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GEOBIOS

Geobios 40 (2007) 51–59

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Article original

Tertiary crocodylians from Puerto Rico: Evidence for Late Tertiary endemic crocodylians in the West Indies?

Crocodiliens tertiaires de Porto Rico : preuve de l'existence de crocodiliens endémiques dans les Antilles ?

Cocodrilos terciarios de Puerto Rico: ¿prueba de la existencia de cocodrilos endémico en las Antillas?

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Received 18 May 2005; accepted 12 October 2005
Available online 16 January 2007

Abstract

Fragmentary fossils from northwestern Puerto Rico document the existence of crocodyliforms during the Late Oligocene and Early Miocene. The remains are insufficient to establish new named species, but they are inconsistent with any other crocodylian known from the western hemisphere during the Cenozoic, including extant *Alligator* and *Crocodylus*. They are thus consistent with the hypothesis that *Crocodylus* is a comparatively recent immigrant into the West Indies and suggest that, as with Australasia and Africa, the Antilles hosted an endemic clade of crocodylians during the Tertiary, later replaced by *Crocodylus*.
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Résumé

Des fragments de fossiles du nord-ouest de Porto Rico démontrent l'existence de crocodyliformes pendant l'Oligocène supérieur et le Miocène inférieur. Les restes sont insuffisants pour nommer de nouvelles espèces, mais ils diffèrent de tous les crocodiliens connus de l'hémisphère ouest pendant le Cénozoïque, y compris *Alligator* et *Crocodylus*, des genres qui existent encore actuellement. Ainsi, ces restes sont-ils conformes à l'hypothèse d'une immigration récente du genre *Crocodylus* dans les Antilles, et suggèrent, comme en Australasie et en Afrique, la présence d'un clade endémique des crocodiliens dans cette région pendant le Tertiaire, remplacé plus tard par *Crocodylus*.
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Resumen

Fragmentos fósiles del noroeste de Puerto Rico evidencian la existencia de crocodyliformes durante el Oligoceno Tardío y el Mioceno Temprano. Los restos son insuficientes para nombrar nuevas especies, pero los mismos son inconsistentes con algún otro cocodrilo conocido del hemisferio Occidental durante el Cenozoico, incluidos los actuales *Alligator* y *Crocodylus*. Por lo tanto estos son consistentes con la hipótesis de

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0016-6995/$ – see front matter © 2006 Published by Elsevier Masson SAS.
doi:10.1016/j.geobios.2005.10.008

que *Crocodylus* es un reciente inmigrante a las Indias Occidentales, y sugiere que al igual que Australasia y Africa, las Antillas alojaron un clado endémico de cocodrilos durante el Terciario, que posteriormente fue reemplazado por *Crocodylus*.
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Keywords: Crocodylia; Puerto Rico; Antilles; Biogeography; *Crocodylus*

Mots clés : Crocodylia ; Porto Rico ; Antilles ; Biogéographie ; *Crocodylus*

Palabras clave: Crocodylia; Puerto Rico; Las Antillas; Biogeografía; *Crocodylus*

Biogeographers debate the origins and present distribution of the Greater Antillean herpetofauna. Some favor vicariance models with speciation driven by landmass division (e.g., Rosen, 1976; Page and Lydeard, 1994; Crother and Guyer, 1996). Others instead prefer dispersal-centered models (e.g., Hedges, 1996a, 1996b; Hass et al., 2001). The complex tectonic and sea level history of the region, along with uncertain phylogenetic relationships and divergence time estimates among many West Indian vertebrates, has made this an especially difficult problem to address.

Crocodiles have played comparatively little role in this debate, in part because only two species occur naturally in the Greater Antilles, one of which (the American crocodile, *Crocodylus acutus*) has a very broad distribution in the region (Varona, 1987; Thorbjarnarson, 1988; Schwartz and Henderson, 1991; Schubert and Santana, 1996; Meshaka et al., 2000; Platt and Thorbjarnarson, 2000) and a demonstrated capacity for crossing marine barriers (Ellis, 1981; Taplin et al., 1982). The other species in the region, the critically-endangered Cuban crocodile (*Crocodylus rhombifer*), was historically restricted to freshwater marshes of Cuba and Isla de Pinos, but there are Holocene occurrences of this species from Grand Cayman Island (Morgan et al., 1993) and outside the Antilles in the Bahamas (Franz et al., 1995). The only other crocodylian found in the Greater Antilles, the common caiman (*Caiman crocodilus*), was introduced by humans on Isla de Pinos and Puerto Rico (Ross, 1998; Schwartz and Henderson, 1991). A third species of *Crocodylus* (the Orinoco crocodile, *Crocodylus intermedius*) has been reported from Trinidad and Grenada (Barbour, 1914), but no sightings have been recorded from the Greater Antilles and the Caribbean island occurrences are thought to be extralimital vagrants from South America (Medem, 1983).

