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

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Abstract

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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^{2-}) 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.

Key Words

Alligator, Florida, fossils, isotopes, Miocene, tomistomines

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 (Figure 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^{2-}) 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 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, 2010; 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 *Gavialosuchus americanus*, because the *Thecachampsa 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; Velez-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 *Thecachampsa 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 “*Gavialosuchus*” *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 *Tomistoma 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; Figure 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 “*Gavialosuchus*” *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 Tessman, 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, deciduous forest, to open-country (Webb et al., 1981; Hulbert, 2005). *Alligator* greatly outnumbers "*G.*" *americanus* at Love Bone Bed, perhaps indicating that the tomistomines were rare visitors to this *Alligator*-dominated fluvial locality. The presence of sharks and other estuarine taxa implies that the locality was either close to the coast or that fluvial transport of marine fossils occurred before the deposition of the locality's clays and phosphatic sands within a limestone solution sinkhole (Webb et al., 1981).

Haile 19A is roughly contemporaneous with McGehee Farm (Hh1; Hulbert, 2005). A solution sinkhole with similar faunal components to Love Bone Bed and especially McGehee Farm (Morgan, 2005), Haile 19A is believed to represent a nearshore marine deposit, primarily because of the abundant fossils of "*G.*" *americanus*. *Alligator* is represented at Haile 19A by

only a few osteoderms with keeled dorsal surfaces, which differentiates them from the large, flat osteoderms of “*G.*” *americanus* (Meylan et al., 2001).

We note here, based on direct examination of specimens curated in the UF Vertebrate Paleontology collection, that all three sites discussed above have numerous unstudied or incompletely studied fossils of marine, estuarine, and freshwater fishes. McGehee Farm and Love Bone Bed also have fossils of sirenians and small cetaceans, whose absence from Haile 19A may be attributable to the small overall sample of fossils from this site.

The presence of “*G.*” *americanus* and *Alligator* at late Miocene Florida localities such as McGehee Farm, Love Bone Bed, and Haile 19A suggests that the two crocodylians were sympatric, and may have shared the same habitats and ecological resources. Finding Miocene “*G.*” *americanus* alongside *Alligator* may not mean that they occupied the same site during the same exact time interval (Meylan et al., 2001), although the poorly defined chronostratigraphy of these localities precludes this determination. Time-averaging and taphonomic biases must be taken into account.

The field notes of UF Curator Emeritus of Vertebrate Paleontology, S. David Webb, from the McGehee Farm excavations in the 1960s and 1970s, mention that all of the tomistomines were found in the lower clayey sand layer, but do not indicate where the *Alligator* fossils were recovered. Because all of the fossils recovered from the coarse gravel layer are heavily water-worn and do not include any identifiable crocodylian remains, we assume that the alligators and tomistomines from McGehee Farm were collected from the same stratigraphic layer, and likely inhabited roughly the same area at the same time.

3. Stable Isotope Analysis of Fossil Crocodylian Teeth

3.1 Background

Previous stable isotope studies of modern and fossil crocodylian tooth enamel have focused on physiological, ecological, evolutionary, and paleoclimatic issues (e.g. Amiot et al., 2004, 2007; Matson and Fox, 2008; Wheatley, 2010; Foreman et al., 2011; Wheatley et al., 2012). To our knowledge, this is the first isotopic study of two broadly contemporaneous fossil crocodylians to specifically assess possible ecological niche partitioning, as well as to test the longstanding hypothesis (Auffenberg, 1954) that “*G.*” *americanus* truly occupied a marine or estuarine habitat.

3.2 Materials and Methods

3.2.1. Sampling and Pretreatment

We selected specimens (n = 20) for sampling based mainly on high-quality enamel preservation and minimal damage to the tooth crown. Our samples are from McGehee Farm, believed to represent a fluvial, estuarine paleoenvironment (Hirschfield and Webb, 1968; Webb and Tessman, 1968; Jackson, 1977; *Alligator*, n = 2; “*G.*” *americanus*, n = 3); Love Bone Bed, believed to represent a fluvial, estuarine paleoenvironment (Webb et al., 1981; *Alligator*, n = 3; “*G.*” *americanus*, n = 3); and Haile 19A, thought to represent a shallow nearshore marine paleoenvironment (Morgan, 2005; *Alligator* extremely rare, n = 0; “*G.*” *americanus*, n = 4). We also sampled specimens from the early Miocene (Hemingfordian NALMA) Thomas Farm locality (*Alligator*, n = 5; “*G.*” *americanus* not present, n = 0), which represents a terrestrial, freshwater paleoenvironment (Pratt, 1990; Hulbert, 2001; Steadman, 2008). The localities from which we obtained our samples are shown geographically in Figure 2.

We used an abrading carbide drill bit mounted on a stationary Brassler dental drill to obtain a fresh, powdered enamel sample (~10 mg) from each tooth, taking care to sample only the outermost surface of the tooth to avoid contaminating enamel powder with underlying dentin. Drilled sample weights ranged from 5.1 mg to 17.6 mg for the 20 teeth, with means of 11.73 mg for “*G.*” *americanus* (n = 10) and 9.14 mg for *Alligator* (n = 10).

Following enamel powder collection, we homogenized each sample with a clean agate mortar and pestle. Powdered samples were placed in 1.5 mL microcentrifuge tubes and treated with 1+ mL of 30% hydrogen peroxide (H₂O₂) for 16 hours to remove any organic contaminants. We pipetted out the H₂O₂ from the microcentrifuge tubes with a fresh pipette tip, and rinsed each sample to neutral (3x) with deionized distilled water. Samples were then treated with 1+ mL of a buffered 1.0 M acetic acid (CH₃COOH) solution for 16 hours to remove secondary carbonates. We pipetted out the CH₃COOH solution from the microcentrifuge tubes with a fresh pipette tip, and rinsed each sample to neutral (3x) with deionized distilled water. Samples were then frozen and lyophilized for 48 hours. Pretreated sample weights ranged from 4.54 mg to 16.66 mg for the 20 teeth, with means of 10.51 mg for “*G.*” *americanus* (n = 10) and 8.40 mg for *Alligator* (n = 10).

Percent of enamel sample retained after pretreatment ranged from 80.46% to 95.26% for “*G.*” *americanus* (mean 89.40%) and 87.87% to 94.66% for *Alligator* (mean 91.36%). Enamel loss following pretreatment did not exceed 13%, except for UF 289203 (“*G.*” *americanus* from Love Bone Bed), which lost 19.54% of its original powdered material.

