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SHEDDING LIGHT ON THE TAXONOMIC DIVERSITY OF THE SOUTH AMERICAN MIOCENE CAIMANS: THE STATUS OF *MELANOSUCHUS FISHERI* (CROCODYLIA, ALLIGATOROIDEA)

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Abstract. *Melanosuchus niger* Spix is distributed throughout the Amazon River basin today. The extinct *Melanosuchus fisheri* Medina from the late Miocene of Venezuela was erected based on two almost complete, but heavily deformed skulls (the holotype MCNC 243 and the referred specimen MCZ 4336), which show morphological differences from each other. The comparison indicates that only the holotype can be referred to *Melanosuchus* Gray. We propose MCZ 4336 is a representative of the caimanine *Globidentosuchus brachyrostris* Scheyer, Aguilera, Delfino, Fortier, Carlini, Sánchez, Carrillo-Briceño, Quiroz and Sánchez-Villagra. Although the taxonomy of *M. fisheri* is taken into question herein, the classification of the holotype still sustains the hypothesis that the genus is registered in South America since the late Miocene.

Key words. Miocene. South America. Caimans. Amazonia. Black caiman. Caimaninae. Neogene.

Resumen. EL ESTATUS TAXONÓMICO DE *MELANOSUCHUS FISHERI* (CROCODYLIA, ALLIGATOROIDEA) ARROJA NUEVA LUZ SOBRE LA DIVERSIDAD DE LOS CAIMANES DEL MIOCENO DE AMÉRICA DEL SUR. *Melanosuchus niger* Spix se distribuye actualmente por toda la cuenca del Río Amazonas. La especie extinta *Melanosuchus fisheri* Medina del Mioceno tardío de Venezuela se erigió sobre la base de dos cráneos casi completos pero muy deformados (el holotipo MCNC 243 y el material referido MCZ 4336), que muestran diferencias morfológicas entre sí. La comparación indica que solo el holotipo puede ser referido a *Melanosuchus* Gray. Aquí se propone que MCZ 4336 es un representante del caimanino *Globidentosuchus brachyrostris* Scheyer, Aguilera, Delfino, Fortier, Carlini, Sánchez, Carrillo-Briceño, Quiroz and Sánchez-Villagra. Si bien la taxonomía de *M. fisheri* es aquí discutida, la clasificación del holotipo aún sostiene la hipótesis de que el género se registra en América del Sur desde el Mioceno tardío.

Palabras clave. Mioceno. América del Sur. Caimanes. Amazonia. Caiman negro. Caimaninae. Neógeno.

CROCODYLIA (*sensu* Benton and Clark, 1988) represents the crown group of neosuchian Mesoeucrocodylia (Pol *et al.*, 2012), which probably diversified during the Late Cretaceous (Brochu, 2003). It comprises three major subclades: Alligatoroidea, Gavialoidea and Crocodyloidea. Caimaninae is a clade nested within alligatoroids that is mostly recorded in South America and includes *Caiman crocodilus* and all crocodylians more closely to it than to *Alligator mississippiensis* (Brochu, 1999). The black caiman (*Melanosuchus niger* Spix, 1825) is the largest extant Caimaninae alligatoroid with adult males surpassing 4–5 m in length and females with a mean total length of 2.8 m (Brazaitis and Merrit, 1973; Thorbjarnarson, 2010). Both molecular and morphological studies place *M. niger* closer to *Caiman* Spix, 1825 than to *Pa-*

leosuchus Gray, 1862, forming the clade Jacarea (*e.g.*, Brochu, 1999, 2003, 2010; Oaks, 2011; Scheyer *et al.*, 2013; Salas-Gismondi *et al.*, 2015). Nowadays, this species is widely distributed throughout the Amazon River basin, in which the biogeographical history of caimanines was significantly impacted by changes of the Pebasian (Miocene) to the Amazonian–Orinoco (Miocene–Pliocene) drainage systems (see Salas-Gismondi *et al.*, 2016).

Although there is only one living species of *Melanosuchus* Gray, 1862, the genus was reported to be present since the late Miocene in South America based on two almost complete skulls (the holotype MCNC 243 and the referred specimen MCZ 4336) from the Urumaco Formation (Falcon State, Venezuela), for which the species *Melanosuchus fisheri*

Medina, 1976 was erected. However, this classification was questioned (Brochu, 1999) because both skulls of *M. fisheri* are fairly damaged, taphonomically deformed (palatal and temporal region) and show some morphological differences from each other. Furthermore, it is particularly difficult to distinguish morphologically the holotype of *M. fisheri* from *M. niger* (Brochu, 1999).

