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Character evolution and the origin of Caimaninae (Crocodylia) in the New World Tropics: new evidence from the Miocene of Panama and Venezuela

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Abstract.—Alligators and caimans share a close relationship, supported by both molecular and morphological characters. The divergence between alligators and caimans has been difficult to discern in the fossil record. Two basal taxa have recently been described from the Miocene of Panama and Venezuela but have not yet been presented in a joint phylogeny. Continued preparation of the type material of the Venezuelan *Globidentosuchus brachyrostris* Scheyer et al., 2013 has revealed new characters for scoring in a cladistic framework. In addition, the first lower jaw of the Panamanian *Centenariosuchus gilmorei* Hastings et al., 2013 is described herein, and additional characters were scored. In total, we conducted five cladistic analyses to better understand the character evolution involved in the establishment of Caimaninae. In each case, *Globidentosuchus* appears as the basal-most of the caimanine lineage, followed by *Culebrasuchus mesoamericanus* Hastings et al., 2013 from Panama. Stepwise character additions of synapomorphies define progressively more derived caimanines, but stratigraphic context creates ghost lineages extending from the Miocene to Paleocene. The persistence of two basal taxa into the Miocene of northern South America and Central America supports the concept of a relict basal population in this region. This further supports biogeographic hypotheses of dispersals in both directions between North and South America prior to full land connection.

Introduction

Caimans are the dominant form of crocodylian in the New World Tropics, with six currently recognized living species in Central and South America as opposed to three currently recognized living species of true crocodiles (Trutnau and Sommerlad, 2006; Grigg and Kirshner, 2015). The caimans are consistently found to be a monophyletic grouping with a close relationship to alligators using both morphological and molecular characters (e.g., Janke et al., 2005; Brochu, 2010; Oaks, 2011). Alligators and caimans are split into separate clades (Alligatorinae and Caimaninae) but are monophyletic in themselves as Alligatoridae (Brochu, 2010). Despite this clear resolution, the split between alligators and caimans has been difficult to interpret.

The earliest alligatorine appears in the early Paleocene of the United States (*Navajosuchus mooki* [Simpson, 1930]; Brochu, 2011), but the oldest caimanines appear in the late Paleocene of southern Argentina (Bona, 2007; Brochu, 2010; Hastings et al., 2013; Pinheiro et al., 2013). Recent studies have revealed basal caimanines persisted in southern Central America and northern South America into the Miocene (Hastings et al., 2013; Scheyer et al., 2013). These fossils retained plesiomorphic characters not found in other caimanines but also possessed traits characteristic of caimans. Independent phylogenetic analyses revealed each as the most basal member of Caimaninae.

Since these publications, new material of the early caimanine, *Centenariosuchus gilmorei* Hastings et al. 2013, has been recovered from Panama. Furthermore, continued preparation has revealed new characters of the holotype of *Globidentosuchus brachyrostris*, allowing for better phylogenetic resolution. In this study, we present new material of *C. gilmorei* as well as phylogenetic analyses combining the newly discovered basal caimanines of Panama and Venezuela. These results are used to discuss character evolution in early caimanines and the nature of the origin of caimans in the New World Tropics. We further place these findings into biogeographic context.

Systematic paleontology

Institutional abbreviations.—AMU-CURS, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; UF, University of Florida, Florida Museum of Natural History, Gainesville, Florida, USA.

Anatomical abbreviations.—Teeth and alveoli of the dentary are referred to with 'd' followed by their position within the jaw, beginning from the anterior end. For example, the first dentary tooth is referred to as 'd1.'

Order Crocodylia Gmelin, 1789
Taxon Alligatoridae Gray, 1844
Subtaxon Caimaninae Brochu, 2003 (following Norell, 1988)
Genus *Centenariosuchus* Hastings et al., 2013
Centenariosuchus gilmorei Hastings et al., 2013
Figure 1.1–1.6

2013 *Centenariosuchus gilmorei* Hastings et al., 2013, p. 246, figs. 5, 6.

Holotype.—Partial skull in direct association with two isolated teeth, one cervical vertebra, and two partial osteoderms (UF 262800) from the Cucaracha Formation of Panama (Hastings et al., 2013, figs. 5, 6).

Occurrence.—The holotype and paratype of *Centenariosuchus gilmorei*, as well as the referred specimen (UF 281065) featured in the following, were recovered from the Hodges Microsite locality of the upper Cucaracha Formation, exposed in the Panama Canal Zone of Panama. The referred specimen, a partial left dentary, was discovered in June of 2011, just three months after the holotype. The site is located at latitude 9.04770°N and longitude 79.65380°W. The Centenario Fauna to which this specimen belongs has been determined as early Hemingfordian in age, from the early Miocene, a modified age from the original publication of *C. gilmorei* (Hastings et al., 2013; MacFadden et al., 2014). This fossil was collected by Maria Camila Vallejo.

Description.—The left dentary (UF 281065) preserves alveoli from d1 to part of d18. The largest alveolus is d4, where a partial tooth root is preserved, showing a nearly circular cross section (Fig. 1). The largest alveolus posterior to this position is d12, which is partially preserved in the fossil. The alveolus for d3 is distinct and nonconfluent with d4. The anterior dentary alveoli extend anterodorsally and are not strongly procumbent. The posteromost alveolus, d18, preserves at least a small part of its posterior wall, and the remaining dentary surface does not seem to indicate further alveoli would have existed during life. The specimen includes a well-preserved symphyseal surface, which extends to d5. The splenial is absent, but its sutural marks near the symphysis are clear. The sutures indicate clearly that the anteromost end of the splenial still lies posterior to the symphysis, meaning it did not contribute at all. The anterior tip of this splenial extension passes dorsal to the Meckelian groove (Fig. 1). Between the fourth and tenth alveoli, the dentary is gently curved ventrally (Fig. 1). The lateral surface bears a smoothed portion immediately lateroventral to the alveoli, beginning with a thin band from d4 and extending posteriorly to d18. The posterior contacts of the splenial, angular, and surangular are not preserved in UF 281065.

Comparison.—According to the paratype of *C. gilmorei*, its upper dentition would have totaled 19 alveoli (premaxilla + maxilla; Hastings et al., 2013), which is appropriate for the 18 preserved alveoli of UF 281065 (Fig. 1). Furthermore, the dentary alveoli of UF 281065 are similarly spaced and shaped as the upper dentition of *C. gilmorei* (Hastings et al., 2013). The premaxilla and maxilla of *C. gilmorei* indicate that the lower dentition occluded lingual to the upper, according to the presence of occlusal pits (Hastings et al., 2013). Consistent with lingual occlusion is the presence of a smoothed band of bone immediately lateral and ventral to the dentition of the UF 281065 dentary, best seen in lateral view (Fig. 1). The pm1 and pm2 alveoli of the premaxilla of the type material of *C. gilmorei* are known to be "separated by a large pit for occlusion of the first dentary tooth" (Hastings et al., 2013, p. 246), consistent with the nonprocumbent d1 alveoli of UF 281065 (Fig. 1). In addition, the premaxilla was noted to have "two small medial depressions for occlusion of d2–3," again consistent with the smaller d2 and d3 alveoli of UF 281065 (Fig. 1). The enlarged d4 alveolus exhibited in UF 281065 was expected from the premaxillary morphology of the type material of *C. gilmorei*: "A small shelf posterior to the pm5 alveolus indicates a deep pit for occlusion of an enlarged tooth in the mandible, likely the d4" (Hastings et al., 2013, p 246). Additional features of the maxilla indicate the same: "The premaxillary-maxillary suture clearly passes through a large depression for the occlusion of d4" (Hastings et al., 2013, p 246). The lateral edge of the maxilla of the type material of *C. gilmorei* exhibits gentle curvature in lateral view, which matches the gentle curvature of the dentary between d4 and d10. Other than the matching maxillary surface for the d4 tooth, the next largest occlusal pit corresponds well with the enlarged d12 of UF 281065. In addition, the dentary symphysis extends to d5, which is consistent with the narrower anterior end of the snout of the *C. gilmorei* type, and the dentary divergence afterward is similar to the widening maxillary (Hastings et al., 2013).

Centenariosuchus gilmorei possessed two of the four diagnostic characters of Caimaninae in the type material, and the other two were simply not preserved. The dentary UF 281065 possesses another of the caimanine characteristics, the anterior splenial projection that ends posterior to the mandibular symphysis. Therefore, both the type and dentary possess characters recognized as identifying caimanines. This does not in itself mean they belong to the same caimanine taxon but at least does not refute the identification and would be inconsistent with other crocodylian groups.

