

## FOSSIL CROCODILIANS FROM THE HIGH GUAJIRA PENINSULA OF COLOMBIA: NEOGENE FAUNAL CHANGE IN NORTHERNMOST SOUTH AMERICA

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**ABSTRACT**—The La Guajira Peninsula, Colombia, has a continuous vertebrate fossil record that includes both the late early–early middle Miocene and the Pliocene. Crocodylians from the early to early middle Miocene Jimol and Castilletes formations include gavialoids, recovered from both coastal and shallow marine deposits, and caimanines representing early records of the specialized caimanine taxa *Purussaurus* and *Mourasuchus*. Crocodyloid specimens from the Pliocene Ware Formation are assigned to *Crocodylus* and represent one of the oldest occurrences of the genus in the New World. Records from the La Guajira Peninsula suggest that diverse crocodylian assemblages were already established by the late early Miocene, including several widely distributed lineages that persisted for several million years. *Crocodylus* is a recent immigrant to South America that occupied habitats left vacant by the extinction of several crocodylian lineages.

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### INTRODUCTION

The greatest diversity of crocodylians during the Cenozoic occurred during the late middle and latest Miocene of equatorial South America (Riff et al., 2009). Our knowledge of this diversity is based on fossils found in Perú (Fitzcarrald), Colombia (La Venta), Brazil (Acre), and Venezuela (Urumaco) (Fig. 1A). In these assemblages, 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). Neogene fossil assemblages were composed of a diverse array of caimanine alligatoroids, gavialoids, and putative tomistomines (Langston, 1965; Souza-Filho and Bocquentin-Villanueva, 1991; Souza-Filho, 1991, 1993; Salas-Gismondi et al., 2007). Taxonomic diversity was accompanied by a high diversity of feeding ecomorphologies, including not only longirostrine and blunt-snouted forms present in modern crocodylians, but also extreme variations such as gavialoids with rostra longer than those of modern longirostrine crocodylians (Sill, 1970; Kraus, 1998; Brochu and Rincón, 2004); durophagous caimans (Scheyer et al., 2013); and *Mourasuchus*, a caimanine with a broad, flat, elongated rostrum and a slender jaw (Price, 1964; Langston, 1966; Bocquentin-Villanueva, 1984). The size range was also greater than in modern communities, with estimated lengths of 8 to 10 m 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 to the high diversity of middle and late Miocene localities, the diversity of South American crocodylians is poorly known for both the early Miocene and Pliocene. High-diversity crocodylian assemblages of the middle and late Miocene are also geographically 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 long and geographically constrained records of crocodylian diversity for the Neogene of tropical South America limits its ability to infer the origins of New World crocodylian diversity, its relationship to environmental factors (climate, hydrography, and faunal composition), and the timing and mode of the origin of modern crocodylian faunas.

Extensive field work in the Cocinetas Basin of the La Guajira Peninsula, Colombia (Fig. 1B), has resulted in the development of a basin-scale stratigraphy, extensive paleontological collections, and a geochronological framework based on strontium isotope (<sup>87</sup>Sr/<sup>86</sup>Sr) chronostratigraphy (Moreno et al., 2015). Crocodylian remains collected in Miocene and Pliocene deposits of the La Guajira Peninsula provide a unique perspective on histories of diversity and faunal change in equatorial South America. In this work, we describe these specimens and discuss their significance in terms of the evolution of crocodylian communities during the Neogene.

### Geological Setting

The Cocinetas Basin is located in the southeast Guajira Peninsula (Fig. 1B), and is delimited by a series of low mountain ranges locally known as ‘serranias’: Cosinas, Jarara, and Macuira. A Cenozoic sedimentary sequence fills the basin, recording a paleo-environmental transition from a shallow marine to a fluvio-deltaic system in the Cocinetas Basin (Moreno et al., 2015). The uppermost components of the Cocinetas Basin are the Jimol, Castilletes, and Ware formations. The Jimol and Castilletes formations are composed mostly of lithic sandstones and mudstones, and the Ware formation is a sequence of conglomerates, sandstones, and mudstones, overlain by fossiliferous limestones (Moreno et al., 2015).

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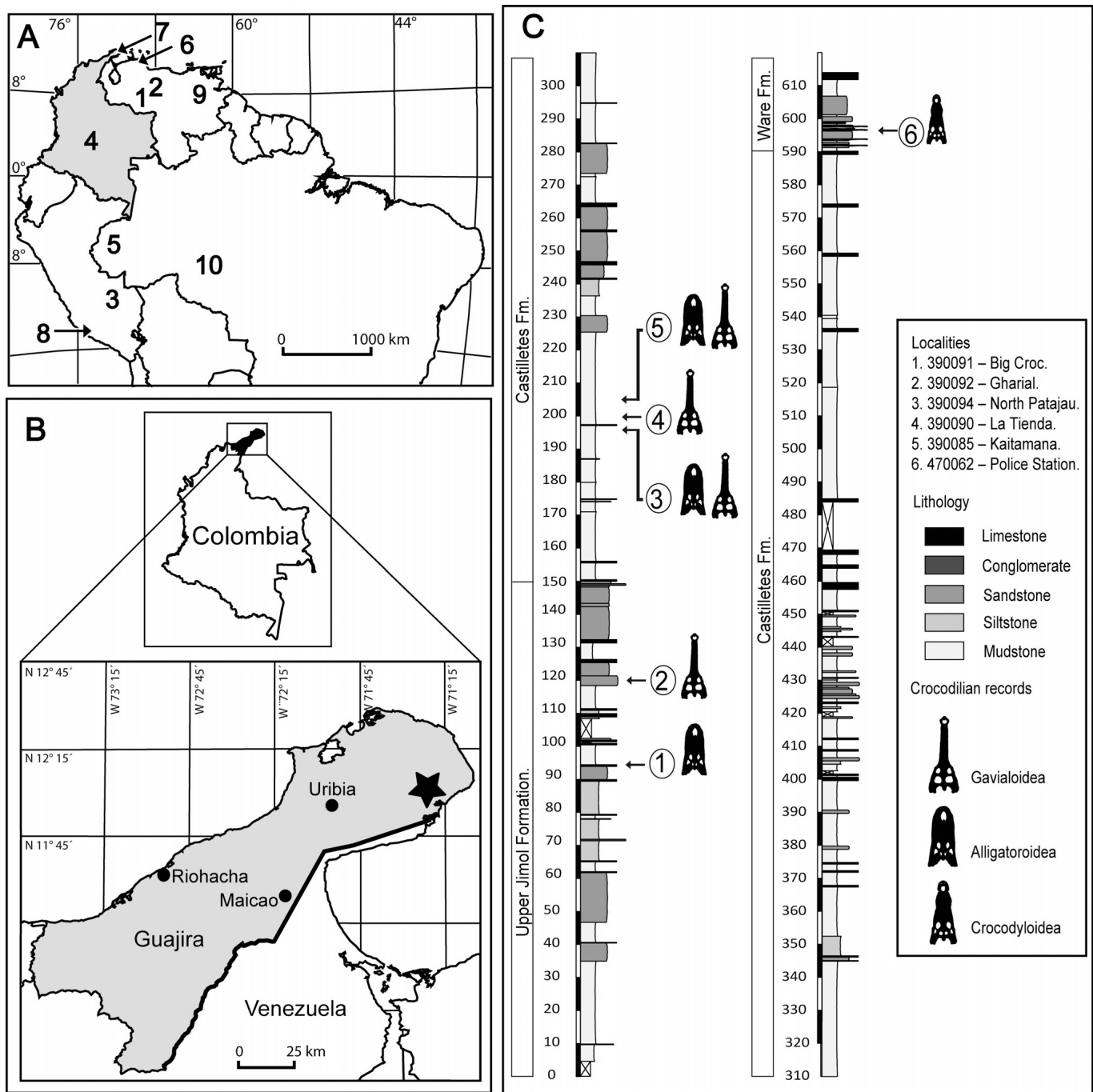


FIGURE 1. **A**, map of equatorial South America showing the geographical positions of Neogene and Quaternary crocodylian localities; **B**, geographical position of the Cocinetas Basin in the La Guajira Peninsula (shaded) of Colombia; **C**, stratigraphic sections of the upper Jimol, Castilletes, and Ware formations in the Cosinetas Basin, showing the stratigraphic position of crocodylian samples. **Abbreviations:** 1, late early Miocene Castillo Formation, 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 faunas in the Cocinetas Basin, Guajira Department, Colombia; 8, late Pliocene Pisco Formation Montemar level, Arequipa Department, Peru; 9, Pleistocene Mesa Formation, Breal de Orocuál, Monagas State, Venezuela; 10, late Pleistocene Rio Madeira Formation, Rondonia State, Brazil.

