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ORIGINAL ARTICLE

Plio-Pleistocene *Crocodylus* (Crocodylia) from southwestern Costa Rica

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Abstract
Mammal and reptile fossils were observed as a lag deposit along a 50 m stretch of a small creek in the Puntarenas Province of southwestern Costa Rica. The fossil deposit, known as El Indio, dates to the late Pliocene – early Pleistocene. Skeletal elements of a crocodylian have characteristics that indicate they belong to a species of *Crocodylus* (Reptilia, Crocodylia). Crocodylian remains were common and recovered with turtles and extinct forms of gomphothere proboscideans, horse, camel, ground sloth (*Eremotherium*), and pampatheres (extinct giant armadillos, *Holmesina* and *Pampatherium*). The record of the crocodylian from El Indo indicates the importance of this new fossil locality and presents the first reported Plio-Pleistocene remains of *Crocodylus* from Costa Rica. Although *Crocodylus* is known to inhabit much of the coastal and large riverine systems of Costa Rica today, the remains from El Indio are the first evidence to indicate that this crocodylian has at least a two million year record in Central America and this important corridor between North and South America.

Keywords: *Crocodylus,* crocodile, Plio-Pleistocene, Costa Rica

Introduction

Costa Rica and adjacent countries form the thoroughfare between North and South America. The geologic evolution of this Central American isthmus has been a complex and extended process over the past 15 million years (Coates & Obando, 1996). The most recent five million years of fossil history (late Neogene) of this critical land bridge is insufficiently understood. Webb and Rancy (1996) provide an overview of the Neotropical mammal evolution beginning with the middle Pliocene (~three million years ago). Vertebrate fossils are not rare in the lowland rainforests or higher premontane forests of Costa Rica, yet they have received little comprehensive attention, especially with the reptiles that are conspicuously absent from published accounts Gómez (1986). Lucas et al. (1997) provided an overview of mammalian species (mainly isolated skeletal remains) known from 41 assumed Pleistocene-age localities in Costa Rica. The importance of their compilation is the conclusion of how little is understood about this land bridge. The reconstruction of the fossil Neotropical floral communities is equally in its infancy (Martin, 1964; Flenley, 1979; Gómez, 1986; Colinvaux, 1996; Hull-Sanders & Howard, 2003). Here we describe the first Plio-Pleistocene remains of *Crocodylus* (Reptilia, Crocodylia) from Costa Rica and provide preliminary details about an important new fossil locality in the southern Puntarenas district. With the timing for the evolution of *Crocodylus* and its dispersal to the Western hemisphere still to be unequivocally determined, the new fossils described here take on additional importance.

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Living crocodilians of Costa Rica

Today there are two crocodylians inhabiting the coastal waters and larger rivers of Costa Rica. The spectacled caiman, *Caiman crocodilus* (Alligatoridae) is the smaller of the two, with total length between 1.25 and 2.50 m. This species occurs today from southern Mexico southward throughout Central America and into South America (and is the only species of *Caiman* to range outside that continent; Ross & Magnusson, 1989). The *Caiman* lives in freshwater lowland habitats such as low-gradient rivers, marshes, and lakes of both the Pacific and Caribbean drainages, and is the more common of the two crocodylians in Costa Rica.

The American crocodile, *Crocodylus acutus* (Crocodylidae), is found from extreme southern Florida to southern Mexico through Central America to Colombia and Venezuela and on several islands within the Caribbean (Ernst et al., 1999). *Crocodylus acutus* inhabits brackish estuaries, swamps, lagoons, and the larger, deep inland rivers along both the Pacific and Caribbean coasts of Costa Rica (Thorbjarnarson, 1989). Individuals today range from 2.5 to 4.0 m in length, and historically reached lengths between 6 and 7 m; the largest individuals restrict their distribution to the low-gradient rivers (Schmidt, 1924; Alvarez del Toro, 1974). *Crocodylus moreletii* (Morelett's crocodile) ranges today north of Costa Rica along Caribbean coastal areas of Belize, Mexico, south to Guatemala (Ross, 1987). Additional species of *Crocodylus* live outside of the immediate region (Alderton, 1998).