The characteristic of an enlarged d4 relative to a smaller and non-confluent d3 in *C. gilmorei* is consistent for both caimanines and alligatorines (Brochu et al., 2012). Similarly, the anterodorsally projecting anterior dentary alveoli are found in *C. gilmorei* and other known caimanines and alligatorines (Brochu et al., 2012). The extent of the symphyseal surface between right and left dentaries does vary among alligatorids. *Centenariosuchus* appears to have the more derived condition, reaching d5, which is found in derived *Alligator* such as *A. sinensis* Fauvel, 1879, *A. mississippiensis* (Daudin, 1802), and *A. olseni* White, 1942. This trait is also found in derived caimanines such as *Purussaurus*, *Caiman*, and *Paleosuchus*. This trait is even seen in the early caimanines *Tsoabichi* and *Necrosuchus* (Brochu et al., 2012). However, basal caimanines and basal *Alligator* species possess a symphyseal surface that extends more posteriorly, to d6–d8 (Brochu et al., 2012). This extended symphysis is found in

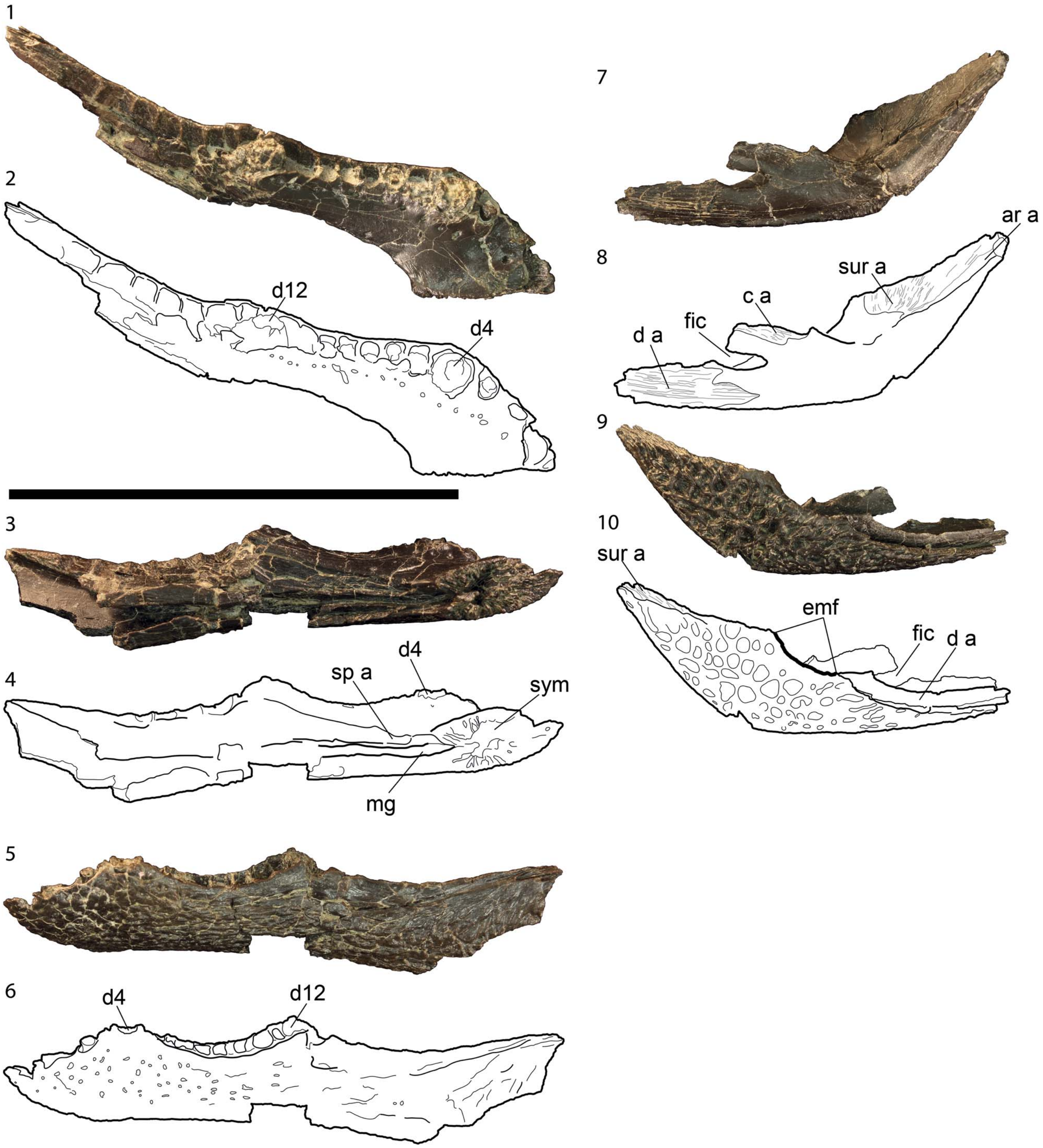


Figure 1. New mandibular caimanine fossil material from the early Miocene Cucaracha Formation of Panama. (**1–6**) Left dentary photos and descriptive illustrations (UF 281065) in (**1, 2**) occlusal view; (**3, 4**) medial view; (**5, 6**) lateral view. (**7–10**) Right angular photos and descriptive illustrations (UF 280923) in (**7, 8**) medial view; (**9, 10**) lateral view. The dentary (**1–6**) is referred to *Centenariosuchus gilmorei*. The angular (**7–10**) is referred to cf. *Centenariosuchus gilmorei*. ar a = articular surface of the articular; c a = articular surface of the coronoid; d4 = fourth dentary alveolus; d12 = twelfth dentary alveolus; d a = articular surface of the dentary; emf = external mandibular fenestra; fic = foramen intermandibularis caudalis; mg = meckelian groove; sp a = articular surface of the splenial; sur a = articular surface of the surangular; sym = symphyseal articular surface. Scale bar = 10 cm.

Alligator prenasalis (Loomis, 1904) and *A. mcgrewi* Schmidt, 1941, as well as *Globidentosuchus* and *Eocaiman* (Brochu et al., 2012; Scheyer et al., 2013). The gently curved dentary, in lateral view, between d4 and d10 of *Centenariosuchus* is similar to most alligatorids, including *Globidentosuchus*, *Caiman*, and *Eocaiman* (Brochu et al., 2012; Scheyer et al., 2013). Only three basal alligatorines are recognized as having a deeply curved dentary: *Alligator prenasalis*, *A. mcgrewi*, and *A. olseni* (Brochu et al., 2012). *Culebrasuchus* and *Mourasuchus* instead have more straight dentaries without notable ventrally directed curvature (Hastings et al., 2013). The largest alveolus of the dentary posterior to d4 is d12 in UF 281065, similar to the caimanines

Caiman, *Melanosuchus*, and *Paleosuchus* (Brochu et al., 2012). This is different from the alligatorine condition of a more posterior enlarged d13 or d14 in *Alligator olseni*, *A. sinensis*, and *A. mississippiensis* (Brochu et al., 2012). In addition, the d12 condition of UF 281065 is different from the enlarged series of posterior teeth found in *Globidentosuchus* and *Alligator prenasalis* (Brochu et al., 2012; Scheyer et al., 2013). The extent of the splenial of UF 281065 is the same as that for derived *Alligator* (*A. sinensis*, *A. mississippiensis*, *A. mefferdi* Mook, 1946, and *A. thomsoni*), *Tsoabichi*, *Mourasuchus*, *Caiman*, *Melanosuchus*, *Paleosuchus*, *Eocaiman*, *Necrosuchus*, and *Culebrasuchus* (Brochu et al., 2012; Hastings et al., 2013). Notable contrasting morphology whereby the splenial extends into the symphysis is seen in *Globidentosuchus* and certain *Alligator* species: *A. prenasalis*, *A. mcgrewi*, and *A. olseni* (Brochu et al., 2012; Scheyer et al., 2013).

Referred specimen.—Partial left dentary (UF 281065), preserving 18 consecutive alveoli (at least partially), a partial tooth base within d3, the tooth root of d4, and the articular surface of the symphysis.

Remarks.—This partial dentary has been referred to *Centenariosuchus gilmorei* because of morphological characters of the jaw that match very well with the known morphology of the taxon (see Comparison). In addition, the fossil was recovered from the same site and formation as the holotype and paratype within the Panama Canal Zone, and no other taxon of similar morphology has been recognized from the Cucaracha Formation.

cf. *Centenariosuchus gilmorei* Hastings et al., 2013
Figures 1.7–1.10, 2

2013 cf. *Centenariosuchus gilmorei* Hastings et al., 2013, p. 249, fig. S2.

Holotype.—Partial skull in direct association with two isolated teeth, one cervical vertebra, and two partial osteoderms (UF 262800) from the Hodges Microsite of the Cucaracha Formation of Panama (Hastings et al., 2013, figs. 5, 6).

Occurrence.—An isolated right angular (UF 245593) was previously described as cf. *Centenariosuchus gilmorei* from a site near the Hodges Microsite (Centenario Bridge locality; 9.03011452°N, 79.636786°W), also in the Cucaracha Formation of the Panama Canal Zone. Three additional specimens, described in the following, were more recently collected from the Hodges Microsite, where the holotype was found, and are assigned here to cf. *C. gilmorei* as well. These fossils are considered to be early Hemingfordian in age, from the early Miocene (MacFadden et al., 2014).

Description.—A second right angular (UF 280923), recovered from the Hodges Microsite, includes well-preserved articular surfaces for the articular, surangular, dentary, and coronoid bones (Fig. 1). These indicate strong contacts with each of these bones, best seen in medial view. The distinction between the surangular and articular surfaces is unclear for the most part, except for a distinct curvature where the edge of the sutural surface passes anteroposteriorly then sharply turns ventrally into a trough that would have led toward the dentary. The medial portion of this surface pertains to the articular, and the lateral portion to the surangular. This sutural surface indicates that the surangular-angular suture contacted the articular dorsal to the ventral-most tip of the articular bone. The sutural surface for the articular, and the posterior end of the angular, are oriented posterodorsally. The smooth medial surface of the mediodorsal projection of the angular indicates that the splenial did not possess a process that separated the angular and the coronoid (Fig. 1). The anteromost extent of this mediodorsal projection is robust and comes near to completing the margin of the foramen intermandibularis caudalis (Fig. 1). The anterior end of the projection appears to have been blunt and not acute. The ventral margin of the external mandibular fenestra is well preserved and smooth. The angular-surangular suture clearly does not pass ventrally along the external mandibular fenestra but ceases dorsally along the opening (Fig. 1). The external mandibular fenestra appears relatively small and to have restricted exposure of the foramen intermandibularis caudalis in lateral view (Fig. 1). The lateral surface is ornamented with deep, mostly circular pits.

The first sacral vertebra (UF 280257) has a strongly procoelus anterior articular facet on the centrum (Fig. 2). The posterior face of the centrum is flattened. The prezygapophyses are widely set at an angle of about 125°. The postzygapophyses appear to have received prezygapophyses at a similar angle. The ventral surface is smooth, with no keels, processes, or ridges (Fig. 2). Only the base of the neural spine is preserved, which is anteroposteriorly long, spanning most of the dorsal surface of the neural canal. Both sacral ribs are fully fused at their base to the centrum of the vertebra (Fig. 2). The capitulum of the sacral rib projects anteriorly, further than the tuberculum, resulting in both being visible dorsally (Fig. 2).