The aim of this study is to re-examine the anatomy of both skulls of *M. fisheri* and compare them with other extinct and extant caimans to test the validity of the previous assignments to *Melanosuchus*.

Institutional Abbreviations. AMU-CURS, Colección de Paleontología de Vertebrados de la Alcaldía de Urumaco, Estado Falcón, Venezuela; FLMNH, Florida Museum of Natural History, Florida, USA; FML, Fundación Miguel Lillo, San Miguel de Tucumán, Argentina; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Ciudad Autónoma de Buenos Aires, Argentina; MCNC, Museo de Ciencias Naturales de Caracas, Caracas, Venezuela; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MFA, Museo Provincial de Ciencias Naturales “Florentino Ameghino”, Santa Fé, Argentina; MG, Museo Provincial de Ciencias Naturales Dr. Ángel Gallardo, Rosario, Argentina; MLP, Museo de La Plata, La Plata, Argentina; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; SMF, Senckenberg Naturmuseum Frankfurt, Frankfurt, Germany; ZSM, Zoologische Staatssammlung München, München, Germany.

MATERIALS AND METHODS

A detailed anatomical study based on a morphological comparative analysis was made on the basis of cranial material of several fossil and extant caimanines (e.g., *Caiman*, *Melanosuchus*, *Globidentosuchus* Scheyer *et al.*, 2013). Specimens were examined with first-hand observations.

The two studied specimens of *M. fisheri* comprise MCNC 243 (holotype, Fig. 1.1–3), a skull lacking pterygoids, part of ectopterygoids, palatines, jugals and premaxillae, left postorbital and quadrate; and the referred specimen MCZ 4336 (Fig. 2.1–2, 5), a skull lacking pterygoids, left quadrate and quadratojugal, part of left jugal, part of basioccipital and left squamosal, and posterior two thirds of both hemimandibles. All specimens considered in this analysis are listed in the Appendix (Online Supplementary Information).

DESCRIPTION AND MORPHOLOGICAL COMPARISONS

Although partially deformed, MCNC 243 presents a caimanine-like skull with an outline resembling subadult specimens of *Melanosuchus niger*, i.e., a rostrum with approximately the same proportions as the extant species and orbits anteroposteriorly larger than other equal sized caimans (Figs. 1.1, 4, S1). The dorsal surface of the skull is partially eroded; however, some of the bone ornamentation can be distinguished. The sculpturing pattern is characterized by the presence of pits with different shapes and sizes irregularly distributed, more concentrated at the skull table. The skull table itself shows a straight posterior border and the squamosals are laterally elevated in occipital view (dorsal margin of the skull table curved in occipital view was listed as an autapomorphy of *M. fisheri*, see discussion below). MCNC 243 has strong “U-shaped” antorbital ridge and prefrontals contacting at midline (see also Mook, 1921: fig. 11 and discussion below). In the holotype the supratemporal fenestra are smaller and more “closed” than in subadult specimens of *M. niger*. In caimans (e.g., *Caiman latirostris* Daudin, 1802, *M. niger*), the supratemporal fenestra tend to get more small and closed during grow, but the size of these fenestrae also varies among specimens of the same ontogenetical stage (e.g., *C. latirostris*). The interorbital bridge, which was described as “arched anteroposteriorly, not concave above, thicker dorsoventrally” (Medina, 1976, p. 2), is arched in the holotype of *M. fisheri* but heavily scraped during preparation, so it is difficult to say if the concavity was originally present.

The palatal bones of MCNC 243 are damaged and eroded medially, so that sutures are largely obscured. Medially, between the premaxillae and the maxillae the suture cannot be traced because the bony surface of the palate is not preserved here, so the presence of the character “vomer exposed in palatal view” (diagnostic feature of the extant *Melanosuchus niger*) cannot be specified in this specimen. The size and shape of the suborbital fenestra are similar to *M. niger* and, as in this species, MCNC 243 also has 13 maxillary alveoli (preserved and counted in the left maxilla, but inferred on the right side, Fig. 1.2). No remains of the lower jaw are preserved in the holotype.