The Jimol Formation is approximately 200 m thick (Moreno et al., 2015) and is characterized by gray calcareous sandstones, yellowish-gray biosparites, and gray to brown siltstones and mudstones. The lower part of the Jimol Formation is composed

mainly of coarse sandstones and biosparites, with occasional beds of siltstones and mudstones. Towards the top, mudstones and fine-grained calcareous sandstone beds dominate the sequence, interbedded with beds of fine- to medium-grained

calcareous sandstones and biosparites (Moreno et al., 2015). The contact with the overlying Castilletes formation is marked by a hardground surface at the top of a biosparite that can be traced along the Cocinetas Basin. A late early Miocene (Burdigalian) age has been assigned to the Jimol Formation, on the basis of invertebrate faunas and  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope chronostratigraphy (Moreno et al., 2015). The  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope chronostratigraphy provides a mean age of 17.3 Ma (range: 16.89–17.51) for the beds at the top of the formation (Moreno et al., 2015).

The Castilletes Formation is composed of thick (~50 m) successions of mudstone, interbedded with thin (50 cm to 2 m) beds of biosparites and sandstones. This interbedding results in a landscape of elongated valleys (mudstones) and ridges (biosparites and sandstones). Sandy and silty facies become more frequent towards the top of the formation (Moreno et al., 2015). The unit was deposited in a very shallow marine to fluvio-deltaic environment (Rollins, 1965; Moreno et al., 2015). The Castilletes Formation is rich both in marine and terrestrial fossils, including plants, bivalves, gastropods, crabs, fishes, turtles, crocodylians, and mammals. The  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope chronostratigraphy indicates a mean age of 16.2 Ma (range: 16.33–16.07) in the lower portion of the Castilletes Formation, and 15.30 Ma (range: 15.14–15.43) for the middle part of the unit (Moreno et al., 2015).

The Ware Formation is composed of light gray mudstones, grayish-yellow fine sandstones, and muddy sandstones, reddish-gray pebbly conglomerates, yellowish-gray packstone biosparites, and sandy to conglomeratic biosparites (Moreno et al., 2015). The lower portion of the unit is composed of a lenticular conglomerate interbedded with mudstones, sandy mudstones, and fossiliferous fine sandstones. The conglomerate is very rich in vertebrate fossils, including sharks, fishes, turtles, crocodylians, and mammals. The middle part of the formation is composed of thick (~15 m) beds of fine and muddy sandstones. The uppermost portion of the unit is composed of fossiliferous biosparites that change laterally to micrites and sandy conglomerates (Moreno et al., 2015). The base of the Ware Formation was deposited in a fluvio-deltaic environment, and the marine invertebrates at the top beds are indicative of exposed open-ocean shelf and nearshore settings near coral reefs (Moreno et al., 2015). Outcrops of the Ware Formation are sparsely distributed as isolated hills, with subhorizontal strata on the eastern side of the Cocinetas Basin. An angular unconformity marks the contact between the Ware and Castilletes formations (Moreno et al., 2015). A late Pliocene (Piacenzian) age was assigned to the Ware Formation (Moreno et al., 2015). Invertebrate fossils from the Ware Formation suggest an age close to the Pliocene-Pleistocene boundary, and  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope chronostratigraphy indicates a mean age of 3.2 Ma (range: 3.40–2.78) for the top of the unit.

Crocodylian fossils representing all three main extant lineages (Alligatoroidea, Crocodyloidea, Gavialoidea) described here were recovered from six localities representing different levels within the Jimol, Castilletes, and Ware formations (Fig. 1C). Undiagnostic crocodylian fossils from the same localities, including isolated vertebrae, skull bone fragments, teeth, and postcranial elements, are listed in Appendix 1. In the Jimol Formation, a fossil crocodylian was found washed on top of a coquina approximately 55 m below the contact with the overlying Castilletes Formation. Another crocodylian was found in a micritic lens with abundant mollusks, within a bed of conglomeratic, coarse-grained sandstones approximately 28 m below the contact with the Castilletes Formation. Fossil crocodylians from the Castilletes Formation described in this work come from three localities in the lower part of the formation, within a sequence of thick mudstones interbedded with thin (<1 m) beds of fossiliferous biosparites. In the Ware Formation, crocodylians and other vertebrates come from the sandstones and conglomerates in the lower part of the unit.

**Institutional Abbreviations**—MUN, Mapuka Museum, Universidad del Norte, Barranquilla, Colombia; STRI, Center for

Tropical Paleocology and Archaeology, Smithsonian Tropical Research Institute, Balboa Ancon, Panama; UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.

## SYSTEMATIC PALEONTOLOGY

CROCODYLIA Gmelin, 1789

GAVIALOIDEA Hay, 1930

Gen. et sp. indet.

(Fig. 2)

**Referred Material**—MUN STRI-16561: portions of the maxillae, nasals, frontal, prefrontals, lacrimals, jugals, and palatines (Fig. 2A, B). MUN STRI-16567: rostrum fragment of longirostrine crocodylian (Fig. 2 C–F). MUN STRI-16791: isolated axis and odontoid (Fig. 2 G, H).

**Localities and Horizons**—MUN STRI-16561 was collected at locality 390092 ‘Gharial Locality,’ approximately 9 km west of Puerto Lopez; Upper Jimol Formation, late early Miocene (Moreno et al., 2015). MUN STRI-16567 was collected at locality 390090 ‘La Tienda,’ approximately 7.7 km southwest of Puerto Lopez and 900 m north of Paraguachon; Lower Castilletes Formation, late early–early middle Miocene (Moreno et al., 2015). MUN STRI-16791 comes from locality 390094 ‘North Patajau Valley,’ approximately 5.7 km northwest of Puerto Lopez; Lower Castilletes Formation, late early to early middle Miocene (Moreno et al., 2015).

## 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 to 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.

**Maxillae**—There are eight preserved fragments of the maxillae in MUN STRI-16561. The maxillae formed an elongated, slender rostrum as in other gavialoids. In dorsal view, the lateral surfaces of the maxillae are undulating, due to the laterally protruding rims of the alveoli. This undulation is more pronounced in two fragments, suggesting that they were more anterior in the rostrum. There are no undulations on the lateral surfaces of those fragments that articulate with the jugals. The suture with the nasals is anteromedially inclined at 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 MUN STRI-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; Langston and Gasparini, 1997; Kraus, 1998; Brochu and Rincón, 2004).