Geologic setting and age

Mammal and reptile fossils were observed as a lag deposit along a 50 m stretch of a 1 – 2 m wide creek in the Puntarenas Province of southwestern Costa Rica. The fossil deposit known as El Indio is located at N 08° 51′ 23.3″ latitude, W 83° 04′ 19.7″ longitude, near the village of San Gerardo and approximately 16 km west of San Vito (Figure 1). El Indio is now at an altitude of 680 m along an unnamed creek of the Río Limón, a major tributary of the Río Térraba, and about 85 km from the Pacific Ocean.

No excavation or systematic screen washing of sediments has occurred at El Indio, but is planned for the near future. All fossils are isolated finds eroding from the sediments; no articulated or semi-articulated skeletons are known. Most of the bones are fragments and demonstrate some rounding due to fluvial tumbling. The larger and denser skeletal remains show little abrasion; an occasional bone has severe abrasion. Fossils are eroding from a weakly cemented, coarse fluvial sandstone and conglomerate of peas-sized pebbles of the Paso Real Formation

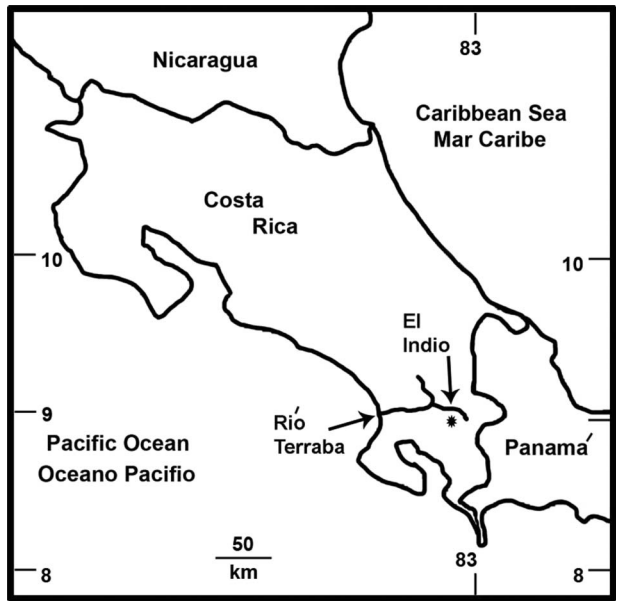

Figure 1. Map of Costa Rica showing the El Indio fossil locality.

(*sensu* Dengo, 1962). Fossils are stratigraphically within two to five meters of an unconformity at the top of the Curré Formation of Miocene age (*sensu* Dengo, 1962).

The low-angle subduction of the Cocos Ridge and seamount domain west of Costa Rica largely controls the landscape evolution of this portion of the Central American volcanic arc (Marshall et al., 2003). Southwestern Costa Rica contains a large structural depression that continues south into Panamá. The Río General heads within this trough in the Cordillera de Talamanca and flows southeast to merge with the north-trending Río Coto Brus and the Río Térraba to flow west about 50 km to the Pacific Ocean (Figure 1). These valleys are situated between the Cordillera de Talamanca and the coastal mountains and have acted as sediment traps during the late Miocene, Pliocene, Pleistocene, and Holocene (Kesel, 1983).

The presence of marine clay (Curré Fm., Middle to Upper Miocene) lining the bottom of these valleys illustrates that an extensive inland embayment existed both north and south within the trough during the late Miocene and Pliocene (Kesel, 1983). Continual up-lift drained the embayment trough out the Río Térraba to the Pacific. Dated volcanic rocks and the presence of the overlying, non-marine Paso Real Formation attest to rapid up-lift (see Adakite stage of andesitic volcanism, Drummond et al., 1995). It is not established conclusively that the marine embayment withdrew simultaneously from the Río General and Río Coto Brus. It has yet to be adequately established that fluvial and alluvial fan sediments from the Cordillera de Talamanca buried the marine clays of the Río General Valley earlier

than the terrestrial transition occurred in the Coto Brus Valley.