In contrast, the specimen MCZ 4336 has a relative small and more robust skull with a wider and rounded rostrum (Fig. 2.1–2). Contrary to MCNC 243, the cranial ornamenta-

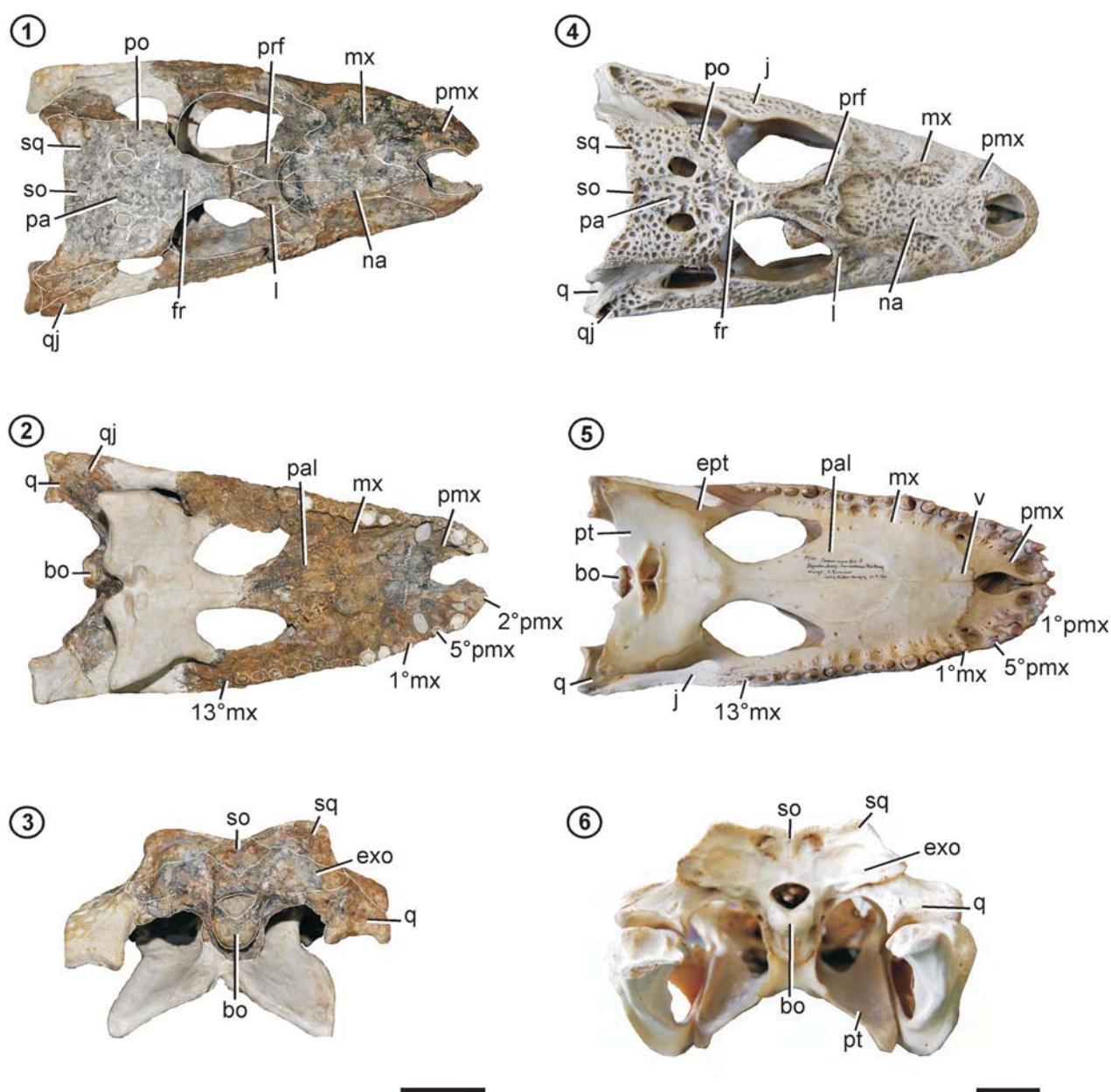


Figure 1. 1–3, Skull of *Melanosuchus fisheri* MCNC 243; 1, dorsal view; 2, ventral view; 3, occipital view. 4–6, Skull of *Melanosuchus niger*; 4–5, ZSM 90/1911; 6, ZSM 77/1911; 4, dorsal view; 5, ventral view; 6, occipital view. Abbreviations: bo, basioccipital; ept, ectopterygoid; exo, exoccipital (exoccipital-opistothic complex); fr, frontal; j, jugal; l, lacrimal; mx, maxilla; na, nasal; pa, parietal; pal, palatine; pmx, premaxilla; po, postorbital; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal; v, vomer; 2°–5° pmx, 2nd to 5th premaxillary alveoli; 1°–13° mx, 1st to 13th maxillary alveoli. Scale bars = 5 cm.