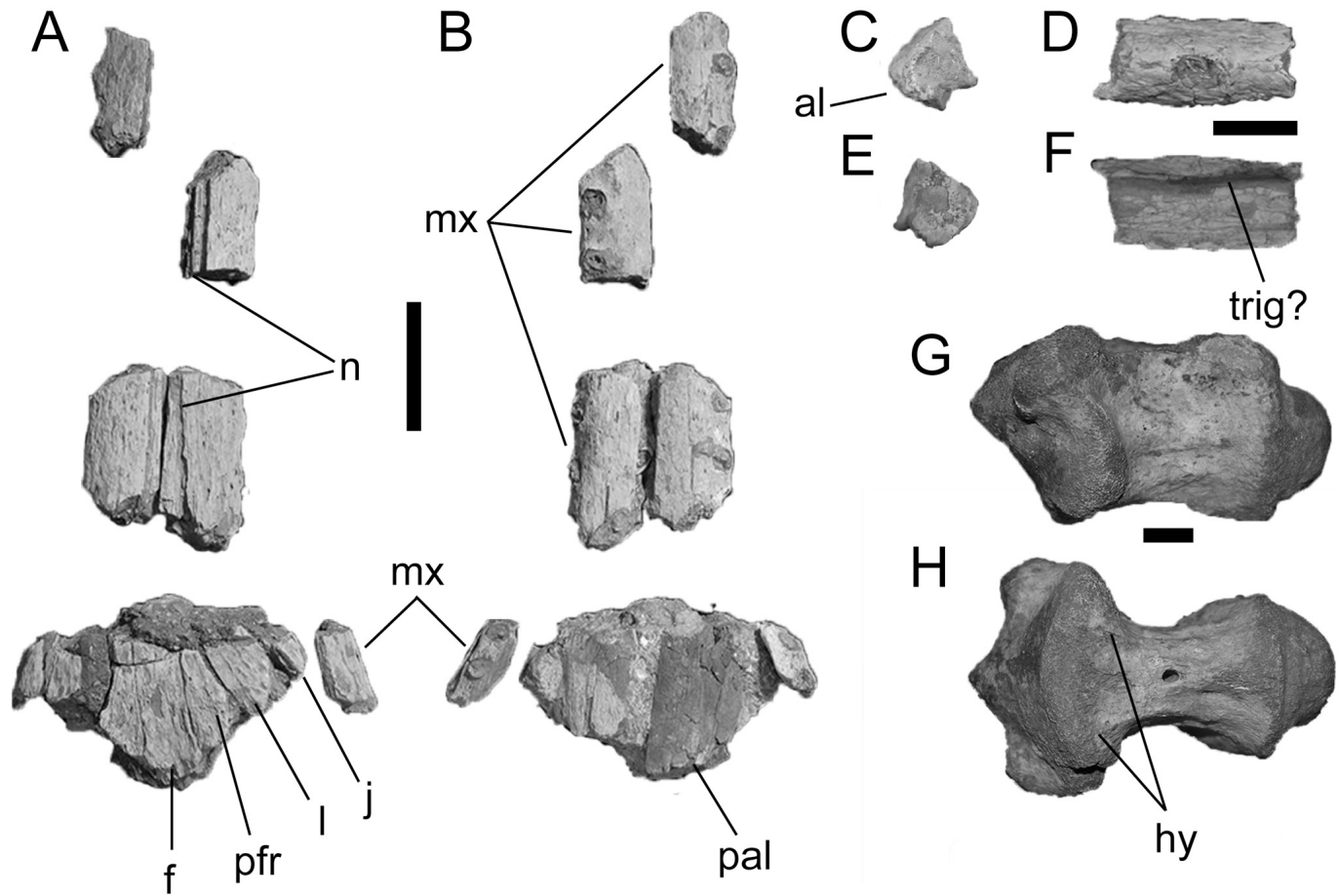


FIGURE 2. Gavioloids from the Jimol and Castilletes formations. **A** and **B**, MUN STRI-16561, portions of the maxillae, nasals, frontal, prefrontals, lacrimals, jugals, and palatines in dorsal and ventral views; **C–E**, MUN STRI-16567, rostral fragment of longirostrine crocodylian in lateral, medial, anterior, and posterior views; **F** and **G**, MUN STRI-16791, partial axis in lateral and ventral views. **Abbreviations:** **al**, alveolus; **f**, frontal; **hy**, axial hypapophyses; **j**, jugal; **l**, lacrimal; **mx**, maxilla; **n**, nasal; **pal**, palatine; **trig?**, possible passage for the trigeminal nerve. Scale bars equal 50 mm (**A**, **B**) and 10 mm (**C–H**).

**Prefrontals**—There are portions of both prefrontals articulated 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.

**Lacrimals**—Portions of the lacrimals are preserved lateral to both prefrontals in MUN STRI-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 crocodylians.

**Palatines**—Portions of the palatines are preserved on the posterior fragment of the rostrum of MUN STRI-16561. In ventral view, they are rectangular, longer than wide. The palatines constitute 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 borders of the suborbital fenestrae were anterior to the orbits.

**Rostrum Fragment from Locality 390090**—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. 2C–F). The lateral surface of MUN STRI-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, because 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 gavioloids (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 the 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. 2G, 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 MUN STRI-16791 suggests that 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. 3)

**Referred Material**—MUN STRI-17145: fragment of right maxilla (Fig. 3A–F), frontal? (Fig. 4G, H), and four incomplete vertebrae (Fig. 3I–P).

**Locality and Horizon**—MUN STRI-17145 was collected at locality 390091 ‘Big Croc,’ approximately 9 km northwest of Puerto Lopez; Upper Jimol Formation, late early Miocene (Moreno et al., 2015).

### Description

**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 views, the maxilla fragment has a roughly square outline. The posterodorsal and anteroventral corners of the fragment project so that the anterior and posterior margins are oblique in lateral and medial views. 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; Di-Poi and Milinkovitch, 2013). 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 tooth row 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.

