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Biogeographic and Systematic Implications of a Caimanine from the Late Miocene of Southern Mexico

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ABSTRACT.—**An isolated supraoccipital from the late Miocene of Chiapas, southern Mexico, can be referred to Caimaninae, a group including the living caimans and their closest extinct relatives. The specimen shares a polygonal shape, indicating lateral contact with the squamosals, with extant *Caiman* and *Melanosuchus*, but some extinct caimanine lineages had a similar morphology. This is the northernmost known caimanine occurrence during the Neogene, suggesting that members of this salt-intolerant lineage were present in North America possibly before the Isthmus of Panama was complete. It might also indicate that extant lineages within *Caiman*, including those found in Mesoamerica today, were distinct earlier than generally believed.**

All of the six recognized species of caimanine alligatorid are found in South America, but one—the Spectacled or Common Caiman, *Caiman crocodilus* Linnaeus 1758—has a range extending into North America (Velasco and Ayarzagüena, 2010; Escobedo-Galván et al., 2011). At first, this seems be a simple case of northward range expansion during the Great American Biotic Interchange (GABI) following closure of the Isthmus of Panama within the past 5 million years (Estes and Báez, 1985; Vanzolini and Heyer, 1985). Divergence points among extant caimanines, including the root, involve South American lineages (Norell, 1988; Gatesy et al., 1993, 2003; Brochu, 1999, 2011; Bona, 2007; Oaks, 2011) and, because alligatorids are less tolerant of salt water than are crocodylids (Taplin et al., 1982; Taplin and Grigg, 1989; Jackson et al., 1996; Pidcock et al., 1997; Leslie and Taplin, 2001), land-based dispersal routes seem more likely. Molecular divergence estimates between the subspecies found in Mesoamerica (*Caiman crocodilus fuscus*, brown caiman) from northernmost South America north to Nicaragua, *Caiman crocodilus chiapasius*, spectacled caiman) in El Salvador, Guatemala, and southernmost Mexico) and populations in the Amazon Basin are broadly consistent with dispersal that is roughly contemporaneous with the GABI (Venegas-Anaya et al., 2008).

We describe a caimanine supraoccipital from the late Miocene Puente Ixcán locality in Chiapas, southern Mexico (Fig. 1). This is the northernmost known occurrence of the lineage during the Neogene, demonstrating that derived caimanines were present in North America two or more million years before the GABI. This, in turn, further reflects a complex biogeographic history, with marine barrier crossings not evident from living species alone.

METHODS AND MATERIALS

Institutional Abbreviations.—FMNH, Field Museum of Natural History, Chicago, IL; IHNFG, Instituto de Historia Natural, Fósil Geográfico, Tuxtla Gutiérrez, Chiapas.

Crocodylia Gmelin, 1789 (sensu Benton and Clark, 1988)
Alligatoridae Gray, 1844 (sensu Norell et al., 1994)
Caimaninae Brochu, 1999 (following Norell, 1988)
(Figure 2)

Referred Material.—IHNFG 4737, complete supraoccipital.

Occurrence.—Late Miocene, Puente Ixcán, Ocosingo Municipality, Chiapas, Mexico. Vertebrate remains from the locality were collected from an unnamed sedimentary sequence comprised of silty sandstones thought to have been deposited in a coastal lagoon or overbank deposits. Other vertebrate remains include stingrays, trionychid and dermetemydid turtles, an anchitheriine horse, and the hippopotamus-like rhinocerotid *Teleoceras hicksi*. Additional crocodyliform remains include procoelous vertebrae and teeth previously referred tentatively to *Crocodylus* (Carbot-Chanona, 2008). The anchitheriine and rhinocerotid strongly suggest a pre-Pliocene age for the deposits, and *T. hicksi* in particular suggests a latest Miocene (Hemphillian) age (Carbot-Chanona, 2011).

Description.—The specimen is a mediolaterally elongate polygon with a pitted planar surface in dorsal view (Fig. 2A). The lateral squamosal sutural surfaces intersect the posterior margin of the skull table at right angles. The parietal sutural surfaces intersect the squamosal surfaces—and each other—at roughly 45° angles. A midsagittal crest divides the occipital surface ventral to the skull table into a pair of concavities (Fig. 2B). Sutural surfaces for the exoccipitals can be seen ventrolaterally (Fig. 2C,D). The posterodorsal roof of the endocranial cavity is preserved on the anteroventral surface (Fig. 2C).