3.2.2. Mass Spectrometry

Isotope Ratio Mass Spectrometry (IRMS) was conducted in the UF Department of Geological Sciences Light Stable Isotope Mass Spectrometry Laboratory. Pretreated samples were loaded into glass vials and inserted into a Kiel III carbonate preparation device and reacted with 100% orthophosphoric acid at 70°C. The resulting evolved CO₂ gas was measured for carbon (δ¹³C) and oxygen (δ¹⁸O) using a Finnigan MAT 252 IRMS. Data are reported in standard delta notation (δ) relative to Vienna Pee Dee Belemnite (VPDB): $\delta X = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$, where X is either carbon or oxygen and R is the ratio of heavy to light isotope (i.e. ¹³C/¹²C or ¹⁸O/¹⁶O). Analytical precision was ±0.04‰ for δ¹³C and ±0.05‰ for δ¹⁸O based on analysis of NBS-19 standards (n=8).

3.2.3 Physiology, Fractionation, Environmental Variables, and Taphonomy

Isotopic signatures in fossils are complex (especially for poikilothermic organisms, such as crocodylians), and are influenced by variables such as temperature, physiology, and diet (e.g. Koch, 1998, 2007; Amiot et al., 2007; Fricke, 2007). Thus, a knowledge of modern ecosystems and life histories is necessary to interpret the fossil record through stable isotope geochemistry.

Understanding how crocodylian teeth are replaced and mineralized can help clarify how quickly geochemical markers become integrated into tooth enamel. Tooth replacement in extant *Alligator mississippiensis* occurs over ~120 days in captive individuals ~0.85 m in length, and tooth replacement rates decrease through ontogeny in crocodylians (Erickson, 1996). Tooth enamel in small alligators mineralizes in just under a third of a year (~4 months), and captures the geochemical signals of the water in which they live and the food they eat during that time. No similar tests have been done on extant tomistomines, although a single Spectacled Caiman (*Caiman crocodilus* [Linnaeus, 1758]) individual studied by Erickson (1996) fell within the same

range of tooth replacement intervals as *A. mississippiensis*; this implies that tooth mineralization and replacement intervals may be similar for crocodylians as a whole, or at least within Alligatoridae. We assume that fossil *Alligator* and “*G.*” *americanus* mineralized and replaced their teeth in a similar fashion to their extant counterparts. Our sampled teeth are not associated with fossilized postcranial skeletal remains that could provide reliable total body length estimates. Nevertheless, most of the teeth we sampled are certainly from individuals >0.85 m in body length, so it is reasonable to conclude that they replaced their teeth over intervals longer than ~120 days, such as the ~10 month interval observed by Edmund (1962).

Isotopic fractionation must also be taken into account when interpreting results from stable isotope analysis of crocodylians. Fractionation may be measured by apparent fractionation (α), trophic discrimination (Δ), or diet-to-tissue enrichment (ϵ^*) factors (Koch, 1998, 2007; Cerling and Harris, 1999). These factors are used to make corrections to raw δ values based on environmental sources of elemental isotopes and trophic position in a given ecosystem, and are especially helpful when interpreting results in physiological and ecological contexts (e.g. Koch, 1998, 2007; Cerling and Harris, 1999; Kelly, 2000; Rubenstein and Hobson, 2004). As stated by Cerling and Harris (1999), Δ and ϵ^* factors are inherently similar, but there are differences in how they are applied in biology (typically Δ) and geology (typically ϵ^*). For simplicity, we refer to Δ factors for modern studies, and ϵ^* factors for fossil studies only. Regardless of which factor is used, very little is known about isotopic fractionation factors in crocodylians. There are very few controlled-diet isotopic studies on extant crocodylians, and none to date address fractionation factors between diet and tooth enamel (or bioapatite, more generally). We discuss fractionations below for $\delta^{13}\text{C}$ only and exclude $\delta^{15}\text{N}$, since nitrogen stable isotope ratios are only

obtainable from subfossil remains with preserved and unaltered collagen (e.g. Wang and Cerling, 1994; Kohn and Cerling, 2002; Hastings et al., 2014).

Rosenblatt and Heithaus (2013) found low $\delta^{13}\text{C}$ Δ factors in small American alligators, which suggests that the $\delta^{13}\text{C}$ values obtained for these animals reflect the original sources of environmental carbon. These values differed slightly depending on which tissue or fluid was analyzed. Bone collagen from osteoderms has a $\delta^{13}\text{C}$ Δ factor of +0.28‰ (corrected for lipid content) to +0.61‰ (control) for a controlled diet consisting of catfish (*Ictalurus* sp.) and catfish pellets; less ^{13}C -enriched values were reported for plasma and red blood cells (RBCs; Rosenblatt and Heithaus, 2013). Caut (2013) found a $\delta^{13}\text{C}$ Δ factor of -0.52‰ to +1.06‰ in the plasma, RBCs, and muscle tissues of juvenile Broad-snouted caimans (*Caiman latirostris* [Daudin, 1801]) based on controlled diets of roach fish (*Rutilus* sp.) and domestic chickens (*Gallus* sp.). Marques et al. (2014) observed a similarly low $\delta^{13}\text{C}$ Δ factor of +0.9‰ to +1.2‰ in *C. latirostris* scutes and claws, respectively, based also on a diet of domestic chickens (*Gallus* sp.). Hanson et al. (2015) observed a $\delta^{13}\text{C}$ Δ factor of +0.6‰ to +2‰ in the plasma, RBCs, collagen, and keratin of juvenile Saltwater crocodiles (*Crocodylus porosus* [Schneider, 1801]) fed a controlled diet of mixed domestic chicken (*Gallus* sp.) and kangaroo (*Macropus* sp.) meat.

The results of these studies suggest that isotopic turnover rates are very low in the collagen, keratin, muscles, and circulatory fluids of living crocodylians, but extrapolation to tooth enamel must be done with caution. Collagen in bone is subject to remodeling and has isotopic values time-averaged over months to years (Koch, 2007), whereas plasma, muscle, and RBCs record shorter time frames and exhibit lower isotopic turnover (Caut, 2013; Rosenblatt and Heithaus, 2013; Hanson et al., 2015). Tooth dentin and tooth enamel, in particular, are more stable than collagen and other soft tissues (i.e. little to no isotopic turnover; Koch, 2007), and are

also less susceptible to diagenetic alteration (Wang and Cerling, 1994; Koch et al., 1997; Kohn and Cerling, 2002). Thus, despite the lack of data on isotopic fractionation between diet and tooth enamel in extant crocodylians, it is reasonable to assume that isotopic fractionation in modern and fossil crocodylian tooth enamel is small, and $\delta^{13}\text{C}$ values obtained from enamel are reflective of diet and the source(s) of environmental carbon.

