


A new crocodylid from the middle Miocene of Kenya and the timing of crocodylian faunal change in the late Cenozoic of Africa

Adam P. Cossette,¹ Amanda J. Adams,² Stephanie K. Drumheller,³ Jennifer H. Nestler,⁴
Brenda R. Benefit,⁵ Monte L. McCrossin,⁵ Frederick K. Manthi,⁶ Rose Nyaboke Juma,⁶ and
Christopher A. Brochu^{2*} 

¹Department of Basic Sciences, NYIT College of Osteopathic Medicine – Arkansas, Jonesboro, AR 72401, USA <acossett@nyit.edu>

²Department of Earth & Environmental Sciences, University of Iowa, Iowa City, IA 52242, USA <chris-brochu@uiowa.edu>, <aadams1290@gmail.com>

³Department of Earth & Planetary Sciences, University of Tennessee, Knoxville, TN 37996 USA <sdrumhel@utk.edu>

⁴Cherokee Nation Businesses, Homestead, FL 33030 USA <jnestler@gmail.com>

⁵Department of Anthropology, New Mexico State University, Las Cruces, NM 88003 USA <bbenefit@nmsu.edu>, <mmccrossin@nmsu.edu>

⁶Department of Earth Sciences, National Museums of Kenya, Nairobi, Kenya <fkmanthi@museums.or.ke>, <nyabokejuma@gmail.com>

Abstract.—*Brochuchus* is a small crocodylid originally based on specimens from the early Miocene of Rusinga Island, Lake Victoria, Kenya. Here, we report occurrences of *Brochuchus* from several early and middle Miocene sites. Some are from the Lake Victoria region, and others are in the Lake Turkana Basin. Specimens from the middle Miocene Maboko locality form the basis of a new species, *Brochuchus parvidens*, which has comparatively smaller maxillary alveoli. Because of the smaller alveoli, the teeth appear to be more widely spaced in the new species. We also provide a revised diagnosis for *Brochuchus* and its type species, *B. pigotti*. A phylogenetic analysis supports a close relationship between *Brochuchus* and tube-snouted *Euthecodon*, but although relationships among crocodylids appear poorly resolved in the set of optimal trees, this is because *Brochuchus* and *Euthecodon*, along with early Miocene “*Crocodylus*” *gariensis* from the early Miocene of Namibia, jointly adopt two distinct positions—either closely related to the living sharp-nosed crocodile (*Mecistops*) or to a group including the living dwarf crocodiles (*Osteolaemus*). Character support for a close relationship with *Mecistops* is problematic, and we suspect a closer relationship to *Osteolaemus* will be recovered with improved sampling, but the results here are ambiguous. In either case, *Brochuchus* is more closely related to living groups not currently found in East Africa. This material helps constrain the timing of crocodylian faunal turnover in the East African Rift Valley System, with endemic lineages largely being replaced by *Crocodylus* in the middle or late Miocene possibly in response to regional xerification and the replacement of continuous rainforest cover with open grasslands and savannas.

UUID: <http://zoobank.org/e6f0b219-5f3e-44e5-bdb9-60a4fae8d126>

Introduction

The modern African dwarf crocodile, *Osteolaemus* Cope, 1861, is a group of at least three crocodylid species (Eaton et al., 2009; Smolensky, 2015; Smolensky et al., 2015). They have comparatively short, deep snouts and extensive dermal armor. These are some of the smallest extant crocodylians, rarely exceeding 2 m in total length (Eaton, 2010), and inhabit streams and pools in rainforests of western and central Africa (e.g., Waitkuwait, 1986; Kofron, 1992; Riley and Huchzermeyer, 1999; Eaton, 2010; Shirley et al., 2018).

Extinct relatives of *Osteolaemus* from the late Cenozoic of Africa and Madagascar represent a much wider range of body size, skull morphology, and (presumably) ecological

preference. Some were gharial-like forms with tubular snouts, and others superficially resembled modern generalized crocodylians (sensu Brochu, 2001) such as *Crocodylus* Laurenti, 1768, bearing moderately long, broad snouts (Brochu, 2000a, 2007; Storrs, 2003; Llinás Agrasar, 2004; Brochu and Storrs, 2012; Conrad et al., 2013). Indeed, most such generalized forms were previously referred to *Crocodylus* (e.g., Fourtau, 1918; Tchernov and Van Couvering, 1978; Tchernov, 1986; Pickford, 2003).

Early osteolaemines also had a broader distribution within continental Africa. One species of *Osteolaemus* formerly occurred as far east as Uganda, but the present range of the genus does not extend into the East African Rift Valley System (EARS; Eaton, 2010). The African sharp-nosed crocodile, *Mecistops* Gray, 1844, is also an osteolaemine in some analyses (e.g., Gatesy et al., 2003; McAliley et al., 2006; Meredith et al., 2011; Oaks, 2011), and it is likewise a Central and West African

*Corresponding Author

lineage not currently found east of Lake Tanganyika or south of the Congo Basin (Shirley et al., 2018). But osteolaemines are known from the early Miocene of Egypt, Libya, Namibia, and Kenya (Fourtau, 1918; Tchernov and Van Couvering, 1978; Brochu, 2000a; Pickford, 2003; Llinás Agrasar, 2004; Brochu and Storrs, 2012; Conrad et al., 2013). Indeed, the only generalized crocodiles known from Africa during the early Miocene are putative osteolaemines.

In the EARS, the generalized osteolaemine *Brochuchus pigotti* (Tchernov and Van Couvering, 1978) and its tube-snouted close relative, *Euthecodon* Fourtau, 1920, have been reported from the ca. 18 Ma Hiwegi Formation on Rusinga Island and correlative units in the Lake Victoria region of Kenya (Tchernov and Van Couvering, 1978; Buffetaut, 1979; Tchernov, 1986; Conrad et al., 2013). By ca. 7 Ma, in the Lower Nawata Formation at Lothagam, near Lake Turkana (Storrs, 2003), the only remaining osteolaemine lineages are *Euthecodon* and, assuming it is an osteolaemine, *Mecistops*, both of which persist in the eastern (Gregory) branch of the EARS into the Pleistocene (Joleaud, 1930; Arambourg, 1947; Tchernov, 1986; Storrs, 2003; Brochu, 2020). Although not to the same degree as *Euthecodon*, *Mecistops* also has a comparatively slender snout (e.g., Busbey, 1994; Pierce et al., 2008; Sadleir and Makovicky, 2008; Piras et al., 2010; Wilberg, 2017; Groh et al., 2020). The generalized crocodylids in these units are species of *Crocodylus* (Brochu and Storrs, 2012; Brochu, 2020).

It is unclear why generalized osteolaemines such as *B. pigotti* appear to have been replaced by *Crocodylus*, largely because of the 11 million years separating early and late Miocene crocodylian assemblages in the region. Whether these changes occurred suddenly or gradually, and whether they can be correlated with specific tectonic events or environmental changes, depends on knowing when generalized osteolaemines disappeared. This, in turn, is reliant on the description of Miocene crocodylids that are intermediate in age between Rusinga and Lothagam.

Here, we report occurrences of *Brochuchus* from several sites throughout the early and middle Miocene of Kenya. Some are from the Lake Victoria region in southwestern Kenya, and others are from the Turkana Basin in the northern part of the country (Fig. 1). Specimens from the middle Miocene at Maboko form the basis of a new species, *Brochuchus parvidens*. These occurrences extend the known stratigraphic range of generalized osteolaemines in East Africa and bear on the timing of crocodylian faunal turnover in the late Cenozoic of the region.

Materials and methods

Phylogenetic analysis.—The new species described here was added to a matrix of 189 discrete morphological characters and 31 ingroup taxa. The characters and codings used here are the same as those of Brochu and Storrs (2012) with modifications (Supplemental Data). First, we added Pleistocene *Crocodylus ossifragus* Dubois, 1908 from Java based on first-hand observation of type and referred specimens. Although it has generally been regarded as a junior synonym of the extant Siamese crocodile (*C. siamensis* Schneider, 1801; Müller,

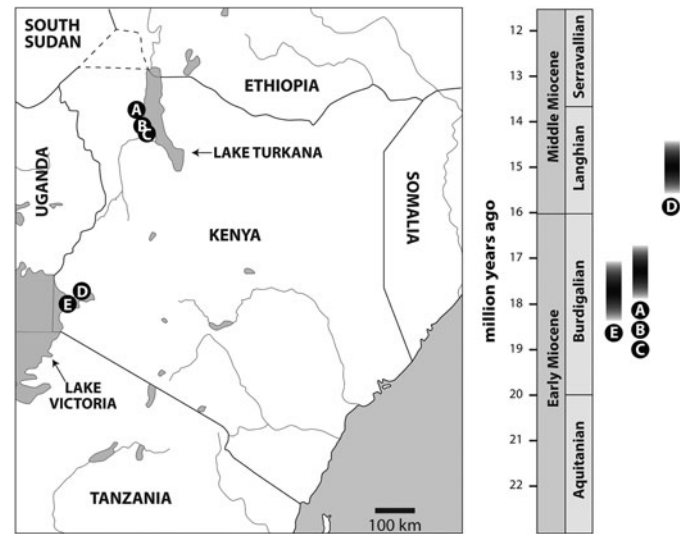


Figure 1. Map showing placements of locations discussed in this manuscript. A: Loncherangan. B: Kalodirr. C: Moruorot. D: Maboko. E: Rusinga Island.

1923; Brochu, 2000a; Delfino and de Vos, 2010), there are subtle but consistent differences between them (Brochu and Sumrall, 2020). We thus treat *C. ossifragus* as a separate species here.

Codings for *B. pigotti* were slightly modified from those used in Brochu and Storrs (2012) to reflect a revised interpretation of sutures surrounding the external naris. Previously, *B. pigotti* was assigned state 0 for character 82, indicating that the nasals contact the naris, but do not bisect it. We no longer hold this interpretation and assign state 2—the nasals do not reach the naris, but the nasals and premaxillae remain in contact—to both species of *Brochuchus*. This is similar to the condition in some other generalized crocodylids, such as *Rimasuchus lloydi* (Fourtau, 1918) and “*Crocodylus*” *gariensis* Pickford, 2003.

As used in this analysis, *Crocodylus niloticus* Laurenti, 1768; *Crocodylus novaeguineae* Schmidt, 1928; and *Mecistops cataphractus* (Cuvier, 1824) can be viewed as representing two species each. All three have been split (Hekkala et al., 2011; Meredith et al., 2011; Shirley et al., 2018; Murray et al., 2019), with *Crocodylus suchus* Geoffroy, 1807 separated from *C. niloticus*; *Crocodylus halli* Murray et al., 2019 separated from *C. novaeguineae*; and *Mecistops leptorhynchus* (Bennett, 1835) separated from *M. cataphractus*. The new or resurrected species are morphologically redundant with their pre-split conspecifics for the characters used here; hence, including them as separate terminals would add nothing to the analysis.

The ingroup sample focused on crocodylids and close crocodyloid relatives. One thousand random addition replicate analyses were performed using PAUP 4.0a (build 165; Swofford, 2002). Branches were collapsed if their minimum length was zero. *Borealosuchus sternbergii* (Gilmore, 1910) and *Leidyosuchus canadensis* Lambe, 1907 were used as outgroups to root the trees.

Nomenclatural notes.—In this manuscript, we apply clade name definitions from a molecular context (Brochu, 2003).

Crocodylidae Cuvier, 1807 corresponds with the last common ancestor of *Crocodylus niloticus* and *Osteolaemus tetraspis* Cope, 1861 and all of its descendants, and Crocodylinae Cuvier, 1807 refers to *C. niloticus* and all crocodylians more closely related to it than to *O. tetraspis*. The definition of Osteolaeminae Brochu, 2003—*O. tetraspis* and all crocodylians more closely related to it than to *C. niloticus*—is context independent.

We refer to the two living species of *Crocodylus* in Africa—*C. niloticus* and *C. suchus*—as Neoafrikan *Crocodylus*. This is to distinguish the modern forms from an extinct clade including *C. anthropophagus* Brochu et al., 2010 and *C. thorbjarnarsoni* Brochu and Storrs, 2012, which is here termed Paleofrikan *Crocodylus*. Neoafrikan *Crocodylus* may not be monophyletic; some analyses draw *C. niloticus* closer to a clade of crocodiles from the Western Hemisphere—Neotropical *Crocodylus*—than to *C. suchus* (Hekkala et al., 2011; Meredith et al., 2011; Oaks, 2011).

