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Oldest record of *Alligator* in southeastern North America

Alexander K. Hastings, Blaine W. Schubert, Jason R. Bourque, and Richard C. Hulbert, Jr.

ABSTRACT

The genus *Alligator* has been represented by large-bodied, predatory species in southeastern North America for at least 18 million years (early Miocene), in what is now the southeastern United States. However, the first occurrences of the genus were from a smaller-bodied species, *A. prenasalis*, known from South Dakota and Nebraska that are about 34 million years old (latest Eocene to earliest Oligocene). Ancestors of *A. prenasalis* were likewise small-bodied and are from the Great Plains. This 16 million-year-gap has left open questions regarding the arrival and body size shift of *Alligator* from what is now the Great Plains to southeastern North America. Recently studied fossil material from Florida exhibits the oldest occurrence of *Alligator* in the region (about 28–26 million years ago). A well-preserved premaxilla (UF 422816) bears the diagnostic premaxillary 'notch' of *Alligator*. Additional material from this and two other Oligocene sites in Florida are indicative of *Alligator* as well. These include well-developed osteoderms, which suggest possible maturity at small body size. As of now, no records of larger *Alligator* from this time (or older) have been recovered from the region, possibly indicating body size may not have increased in *Alligator* until the Miocene.

Alexander K. Hastings. Science Museum of Minnesota, Saint Paul, Minnesota 55102, USA. ahastings@smm.org
Blaine W. Schubert. Center of Excellence in Paleontology and Department of Geosciences, East Tennessee State University, Johnson City, Tennessee 37614, USA. schubert@etsu.edu
Jason R. Bourque, Division of Vertebrate Paleontology, Florida Museum of Natural History, Gainesville, Florida 32611, USA. jbourque@flmnh.ufl.edu
Richard C. Hulbert, Jr. Division of Vertebrate Paleontology, Florida Museum of Natural History, Gainesville, Florida 32611, USA. rhulbert@flmnh.ufl.edu

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INTRODUCTION

The earliest records of *Alligator* Cuvier, 1807, are small-bodied (1.1–2.6 m estimated total body length) and come from the latest Eocene of South Dakota (Higgins, 1971) and Nebraska (Figure 1; Whiting and Hastings, 2015). These belong to the basal species for the genus, *Alligator prenasalis* (Loomis, 1904), which are also found in earliest Oligocene strata from South Dakota (Higgins, 1971, with dates revised by Walker and Geissman, 2009). Alligatorine phylogeny is often poorly

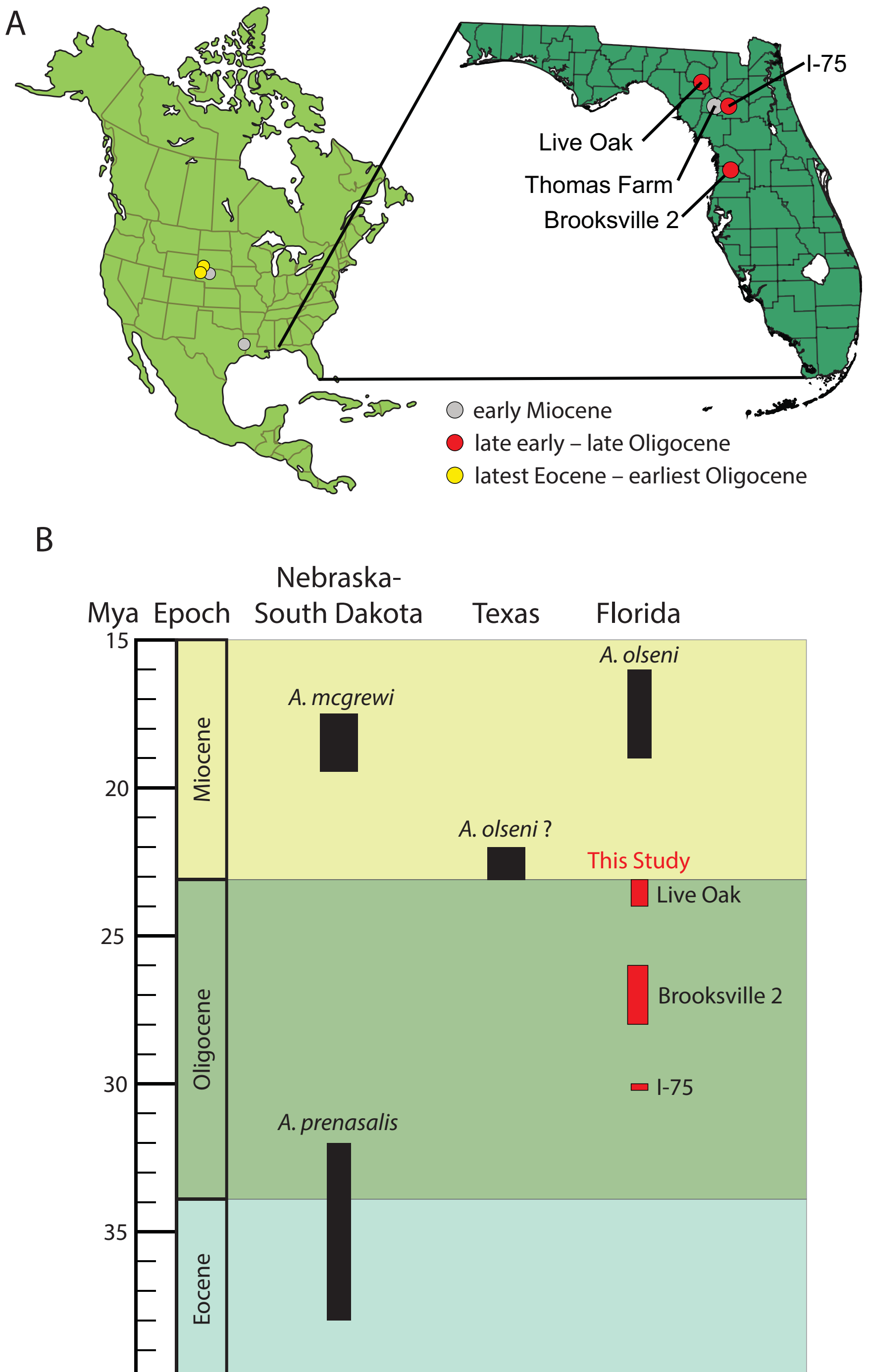

FIGURE 1. A: Map showing late Eocene – early Miocene fossil localities of *Alligator* in North America, with Florida enlarged. **B**: Geologic timescale showing occurrences of fossil *Alligator* in different regions.

resolved at the node basal to *Alligator*, but typically the small-bodied *Wannaganosuchus brachymanus* Erickson, 1982 (Paleocene; North Dakota) is recovered as the next most basal form (e.g., Brochu, 2004; Piras and Buscalioni, 2006; Snyder, 2007; Brochu, 2011; Hastings et al., 2016). Moreover, other species commonly recovered as very closely related to *Alligator* are also small-bodied and from high latitude regions of western North America, including: *Allognathosuchus wartheni* Case, 1925 (early Eocene, Wyoming), *Allognathosuchus polyodon* (Cope, 1873) (early Eocene, Wyoming; Mook, 1961), *Procaimanoidea kayi* Mook, 1941 (early Eocene, Wyoming), and *Procaimanoidea utahensis* Gilmore, 1946 (middle Eocene, Utah).