That *Crocodylus* is capable of prolonged exposure to salt water suggests that dispersal was a factor in the group's historical biogeography. But *Crocodylus* was long viewed as an ancient genus with a widespread distribution (e.g., Steel, 1973). Tertiary fossils from the Americas were often assigned to *Crocodylus*, and these were sometimes implied to have been the ancestors of West Indian crocodiles (Sill, 1968; Hedges, 1996a). Depending on how one classified the fossils, the divergence times could have fit within the framework of regional landmass separation (Brooks and O'Grady, 1989). *Crocodylus* could therefore be consistent with either a dispersal or vicariance model, depending on when members of the group first arrived in the region. An early arrival would allow geological factors to impact crocodile populations and drive allopatric speciation.

Recent phylogenetic work challenges this view. Molecular and fossil evidence indicates that all living species of *Crocodylus* last shared a common ancestor within the past 15 million years, with the group first appearing in the Old World (Densmore, 1983; Densmore and Owen, 1989; Hass et al., 1992; Brochu, 2000; Head, 2001; Schmitz et al., 2003). Older fossils formerly classified as forms of *Crocodylus* are more distant relatives, and *Crocodylus* does not appear in the western hemisphere until the Late Miocene or Pliocene (Mook, 1959; Miller, 1980; Castillo-Ceron, 2000; Mead et al., 2004).

Large portions of the present range of *Crocodylus* were already separated by large stretches of seawater by that time, and the Beringian connection between the eastern and western hemispheres was well outside the thermal tolerance zone for crocodiles (Markwick, 1998). We are thus forced to assume transoceanic dispersal. The four living species of New World *Crocodylus* may form a clade, implying a single dispersal event either across the Atlantic from Africa or (less likely) across the Pacific from Asia (Densmore and White, 1991; Brochu, 2000).

Discovery of Antillean *Crocodylus* in units older than 15 million years would force us to reconsider this scenario. Unfortunately, little is known about the pre-Holocene record of Antillean crocodylians. The best-sampled record is from Cuba, where fossils document the presence of *Crocodylus rhombifer* in the Quaternary (Brown, 1913; Varona, 1966, 1984). Less complete Quaternary material has been considered to represent extinct species (Leidy, 1868; Varona, 1984), but we are not convinced that it can be distinguished from *C. rhombifer* (Brochu, 2000). The Tertiary crocodile record in Cuba extends at least as far back as the Early Miocene (MacPhee et al., 2003), but to date nothing diagnosable has been published. Fragmentary crocodylian remains are known from the Quaternary of New Providence Island (Pregill, 1982), San Salvador (Olson et al., 1990), Jamaica (Morgan, 1993), and Isla de Mona (Frank and Benson, 1998), but in these cases not enough was found to allow specific identification. The only described pre-Miocene crown-group crocodylian from the region is *Charactosuchus kugleri*, a long-snouted form probably related to *Tomistoma* (the living Indonesian false gharial) from the Eocene of Jamaica (Berg, 1969; Donovan et al., 1990; Domning and Clark, 1993; Portell et al., 2001).

Previous accounts of Tertiary vertebrates from Puerto Rico reported crocodylians in units of Oligocene and Early Miocene age (MacPhee and Wyss, 1990). Although insufficient for species-level diagnosis, this material is sufficient to rule out any crocodylian currently found in the Americas, including *Crocodylus*. It is also dissimilar from any of the longirostrine crocodylians known from the region in the Tertiary. Some morphological aspects suggest the possibility of a group of endemic crocodylians from the Greater Antilles during the Neogene, a concept congruent with the trans-Atlantic dispersal model of New World *Crocodylus* biogeography and the presence of similar endemic radiations in the Neogene of Australasia (Willis et al., 1993; Salisbury and Willis, 1996) and Africa (Brochu, 2000; Llinás Agrasar, 2004). The purpose of this paper is to briefly describe these Puerto Rican remains.

Institutional/Collection Abbreviations: AMNH, American Museum of Natural History, New York; RC, collection of Narciso Rabell Cabreri maintained by the University of Puerto Rico at Río Piedras; TMM, Vertebrate Paleontology Laboratory, Texas Memorial Museum, Austin; UPRMP, University of Puerto Rico Department of Geology, Paleontology Collection, Mayagüez.