The ilium of UF 280256 is well preserved in three dimensions and is fully fused anteriorly and posteriorly to the ischium (Fig. 2). The anterior articulation is thin relative to the much thicker and well-sutured surfaces of the posterior contact. The anterior process of the ilium is distinct but not prominent. The dorsal margin of the iliac blade is rounded with a modest, ventrally directed indentation. The posterior end of the blade is relatively narrow, dorsoventrally, and would not be classified as ‘wasp-waisted’ (Fig. 2). The ventral surface of the posterior end of the blade is indented dorsally. The supraacetabular crest forms a narrow lip over the articular area. The ischium’s articular surface for the pubis is relatively small. The ventral extension of the ischium of UF 280256 slopes posteroventrally and tapers mediolaterally from its thickest near the ilium to the ventral tip (Fig. 2). The anterior surface of the ischium runs mostly dorsoventrally, with only a slight anteroposterior slant.

Comparison.—The right angular bone, UF 280923, presented in this paper preserves much more morphology than the only other crocodylian angular described from the Cucaracha Formation, UF 245593, recovered from a different site, near the Centenario Bridge (Hastings et al., 2013). This angular was also referred to cf. *C. gilmorei*.

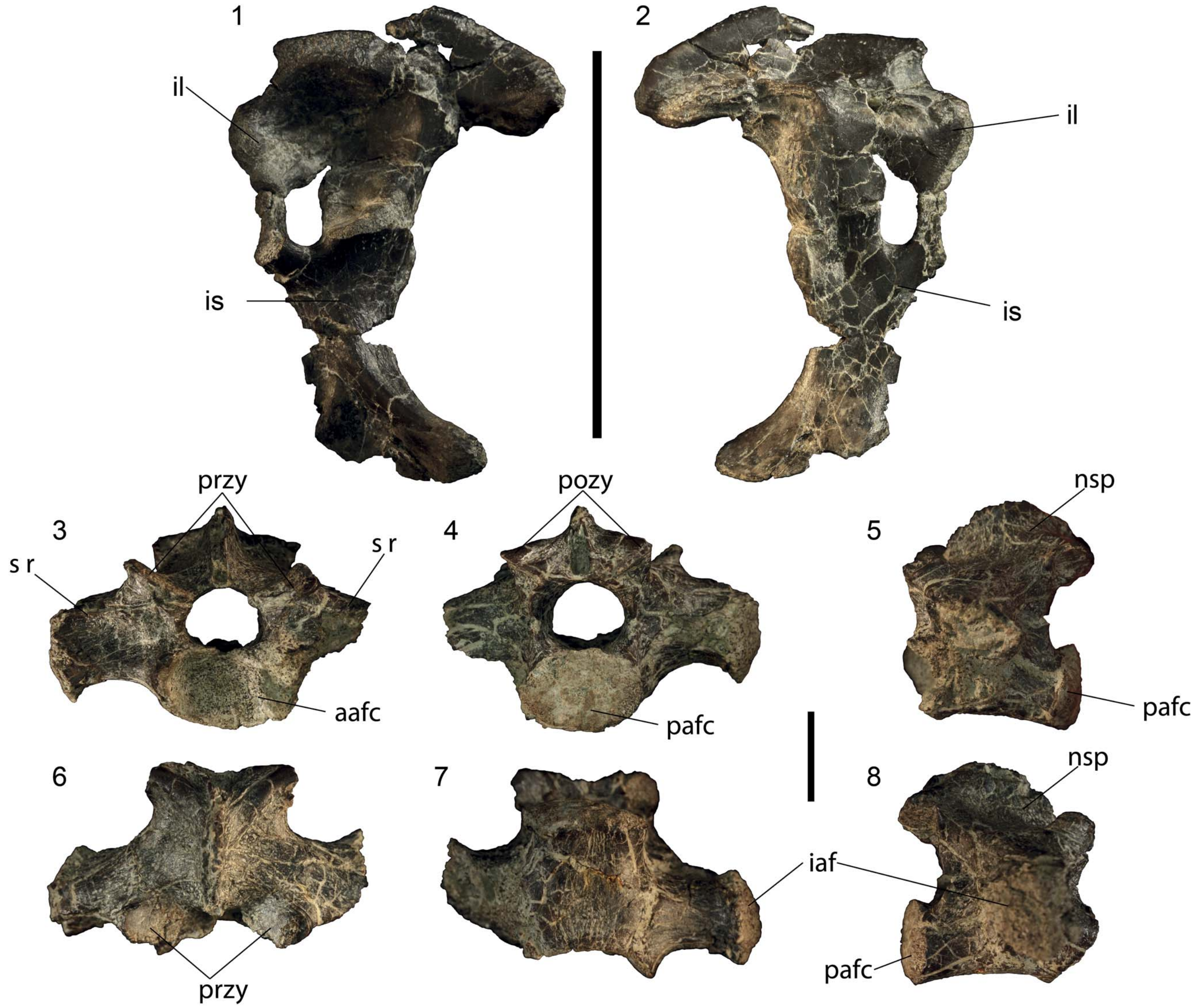


Figure 2. New pelvic caimanine fossil material from the early Miocene Cucaracha Formation of Panama, all referred to cf. *Centenariosuchus gilmorei*. (**1, 2**) Left ilium and ischium (UF 280256; fused) in lateral and medial views, respectively. (**3–8**) First sacral vertebra (UF 280257) in (**3**) anterior view; (**4**) posterior view; (**5**) left lateral view; (**6**) dorsal view; (**7**) ventral view; (**8**) right lateral view. aafc = anterior articular facet of the centrum; iaf = ilial articular facet; il = ilium; is = ischium; nsp = neural spine; pafc = posterior articular facet of the centrum; pozy = postzygapophyses; przy = prezygapophyses; s r = sacral rib. Scale bars = 1 cm.

The Hodges Microsite angular described in this paper possesses a sutural surface of the coronoid that indicates the coronoid contacted the angular directly and was not separated by the splenial. This condition is similar to all caimanines for which this characteristic is known as well as extant *Alligator* (Brochu et al., 2012). No part of the coronoid sutural surface was preserved in the Centenario Bridge Site angular.

One of the most typical traits of Caimaninae is possession of a relatively small external mandibular fenestra that limits exposure of the foramen intermandibularis caudalis from lateral view (Brochu, 2011). Although a recognized caimanine, *Purussaurus* does not possess this characteristic and instead has an enlarged external mandibular fenestra (Brochu, 2010; Brochu et al., 2012). In addition, the external mandibular fenestra of the older *Culebrasuchus* of Panama was also enlarged (Hastings et al., 2013). However, the smaller external mandibular fenestra characteristic is present in the Hodges Microsite angular (Fig. 1) and the Centenario Bridge Site angular (Hastings et al., 2013, fig. S2), as well as in every other caimanine including *Globidentosuchus* (Brochu, 2010; Scheyer et al., 2013). A second common trait to caimanines is a mediodorsal projection of the angular that has a blunt anterior margin, noted in medial view in all caimanines with the characteristic preserved (Brochu et al., 2012). Conversely, all recorded *Alligator* possess a projection that comes to an acute point (Brochu et al., 2012). The Hodges Microsite angular appears to have a robust projection that is not acute (Fig. 1). The Centenario Bridge Site angular only possesses the base of this projection, and its anterior extent cannot be evaluated (Hastings et al., 2013). A third common trait of caimanines is a surangular-angular suture that meets the articular bone dorsal to its ventral-most tip (Brochu, 1999). This trait is seen in all recorded caimanines, whereas all recorded *Alligator* possess a suture that meets the articular at the ventral-most tip (Brochu et al., 2012). The Hodges Microsite angular preserves this sutural distinction and is consistent with the caimanine condition.

These three traits are not recognized diagnostic characters of Caimaninae but are relatively consistent indicators of alligatorine versus caimanine taxa. A recognized diagnostic trait of Caimaninae is a surangular-angular suture that passes along the ventral margin of the external mandibular fenestra (Brochu, 2010). This character is recorded for all caimanine taxa that preserve it except *Mourasuchus* and the putative caimanines *Culebrasuchus* and *Globidentosuchus* (Brochu et al., 2012; Hastings et al., 2013; Scheyer et al., 2013). These taxa instead have a surangular suture that ends at the posterior margin of the external mandibular fenestra, much like the Hodges Microsite angular (Fig. 1). The ornamentation of the lateral surface of the Hodges Microsite angular is deep with rounded pits, similar to the deep pitting found in mature specimens of *Alligator* and *Caiman* (personal communication, A.K. Hastings, 2015). This likely indicates that UF 280923 was an adult individual and that these characteristics are not merely indicative of juvenile morphology.

The first sacral vertebra (UF 280257) has a strongly concave anterior articular facet on the centrum, indicating it received a procoelus presacral centrum. This would be consistent with most derived crocodyliforms, particularly eusuchians (Brochu, 2003), but inconsistent with the amphicoelus condition evidently present in *Sebecus* from the Miocene of Colombia (Busbey, 1986; Pol et al., 2012). UF 280257 also has the alligatorid characteristic of a sacral capitulum that projects strongly anterior to the tuberculum, resulting in both being visible in dorsal view (Brochu et al., 2012; Fig. 2). This contrasts the condition typical to crocodylids like *Crocodylus* with a capitulum and tuberculum that extend to essentially the same level anteriorly, obscuring most of the capitulum from dorsal view (Brochu et al., 2012).