Fossil *Alligator* in Nebraska are not recovered again until the early Miocene, with *Alligator mcgrewi* Schmidt, 1941, in what was then referred to as the Marsland Formation, but is now split into the Runningwater Formation and Anderson Branch Formation (Tedford et al., 2004). *Alligator mcgrewi* possesses more derived features than *A. prenasalis*, including a dorsally facing external naris, also present in extant *Alligator* (Brochu, 1999; Brochu, 2011). Definitively identifiable *Alligator* fossils from southeastern North America first appeared in Florida from the early Miocene, belonging to the notably larger species *Alligator olseni* White, 1942 (Snyder, 2007), best known from the Thomas Farm site. Further reports of *A. olseni* have been assigned to material from the early Miocene of the Texas Gulf Coastal Plain (Albright, 1994). This has left a sizable gap between early Oligocene and early Miocene *Alligator* records (at least 9 million years; Figure 1).

We describe here the first published record of identifiable *Alligator* material from the late Oligocene Brooksville 2 site in central Florida (Figure 1). Brooksville 2 has a diverse fauna, including the burrowing toad *Rhinophrynus* Duméril and Bibron, 1841 (Blackburn et al., 2019), kinosternid turtle *Xenochelys* Hay, 1906 (Bourque, 2013), lizard *Anolis* Daudin, 1802 (Chovanec, 2014), mormoopid bat *Koopmanycteris* Morgan, Czaplewski, and Simmons, 2019 (Morgan et al., 2019), and the early horse *Miohippus* Marsh, 1874 (Hayes, 2000). We report additional fossil material from two other Oligocene sites in Florida, the I-75 site (Patton, 1969; Morgan et al., 2019) and Live Oak site (Frailey, 1978), that also appear to come from a small species of *Alligator*. While the *Alligator* fossils described here are not diagnostic beyond genus, they significantly extend its temporal range in the region by 10–8 million years (see Locality and Horizon).

Institutional Abbreviation

UF, University of Florida, Florida Museum of Natural History, Division of Vertebrate Paleontology, Gainesville, Florida, USA.

SYSTEMATIC PALEONTOLOGY

CROCODYLIA Gmelin, 1789,
sensu Benton and Clark, 1988
ALLIGATORIDAE Gray, 1844,
sensu Norell et al., 1994
ALLIGATORINAE Kälin, 1939

Alligator Cuvier, 1807
Crocodilia Hayes, 2000, table 1
dwarf alligatorid Bourque, 2013, p. 461

Referred specimens. Right premaxilla (UF 422816; Figure 2); complete parietal (UF 333984; Figure 3), fragment of a dorsal cranial bone (position uncertain; UF 425424; Figure 3), right articular (UF 422817; Figure 3), fragment of dentary (UF 425402; Figure 3), 12 isolated teeth (for catalog numbers, see Appendix 1; select teeth in Figure 3), neural arch of a dorsal vertebra (UF 424653; Figure 3), caudal vertebra (UF 425435; Figure 3), two unguals (UF 424655, UF 425405; Figure 3), and 83 partial to complete osteoderms (for catalog numbers, see Appendix 1; select osteoderms in Figure 3).

Locality and horizon. Brooksville 2 is a series of at least five fissure-fill deposits of laminated clay and sand, formed within the older Suwannee Limestone, 35.5–33.3 Ma (Hayes, 2000). The site is near the town of Brooksville, in Hernando County, Florida (Figure 1). The age of the deposit was considered to be 26–25 Ma by Tedford et al. (2004) based on mammalian biochronology. Later analysis by Czaplewski and Morgan (2012) and Morgan et al. (2019) suggested a slightly older age range of 28–26 Ma for Brooksville 2. The premaxilla is from Quarry 1E, although some specimens are from Quarries 1A, 1B, 1D, and some of uncertain provenience within the site (further details in Appendix 1). Much of the material at this quarry is thought to have arrived via subaqueous transport through karst solution pipes (Hayes, 2000). There were no fissures or sinkholes with younger fossils in this part of the quarry, and the unusual orange color of the *Alligator* tooth enamel (Figure 3E–J) is also observed on Oligocene mammals from the same fissure-fills (e.g., Czaplewski and Morgan, 2012).