1. Stratigraphic setting and history of collection

The material described here is from Oligocene through Lower Miocene marginal marine sequences. During this time, changes in sea level resulted in shifting zones of carbonate and noncarbonate shelf deposition. On the northern coast of Puerto Rico, the Oligocene San Sebastián Formation and Early Miocene Cibao Formation represent noncarbonate nearshore facies, with an intervening limestone unit (the Lares Limestone) straddling the Oligocene-Miocene boundary (Monroe, 1980; MacPhee et al., 2003). Vertebrate fossils are much more abundant in the noncarbonate units, and the material in this paper is from the San Sebastián and Cibao Formations and Lares Limestone.

Oligocene noncarbonate units along the southern coast of Puerto Rico (the Juana Díaz Formation) have also preserved vertebrate material, including crocodylian teeth and fragments of vertebrae (MacPhee and Wyss, 1990; MacPhee et al., 2003; Nieves-Rivera and Vélez-Juarbe, unpublished observations). At least some of the Lares Limestone material is from road cuts along road PR-448 (UPRMP-2820, 2821, and 2822) and PR-111 (UPRMP-2775) near San Sebastián, where exposures pertain to the Early Miocene and Late Oligocene respectively based on the occurrence of biostratigraphically informative foraminifera and stratigraphy (Vélez-Juarbe, unpublished data). Although demonstrating the presence of crocodyliforms in the region at these times, isolated teeth are of limited taxonomic value and cannot tell us which crocodyliform lineages were present.

Some specimens were collected by Narciso Rabell Cabreri in the early 20th century, most of which was brought to the AMNH in 1987. The collection included a pelomedusid turtle (Wood, 1972), mammals, sharks, bony fishes, and marine invertebrates as well as crocodylians (Wood, 1972; MacPhee and Wyss, 1990). A few teeth remain in the collections of the University of Puerto Rico–Rio Piedras campus, where they maintain the original Rabell Cabreri collection numbers. Precise locality information was evidently collected along with the fossils, but this information was lost after Rabell Cabreri's death (MacPhee and Wyss, 1990). We can be reasonably sure the material derives from the San Sebastián Formation, as it was collected from a silty matrix in the vicinity of San Sebastián and Lares, and the only other rock unit exposed in that region (the Lares Limestone) is a carbonate unit lacking silty layers.

Field work by the AMNH (MacPhee and Wyss, 1990) and H. Santos and J. Vélez-Juarbe of the University of Puerto Rico at Mayagüez Department of Geology has expanded the amount of material available. Locality information for AMNH material is provided by MacPhee and Iturralde-Vinent (1995) and MacPhee and Wyss (1990). Most San Sebastián Formation material from the UPRMP collections is from the vicinity of the town of San Sebastián, with the exception of UPRMP 2824, which is from near Lares. Cibao material from the UPRMP is from the Montebello Limestone Member near Arecibo. Additional crocodylian teeth from the Cibao Formation near Bayamón are deposited in the División de Arqueología (Instituto de Cultura Puertorriqueña, San Juan).

2. Description

2.1. San Sebastián Formation

Referred specimens: AMNH 24484, AMNH 24485, teeth; AMNH 24487, two dorsal osteoderms; AMNH 24488, left quadrate ramus; AMNH 24489, four partial vertebrae; AMNH 24558, fragmentary?anterior sacral vertebra; RC 238, RC 1579, RC 1584, RC 1585, RC 1615, RC 1616, RC 2912, teeth; UPRMP 372, UPRMP 2824, teeth.

Several isolated teeth are known (Fig. 1L–P). The crowns are conical and bear a pair of carinae. The surface of the enamel is striated. These teeth are consistent with almost any lineage and can only be identified to the level of Crocodyliformes, although some are slender and resemble those of longirostrine crocodylians.

An isolated left quadrate ramus (Fig. 2A,B) is incomplete, but preserves most of the condylar surface. The distalmost part of the paraoccipital process (including the exoccipital and squamosal) is preserved on the dorsal surface of the ramus, and a lineation on that surface represents the quadrate-quadratojugal suture. The foramen aereum is not preserved, but it would have been visible had it taken a dorsal position, as in alligatoroids. We therefore assume that the foramen was placed medially on the ramus. The condylar region is not complete, but the dorsal margin of the medial hemicondyle (as preserved) is ventromedial to the dorsal margin of the lateral hemicondyle. Although the medial hemicondyle is not complete, its dorsal margin probably continued ventromedially and did not curve dorsally.