Dietary enrichment (ϵ^*) factors in mammals have been studied in some detail, and relate mammalian diets directly to food sources consumed (e.g. Tieszen and Fagre, 1993; Koch, 1998, 2007; Cerling and Harris, 1999). The ϵ^* factor for $\delta^{13}\text{C}$ in terrestrial and aquatic herbivorous mammals is generally given as ~10–14‰ (Cerling and Harris, 1999; Clementz and Koch, 2001; MacFadden et al., 2004; Clementz et al., 2006; Koch, 2007), whereas the ϵ^* factor of carnivorous mammals is considered to be ~9‰ (Tieszen and Fagre, 1993; Clementz et al., 2006; Koch, 2007). These values are likely more taxon-specific (Koch, 2007), and may not be reflective of overall trends for all herbivorous and carnivorous mammals (both terrestrial and aquatic). Since crocodylians are not mammals and there is a lack of fundamental information about isotopic fractionations in crocodylian bioapatite (see above), we did not attempt to correct our $\delta^{13}\text{C}$ values based on the ϵ^* factors of aquatic mammals. In addition to the physiological and trophic fractionation factors discussed above, environmental variables also affect stable isotope ratios in the tooth enamel of aquatic tetrapods, such as crocodylians. These include water temperature, dissolved inorganic carbon (DIC) content, and salinity, distance from a fluvial source (and where that fluvial water originated), drought/water stress, and several other parameters (e.g. Hemminga and Mateo, 1996; Koch, 1998, 2007; Clementz and Koch, 2001; Rubenstein and Hobson, 2004; Clementz et al., 2006; Fricke, 2007; Silva et al., 2011; Wheatley et al., 2012). Marine producers and consumers tend to be more enriched in ^{13}C , which translates

to more positive $\delta^{13}\text{C}$ values in marine organisms than in terrestrial or freshwater producers and consumers (Clementz and Koch, 2001; Clementz et al., 2006; Koch, 2007; Newsome et al., 2010; Wheatley et al., 2012). While $\delta^{13}\text{C}$ values change slightly (usually $\sim 1\%$) as carbon moves from consumer to consumer, making them useful for estimating the original source(s) of environmental carbon, trophic status is typically more evident in $\delta^{15}\text{N}$ values (e.g. Peterson and Fry, 1987; Fry, 1991; Koch, 1998, 2007; Rubenstein and Hobson, 2004). However, because $\delta^{15}\text{N}$ values can be obtained only for subfossils preserving unaltered organic material (see above), we could not obtain any $\delta^{15}\text{N}$ data from our Miocene samples.

Oxygen isotope values are the result of a complicated interplay of temperature, season, latitude, altitude, precipitation, evaporation, upwelling, ocean currents, and water sources (e.g. Koch, 1998, 2007; Clementz and Koch, 2001; Kohn and Cerling, 2002; MacFadden et al., 2004; Rubenstein and Hobson, 2004; Fricke, 2007). Marine tetrapods typically have $\delta^{18}\text{O}_{\text{VPDB}}$ values closer to 0‰ ($\delta^{18}\text{O}_{\text{VSMOW}} \approx 30\%$), because this is the approximate $\delta^{18}\text{O}$ value of ocean water (Clementz and Koch, 2001; MacFadden et al., 2004; LeGrande and Schmidt, 2006; Wheatley et al., 2012). However, because of the variables affecting $\delta^{18}\text{O}$, especially in coastal settings (MacFadden et al., 2004), the standard deviation (σ) of $\delta^{18}\text{O}$ values in a sample has been suggested to be a better measure of marine versus freshwater habits; a lower $\delta^{18}\text{O}$ σ usually correlates to marine habits, whereas greater variability in $\delta^{18}\text{O}$ values is associated with freshwater or terrestrial habits (Clementz and Koch, 2001; Clementz et al., 2006; Wheatley et al., 2012).

Taphonomic factors must also be accounted for when interpreting stable isotope results. We sampled only tooth enamel because its bioapatite is more diagenetically-resistant than the collagen or bioapatite in bone or dentin (Wang and Cerling, 1994; Koch et al., 1997; Kohn and

Cerling, 2002). The apparent stability of isotopic ratios in fossil tooth enamel dating back to the Late Paleogene (Kohn and Cerling, 2002) suggests that our isotope values from Miocene tooth enamel are probably not altered, except for one outlier (UF 289204; “*G.*” *americanus* from Haile 19A) with a spurious $\delta^{18}\text{O}$ value compared to our other assayed samples (see Results); this might be explained by potential contamination of the enamel sample with dentin, especially given the greater susceptibility of $\delta^{18}\text{O}$ to diagenetic alteration compared to $\delta^{13}\text{C}$ (Wang and Cerling, 1994; Koch et al., 1997).

3.3 Results

3.3.1. Raw Data

Our raw $\delta^{18}\text{O}_{\text{VPDB}}$ values range from -3.64‰ to -0.3‰ for all of our samples (n=19). Because of its anomalous (and possibly diagenetically altered) $\delta^{18}\text{O}_{\text{VPDB}}$ value of -7.35‰, the results for UF 289204 (“*G.*” *americanus* from Haile 19A) were excluded from our corrections and statistical analyses. Overall, “*Gavialosuchus*” *americanus* exhibits more positive $\delta^{18}\text{O}$ values (^{18}O -enriched) compared to *Alligator*. The mean for “*G.*” *americanus* (n=9) is -1.05‰ (range -2.09‰ to -0.52‰). The mean for *Alligator* (n=10) is -2.3‰ (range -3.64‰ to -0.30‰).

Our raw $\delta^{13}\text{C}$ values range from -10.95‰ to 0.90‰ for all of our samples (n=19). Overall, $\delta^{13}\text{C}$ values for “*G.*” *americanus* are more positive (^{13}C -enriched) than for *Alligator*. The mean for “*G.*” *americanus* (n=9) is -1.32‰ (range -4.58‰ to 0.9‰). The mean for *Alligator* (n=10) is -8.55‰ (range -10.95‰ to -6.37‰). We present our resulting raw $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values and descriptive statistics in Tables 1 and 2, respectively, as well as graphically in Figure 3.