Although the Paso Real Fm. is not satisfactorily dated throughout its stratigraphic sequence, it is believed that deposition continued from the Pliocene into the early Pleistocene (approximately two million years ago; Kesel, 1983). A reconstruction of the depositional and ecological environments includes a fluvial deltaic setting into a marine embayment habitat. Isolated horse teeth recovered from El Indio (associated with the crocodylian material described here and numerous additional reptilian and mammalian skeletal remains) have plesippine traits, such as a well-developed prehypoconual groove, short protocone, and a long ectoflexid that penetrates the molar isthmus. These characters are consistent with plesippine horses of a later Pliocene to earliest Pleistocene age (Eric Scott, pers. comm. 2004).

Materials and methods

Fossils described here are catalogued into the fossil collections of the Museo Nacional de Costa Rica, San José (CFM, Colección Fosiles del Museo). Identifications of the crocodylian bones are based on phenetic similarities with modern comparative specimens and characters discussed in Brochu (1999, 2000). We feel that at this time many isolated skeletal elements of modern species of *Crocodylus* are not understood well enough to permit a detailed apomorphic approach to their identifications. Brochu (2000) provides a developing list of apomorphies and diagnostic characters for clades within *Crocodylus*. Unfortunately none of these diagnostic characters could be used on the recovered specimens from El Indio.

Results

Surangular-articular-angular

CFM-949 is a fragment of a left lower jaw preserving the contact between the angular, articular, and surangular, ventral to the lingual foramen for the articular artery and alveolar nerve (faaan) (Figure 2A). The angular ventral to the articular on the fossil is narrow as observed on *Crocodylus* and not the dorsoventrally wide and robust angular found on alligatorids.

CFM-947 is a fragment of a right surangular and articular (Figure 2B). The faaan is located on CFM-947 on the articular and surangular suture, as is found with *Crocodylus* spp. and most species of *Alligator* (Brochu, 1999: character 45(1)). However, it is located entirely on the surangular (0) on *Caiman*, *Melanosuchus*, *Paleosuchus*, and with *Gavialis* (Gavialoidea) (Brochu, 1999). The suture of the angular and surangular is simple on *Alligator* and *Paleosuchus* (Brochu, 1999: character 44 (0)), more complex and more anterior to the lingual foramen on CFM-947 (Figure 2B) and *Crocodylus* (1), or with an anterior process ventral to the lingual foramen on *Caiman* and *Melanosuchus* (2).

Dentary

All edentulous dentaries (CFM-945, 946, 949, 950, 1393) are fragmented, representing entire cross-sections of the element, and only a small portion of the entire length. CFM-950 is from a left dentary at the mesial portion of the mandibular symphysis (Figure 2C, D). Alveoli 3 and 4 are entire; the latter measures 17.7 by 16.3 mm. The mediolateral width at the mandibular symphysis immediately posterior to the articulation measures 42.5 mm on a modern *C. acutus* of 4.3 m length from Costa Rica. This same measurement on CFM-950 is 38.6 mm, indicating that this fossil is from a relatively large individual. The splenial is excluded from the mandibular symphysis (Brochu, 1999: character 43) on CFM-950. Clearly this would omit the specimen from belonging to the extinct *Gavialosuchus* that occurred in the Miocene – Pliocene of Florida (Sellards, 1915; Mook, 1921a). A slight roughness ventral to the meckelian groove on CFM-950 appears to be locating the position of the mesial tip of the splenial (mts in Figure 2D). If this is correct, then the specimen belongs to *Crocodylus* (Brochu, 1999: character 43(1)) and not to *Caiman*, *Alligator*, *Melanosuchus* (Black caiman), or *Paleosuchus* (dwarf caiman) that have the contact dorsal to the groove (43(2); see modern, Figure 2 top).

The posterior extremity of the mandibular symphysis does not extend posterior to dentary (d) tooth 8 in any species of *Crocodylus*, and typically is not posterior to d5 (Mook, 1921b). Figure 2C illustrates that the posterior terminus of the symphysis on CFM-950 is opposite the contact between d3 and d4; we infer that this represents a robust jaw. Our analysis indicates that the posterior terminus of the symphysis on large *C. acutus* (adults) is between d4 and d5. This terminus is between d4 and d5 on medium-sized *C. rhombifer* (Cuban crocodile) and between d7 and d8 on the narrow-snouted *C. intermedius* (Orinoco crocodile) (Mook, 1921b). *Alligator mississippiensis* (American alligator) has the relatively shortest symphysis of the living Crocodilia (Iordansky, 1973). The terminus occurs between d3 and d5 on this alligator, and between d4 and d5 on *Caiman crocodilus* (our data and Mook, 1921b). The position of this terminus is not understood on the living *C. moreletii*. A dentary from southern Baja California (Mexico) of Pliocene age is referred to *C. moreletii*; the terminus of the symphysis is opposite the posterior edge of d4 (Miller, 1980: Figure 7).

