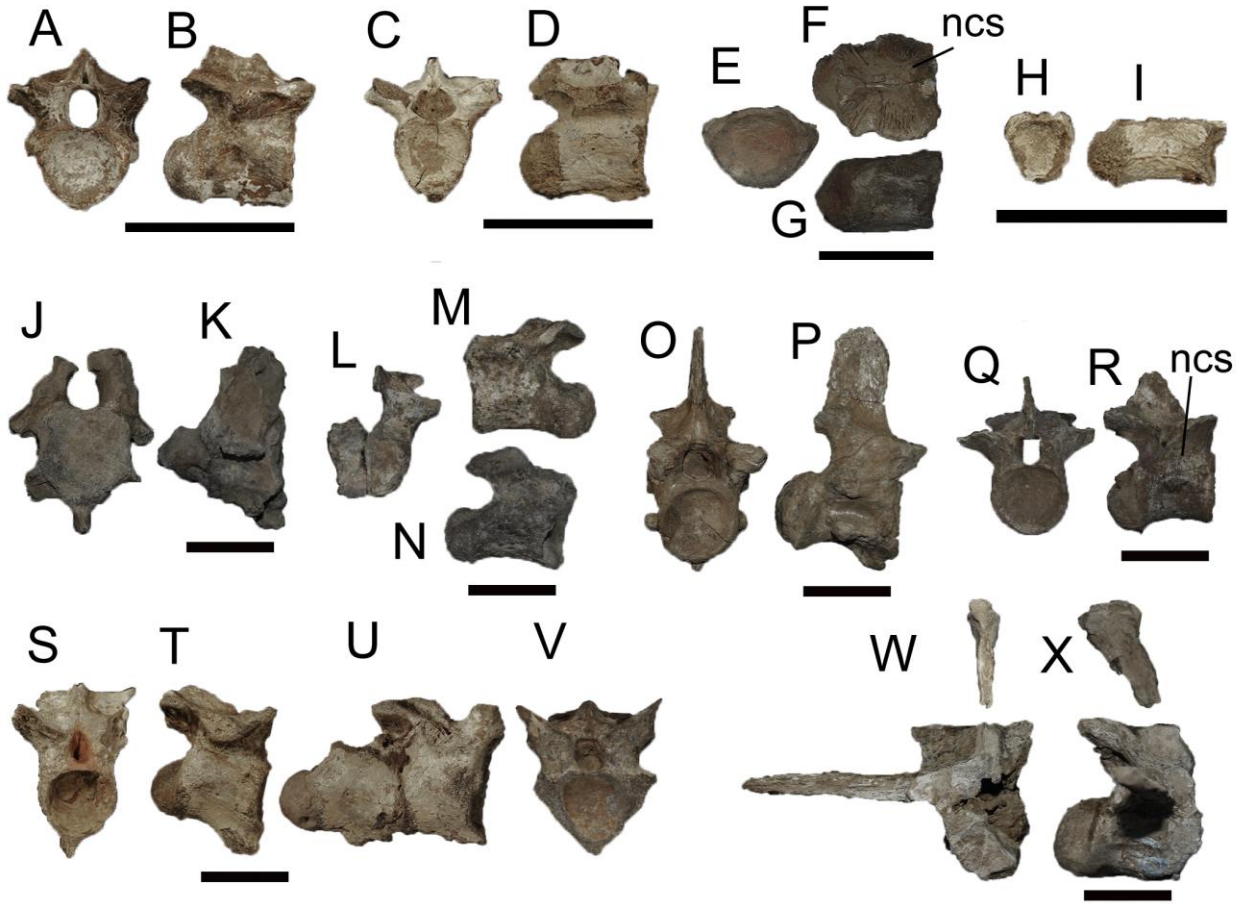
bowed sa-ar suture

lamina dorsal to faan

faan on suture

narrow exposure of an

FIGURE 8

FIGURE 9

FIGURE 10

FIGURE 11