A set of four partial vertebrae (one cervical, two dorsal, and one caudal), possibly pertaining to the same individual, is catalogued as AMNH 24489. A fragmentary sacral vertebra (probably the anterior element, AMNH 24558) is also preserved. The dorsal, sacral, and caudal elements are not very informative, but the cervical vertebra is interesting (Fig. 1A–C). The parapophysis and diapophysis on each side are very close together, strongly suggesting that this derives from the cranial portion of the neck. It is consistent with the first

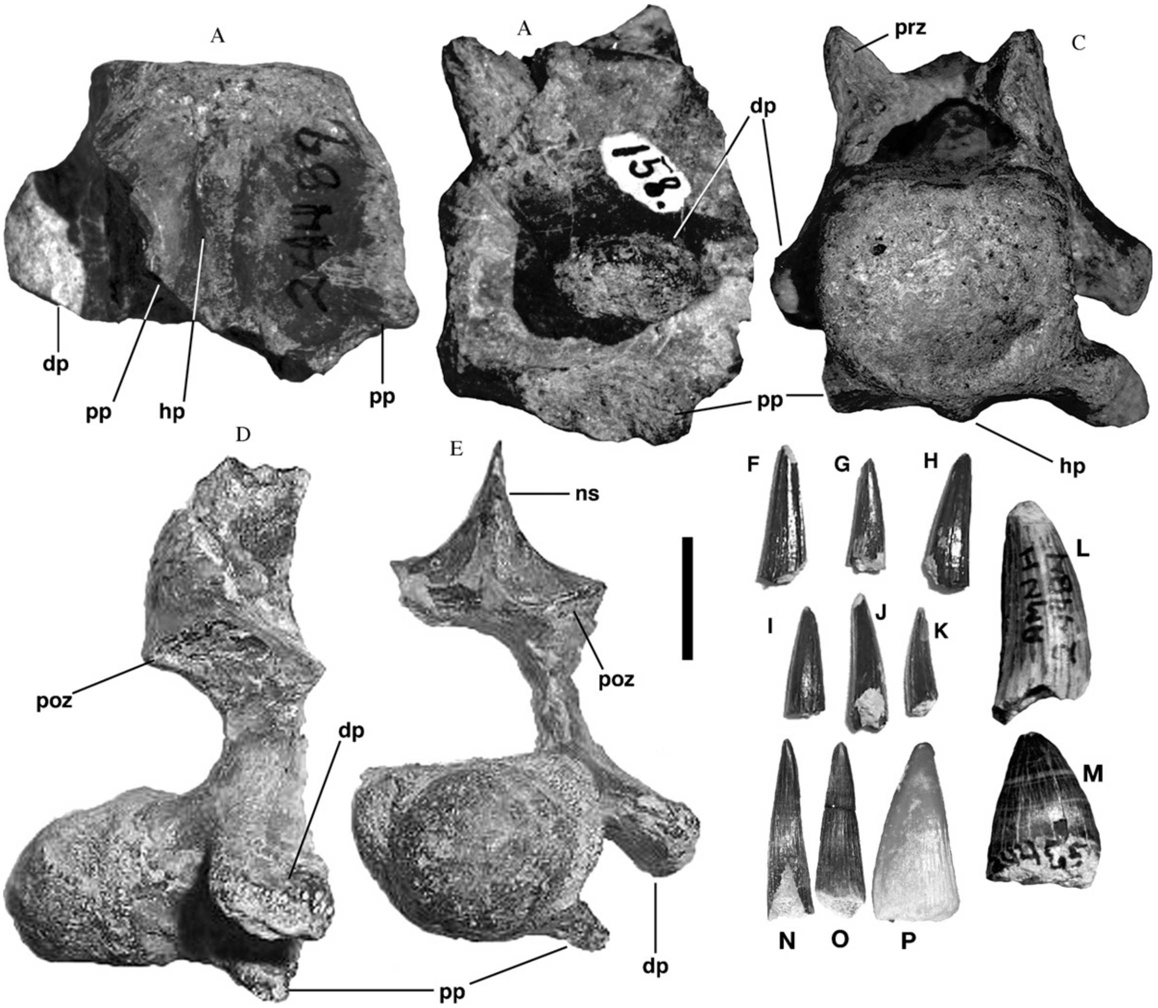

Fig. 1. Crocodyliform remains. (A–C, L–P) San Sebastián Formation (Late Oligocene) and (D–K) Lares Formation, Puerto Rico. AMNH 24489, partial cervical vertebra, ventral (**A**), left lateral (**B**), and anterior (**C**) view. UPRMP 2822, cervical vertebra, right lateral (**D**) and posterior (**E**) view. Isolated teeth: F, H, I, UPRMP 2820; G, I, K, UPRMP 2821, posterior (**F, G**), labial (**H, I**), lateral (**J, K**) view; **L**, AMNH 24424; **M**, AMNH 24485; **N, O**, RC 1585; **P**, RC 1579. Scale = 1 cm. Abbreviations: dp, diapophysis; hy, hypophysis; poz, postzygapophysis; pp, parapophysis; prz, prezygapophysis.

postaxial element (third cervical) in most crocodylians. This specimen bears a very short ventral midline keel.