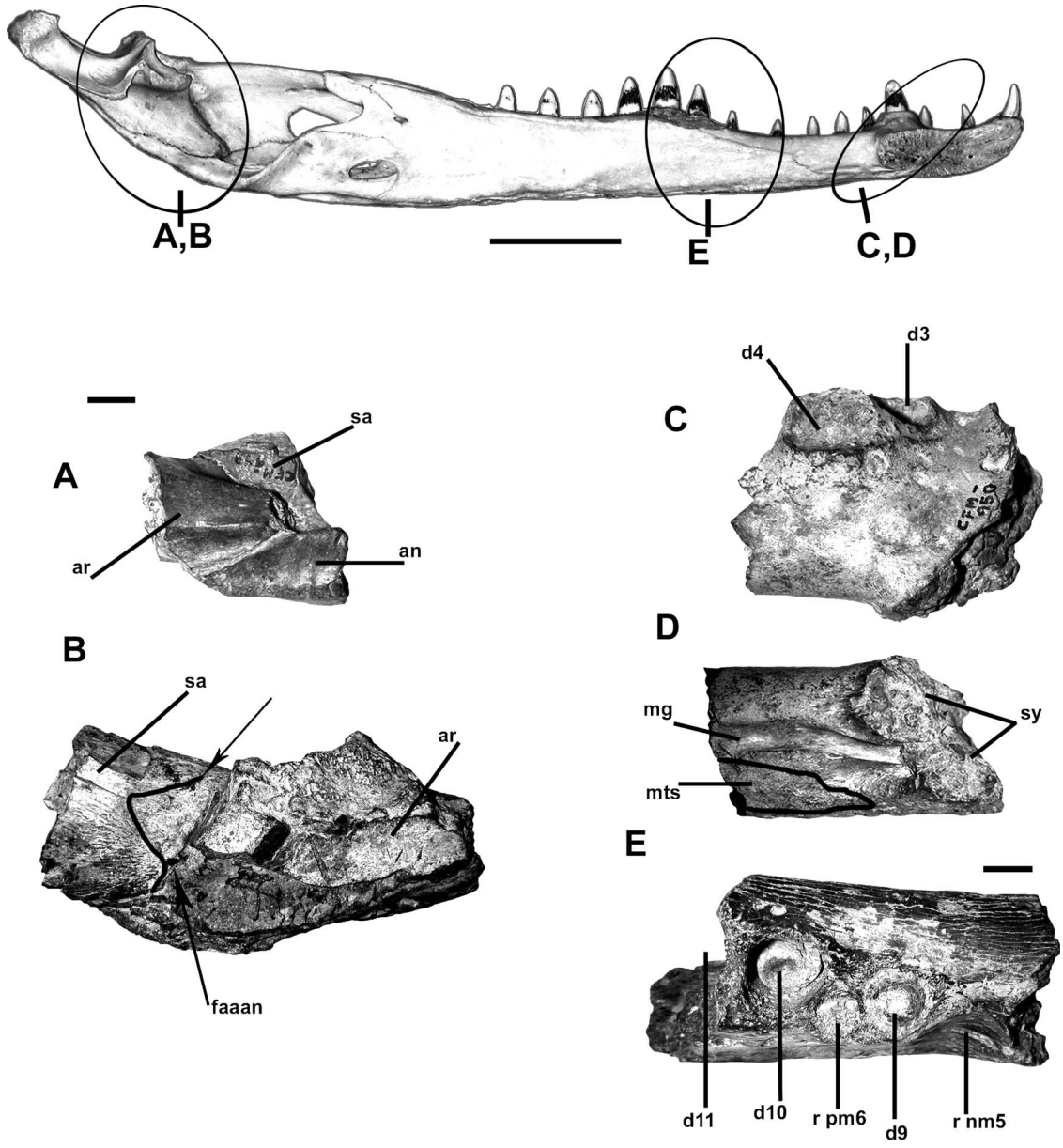

Figure 2. Modern (top; *Crocodylus acutus*; left, lingual view; anterior to right; scale bar equals 10 cm) and fossil (A–E) *Crocodylus* mandible elements (scale bars equal 10 mm). (A) Lingual view of left angular, articular, and surangular (CFM-949). (B) Lingual view of a right articular and surangular fragment (CFM-947). Line is the suture between the articular and the surangular. Left dentary fragment (CFM-950) with alveoli for dentary teeth, d3 and d4 in (C) dorsal and (D) lingual views. Anterior to right. (E) Right dentary fragment (CFM-946) dorsal view, showing notch for five maxillary teeth, two adjacent alveoli, and a reception pit for m6; anterior to right. Abbreviations: an, angular; ar, articular; d, dentary tooth number; faaan, foramen for articular artery and alveolar nerve; mg, meckelian groove; mts, possible contact area for mesial tip of splenial showing location ventral to mg; rnm5, reception notch for maxillary tooth 5; rpm6, reception pit for maxillary 6th tooth; sa, surangular; sy, symphysis. Scale bar equals 10 mm.

This Mexican specimen and its identification deserve new attention. The ultimate significance of the termination of the symphysis between d3 and d4 on CFM-950 is not resolved.

CFM-946 is a fragment from the right dentary where the 5th maxillary tooth fits into the dentary notch. Complete alveoli for the next posterior teeth and a reception pit for m6 are present (Figure 2E). The dorsoventral height of the dentary is 42.9 mm; the mediolateral width at the maxillary tooth notch is 27.4 mm.

Tooth

The isolated tooth (CFM-1200) is keeled and measures 16.5 by 15.6 mm at its base. Isolated teeth of most crocodylians are not diagnostic to genus or species.

Frontal