Some characteristics of the morphology of the UF 280256 ilium are preserved well enough for comparison to other known crocodyliforms. The anterior process of the ilium for example is reduced as in alligatorids and is not the prominent feature seen in gavialids (Brochu et al., 2012). The supraacetabular crest of UF 280256 is narrow as in other alligatorids, and not broad as in the dwarf crocodile, *Osteolaemus* (Brochu et al., 2012). Most significantly though, the dorsal margin of the iliac blade of UF 280256 is modestly ventrally indented (Fig. 2) with a narrow posterior extension. This aspect is most similar to extant *Paleosuchus* and the early caimanine *Necrosuchus* (Brochu, 1999, 2011). The posterior extension of the ilium is more rounded and less dorsoventrally narrow in extant *Caiman*, *Melanosuchus*, and *Alligator*. The ischium of UF 280256 is much more similar to extant *Caiman* than to the widely spatulate shape of *Necrosuchus* (Brochu, 2011); its anterior articulation surface with the ilium is also much smaller. Despite being relatively small, the ilium and ischium of UF 280256 are fully fused, which is more consistent with fully adult extant specimens of Crocodylia (personal communication, A.K. Hastings, 2015).

Referred specimens.—Right angular (UF 280923), first sacral vertebra with articulated right and partial left sacral ribs (UF 280257), left ilium and ischium (UF 280256).

Remarks.—Although these three bones were recovered from the type locality of *Centenariosuchus gilmorei* (Hastings et al., 2013), they do not possess the necessary complementary morphology of the type material needed for taxonomic identification. The size and morphology of these specimens are consistent with that expected of *C. gilmorei*. However, although the dentary possesses characters that can be inferred from the preserved morphology of the type specimens, morphology of these three specimens cannot be definitively identified as belonging to *C. gilmorei*. Much like the angular described in the same work as the holotype (Hastings et al., 2013), we qualify the identification of these three specimens as cf. *C. gilmorei*. Should a more complete *C. gilmorei* specimen be recovered, these specimens may receive a more definitive identification.

Phylogenetic analysis

The character matrix of 179 morphological characters used for this analysis is that of Scheyer et al. (2013), with the addition of *Culebrasuchus mesoamericanus* and *Centenariosuchus gilmorei*. These character scores utilized the matrix of Brochu et al. (2012), with the addition of characters scored for *Necrosuchus* from Brochu (2011). Character scores were revised from Scheyer et al. (2013) for *Globidentosuchus* and revised from Hastings et al. (2013) for *Centenariosuchus.* Scorings for *Culebrasuchus* are unmodified from Hastings et al. (2013) except for adaptation into the new matrix. The newly described caimanines from the late middle Miocene of Peru (e.g., *Gnatusuchus* and *Kuttanacaiman*) could not be included in this analysis as the cladistic matrix of the current analysis was very different from that of Salas-Gismondi et al. (2015). For a complete list of characters and the cladistic data matrix used in these analyses, see supplemental data.

New scorings for Globidentosuchus.—Continued preparation of the holotype of *Globidentosuchus brachyrostris*, AMU-CURS-222, allowed for three character state changes to be scored for the taxon. The first of these concerns character 57, whether the inferior process of the coronoid laps strongly over the inner surface of the Meckelian fossa, state 0, or remains largely on the medial surface of the mandible, state 1 (Brochu et al., 2012). The right mandibular ramus of the holotype had a portion of the pterygoid emplaced over the coronoid, obscuring it from view, leading to the original score of '?.' Continued preparation was able to remove the displaced pterygoid, making it possible to assess the character (Fig. 3). The coronoid was preserved in the mandible, and the character could be scored as state 1, that the coronoid remains largely on the medial surface of the mandible. The rare preservation of the coronoid was likely due to the pterygoid holding it in place as the skull was pressed into the mandible after burial. Most often, this small, thin bone with a small contact with the mandible is lost prior to fossilization.

The second revision for *Globidentosuchus* concerns character 72, whether the surangular extends to the posterior end of the retroarticular process, state 0, or is 'pinched off' anterior to the tip of this process, state 1 (Brochu et al., 2012). After careful revision of the specimens and examples of scorings from modern and figured fossil specimens, we concluded that this character should

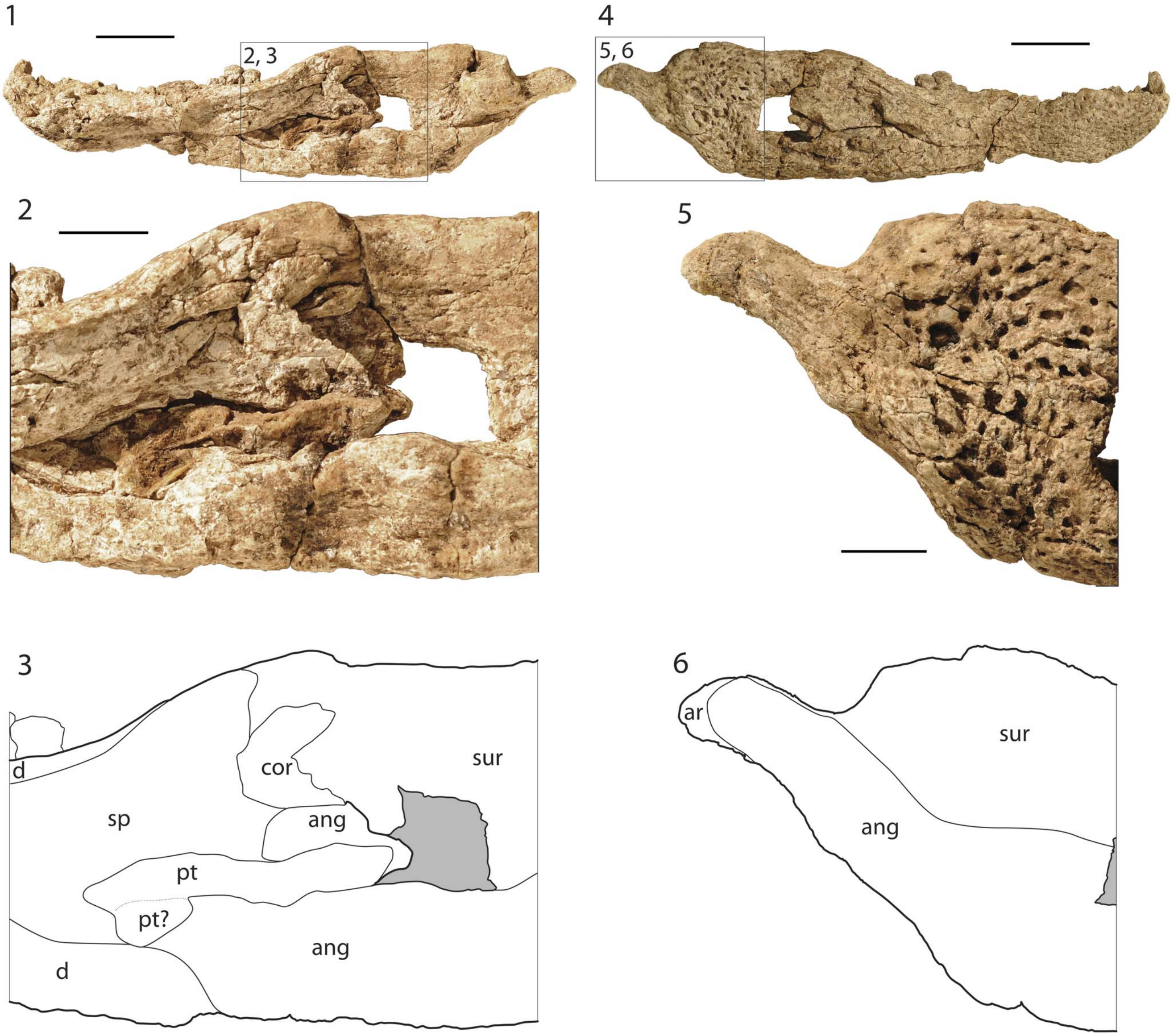


Figure 3. Right half of the mandible of the holoytpe of *Globidentosuchus brachyrostris* (AMU-CURS-222). (**1**) Medial view of lower jaw, with enlarged section labeled. (**2, 3**) Enlarged section from (**1**) with photos and lines indicating individual bones. (**4**) Lateral view of lower jaw, with enlarged section labeled. (**5, 6**) Enlarged section from (**4**) with photos and lines indicating individual bones. Note that due to taphonomy, part of the pterygoid was wedged into and fused with the mandible. ang = angular; ar = articular; cor = coronoid; d = dentary; pt = pterygoid; pt? = possible fragment of pterygoid; sp = splenial; sur = surangular. (**1, 4**) Scale bars = 5 cm. (**2, 3, 5, 6**) Scale bars = 2 cm.

be scored as the surangular extending to the posterior end of the retroarticular process (state 0; Fig. 3) instead of being pinched off (state 1). The condition is most similar to that scored for *Caiman*, and they are now scored the same for this character in the revised matrix presented here.

The third character alteration for *Globidentosuchus* is for character 127, whether the lacrimal makes a broad contact with the nasal with no posterior maxillary process, state 0, a maxillary process is present within the lacrimal, state 1, or the maxilla possesses a posterior process between the lacrimal and prefrontal, state 2 (Brochu et al., 2012). After careful reevaluation, we were able to determine the lacrimal-maxilla suture has a small, posteriorly directed indentation in the suture that indicates state 1 (Fig. 4). Furthermore, this is consistent with figures produced in Brochu (1999).

New scorings for Centenariosuchus.—The new material recovered of *Centenariosuchus gilmorei* allowed for six new scores for the taxon. These were limited to the new material and did not result in changing any characters that had already been scored. Furthermore, all material attributed to cf. *Centenariosuchus gilmorei* were not included due to the uncertainty of the taxonomic identification. The potential implications of characters that could be scored from this material are discussed in the following. The six additional characters are all scored from the dentary (UF 281065).