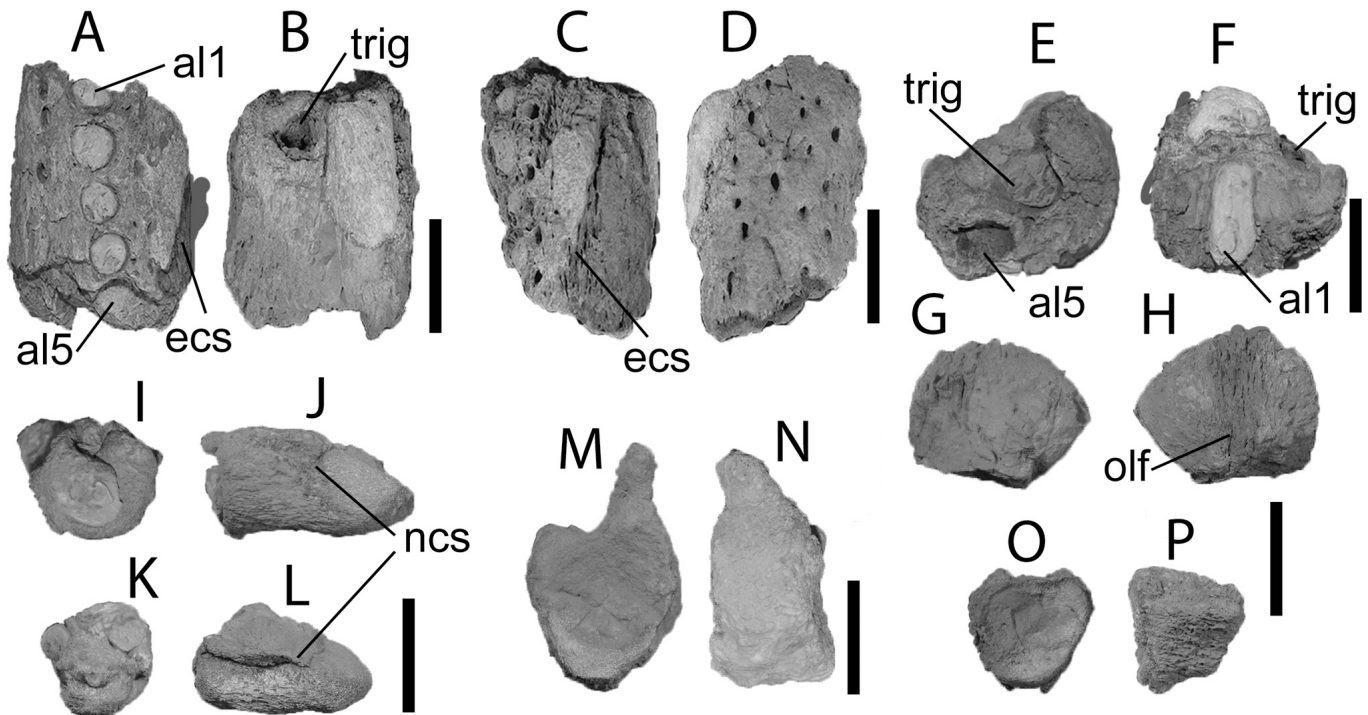
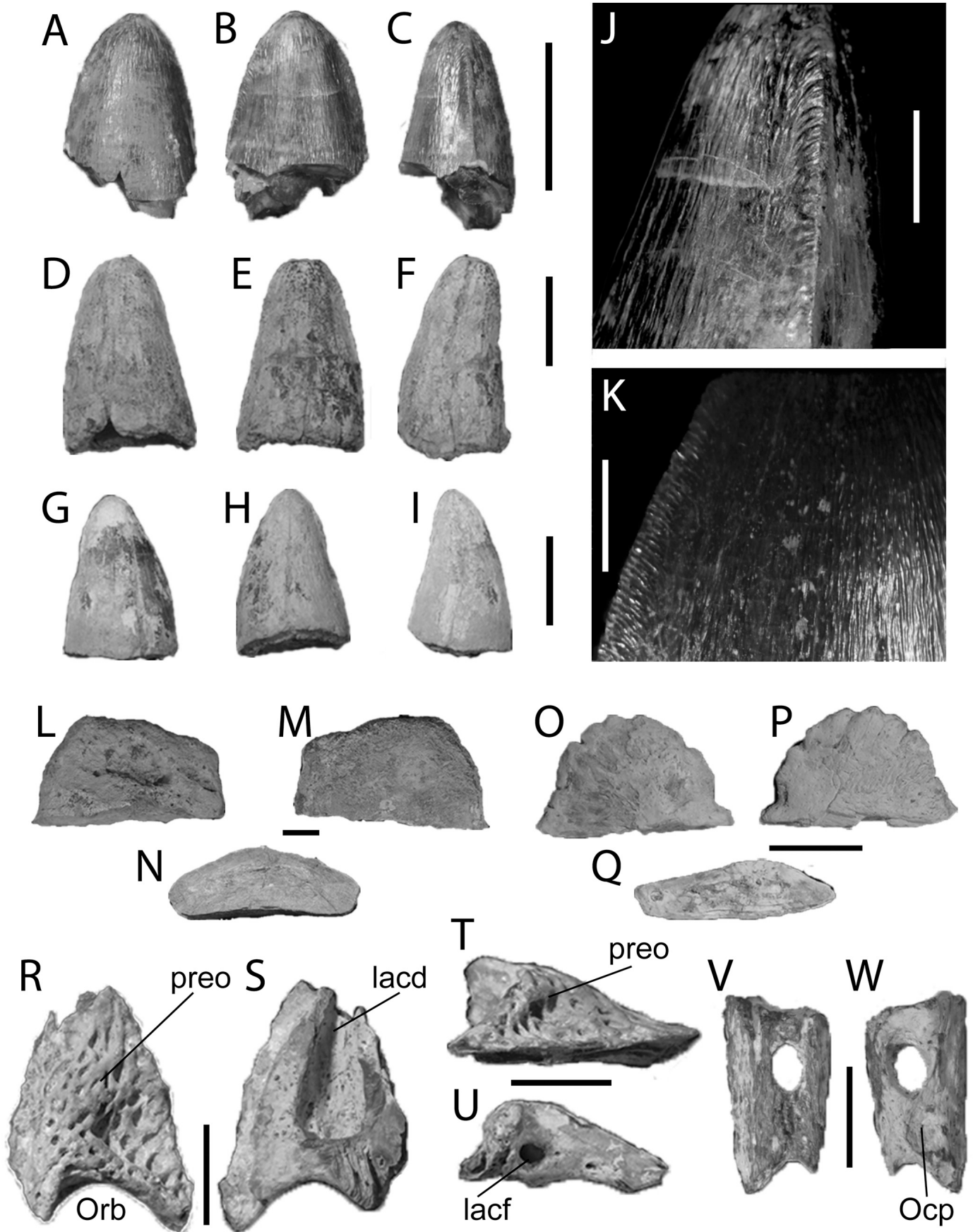


FIGURE 3. Alligatoroidea, gen. et sp. indet, MUN STRI-17145, from the upper Jimol Formation. A–F, fragment of posterior left maxilla in A, ventral view; B, dorsal view; C, medial view; D, lateral view; E, posterior view; and F, anterior view. G–H, partial frontal in G, dorsal view; and H, ventral view. I–P, partial vertebrae in I, K, M, O, anterior view; and J, L, N, P, lateral view. **Abbreviations:** al1, anterior alveolus; al5, posterior alveolus; **ecmx**, suture with the ectopterygoid; **ncs**, neurocentral suture; **olf**, groove for the olfactory tract; **trig**, passage for the trigeminal nerve. All scale bars equal 50 mm.



**Frontal**—A partial frontal is preserved in MUN STRI-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 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 MUN STRI-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 immature animal. The most complete centrum (Fig. 3I, J) is 90.35 mm long.

CAIMANINAE Brochu, 1999

*PURUSSAURUS* Barbosa-Rodrigues, 1892

(Fig. 4A–Q)

**Referred Material**—MUN STRI-16800: tooth fragment. MUN STRI-16802: isolated tooth. MUN STRI-16803: isolated tooth. MUN STRI-16804: small incomplete osteoderm. MUN STRI-16806, incomplete osteoderm.

**Locality and Horizon**—All specimens come from locality 390094 ‘North Patajau Valley,’ approximately 5.7 km northwest of Puerto Lopez; Lower Castilletes Formation, late early–early middle Miocene (Moreno et al., 2015).

#### Description

**Teeth**—Referred teeth are thick and blunt, and their basal section is round. The basal diameter is approximately 0.8 times the crown height for MUN STRI-16802 and MUN STRI-16803; MUN STRI-16800 is represented by the upper half of the crown only. The preserved portions of enamel have a wrinkled surface, which is more marked near the tip of MUN STRI-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. The 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 Lapparent de 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 to the perpendicular crests of false-ziphodont teeth, as those on the teeth of *Purussaurus neivensis* (Fig. 4K).

**Osteoderms**—In external view, these osteoderm fragments have flat, linear, broken surfaces. The preserved outline is roughly semicircular in MUN STRI-16804 and trapezoidal in MUN STRI-16806. The external surface is smooth and has small

foramina, but lacks the ornamentation pits typical of crocodylian osteoderms (Buffrénil, 1982). Both specimens are very thick compared with crocodylian osteoderms of similar size. There are no sharply defined keels; the external surface is raised in the middle and slopes to the sides at an angle of 20–25°. The ventral surface is flat in MUN STRI-16804, whereas there is a soft concavity in MUN STRI-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-Bernal, 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*.

*MOURASUCHUS* Price, 1964

(Fig. 4R–W)

**Referred Material**—MUN STRI-16558: maxillary fragment and associated lacrimal.

**Locality and Horizon**—This specimen comes from locality 390085 ‘Kaitamana,’ 4.5 km west of Castilletes and 1.2 km north of the Venezuelan border; Lower Castilletes Formation, late early–early middle Miocene (Moreno et al., 2015).

#### Description

This specimen comprises a small fragment of a maxillary and a lacrimal, found less than 5 cm from each other.

**Maxilla**—The 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 the 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 crocodylians, making it 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 the alveoli; its lateral rim is thicker and higher than the medial one.

