

Paleoecology of Miocene crocodylians in Florida: Insights from stable isotope analysis



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ABSTRACT

Fossils from late Miocene localities in north Florida offer new information about the paleoecological relationships between sympatric alligatorine and tomistomine crocodylians. Large, robust tomistomines (traditionally referred to *Gavialosuchus americanus*) outnumber *Alligator* fossils at localities representing coastal/estuarine depositional environments. Stable isotope analysis of carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) values in fossil crocodylian tooth enamel carbonate (CO_3) provides evidence for niche partitioning between these two taxa, which may have co-inhabited estuarine paleoenvironments. Our isotopic results imply that alligators procured prey from primarily freshwater or terrestrial sources, whereas tomistomines fed mainly on marine-based prey items. As indicators of saltwater paleoenvironments, the fossil tomistomines may therefore be informative for tracking Miocene sea level change.

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1. Introduction

Crocodylian fossils occur in Florida from the Eocene onward, spanning nearly the entire geologic history of Florida's developing terrestrial landmass (Hulbert, 2001; Meylan et al., 2001). Crocodylians have an especially good fossil record in Florida from the early Miocene and thereafter, with a peak in abundance during the late Miocene (Brochu, 1999; Meylan et al., 2001). Two distinct types of crocodylians are preserved in Florida's late Miocene fossil deposits: (1) short, broad-snouted alligators and (2) long, slender-snouted tomistomines (Fig. 1).

In this study, we present stable isotope ratios of carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) derived from fossil tooth enamel carbonate (CO_3) to evaluate the paleoecology of Miocene alligatorine and tomistomine crocodylians from several Florida localities with proposed paleoenvironments of varying salinities. We then discuss these data with respect to their implications for Miocene sea levels and the emergence of Florida's terrestrial landmass. Understanding the co-existence of alligatorines and tomistomines in Florida could help inform modern crocodylian ecology and conservation, especially in light of anthropogenically-induced global warming and associated sea level rise

(e.g. Scavia et al., 2002; Meehl et al., 2005; IPCC, 2007, 2014; Hoegh-Guldberg and Bruno, 2010).

2. Miocene crocodylians in Florida

2.1. Alligators

Florida has the world's best fossil record for the well-known extant genus, *Alligator*, spanning from the late Oligocene to Holocene (Brochu, 1999; Hulbert, 2001; Meylan et al., 2001; Snyder, 2007; Bourque, 2013). At least two species are represented: the extinct *Alligator olseni* (White, 1942) and the extant *Alligator mississippiensis* (Daudin, 1801). *Alligator mefferdi* (Mook, 1946), a metataxon lacking autapomorphic characters (Brochu, 1999), was also reported (Snyder, 2007), although its taxonomic status and presence in Florida are questionable (Whiting et al., In press). Malone (1979) considered *A. mefferdi*, as well as another named species lacking unambiguous diagnostic character support, *Alligator thomsoni* (Mook, 1923), to be synonymous with *A. mississippiensis*.

Alligator first appeared in Florida in the late Oligocene during the late Arikareean North American Land Mammal Age (NALMA; Bourque, 2013), but was not truly prominent in fossil faunas until the early Miocene (Hemingfordian NALMA), when *A. olseni* inhabited what was exposed of north Florida (White, 1942; Auffenberg, 1957; Olsen, 1964, 1968; Stoutamire, 1975; Snyder, 2007). In the middle to late Miocene (Barstovian, Clarendonian, and Hemphillian NALMAs), *Alligator* became