Character 47 could be scored as state 1, that the d4 alveolus is larger than and nonconfluent with the d3 alveolus (Fig. 1). This character is not surprising given the known morphology of the premaxilla that received this dentition in the type material of *Centenariosuchus* (Hastings et al., 2013). Also consistent with the premaxilla of the type of *Centenariosuchus*, the anterior

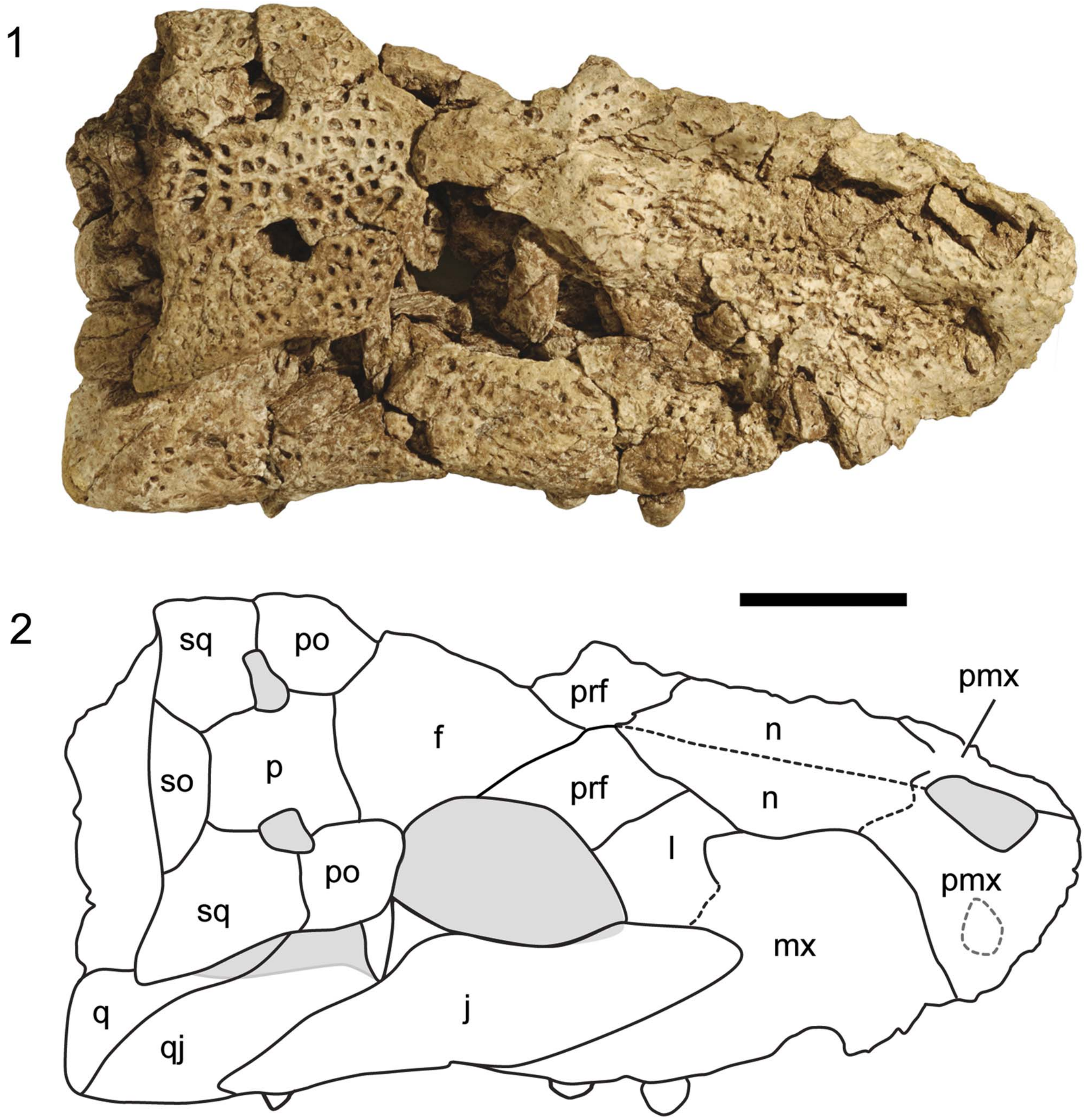


Figure 4. Revised interpretation of cranial elements in the holotype of *Globidentosuchus brachyrostris* (AMU-CURS-222). (**1**) Photo in dorsal view; (**2**) interpretive sketch. Dotted lines indicate sutures that are not completely clear. f = frontal; j = jugal; l = lacrimal; mx = maxilla; n = nasal; p = parietal; pmx = premaxilla; prf = prefrontal; po = postorbital; q = quadrate; qj = quadratojugal; so = supraoccipital; sq = squamosal. Scale bar = 5 cm.

dentary teeth are not procumbent, but instead project dorsally in UF 281065 (state 1 for character 48; Hastings et al., 2013). The dentary symphysis extends to the d5 alveolus for UF 281065 (Fig. 1), representing state 0 for character 49. Because of the overall similarity of *Centenariosuchus* to derived caimanines, this too is not surprising (Brochu et al., 2012; Hastings et al., 2013). Matching the contour of the tooth row of the maxilla of the type of *Centenariosuchus*, the dentary is gently curved in lateral view between d4 and d10 in UF 281065 (Hastings et al., 2013). character 51 could be scored as state 2, considering that the d12 alveolus is the largest dentary alveolus posterior to d4. Last, character 54 regarding the splenial participation with the symphysis was scored as state 2 since the splenial sutures clearly indicate that the splenial ended posterior to the dentary symphyseal surface, dorsal to the Meckelian groove (Fig. 1).

All-inclusive analysis.—All analyses were run using the ‘Traditional Search’ setting in the program TNT (Goloboff et al., 2008). Searches were run with 1,000 replicates, 100 trees saved per repetition, and Tree Bisection R (TBR) mode activated. A total of 100 crocodylian taxa were included, ranging across all forms and including all living species, and

179 morphological characters were scored. In addition, analyses were run in PAUP for Windows, version 4.0b10, using heuristic searches with 1,000 replicates and 100 trees retained per repetition (Swofford, 2004). In PAUP, due to the large data set, the 'Maxtrees' setting was limited to 20,000. For subsequent computation of consensus trees, cladograms had to be divided into two sets of 10,000. The resulting strict consensus cladograms and branch lengths from PAUP were identical to those generated by TNT. The Adams consensus cladograms were generated in PAUP. A total of 11 characters were recognized as parsimoniously uninformative (see supplemental data).

With all taxa included, the analysis recovered 37,300 equally most-parsimonious cladograms, or trees (EMTs), with a tree length (TL) of 656 steps. From TNT, the retention index (RI) was 0.811, and the consistency index (CI) was 0.348. In general, the topology of the strict consensus (Fig. 5) recovered poor resolution. The target taxa, *Culebrasuchus* and *Globidentosuchus*, were included in a large polytomy at the base of Alligatoridae, along with many other basal alligatorids. However, even in this topology, all other caimanines, including *Centenariosuchus*, were recovered in a monophyletic grouping with *Eocaiman* as sister to all other caimanines. The Adams consensus cladogram also placed *Culebrasuchus* in a polytomy at the unresolved base of a clade that included both Alligatorinae and Caimaninae, as well as *Hassiacosuchus*, a monophyletic *Brachychampsa*, and the sister taxa *Navajosuchus* and *Ceratosuchus* (Fig. 6). *Globidentosuchus* was recovered as basal to Caimaninae, sister to a clade uniting all other caimanines. The Adams consensus also placed *Stangerochampsa* as sister to the clade uniting *Globidentosuchus* to all other Caimaninae. *Centenariosuchus* placed within a polytomy at the base of a clade uniting all other caimanines except *Eocaiman*.

Tests with removing or revising selected taxa.—For these analyses, we analyzed using all taxa except for the minor revisions described in the following. However, we only present alligatorid taxa (and closely related taxa) in Figures 7–9 in order to save space and make text larger. The main focus of the subsequent analyses was within Alligatoridae, and the positions of non-alligatorid taxa did not shift within the topology regardless of the changes implemented in the following.

Removal of Globidentosuchus.—The same analysis as above was run again using the same parameters except with the removal of *Globidentosuchus* (Fig. 7). The number of EMTs increased to 43,500, with 649 steps (RI: 0.815; CI: 0.351). Both the strict consensus and Adams consensus topologies show a monophyletic Caimaninae with *Culebrasuchus* as the most basal member, sister to all other caimanine taxa. *Centenariosuchus* was recovered in a polytomy including all caimanines except *Culebrasuchus* and *Eocaiman*. Both consensus cladograms also depict a well-resolved Alligatorinae. *Stangerochampsa* was placed in a basal polytomy outside of the caimanine clade, not sister to it as in the all-inclusive analysis.

Removal of Culebrasuchus.—The same analytical parameters were again used, but *Culebrasuchus* was removed and *Globidentosuchus* was restored. The analysis resulted in 40,800 EMTs with tree lengths of 652 steps (RI: 0.813; CI: 0.350). The results of this analysis are nearly identical to when *Globidentosuchus* is removed, with *Globidentosuchus* instead placed as the basal-most member of a monophyletic Caimaninae (Fig. 7). All caimanine relationships are the same, including *Centenariosuchus*. The major difference in the Adams consensus was that *Stangerochampsa* again placed as sister to a clade uniting *Globidentosuchus* with all other caimanines.

Removal of Necrosuchus.—The Paleocene *Necrosuchus* of Argentina is known from only fragmentary remains (Brochu, 2011) and has been recognized as a wildcard taxon in the past (Hastings et al., 2013). *Necrosuchus* was only scored with 16.2% of the total number of characters. When the analysis was run with *Globidentosuchus* and *Culebrasuchus*, but not *Necrosuchus*, the result was 33,100 EMTs with tree lengths of 656 steps (RI: 0.811; CI: 0.348). The topologies of the resultant strict and Adams consensus diagrams are very similar to those of the all-inclusive analysis (Figs. 5, 6, 8) but with slightly better resolution within Caimaninae. *Tsoabichi* was sister to a monophyletic *Paleosuchus*, and *Mourasuchus* and *Orthogenysuchus* were sister taxa (Fig. 8). In the Adams consensus cladogram, *Culebrasuchus* remains in an unresolved position at the base of the clade uniting Alligatorinae, Caimaninae, and other alligatorids. In addition, the Adams consensus cladogram showed a sister taxon relationship between a clade uniting *Purussaurus*, *Mourasuchus*, and *Orthogenysuchus* and a clade uniting all *Caiman* and *Melanosuchus* species.