Three frontal specimens were recovered (CFM-975, 977, 980). CFM-975 is from a large, adult individual (Figure 3A, B). The smallest diameter between the orbital rims is 49.7 mm (44.6 mm on CFM-977). The frontal of *Crocodylus* and from El Indio are deeply rugose. The depth between the orbital rims and the medial ridge is slight on adult *Crocodylus* (slightly deeper on juveniles) and those from El Indio, whereas *Caiman* and *Alligator* have prominent orbital rims with a deep curvature down to a medial trough; that area on *Paleosuchus* is rather shallow compared to the former yet deeper than observed on *Crocodylus*.

Nasal

A fragment of the paired nasal (CFM-1392) is preserved from the articulation with the prefontals to about 30% of its possible length; the small process that articulates with the frontal is not preserved (Figure 3C). The frontal constricts mesially on crocodylians due to the prefontals and articulates with the nasals at a minor suture. The frontal on *Alligator* has a deep curvature that meets with an equally curved prefrontal, both of which proceed to an entrenched articulation with the nasals. *Caiman* and *Paleosuchus* have the deeply curved frontal but a distinct transverse ridge on the prefrontals breaks the trough appearance; the contact of prefontals with the nasals is broad but still somewhat entrenched. *Crocodylus* does not have the deeply curved frontal (see above); the suture with the prefontals and the nasals is not entrenched. The nasal–prefrontal–frontal contact on *C. acutus* forms a broad ''dorsal bulge'', or median boss (see Mook, 1921b). CFM-1392 appears relatively flat, not bulged with the median boss, but this conclusion could be erroneous due the shortened length preserved; it would appear to belong to a *Crocodylus*. The median boss feature is