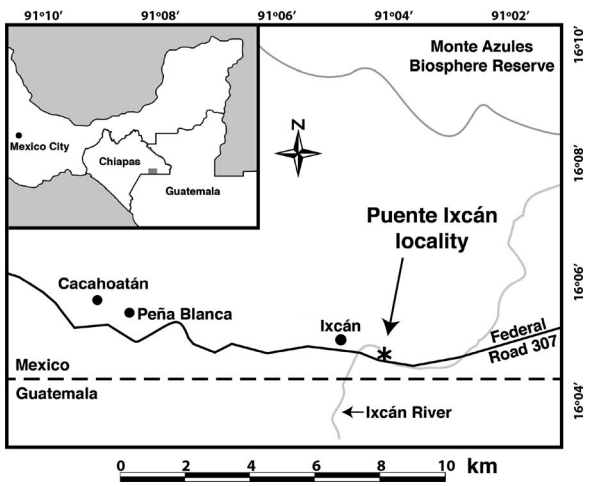

FIG. 1. Map of southern Mexico showing location of the Puente Ixcán locality.

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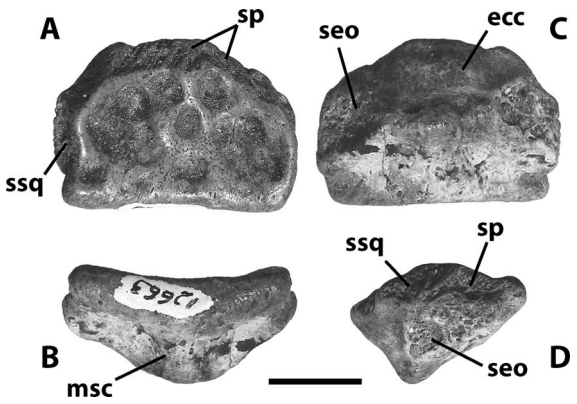

FIG. 2. IHNFG 4737, Caimaninae, late Miocene, Chiapas. Supraoccipital in dorsal (A), posterior (B), ventral (C), and right lateral (D) view. Scale bar = 1 cm. Abbreviations: ecc, roof of endocranial cavity; msc, mid-sagittal crest; seo, sutural surface for exoccipital; sp, sutural surface for parietal; ssq, sutural surface for squamosal.

DISCUSSION

Phylogenetic Position.—Although limited to a supraoccipital, the specimen preserves morphology diagnostic of several caimanine lineages, including extant *Caiman*. The supraoccipital is visible dorsally on the skull table in most crocodylians but, in all caimanines with sufficiently preserved cranial material, dorsal expression of the supraoccipital is expanded. In some basal forms, such as *Paleosuchus* (Fig. 3A) and *Tsoabichi*, the dorsal supraoccipital exposure is triangular and, as with most crocodyliforms, bound laterally by the parietal. In others, including members of Jacarea (the last common ancestor of *Caiman crocodilus*, *Caiman yacare*, *Caiman latirostris*, and *Melanosuchus niger* and all of its descendents), the supraoccipital has an even larger presence on the skull table and blocks the parietal from the posterior skull table margin (Norell, 1988; Brochu, 1999, 2010). The shape of the supraoccipital varies within living jacarean species, but the anterior margin is usually linear and perpendicular to the sagittal plane. In some cases, the lateral margins are oriented anteromedially, giving the supraoccipital a trapezoidal shape. In others, the parietal bears a pair of short triangular posterior processes that extend along the anterolateral margins of the supraoccipital (Fig. 3B). This results in a polygonal shape similar to that seen on IHNFG 4737. Polygonal supraoccipitals only occur when the parietal is excluded from the posterior skull table surface.

Among members of Jacarea, IHNFG 4737 most closely approximates the supraoccipitals of living *Caiman crocodilus*, *C. yacare* (yacare caiman), and *C. latirostris* (broad-snouted caiman). In *Caiman lutescens* and *Caiman gasparinae* from the late Miocene of Argentina (Bona et al., 2013b), the posterior margin of the skull table is more-deeply concave in dorsal view, and the posterior edge of the supraoccipital is not as linear as in IHNFG 4737. The same is usually, though not always, true for modern *Melanosuchus niger*—black caiman (Brochu, pers. obs.). *Caiman niteroiensis* from the late Miocene of Brazil bears a pair of squamosal "horns" that would have imparted a concave dorsal surface to the supraoccipital (Riff et al., 2010:fig. 16.4).