3.3.4. Corrected Data

We corrected our raw $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from assayed fossil crocodylian tooth enamel (+1.2‰ for each $\delta^{18}\text{O}_{\text{VPDB}}$ value and -0.5‰ for each $\delta^{13}\text{C}$ value) to account for a warmer planet during the Miocene with less ice, higher concentrations of atmospheric carbon dioxide (CO_2), and depleted carbon reservoirs (Zachos et al., 2001; Tipple et al., 2010). Our paleoecological and paleoenvironmental inferences are based on these corrected values (Table 1, Fig. 4). For reasons discussed at length above, we did not correct our raw $\delta^{13}\text{C}$ values with a fractionation factor. However, we do keep in mind the slight trophic effect (~1‰) between consumers in most food webs (Peterson and Fry, 1987). To aid in comparison with other published data (i.e. MacFadden et al., 2004), both raw and corrected $\delta^{18}\text{O}$ values were converted from VPDB to VSMOW (Vienna Standard Mean Ocean Water) using the equation of Friedman and O'Neil (1977): $\delta^{18}\text{O}_{\text{VSMOW}} = 1.03086(\delta^{18}\text{O}_{\text{VPDB}}) + 30.86$. After this conversion, the mean raw $\delta^{18}\text{O}_{\text{VSMOW}}$ value for “*G. americanus*” (n=9) is 29.78‰ and the mean corrected $\delta^{18}\text{O}_{\text{VSMOW}}$ value is 31.02‰ (excluding the outlier, UF 289204). For *Alligator*, the mean raw $\delta^{18}\text{O}_{\text{VSMOW}}$ value is 28.49‰ and the mean corrected $\delta^{18}\text{O}_{\text{VSMOW}}$ value is 29.73‰.

3.3.5 Statistical Analyses

We analyzed our raw and corrected data using PAST v. 2.17 (Hammer et al., 2001) to test for any statistically significant ($p < 0.05$) differences between our data sets for *Alligator* (n = 10) and “*Gavialosuchus*” *americanus* (n = 9; UF 289204 excluded, see above). Because we cannot assume normal distributions for the data (especially at the locality level, for which sample sizes are very small), we also conducted nonparametric analyses to supplement the parametric tests.

First, we conducted a Kolmogorov-Smirnov test (a nonparametric method assuming a non-normal data distribution) to evaluate if our *Alligator* and “*Gavialosuchus*” samples all originated from the same, non-normal sample distribution on each set of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements (raw and corrected; VPDB and VSMOW). We observed significantly different p-values for raw and corrected $\delta^{13}\text{C}$ values ($p = 0.00003286$), barely significantly different p-values of 0.04384 for raw, corrected, and converted $\delta^{18}\text{O}_{\text{VPDB}}$ and $\delta^{18}\text{O}_{\text{VSMOW}}$ values, and a not statistically significantly different p-value of 0.1273 for corrected $\delta^{18}\text{O}_{\text{VSMOW}}$ values. These analyses show that $\delta^{13}\text{C}$ values can be used to distinguish *Alligator* from “*G.*” *americanus*, whereas this is not necessarily the case for the $\delta^{18}\text{O}$ values, which are barely significantly different or not significantly different at all.

Next, we conducted simple t-tests and one-way ANOVAs (parametric methods assuming normality of the data distributions) to analyze the probability that both data sets (*Alligator* and “*Gavialosuchus*”) originated from a single sample population with given mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, based on comparing the raw and corrected isotopic means for both data sets. We obtained a highly significant p-value of 0.0000000299 for the raw $\delta^{13}\text{C}$ values from both the t-test and ANOVA. For the raw $\delta^{18}\text{O}_{\text{VPDB}}$ and $\delta^{18}\text{O}_{\text{VSMOW}}$ values, a p-value of 0.009871 implies that they too are significantly different, although to a lesser degree than the raw $\delta^{13}\text{C}$ values. Our t-test p-values for corrected $\delta^{13}\text{C}$ and $\delta^{18}\text{O}_{\text{VPDB}}$ values are similar to those for the raw data sets; the t-test and ANOVA p-values for corrected $\delta^{18}\text{O}_{\text{VSMOW}}$ were both 0.02893, implying that the conversion from VPDB to VSMOW enhanced the degree of similarity between the *Alligator* and “*G.*” *americanus* $\delta^{18}\text{O}$ data sets. The t-tests and ANOVAs on both the raw and corrected data suggest that $\delta^{13}\text{C}$ differentiates *Alligator* from “*G.*” *americanus* with great statistical significance; $\delta^{18}\text{O}$ values are also significantly different, but not to the same degree.

Mann-Whitney and Kruskal-Wallis tests (nonparametric substitutes for t-tests and ANOVAs not assuming data normality) on raw and corrected $\delta^{13}\text{C}$ and $\delta^{18}\text{O}_{\text{VPDB}}$ and raw $\delta^{18}\text{O}_{\text{VSMOW}}$ values resulted in significantly different $\delta^{13}\text{C}$ p-values of 0.0002797 (Mann-Whitney) and 0.0002386 (Kruskal-Wallis), and slightly significantly different $\delta^{18}\text{O}$ p-values of 0.02474 (Mann-Whitney) and 0.02224 (Kruskal-Wallis). Conducting the same tests on the corrected $\delta^{18}\text{O}_{\text{VSMOW}}$ values resulted in Mann-Whitney and Kruskal-Wallis p-values of 0.06619 and 0.06039, respectively (no statistically significant differences). These nonparametric methods also suggest that $\delta^{13}\text{C}$ values readily distinguish “*G.*” *americanus* from *Alligator*, whereas $\delta^{18}\text{O}$ values do so with less statistical rigor.

We also tested for significant differences between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of alligatorines and tomistomines at each locality for which we sampled both crocodylians (McGehee Farm and Love Bone Bed). Given our statistical findings above and for simplicity, we only analyzed corrected $\delta^{13}\text{C}$ and $\delta^{18}\text{O}_{\text{VPDB}}$ values for each taxon. For McGehee Farm, we found a significant difference ($p = 0.0026575$, t-test) between *Alligator* and “*G.*” *americanus* $\delta^{13}\text{C}$ values, although this was not upheld by a Mann-Whitney test ($p = 0.14891$). This is most likely attributable to small sample sizes at the locality level, since the McGehee Farm alligators and tomistomines have clearly distinct $\delta^{13}\text{C}$ values (Fig. 4). We found no significant difference ($p = 0.9304$; t-test) between *Alligator* and “*G.*” *americanus* $\delta^{18}\text{O}$ values, which was upheld by Mann-Whitney ($p = 0.77283$) and Kolmogorov-Smirnov ($p = 0.99062$) tests.

For Love Bone Bed, we found a significant difference ($p = 0.0058787$, t-test; $p = 0.032622$, Kolmogorov-Smirnov) between *Alligator* and “*G.*” *americanus* $\delta^{13}\text{C}$ values, although this was not upheld by a Mann-Whitney test ($p = 0.080856$). This is again most likely attributable to small sample sizes, since the Love Bone Bed alligators and tomistomines also

have clearly distinct $\delta^{13}\text{C}$ values (Fig. 4). We found no significant difference ($p = 0.28176$; t-test) between *Alligator* and “*G.*” *americanus* $\delta^{18}\text{O}$ values, which was upheld by Mann-Whitney ($p = 0.66252$) and Kolmogorov-Smirnov ($p = 0.31972$) tests.