tion is given by sub circular pits uniformly distributed all over the surface of the bones. Interorbital ridges are absent and preorbital ridges are weak and practically absent at the maxilla. In MCZ 4336, the frontals have a different morphology than in extant *Melanosuchus* and *Caiman* species with extremely short anterior processes, probably articu-

lating in a V-shaped suture with the prefrontals rostrally. The supraoccipital is widely exposed on the skull roof and, as in other caimans, it excludes the parietal from the posterior edge of the skull table. As in MCNC 243, the interorbital bridge is crushed (Scheyer and Delfino, 2016) so that its original morphology cannot be verified. In contrast to MCNC

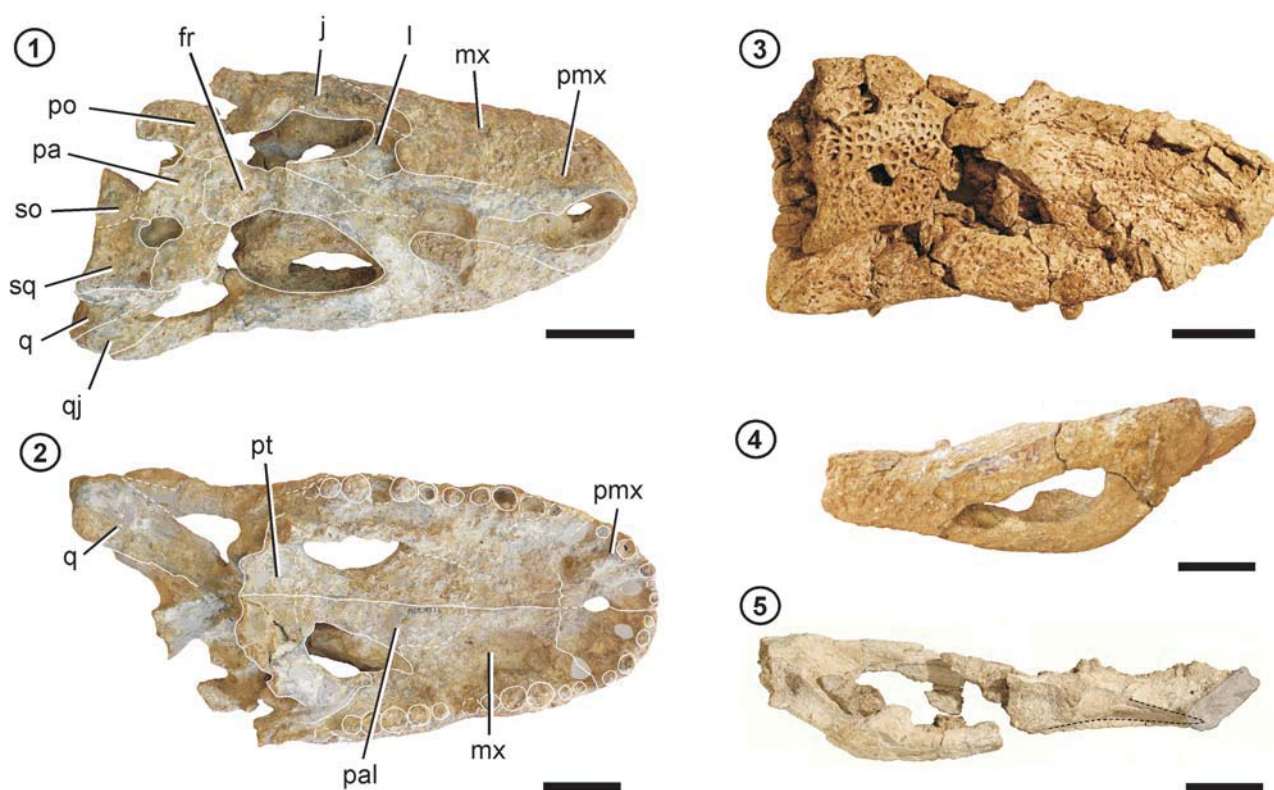


Figure 2. 1–2, 5, MCZ 4336; 1, dorsal view of the skull; 2, ventral view of the skull; 5, lateral view of left hemimandible. 3–4, *Globidentosuchus brachyrostris* AMU-CURS-222; 3, dorsal view of the skull; 4, lateral view of right hemimandible (mirrored). Abbreviations: fr, frontal; j, jugal; l, lacrimal; mx, maxilla; pa, parietal; pal, palatine; pmx, premaxilla; po, postorbital; pt, pterygoid; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal. Scale bars= 5 cm.