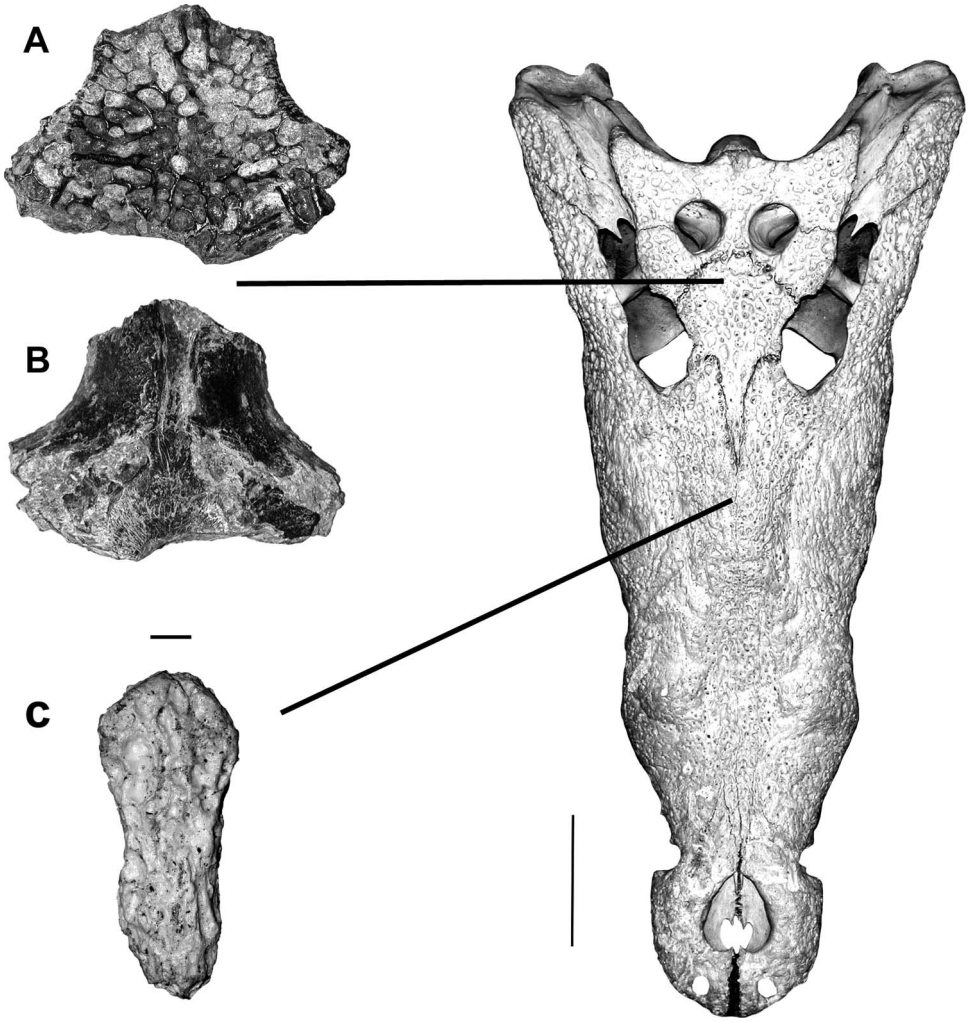

Figure 3. Modern (right) *Crocodylus acutus* (scale bar equals 10 cm). Fragmented fossil *Crocodylus* frontal (CFM-975) in (A) dorsal and (B) ventral views; posterior fragment of *Crocodylus* paired nasals (C) in dorsal view (CFM-1392) (scale bar equals 10 mm).

not understood by us for *C. moreletii*, *C. rhombifer* (Cuban crocodile), or the Venezuelan *C. intermedius* (Orinoco crocodile).

Jugal

The fragmented portion of the jugal (CFM-978) was recovered; however, it is not complete enough to determine the species.

Prefrontal

A small, thick fragment appears to be from the left prefrontal (CFM-981) that contains a portion of the orbital rim; however, it is not complete enough to determine the taxon.

Dermal ossicles

Dermal ossicles (osteoderms; CFM-960-962, 982) are varied in size and shape. Most are rectangular in form (approximately 48 by 43 mm) and have a conspicuous rugose dorsal ridge (keel) typical of *Crocodylus* and alligatorids and unlike those of *Gavialosuchus* that have no ridge.

Discussion and conclusions

The El Indio fauna contains numerous skeletal remains recovered as a lag deposit along a 50 m stretch of a tributary of the Río Limón (a major stream of the Río Térraba; about 85 km from the Pacific Ocean) in southern Costa Rica. Vertebrate fossils are eroding from a weakly cemented, coarse fluvial sandstone and conglomerate of the Paso Real Formation of late Pliocene to earliest Pleistocene age.