Single character state change for Globidentosuchus.—Character 174, whether or not the exoccipitals send slender branches to the basioccipital tubera, is a character thought to be monophyletic within Caimaninae (Brochu, 2010). All caimanines with this character scored exhibited presence (state 2), with the exception of *Culebrasuchus*. This character could not be assessed from the preserved material of *Globidentosuchus*. We ran the analysis again, with this character scored for *Globidentosuchus* as being the typical caimanine condition (Fig. 9). The result was 40,600 EMTs with tree lengths of 656 steps (RI: 0.812; CI: 0.348). The strict consensus of this analysis places *Globidentosuchus* as the basal-most member of Caimaninae, sister to a clade uniting all other members. Again, *Stangerochampsa* was sister to this clade (*Globidentosuchus* + Caimaninae) in the Adams consensus (Fig. 9). However, *Culebrasuchus* was placed outside of Caimaninae entirely, and was instead nested well within *Alligator* of Alligatorinae. This is very likely due to the presence of the noncaimanine trait for this specific character in *Culebrasuchus* (Hastings et al., 2013). This drastically different placement renders necessary reversals for characters of *Culebrasuchus* in order to account for its position in Alligatorinae. *Centenariosuchus* remained in a polytomy at the base of the clade uniting all caimanines except *Globidentosuchus* and *Eocaiman* (as well as *Culebrasuchus*).

Discussion

Characters diagnosing Caimaninae.—Four characters were found to be monophyletic for Caimaninae (Brochu, 2010) prior to the discoveries of *Globidentosuchus* and *Culebrasuchus*. Only one of these four is shared by Caimaninae and both

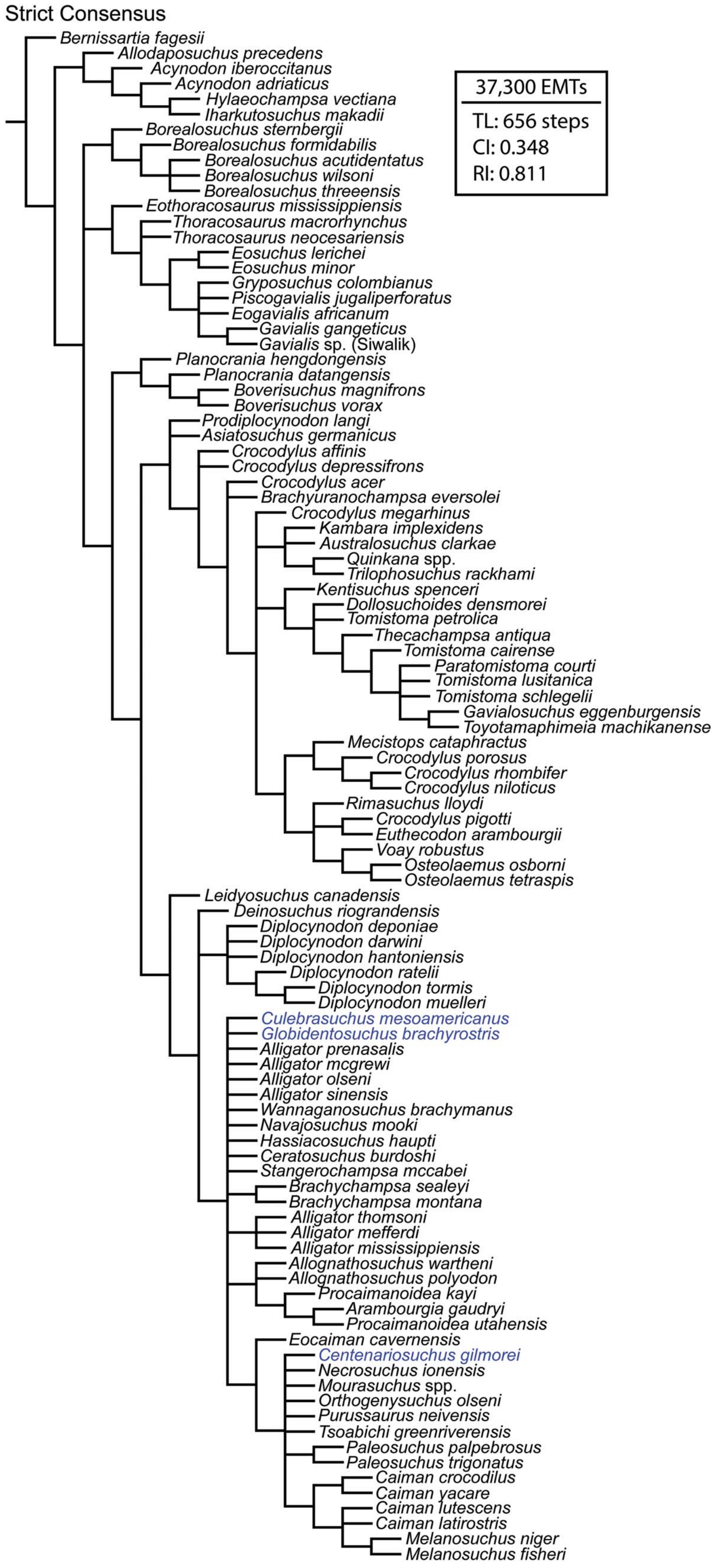


Figure 5. Strict consensus cladogram from a phylogenetic analysis including all 100 taxa and 179 characters. The main focus of the present study is on the relative positions of *Culebrasuchus mesoamericanus* and *Centenariosuchus gilmorei* (both from the Miocene of Panama) and *Globidentosuchus brachyrostris* (from the Miocene of Venezuela). All three taxa are highlighted. CI = consistency index; EMTs = equally most-parsimonious topologies; RI = retention index; TL = tree length.

Figure 6. Adams consensus cladogram with all 100 taxa included and 179 characters. Numbers at nodes represent percentage of topologies in agreement. The main focus of the present study is on the relative positions of *Culebrasuchus mesoamericanus* and *Centenariosuchus gilmorei* (both from the Miocene of Panama) and *Globidentosuchus brachyrostris* (from the Miocene of Venezuela). All three are highlighted. CI = consistency index; EMTs = equally most-parsimonious topologies; RI = retention index; TL = tree length.

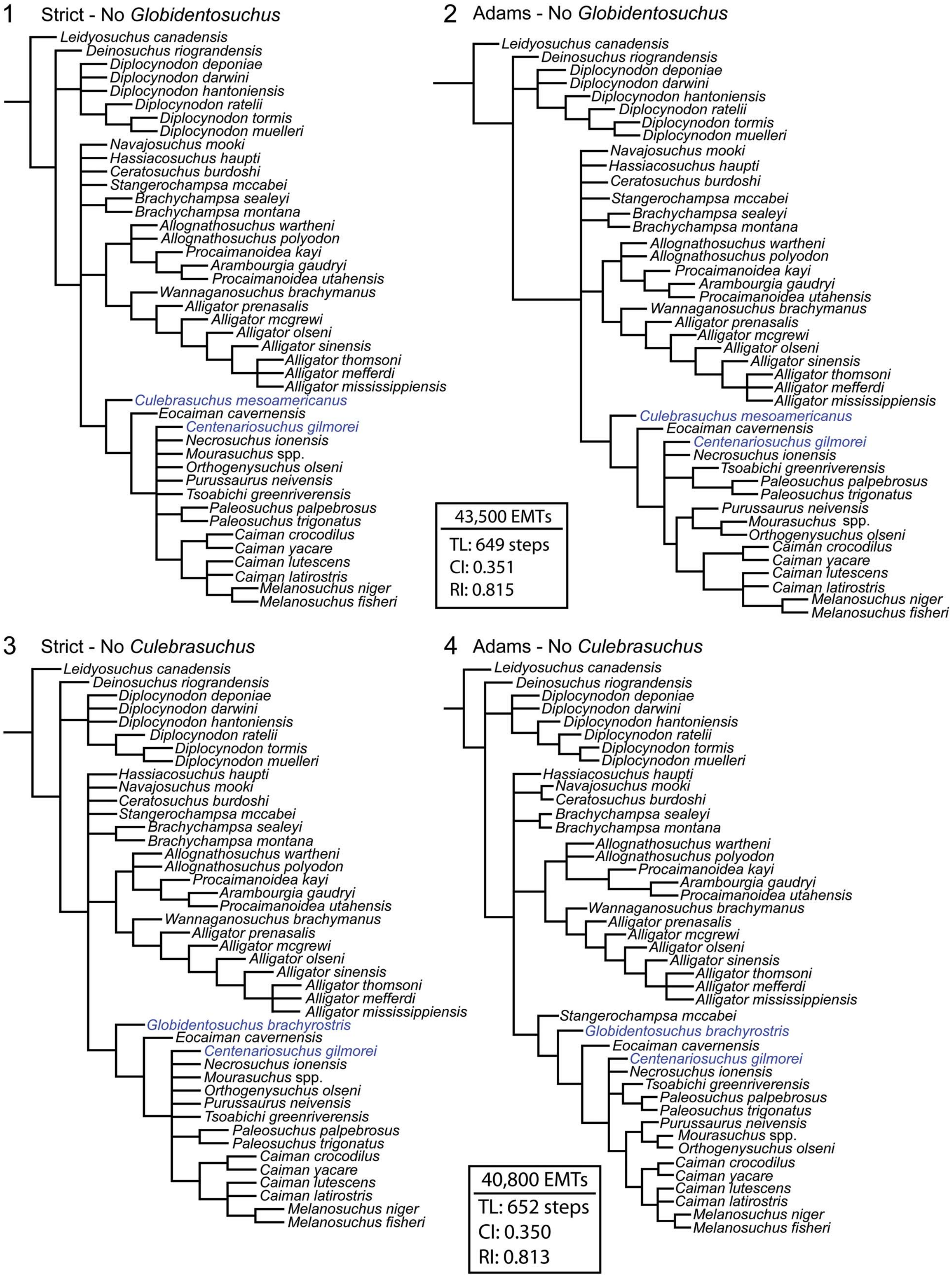


Figure 7. Phylogenetic analyses with selected removal of *Globidentosuchus brachyrostris* and *Culebrasuchus mesoamericanus*; 99 taxa were included in each analysis, although only Alligatoroidea is presented. The three taxa of primary interest are highlighted. (**1**) Strict consensus cladogram for analysis excluding *G. brachyrostris*. (**2**) Adams consensus cladogram for analysis excluding *G. brachyrostris*. (**3**) Strict consensus cladogram for analysis excluding *C. mesoamericanus*. (**4**) Adams consensus cladogram for analysis excluding *C. mesoamericanus*. CI = consistency index; EMTs = equally most-parsimonious topologies; RI = retention index; TL = tree length.