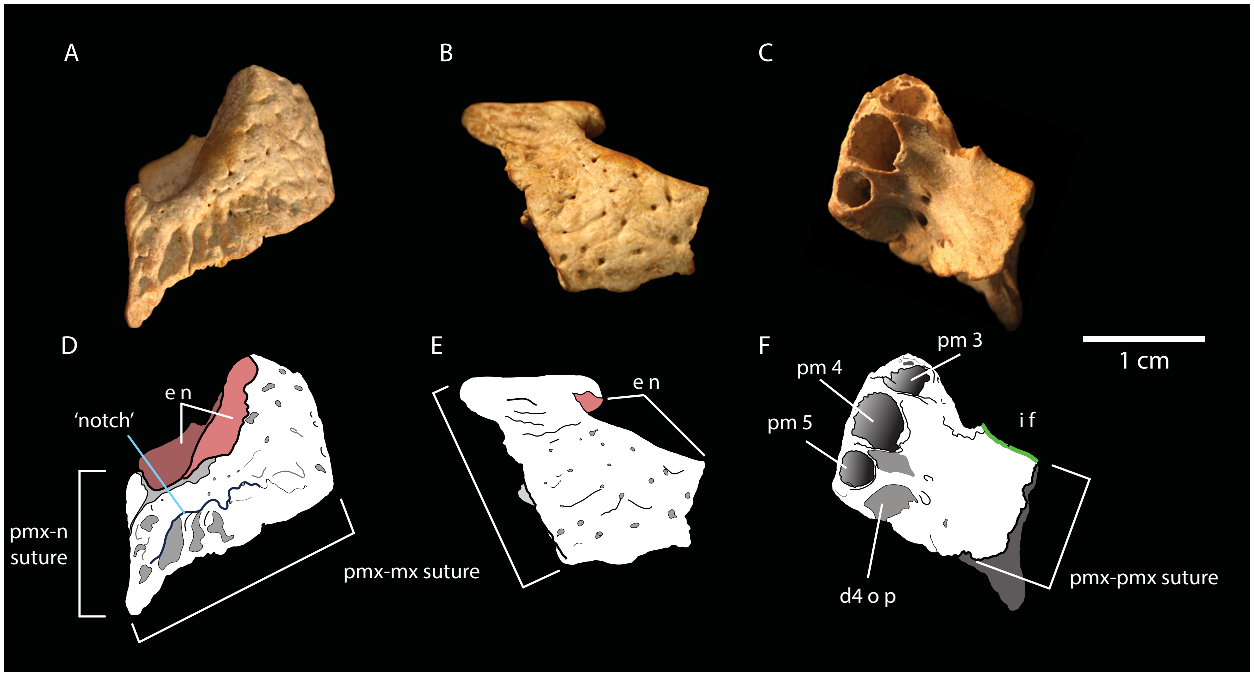

FIGURE 2. Right premaxilla of *Alligator* from the late Oligocene Brooksville 2 site in northern Florida (UF 422816). Element shown in dorsal (**A, D**), lateral (**B, E**), and ventral (**C, F**) views, with photos and interpretive sketches. Abbreviations: **d4 o p,** occlusal pit for the fourth dentary tooth; **e n**, external naris; **i f**, incisive foramen; **pm 3–5**, premaxillary alveoli 3–5; **pmx-mx**, premaxillary-maxillary; **pmx-n**, premaxillary-nasal; **pmx-pmx**, premaxillary-premaxillary.

Description. The premaxilla recovered from Brooksville 2 (UF 422816) bears the characteristic premaxillary 'notch' alongside the naris that defines the genus *Alligator* (Figure 2; Brochu, 1999; Brochu, 2011). Moreover, it has a forward-facing external naris, consistent with *A. prenasalis* (Brochu, 1999). This is counter to the more dorsal-facing naris of *A. olseni* and the extant *Alligator mississippiensis* (Daudin, 1802) (Brochu, 1999). Because the anterior end of the premaxilla is missing, and no part of the nasal is preserved, it is unclear whether or not the naris would have been fully bisected, as in other *Alligator* (Brochu, 1999). However, as the premaxilla curves back anteriorly along the nasal suture, we can say the nasal almost certainly penetrated well into the naris. UF 422816 bears three preserved alveoli, although more were likely present in the anterior broken portion. Based on the presence of the suture with the maxillary, these would be the third through fifth positions. Of these three preserved alveoli, the fourth is the largest, followed by the third, then the fifth (see measurements in Table 1). Sutural surfaces are preserved with the right maxilla (posteriorly), left premaxilla (ventrally), and right nasal (medially). Part of an occlusal pit is preserved at the sutural contact with the right maxilla, for reception of the fourth dentary tooth. This character is consistent across all *Alligator* species (Brochu, 1999; Brochu, 2011), and is distinct from Crocodylidae as well as Oligocene *Thecachampsa antiquus* Leidy, 1852 (synonymized with *Gavialosuchus*; Myrick, 2001; Brochu, 2011). The dorsal premaxillary process extends posteriorly only slightly between the nasal and maxillary bones, indicating a rather short snout. This process is also short in the fairly brevirostrine *Alligator* species, *A. mcgrewi* (Schmidt, 1941), and makes a similar angle from the acute posterior end between the nasal and maxillary sutures. This angle of the dorsal premaxillary process is wider in other *Alligator* species, including extant *A. mississippiensis*. The dorsal ornamentation is highly developed and rugose for such a small bone. The degree of pitting is typical of extant *Alligator* that are well beyond sexual maturity, yet the size is similar to an immature individual.

The parietal recovered from Brooksville 2 (UF 333984) is isolated, but complete, including sutures with the frontal, postorbital, squamosal, and supraoccipital (Figure 3). The frontoparietal suture is convex and remains on the skull table. The dermal part of the parietal overhangs the supratemporal fenestra weakly. There is a shallow fossa at the anteromedial corner of the supratemporal fenestra, and the medial parietal wall is