Some non-jacarean fossils share a similar configuration of the skull table elements, including *Centenariosuchus gilmorei* from the early-middle Miocene of Panama and the bizarre, gigantic Miocene caimanines *Mourasuchus* and *Purussaurus*. The supraoccipital of *C. gilmorei* is very similar to IHNFG 4737 (Hastings et al., 2013; Surname, pers. obs.). The supraoccipital is much narrower in dorsal view in *Mourasuchus*, and it sits in a furrow within a greatly expanded skull table posterior to the supratemporal fenestrae, giving the element a sagittally convex and frontally concave dorsal surface (Price, 1964; Bocquentin and Souza Filho, 1990; Bona et al., 2013a; Scheyer et al., 2013). The supraoccipital in *Purussaurus* has a dorsal outline similar to that of IHNFG 4737, but it does not contact the squamosals and the posterior margin is markedly concave (Langston, 1965; Bocquentin et al., 1989; Brochu, 1999; Aguilera et al., 2006).

Enlarged supraoccipitals are also sometimes seen in non-caimanine crocodylians. The best-known example is the Late Cretaceous globidontan alligatoroid *Brachychampsa* from western North America in which the supraoccipital is large and trapezoidal. The supraoccipital in *Brachychampsa*, however, does not contact the squamosals (Norell et al., 1994). The polygonal condition seen in IHNFG 4737 is only found in caimanines in which the supraoccipital contacts the squamosals.

The distribution of supraoccipital-squamosal contact among caimanines is complex. Some analyses (e.g., Brochu, 1999, 2010, 2011) considered the basal Patagonian caimanine *Eocaiman cavernensis* to have this condition, but the supraoccipital is not preserved on the holotype (Simpson, 1933), and other analyses have left this character state uncoded for the species (e.g., Scheyer et al., 2013). Two newly-described basal caimanines, *Globidentosuchus brachyrostris* from the late Miocene of Venezuela (Scheyer et al. 2013) and *Culebrasuchus mesoamericanus* from the early Miocene of Panama (Hastings et al., 2013), have both been reconstructed as having a jacarean-like supraoccipital. The supraoccipital of *Globidentosuchus* does, indeed, resemble that of extant *Caiman* and *Melanosuchus*, but that of *Culebrasuchus* appears to have had an acute anterior margin different from that of IHNFG 4737 and more similar to that of *Paleosuchus*.

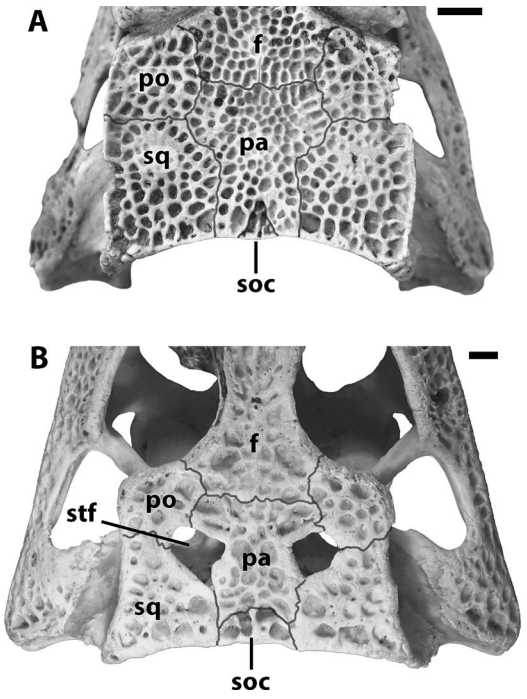

FIG. 3. Morphology of the skull table in extant caimanines. (A) FMNH 69871, *Paleosuchus trigonatus* (smooth-fronted caiman). (B) FMNH 73739, *Caiman crocodilus fuscus*. Suture lines emphasized. Scale bar = 1 cm. Abbreviations: f, frontal; pa, parietal; po, postorbital; soc, supraoccipital; sq, squamosal; stf, supratemporal fenestra.

Because the caimanine fossil record is so uneven, there is reason to be skeptical that these new Miocene caimanines are basal to the group. A few poorly-known caimanines have been found in Paleocene and early Eocene deposits (Simpson, 1937; Bona, 2007; Pinheiro et al., 2013), some of which are incomplete enough to render the base of the group highly labile (Brochu, 2011). Almost nothing is known about the group during the later Eocene and Oligocene. By the time observed caimanine diversity picks up again in the Miocene, the group includes some of the most-highly derived crocodyliforms ever found (Langston, 1965; Riff et al., 2010; Scheyer and Moreno-Bernal, 2010; Bona et al., 2013a,b). Character state polarity assessment is hazardous under these circumstances.