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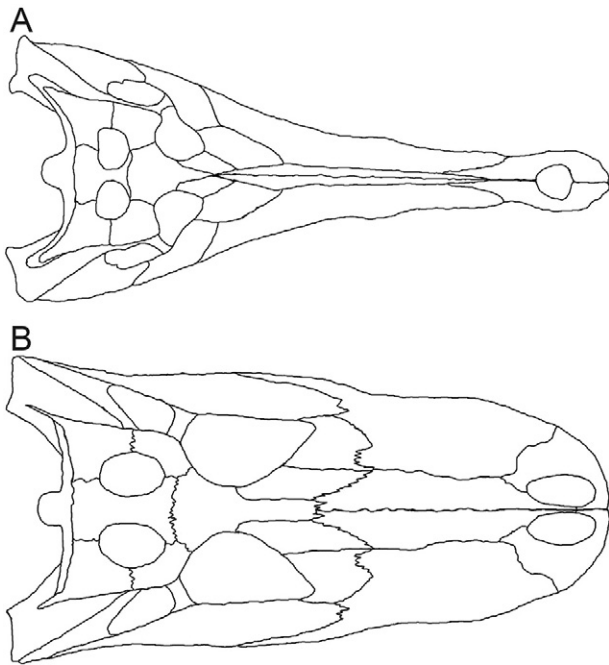


Fig. 1. Comparison of (A) “*Gavialosuchus*” *americanus* and (B) *Alligator* skull morphology. Note the differences in snout shape, which are primarily driven by the evolution of different feeding strategies (Brochu, 2003). Skull sizes are not to scale. (A) is adapted from Auffenberg (1954); Fig.2); (B) is adapted from White (1942); Fig.1).

more widespread and common in Florida (Meylan et al., 2001); the possible evolutionary transition from *A. mefferdi/thomsoni* to *A. mississippiensis* also may have occurred during this time (Brochu, 1999; Snyder, 2007; Whiting et al., in press).

Extant *Alligator* primarily lives in and is dependent upon freshwater, and has a varied, generalist diet (e.g. Valentine et al., 1972; Gabrey, 2010; Rice, 2004; Saalfeld et al., 2011; Nifong and Silliman, 2013; Nifong et al., 2012, 2015). Their brevirostrine snout morphology allows them to consume a variety of different-sized prey items, unlike the highly specialized, stenorostrine snouts of true gharials (Gavialidae, see below), which are mostly piscivorous (Whitaker and Basu, 1983). Alligators, though lacking lingual salt-secreting glands (Taplin et al., 1982, 1985; Taplin and Grigg, 1989), do display a degree of saltwater tolerance when feeding in coastal settings, but must always return to freshwater to maintain proper osmotic balance (Nifong et al., 2012, 2015).

2.2. Tomistomines

Tomistomines are long, slender-snouted crocodylians placed in the Crocodylidae based on morphology, but in the Gavialidae based on molecular data (e.g. Brochu, 2003; Willis et al., 2007; Piras et al., 2010; Gold et al., 2014). The Tomistominae and Gavialidae are each represented by a single extant species in Asia: *Tomistoma schlegelii* (Müller, 1838) and *Gavialis gangeticus* (Oppel, 1811), respectively (Brochu, 2003).

Fossils of large, robust tomistomine crocodylians have been collected from Miocene deposits in Florida for over a century (Sellards, 1915; Mook, 1921, 1924; Auffenberg, 1954, 1957; Morgan, 1986; Meylan et al., 2001). Traditionally, these fossils were referred to *Gavialosuchus americanus* (Sellards, 1915), although many authors question or discuss the validity of this name (e.g. Myrick, 2001; Brochu, 2006, 2007; Piras et al., 2007; Laurito and Valerio, 2008; Shan et al., 2009; Brochu and Storrs, 2012; Hastings et al., 2013).

Thecachampsa antiqua (Leidy, 1852), originally described from a single tooth from the early-middle Miocene Calvert Formation of Virginia, was proposed to also include tomistomine specimens collected from the

Miocene of New Jersey, Maryland, North Carolina, Florida, California, and Portugal (Myrick, 2001). Meylan et al. (2001) advocate using the name *G. americanus*, because the *T. antiqua* holotype is not diagnosable. However, the type species of the genus *Gavialosuchus*, *Gavialosuchus eggenburgensis* from the Miocene of Austria (Toula and Kail, 1885), is not closely related to *G. americanus* (e.g. Brochu and Gingerich, 2000; Brochu, 2003, 2006, 2007; Piras et al., 2007; Vélez-Juarbe et al., 2007; Shan et al., 2009; Brochu and Storrs, 2012). Therefore, the genus *Gavialosuchus* should not be applied to North American specimens. The lack of a diagnosable holotype for *T. antiqua* (Leidy, 1852) precludes assignment of North American specimens to that taxon as well. Pending a thorough review of the systematics and nomenclature of Miocene tomistomines from Florida, we refer to the Miocene Florida tomistomines as “*G.*” *americanus*, with an understanding that a new generic name may be appropriate for this taxon.