← FIGURE 4. Caimanine alligatoroids from the lower Castilletes Formation. **A–I**, *Purussaurus* sp., isolated tooth in labial, lingual, and lateral views. **A–C**, MUN STRI-16800; **D–F**, MUN STRI-16802; **G–I**, MUN STRI-16803. **J**, detail of teeth in MUN STRI-16800 in lateral view, showing the wrinkled ornamentation of the enamel. **K**, *Purussaurus neivensis*, UCMP 38932, detail of teeth in labial view, showing the wrinkled enamel surface. **L–Q**, *Purussaurus* sp., incomplete osteoderms in dorsal, ventral, and lateral views. **L–M**, MUN STRI-16806; **O–Q**, MUN STRI-16804. **R–W**, *Mourasuchus* sp. **R–U**, MUN STRI-16558, lacrimal in **R**, dorsal; **S**, ventral; **T**, lateral; and **U**, posterior views. **V–W**, maxilla fragment in **V**, dorsal; and **W**, ventral views. **Abbreviations:** **lacd**, lacrimal duct; **lacf**, lacrimal foramen; **preo**, preorbital canthus; **ocp**, occlusal pit. Scale bars equal 10 mm (**A–I**, **R–W**) and 5 mm (**J–Q**).

**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 lies entirely on the lacrimal, because the surface medial to it is flat and 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 crocodylians (Busbey, 1995). 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 in gavialoids, in which the lateral portion of the lacrimal orbital rim is raised. 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 lie 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 teardrop-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.

**Discussion**—The morphology of the lacrimal in MUN STRI-16558, with an open concavity surrounded by the orbital margin and a rostral canthus, is shared by several caimanine taxa, such as *Caiman latirostris*, *Melanosuchus niger*, *Mourasuchus*, and *Purussaurus*. Most caimanines have short- to medium-length rostra, with closely spaced maxillary alveoli. Species of *Mourasuchus*, in contrast, have small, widely spaced alveoli in their elongated maxillae (Langston, 1965; Bocquentin-Villanueva, 1984). Wide spaces between alveoli are also present in other longirostrine crocodylians, such as South American gavialoids. However, the presence of occlusal pits, medial to the row of alveoli, in MUN STRI-16558 indicates that the mandibular tooth occluded medially to the maxillary tooth row, as in alligatorids. Among known fossil and living caimanines, the combination of characters in the lacrimal and maxilla of MUN STRI-16558 is only consistent with the genus *Mourasuchus*.

#### CROCODYLIDAE Cuvier, 1807

Gen. et sp. indet

(Figs. 5, 6)

**Referred Material**—MUN STRI-12939: partial premaxilla (Fig. 5). MUN STRI-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. 6).

**Locality and Horizon**—These specimens come from locality 470062 ‘Police Station,’ near the border with Venezuela. They were collected in fluvial sandstones of the lower Ware Formation; late Pliocene (Moreno et al., 2015).

**Partial Premaxilla**—The MUN STRI-12939 specimen 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

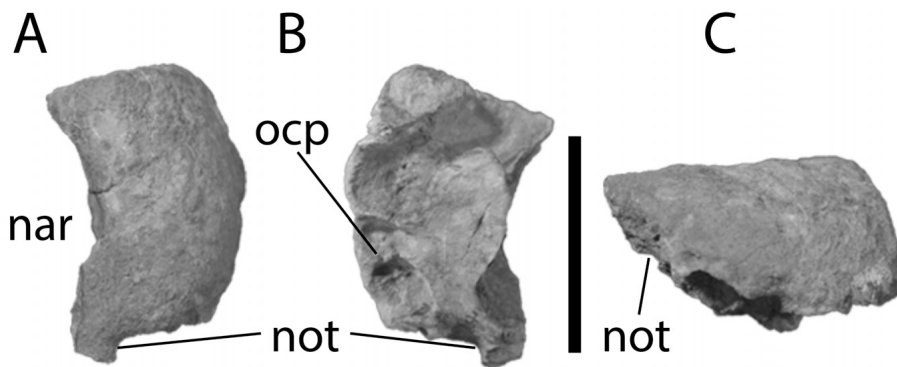


FIGURE 5. Crocodyloidea, gen. et sp. indet, MUN STRI-12939, from the Ware Formation. Right premaxilla in **A**, dorsal; **B**, ventral; and **C**, lateral views. **Abbreviations:** nar, narial rim; not, notch for the fourth mandibular tooth; ocp, occlusal pit. Scale bar equals 50 mm.