243 and *M. niger*, MCZ 4336 possesses a reduced number of maxillary alveoli (11 partially preserved on the left side; Fig 2.2). The external mandibular fenestra is large and low, but given the distortion of the material it might have been dorsoventrally higher in life (Fig. 2.5). There are at least two posterior teeth preserved in the right mandible of this specimen. They are robust with sub-spherical crowns, contrasting with the teeth morphology present in extant crocodylians (Fig. 2.5). MCZ 4336 also has preserved posterior fragments of both hemimandibles, but they are not very informative.

DISCUSSION

Melanosuchus is nested within the taxon *Caiman* in morphology-based phylogenetic analyses (e.g., Brochu 2011, Salas-Gismondi *et al.*, 2015; Hastings *et al.*, 2016), while molecular studies found *Melanosuchus* as sister group to the *Caiman* clade (Poe, 1996; Oaks, 2011). Thus, based on this

discrepancy, we provisionally retain *Melanosuchus* as a valid genus until more conclusive studies are conducted on the taxonomy of South American alligatorids.

The taxonomic validity of *Melanosuchus fisheri* was based on a combination of morphological features taken from both MCNC 243 and MCZ 4336, considered by Medina (1976) as the same taxon by their overall morphological similarities and their similar skull proportions. After detailed anatomical comparisons, we conclude, however, that these two specimens do not represent the same taxon, as they show a number of significant morphological differences, namely in the skull ornamentation, number of maxillary teeth, the occurrence of interorbital and preorbital ridges, and the shape of the frontal and supraoccipital. This outcome has far reaching consequences for the diagnosis of the species *M. fisheri* (see below), which was based on the two specimens (Medina, 1976).

The holotype of *M. fisheri* preserves several skull fea-

tures that can be found in *M. niger* and other jacarean caimanines or fall within its intraspecific morphological range of variation. Like *M. niger* (Fig. S1), MCNC 243 has anteroposteriorly longer orbits (only present in *M. niger*) than other similar sized caimans and shows also strong “U-shaped” antorbital ridges (also present in *C. latirostris* and *C. crocodilus*). Although partially deformed, the proportions of the rostrum of the holotype is very similar to that of *M. niger*. The prefrontals of MCNC 243 are contacting at the midline as is the case in some specimens of *M. niger* (e.g., ZSM 73/1911; ZSM 74/1911; ZSM 77/1911; ZSM 90/1911; see also Mook, 1921: fig. 11). Regarding the skull table, MCNC 243 shows a straight posterior border as was described by Medina (1976). However, this feature varies individually within *M. niger* with the posterior margin being straight (e.g., FLMNH 53600; SMF 30102; SMF 40172; ZSM 46/1911; ZSM 85/1911) to deeply curved, being “U-” (e.g., SZM 12/1911) or “V-shaped” (e.g., SZM 14/1911). Another important feature shared by the holotype MCNC 243 and large specimens of the extant *M. niger* is the dorsolateral elevation of the squamosals at the dorsal margin of the occipital table in occipital view (Fig. 1.3, 6). They further conform in the number of maxillary teeth (13), also present in *C. latirostris* (and contrary to *Caiman yacare*, which presents 14 maxillary teeth). In extant Caimaninae, the latter character is conserved throughout the whole ontogeny and not affected by individual variation. The exposure of the vomer at the palate, contacting with premaxillae and maxillae is a distinctive feature of *Melanosuchus niger* (Mook, 1921; Fig. 1.5), but unfortunately, the preservation of the damaged palatal region in the holotype of *M. fisheri* (with sutures largely obscured), allows only an ambiguous interpretation of this feature (Fig. 1.2). However, based on the number of similarities listed above, MCNC 243 can be confidently assigned to jacarean caimanines, sharing similarities (e.g., enlarged orbits, rostral shape) with *M. niger*. Neither its affiliation to *Melanosuchus* nor its classification as its own species is possible to support at the moment, as a number of shared characters listed are also present in other jacarean caimanines, while most diagnostic features of *M. fisheri* are based on the referred specimen (MCZ 4336), which differs from both MCNC 243 and *Melanosuchus* (see above). The lack of diagnostic features in the holotype MCNC 243 (because of its poor preservation, especially at the orbital and rostral

portions) prevents a conclusive decision regarding the taxonomic status of *Melanosuchus fisheri* and therefore this taxon could be regarded as a *nomen dubium*. However, there are some cranial shape differences and similarities among MCNC 243 with extant caimanine taxa (e.g., *Caiman crocodilus/C. jacare* and *C. latirostris/Melanosuchus niger*, respectively), which can offer new information on the taxonomic status of *M. fisheri* through a geometric morphometric analysis (Foth *et al.*, 2017).