Many of these extinct North American fossil tomistomines were large, attaining estimated total body lengths of ~4–12 m (Mook, 1921; Auffenberg, 1954, 1957; Myrick, 2001; Farlow et al., 2005). They typically occur in shallow marine or estuarine deposits containing abundant potential prey items such as sharks, bony fish, and marine mammals (e.g. Auffenberg, 1954, 1957; Morgan, 1986; Erickson, 1990; Erickson and Sawyer, 1996; Myrick, 2001; Meylan et al., 2001; Brochu, 2003; MacFadden et al., 2004; Laurito and Valerio, 2008).

Extant *Tomistoma* inhabits freshwater rivers, swamps, and peat bogs in Southeast Asia (Stuebing et al., 2006, 2015; Bezuijen et al., 2010). *Tomistoma* has a more robust skull than the primarily piscivorous and more gracile *Gavialis*, but its diet and ecology are not very well known. *Tomistoma* has been reported to feed on fish more than anything else, but also on a variety of larger semi-terrestrial and terrestrial prey items including frogs, birds, monkeys, and small artiodactyls (Rachmawan and Brend, 2009; Selvaraj, 2012; Stuebing et al., 2015 and unpublished references therein). There is even a report of a larger individual attacking a cow (*Bos* sp.; Bezuijen et al., 2010), although this constitutes extremely atypical behavior for *Tomistoma*. Since modern *Tomistoma* occupies a very different environment and niche than its extinct relatives, it is likely that the ecology and diet of *T. schlegelii* are not good analogs for fossil tomistomines. It is important to note, however, that *Tomistoma* appears to have secondarily lost lingual salt-secreting glands from a saltwater-tolerant ancestor (Taplin et al., 1985; Taplin and Grigg, 1989), which provides support for adaptations to marine habitats in extinct members of Tomistominae.

2.3. Fossil localities with alligators and tomistomines

Three late Miocene fossil localities in north Florida (McGehee Farm, Love Bone Bed, and Haile 19A; Fig. 2) provide evidence that alligators and tomistomines once coexisted sympatrically. The locality of most interest in this respect is McGehee Farm, a very early Hemphillian NALMA (Hh1) site with numerous fossils of *Alligator* cf. *A. mississippiensis* as well as “*G.*” *americanus* (Hirschfield and Webb, 1968; Morgan, 1986; Hulbert, 2005). McGehee Farm is similar to many other Miocene vertebrate fossil localities in Florida in being a clay- and sand-filled solution sinkhole in limestone bedrock (Hirschfield and Webb, 1968; Lambert, 1994; Hulbert, 2001). Paleoenvironmental interpretations of McGehee Farm generally suggest an estuarine or fluvial setting inhabited by fish, turtles, and other possible prey for crocodylians (Rose and Weaver, 1966; Hirschfield and Webb, 1968; Webb and Tesson, 1968; Jackson, 1977; Becker, 1985; Meylan et al., 2001). In a 1964 letter, the late Florida Museum of Natural History (UF) Curator of Herpetology, Walter Auffenberg, described the McGehee Farm paleoenvironment as “...a slow moving stream of considerable dimensions, probably near the sea, and perhaps the upper, freshwater part of an estuary, and a swifter moving stream of much smaller dimensions.”

Love Bone Bed is slightly older than McGehee Farm, and has a diverse, mixed fauna from the latest Clarendonian (Cl3) NALMA with faunal elements representing habitats ranging from estuary, inland stream,

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