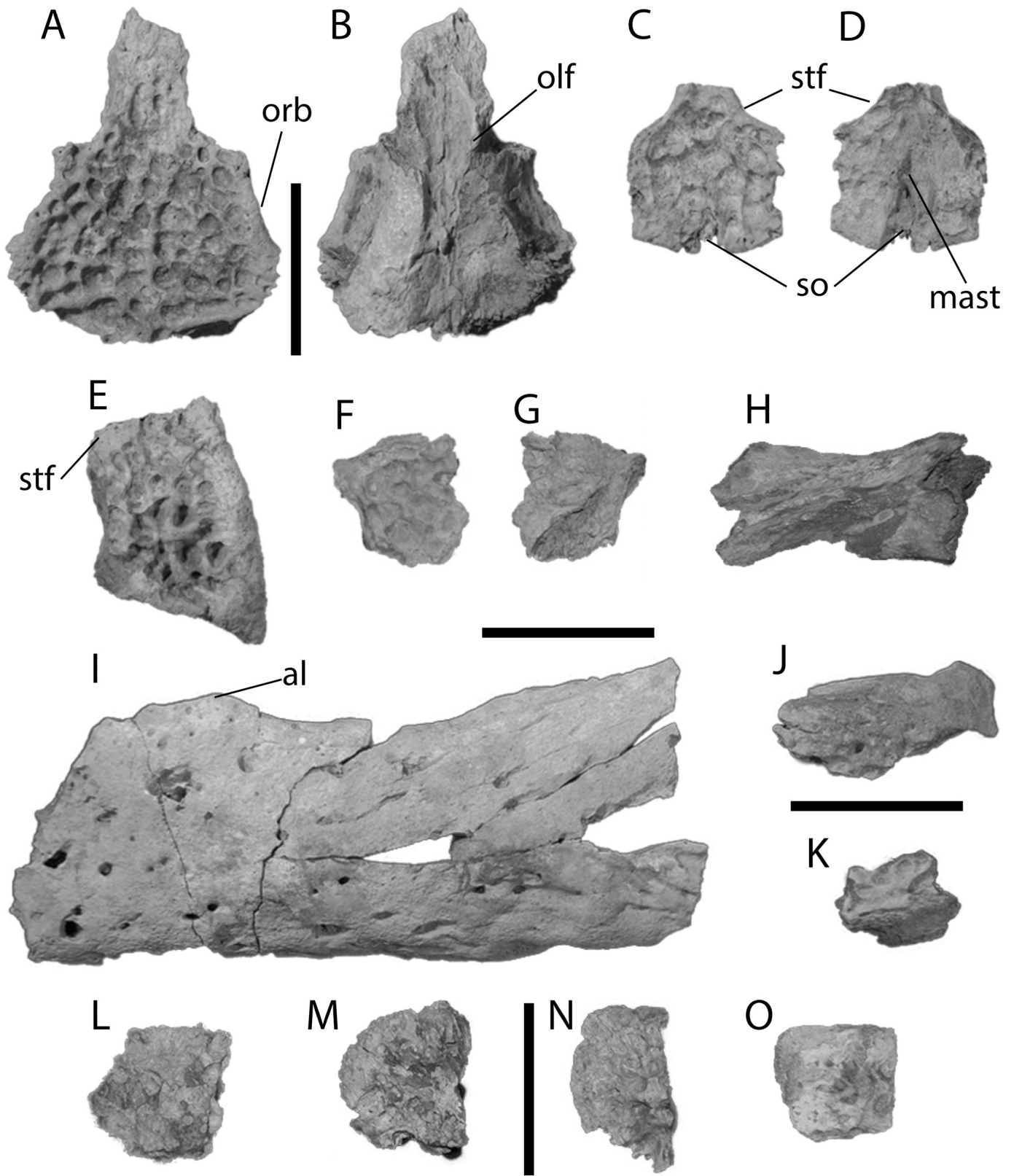


FIGURE 6. *Crocodyloidea*, gen. et sp. indet, MUN STRI-16180, fragments of skull, mandible, and osteoderms from the Ware Formation. **A, B**, frontal in **A**, dorsal; and **B**, ventral views. **C, D**, parietal and supraoccipital in **C**, dorsal; and **D**, ventral views. **E**, partial right squamosal. **F, G**, partial right postorbital in **F**, dorsal; and **G**, ventral views. **H**, partial left jugal. **I**, fragment of right dentary in lateral view. **J**, fragment of right surangular in lateral view. **K**, angular fragment in lateral view. **L–O**, partial osteoderms in dorsal view. **Abbreviations:** **al**, external rim of 11th? alveolus; **olf**, groove for the olfactory tract; **orb**, orbital rim; **so**, supraoccipital; **stf**, supratemporal fenestrae rim. All scale bars equal 50 mm.

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 undulating 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 of neurovascular foramina close to the alveolar margin. The internal surfaces of the fourth alveolus and the narial opening are visible in medial view. A deep cylindrical cavity projects anterodorsally from the rim of the fourth alveolus and may represent the internal cavities of both the third and fourth alveoli. The internal cavity of the narial opening can be seen in medial view as a 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 posterolateral 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 alveoli, 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**—Specimen MUN STRI-16180 comprises several associated fragments with ornamentation patterns consistent with skull or mandibular fragments. It includes 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 convex. 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 MUN STRI-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 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 indicates that 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. In dorsal view, the posterior plate of the parietal is roughly square. The posteromedial 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 plate is 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. Anterior to this cavity, the cancellous bone is exposed, and it cannot be determined if the atrium continues anteriorly into an expanded parietal sinus as in alligatorids and gavialoids, or the sinus is absent, as in crocodyloids (Brochu, 1997).

**Squamosal**—The dorsal surface of the right squamosal is preserved. In dorsal view, the anterior portion of the squamosal is 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 because 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 MUN STRI-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, except 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 anterior two-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.

**Osteoderms**—There are four osteoderms preserved in MUN STRI-16180: 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 of between 5 and 10 mm.

**Discussion**—Despite not having any synapomorphies preserved, MUN STRI-16180 has several features consistent with those found in Crocodyloidea. 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 posterior plate of the parietal of MUN STRI-16180, anteroposteriorly broad posterior to the supratemporal fenestrae, is different from those of tomistomines such as *Maroccosuchus zennaroi*, *Thecachampsia carolinensis*, and *Tomistoma schlegelii*, in which the posterior parietal plate is anteroposteriorly narrow (Myrick, 2001; Jouve, et al., 2014). In other tomistomine taxa such as *Dollosuchoides densmorei* and *Toyotamaphimeia machikanensis*, as well as in South American gavialoids and *Gavialis*, the parietal is even narrower posterior to the supratemporal fenestrae, forming a very narrow, unornamented bar (Jouve, 2004; Kobayashi et al., 2006; Brochu, 2007b). The robusticity of the dentary fragment relative to other elements of MUN STRI-16180 also indicates that MUN STRI-16180 does not represent a longirostrine form, such as tomistomines or gavialoids. Thus, MUN STRI-16180 represents a crocodyloid, likely a species of *Crocodylus*, but it lacks any synapomorphies that allow assigning it to genus.

*CROCODYLUS* Laurenti, 1769

*CROCODYLUS* sp.

(Fig. 7)

**Referred Material**—MUN STRI-17702: posterior fragment of a right mandibular ramus (Fig. 7).

**Locality and Horizon**—This specimen comes from locality 470062 ‘Police Station,’ near the border with Venezuela; Lower Ware Formation, late Pliocene (Moreno et al., 2015).

### Description

Specimen MUN STRI-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 MUN STRI-17702 is truncated, and a portion of the articular can be seen laterally, as in *Crocodylus* and *Voay robustus* (Brochu, 2000, 2007a). 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 fossa 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 aereum is located in the medial margin of the articular, just posterior to the glenoid fossa, in contrast to the dorsally shifted position seen in all alligatoroid crocodylians (Brochu, 1999). The retroarticular process of MUN STRI-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., 2006).

**Discussion**—This specimen 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 aereum in MUN STRI-17702 is located in the medial margin or the articular, and not dorsally shifted as in all alligatoroids (Brochu, 1999). The truncated dorsal process of the surangular in MUN STRI-17702 differentiates it from most crocodylians, including tomistomines and *Osteolaemus*, in which this process is not truncated and the articular is not visible in lateral view. A truncated dorsal process of the surangular is also found in the osteolamine *Voay robustus* (Brochu, 1999). However, in *V. robustus*, the retroarticular process is shorter, less curved, and lower than the posterior edge of the articular fossa (Brochu, 2007a). The retroarticular process in MUN STRI-17702 is more curved and higher than the edge of the articular fossa in lateral view, more similar to species of *Crocodylus*.