Conrad et al. (2013) informally referred to a group including *Osteolaemus* and *Voay* Brochu, 2007 as “osteolaemins.” Here, we define Osteolaemini on the basis of *Osteolaemus tetraspis* and all taxa more closely related to it than to *Mecistops cataphractus*, *Crocodylus niloticus*, or *Euthecodon nitriae* Fourtau, 1920. We define Euthecodonini as *Euthecodon nitriae* and all taxa more closely related to it than to *Osteolaemus tetraspis*, *Mecistops cataphractus*, or *Crocodylus niloticus*. In some published trees (e.g., those of Conrad et al., 2013), Osteolaemini is redundant with Osteolaeminae.

Because we have not studied it first-hand, the ingroup sample in our analysis does not include the type species of *Euthecodon*, *E. nitriae* from the Pliocene of Egypt. One could thus argue that our analysis does not actually explore the membership of Euthecodontini, the definition of which is anchored on the type species. However, *E. nitriae* and one of the species included here, Plio-Pleistocene *Euthecodon brumpti* (Joleaud, 1920) from Kenya and Ethiopia, are extremely similar (Ginsburg and Buffetaut, 1978; Tchernov, 1986). *Euthecodon brumpti* can reasonably be used as a stand-in for *E. nitriae* when discerning putative euthecodontins.

Dental abbreviations.—Dental alveolar positions are indicated with a letter representing the tooth-bearing bone (p for premaxilla, m for maxilla, d for dentary) and a number indicating the position of the tooth or alveolus in the tooth row.

Repositories and institutional abbreviations.—All specimens discussed in this manuscript are housed at the National Museums of Kenya, Nairobi (KNM) or the Natural History Museum, London, UK (NHMUK).

Systematic paleontology

Crocodylia Gmelin, 1789

Crocodylidae Cuvier, 1807

Brochuchus Conrad et al., 2013

Type species.—*Brochuchus pigotti* (Tchernov and Van Couvering, 1978).

Revised diagnosis.—Crocodylid with flat, slender rostrum. Five premaxillary, 14 maxillary, and 15 dentary teeth; teeth are circular in cross-section. Deep occlusal pits between maxillary alveoli, and the first eight alveoli are widely spaced. Alveoli project beyond surrounding surface, giving them a collared appearance. Nasals excluded from the external naris on dorsal surface of rostrum (shared with most longirostrine crocodylians, including *Euthecodon*). Naris opens anterodorsally. W-shaped maxillary-premaxillary suture on the palate, with the premaxilla extending back to the level of m2. Maxillary ramus of ectopterygoid forked (shared with *Crocodylus*). Dentary symphysis extends to a level between d5 and d6. The following characters are true for *B. pigotti*, but unknown in *B. parvidens* n. sp.: suborbital fenestra elliptical, and there are no concavities in its outline caused by laminae of the maxilla, palatine, or ectopterygoid. Palatine process slender and pointed, and extends anteriorly to the level of m7. Collared internal choana surrounded by a thin lamina of the pterygoid (shared with other osteolaemines). Prominent preorbital ridges; linear frontoparietal suture; skull table planar, and supratemporal fenestrae not constricted; supraoccipital exposed on dorsal skull table surface. Quadrate foramen aëreum on dorsomedial surface of quadrate ramus. Dorsal margin of axial neural spine oriented anterodorsally.

Remarks.—*Brochuchus pigotti* was a relatively small animal—the largest cranial specimens suggest individuals ~2.5 m in total length (Conrad et al., 2013). Its skull is gracile but not tubular, and like most such Cenozoic crocodyloids, the species was originally referred to *Crocodylus* (Tchernov and Van Couvering, 1978). The forms described here are broadly similar in size and skull shape.

The type species is known from a large number of specimens from the Hiwegi Formation (early Miocene, ca. 18 Ma) on Rusinga Island that collectively make it one of the best-sampled Neogene crocodylids. Phylogenetic analyses have consistently drawn the type species closer to *Osteolaemus* than to *Crocodylus* (Brochu, 2006, 2007; Brochu et al., 2010; Brochu and Storrs, 2012). This prompted Conrad et al. (2013) to transfer the species to the new genus *Brochuchus*.

At present, *Brochuchus* is known with certainty only from sites in the Victoria and Turkana Basins in Kenya. Specimens referred to *B. pigotti* have been reported from Italy (Kotsakis et al., 2004), but these were not figured and, not having seen them, we are unable to assess these referrals. Conrad et al. (2013) questioned whether mandibular material from the early Miocene of Saudi Arabia referred to *B. pigotti* (Buffetaut, 1984) was sufficient to support this conclusion. Indeed, the Saudi dentaries figured by Buffetaut (1984) differ from Kenyan *Brochuchus* dentaries in important respects—there is greater size disparity between d4 and much smaller neighboring alveoli, the fourth alveolus is substantially larger relative to other dentary alveoli, alveoli behind the fourth are not as widely separated, the dentary symphysis is narrower, and the tooth row between d1 and d5 is more arcuate. Referral to *Brochuchus* is possible, but not yet demonstrable.

Tchernov and Van Couvering (1978) included a dorsal premaxillary process extending to m2 in their diagnosis of *B.*

pigotti. The dorsal premaxillary process extends between the maxilla and nasal on the rostral surface, and it does indeed terminate at the level of m2 in *B. pigotti*. It is somewhat longer in *B. parvidens* n. sp. (see below).

The morphological restoration of *B. pigotti* presented by Conrad et al. (2013) is generally accurate, but we disagree on one point. Conrad et al. (2013) reconstructed the skull with nasals that penetrate the narial aperture (Fig. 2.2). This was the condition assigned to *B. pigotti* by Brochu and Storrs (2012), although they interpreted the nasals as being restricted to a pair of slender processes approaching the naris, much like the nasals of *Voay*, and not the more robust structures depicted by Conrad et al. (2013). Further examination of material at the NHMUK (including the holotype) and KNM compels us to reinterpret the rostrum of *B. pigotti*. The premaxillae meet behind the naris, excluding the nasals from the narial rim (Fig. 2.3).

Conrad et al. (2013) distinguished *Brochuchus* from *Osteolaemus* and *Voay* on the absence in *Brochuchus* of anterolateral processes on paramedian osteoderms, but these are absent from all crocodylids, including *Osteolaemus* and *Voay*.

Brochuchus parvidens new species
Figures 3.3–3.6, 4.

Holotype.—KNM-MB 36682, partial rostrum including most of both premaxillae, the right maxilla to m5, the left maxilla to m6, and the nasals between them (Fig. 3.3–3.6).

Diagnosis.—*Brochuchus* differing from *B. pigotti* in having slender premaxillary processes on the dorsal surface of the rostrum and more widely spaced maxillary and dentary alveoli; among the first four maxillary alveoli, the gap between two alveoli is approximately as long as the diameter of the alveolus behind the gap.

Occurrence.—Middle Miocene Maboko Formation, Maboko Main Locality, Maboko Island, Kenya (Fig. 1). All specimens were excavated in situ from Bed 3 at Maboko Main (see map in Geraads et al., 2012). Laser fusion $^{40}\text{Ar}/^{39}\text{Ar}$ dating of alkali feldspar from the tuff of Bed 8 (K87-4149) up-section from Beds 3 and at Maboko Cliffs yielded six reasonable isotopic ages with a mean age of 15.4 Ma and most recent date of 14.7 Ma (Feibel and Brown, 1991). Biostratigraphic

markers indicate an age younger than 16–18 Ma deposits at Rusinga (Van Couvering and Van Couvering, 1976; Pickford, 1981, 1983).

Bed 3 is a fossil-rich ~1 m thick unconsolidated oolitic packstone overlying the Bed 2 bentonite and capped by the hard Bed 4 calcrete. Several researchers suggest Maboko was part of a large floodplain (Van Couvering and Van Couvering, 1976; Andrews et al., 1981; Pickford, 1981, 1983). Sedimentological analysis of the ooids and oncoids in Bed 3, along with faunal and isotopic evidence, indicate likely deposition as a low energy freshwater beach ramp or littoral environment in a forest or woodland setting (McCrossin et al., 1998; Benefit, 1999; Retallack et al., 2002; Watkins, 2004; Arney et al., 2018). Water appears to have receded late in the history of Bed 3, leading to deposition of the Bed 4 calcrete. This may explain the absence of *Brochuchus* above Bed 3. A local habitat change at Maboko Main is indicated by the transition to Bed 4 calcrete overlain by Bed 5b mudstone, both with horizontal bedding (Watkins, 2004). Faunal transitions between Bed 3 and 5b include dramatic increases in the relative abundance of tragulids and the highly arboreal ape *Mabokopithecus*, accompanied by a decrease in the abundance of the presumably woodland giraffoid *Climacoceras* (Benefit, 1999; Retallack et al., 2002). Whereas numerous birds typically associated with large expanses of water occur higher in the sequence in Bed 5w (pelican, stork, cormorant, and flamingo), the only bird known from Bed 5b is a wader (Charadrii) typically associated with mudflats, and the only bird known from Bed 3 is a hornbill, which can occur in a range of habitats from forest to savanna (Mayr, 2014). Bed 5b may have been a forested wetland or swamp environment (Benefit, 1999).

Description.—Each premaxilla of the holotype preserves the distalmost three alveoli (Fig. 3.4, 3.6). The incisive foramen was evidently small, but its outline is not preserved. A deep occlusal pit separates p3 and p4, and there was evidently a large pit on the palatal surface mesial to p3. The fourth and fifth alveoli are close together. The premaxillae are dorsoventrally narrower anteriorly than posteriorly, and the naris opens anterodorsally.

The left and right sides of the holotype are displaced, with the left side elevated relative to the right. The premaxillae are no longer in contact, and the nasals separate anteriorly. As a result, sutural relationships around the naris are open to interpretation. Nevertheless, we are reasonably certain the nasals did not reach the naris on the external surface (Fig. 3.3, 3.5). The anterior end of the left nasal, as preserved, is acute. The medial sutural surface on the premaxilla behind the naris is parasagittal, suggesting it was contacting something on the sagittal plane. The apparent groove posterior to the naris is caused by depression of the right nasal and premaxilla relative to their left counterparts.

The dorsal premaxillary processes are very slender and appear to be rather long (Fig. 3.3, 3.5). That it appears shorter on the right is because the anterior tip of the right nasal is broken away. Despite their length, they only reach the level of m3. This can be seen both on the holotype and on KNM-MB 25736, which does not preserve the premaxilla itself, but which preserves a clear sutural surface for it (Fig. 4.1). Indeed, on the

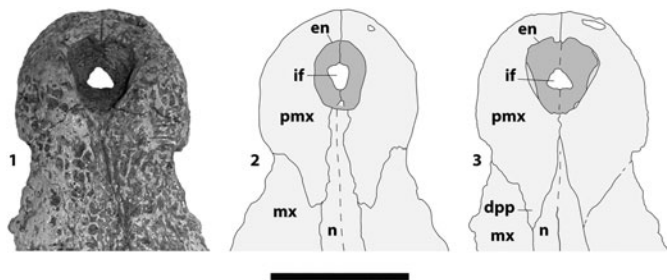


Figure 2. Anterior end of rostrum of NHMUK PV R 7729, holotype, *Brochuchus pigotti*. (1) Photograph of specimen. (2) Sutural interpretation based on Conrad et al., 2013. (3) Sutural interpretation used in this study. dpp = dorsal posterior premaxillary process; en = external naris; if = incisive foramen; mx = maxilla; n = nasal; pmx = premaxilla. Scale = 5 cm.