4. Discussion

4.1 Paleoecology

The $\delta^{13}\text{C}$ values of tooth enamel CO_3^{2-} are significantly more positive in the tomistomine “*Gavialosuchus*” *americanus* than in the alligatorine *Alligator*, whereas $\delta^{18}\text{O}$ values distinguish between these two crocodylians less reliably. This overall trend is less certain at the locality level, due to small sample sizes, but is still evident in the isotopic partitioning of each crocodylian at each locality (Fig. 4). We interpret our results as showing that alligators and tomistomines procured prey from different sources, including at localities for which both taxa are present, thus constituting ecological niche partitioning. The tomistomines are greatly enriched in ^{13}C compared to the alligators. Therefore, we can infer that tomistomines display a more consistent affinity for marine or estuarine habitats and food sources, which typically exhibit more positive $\delta^{13}\text{C}$ values than freshwater habitats and organisms (e.g. Clementz and Koch, 2001; Rubenstein and Hobson, 2004; Clementz et al., 2006; Silva et al., 2011; Wheatley et al., 2012). Our corrected $\delta^{18}\text{O}_{(\text{VPDB and VSMOW})}$ values also support this hypothesis. Generally, $\delta^{18}\text{O}_{\text{VPDB}}$ values closer to 0‰ ($\delta^{18}\text{O}_{\text{VSMOW}} \approx 30\text{‰}$) are indicative of marine environments and saltwater affinities (Clementz and Koch, 2001; MacFadden et al., 2004; Wheatley et al., 2012). Our mean corrected “*G.*” *americanus* $\delta^{18}\text{O}_{(\text{VPDB and VSMOW})}$ values of 0.15‰ and 31.02‰, respectively, provide evidence for our hypothesis, since they are very close to the oceanic $\delta^{18}\text{O}_{(\text{VPDB and VSMOW})}$

values of 0‰ and 30‰, respectively. However, we also obtained relatively high $\delta^{18}\text{O}_{(\text{VPDB and VSMOW})}$ values for *Alligator* (-1.1‰ and 29.73‰, respectively), so another method must be invoked to parse the two crocodylians apart based on their $\delta^{18}\text{O}$ values.

Several authors (Clementz and Koch, 2001; Clementz et al., 2006; Wheatley et al., 2012) advocate using the standard deviations (σ) of $\delta^{18}\text{O}$ values in order to separate marine and freshwater tetrapods, since lower $\delta^{18}\text{O}$ variability is expected in more homogenous ocean habitats than freshwater habitats (which have more inputs and confounding variables). We observed lower $\delta^{18}\text{O}$ σ values in the tomistomines overall, with the exception of *Alligator* from McGehee Farm, which overlapped with “*G.*” *americanus* from McGehee Farm and Haile 19A (Fig. 5). Curiously, however, the two most disparate $\delta^{18}\text{O}$ σ values are for alligators and tomistomines at Love Bone Bed. The “*G.*” *americanus* at Love Bone Bed has the lowest $\delta^{18}\text{O}$ σ of all of our localities, while *Alligator* from Love Bone Bed has the highest $\delta^{18}\text{O}$ σ (surprisingly, even higher than for Thomas Farm, which was definitely a freshwater, terrestrial environment; Pratt, 1990; Hulbert, 2001; Steadman, 2008). This could indicate that alligators living in the Love Bone Bed depositional environment inhabited a wider breadth of microhabitats (particularly in freshwater settings) than “*G.*” *americanus*, which was restricted to marine habitats and only occurred as a rare visitor to the area during the time of deposition (Cl3). The relative spatiotemporal proximity of McGehee Farm and Haile 19A (Hh1; see also Fig. 2) may account for some of the similarity in $\delta^{18}\text{O}$ σ values between sympatric alligators and tomistomines, although it appears that the alligators inhabiting this area were living in saltwater at least part of the time ($\delta^{18}\text{O}$ σ < 1‰). However, the large differences in $\delta^{13}\text{C}$ values between the two taxa imply niche partitioning in the estuarine paleoenvironment represented at McGehee

Farm (i.e. *Alligator* consumed more ^{13}C -depleted food, probably from freshwater or terrestrial settings, than “*G.*” *americanus*, which consumed more ^{13}C -enriched foods from marine habitats).

Assuming low $\delta^{13}\text{C}$ trophic fractionations ($\sim 1\text{‰}$; see Materials and Methods), we can proffer some ideas about the potential diets and prey items for both Miocene alligators and tomistomines in Florida. Modern alligators consume a wide variety of prey items, including terrestrial animals (see above). Our mean $\delta^{13}\text{C}$ value of -9.05‰ for *Alligator* at all localities (except for Haile 19A, for which no alligators were sampled) is similar to the mean modern coastal American Alligator $\delta^{13}\text{C}$ value (10.3‰) of Wheatley et al. (2012). Since we know that the Thomas Farm alligators were not feeding on any marine prey items, and they have similar $\delta^{13}\text{C}$ values to the alligators from Love Bone Bed and McGehee Farm, it is possible that our greater $\delta^{13}\text{C}$ values for Miocene alligators do not actually indicate marine dietary components. Higher amounts of dissolved inorganic carbon (DIC) in the water, varied carbon inputs from terrestrial prey (possibly including herbivorous mammals feeding on water-stressed C_3 vegetation, which is isotopically close to ^{13}C -enriched C_4 grasses; e.g. Kita et al., 2014), or diagenesis could be inflating our $\delta^{13}\text{C}$ values for Miocene alligators.

Our mean corrected $\delta^{13}\text{C}$ value of -1.32‰ for “*G.*” *americanus* is much higher than the extant American Crocodile (*Crocodylus acutus* [Cuvier, 1807]) mean $\delta^{13}\text{C}$ value (-9.6‰) found by Wheatley et al. (2012), indicating that Miocene tomistomines were most likely feeding in marine environments that were much more ^{13}C -enriched than those frequented by *C. acutus* today in Florida (mainly coastal mangrove swamps [Kushlan and and Mazzotti, 1989], which have reported $\delta^{13}\text{C}$ values ≈ -26 – -27‰ ; Rodelli et al., 1984; Cifuentes et al., 1996). Our tomistomine $\delta^{13}\text{C}$ values are also much higher than those reported for large Saltwater crocodiles (*C. porosus*) from a tidal river in northern Australia, which primarily consumed freshwater prey

items ($\delta^{13}\text{C} \approx -19\text{--}20\text{‰}$; Hanson et al., 2015). Comparison of our tomistomine $\delta^{13}\text{C}$, $\delta^{18}\text{O}_{\text{VSMOW}}$, and $\delta^{18}\text{O}_{\text{VPDB}}$ σ values to those of different aquatic environments indicates a close affinity to seagrass estuaries ($\delta^{13}\text{C} < -10\text{‰}$, $\delta^{18}\text{O}_{\text{VSMOW}} \approx 30\text{‰}$, $\delta^{18}\text{O}_{\text{VPDB}}$ $\sigma < 1\text{‰}$; Hemminga and Mateo, 1996; Clementz and Koch, 2001; MacFadden et al., 2004; Clementz et al., 2006).