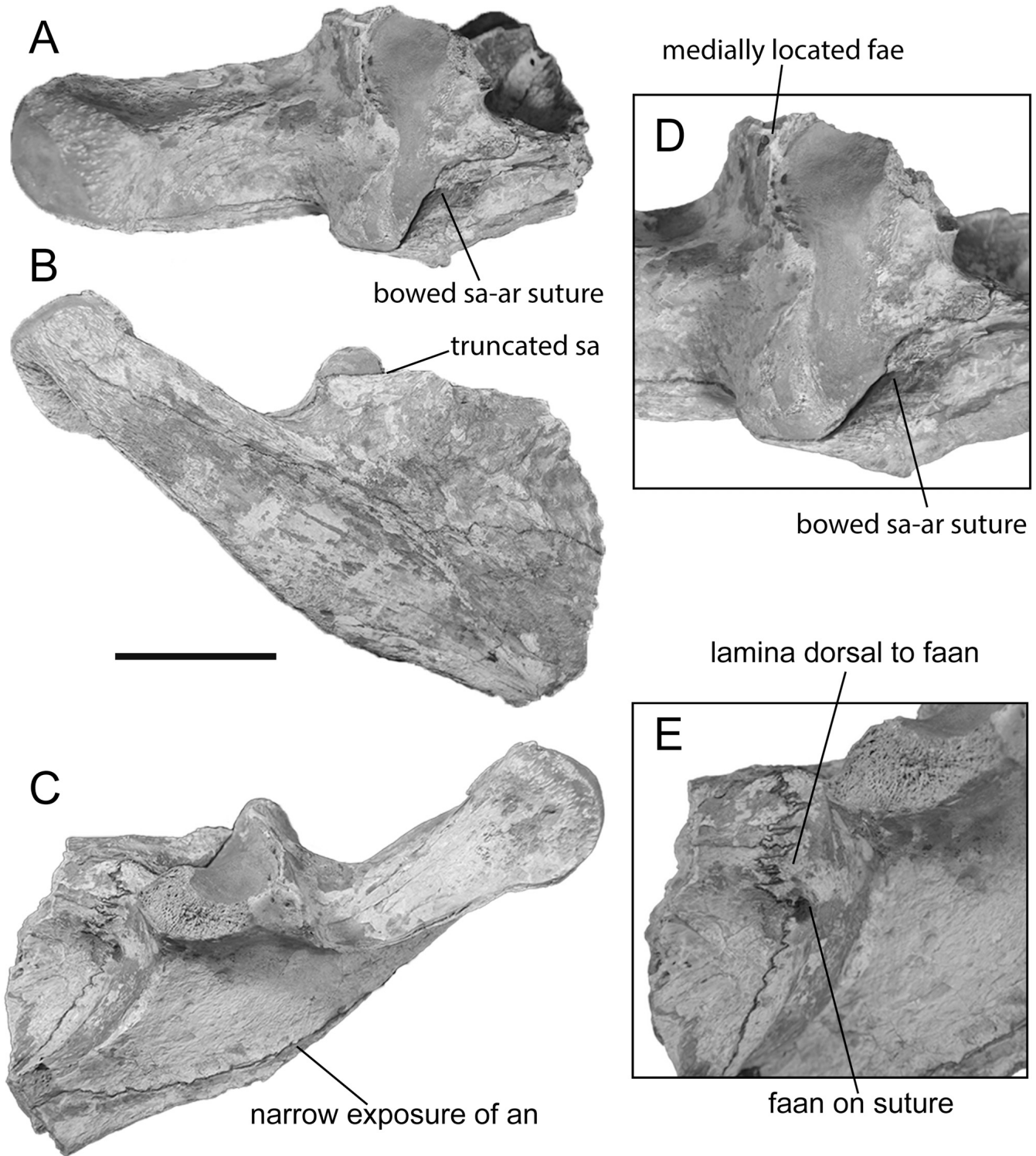


FIGURE 7. *Crocodylus* sp. from the Ware Formation. **A–C**, MUN STRI-17702, posterior fragment of right mandibular ramus in **A**, dorsal; **B**, lateral; and **C**, medial views. **D**, detail of glenoid fossa in dorsal view. **E**, detail of surangular-articular suture in medial view. **Abbreviations:** an, angular; ar, articular; faan, foramen for articular artery and alveolar nerve; fae, foramen aereum; sa, surangular. Scale bar equals 50 mm.

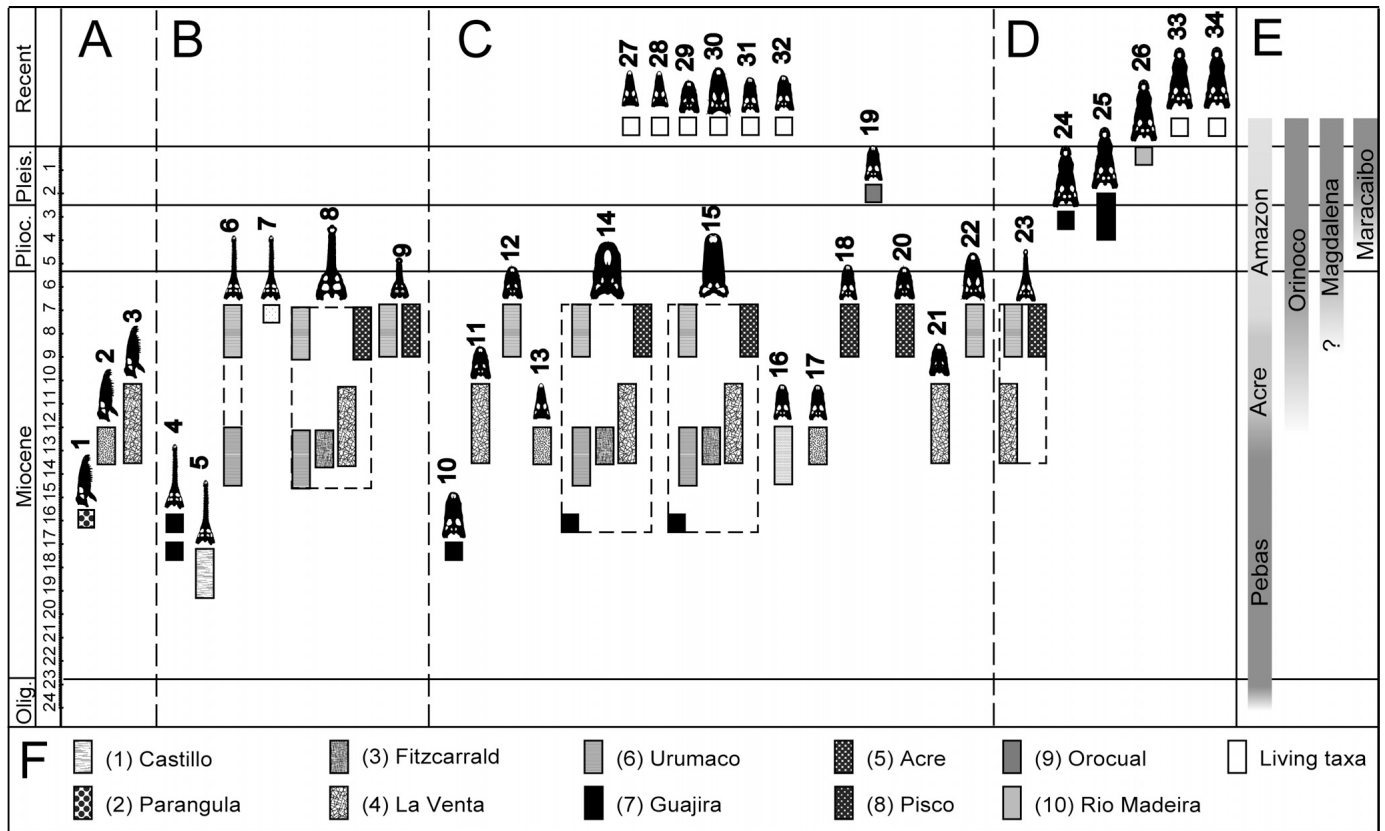


FIGURE 8. Crocodylian faunas and hydrographic change in equatorial South America during the Neogene and Quaternary. **A–C**, crocodylian taxa through time. **A**, sebecids; **B**, gavialoids; **C**, caimanine alligatoroids; **D**, crocodyloids. Individual taxon names from Riff et al. (2009) and Scheyer et al. (2013). Age of the Castillo formation follows Rincón et al. (2014). **E**, 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; **F**, key to fossil crocodylian sites. Numbers are as in Figure 1. **Abbreviations:** 1, *Barinasuchus arveloi*; 2, Sebecidae, gen. et sp. indet.; 3, *Langstonia huilensis*; 4, Gavialoidea, gen. et sp. indet.; 5, *Siquisiquesuchus venezuelensis*; 6, *Ikanogavialis gameroi*; 7, *Piscogavialis jugaliperforatus*; 8, *Gryposuchus* spp.; 9, *Hesperogavialis* spp.; 10, Alligatoridae, gen. et sp. indet.; 11, *Eocaiman* sp.; 12, *Globidentosuchus brachyrostris*; 13, *Paleosuchus* sp.; 14, *Purussaurus* spp.; 15, *Mourasuchus* spp.; 16, *Caiman* sp. from the Socorro Formation; 17, *Caiman* sp. from the Ipururo Formation; 18, *Caiman niteroiensis*; 19, *Caiman venezuelensis*; 20, *Caiman brevirostris*; 21, *Caiman* cf. *lutescens*; 22, *Melanosuchus fisheri*; 23, *Charactosuchus* spp.; 24, *Crocodylus* sp.; 25, *Crocodylus falconensis*; 26, *Crocodylus* sp. from the Rio Madeira Formation; 27, *Paleosuchus trigonatus*; 28, *Paleosuchus palpebrosus*; 29, *Caiman latirostris*; 30, *Melanosuchus niger*; 31, *Caiman yacare*; 32, *Caiman crocodilus*; 33, *Crocodylus intermedius*; 34, *Crocodylus acutus*.