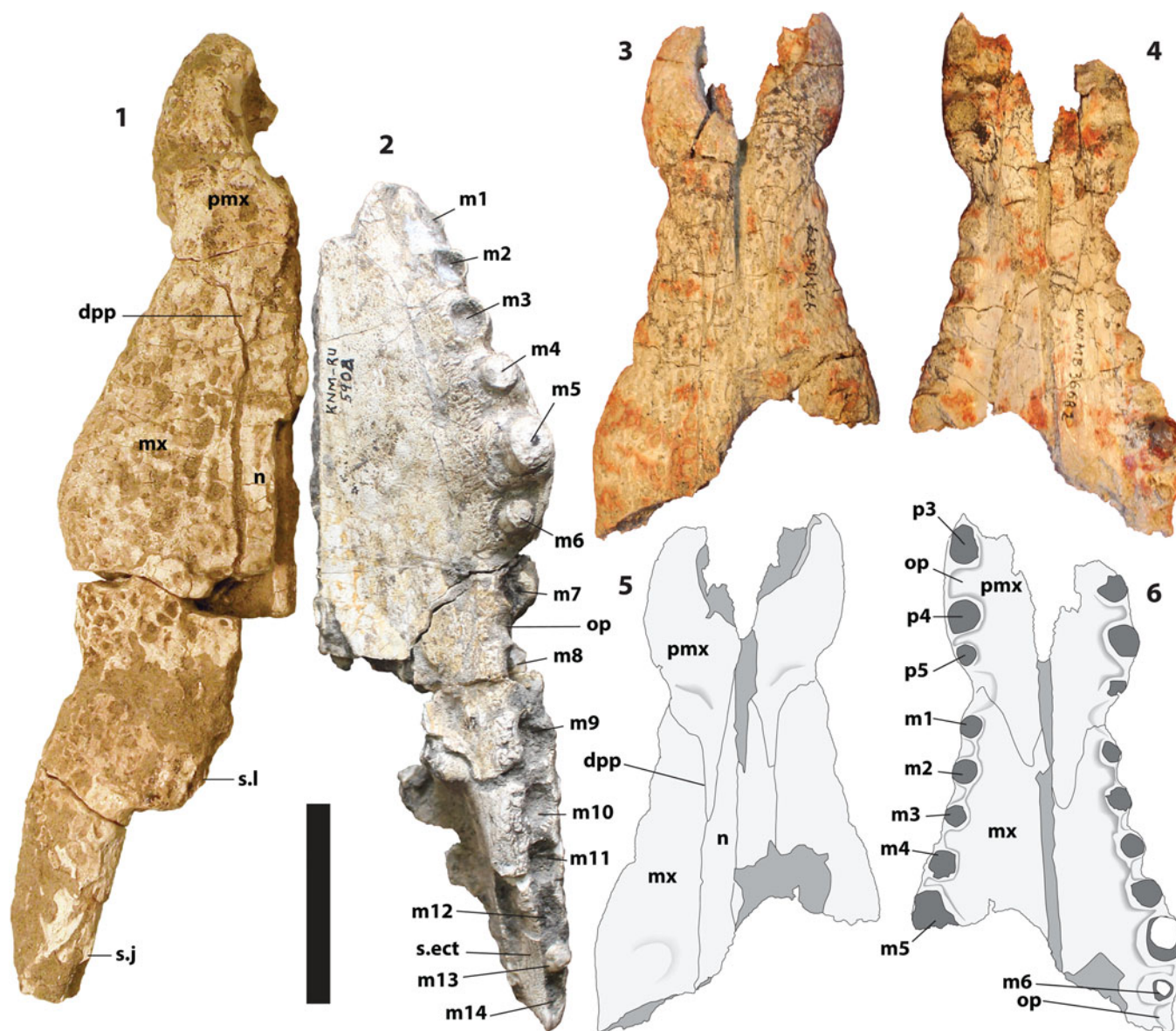


Figure 3. (1) NHMUK PV R 37517, *Brochuchus pigotti*, partial rostrum, dorsal view. (2) KNM RU-5904, *Brochuchus pigotti*, partial rostrum, ventral view. KNM-MB 36682, holotype, *Brochuchus parvidens* n. sp., partial skull in dorsal (3, 5) and ventral (4, 6) view. dpp = dorsal posterior premaxillary process; m1–m14 = maxillary dental/alveolar positions; mx = maxilla; n = nasal; op = occlusal pit; p3–p5 = premaxillary dental/alveolar positions; pmx = premaxilla; s.ect = sutural surface for ectopterygoid; s.j = sutural surface for jugal; s.l = sutural surface for lacrimal. Scale = 5 cm.

right side of the holotype, the process appears to reach a level between m2 and m3. Normally, processes as long as these would extend beyond m3. In this case, the alveoli are more widely spaced than in most other crocodylians. In effect, the alveoli moved posteriorly relative to the process.

The premaxillary-maxillary sutural surface on the palate is convex posteriorly, with the premaxilla extending to the level of the second maxillary alveolus (Fig. 4.2). The suture as a whole is W-shaped (Fig. 3.4, 3.6).

Four complete alveoli are preserved on the right maxilla of the holotype (Fig. 3.4, 3.6). The fifth alveolus is partially preserved. The same is true of KNM-MB 25736 (Fig. 4.2). The left maxilla of the holotype preserves six alveoli and an occlusal pit posterior to the sixth. The tooth row has an almost linear arrangement from m1 through m5 (Fig. 3.4, 3.6). The fifth

alveoli are the largest, and the left m5 bears a slender, lingually recurved tooth with low unserrated mesiodistal carinae. The alveoli are widely separated, and occlusal pits between the first four alveoli are almost as large as the preceding alveolus. The fourth and fifth alveoli are not as widely spaced from each other. A small boss for the fifth tooth root is preserved on the dorsal surface of the left maxilla of the holotype and, indistinctly, KNM-MB 25736.

The medial wall of the caviconchal recess is exposed on KNM-MB 25736. There are three or four shallow pits dorsal to the first two alveoli, but the surface is smooth otherwise.

The preserved dentaries are from substantially smaller animals than the holotype. Neither preserves the anteriormost alveoli, but we assume the largest preserved on both specimens is d4 (Fig. 4.4, 4.7); in other generalized crocodyliids, there is

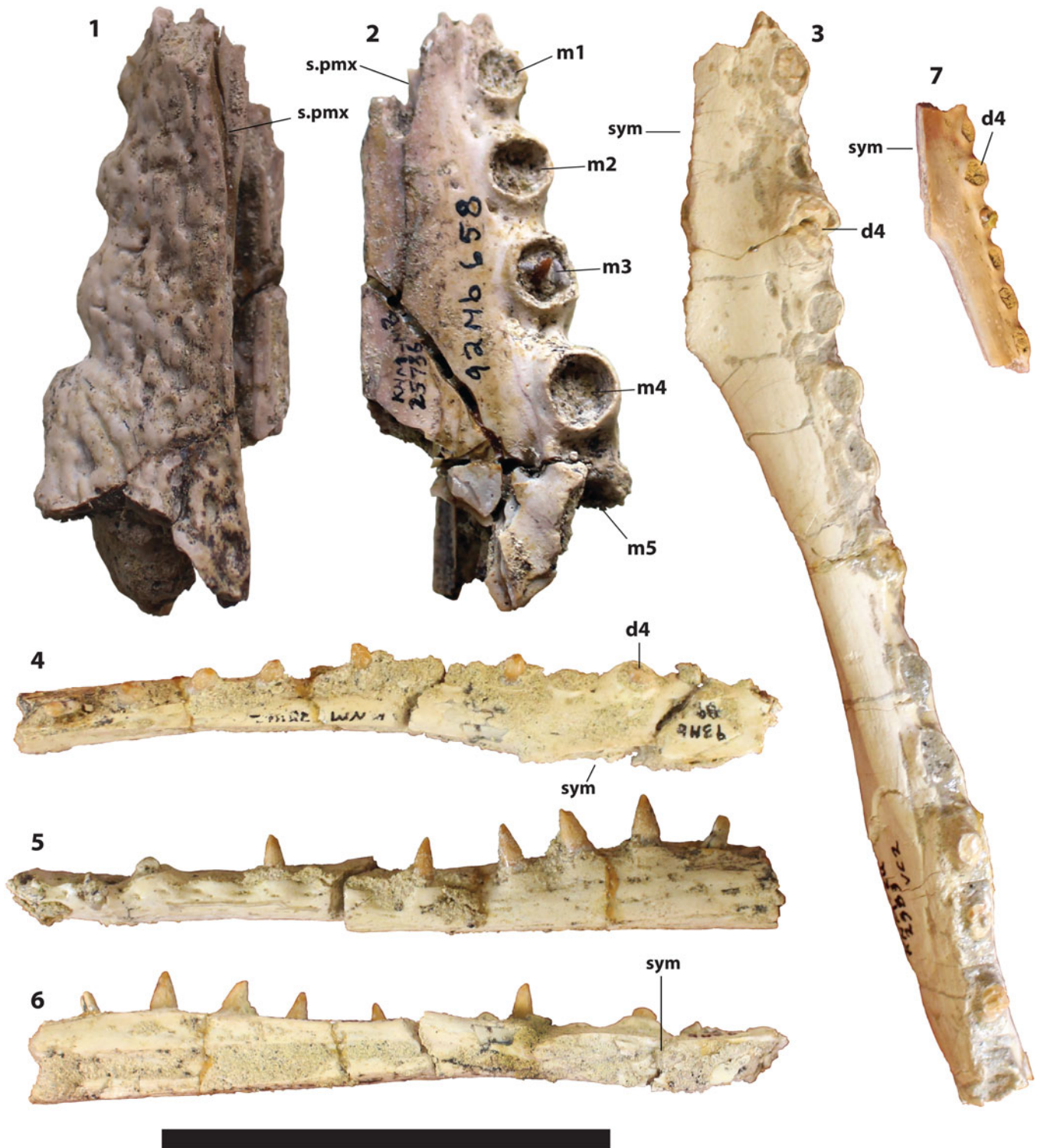


Figure 4. KNM-MB 25736, *Brochuchus parvidens* n. sp., partial left maxilla, dorsal (1) and ventral (2) view. (3) KNM-RU 2583, *Brochuchus pigotti*, right dentary, dorsal view. KNM-MB 28142, *Brochuchus parvidens* n. sp., left dentary, dorsal (4), lateral (5), and medial (6) view. (7) KNM-MB 22102, *Brochuchus parvidens* n. sp., partial right dentary, dorsal view. d4 = fourth dentary tooth/alveolus; m1–m5 = maxillary dental/alveolar positions; s.pmx = sutural surface for premaxilla; sym = dentary symphysis. Scale = 5 cm.

minimal difference in diameter among other mesial dentary alveoli. Based on this, the dentary symphysis extends either to the level of d6 (KNM-MB 28142; Fig. 4.4) or to a level between d5 and d6 (KNM-MB 22102; Fig. 4.7). The symphyseal part of

the mandible would have been mediolaterally narrow, and the dentary posterior to the symphysis remains slender, with only a modest amount of dorsal expansion approaching d10 and d11. Alveoli are widely spaced, with a larger diastema between

d8 and d9. The third and fourth alveoli are also widely separated. The splenial did not reach the symphysis, and based on the sutural surface on KNM-MB 22102 (Fig. 4.6), it terminated at the level of d7.

Etymology.—*parvi*, from Latin *parvus*, small; *dens*, Latin, tooth. The name refers to the relatively small alveoli in the maxilla and dentary compared with homologues in *B. pigotti*.

Materials.—KNM-MB 22099, partial maxilla; KNM-MB 22102, partial right dentary (Fig. 4.7); KNM-MB 25736, partial left maxilla (Fig. 4.1, 4.2); KNM-MB 28142, left dentary (Fig. 4.4–4.6).

Remarks.—Differences between *B. pigotti* and *B. parvidens* n. sp. are modest but consistent across multiple specimens. The most obvious is the shape of the premaxillary process on the dorsal surface. The process is triangular in both species, but it is visibly narrower in *B. parvidens* n. sp. than in *B. pigotti*. The condition in *B. parvidens* n. sp. is most evident in the holotype (Fig. 3.3), which preserves the premaxillae, but it can also be discerned on the much smaller isolated left maxilla (KNM-MB 25736), which preserves the sutural surface for the premaxilla (Fig. 4.1). The process is consistently more robust in *B. pigotti* (Figs. 2.3, 3.1). That the premaxillary process of *B. parvidens* n. sp. is slender in two specimens of very different size, the largest of which are of similar size to large specimens of *B. pigotti*, argues against an ontogenetic explanation.