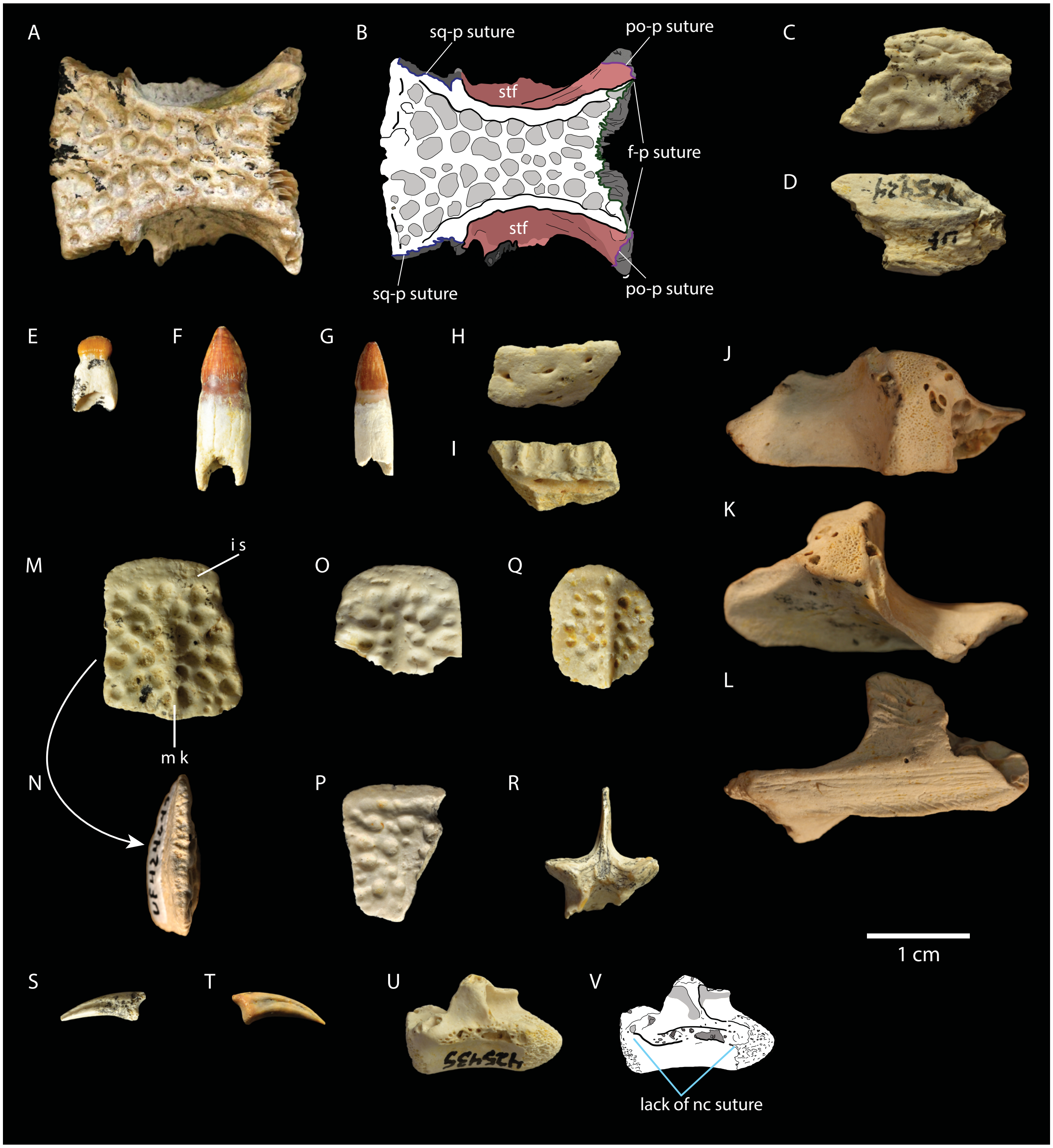

FIGURE 3. *Alligator* fossils from the late Oligocene Brooksville 2 site in northern Florida. **A**, **B**: Dorsal view of parietal (UF 333984). **C**, **D**: Cranial fragment (UF 425424) in dorsal (**C**) and ventral (**D**) views; position is uncertain. **E**: Alligatorid tooth from posterior dentition (UF 422818). **F**: Alligatorid tooth from middle dentition (UF 422819). **G**: Alligatorid tooth from middle dentition (UF 422820). Fragment of right dentary (UF 425402) in lateral (**H**) and medial (**I**) views. Right articular (UF 422817) in dorsal (**J**), lateral (**K**), and medial (**L**) views. Dorsal osteoderm (UF 424647) in dorsal view (**M**) and left lateral view (**N**). Anterior portion of osteoderm (UF 425398) in dorsal view (**O**). Partial osteoderm (UF 422827) in dorsal view (**P**). Osteoderm (UF 425395) in dorsal view (**Q**). Neural arch of a dorsal vertebra (UF 424653) in posterior view (**R**). Ungual (UF 424655) in lateral view (**S**). Ungual (UF 425405) in lateral view (**T**). **U**, **V**: Caudal vertebra in left lateral view (UF 425435). Abbreviations: **f-p**, frontoparietal; **i s**, imbricating shelf; **m k**, median keel; **nc**, neurocentral; **po-p**, postorbital-parietal; **sq-p**, squamosal-parietal; **stf**, supratemporal fenestra.

TABLE 1. Measurements of the premaxilla UF 422816 from the Brooksville 2 fossil site. All measurements given in mm. Note: Measurements of the 3rd premaxillary alveolus are not provided here because it is incomplete.

4th Premaxillary Alveolus	Length	4.28
	Width	3.92
5th Premaxillary Alveolus	Length	2.78
	Width	2.63
Premaxillary-Maxillary Suture	Length	19.74
Premaxillary-Premaxillary Suture	Length	10.91
Premaxillary-Nasal Suture	Length	12.05

imperforate. The parietal and squamosal meet along the posterior wall of the supratemporal fenestra. The skull table is planar at maturity and does not slope ventrally. There is no supraoccipital exposure on the dorsal surface of the parietal (Figure 2), which is consistent with *A. mcgrewi, A. olseni* and *A. mississippiensis* but not with *A. prenasalis* (Brochu, 1999). The supratemporal fenestra is longer than wide, with a thick posterior bar. There is a recess that connects with the pneumatic system (sensu Brochu, 2011).

The 12 preserved teeth from Brooksville 2 exhibit morphology that is consistent with *Alligator* (Figure 3). These include the globidontan morphology of posterior dentition (Figure 3E), as well as spade-shaped morphology from the middle of the jaw (Figure 3F-G). Several specimens include full roots, indicating they were likely not shed teeth. These teeth are also consistent in size with the premaxilla (UF 422816) and are inconsistent with that of contemporary *Thecachampsa*, which are longer and recurved in the middle of the jaw and more triangular in the rear (Myrick 2001).

A caudal vertebra was recovered at Brooksville 2 (Figure 3U-V). Although only partial, it appears to represent roughly the mid-section of the tail. This vertebra is of small size (14.78 mm centrum length) and exhibits a fully closed neurocentral suture.

A total of 83 partial to complete osteoderms were recovered from Brooksville 2 (Figure 3). These have the characteristic patterns of a square or anteroposteriorly rectangular shape, median keel, anterior imbricating shelf, and dorsal pitting found in *Alligator*. The more complete osteoderms can be recognized as belonging to the dorsal shield, rather than the nuchal shield, due to the development of the highly rectangular shape. Several osteoderms are complete enough to exhibit fully-developed edges and lateral sutures (Figure 3), which are consistent with individuals well beyond yearling age (see Discussion). The presence of a keel is inconsistent with *Thecachampsa*, which also has mediolaterally rectangular osteoderms, rather than anteroposteriorly rectangular ones (Myrick, 2001).

CROCODYLIA Gmelin, 1789,
sensu Benton and Clark, 1988
ALLIGATORIDAE Gray, 1844,
sensu Norell et al., 1994

Referred specimens. Material from Live Oak (Figure 4) includes: three isolated teeth (UF 424639–41), two caudal vertebrae (UF 424637–8), and four osteoderms (UF 424633–36). A partial osteoderm (UF 16729; Figure 5) from the I-75 site is referred as well.

Localities and horizons. The Live Oak fossil site (a.k.a. SB-1A; Figure 1) represents an unstratified sequence of conglomerate deposited in a single fissure in the Suwanee Limestone (Frailey, 1978). Mammalian biochronology suggests this site is slightly younger than Brooksville 2, at about 25–24 Ma (Figure 1; Tedford et al., 2004). Fossils from the I-75 site (Figure 1) were recovered from a small karst solution fill, exposed during road construction. The geologic age is around 30 Ma, either late Whitneyan or early Arikareean (Patton, 1969; Hayes, 2000; Morgan et al., 2019). Other than the fossils of shark teeth and other marine fishes from the limestone bedrock, all the age-diagnostic fossils from these two localities provide a consistent date with no evidence of contamination of younger material.

Description. The additional three teeth preserved from Live Oak likewise display morphology entirely consistent with *Alligator* (Figure 4). More specifically, these teeth display the typical spade-shaped morphology from the middle of the jaw. One specimen also includes a full root, suggesting it was likely not a shed tooth (UF 424639; Figure 4B). Again, these teeth are consistent in size with the premaxilla from Brooksville 2 (UF 422816) and are inconsistent with that of contemporary *Thecachampsa* (Myrick, 2001).

Two caudal vertebrae were recovered at Live Oak (Figure 4). Similar to Brooksville 2, these seem to represent the mid-section of the tail. These vertebrae are of even smaller size (10.34–12.00 mm centrum length) and also exhibit fully closed neurocentral sutures.