A pair of rectangular osteoderms from the dorsal shield is preserved (AMNH 24487, Fig. 3). They bear circular pits and a smooth bevelled surface along the anterior margin. The anterior margin is concave, and each osteoderm bears a very small keel toward the rear of the dorsal surface.

2.2. Lares Limestone

Referred specimens: UPRMP-2775, 2820, 2821, teeth; UPRMP-2822, vertebra.

An abraded trunk vertebra (Fig. 1D,E) and several isolated teeth (Fig. 1F–K) are preserved. The teeth, like those from the San Sebastián Formation, can be identified only to the level of Crocodyliformes, though the slender teeth resemble those often found in longirostrine crocodylians. The vertebra is procoelous and probably comes from a crown-group crocodylian, but there is insufficient information to identify it more precisely.

2.3. Cibao Formation

Referred specimens: AMNH 24494, cranial and mandibular elements including frontal, partial left squamosal, and anterior end of right dentary; AMNH 24497, AMNH 24498, AMNH 24499, fragmentary vertebrae; AMNH 24496, teeth UPRMP 2845, teeth.

Some fragments from the Cibao Formation can be identified to the level of Eusuchia (e.g., procoelous vertebral fragments, AMNH 24497, 24498, and 24499) and others only to the level of Crocodyliformes (e.g., tooth fragments, AMNH 24496). Most of these do little beyond establishing the presence of crocodyliforms (probably crocodylians) in the Cibao Formation, and size differences among the vertebrae indicate the presence of more than one individual. Any comparisons must consider the abrasion that has, to varying degrees, affected all crocodyliform remains from this unit. However, several skull fragments (catalogued as AMNH 24494) are consistent in size and may represent a single individual.

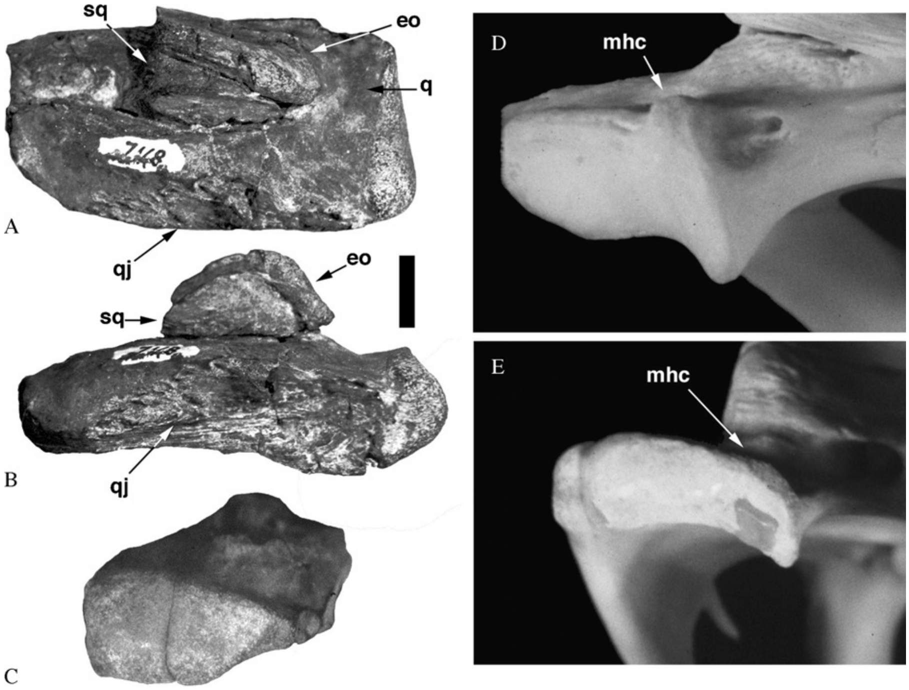

Fig. 2. AMNH 24488, crocodylian partial left quadrate ramus, San Sebastián Formation (Late Oligocene), Puerto Rico, in dorsal (**A**), left lateral (**B**), and posterior (**C**) view. **D**, TMM m-6342, *Tomistoma schlegelii*, left quadrate, posterior view; **E**, TMM m-5485. *Gavialis gangeticus*, left quadrate, posterior view. Scale = 1 cm. Abbreviations: eo, exoccipital; mhc, medial hemicondyle; q, quadrate; qj, surface for quadratojugal on quadrate; sq, squamosal.

The frontal (Fig. 4C) bears a prominent anterior process that would have separated the caudalmost tips of the nasals. It flares ventrally and is triangular in cross-section. The margins of the orbits are upturned, but not to the same degree seen in extant *Alligator* or *Crocodylus*. The posterior margin, which would have contacted the parietal, is posteriorly convex and would not have contributed to the supratemporal fenestrae. A deep groove for the olfactory tract is visible on the ventral surface of the frontal.