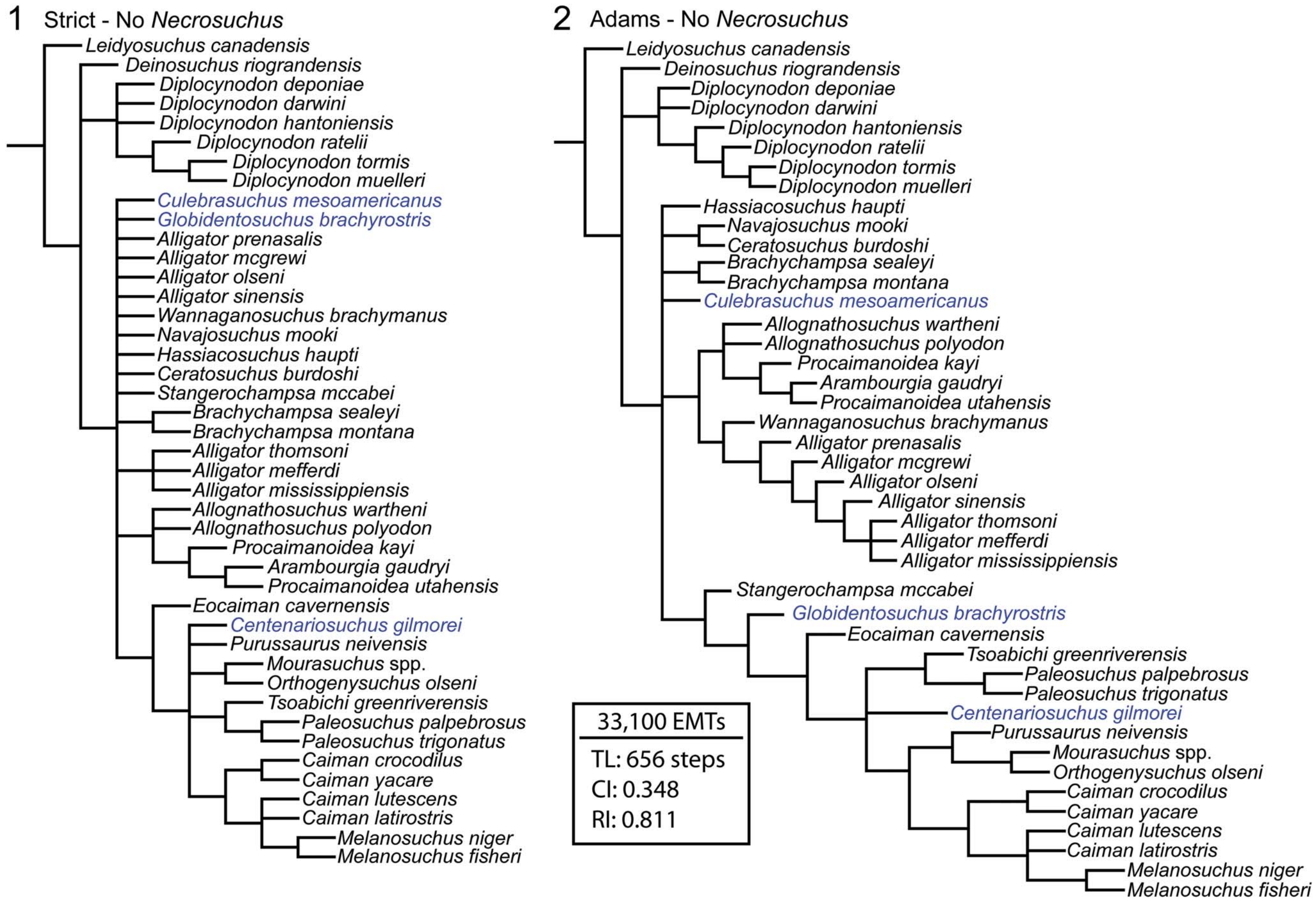


Figure 8. Phylogenetic analysis with removal of *Necrosuchus ionensis*; 99 taxa were included, although only Alligatoroidea is presented. The three taxa of primary interest are highlighted. (**1**) Strict consensus cladogram for analysis excluding *N. ionensis*. (**2**) Adams consensus cladogram for analysis excluding *N. ionensis*. CI = consistency index; EMTs = equally most-parsimonious topologies; RI = retention index; TL = tree length.

Globidentosuchus and *Culebrasuchus*. This uniting character is a large exposure of the supraoccipital on the dorsal skull roof (character 158). This trait is reduced in the more derived taxa *Paleosuchus* and *Tsoabichi* (Brochu, 2010) but is also seen in older species of *Alligator* (Brochu, 1999). This latter fact likely contributed to the alligatorine position of *Culebrasuchus* when character 174 was revised in the preceding analysis. *Gnatusuchus* of the Miocene of Peru was independently recovered as a stem caimanine in a separate analysis, and this character was mentioned as being prevalent in the holotype (Salas-Gismondi et al., 2015). Both *Globidentosuchus* and *Culebrasuchus* possess the noncaimanine trait of an angular-surangular suture that meets the external mandibular fenestra at the dorsal corner, not passing along the ventral margin (character 60). It should be noted, however, that there is a known reversal of this character to the more alligatorine condition of a surangular-angular suture that does not pass along the ventral margin of the external mandibular fenestra in *Mourasuchus* (Brochu et al., 2012). The third character thought to unite Caimaninae is that the splenial does not reach the mandibular symphysis, present in *Culebrasuchus* and all other caimanines (character 54). However, the splenial does reach the symphysis in *Globidentosuchus* (Scheyer et al., 2013) and *Gnatusuchus* (Salas-Gismondi et al., 2015). The last caimanine character is the presence of slender processes of the exoccipital extending to the basioccipital tubera (character 174). *Culebrasuchus* instead preserves the alligatorine condition of shorter processes. The trait is not preserved in *Globidentosuchus*, so it remains unknown. This trait was noted as present in *Gnatusuchus* (Salas-Gismondi et al., 2015). Overall, *Culebrasuchus* possesses two of these four and possesses noncaimanine traits for the other two. *Globidentosuchus* possesses only one caimanine state, two noncaimanine states, and one unknown. *Gnatusuchus* possesses at least two of the caimanine traits as well as one noncaimanine trait (Salas-Gismondi et al., 2015).

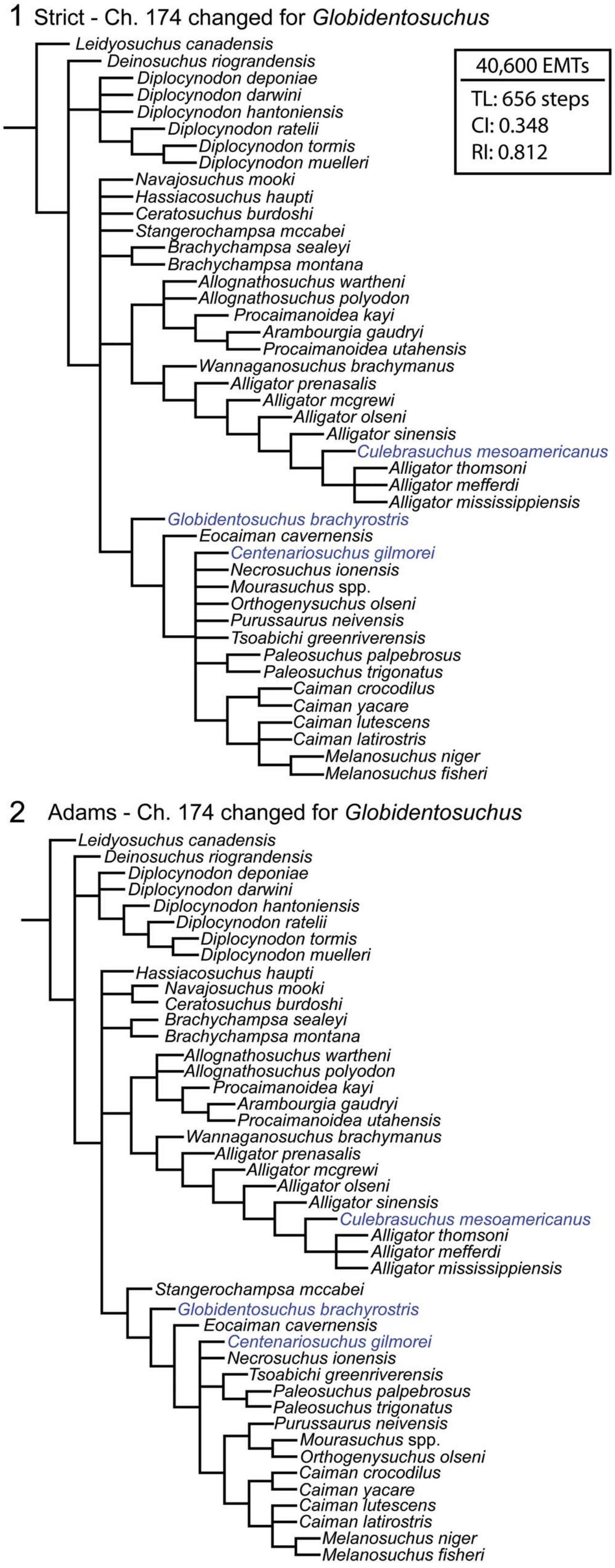
Despite having only one of the unambiguous synapomorphies of Caimaninae, *Globidentosuchus* possesses two traits that are typical of more derived caimanines. These are a small external mandibular fenestra and reduced supratemporal fenestrae, both found in nearly all caimanines. *Culebrasuchus* instead possesses a large external mandibular fenestra and nonreduced supratemporal fenestrae, characteristics more typical of Alligatorinae. Although these characteristics are not unique to Alligatorinae, these features combined with many unscored characters for *Culebrasuchus* result in a more tentative position near the base of Caimaninae. This study mostly highlights the uncertainty around the base of the alligatorine-caimanine split and the need for more complete representatives of the taxa recovered near this divergence.