Four osteoderms have been recovered at Live Oak (Figure 4) and a partial osteoderm has been recovered from the I-75 fossil site (Figure 5). Much like the remains at Brooksville 2, these are all of

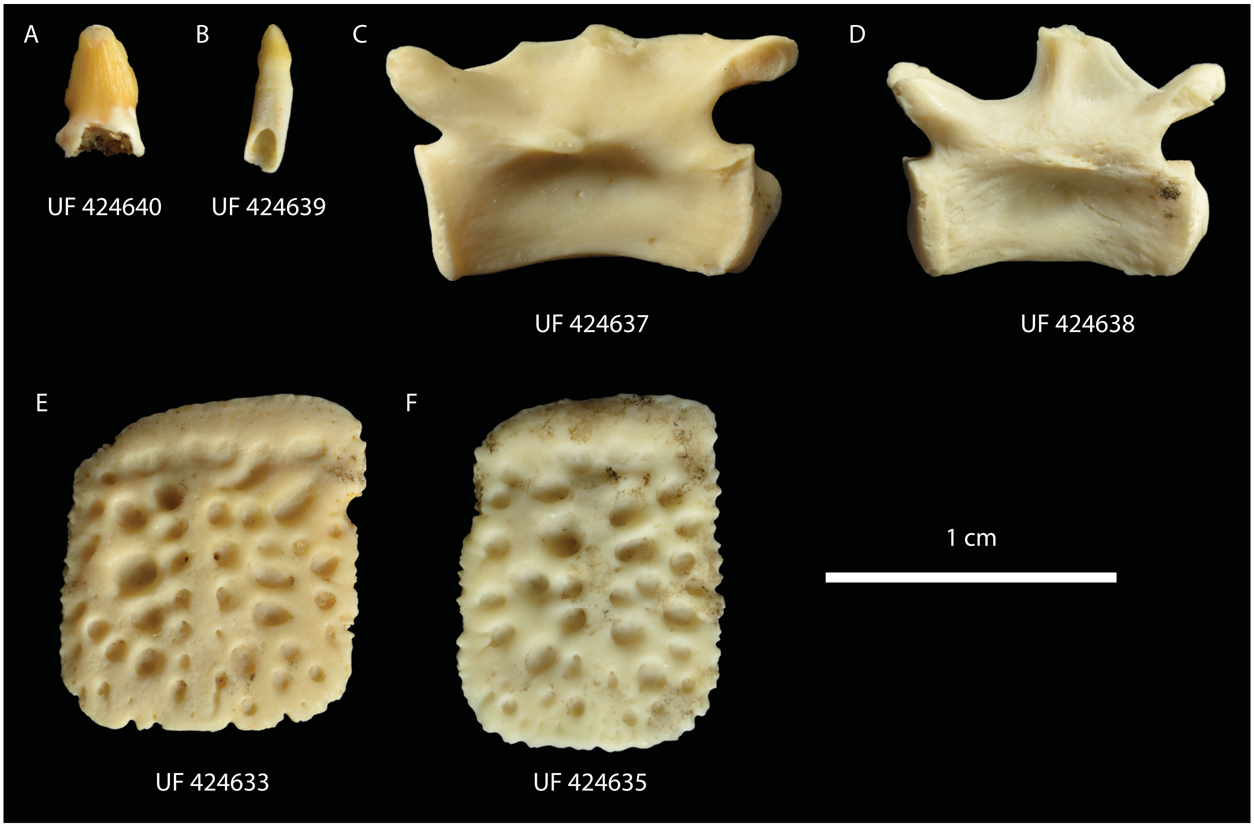

FIGURE 4. Alligatorid fossils from the Live Oak fossil site. **A**: Isolated tooth, likely mid-rostral position (UF 424640) in lingual view. **B**: Isolated tooth, likely anterior position (UF 424639) in lingual view. **C**: Caudal vertebra exhibiting a fully fused neurocentral suture (UF 424637) in left lateral view. **D**: Caudal vertebra exhibiting a fully fused neurocentral suture (UF 424638) in left lateral view. **E**: Osteoderm (UF 424633) in dorsal view. **F**: Osteoderm (UF 424635) in dorsal view.

small size, are anteroposteriorly rectangular, and possess a median keel, an anterior imbricating shelf, and dorsal pitting like that found in *Alligator*. The more complete osteoderms can be recognized as belonging to the dorsal shield. Again, these appear to represent individuals that were at least beyond yearling age (see Discussion). Not only are they much smaller, but they are inconsistent with the contemporary *Thecachampsa* (Myrick, 2001).

DISCUSSION

The premaxilla, UF 422816, exhibits the diagnostic character of a premaxillary 'notch' adjacent to the external naris, placing it within the genus *Alligator*. The morphology of the *Alligator* premaxilla indicates the ancestral condition of a forward-facing external naris, much like the older *A. prenasalis* of Nebraska and South Dakota (Whiting and Hastings, 2015). Likewise, the small size of the premaxilla, paired with its notable dorsal ornamentation indicates small body size despite relative maturity.

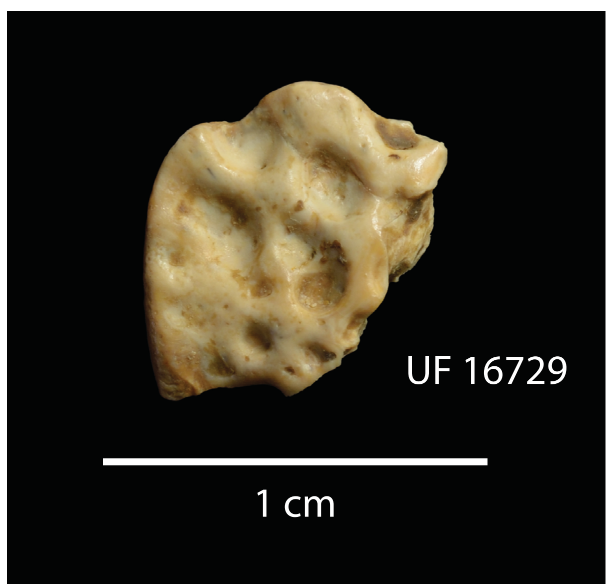

FIGURE 5. Isolated osteoderm fragment attributed to Alligatoridae from the I-75 fossil site (UF 16729) in dorsal view.

Alligator prenasalis has been estimated at 1.30–1.92 m in body length at adult size (Whiting and Hastings, 2015). In addition to similar morphology, UF 422816 has comparable size to the premaxillae of more completely preserved *A. prenasalis*. Conversely, this element is much smaller than the premaxillae of adult *A. olseni*, which typically has a larger body size of 1.71–2.41 m (calculated from data in Snyder, 2007, equations in Farlow et al., 2005). However, the lack of supraoccipital exposure of the parietal (UF 333984) is not characteristic of *A. prenasalis*, but would be consistent with *A. olseni* (Brochu, 1999). Thus, the *Alligator* from Brooksville 2 may indicate a transitional form between these two species; however, having material that can reliably connect both features as belonging to a single specimen would be needed.