A partial left squamosal is also preserved (Fig. 4D,E). Neither the skull table sutures (for the postorbital and parietal) nor the margin of the supratemporal fenestra are present, but the lateral skull table margin bears a shallow anteroposterior groove for attachment of the external ear muscles. The lateral margin also bears a modest ventral process anterior to the external otic recess, a feature found in most extant crocodylian skulls. The posterolateral corner is extended into a prominent posterior process that is continuous with the lateral skull table margin and, as in most crocodylians, is not deflected laterally.

A partial right dentary (Fig. 4A,B) preserves six complete alveoli and a partial alveolus on the broken anterior surface. The lateral margin is strongly convex, and the mandibular ramus expands in mediolateral width behind the symphysis. Sulci between alveoli are very modest. Size relationships among alveoli are consistent with a placement for this fragment very close to the anterior tip – we interpret the largest complete alveolus as the fourth, and the incomplete alveolus as the first. The fourth occurs where the specimen is widest mediolaterally. The medial surface is flattened and, for much of its length, bears a long groove for the mandibular nerve. No splenial scar is apparent, but the specimen is worn and it might not have been preserved. The medial surface is broken anteriorly. The length

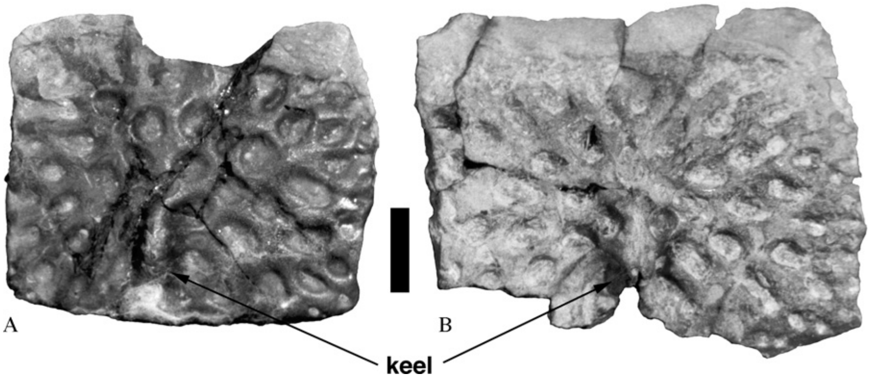

Fig. 3. AMNH 24487, crocodylian osteoderms, San Sebastián Formation (Late Oligocene), Puerto Rico, dorsal view. Scale = 1 cm.

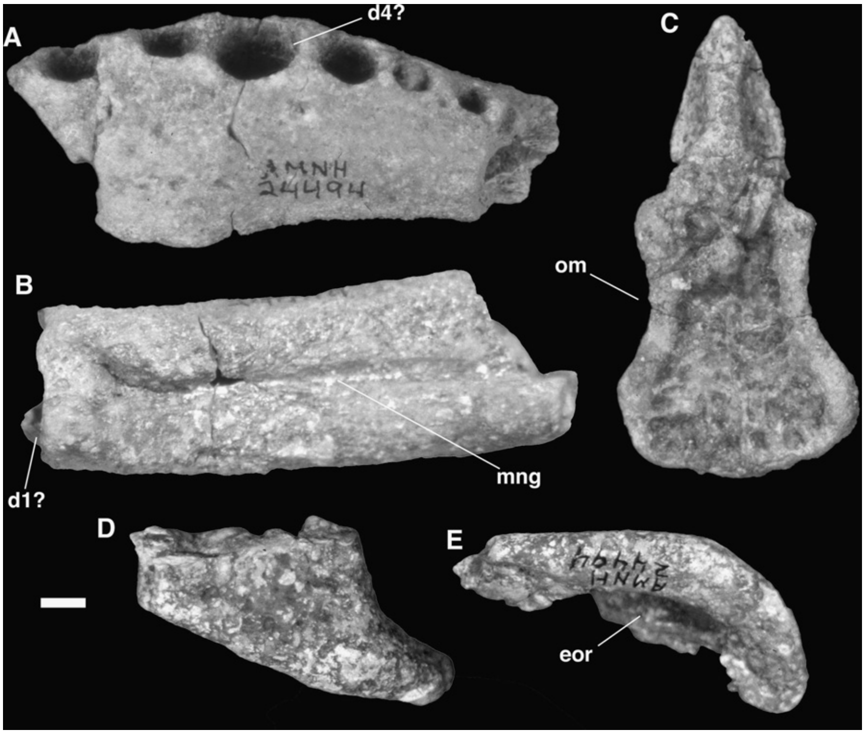

Fig. 4. AMNH 24494, crocodylian skull and mandible fragments, Cibao Formation (Early Miocene), Puerto Rico. **A**, anterior end of right dentary, dorsal view. **B**, anterior end of right dentary, medial view. **C**, frontal, dorsal view. **D**, partial left squamosal, dorsal view. **E**, partial left squamosal, medial view. Scale = 1 cm. Abbreviations: d1, first dentary alveolus; d4, fourth dentary alveolus; eor, external otic recess; om, margin of orbit.

of the dentary symphysis is unknown, but it must have been very short, as the medial surface at least as far forward as the fourth alveolus was not symphyseal.