The closest isotopic analogs to our tomistomines are sympatric Miocene dugongs (Mammalia, Sirenia) from Florida allied with the “marine seagrass diet” category of MacFadden et al. (2004: fig. 3). This isotopic similarity, paired with low trophic fractionation factors (see above), could suggest predation on sirenians by tomistomines during the Miocene. This is unprecedented in a modern context; only one reliable record exists documenting consumption of a sirenian carcass by a living crocodylian, but this was isolated and probably atypical behavior (Marsh et al., 2011). “*G. americanus*” grew to be very large (~4–12 m in body length) and, despite being stenorostrine, had large, robust skulls. These giant tomistomines could have easily taken large mammalian prey, such as dugongs, although this claim lacks more explicit, direct evidence (e.g. crocodylian bite marks on dugong bones).

Sea turtles (Cheloniidae) could be another potential “*G. americanus*” prey source in Miocene Florida estuaries and nearshore seagrass ecosystems, given their high $\delta^{13}\text{C}$ (Biasatti, 2004) and low $\delta^{18}\text{O}_{\text{VPDB}}$ σ (Wheatley et al., 2012) values. However, fossil sea turtles in Florida (Dodd and Morgan, 1992) do not regularly occur at the same localities as tomistomines, and there is no direct evidence supporting durophagy in Tomistominae. Fossil sea turtles are common in Florida during high sea level stands in the Pliocene, after the local extinction of tomistomines.

Isotopic data for modern subtropical sharks show low $\delta^{13}\text{C}$ values in near equilibrium with seawater DIC content (Vennemann et al., 2001). Shark fossils are abundant at all three of our estuarine localities (see above), which could have provided a steady food source for

tomistomines. Additionally, our tomistomines could be tracking local marine DIC and/or bicarbonate (HCO_3^-) levels, but this would need to be tested by sampling other taxa or sediments from each locality. Hemminga and Mateo (1996) found a $\delta^{13}\text{C} \approx 0\text{‰}$ for HCO_3^- in open ocean environments, which could possibly help explain the ^{13}C -enriched isotopic signatures we found in the marine/estuarine tomistomine, “*G.*” *americanus*.

Fossils of “*G.*” *americanus* occur in Florida into the early Hemphillian NALMA, but no Plio-Pleistocene records exist (Morgan, 1986; Meylan et al., 2001). The cooling of Earth’s climate associated with the development of northern hemisphere ice sheets (Zachos et al., 2001, 2008), as well as ensuing drops in global sea levels (Miller et al., 2005), might have been key factors in the loss of tomistomines from Florida and North America.

In the post-Miocene absence of tomistomines, *Alligator* may have begun to feed more from estuarine or marine food webs. While living primarily in freshwater, extant *A. mississippiensis* has some estuarine and coastal populations in the southeastern United States; these alligators feed on many types of marine prey, but must return to freshwater to avoid excessive absorption of salt, given their lack of lingual salt-excreting glands (Taplin et al., 1982; Rosenblatt and Heithaus, 2011; Nifong et al., 2012, 2015; Nifong and Silliman, 2013; Rosenblatt et al., 2013). Modern coastal populations of alligators may represent an expanded ecological niche for what once was a more restricted freshwater genus, which originated during the late Eocene in the Great Plains (Brochu, 1999; Whiting and Hastings, 2015). This idea could be tested by stable isotope analysis of fossil tooth enamel from Plio-Pleistocene and modern *A. mississippiensis* in Florida, and comparing resulting values to the Miocene values we present in this study.

4.2. Sea Levels and Paleoclimate

During most of the late Miocene, sea levels in Florida (and worldwide) were higher than those of today (Webb and Tessman, 1968; Miller et al., 2005). From ~7–10 million years ago (Ma), sea levels fluctuated from slightly below to ~20+ m above modern sea levels (Miller et al., 2005; fig. 4). Higher sea level stands would have inundated much of Florida’s current land area (Emslie 1998: fig. 17), and made what is now peninsular Florida a transient archipelago during the Neogene, with topographic high points acting as temporary islands during periods of higher sea levels (Riggs, 1984; Bert, 1986). These conditions are reflected in Florida’s fossil record as mixed assemblages of terrestrial and marine faunas (Hulbert, 2001).

In the late Miocene, sea levels were higher than at present during the late Clarendonian (Cl3; ~9–10 Ma) and early Hemphillian (Hh1; ~7.5–9 Ma; NALMA dates from Tedford et al., 2004; sea level data from Miller et al., 2005). Tomistomines were most prevalent in Florida during these time intervals (Hulbert, 2001; Meylan et al., 2001), which may be related to an affinity for shallow marine habitats, as suggested by Auffenberg (1954, 1957) and our isotopic data (see above). We therefore propose that the presence of “*G.*” *americanus* at currently inland fossil bearing localities reflects higher sea level stands during the late Miocene; these localities were close to the coastline when the fossils were deposited, although they are now farther from the coast because of decreased sea levels. This is especially evident for the Bone Valley localities (Hh2) of central Florida (Hulbert, 2005), which yielded the holotype and many other specimens of “*G.*” *americanus* (Sellards, 1915; Mook, 1924; Morgan, 1986) and abundant vertebrate and invertebrate fossils indicating a shallow marine paleoenvironment (Hulbert, 2001). In turn, late Miocene (Hh1 and 2) localities in Florida lacking tomistomines but preserving alligators, such as

Mixon's Bone Bed, Moss Acres Racetrack, Tyner Farm, and Withlacoochee 4A, may represent times of lower sea levels.