The features of the material included here likely indicate a new species of *Alligator*, but due to the lack of material from other parts of the skull typically used to diagnose *Alligator* species, we refrain from assigning a new taxon here. We included the postcranial remains from Brooksville 2 as referred specimens due to the total lack of other crocodylian material from the site and their close proximity in size to the individual that would have yielded the premaxilla. Due to the nature of fossil preservation, it is not possible to confidently assign any two bones as having belonged to the same individual. Although all seem to indicate small body size, they do seem to have some size variation, indicating that this was almost certainly more than one individual.

Given the presence of early caimanines in North America during the Paleogene, it is worth some comparison to this group. For example, *Tsoabichi* is known from multiple individuals in southwest Wyoming from the early Eocene, ranging from 51.98 to 49.25 million years old (Walter et al., 2021). This taxon is similar to the Brooksville 2 *Alligator* in having an anterodorsally facing naris, but is missing the diagnostic thin crest encircling it. In addition, *Tsoabichi* has a broad exposure of the supraoccipital bone on the skull table (Walter et al., 2021), which the Brooksville 2 specimen does not. Similarly, the parietal of *Protocaiman* (Paleocene of Argentina) also possesses dorsal exposure of the supraoccipital bone on the skull table (Bona et al., 2018). Unfortunately, the premaxilla is unknown for this taxon. A newly described taxon from the Eocene of Texas, *Chinatichampsus wilsonorum* includes a skull with a partial premaxilla (Stocker et al., 2021). This bone preserves an occlusal pit lying medial to the tooth row and nearly entirely anterior to the premaxillary-maxillary suture. This is unlike the occlusal pit of UF 422816, which is much more in-line with the tooth row and split across the suture. Premaxillary tooth positions were not assigned for *Chinatichampsus*, but images indicate the relative proportions of the alveoli anterior to the premaxillary-maxillary suture are in quite different proportions from UF 422816 (Stocker et al., 2021). Moreover, *Chinatichampsus* also has dorsal exposure of the supraoccipital bone (Stocker et al., 2021).

Another alligatoroid that could potentially have occurred in Florida at one time, *Bottosaurus harlani*, a Cretaceous–Paleocene taxon known from New Jersey, lacks the premaxillary notch and has four alveoli rather than five; the incisive foramen is also much larger (Cossette and Brochu, 2018). In addition, *Bottosaurus* has broad exposure of the supraoccipital on the skull table (Cossett and Brochu, 2018). There is very little overlapping material of *Bottosaurus fustidens* from the Paleocene of Texas, only a small portion of one premaxilla and the anterior portion of the parietal (Cossette, 2021). These are not known well enough for a meaningful comparison with the Brooksville 2 fossil *Alligator*.

There are fossil crocodyliforms from the Oligocene and Miocene of the Caribbean that do not (as of yet) have a record from the mainland, but hypothetically could have appeared in Florida. *Aktiogavialis* is a gryposuchine gavialoid known from a braincase in the Oligocene of Puerto Rico (Velez-Juarbe et al., 2007). The parietal from Brooksville 2 differs significantly from *Aktiogavialis*, in that the suproccipital has no dorsal exposure, and the mid-point of the posterior edge does not form a point with indentations directed anteriorly on either side (Figure 3; Velez-Juarbe et al., 2007). Moreover, other gryposuchines have premaxillae with a very different shape, including: (1) four alveoli rather than five, (2) very elongate dorsal and ventral posterior processes, (3) no 'notch' present on the dorsal surface, and (4) do not have the deep pit for occlusion with the lower jaw seen at the premaxillary-maxillary suture, and instead have a tight constriction allowing for the lower dentition to sit outside of the premaxilla entirely (e.g., De Souza et al., 2018). Additional unidentified crocodyliform remains from the Oligocene and Miocene of Puerto Rico, as well as the Miocene of Cuba are rather fragmentary, and there is very little overlap from which to compare the material (Brochu and Jimenez-Vazquez, 2014). The two osteoderms from the late Oligocene of Puerto Rico bear more resemblance to the rectangular and low, small

TABLE 2. Length measurements of the premaxillary-maxillary suture in *Alligator*. When possible, these were measured on both the left (L) and right (R) sides. In these cases, the value is an average of those two measurements. All *A. mississippiensis* specimens were from wild populations. Institutional abbreviations: **ETMNH-Z,** East Tennessee State University Museum of Natural History - Zoology Collection; **UF,** Vertebrate Paleontology Collection at the University of Florida, Florida Museum of Natural History.

Taxon	Catalog Number	Premax-Max Suture Length (mm)	Side	Dorsal Skull Length (mm)
A. mississippiensis	ETMNH-Z 7217	37.72	L	271.00
A. mississippiensis	ETMNH-Z 507	22.71	R	177.46
A. mississippiensis	ETMNH-Z 265	76.21	L/R	506.00
A. mississippiensis	ETMNH-Z 7207	41.23	L/R	291.00
A. mississippiensis	ETMNH-Z 3036	65.35	L/R	438.00
A. mississippiensis	ETMNH-Z 7203	45.92	L/R	315.00
A. mississippiensis	ETMNH-Z 6920	53.85	L/R	390.00
A. mississippiensis	ETMNH-Z 7208	63.50	L/R	420.00
A. mississippiensis	ETMNH-Z 7205	54.11	L/R	375.00
A. mississippiensis	ETMNH-Z 5025	22.59	L/R	181.00
A. mississippiensis	ETMNH-Z 2957	51.53	L/R	362.00
A. mississippiensis	ETMNH-Z 509	39.51	L/R	286.00
A. mississippiensis	ETMNH-Z 3024	45.89	L	328.00
A. mississippiensis	ETMNH-Z 3366	48.28	L/R	357.00
A. mississippiensis	ETMNH-Z 487	38.88	L/R	285.00
A. mississippiensis	ETMNH-Z 17916	19.81	L/R	163.00
A. mississippiensis	ETMNH-Z 5289	21.98	L/R	172.00
A. mississippiensis	ETMNH-Z 3371	38.93	L/R	296.00
A. mississippiensis	ETMNH-Z 10937	18.27	L/R	149.00
A. mississippiensis	ETMNH-Z 7144	30.31	L/R	220.00
A. mississippiensis	ETMNH-Z 266	75.31	L/R	480.00
Alligator sp.	UF 422816	19.74	R	See Table 3

keels of gavialoids than the ones presented here (Brochu et al., 2007). Of the two crocodyliform osteoderms described from the Miocene of Cuba, one is square and has a modest keel that somewhat resembles the Florida material described here. The other is very round with a prominent keel, which does not match the ones described here. Both are significantly larger as well.