## DISCUSSION

### Stratigraphic Distributions and Historical Implications of Guajira Crocodylians

The number of described South American crocodylians is higher for the Miocene than for any other epoch of the Cenozoic (Riff et al., 2009; Scheyer et al., 2013). Most species come from four assemblages assigned to the late middle Miocene Laventan (13.8–11.8 Ma) and the late Miocene Huayquerian (9.0–6.8 Ma) South American Land Mammal ages (SALMAs; Guerrero, 1997; Cozzuol, 2006; Antoine et al., 2007) (Fig. 8A). Older crocodylian 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. 8A). 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 Fitzcarrald 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 late early–early middle Miocene Jimol and Castilletes formations are characterized by both gavialoids and caimanine alligatoroids. Gavialoid remains from localities 390090 and 390091 were found in shallow marine deposits, similar to the oldest Neotropical gavialoid records from latest Oligocene or earliest Miocene marginal marine deposits in Antillean, Atlantic, and Caribbean localities (Brochu and Rincón, 2004; Velez-Juarbe et al., 2006; Moraes-Santos et al., 2011). These records are consistent with coastal and eustarine habitats

inferred for the oldest known gavialoids (e.g., Troxell, 1925; Brochu, 2004, 2006a, 2006b; Hua and Jouve, 2004; Delfino et al., 2005; Jouve et al., 2006, 2008).

Fossil caimans from the Paleogene are small, comparable in size to living species of *Caiman* and *Paleosuchus* (e.g., Bona, 2007; Brochu, 2010, 2011; 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, are known only from the middle and late Miocene. The size of alligatorid remains from the upper Jimol formation (locality 390092) indicates that large caimanine taxa were already present by the early Miocene.

Remains of the caimans *Purussaurus* and *Mourasuchus* from the lower Castilletes formation (North Patajau Valley and Kaitamana Cemetery, respectively) represent taxa already known from the younger Laventan and Huayquerian faunas, thus extending the temporal range of these specialized lineages. The presence of gavialoids together with *Purussaurus* indicates further similarities with Laventan and Huayquerian faunas, suggesting that by the early Miocene a diverse gavialoid-caimanine assemblage was already established.

Crocodylian specimens from the Ware Formation represent crocodyloids; one of them includes the extant genus *Crocodylus*. Fossils of *Crocodylus* in the Neotropics are restricted to the Plio-Pleistocene and Holocene. A complete skull from the late Pleistocene of Rondonia, Brazil (Fortier et al., 2007), and remains of *Crocodylus rhombifer* from the late Holocene of the Antilles (Morgan and Albury, 2013) indicate that in the recent past, the genus had a greater distribution within the Neotropics. Pliocene records of Neotropical *Crocodylus* are even scarcer. The fossil record of *Crocodylus moreleti* in the late Pliocene of Mexico (Miller, 1980) is based on jaw fragments consistent with the morphology of the genus. Unequivocal fossils of *Crocodylus* have been reported from the Plio-Pleistocene of Costa Rica (Mead et al., 2006). The oldest Neotropical representative of the genus is *Crocodylus falconensis* from the middle-late Pliocene San Gregorio Formation of the Urumaco sequence in northwestern Venezuela (Scheyer et al., 2013). The Ware Formation record expands the geographical range of Neotropical *Crocodylus* to include the northernmost edge of South America.

### Crocodylian Faunas and Environmental Change

The Neogene was a time of extensive climatic and hydrographic change in equatorial South America (Fig. 8B), related in part to the isolation of drainage basins caused by Andean uplift (Wesselingh et al., 2009). Peripheral drainages such as those of the Magdalena and Maracaibo basins had extensive connections with the Amazon and Orinoco until the late Neogene (Lundberg et al., 1998). These connections may have facilitated cosmopolitan distributions of Miocene crocodylian assemblages in equatorial South America. The presence in the lower Castilletes Formation of two caimanine taxa (*Purussaurus* and *Mourasuchus*) shared with other Miocene South American assemblages suggests that by the early Miocene, drainage connections extended to the northernmost part of the continent.

During the latest Miocene and Pliocene (7.0–2.5 Ma), 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 Orinoco-Amazonia (Lundberg et al., 1998). Aridity increased by both the generation of rain shadows (Bookhagen and Streecker, 2009; Mora et al., 2009) and drastic changes in the northern position of the Intertropical Convergence Zone (Vonhof and Kaandorp, 2009), leading to the disappearance of rain forests and the local extirpation of several groups of fishes (Lundberg et al., 2009). The extinction of many

crocodylian taxa typical of Laventan and Huayquerian faunas has been attributed to these climatic and hydrographic changes (Riff et al., 2009; Scheyer et al., 2013).

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

### Conclusions

Fossil crocodylians of the late early–early middle Miocene Jimol and Castilletes formations include gavialoids and large caimanines. The occurrences of the specialized caimanines *Purussaurus* and *Mourasuchus* in the Castilletes Formation expand the temporal range of these genera to the late early–early middle Miocene, thus persisting for approximately 9 million years. The Castilletes Formation record also expands the geographic range of these taxa to the northernmost edge of South America. The presence of taxa shared with other localities suggests that the La Guajira Peninsula was connected to other hydrographical basins in tropical South America.

Crocodyloids from the Pliocene Ware Formation represent an early record of *Crocodylus*, an immigrant taxon that occupied hydrographic basins after the extinction of Miocene assemblages. This record potentially expands the geographic range of the genus during the Pliocene in South America, indicating that crocodylian faunal turnover had already occurred by the late Pliocene, at least in the northern portion of the continent.

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APPENDIX 1. List of undiagnostic crocodylian specimens. Numbers in parenthesis refer to localities explained in the text.

- Procoelus vertebrae: MUN STRI-16422 (390085), MUN STRI-16788 (390094), MUN STRI-16789 (390094), MUN STRI-16805 (390094), MUN STRI-16197 (390075), MUN STRI-16203 (390075), MUN STRI-16296 (390075), MUN STRI-16320 (390075; dorsal vertebra and rib fragments), MUN STRI-17704 (390075; three articulated vertebrae), MUN STRI-19554 (390075).
- Skull fragments: MUN STRI-16334 (390085; rostrum fragment), MUN STRI-16563 (390085), MUN STRI-13109 (390075; articulated lacrimal and jugal), MUN STRI-19823 (390075; rostrum fragment and associated fragments), MUN STRI-16352 (390075; fragment of squamosal).
- Isolated teeth: MUN STRI-16554 (390085), MUN STRI-17158 (390094), MUN STRI-13112 (390075), MUN STRI-13113 (390075), MUN STRI-16181 (390075), MUN STRI-16191 (390075), MUN STRI-16192 (390075), MUN STRI-16194 (390075), MUN STRI-16213 (390075), MUN STRI-16217 (390075), MUN STRI-16218 (390075), MUN STRI-16222 (390075), MUN STRI-16228 (390075), MUN STRI-16232 (390075), MUN STRI-16243 (390075), MUN STRI-16277 (390075), MUN STRI-16278 (390075), MUN STRI-16279 (390075), MUN STRI-16280 (390075), MUN STRI-16281 (390075), MUN STRI-16282 (390075), MUN STRI-16310 (390075), MUN STRI-16319 (390075), MUN STRI-16322 (390075), MUN STRI-16326 (390075), MUN STRI-16329 (390075), MUN STRI-16360 (390075), MUN STRI-16410 (390075; six isolated teeth), MUN STRI-16498 (390075), MUN STRI-16539 (390075), MUN STRI-17134 (390075), MUN STRI-20368 (390075; three isolated teeth), MUN STRI-31304 (390075).
- Osteoderms: MUN STRI-16336 (390085), MUN STRI-16424 (390085), MUN STRI-16425 (390085), MUN STRI-16426 (390085), MUN STRI-16215 (390075), MUN STRI-16240 (390075), MUN STRI-17136 (390075), MUN STRI-19620 (390075), MUN STRI-20337 (390075), MUN STRI-20432 (390075).
- Postcranial elements: MUN STRI-16781 (390094; left ilium), MUN STRI-16189 (390075; incomplete scapula).