Based on data from stable isotopes, sea levels, and fossil crocodylian presence/absence, we can generate a narrative of late Miocene crocodylian distributions in Florida (Fig. 6). During Cl3 (~9–10 Ma), sea levels were higher than today, and both alligators and tomistomines inhabited the estuarine fluvial system preserved at Love Bone Bed. Alligators are much more common at Love Bone Bed than tomistomines, and their isotopic values suggest that this locality had a relatively large freshwater influence and minor marine component. Sea levels remained high during Hh1 (~9–7.5 Ma), and tomistomines reached their highest abundance in north Florida (typified at McGehee Farm and Haile 5B and 19A). Because tomistomines are much more common than alligators in most Hh1 fossil assemblages, we propose that Hh1 sea levels were higher than Cl3 sea levels. Sea levels dropped after Hh1, exposing more land and allowing more terrestrial and freshwater faunas to dominate the region, as typified by the Hh2 (~7.5–6.8 Ma) Moss Acres Racetrack and Tyner Farm localities. Sea levels rose again during part of this same biochronologic interval (Hh2), when a number of "*G.*" *americanus* fossils were preserved in the shallow marine sediments of the Bone Valley localities (Morgan, 1986; Meylan et al., 2001). These last records of "*G.*" *americanus* in North America occur during the last late Miocene high sea level stands prior to the onset of northern hemisphere cooling and sustained glaciation (Morgan, 1986; Hulbert, 2001; Zachos et al., 2001, 2008; Miller et al., 2005). Late Miocene (~10–7 Ma) sea levels in Florida and around the world were highly variable (Hulbert, 2001; Miller et al., 2005). Imprecise chronostratigraphic resolution at most fossil bearing localities in Florida limits our ability to pinpoint exact time intervals and quantify sea levels.

Nevertheless, we still propose that tomistomine presence suggests periods of higher sea level stands, which could help in future research on Neogene sea level change in peninsular Florida.

5. Summary and Conclusions

This study provides isotopic evidence for crocodylian paleoecology during the Miocene in Florida. The major findings are summarized here: (1) The tooth enamel carbonate of fossil alligators and tomistomines can be differentiated definitively by $\delta^{13}\text{C}$ values, and less reliably by $\delta^{18}\text{O}$ values. (2) The more positive $\delta^{13}\text{C}$ values of fossil tomistomines suggest that they procured prey items primarily from estuarine/marine ecosystems. This supports the hypothesis of Auffenberg (1954); “*Gavialosuchus*” *americanus* likely inhabited shallow marine ecosystems. The more negative $\delta^{13}\text{C}$ values of alligators suggest that they fed mainly in freshwater ecosystems, or from different estuarine microhabitats than the tomistomines did. (3) Sympatric alligators and tomistomines co-inhabiting estuarine paleoenvironments likely partitioned ecological resources by feeding on different prey items in waters of differing salinities. This is primarily supported by $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ σ values showing marine affinities for tomistomines and mostly freshwater affinities for alligators. (4) The presence and abundance of fossil tomistomines and alligators can help track late Miocene sea level changes in Florida. The loss of “*G.*” *americanus* from North America may be related to decreasing global sea levels and temperatures at the end of the Miocene, as well as roughly temporally equivalent faunal changes. *Alligator* may have shifted into the ‘empty’ estuarine niche space left behind by the extinct tomistomines in the ensuing Plio-Pleistocene.

These findings are important for a number of reasons. Perhaps most notably, we find that $\delta^{13}\text{C}$ values can readily distinguish between fossil crocodylians that fed on prey from different

biomes or microhabitats (i.e. marine versus freshwater). We also verify the utility of testing saltwater tolerance in extinct crocodylians using stable isotopes, as pioneered by Wheatley (2010). Saltwater tolerance is minimal or absent in most extant crocodylians, but this character was once more widespread across Crocodylia (Taplin et al., 1982, 1985; Taplin and Grigg, 1989; Wheatley et al., 2012). Conducting isotopic studies on extant populations of ocean-voyaging Saltwater crocodiles (*Crocodylus porosus*) could provide a better understanding of how tooth enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are affected by forays into the open seas between extended intervals in fluvial systems (Campbell et al., 2010). “*G.*” *americanus* and other extinct crocodylians might have engaged in behaviors most similar to those of extant *C. porosus* among living crocodylians, which could be evaluated using stable isotope analysis.

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1 **Whiting, Steadman, and Krigbaum Table Captions**

2

3 **Table 1.** Relevant data for sampled specimens in stable isotope analyses in this study. *Isotopic
4 values for UF 289204 (“*Gavialosuchus*” *americanus* from Haile 19A) were not corrected
5 because of its anomalous raw $\delta^{18}\text{O}$ value (see Results). Abbreviations: UF¹, BCL², NALMA³.
6 [Table intended to fit 2 columns of text.]

7

8 **Table 2.** Descriptive statistics for raw $\delta^{13}\text{C}$ (‰, vs. VPDB), $\delta^{18}\text{O}$ (‰, vs. VPDB) and $\delta^{18}\text{O}$ (‰,
9 vs. VSMOW) values for Miocene crocodylian tooth enamel sampled in this study. *UF 289204
10 (“*Gavialosuchus*” *americanus* from Haile 19A) is excluded because of its anomalous $\delta^{18}\text{O}$ value
11 (see Results). [Table intended to fit 1.5 columns of text.]

Table 1

Table 1.

					RAW	RAW	RAW	CORRECTED	CORRECTED	CORRECTED
UF Number	BCL Number	Taxon	Locality	Age (NALMA)	$\delta^{13}\text{C}$ (‰, vs VPDB)	$\delta^{18}\text{O}$ (‰, vs VPDB)	$\delta^{18}\text{O}$ (‰, vs VSMOW)	$\delta^{13}\text{C}$ (‰, vs VPDB)	$\delta^{18}\text{O}$ (‰, vs VPDB)	$\delta^{18}\text{O}$ (‰, vs VSMOW)
UF 289204	EN-13-2644	"Gavialosuchus"	Haile 19A	Hemphillian 1	-4.35	-7.35	*excluded			
UF 289205	EN-13-2642	"Gavialosuchus"	Haile 19A	Hemphillian 1	-2.88	-0.52	30.32	-3.38	0.68	31.56
UF 289206	EN-13-2649	"Gavialosuchus"	Haile 19A	Hemphillian 1	-4.58	-1.47	29.34	-5.08	-0.27	30.58
UF 053000	EN-13-2647	"Gavialosuchus"	Haile 19A	Hemphillian 1	0.21	-0.90	29.93	-0.29	0.30	31.17
UF 289203	EN-13-2643	"Gavialosuchus"	Love Bone Bed	Clarendonian 3	-1.74	-0.85	29.98	-2.24	0.35	31.22
UF 289202	EN-13-2645	"Gavialosuchus"	Love Bone Bed	Clarendonian 3	0.90	-0.74	30.10	0.40	0.46	31.33
UF 289201	EN-13-2646	"Gavialosuchus"	Love Bone Bed	Clarendonian 3	-0.67	-0.73	30.11	-1.17	0.47	31.34
UF 289209	EN-13-2650	Alligator sp.	Love Bone Bed	Clarendonian 3	-6.37	-0.30	30.55	-6.87	0.90	31.79
UF 289207	EN-13-2652	Alligator sp.	Love Bone Bed	Clarendonian 3	-10.36	-1.96	28.84	-10.86	-0.76	30.08
UF 289280	EN-13-2659	Alligator sp.	Love Bone Bed	Clarendonian 3	-10.95	-2.85	27.92	-11.45	-1.65	29.16
UF 041602	EN-13-2648	"Gavialosuchus"	McGehee Farm	Hemphillian 1	-0.73	-0.78	30.06	-1.23	0.42	31.29
UF 041632	EN-13-2660	"Gavialosuchus"	McGehee Farm	Hemphillian 1	-0.36	-1.33	29.49	-0.86	-0.13	30.73
UF 289279	EN-13-2661	"Gavialosuchus"	McGehee Farm	Hemphillian 1	-2.02	-2.09	28.71	-2.52	-0.89	29.94
UF 289211	EN-13-2651	Alligator sp.	McGehee Farm	Hemphillian 1	-7.30	-1.04	29.79	-7.80	0.16	31.02
UF 028912	EN-13-2653	Alligator sp.	McGehee Farm	Hemphillian 1	-8.14	-1.87	28.93	-8.64	-0.67	30.17
UF 272294	EN-13-2654	Alligator olseni	Thomas Farm	Hemingfordian 1	-10.00	-3.36	27.40	-10.50	-2.16	28.63
UF 258805	EN-13-2655	Alligator olseni	Thomas Farm	Hemingfordian 1	-6.89	-3.64	27.11	-7.39	-2.44	28.34
UF 272288	EN-13-2656	Alligator olseni	Thomas Farm	Hemingfordian 1	-7.11	-3.60	27.15	-7.61	-2.40	28.39
UF 272789	EN-13-2657	Alligator olseni	Thomas Farm	Hemingfordian 1	-8.94	-1.13	29.70	-9.44	0.07	30.93
UF 272292	EN-13-2658	Alligator olseni	Thomas Farm	Hemingfordian 1	-9.46	-3.25	27.51	-9.96	-2.05	28.75