Given the limited material available, a new method was developed to estimate the body size of UF 422816. A study set of 22 extant *Alligator* skulls were measured for six dimensions that could be compared to UF 422816: length of the premaxillary-maxillary suture, length of the premaxillary-premaxillary suture, length and width of the fourth premaxillary alveolus, and length and width of the fifth premaxillary alveolus. These were then compared to dorsal skull length. Of these six, by far the greatest correlation between premaxillary measurement (Table 2) and dorsal skull length (Table 3) was the length of the premaxillary-maxillary suture (R^2 = 0.9917; Table 4). Using a best-fit linear regression, determined from this study set (Figure 6), the dorsal skull length of UF 422816 is estimated as 15.9 cm. Established correlations have been found between dorsal skull length and total body length in *Alligator* (Woodward et al., 1995; Young et al., 2011). Applying a known regression for extant *Alligator* yields an estimated total body length for UF 422816 as 1.18 m.

The osteoderms, which come from the dorsal shield over the trunk, are at least somewhat informative in terms of relative maturity. A study of development in *Alligator* has shown that osteoderm calcification occurs relatively late in ontogeny: "In *A. mississippiensis* the earliest sign of calcification

TABLE 3. Dorsal skull lengths used as a proxy for body size in basal *Alligator* and its ancestors. *Alligator mississippiensis* with locations specified are from wild populations; specimens with "No Data" may be from either wild or captive populations. ETMNH-Z 10937 and 17916 are known captive specimens. Data are plotted in Figure 7. Institutional Abbreviations: **AMNH**, American Museum of Natural History, New York, New York, USA; **CM**, Carnegie Museum of Natural History, Pittsburg, Pennsylvania, USA; **ETMNH-Z**, East Tennessee State University Museum of Natural History - Zoology Collection, Johnson City, Tennessee, USA; **FMNH**, Field Museum of Natural History, Chicago, Illinois, USA; **MCZ**, Museum of Comparative Zoology, Vertebrate Paleontology Collection, Harvard University, Cambridge, Massachusetts, USA; **SDSM**, South Dakota School of Mines Museum of Natural History, Rapid City, South Dakota, USA; **SMM P**, Science Museum of Minnesota Paleontology Collection, Saint Paul, Minnesota, USA; **UF**, Vertebrate Paleontology Collection at the University of Florida, Florida Museum of Natural History, Gainesville, Florida, USA; **USNM;** United States National Museum of Natural History, Vertebrate Paleontology Collection, Washington, D.C., USA; **YPM-PU**, Yale Peabody Museum and Princeton University Vertebrate Paleontology Collection, New Haven, Connecticut, USA. (Continued on next page.)

Taxon	Geologic Age	Skull Length (mm)	Location	Reference	Specimen Number
Allognathosuchus wartheni	early Eocene	106	Wyoming	Miller-Camp, 2016	YPM-PU 8357
Allognathosuchus wartheni	early Eocene	163	Wyoming	Miller-Camp, 2016	YPM-PU 8449
Allognathosuchus wartheni	early Eocene	136	Wyoming	Miller-Camp, 2016	MCZ 4367
Allognathosuchus polyodon	early Eocene	172	Wyoming	Mook, 1961	AMNH 6049[1]
Procaimanoidea kayi	early Eocene	98	Wyoming	Mook, 1941	CM 9600
Procaimanoidea utahensis	middle Eocene	115	Utah	Gilmore, 1946	USNM 15996[2]
Wannaganosuchus brachymanis	Paleocene	144	North Dakota	This Study	SMM P76.28.247
Alligator prenasalis	early Oligocene	198	South Dakota	This Study	MCZ 1014
Alligator prenasalis	Eocene/ Oligocene	215	South Dakota	This Study	MCZ 1015
Alligator prenasalis	Eocene/ Oligocene	223	South Dakota	Miller-Camp, 2016	YPM 13799
Alligator prenasalis	Eocene/ Oligocene	215	South Dakota	Miller-Camp, 2016	YPM 14063
Alligator prenasalis	late Eocene	278	South Dakota	Miller-Camp, 2016	YPM 16273
Alligator prenasalis	Eocene/ Oligocene	218	South Dakota	Miller-Camp, 2016	SDSM 243
Alligator olseni	early Miocene	257	Florida	This Study	MCZ 1899
Alligator olseni	early Miocene	223	Florida	This Study	MCZ 1887 [Type]
Alligator olseni	early Miocene	299	Florida	This Study	MCZ 101578
Alligator mcgrewi	middle Miocene	157	Nebraska	Miller-Camp, 2016	AMNH 7905
Alligator mcgrewi	middle Miocene	150	Nebraska	Miller-Camp, 2016	FMNH P 26242
Alligator mississippiensis	Modern	149	No data	This Study	ETMNH-Z 10937
Alligator mississippiensis	Modern	163	No data	This Study	ETMNH-Z 17916
Alligator mississippiensis	Modern	172	No data	This Study	ETMNH-Z 5289
Alligator mississippiensis	Modern	177	No data	This Study	ETMNH-Z 507
Alligator mississippiensis	Modern	181	Georgia	This Study	ETMNH-Z 5025
Alligator mississippiensis	Modern	220	Georgia	This Study	ETMNH-Z 7144
Alligator mississippiensis	Modern	271	Georgia	This Study	ETMNH-Z 7217

TABLE 3 (continued).

Taxon	Geologic Age	Skull Length (mm)	Location	Reference	Specimen Number
Alligator mississippiensis	Modern	285	Georgia	This Study	ETMNH-Z 487
Alligator mississippiensis	Modern	286	No data	This Study	ETMNH-Z 509
Alligator mississippiensis	Modern	291	Georgia	This Study	ETMNH-Z 7207
Alligator mississippiensis	Modern	296	Louisiana	This Study	ETMNH-Z 3371
Alligator mississippiensis	Modern	315	Georgia	This Study	ETMNH-Z 7203
Alligator mississippiensis	Modern	328	Georgia	This Study	ETMNH-Z 3024
Alligator mississippiensis	Modern	357	Louisiana	This Study	ETMNH-Z 3366
Alligator mississippiensis	Modern	362	South Carolina	This Study	ETMNH-Z 2957
Alligator mississippiensis	Modern	375	Georgia	This Study	ETMNH-Z 7205
Alligator mississippiensis	Modern	390	No data	This Study	ETMNH-Z 6920
Alligator mississippiensis	Modern	420	Georgia	This Study	ETMNH-Z 7208
Alligator mississippiensis	Modern	438	Georgia	This Study	ETMNH-Z 3036
Alligator mississippiensis	Modern	480	Arkansas	This Study	ETMNH-Z 266
Alligator mississippiensis	Modern	506	Arkansas	This Study	ETMNH-Z 265
Alligator sp.	Oligocene	158.97	Florida	This Study	UF 422816

[1]Estimated from Mook (1961; figure 1) using the preserved craniomandibular joint to approximate distal end of skull.
[2]Determined from Plate 11, figure 3 of Gilmore, 1946.

occurs approximately 1 year after hatching, in the area of the presumptive nuchal shield" (Vickaryous and Hall, 2008). Even at this stage, osteoderms begin development along the center, where the median keel eventually forms, then grow outward to the lateral edges (Vickaryous and Hall, 2008). Development of additional features such as lateral sutures and imbricating shelves occurs even later in ontogeny, further indicating growth well past the yearling stage for the Oligocene individuals. However, without morphological studies that track osteoderm features with maturity, there is not currently a way to be more definitive about how old these individuals were outside osteohistological analyses, which are beyond the scope of this paper.