3. Comparisons

3.1. San Sebastián Formation

The osteoderms from the San Sebastián Formation are rectangular in outline. Dorsal shield osteoderms from modern alligatorids and *Crocodylus* tend to be square in outline, although some midline dorsal osteoderms from large *Crocodylus* approach the shape seen in the present material. But they universally lack the anterior concavity seen in these specimens. Members of basal crocodylian lineages (e.g., Gavialoidea, *Borealosuchus*) bear a prominent anteromedial process that imparts a concavity to the anterior margin. The anterior osteoderm margin may still be concave in basal members of Alligatoroidea and Crocodyloidea, but these osteoderms lack a discrete process.

In extant alligatorids or *Crocodylus*, the dorsal osteoderm keel is anteroposteriorly long and extends along at least half of the osteoderm's length. Dorsal osteoderms from New World *Gavialosuchus* have no keels (Auffenberg, 1954; Erickson and Sawyer, 1996). In contrast, the keels of AMNH 24487 are short and restricted to the posterior half of the dorsal surface. Their shape is reminiscent of those of derived gavialoids, including those from the Tertiary of South America (e.g., Rovereto, 1912: Pl. 18), or of some Late Tertiary European tomistomines (e.g., Antunes, 1961: Pl. 12). Restriction of the keel to the posterior half of the scute occurs variably in both groups, but the flatness and anterior concavity of AMNH 24487 are much more like the dorsal osteoderms of gavialoids.

The medial hemicondyle of the San Sebastián Formation quadrate is incomplete, but we believe its dorsal margin passed medioventrally from the lateral hemicondyle. In this regard, it resembles the quadrate of most non-crocodyloid crocodylians (Fig. 3). In contrast, the crocodyloid medial hemicondyle is dorsally expanded and its dorsal margin is dorsomedial to that of the lateral hemicondyle. This is true for *Crocodylus* and for all living and extinct tomistomines, including New World *Gavialosuchus*. Because of the dorsally shifted foramen aereum, the medial hemicondyle of an alligatorid is often offset by a distinct groove on the ramial dorsal surface; this is not universally true, but the apparent medial placement of the foramen aereum in AMNH 24488 rules out an alligatorid.

The San Sebastián cervical vertebra is unlike that of any extant crocodylian. The hypapophysis is anteroposteriorly long, but dorsoventrally low. In this regard, it most closely resembles some of the cervicals of some gavialoids, although in gavialoids keels like this do not occur in the third cervical and the keel is more restricted to the anterior half of the centrum.

3.2. Cibao Formation

The frontal from the Cibao differs from contemporary New World *Crocodylus* in having a broadly convex posterior margin for articulation with the parietal; in contrast, the frontoparietal suture of extant *Crocodylus* forms an anteriorly concave "V," and the posterior margin of the frontal is more angular at the midline. The frontal of extant *Crocodylus* also has a more acute transition from rostral process to interorbital region. The Cibao frontal also differs from modern *Crocodylus, Alligator, Caiman*, or *Melanosuchus* in having less prominent dorsally upturned orbital rims. The amount of upturning is similar to what is found in *Paleosuchus*, but the slender rostral process rules out extant *Paleosuchus*. However, abrasion to the bone after death could have muted the orbital rims and any angularity to the posterior surface that might have existed. Upturning is much more extreme in *Alligator* and *Caiman* than in *Crocodylus*, and the interorbital region is concave in the alligatorids; moreover, the frontal lacks any indication of the preorbital ‘‘spectacle’’ ridge found on the frontal of *Caiman*. An alligatorid affinity is unlikely, but the frontal is not sufficient by itself to exclude *Crocodylus*.

The squamosal also differs from that of extant *Crocodylus*. The posterolateral process that, in an intact skull, would lie against the paroccipital process of the exoccipital projects posteriorly from the bone, and the posterodorsal angle of the squamosal between the skull table and posterolateral process is very broad. In contrast, the posterolateral process of extant *Crocodylus* extends posterolaterally, and the transition from skull table to posterolateral process is more abrupt. The same is true for *Alligator* and *Caiman*, though the angularity of the transition varies among individuals to some degree. But again, postmortem abrasion cannot be ruled out as the cause for any differences between this specimen and homologues from extant crocodylians.