Phylogenetic implications.—Overall, the results of the present analyses agree with topologies reported previously that included

Caimaninae (Brochu, 2010, 2011; Hastings et al., 2013; Scheyer et al., 2013; Salas-Gismondi et al., 2015). *Globidentosuchus* was recovered as a basal taxon with respect to Caimaninae, as was *Culebrasuchus* in one analysis, and both likely did play a significant part in the evolutionary split between Alligatorinae and Caimaninae. Given that Adams consensus cladograms place labile taxa in their most inclusive position, it is no surprise that *Culebrasuchus* was not placed as sister to or within Caimaninae in the all-inclusive analysis. The retention of *Globidentosuchus* as a basal caimanine would leave one synapomorphy for Caimaninae, the large dorsal exposure of the supraoccipital bone. Uniting *Culebrasuchus* and all other caimanines is the synapomorphy of a lack of splenial involvement in the dentary symphysis. Uniting *Eocaiman* and all other caimanines is the synapomorphy of a surangular-angular suture that passes ventrally along the external mandibular fenestra. If *Culebrasuchus* were retained with Caimaninae, this would create three steps of progression, showing these traits coming into caimanine evolution one at a time (Fig. 6). Much of the early caimanine fossil record is unavoidably poorly scored at present. Many of the taxa are known from partial skulls, and most postcranial material is unknown. Higher resolution would greatly improve the ability of the cladistic application to better understand the evolutionary split that led to the alligators and caimans of the New World.

Had the referred material been scored for *Centenariosuchus gilmorei*, its position in the cladogram may have been more solid. In particular, the possession of an angular-surangular suture that meets at the posterior angle is not seen often in Caimaninae, only *Mourasuchus*, *Globidentosuchus*, and *Culebrasuchus* (Brochu et al., 2012; Hastings et al., 2013; Scheyer et al., 2013). Given its proximity to *Mourasuchus* in the above analysis, this would likely only bring these taxa closer together, instead of remaining in a polytomy outside of the *Mourasuchus* + *Orthogenysuchus* clade (Figs. 6–9). The reduced external mandibular fenestra of the UF 280923 angular would provide some distinction from the also closely related genus *Purussaurus*, which has an enlarged fenestra (Aguilera et al., 2006). The cladistic similarity to the *Mourasuchus* and *Paleosuchus* taxa would be stronger with inclusion of the ilium UF 280256. These taxa have narrow iliac blades with dorsal indentations, as opposed to most caimanines, which have rounded dorsal margins and modest dorsal indentations. If future specimens can be found that more reliably align these bones with known material of *C. gilmorei*, then phylogenetic coding of the taxon can expand.

Biogeographic and temporal implications.—Both the full phylogenetic analysis and the test with removal of *Necrosuchus* recovered consensus cladograms with *Globidentosuchus* as a basal caimanine, but with less conclusive positioning of *Culebrasuchus*. Furthermore, *Gnatusuchus* was independently recovered as more basal than *Globidentosuchus* (Salas-Gismondi et al., 2015). However, all three taxa were recovered from Miocene deposits, much younger than the oldest


1 Strict - Ch. 174 changed for *Globidentosuchus*

2 Adams - Ch. 174 changed for *Globidentosuchus*

Figure 9. Phylogenetic analysis when Character 174 is changed for *Globidentosuchus brachyrostris* from '?' to '2' (exoccipitals send slender process ventrally to the basioccipital tubera; Brochu et al., 2012). All 100 taxa and 179 characters are included in the analysis, and this character state was not changed for any other taxon. Only Alligatoroidea is presented although the analysis was run with all taxa. (**1**) Strict consensus cladogram. (**2**) Adams consensus cladogram. CI = consistency index; EMTs = equally most-parsimonious topologies; RI = retention index; TL = tree length.

caimanines. *Culebrasuchus* is stratigraphically the oldest taxon (early Miocene) as *Globidentosuchus* and *Gnatusuchus* come from later Miocene deposits (middle to late Miocene and late middle Miocene, respectively; Salas-Gismondi et al., 2015). The earliest caimanine records are of *Necrosuchus* and *Eocaiman* from the Paleocene and Eocene of southern Argentina and Brazil in South America (Bona, 2007; Brochu, 2011; Pinheiro et al., 2013) and *Tsoabichi* and *Orthogenysuchus* from the early Eocene of Wyoming in North America (Brochu, 2010). An additional record of an indeterminate caimanine was recovered from the middle Eocene of Texas (Westgate, 1989). This temporal disconnect creates ghost lineages of basal caimanines extending back from the Miocene into the Paleocene.

The origination of caimanines has been explained as an early dispersal from basal alligatorids in North America dispersing to southern South America. Phylogenetic and biogeographic analyses by Hastings et al. (2013) led them to suggest dispersal of a caimanine ancestor during the Late Cretaceous from North America to South America, previously supported by Brochu (2010). Hastings et al. (2013) proposed a potential relict population of basal caimanines persisting in Central America and/or northern South America well into the Miocene, accounting for occurrences of *Culebrasuchus*, *Globidentosuchus*, and now *Gnatusuchus*. These analyses further provide support for a back dispersal from this ancestral population to North America during the Eocene (Hastings et al., 2013). Although both *Culebrasuchus* and *Globidentosuchus* are admittedly younger than this dispersal event, the potential that the ancestor of *Culebrasuchus* came from northern South America would support this back-dispersal event. Older and more primitive caimanine fossils, lacking derived synapomorphies, recovered from Central America and northern South America would help to further support this working hypothesis.

The remaining issue surrounding these dispersal events is that during the Paleocene through Miocene, Panama was not connected to South America by a continuous land bridge (Fig. 10; Montes et al., 2012). During the Miocene, the gap was thought to have been roughly 200 km wide between northern South America and Central America (Montes et al., 2012). Recent geological evidence now suggests the isthmus had formed a continuous mass as far back as the middle Miocene, reducing the barrier to shallow or transient channels (Montes et al., 2015). Another study found that a significant wave of terrestrial organisms had dispersed between North and South America around 20 million years ago (Bacon et al., 2015), which would likely account for the occurrence of *Centenariosuchus gilmorei* in Panama during the early Miocene. However, this still does not account for dispersal events across a marine barrier before the Miocene. Modern caimanines and alligatorines lack the salt glands of marine crocodylids (Taplin and Grigg, 1989), and phylogenetic parsimony would indicate that the ancestors of both alligators and caimans also lacked salt glands that would have improved dispersal ability across marine barriers. A study involving extant *Caiman latirostris* (Daudin, 1802) found these animals would make short trips into saltwater habitats to feed, but afterward return to nearby freshwater habitats (Grigg et al., 1998). However, even fully marine reptiles such as sea snakes (e.g., *Pelamis platurus* [Linnaeus, 1766]) are known to require freshwater intake despite living in a saltwater habitat (Lillywhite et al., 2012). Researchers have suggested that the snakes obtained freshwater from surface lenses that occur during heavy rainfall (Lillywhite et al., 2012). In any case, the sizable marine gap between northern South America and Central America was evidently not an impassable barrier for early caimanines.

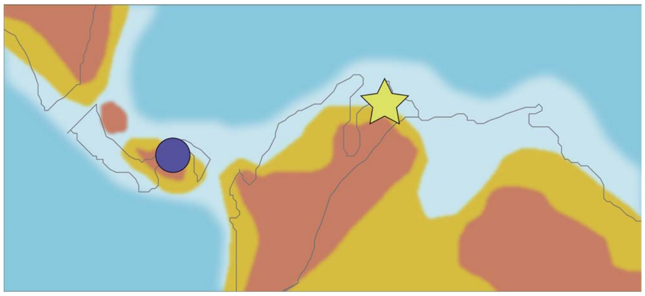


Figure 10. Miocene map of Central America and northern South America. Circle indicates the fossil localities of the early Miocene caimanines *Culebrasuchus* and *Centenariosuchus*. Star indicates locality of the middle to late Miocene *Globidentosuchus* fossil locality. The marine gap between the two landmasses at this time is estimated to have been approximately 200 km (Montes et al., 2012). Map adapted from Scotese (2001).

Summary

We have expanded the known morphology of the early caimanines *Globidentosuchus* and *Centenariosuchus*, from the Miocene of Venezuela and Panama, respectively. The phylogenetic analyses support an origination of Caimaninae within northern South America, with close relations in nearby Central America. Progressive, stepwise evolution occurs within the caimanine line, with the most diagnostic trait being the large dorsal exposure of the supraoccipital bone. Multiple dispersal events across the marine barrier between the two landmasses are necessary to explain the close relationships between taxa in North and South America. Ghost lineages are implied that extend from the Miocene caimanines into the Paleocene where the oldest, still more derived caimanines have been recovered in southern South America (Brochu, 2010). New fossil discoveries from the Paleogene of northern South America and southern Central America would further support the concept of a relict population of caimanines persisting in the region from the time of first dispersal to South America until at least the Miocene.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: http://datadryad.org/handle/10255/dryad.101085

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