Comparing the referred specimen MCZ 4336 with other neogene caimanines, it shows the same general morphology, outline, proportions and skull ornamentation as *Globidentosuchus brachyrostris*. This taxon is a basal caimanine that comes from the same levels of the Urumaco Formation (Scheyer *et al.*, 2013; Scheyer and Delfino, 2016; Fig. 2.3–4). Some of the original diagnostic characters of *M. fisheri*, such as “skull more robust; snout deeper heavier; preorbital ridges on snout faint rather than strong” (Medina, 1976, p. 2), are based on this specimen and fit the morphology of *G. brachyrostris*. As in the latter species, MCZ 4336 is a relative small caimanine with an U-shaped, short and wide skull (and rostrum); deep and robust mandibles; weak preorbital ridges and absent interorbital ridges; frontals without anterior processes, articulating in a V-shaped suture with the prefrontals rostrally; rectangular-shaped prefrontals, meeting in midline; supraoccipital well exposed on skull roof, excluding the parietal from posterior skull table edge; sub-spherical or globular posterior mandibular teeth (there are at least two globular teeth preserved in the right mandible of MCZ 4336); superior edge of coronoid slopes almost horizontally, and margin of orbit flush with skull surface (Fig. 2). Furthermore, the bone configuration of the skull roof of MCZ 4336 is very similar to *G. brachyrostris* (see Scheyer *et al.*, 2013; Hastings *et al.*, 2016), as the supraoccipital is crescent-shaped and more exposed on the skull roof of MCZ 4336. In addition, the mandibular fenestra of MCZ 4336 is large and probably low as in *G. brachyrostris*, but given the distortion of the material the fenestra might have been higher in life. Based on these features we refer MCZ 4336 to *G. brachyrostris*. Finally, the morphology of both posterior fragments of hemimandibles of MCZ 4336 also resembles that of *G. brachyrostris* (Fig. 2.4, 5; see also Scheyer and Delfino, 2016).

CONCLUSIONS

According to the discussed morphological evidence, we assign MCZ 4336 to the basal caimanine *Globidentosuchus brachyrostris*, whereas the holotype specimen of *M. fisheri* (MCNC 243) shows clear affinities with jacarean caimanines, and most likely can be referred to the genus *Melanosuchus*. However, at this point there are no morphological characters that can be used to assign this material to its own species and to distinguish it from *M. niger*. Further comparisons with other jacarean caimans including geometric morphometric analyses are needed to verify its finer differences and similarities with *Melanosuchus niger* (Foth *et al.*, 2017). Up to now, one taxonomical hypothesis is to consider *Melanosuchus fisheri* as a *nomen dubium* and assign MCNC 243 to *Melanosuchus* sp. on the basis of the rostral shape and the enlarged orbits (Mook, 1921; Kälin, 1933). Accordingly, material previously assigned to Caimaninae aff. *Melanosuchus fisheri*, such as AMU-CURS-234 (see Scheyer and Delfino, 2016), should be reassigned to *Melanosuchus* sp. as well.

Despite these uncertainties on the taxonomic status of *M. fisheri*, our study corroborates that *Melanosuchus* and other jacarean caimanines were already present in South America since the late Miocene (Bona *et al.*, 2014), which is further supported by molecular clock estimations (Oaks, 2011). Together with *G. brachyrostris* and other caimanines (e.g., *Caiman brevirostris* Souza-Filho, 1987, *Mourasuchus arendsi* Bocquentin-Villanueva, 1984, *Purussaurus mirandai* Aguilera, Riff and Bocquentin-Villanueva, 2006, *Purussaurus brasiliensis* Barbosa-Rodrigues, 1892; see Scheyer *et al.*, 2013; Salas-Gismondi *et al.*, 2015; Scheyer and Delfino, 2016), the black caiman could have formed part of the crocodylian assemblage that evolved in Amazonia during the Neogene.

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