The slender premaxillary process may reflect a mediolaterally contracted snout overall. The holotype of *B. parvidens* n. sp. is of approximately equivalent size with the holotype and several referred specimens of *B. pigotti*, but the rostrum appears broader between the fifth maxillary teeth in *B. pigotti* than in *B. parvidens* n. sp. The symphyseal surface of the dentary is also visibly narrower in *B. parvidens* n. sp., although because the only known dentaries of *B. parvidens* n. sp. are from small individuals, this could be a matter of scaling.

Alveolar separation also distinguishes the two species. The second, third, and fourth maxillary alveoli are only slightly wider than the diastemata anterior to them; the average ratio between the diameter of an alveolus and the length of the diastema in front of it (e.g., diameter of m2/distance between m1 and m2) is 1.16 (m2), 1.15 (m3), and 1.29 (m4) for two specimens of *B. parvidens* n. sp. (KNM-MB 36682 and KNM-MB25736). Conversely, the same alveoli are more than twice as wide as their preceding diastemata in *B. pigotti*, with ratios 2.10 (m2), 2.06 (m3), and 2.32 (m4) for three specimens (NHMUK PV R 7729, KNM-RU 5904, KNM-RU 2597). The third and fourth dentary alveoli also seem to be more widely spaced in *B. parvidens* n. sp.

Relative distances between centers of maxillary alveoli are the same in both species. Wider separation in *B. parvidens* n. sp. results from smaller alveolar diameter, which increases interalveolar space. This, too, might reflect decreased snout width; most living and extinct slender-snouted crocodylians, including gharials and *Mecistops*, have comparatively gracile teeth, although these forms also have elongated snouts that, in most cases, spread the alveoli further apart.

The dentary symphysis might be longer in *B. parvidens* n. sp. than in *B. pigotti*. On the more complete *B. parvidens* n. sp. dentary (KNM-MB 28142; Fig. 4.4–4.6), its posterior limit is somewhat closer to d6 than in most *B. pigotti* dentaries (e.g., Fig. 4.3). But this is not the case with the other dentary fragment referred to *B. parvidens* n. sp. (Fig. 4.7), and this is subject to minor amounts of variation among living crocodylians (Brochu, 2000b). A larger sample is needed to assess the consistency of this difference.

Brochuchus sp.
Figure 5.1–5.3.

Occurrence.—Kalodirr Member, Lothidok Formation, Moruorot (Fig. 1). Deposits at this site west of Lake Turkana are correlative with those at Kalodirr to the southeast (see below).

Materials.—KNM-MO 91, right maxilla (Fig. 5.1–5.3).

Remarks.—This specimen preserves, either completely or in part, fourteen maxillary alveoli surrounded by thin crests, imparting a collared appearance (Fig. 5.1). There are deep occlusal pits between m6 through m8, and the pit between m7 and m8 is especially deep with a scalloped lateral surface expressed as a discrete concavity on the ventral margin of the bone in lateral view (Fig. 5.1, 5.3). The suborbital fenestra extends anteriorly to a level between m9 and m10, and the ectopterygoid was adjacent to the last four maxillary alveoli. Matrix covers most of the medial surface, preventing us from assessing the shape of the ectopterygoid, and although a small uncovered section of the medial surface at the anterior end lacks pits on the caviconchal recess wall, we do not know whether such pits were absent posteriorly. The maxilla-premaxilla suture is not preserved on the palate.

The sutural surface for the premaxilla is visible dorsally (Fig. 5.2). It suggests a rather robust premaxillary process. The surface appears to be oriented medially more than anteriorly toward its posterior end, which would suggest a slender process, but it is unclear whether this is an actual sutural surface or breakage. In either case, even if the process was slender posteriorly, it was robust anteriorly. The jugal sutural surface is visible as a smooth patch toward the posterior end of the specimen.

Brochuchus sp.
Figure 5.4–5.6.

Occurrence.—Kalodirr Member, Lothidok Formation, Kalodirr, west of Lake Turkana (Fig. 1). These deposits have been constrained by radiometric dates from under- and overlying tuffs to between 17.7 Ma and 16.6 Ma (Boschetto et al., 1992).

Materials.—KNM-WK 18210, right dentary (Fig. 5.6); KNM-WK 18211, right maxilla (Fig. 5.4, 5.5).

Remarks.—The maxilla (KNM-WK 18211; Fig. 5.4, 5.5) preserves sutural contacts for the premaxilla anteriorly, nasal medially, and ectopterygoid posteromedially. The medial surface is covered with matrix. Thirteen or 14 alveoli were present; the number is unclear because the posterior end of the

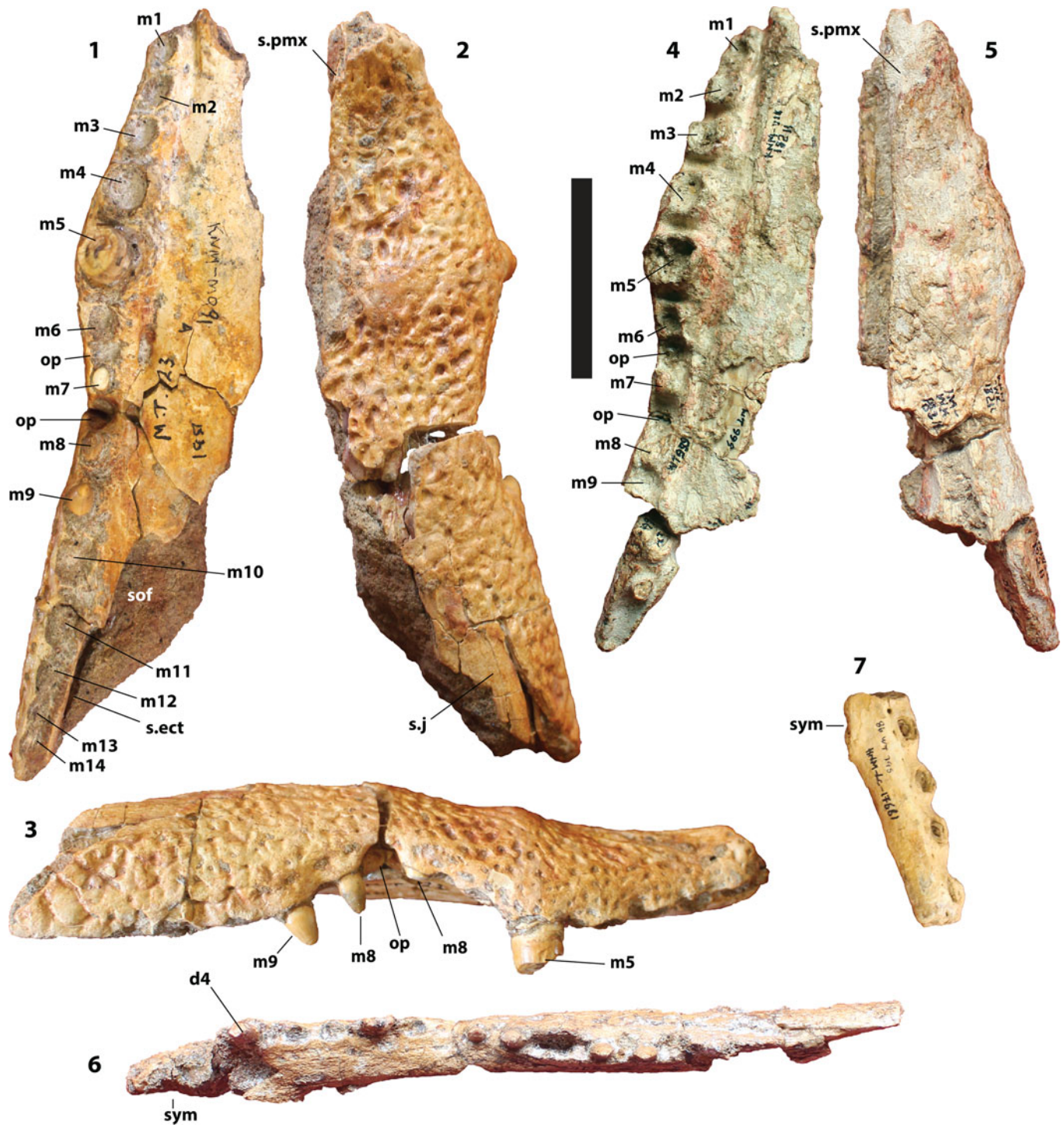


Figure 5. KNM-MO 91, *Brochuchus* sp. from Morurorot, right maxilla, ventral (1), dorsal (2), and lateral (3) view. KNM-WK 18211, *Brochuchus* sp. from Kalodirr, right maxilla, ventral (4) and dorsal (5) view. (6) KNM-WK 18210, *Brochuchus* sp. from Kalodirr, partial right dentary, dorsal view. (7) KNM-LC 17661, *Brochuchus* sp. from Loncherangan, partial right dentary, dorsal view. d4 = fourth dentary tooth/alveolus; m1–m14 = maxillary dental/alveolar positions; op = occlusal pit; s.ect = sutural surface for ectopterygoid; s.j = sutural surface for jugal; s.pmx = sutural surface for premaxilla; sof = suborbital fenestra; sym = dentary symphysis. Scale = 5 cm.

maxilla is not attached to the rest of the element, but the alveoli are surrounded by thin crests and separated by deep occlusal pits. The sutural contact for the premaxilla is preserved on the maxilla, but the dorsal premaxillary process itself is not preserved.

The symphysis of the right dentary (Fig. 5.6) extends to a level between d5 and d6. The splenial terminated behind the symphysis at the level of d7. Alveoli are widely spaced and were evidently surrounded by tall collars, although these are imperfectly preserved.

The teeth preserved with the maxilla and dentary are slender and, where the apex is preserved, conical. They bear modest unserrated mesiodistal carinae.

Brochuchus sp.

Figure 5.7.

Occurrence.—Loncherangan, west of Lake Turkana (Fig. 1). An underlying ash bed gives a radiometric age of ca. 17.5 Ma, and the mammalian fauna is similar to those of Kalodirr and Moruorot (Anyonge, 1991).

Materials.—KNM-LC 17661, partial right dentary (Fig. 5.7); KNM-LC 17672, maxilla fragment; KNM-LC 18458, left dentary fragment; KNM-LC 18460, maxilla fragment.

Remarks.—Although fragmentary, this material is sufficient to establish a form of *Brochuchus* at Loncherangan. The dentary symphysis (Fig. 5.7) extended to d6, and the alveoli are widely spaced and collared. Maxillary alveoli are likewise surrounded by collars, and there are deep occlusal pits between them. KNM-LC 17672 may preserve m5—one of the two preserved alveoli is large, and the dorsal surface is expanded in the manner of a boss over the fifth tooth root.

Comparisons

Several character states allow referral of these specimens to *Brochuchus*. The most notable is the configuration of the maxillary alveoli. They are surrounded by prominent collars and separated by deep occlusal pits (Figs. 2.3, 3.2, 3.4, 4.2, 5.1, 5.4). Most crocodylid maxillary teeth are separated by occlusal pits and surrounded by collars, but the pits of *Brochuchus* are especially deep, and their depth is accentuated by the more prominent circumalveolar collars.

These specimens share additional features with *B. pigotti*, although these may have a broader distribution among crocodylids. The nasals did not reach the external naris, for example, but this is also true for *Rimasuchus lloydi*, “*Crocodylus*” *gariopensis*, and almost any tube-snouted crocodyliform, including *Euthecodon* and *Mecistops*.

Moruorot and Kalodirr are equivalent in age and in close physical proximity, and we would expect *Brochuchus* from both to be conspecific. In both cases, the maxillae more closely resemble those of *B. pigotti*. In particular, the dorsal premaxillary process appears to be robust. Distances between alveoli on the Moruorot form are also similar to those of *B. pigotti* (Fig. 5.1). At first glance, they appear to be greater and more like those of *B. parvidens* n. sp. on the Kalodirr maxilla (Fig. 5.4), but the appearance of greater distance results from better preserved alveolar collars.

Referral of the Moruorot and Kalodirr material to *B. pigotti* might be a reasonable approach, but we are hesitant because the maxillae from Moruorot and Kalodirr appear to be somewhat narrower than in *B. pigotti*. This is most apparent on the Kalodirr maxilla, which preserves the midline palatal suture (Fig. 5.4). But this is also from a smaller individual than most maxillae from Rusinga. The difference could be ontogenetic. In the absence of a larger sample, we would rather not identify this material beyond the level of *Brochuchus*.