Many of the turtle shells and mammalian long bones are broken, some with fractured edges that are slightly abraded, indicating breakage prior to fluvial transport. Numerous bones of turtle, horse, and camel exhibit conical marks (Figure 4), which appear to be punctures and are consistent with those produced by isodont teeth. This suggests that many of the fossils could be the result of prey breakage by crocodilians (see Fisher, 1981). Detailed analysis of the cross-sections of the pits has not been conducted.

Crocodylian remains were common and recovered with turtles and extinct forms of horse, camel, ground sloth (*Eremotherium*), pampatheres (extinct armadillos, *Holmesina* and *Pampatherium*—the first record for Costa Rica), and gomphothere proboscideans. The crocodylian remains have characteristics that indicate they belong to a species of *Crocodylus*, and do not belong to *Alligator*, *Caiman*, *Paleosuchus*, *Melanosuchus*, or the extinct *Gavialosuchus*. The fragmented crocodylian specimens from El Indio do not have characters that permit species identification.

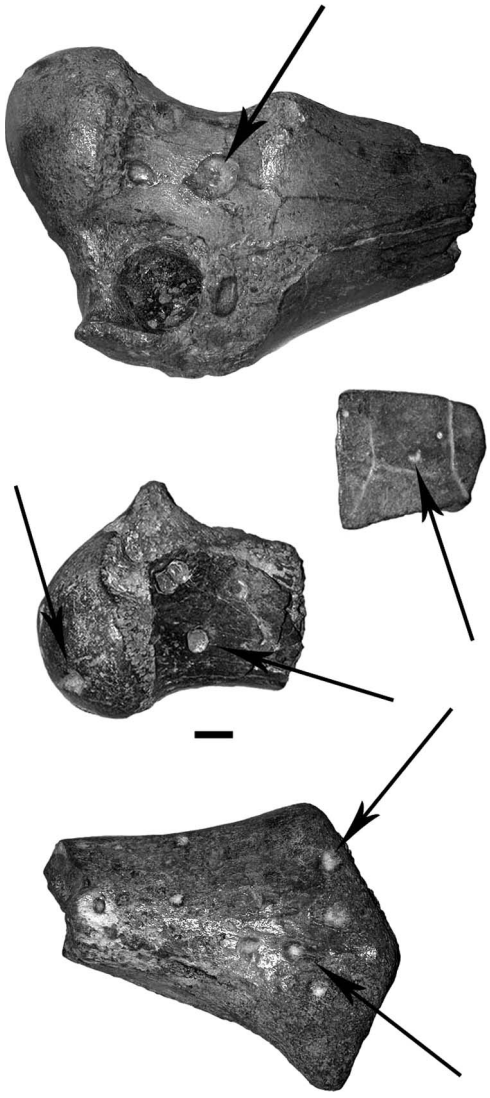

Figure 4. Arrows locate some of the puncture marks on broken bones of horse and turtles possibly produced by the isodont teeth, and are believed to indicate prey items of crocodylians such as *Crocodylus*.

Using the results of a parsimony analysis of morphological characters for living and fossil crocodylians, Brochu (2000) determined that the fossil record closely supports protein divergence timing estimates for the crown group *Crocodylus*. The oldest *Crocodylus* is of Miocene age (Brochu, 2000, 2003). The oldest *Crocodylus* in the Western hemisphere is *C. moreletii* from the Pliocene (early Blancan North American Land Mammal Age) deposits at Las Tunas, southern-most Baja California, Mexico (Miller, 1980). This species is also referred to fossils from the Pleistocene of Guatamala (Mook, 1959). *C. rhombifer* remains are reported from the Pleistocene of Cuba and Holocene of Grand Cayman Island and Bahamas (Varona, 1966, 1984; Morgan et al., 1993; Franz et al., 1995).

This brief overview of the fossil record of the Americas indicates that evidence exists for *Crocodylus*,

yet there is desperate need for more attention. Details of chronology and the recovery of specimens that permit species-specific identification are required. The above results from El Indo indicate the importance of this new fossil locality and present the first reported Plio-Pleistocene remains of *Crocodylus* from Costa Rica. Although *Crocodylus* is known to inhabit much of the coastal and large riverine systems of Costa Rica today, and is expected in the local fossil record, the remains from El Indio are the first evidence to indicate that *Crocodylus* has at least a two million year record in Central America, an important corridor between North and South America.

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