Depending on how polytomies are resolved and the status of the supraoccipital is coded in key taxa (such as *Eocaiman*), the morphology seen in Jacarea could either be plesiomorphic for Caimaninae or something that arose two or more times (Brochu, 2010). This makes it impossible to refer IHNFG 4737 to any particular caimanine lineage. We can, however, refer it to Caimaninae.

Biogeographic Implications.—IHNFG 4737 is the northernmost Neogene caimanine and the only known North American occurrence for the group in the late Miocene. It predates the GABI, as classically understood, which began at around 3 million years ago (Ma) (e.g., Webb, 1976, 2006; Woodburne, 2010). At first, this seems puzzling; alligatorids are believed to be salt intolerant, and the GABI was thought to correspond with final closure of the Isthmus of Panama.

In fact, the biogeographic simplicity indicated by extant caimanines overprints historical complexity. In addition to the early Miocene Panamanian fossils, caimanines are known from the Eocene of North America (Busbey, 1989; Westgate, 1989; Brochu, 1999, 2010). Phylogenetic analyses reject a close relationship between the North American forms, and simple vicariance or single-dispersal models are insufficient to explain the data. Multiple crossings of the seaway separating North and South America must have occurred. Modern alligatorids are found periodically in estuarine and coastal areas (Grigg et al., 1998; Elsey, 2005; Mazzotti et al., 2009; Nifong et al., 2014) and are prone to long-distance, storm-driven dispersal along coastal regions (Elsey and Aldrich, 2009). These facts suggest physiological limits but do not preclude the possibility of the animals crossing marine barriers.

There is also geological evidence that the straits dividing the Isthmus of Panama may have been narrower and shallower by the Miocene than previously believed (e.g., Farris et al., 2011; Montes et al., 2012). The likelihood that a salt-intolerant freshwater animal will cross a marine barrier presumably increases as barrier width and depth decrease. This, in addition to fossil and molecular phylogenetic evidence for faunal and floral exchange prior to 3 Ma (e.g., Flynn et al., 2005; Cody et al., 2010; Woodburne, 2010; Head et al., 2012; Bacon et al., 2013), diminishes the surprise we might express over the presence of a caimanine in southern Mexico before the Pliocene.

Depending on its taxonomic affinity, though, IHNFG 4737 might be of relevance to the origins of modern Mesoamerican caimanine populations. Divergence time estimates based on mitochondrial data put the split between northern subspecies of *C. crocodilus* (*C. c. fuscus* and *C. c. chiapasius*) from their southern conspecifics in the late Miocene (5.7–6.7 Ma) and between *C. c. fuscus* and *C. c. chiapasius* in the Plio-Pleistocene (2.5–2.9 Ma). This led Venegas-Anaya et al. (2008) to conclude that Mesoamerican *C. crocodilus* arrived during the GABI and subsequently diversified.

Given its age, geographic location, and morphology, it is tempting to refer IHNFG 4737 to *C. crocodilus*, which would put the species in Mesoamerica before the GABI and prior to the arrival predicted by mitochondrial data. This is consistent with other fossil evidence showing that closely-related extant lineages within *Caiman* have been distinct longer than molecular data suggest; Oaks (2011), for example, put the divergence between *C. crocodilus* and *C. yacare* (which is sometimes treated as a subspecies of *C. crocodilus*) in the Quaternary, but fossils referable to *C. yacare* or a close extinct relative are known from the Miocene (Fortier et al., 2009; Bona et al., 2013b). Earlier divergences reinforce the notion that Mesoamerican *C. crocodilus*—all of which are under considerable pressure from habitat loss and hunting—are units of diversity worthy of conservation (Amato and Gatesy, 1994; Venegas-Anaya et al., 2008; Escobedo et al., 2011).

IHNFG 4737 is too incomplete to exclude other possibilities. It could, for example, come from an extinct lineage present in Mexico prior to the arrival of *C. crocodilus*. Regardless, this fossil shows that caimanines lived in southern Mexico earlier than we previously believed. Future work in this region will likely uncover more material that will shed light on the historical biogeography of Mesoamerican alligatorids during a time of great climatic, tectonic, and sea level changes.

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