Results

The analysis recovered 46 equally optimal trees with a length of 214, CI excluding uninformative characters of 0.541, and an RI of 0.719 (Fig. 6). Most aspects of the optimal trees are consistent with those from previous analyses—extant *Crocodylus* forms a clade with Paleoafrican *Crocodylus* and *Crocodylus checchiai* Maccagno, 1948, and there is a well-supported Crocodylidae excluding mekosuchines and “*Crocodylus*” *megarhinus* Andrews, 1905. Moreover, as with most recent analyses using this matrix (e.g., Brochu and Storrs, 2012; Drumheller and Brochu, 2016), although there are groups including *Osteolaemus* and *Voay* (Osteolaemini) and *Euthecodon*, *Brochuchus*, and “*Crocodylus*” *gariopensis* (Euthecodonini), this analysis failed to unambiguously support a monophyletic Osteolaeminae including both groups. In fact, relationships at the root of Crocodylidae appear poorly resolved.

Dampened resolution arises in part from incomplete coding of fossils, but character conflict is also a factor. One of the topological miscreants is *Crocodylus checchiai*, which shares a derived midrostral boss (character 95) with Neotropical *Crocodylus*, but a plesiomorphic sutural configuration around the infratemporal fenestra (character 145) with Paleoafrican *Crocodylus*. Paleoafrican *Crocodylus* and *C. checchiai* are basal to extant *Crocodylus* in some optimal trees, but *C. checchiai* and sometimes Paleoafrican *Crocodylus* are closer to Neotropical *Crocodylus* in others.

The relationships among *Crocodylus*, *Mecistops*, osteolaemins, and euthecodonins are unresolved in the strict consensus tree (Fig. 6), but the number of optimal trees is small compared with number of possible resolutions of this polytomy, suggesting conserved structure masked by a strict consensus approach. *Mecistops* is closer to *Crocodylus* than to other crocodylids in the Adams consensus tree, and *Mecistops* is always closer to *Crocodylus* than to *Osteolaemus* in the individual optimal trees. This is incongruent with molecular analyses (e.g., Gatesy et al., 2003; McAliley et al., 2006; Li et al., 2007; Meganathan et al., 2010; Meredith et al., 2011; Oaks, 2011), but consistent with previous morphological analyses (e.g., Brochu, 2000a, 2007; Piras et al., 2007; Brochu and Storrs, 2012; Scheyer et al., 2013; Wu and Brinkman, 2015; Narváez et al., 2016; Massonne et al., 2019; Groh et al., 2020).

Relationships at the root of Crocodylidae collapse because Euthecodontini assumes two different positions in the set of optimal trees. This group is either closer to *M. cataphractus* (Fig. 7.1) or to Osteolaemini (Fig. 7.2). *Rimasuchus* Storrs, 2003 is always an osteolaemine, but whether it is an osteolaemin depends on the placement of euthecodontins. Bimodally labile taxa cause a loss of resolution disproportionate to the number of trees recovered (e.g., Sumrall et al., 2001; Wilkinson and Thorley, 2001; Sharkey et al., 2013), though in this case, the labile taxon is a clade rather than a single wildcard terminal.

There are compelling reasons to question a grouping of Euthecodontini (including *Mecistops* and *Crocodylus*). The three unambiguous synapomorphies supporting this clade are problematic. One is a wasp-waisted iliac blade (character 34; Brochu, 2000a). The ilium is currently unknown for *Euthecodon* and “*C.*” *gariopensis*, and although an ilium has been referred to *B. pigotti*, its blade is missing (Conrad et al., 2013).

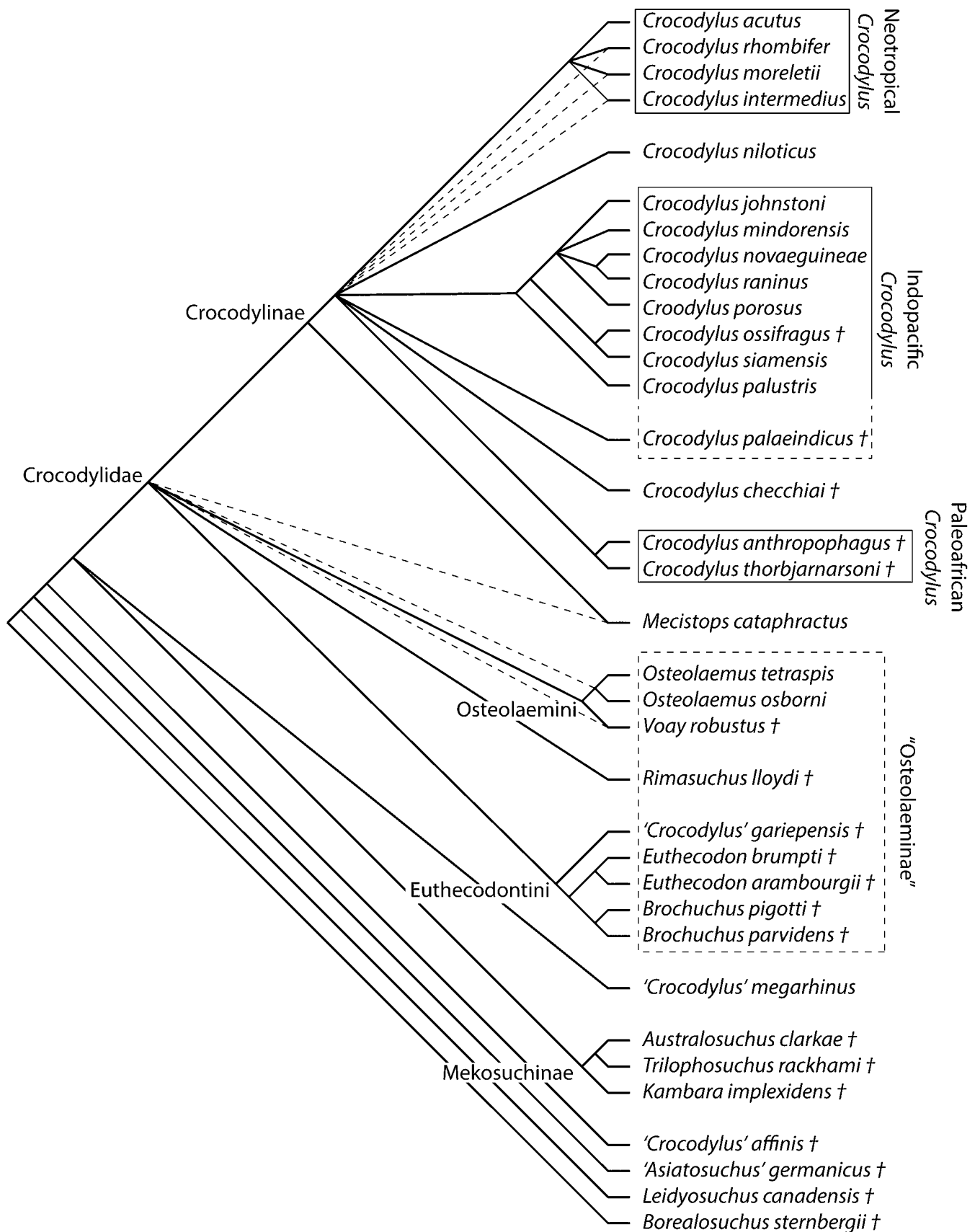


Figure 6. Adams consensus of 46 equally optimal trees (length = 214, CI = 0.54, RI = 0.719) based on maximum parsimony analysis of 33 ingroup taxa and 189 morphological characters. *Borealosuchus sternbergii* and *Leidyosuchus canadensis* were used as outgroups. Dashed branches on tree indicate collapsed resolution in a strict consensus of these trees.

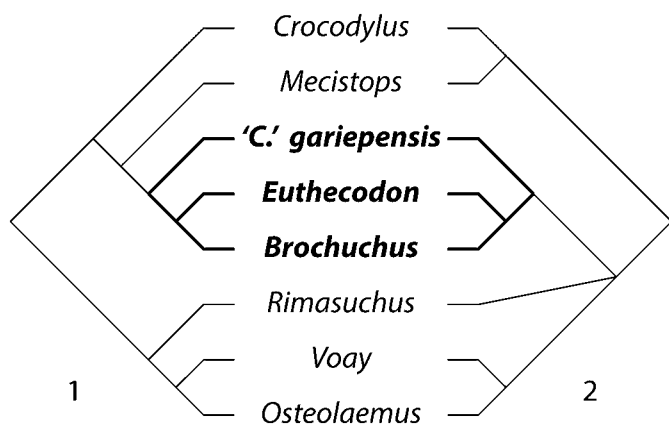


Figure 7. Alternative phylogenetic positions of Euthecodontini in the optimal trees recovered in this analysis. (1) Euthecodontini includes *Mecistops* and is closer to *Crocodylus*. (2) Euthecodontini excludes *Mecistops* and is closer to *Osteolaemus*. Euthecodontini is subordinate to Crocodylinae in (1) and Osteolaeminae in (2).

The second is the absence of ventral armor (character 42). The known absence of such armor in *Mecistops* and *Crocodylus*, along with its known presence in *Osteolaemus* and in the outgroups used in this study, does render the condition in *Crocodylus* and *Mecistops* derived; but a broader ingroup sample (including tomistomines) would have called this polarity into question, and although definitive ventral osteoderms have never been found associated with the fossil crocodylids in this analysis, we cannot say these forms lacked ventral armor.

The third unambiguous synapomorphy, passage of the surangular-angular suture along the posteroventral margin of the mandibular fenestra on the lateral surface of the mandible (character 60), has a complex distribution among crocodylids. *Euthecodon brumpti* was coded on the basis of Plio-Pleistocene specimens from Omo (where the holotype was collected) and Koobi Fora; although the derived state pertains to this material, it does not to *Euthecodon* from earlier Pliocene deposits at Kanapoi (CAB, personal observation), and the condition is unknown in *Euthecodon arambourgi* Ginsburg and Buffetaut, 1978. The derived state is also found in *Osteolaemus tetraspis*, but not *O. osborni* (Schmidt, 1919).

A fourth character state may diagnose this group—a truncated ascending surangular lamina (character 67). This refers to a structure adjacent to the posterior wall of the glenoid fossa. In most crocodylians, it extends all the way to the dorsal tip of the articular. In *Crocodylus* and *Mecistops*, the lamina is truncated and does not extend substantially beyond the adjacent dorsal surface of the mandible (Brochu, 2000a). This is true of *'C.' gariensis*, *E. brumpti*, and *B. pigotti*, but also of *Voay robustus* (Grandidier and Vaillant, 1872), and so the derived state could either pertain to Crocodylidae with a reversal in *Osteolaemus* or independent gains in *Crocodylus* + Euthecodontini and *Voay*.

Support for a basal *Mecistops* among euthecodontins is equally problematic. In some trees, this group is united by external exclusion of the nasals from the naris (character 82). But this is only unambiguously true when *Crocodylus checchiai*, which also shares this feature, is close to Neotropical *Crocodylus* and not part of a basal Paleoafrican *Crocodylus* assemblage.

Mecistops and *Euthecodon* also share an anterior surangular spur extending along the lingual margin of at least one dentary alveolus (character 62), but this is true of many tube-snouted crocodylians (Brochu, 1997) and is unknown in *Brochuchus* or *'C.' gariensis*.

In trees uniting osteolaemins and euthecodontins, osteolaemine monophyly is supported by three unambiguous synapomorphies—prominent preorbital ridges (character 97); a thin bony crest, or “neck,” surrounding the internal choana (character 123); and extension of the squamosal over the dorsal surface of the quadrate ramus (character 159). This last character was discussed and figured by Brochu (2007). Expanded sampling of these taxa suggests more variable expression than previously thought, and continued use of this character may not be advisable.

In all optimal trees, Euthecodontini (excluding *Mecistops*) is supported by an anterodorsally opening external naris (character 81). The naris ancestrally opens dorsally in crocodylids, and this is the condition in *Crocodylus*, *Mecistops*, and osteolaemins. In euthecodontins, the anterior margin of the naris is depressed relative to the posterior margin. Euthecodontini is supported by exclusion of the nasals from the naris when the group is within Osteolaeminae, and by preorbital ridges when linked to *Mecistops* and *Crocodylus*.