The Cibao dentary is more conclusively different from those of any extant crocodylian. It clearly does not come from a longirostrine form. In *Crocodylus*, the dentary does not expand significantly behind the symphysis and the lateral margin in the symphyseal region is not as strongly convex as in the Cibao dentary. In these features, the dentary is more similar to that of an alligatorid. However, the specimen is inconsistent with an alligatorid because the alveoli behind what we interpret as the fourth are widely spaced and the difference in size between the fourth and fifth is not as extreme. None of these differences can be attributed to postmortem wear.

4. Discussion

However, fragmentary and abraded, these specimens are sufficiently informative to rule out several possibilities, including any currently extant New World crocodylian. The specimens from the Cibao Formation are also inconsistent with any of the longirostrine clades that have been found in the New World.

Some aspects of the Oligocene San Sebastián material are reminiscent of what is seen in basal crocodylian lineages. The osteoderms and quadrate, for example, are consistent with basal crocodylian lineages, although the incompleteness of the preserved quadrate makes absolute determination impossible. The Miocene Cibao material is more difficult to characterize, but again it does not appear to represent *Crocodylus*.

This is consistent with the hypothesis that *Crocodylus* was a comparatively recent immigrant to the Americas. The last land connections between the Americas and the Old World (other than high-latitude routes) predate the Cenozoic (Pindell, 1994; Smith et al., 2004). Although not strictly falsified, vicariance would require a six- to eightfold increase in the known stratigraphic range of *Crocodylus*.

These Oligocene and Miocene remains also raise the possibility that the Antilles were part of a global pattern in crocodylian phylogeny during the Neogene. Endemic clades of crocodylians occurred in the Neogene of Africa (Brochu, 2000; Llinás Agrasar, 2004) and Australia and nearby islands (Willis et al., 1993; Salisbury and Willis, 1996). The Australasian radiation (Mekosuchinae) is now extinct, and the African radiation (Osteolaeminae) today includes only the African dwarf crocodiles (*Osteolaemus tetraspis* and *O. osborni*). In both regions, *Crocodylus* first appears in the Pliocene (Willis, 1997; Brochu, 2000). Both endemic clades persisted into the Quaternary, but with diminished diversity. Whether *Crocodylus* helped cause the reduction or extinction of these groups or merely filled an ecological void left by their absence is unknown, but the timing of replacement is similar and intriguing in both instances.

Did a similar pattern of replacement by *Crocodylus* occur in the Antilles during the Neogene? And if so, what group was replaced? Alligatorids are less tolerant of salt water than other crocodylians (Taplin and Grigg, 1989; Jackson et al., 1996; Pidcock et al., 1997). Although they doubtless occurred in the region at various times during the Cenozoic, the fact that alligatorids are less likely to thrive in coastal habitats raises the suspicion that different crocodylian clades were involved in the Antilles.

More complete material is needed to determine the identity of crocodylians inhabiting the Caribbean during the Tertiary. Tantalizingly, some might already have been collected – Ortiz Rivera (1980) documented what appear to be portions of crocodylian skulls and jaws, at least some of which appears to have come from a slender-snouted form. The identity is unclear. Ortiz Rivera also figured fish and turtle bones, human remains, and cultural material (such as fragments of aboriginal pottery), suggesting that material from multiple stratigraphic horizons is represented. Information on location and stratigraphic context is unknown. Without this information, these fossils remain minimally informative.

Finally, these observations indicate the need for additional information from two sources. First, we need more complete and better preserved crocodylian fossils from the region. Full characterization of these crocodiles awaits more complete specimens, and the different biogeographic scenarios described herein can only be tested if more informative material is collected. Second, we need improved species-level phylogenetic hypotheses for *Crocodylus*. The value of unambiguous *Crocodylus* in units older than five to 15 million years is greatly improved if we can demonstrate whether the fossils are more closely aligned to any particular group of extant species.

Acknowledgments

We thank M. Ruiz-Yantín, M. M. Sánchez, M. Martínez, and O. Saneaux (Department of Geology, University of Puerto

Rico, Mayagüez) for field assistance. M. Norell and R. MacPhee provided discussion and access to collections. Thanks are expressed to P. Rocafort and L.A. Padilla for assistance with some of the photographs. J. Mead and S. Jouve carefully reviewed a previous version of this paper and made invaluable suggestions for its improvement. This project was partially supported by the University of Puerto Rico Alliance for Graduate Education and Professorate Fellowship (Grant No. NSF/AGEP–HRD # 0302696) to ÁMNR.

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