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³North American Land Mammal Age

Table 2.

Taxon	<i>"Gavialosuchus" americanus</i> = Tomistominae				<i>Alligator</i> sp. = Alligatorinae		
Locality	Haile 19A	Love Bone Bed	McGehee Farm		Love Bone Bed	McGehee Farm	Thomas Farm
n	*(n = 3)	(n = 3)	(n = 3)		(n = 3)	(n = 2)	(n = 5)
$\delta^{13}\text{C}$ (‰, vs. VPDB)							
Mean	-2.90	-0.50	-1.04		-9.23	-7.72	-8.48
Std. Dev. (σ)	2.21	1.33	0.87		2.49	0.59	1.40
Range	-4.58 to 0.21	-1.74 to 0.90	-2.02 to -0.36		-10.95 to -6.37	-8.14 to -7.30	-10.00 to -6.89
$\delta^{18}\text{O}$ (‰, vs. VPDB)							
Mean	-0.96	-0.77	-1.40		-1.70	-1.46	-3.00
Std. Dev. (σ)	0.48	0.07	0.66		1.29	0.59	1.06
Range	-1.47 to -0.52	-0.85 to -0.73	-2.09 to -0.78		-2.85 to -0.30	-1.87 to -1.04	-3.64 to -1.13
$\delta^{18}\text{O}$ (‰, vs. SMOW)							
Mean	29.87	30.06	29.42		29.10	29.36	27.77
Std. Dev.	0.49	0.07	0.68		1.33	0.61	1.09
Range	29.34 to 30.32	29.98 to 30.11	28.71 to 30.06		27.92 to 30.55	28.93 to 29.79	27.11 to 29.70

Whiting, Steadman, and Krigbaum Figure Captions

Figure 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; figure 2); (B) is adapted from White (1942; figure 1). [Figure intended to fit 1 column of text. Should have white background with black letters and lines indicating skull bone sutures.]

Figure 2. Map of the continental USA highlighting Florida. Inset shows Miocene crocodylian fossil localities in Alachua and Gilchrist counties analyzed in this study. [Figure intended to fit 2 columns of text and be available in color online only.]

Figure 3. Resulting raw $\delta^{13}\text{C}$ and $\delta^{18}\text{O}_{\text{VPDB}}$ values from stable isotope analysis sorted by taxon. Values to the left of the dashed line represent *Alligator* (blue dots), whereas values to the right of the dashed line represent “*Gavialosuchus*” *americanus* (red diamonds). UF 289204 (“*Gavialosuchus*” *americanus* from Haile 19A) is excluded because of its anomalous $\delta^{18}\text{O}$ value (see Results). Skull silhouettes adapted from Figure 1. [Figure intended to fit 2 columns of text and be available in color online only.]

Figure 4. Resulting corrected $\delta^{13}\text{C}$ and $\delta^{18}\text{O}_{\text{VPDB}}$ values from stable isotope analysis sorted by taxon and locality. Values to the left of the dashed line represent *Alligator*, whereas values to the right of the dashed line represent “*Gavialosuchus*” *americanus*. UF 289204 (“*Gavialosuchus*” *americanus* from Haile 19A) is excluded because of its anomalous $\delta^{18}\text{O}$ value (see Results).

Means and standard deviations ($\pm 1\sigma$) are indicated by symbols and error bars, respectively. Skull silhouettes adapted from Figure 1. [Figure intended to fit 2 columns of text and be available in color online only.]

Figure 5. Resulting corrected $\delta^{13}\text{C}$ and $\delta^{18}\text{O}_{\text{VPDB}}$ standard deviation ($\delta^{18}\text{O} \sigma$) values from stable isotope analysis sorted by taxon and locality. Values to the left of the dashed line represent *Alligator*, whereas values to the right of the dashed line represent “*Gavialosuchus*” *americanus*. UF 289204 (“*Gavialosuchus*” *americanus* from Haile 19A) is excluded because of its anomalous $\delta^{18}\text{O}$ value (see Results). Means and standard deviations ($\pm 1\sigma$) are indicated by symbols and error bars, respectively. Skull silhouettes adapted from Figure 1. [Figure intended to fit 2 columns of text and be available in color online only.]

Figure 6. Qualitative crocodylian sea level proxy for the late Miocene of Florida. Presence and/or predominance of the marine- or estuarine-dwelling tomistomine crocodylian, “*Gavialosuchus*” *americanus* (such as at McGehee Farm and Haile 19A, two primarily estuarine early Hemphillian [Hh1] localities), suggests much higher sea levels than at present. On the other hand, predominance of the mostly freshwater-dwelling alligatorine crocodylian, *Alligator* (such as at Love Bone Bed, a chiefly freshwater, late Clarendonian [Cl3] locality), is more indicative of sea levels closer to those at present. Imprecise chronostratigraphic resolution at our fossil localities precludes quantification of sea levels using the sea level data of Miller et al. (2005). Skull silhouettes adapted from Figure 1. [Figure intended to fit 1.5 columns of text and be available in color online only.]

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6