Euthecodon and *B. pigotti* share a linear frontoparietal suture (character 151). The suture is anteriorly concave in most crocodylids, including *R. lloydi* and *V. robustus*, though it is also linear in all forms of *Osteolaemus*. The absence of a septum within the internal choana (character 125), evident in both species of *Euthecodon* and in *B. pigotti*, may also diagnose a *Euthecodon* + *Brochuchus* clade, although this is also true for *Crocodylus thorbjarnarsoni*.

In all trees, *B. pigotti* and *B. parvidens* n. sp. unambiguously share a notch on the dorsal surface of the premaxilla posterolateral to the external naris (character 86). Beyond *Brochuchus* among crocodylians, such a notch is only seen in alligatoroids (Brochu, 1999; Piras and Buscalioni, 2006). *Brochuchus pigotti* is characterized by a wedge-shaped palatine process (character 116) and tall, prominent posterior pterygoid processes lateral to the eustachian foramina (character 171). Neither of these could be assessed for *B. parvidens* n. sp., and the tall pterygoid processes are a reversal to the plesiomorphic eusu-chian condition.

Comparison with other studies.—Conrad et al. (2013) and some subsequent analyses (e.g., Lee and Yates, 2018; Groh et al., 2020) recovered *Brochuchus* as an osteolaemine, but *Euthecodon* as a close relative of *Mecistops*, with *Euthecodon* + *Mecistops* closer to *Crocodylus* than to *Osteolaemus*. This is not surprising because *Euthecodon* and *Mecistops* are both derived crocodylids with long, slender snouts, and some of the characters used in crocodyliform phylogenetics are correlated with this condition (e.g., Clark, 1994; Pol and Gasparini, 2009; Iijima, 2017; Drumheller and Wilberg, 2020; Groh et al., 2020). Moreover, because Lee and Yates (2018) drew much of their information for *B. pigotti* from Conrad et al. (2013), whose analysis separated *B. pigotti* from *Euthecodon*, a similar outcome would be expected.

Although the matrix used here and that used by Conrad et al. (2013) are both based on the data set of Brochu and Storrs

(2012), there are several differences. Conrad et al. (2013) included two additional terminals—what they called “*Crocodylus*” *niloticus* from the Pliocene of Kanapoi and a specimen from the late Miocene of Lothagam (KNM-LT 24081), both of which fell out as related to *Osteolaemus* in their analyses. This material is all referable to *Crocodylus* (Brochu and Storrs, 2012; Brochu, 2020).

Brochuchus and *Euthecodon* take different positions in Conrad et al. (2013) and our analysis because of different codings for *B. pigotti* in the two studies. We replaced ours for theirs, and in the absence of their interpretations of Kanapoi and Lothagam *Crocodylus* (and in the absence of *B. parvidens* n. sp.), we replicated their results. Many of the differences reflect a more conservative approach to character assessment in this study; in several cases, Conrad et al. (2013) made a determination we were unwilling to make. Others indicate differences of opinion about the character state preserved in the material. All such differences are indicated in the supplemental data.

Three characters appear to be most responsible for the different outcomes. First, Conrad et al. (2013) agreed with Brochu (2007) and Brochu and Storrs (2012) in believing the nasals contributed to the narial rim in *B. pigotti*. Exclusion of the nasals from the naris thus links *Euthecodon* and *Mecistops* to the exclusion of *Brochuchus* in their study. Second, Conrad et al. (2013) interpreted the surangular-angular suture as intersecting the mandibular fenestra posteriorly rather than posteroventrally. Whether the derived condition (posteroventral intersection) actually pertains to *Euthecodon* as a whole is an open question (see above), but it does link *Euthecodon* and *Mecistops* in their study. We disagree that the specimens available are sufficient to make a determination for *B. pigotti*.

Third, Conrad et al. (2013) coded *B. pigotti* as having an incisive foramen that abuts the premaxillary toothrow (character 89). This is actually not the case in either species of *Brochuchus*, but it would have linked *B. pigotti* with *Euthecodon*, which has this condition. Lee and Yates (2018) further assigned this state (incorrectly) to other crocodyloids, including *M. cataphractus*, all extant species of *Crocodylus* except *C. acutus* Cuvier, 1807, Paleoafrican *Crocodylus*, both *Osteolaemus*, *Kambara* Willis et al., 1993, and “*Crocodylus*” *megarhinus*. In all of these except “*C.*” *megarhinus*, the incisive foramen is demonstrably situated farther back on the palate and does not abut the premaxillary tooth row; none of the specimens of “*C.*” *megarhinus* has a completely preserved incisive foramen, and the state cannot be assessed. Lee and Yates (2018) also miscoded *B. pigotti* as unknown for the extent of the dorsal surangular lamina—nearly flush with the surrounding dorsal mandibular surface rather than extending to the dorsal tip of the glenoid fossa—which further diminished similarities between *Brochuchus* and *Euthecodon* in their analysis.

New characters added by Lee and Yates (2018) supporting a close relationship between *Mecistops* and *Euthecodon* are generally correlated with having a long, slender snout, such as deep occlusal sulci on the lateral margin of the premaxilla. Slender-snouted forms, such as *Euthecodon* and *Mecistops*, generally do have deeper sulci in the premaxillary outline, especially between p1 and p2 or p3. There is less room in the rostrum for occlusal pits between alveoli, and so the dentary teeth occlude externally to a greater degree. Nearly all slender-snouted forms

in their analysis were coded as having this condition. It is unclear, though, why Lee and Yates (2018) scored *Brochuchus* this way, as the condition in *Brochuchus* is indistinguishable from that of the majority of generalized crocodyliforms.

Discussion

Differences between *Brochuchus parvidens* n. sp. and *B. pigotti* are minor. Although some might regard them as insufficient to support species-level separation, we now know that many extant crocodylids are cryptic complexes of two or more species with very similar morphology (e.g., Eaton et al., 2009; Meredith et al., 2011; Smolensky, 2015; Milián-García et al., 2018; Shirley et al., 2018; Murray et al., 2019). Osteological distinctions between these, where documented, are very subtle. Differences between *B. pigotti* and *B. parvidens* n. sp. may be modest, but they are consistent among multiple specimens of similar size and can be used to distinguish morphologically distinct assemblages.

One is tempted to regard *Brochuchus parvidens* n. sp. as part of a continuously evolving lineage, also including *B. pigotti*. The two forms are very similar, and they occur in close geographic proximity; indeed, isolation of the Lake Turkana depositional basin postdates the Miocene, and sites proximate to present-day Lake Victoria and Lake Turkana might have been fluvially connected in the early to middle Miocene (e.g., Feibel, 2011; Macgregor, 2015). This might even be seen as the most parsimonious explanation, and depending on the species concept one chooses to adopt (e.g., Polly, 1997; Hunt and Rabosky, 2014; Allmon, 2016; Haug and Haug, 2017), *B. parvidens* n. sp. would be a late-occurring form of *B. pigotti*.

Such interpretations—that fossils in stratigraphic sequence reflect discontinuous sampling of a continuous lineage—may no longer be tenable. In part, this arises from the ongoing discovery of cryptic species complexes among crocodylians. Because geographic ranges of species within these complexes, including Neoafrican *Crocodylus*, are known to have shifted during historical times (Hekkala et al., 2011), we cannot assume that the crocodiles found in a particular depositional sequence represent an indigenous lineage (Brochu and Sumrall, 2020). *Brochuchus parvidens* n. sp. and *B. pigotti* may indeed be end members of a continuum, but other explanations cannot be discounted.

However one wishes to perceive the underlying evolutionary pattern, this study extends the range of *Brochuchus* into the middle Miocene. Among generalized crocodylids, neither *Crocodylus* nor anything unambiguously more closely related to it than to *Osteolaemus* has been found prior to the late Miocene in the region. This is consistent with previous suggestions that endemic crocodylid faunas were replaced by *Crocodylus* at some point during the Miocene (Brochu, 2007; Brochu and Storrs, 2012).

But the details have grown murky. Based on our phylogenetic analysis, a division between osteolaemines, *Mecistops*, and *Crocodylus* among late Cenozoic African crocodylids (e.g., Brochu, 2007) may be an oversimplification. Two distinct groups of erstwhile osteolaemines can be recognized—one including *Osteolaemus*, another including *Euthecodon*—but whether these are closely related is ambiguous. We believe the characters supporting osteolaemine affinities for euthecodontins

are more compelling, but without additional character evidence, we cannot reject equally parsimonious alternatives. This, along with conflicting phylogenetic hypotheses for *Mecistops*, makes biogeographic assessment difficult.

Nevertheless, there appears to be a fundamental difference in crocodylid faunas between the last known appearance of *Brochuchus* at 15 Ma and the first known appearance of *Crocodylus* at ca. 7 Ma. This interval in the EARS preserves profound climatic and tectonic change. A period of increased basaltic volcanism began ca. 12 Ma in the eastern branch of the EARS (Rooney, 2020). Continuous forest cover began to give way to open grasslands and savannahs at this time, largely in response to drier conditions (Jacobs et al., 2010; Feibel, 2011; Feakins et al., 2013; Wichura et al., 2015; Linder, 2017). Unlike *Crocodylus*, modern *Osteolaemus* is found only in forested wetlands (Eaton, 2010). If these ecological preferences apply to putative extinct relatives of *Osteolaemus*, the change from osteolaemine- or euthecodontin-dominated to *Crocodylus*-dominated crocodylid faunas in the EARS may reflect changes in vegetation cover. These changes are often thought to have played a role in human origins (e.g., Bonnefille, 2010; Mearns et al., 2015). If so, then evolutionary pathways followed by early humans and crocodylids may have been linked to similar causal factors.

Such conclusions are preliminary. Further testing requires improved sampling in three areas. First, additional crocodylid material from the early and middle Miocene of the EARS must be described. *Brochuchus* is the only generalized crocodylid currently known from this interval, but it was a comparatively small animal, and larger generalized crocodylids may have occurred in the region at the time. Second, discovery and description of crocodylids between 7 and 15 Ma is needed to more precisely document the timing and manner of Miocene crocodylid replacement. Third, and most importantly, additional morphological characters expressing variation among late Cenozoic African crocodylids are needed to clarify the phylogeny of this assemblage.

Acknowledgments

The preparation and collections staff at the National Museums of Kenya in Nairobi are acknowledged for superlative assistance and friendship. L. Steel, S. Maidment, D. Schwarz, and N. den Ouden are thanked for collections access. Interactions with K. McNulty, C. Ward, J.M. Plavcan, T. Lehmann, A. Grossman, E. Hekkala, C. Liutkus-Pierce, J. Conrad, and M. Leakey were especially helpful in better understanding regional stratigraphy, paleoenvironments, and phylogenetic issues. Comments by two anonymous reviewers and the editor improved this contribution. This work was supported by NSF DEB 1257786 (to CAB) and the Leakey Foundation (to CAB and SKD).

Accessibility of supplemental data

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.15dv41nvf>.

References

Allmon, W.D., 2016. Studying species in the fossil record: a review and recommendations for a more unified approach, in Allmon, W.D., and Yacobucci,

- M.M., eds., *Species and Speciation in the Fossil Record*: Chicago, University of Chicago Press, p. 59–120.
- Andrews, C.W., 1905. Notes on some new Crocodylia from the Eocene of Egypt: *Geological Magazine* (n.s.), v. 2, p. 481–484.
- Andrews, P., Meyer, G.E., Pilbeam, D.R., Van Couvering, J.A., and Van Couvering, J.A.H., 1981. The Miocene fossil beds of Maboko Island, Kenya: geology, age, taphonomy and palaeontology: *Journal of Human Evolution*, v. 10, p. 35–48.
- Anyonge, W., 1991. Fauna from a new lower Miocene locality west of Lake Turkana, Kenya: *Journal of Vertebrate Paleontology*, v. 11, p. 378–390.
- Arney, I.D., Maclatchy, L., Benefit, B.R., McCrossin, M.L., and Kingston, J.D., 2018. Environmental change and African early to middle Miocene catarrhine evolution: *American Journal of Physical Anthropology*, v. 165, p. 12–13.
- Arambourg, C., 1947. Contribution à l'étude géologique et paléontologique du Bassin du Lac Rodolphe et de la Basse Vallée de l'Omo, in Arambourg, C., ed., *Mission Scientifique de l'Omo 1932–1933, Tome I: Géologie–Anthropologie*: Paris, Muséum National d'Histoire Naturelle, p. 231–562.
- Benefit, B.R., 1999. *Victoriapithecus*: the key to Old World monkey and catarrhine origins: *Evolutionary Anthropology*, v. 7, p. 155–174.
- Bennett, E.T., 1835. *Crocodylus leptorhynchus*: *Proceedings of the Zoological Society of London*, v. 3, p. 128–132.
- Bonnefille, R., 2010. Cenozoic vegetation, climate changes and hominid evolution in tropical Africa: *Global and Planetary Change*, v. 72, p. 390–411.
- Boschetto, H.B., Brown, F.H., and McDougall, I., 1992. Stratigraphy of the Lothidok Range, northern Kenya, and K/Ar ages of its Miocene primates: *Journal of Human Evolution*, v. 22, p. 47–71.
- Brochu, C.A., 1997. Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*: *Systematic Biology*, v. 46, p. 479–522.
- Brochu, C.A., 1999. Phylogeny, systematics, and historical biogeography of Alligatoroidea: *Society of Vertebrate Paleontology Memoir*, v. 6, p. 9–100.
- Brochu, C.A., 2000a. *Borealosuchus* (Crocodylia) from the Paleocene of Big Bend National Park, Texas: *Journal of Paleontology*, v. 74, p. 181–187.
- Brochu, C.A., 2000b. Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record: *Copeia*, v. 2000, p. 657–673.
- Brochu, C.A., 2001. Crocodylian snouts in space and time: phylogenetic approaches toward adaptive radiation: *American Zoologist*, v. 41, p. 564–585.
- Brochu, C.A., 2003. Phylogenetic approaches toward crocodylian history: *Annual Review of Earth and Planetary Sciences*, v. 31, p. 357–397.
- Brochu, C.A., 2006. A new miniature horned crocodile from the Quaternary of Aldabra Atoll, western Indian Ocean: *Copeia*, v. 2006, p. 149–158.
- Brochu, C.A., 2007. Morphology, relationships and biogeographic significance of an extinct horned crocodile (Crocodylia, Crocodylidae) from the Quaternary of Madagascar: *Zoological Journal of the Linnean Society*, v. 150, p. 835–863.
- Brochu, C.A., 2020. Pliocene crocodiles from Kanapoi, Turkana Basin, Kenya: *Journal of Human Evolution*, v. 140, p. 102410.
- Brochu, C.A., and Storrs, G.W., 2012. A giant crocodile from the Plio-Pleistocene of Kenya, the phylogenetic relationships of Neogene African crocodylines, and the antiquity of *Crocodylus* in Africa: *Journal of Vertebrate Paleontology*, v. 32, p. 587–602.
- Brochu, C.A., and Sumrall, C.D., 2020. Modern cryptic species and crocodylian diversity in the fossil record: *Zoological Journal of the Linnean Society*, v. 189, p. 700–711.
- Brochu, C.A., Njau, J.K., Blumenshine, R.J., and Densmore, L.D., 2010. A new horned crocodile from the Plio-Pleistocene hominid sites at Olduvai Gorge, Tanzania: *PLoS One*, v. 5, p. e9333.
- Buffetaut, E., 1979. Présence du crocodylien *Euthecodon* dans le Miocène inférieur d'Ombo (Golfe de Kavirondo, Kenya): *Bulletin de la Société Géologique de France*, v. 21, p. 321–322.
- Buffetaut, E., 1984. On the occurrence of *Crocodylus pigotti* in the Miocene of Saudi Arabia, with remarks on the origin of the Nile crocodile: *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, v. 1984, p. 513–520.
- Busbey, A.B., 1994. The structural consequences of skull flattening in crocodylians., in Thomason, J.J., ed., *Functional Morphology in Vertebrate Paleontology*: New York, Cambridge University Press, p. 173–192.
- Clark, J.M., 1994. Patterns of evolution in Mesozoic Crocodyliformes, in Fraser, N.C., and Sues, H.-D., eds., *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*: New York, Cambridge University Press, p. 84–97.
- Conrad, J.A., Jenkins, K., Lehmann, T., Manthi, F.K., Peppe, D.J., Nightingale, S., Cossette, A., Dunsforth, H.M., Harcourt-Smith, W.E.H., and McNulty, K.P., 2013. New specimens of '*Crocodylus*' *pigotti* (Crocodylidae) from Rusinga Island, Kenya, and generic reallocation of the species: *Journal of Vertebrate Paleontology*, v. 33, p. 629–646.
- Cope, E.D., 1861. List of the Recent species of emydosaurian reptiles in the Museum of the Academy of Natural Sciences: *Proceedings of the Academy of Natural Sciences of Philadelphia*, v. 12, p. 549–550.
- Cuvier, G., 1807. Sur les différentes espèces de crocodiles vivans et sur leurs caractères distinctifs: *Annales du Muséum d'Histoire Naturelle de Paris*, v. 10, p. 8–66.

- Cuvier, G., 1824, Recherches Sur les Ossemens Fossiles, où l'On Rétablit les Caractères de Plusieurs Animaux Dont les Révolutions du Globe Ont Détruit les Espèces: Paris, G. Doufour et Ed. D'Ocagne, v. 5 (pt. 2), 547 p.
- Delfino, M., and De Vos, J., 2010, A revision of the Dubois crocodylians, *Gavialis bengawanicus* and *Crocodylus ossifragus*, from the Pleistocene *Homo erectus* beds of Java: *Journal of Vertebrate Paleontology*, v. 30, p. 427–441.
- Drumheller, S.K., and Brochu, C.A., 2016, Phylogenetic taphonomy: a statistical and phylogenetic approach for exploring taphonomic patterns in the fossil record using crocodylians: *Palaeos*, v. 31, p. 463–478.
- Drumheller, S.K., and Wilberg, E.W., 2020, A synthetic approach for assessing the interplay of form and function in the crocodyliform snout: *Zoological Journal of the Linnean Society*, v. 188, p. 507–521.
- Dubois, E., 1908, Das Geologische alter der Kendeng-oder Trinilfauna: *Tijdschrift van het Koninklijk Nederlandsch Aardrijkskundig Genootschap*, v. 25, p. 1235–1270.
- Eaton, M.J., 2010, Dwarf crocodile *Osteolaemus tetraspis*, in Manolis, S.C., and Stevenson, C., eds., Crocodiles: Status Survey and Conservation Action Plan: Darwin, Australia, IUCN Crocodile Specialist Group, p. 127–132.
- Eaton, M.J., Martin, A., Thorbjarnarson, J., and Amato, G., 2009, Species-level diversification of African dwarf crocodiles (genus *Osteolaemus*): a geographic and phylogenetic perspective: *Molecular Phylogenetics and Evolution*, v. 50, p. 496–506.
- Feakins, S.J., Levin, N.E., Liddy, H.M., Sieracki, A., Eglinton, T.I., and Bonnefille, R., 2013, Northeast African vegetation change over 12 m.y.: *Geology*, v. 41, p. 295–298.
- Feibel, C.S., 2011, A geological history of the Turkana Basin: *Evolutionary Anthropology*, v. 20, p. 206–216.
- Feibel, C.S., and Brown, F.H., 1991, Age of the primate-bearing deposits on Maboko Island, Kenya: *Journal of Human Evolution*, v. 21, p. 221–225.
- Fourtau, R., 1918, Contribution à l'étude des vertèbres miocènes de l'Égypte: Cairo, Egypt Survey Department, 99 p.
- Fourtau, R., 1920, Supplément, in Fourtau, R., ed., Contribution à l'étude des vertèbres miocènes de l'Égypte: Cairo, Egypt Survey Department, p. 111–121.
- Gatesy, J., Amato, G., Norell, M., Desalle, R., and Hayashi, C., 2003, Combined support for wholesale taxic atavism in gavialine crocodylians: *Systematic Biology*, v. 52, p. 403–422.
- Geoffroy Saint-Hilaire, E., 1807, Description de deux crocodiles qui existent dans le Nil, comparés au crocodile de Saint-Domingue: *Annales du Muséum d'Histoire Naturelle*, v. 10, p. 67–86.
- Geraads, D., McCrossin, M.L., and Benefit, B.R., 2012, A new rhinoceros, *Victoriaceros kenyensis* gen. et sp. nov., and other Perissodactyla from the middle Miocene of Maboko, Kenya: *Journal of Mammalian Evolution*, v. 19, p. 57–75.
- Gilmore, C.W., 1910, *Leidyosuchus sternbergii*, a new species of crocodile from the Cretaceous Beds of Wyoming: *Proceedings of the United States National Museum*, v. 38, p. 485–502.
- Ginsburg, L., and Buffetaut, E., 1978, *Euthecodon arambourgi* n. sp., et l'évolution du genre *Euthecodon*, crocodilien du Néogène d'Afrique: *Géologie Méditerranéenne*, v. 5, p. 291–302.
- Gmelin, J., 1789, *Linnei Systema Naturae*: Leipzig, G. E. Beer, 1057 p.
- Granddier, A., and Vaillant, L., 1872, Sur le crocodile fossile d'Amboulinstare (Madagascar): *Comptes Rendus de l'Académie des Sciences de Paris*, v. 75, p. 150–151.
- Gray, J.E., 1844, Catalogue of Tortoises, Crocodylians, and Amphisbaenians in the Collection of the British Museum: London, British Museum (Natural History), 80 p.
- Groh, S.S., Upchurch, P., Barrett, P.M., and Day, J.J., 2020, The phylogenetic relationships of neosuchian crocodiles and their implications for the convergent evolution of the longirostrine condition: *Zoological Journal of the Linnean Society*, v. 188, p. 473–506.
- Haug, J.T., and Haug, C., 2017, Species, populations and morphotypes through time—challenges and possible concepts: *Bulletin de la Société Géologique de France*, v. 188, p. 1–14.
- Hekkala, E., Shirley, M.H., Amato, G., Austin, J.D., Charter, S., Thorbjarnarson, J., Vliet, K.A., Houck, M.L., Desalle, R., and Blum, M.J., 2011, An ancient icon reveals new mysteries: mummy DNA resurrects a cryptic species within the Nile crocodile: *Molecular Ecology*, v. 20, p. 4199–4215.
- Hunt, G., and Rabosky, D.L., 2014, Phenotypic evolution in fossil species: pattern and process: *Annual Review of Earth and Planetary Sciences*, v. 42, p. 421–441.
- Iijima, M., 2017, Assessment of trophic ecomorphology in non-alligatoroid crocodylians and its adaptive and taxonomic implications: *Journal of Anatomy*, v. 231, p. 192–211.
- Jacobs, B.F., Pan, A.D., and Scotese, C.R., 2010, A review of the Cenozoic vegetation history of Africa, in Werdelin, L. and Sanders, W.J., eds., *Cenozoic Mammals of Africa*: Berkeley, University of California Press, p. 57–72.
- Joleaud, M.L., 1920, Sur la présence d'un Gavialidé du genre *Tomistoma* dans le Pliocène d'eau douce de l'Éthiopie: *Comptes Rendus de l'Académie des Sciences de Paris*, v. 170, p. 816–818.
- Joleaud, M.L., 1930, Les crocodyliens du pliocène d'eau douce de Omo, *Livre Jubilaire, Centenaire de la Société Géologique de France*: Paris, Société Géologique de France, p. 411–429.
- Kofron, C.P., 1992, Status and habitats of the three African crocodiles in Liberia: *Journal of Tropical Ecology*, v. 8, p. 265–273.
- Kotsakis, A., Delfino, M., and Piras, P., 2004, Italian Cenozoic crocodylians: taxa, timing and palaeobiogeographic implications: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 210, p. 67–87.
- Lambe, L.M., 1907, On a new crocodylian genus and species from the Judith River Formation of Alberta: *Transactions of the Royal Society of Canada*, v. 4, p. 219–244.
- Laurenti, J.N., 1768, Specimen Medicum, Exhibens Synopsin Reptilium Emendatum cum Experimentatis Circa Venena et Antiodota Reptilium Austriaeorum: Vienna, J. T. de Trattner, 214 p.
- Lee, M.S.Y., and Yates, A.M., 2018, Tip-dating and homoplasy: reconciling the shallow molecular divergences of modern gharials with their long fossil record: *Proceedings of the Royal Society of London B*, v. 285, p. 20181071.
- Li, Y., Wu, X.-B., Ji, X.-F., Yan, P., and Amato, G., 2007, The complete mitochondrial genome of salt-water crocodile (*Crocodylus porosus*) and phylogeny of crocodylians: *Journal of Genetics and Genomics*, v. 34, p. 119–128.
- Linder, H.P., 2017, East African Cenozoic vegetation history: *Evolutionary Anthropology*, v. 26, p. 300–312.
- Llinás Agrasar, E., 2004, Crocodile remains from the Burdigalian (lower Miocene) of Gebel Zelten (Libya): *Geodiversitas*, v. 26, p. 309–321.
- Maccagno, A.M., 1948, Descrizione di una nuova specie di "*Crocodylus*" del giacimento di Sahabi (Sirtica): *Atti della Reale Accademia Nazionale dei Lincei: Memorie della Classe di Scienze fisiche, Matematiche e Naturale*, Serie 8, v. 1, p. 63–96.
- Macgregor, D., 2015, History of the development of the East African Rift System: a series of interpreted maps through time: *Journal of African Earth Sciences*, v. 101, p. 232–252.
- Marean, C.W., Anderson, R.J., Bar-Matthews, M., Braun, K., Cawthra, H.C., Cowling, R.M., Engelbrecht, F., Esler, K.J., Fisher, E., Franklin, J., Hill, K., Janssen, M., Potts, A.J., and Zahn, R., 2015, A new research strategy for integrating studies of paleoclimate, paleoenvironment, and paleoanthropology: *Evolutionary Anthropology*, v. 24, p. 62–72.
- Massonne, T., Vasilyan, D., Rabi, M., and Böhme, M., 2019, A new alligatoroid from the Eocene of Vietnam highlights an extinct Asian clade independent from extant *Alligator sinensis*: *PeerJ*, v. 7, p. e7562.
- Mayr, G., 2014, On the middle Miocene avifauna of Maboko Island, Kenya: *Geobios*, v. 47, p. 133–146.
- McAliley, L.R., Willis, R.E., Ray, D.A., White, P.S., Brochu, C.A., and Densmore, L.D., 2006, Are crocodiles really monophyletic?—evidence for subdivisions from sequence and morphological data: *Molecular Phylogenetics and Evolution*, v. 39, p. 16–32.
- McCrossin, M.L., Benefit, B.R., Gitau, S.R., Palmer, A., and Blue, K., 1998, Fossil evidence for the origins of terrestriality among Old World monkeys and apes, in Fleagle, J.G., McHenry, H.M., and Rosenberger, A.L., eds., *Primate Locomotion: Recent Advances*: New York, Plenum Press, p. 353–376.
- Meganathan, P.R., Dubey, B., Batzer, M.A., Ray, D.A., and Haque, I., 2010, Molecular phylogenetic analyses of genus *Crocodylus* (Eusuchia, Crocodylia, Crocodylidae) and the taxonomic position of *Crocodylus porosus*: *Molecular Phylogenetics and Evolution*, v. 57, p. 393–402.
- Meredith, R.W., Hekkala, E.R., Amato, G., and Gatesy, J., 2011, A phylogenetic hypothesis for *Crocodylus* (Crocodylia) based on mitochondrial DNA: evidence for a trans-Atlantic voyage from Africa to the New World: *Molecular Phylogenetics and Evolution*, v. 60, p. 183–191.
- Milián-García, Y., Castellanos-Labarena, J., Russello, M.A., and Amato, G., 2018, Mitogenomic investigation reveals a cryptic lineage of *Crocodylus* in Cuba: *Bulletin of Marine Science*, v. 94, p. 329–343.
- Müller, L., 1923, *Crocodylus siamensis* Schneid. und *Crocodylus ossifragus* Dubois: *Palaeontologia Hungarica*, v. 1, p. 109–114.
- Murray, C.M., Russo, P., Zorrilla, A., and McMahan, C.D., 2019, Divergent morphology among populations of the New Guinea crocodile, *Crocodylus novaeguineae* (Schmidt, 1928): diagnosis of an independent lineage and description of a new species: *Copeia*, v. 2019, p. 517–523.
- Narváez, I., Brochu, C.A., Escaso, F., Pérez-García, A., and Ortega, F., 2016, New Spanish Late Cretaceous eusuchian reveals the synchronic and sympatric presence of two allodaposuchids: *Cretaceous Research*, v. 65, p. 112–125.
- Oaks, J.R., 2011, A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles: *Evolution*, v. 65, p. 3285–3297.
- Pickford, M., 1981, Preliminary Miocene mammalian biostratigraphy for western Kenya: *Journal of Human Evolution*, v. 10, p. 73–97.

- Pickford, M., 1983. Sequence and environments of the lower and middle Miocene hominoids of western Kenya, in Ciochon, R.L. and Corruccini, R.S., eds., *New Interpretations of Ape and Human Ancestry*: New York, Plenum Press, p. 421–439.
- Pickford, M., 2003. A new species of crocodile from Early and Middle Miocene deposits of the Lower Orange River Valley, Namibia, and the origins of the Nile crocodile (*Crocodylus niloticus*): *Geological Survey of Namibia Memoir*, v. 19, p. 51–65.
- Pierce, S., Angielczyk, K.D., and Rayfield, E.J., 2008. Patterns of morphospace occupation and mechanical performance in extant crocodylian skulls: a combined geometric morphometric and finite element modeling approach: *Journal of Morphology*, v. 269, p. 840–864.
- Piras, P., and Buscalioni, A.D., 2006. *Diplocynodon muelleri* comb. nov., an Oligocene diplocynodontine alligatoroid from Catalonia (Ebro Basin, Lleida Province, Spain): *Journal of Vertebrate Paleontology*, v. 26, p. 608–620.
- Piras, P., Delfino, M., Del Favero, L., and Kotsakis, T., 2007. Phylogenetic position of the crocodylian *Megadontosuchus arduini* and tomistomine palaeobiogeography: *Acta Palaeontologica Polonica*, v. 52, p. 315–328.
- Piras, P., Colangelo, P., Adams, D.C., Buscalioni, A.D., Cubo, J., Kotsakis, A., Meloro, C., and Raia, P., 2010. The *Gaviais-Tomistoma* debate: the contribution of skull ontogenetic allometry and growth trajectories to the study of crocodylian relationships: *Evolution and Development*, v. 12, p. 568–579.
- Pol, D., and Gasparini, Z., 2009. Skull anatomy of *Dakosaurus andintiensis* (Thalattosuchia: Crocodylomorpha) and the phylogenetic position of Thalattosuchia: *Journal of Systematic Palaeontology*, v. 7, p. 163–197.
- Polly, P.D., 1997. Ancestry and species definition in paleontology: a stratocladistic analysis of Paleocene–Eocene Viverravidae (Mammalia, Carnivora) from Wyoming: *Contributions from the Museum of Geology, University of Michigan*, v. 30, p. 1–53.
- Retallack, G.J., Wynn, J.G., Benefit, B.R., and McCrossin, M.L., 2002. Paleosols and paleoenvironments of the middle Miocene, Maboko Formation, Kenya: *Journal of Human Evolution*, v. 42, p. 659–703.
- Riley, J., and Huchzermeyer, F.W., 1999. African dwarf crocodiles in the Likouala swamp forests of the Congo Basin: habitat, density, and nesting: *Copeia*, v. 1999, p. 313–320.
- Rooney, T.O., 2020. The Cenozoic magmatism of East Africa: Part II—rifting of the mobile belt: *Lithos*, v. 360–361, p. 105291.
- Sadleir, R.W., and Makovicky, P.J., 2008. Cranial shape and correlated characters in crocodylian evolution: *Journal of Evolutionary Biology*, v. 21, p. 1578–1596.
- Scheyer, T.M., Aguilera, O.A., Delfino, M., Fortier, D.C., Carlini, A.A., Sánchez, R., Carrillo-Briceño, J.D., Quiroz, L., and Sánchez-Villagra, M.R., 2013. Crocodylian diversity peak and extinction in the late Cenozoic of the northern Neotropics: *Nature Communications*, v. 4, p. 1907.
- Schmidt, K.P., 1919. Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo expedition, 1909–1915. I. Turtles, crocodiles, lizards, and chameleons: *Bulletin of the American Museum of Natural History*, v. 39, p. 385–624.
- Schmidt, K.P., 1928. A new crocodile from New Guinea: *Field Museum of Natural History Zoological Series*, v. 12, p. 176–181.
- Schneider, J.G., 1801. *Historiae Amphibiorum Naturalis et Literariae Fasciculus Secundus*: Jena, F. Frommann, 364 p.
- Sharkey, M.J., Stoelb, S., Miranda-Esquivel, D.R., and Sharanowski, B.J., 2013. Weighted compromise trees: a method to summarize competing phylogenetic hypotheses: *Cladistics*, v. 29, p. 309–314.
- Shirley, M.H., Carr, A.N., Nestler, J.H., Vliet, K.A., and Brochu, C.A., 2018. Systematic revision of the living African slender-snouted crocodiles (*Mecistops* Gray, 1844): *Zootaxa*, v. 4504, p. 151–193.
- Smolensky, N.L., 2015. Co-occurring cryptic species pose challenges for conservation: a case study of the African dwarf crocodile (*Osteolaemus* spp.) in Cameroon: *Oryx*, v. 49, p. 584–590.
- Smolensky, N.L., Hurtado, L.A., and Fitzgerald, L.A., 2015. DNA barcoding of Cameroon samples enhances our knowledge on the distributional limits of putative species of *Osteolaemus* (African dwarf crocodiles): *Conservation Genetics*, v. 16, p. 235–240.
- Storrs, G.W., 2003. Late Miocene–Early Pliocene crocodylian fauna of Lothagam, southwest Turkana Basin, Kenya, in Leakey, M.G., and Harris, J.M., eds., *Lothagam: The Dawn of Humanity in Eastern Africa*: New York, Columbia University Press, p. 137–159.
- Sumrall, C.D., Brochu, C.A., and Merck, J.W., 2001. Global lability, regional resolution, and majority-rule consensus bias: *Paleobiology*, v. 27, p. 254–261.
- Swofford, D.L., 2002. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*: Sunderland, MA, Sinauer Associates.
- Tchernov, E., 1986. *Evolution of the crocodiles in East and North Africa*: Paris, CNRS, 65 p.
- Tchernov, E., and Couvering, J.V., 1978. New crocodiles from the Early Miocene of Kenya: *Palaeontology*, v. 21, p. 857–867.
- Van Couvering, J.A.H., and Van Couvering, J.A., 1976. Early Miocene mammal fossils from East Africa: aspects of geology, faunistics and paleoecology, in Isaac, G.L., and McCown, E., eds., *Human Origins: Louis Leakey and the East African Evidence*: Menlo Park, California, W.A. Benjamin Press, p. 155–207.
- Waitkuwait, W.E., 1986. Contribution à l'étude des crocodiles en Afrique de l'ouest: *Nature et Faune*, v. 1, p. 13–29.
- Watkins, B., 2004. The middle Miocene Maboko Island primate locality: new data and the integration and reinterpretation of existing data suggest the paleoenvironment was lacustrine: *American Journal of Physical Anthropology*, v. 123, p. 204.
- Wichura, H., Jacobs, L.L., Lin, A., Polcyn, M.J., Manthi, F.K., Winkler, D.A., Strecker, M.R., and Clemens, M., 2015. A 17-My-old whale constrains onset of uplift and climate change in east Africa: *Proceedings of the National Academy of Sciences of the U. S. A.*, v. 112, p. 3910–3915.
- Wilberg, E., 2017. Investigating patterns of crocodyliform cranial disparity through the Mesozoic and Cenozoic: *Zoological Journal of the Linnean Society*, v. 181, p. 189–208.
- Wilkinson, M., and Thorley, J.L., 2001. Efficiency of strict consensus trees: *Systematic Biology*, v. 50, p. 610–613.
- Willis, P.M.A., Molnar, R.E., and Scanlon, J.D., 1993. An early Eocene crocodylian from Murgon, southeastern Queensland: *Kaupia*, v. 3, p. 27–33.
- Wu, X.-C., and Brinkman, D.B., 2015. A new crocodylian (Eusuchia) from the uppermost Cretaceous of Alberta, Canada: *Canadian Journal of Earth Sciences*, v. 52, p. 590–607.

Accepted: 27 June 2020