TABLE 4. Statistical support for linear regressions of different premaxillary measurements against dorsal skull length for study set of extant *Alligator mississippiensis* specimens (n = 22; see Table 2). R^2 values are calculated for a 'best fit' line. Due to its higher congruence with the data, we selected the premaxillary-maxillary suture length as the best proxy for estimating dorsal skull length.

Premaxillary Measurement	R^2 Value
Overall Width	0.9125
Length of premaxillary-maxillary suture	0.9917
Length of left-right premaxillary suture	0.7712
Width of 4th Premaxillary Alveolus	0.9221
Length of 4th Premaxillary Alveolus	0.9149
Length of 5th Premaxillary Alveolus	0.9101

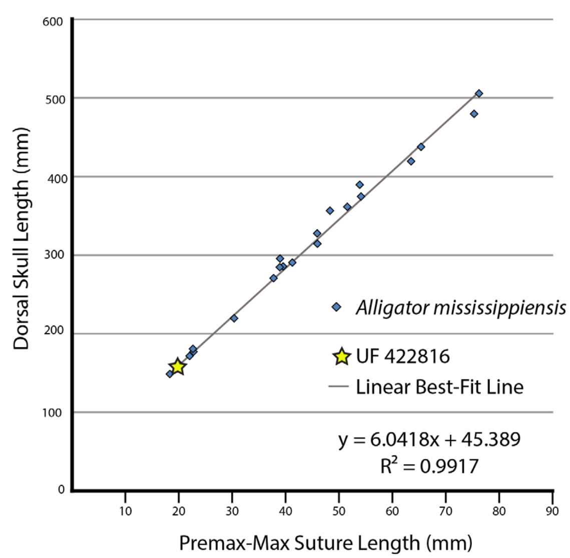

FIGURE 6. X-Y scatter plot of premaxillary-maxillary suture lengths compared to dorsal skull length of extant *Alligator* (n = 22). Linear regression is best-fit line (R^2 = 0.9917).

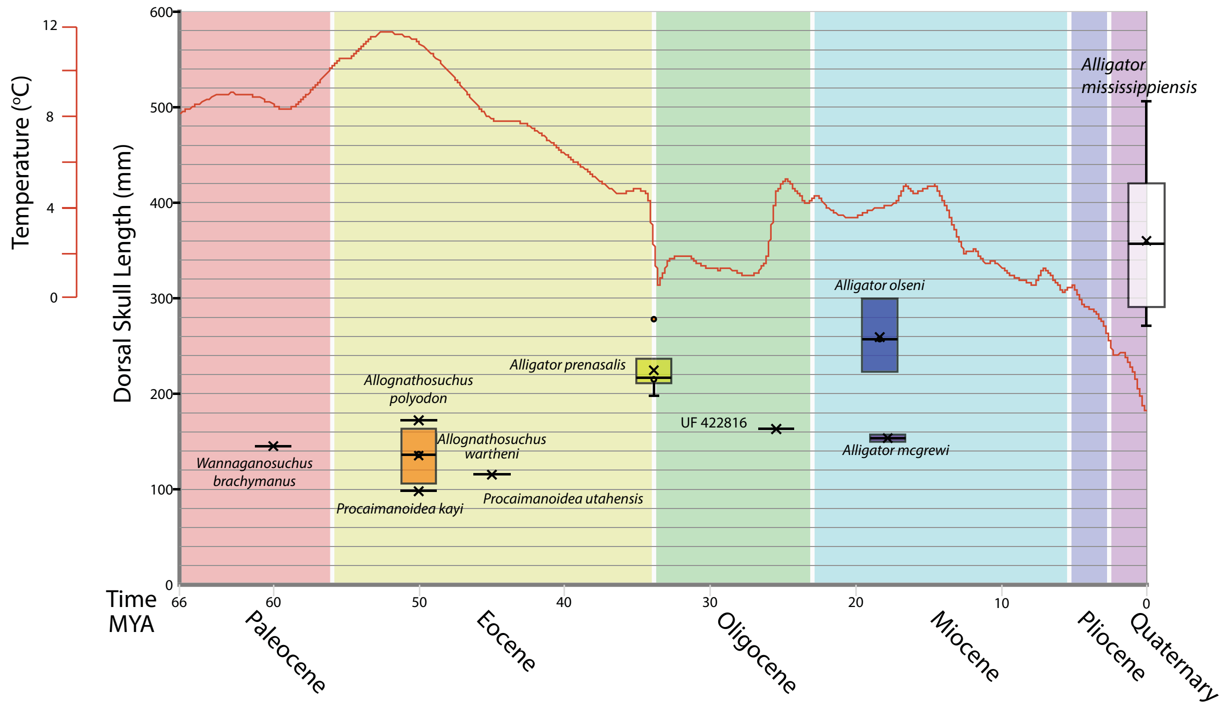

FIGURE 7. Box and whisker plots of dorsal skull length of published fossil *Alligator* specimens and extant *Alligator mississippiensis* (this study). For data, see Table 3. Time shown in millions of years ago (MYA). UF 422816, an isolated right premaxilla, was estimated following methods outlined in the main document. Most notable is that the estimated dorsal skull length for UF 422816 is small, similar to ancestral forms such as *Allognathosuchus*, *Procaimanoidea*, and *Wannaganosuchus*. Global temperature curve from Zachos et al. (2001).

Shortly after *Alligator* appears in the fossil record of the Great Plains, the region experienced a massive drop in mean annual temperature (8.2±3.1°C), at the beginning of the Oligocene (Zanazzi et al., 2007). Following this, temperature generally warmed through the Oligocene, particularly at the time of the Brooksville 2 fauna (Zachos et al., 2001), which has been further supported by pollen analysis on the eastern coast of North America (Kotthoff et al., 2015; Figure 7). Body size in ectothermic vertebrates often relates to mean annual temperature (Makarieva et al., 2005 a,b; Head et al., 2009). Paleotemperature data are currently lacking for the Oligocene of Florida, and thus temperature differences between the Great Plains and Florida at this time remain unknown. Given our current knowledge, *Alligator* may have originated in the Great Plains during the middle Paleocene–late Eocene and dispersed to the southeastern region of North America sometime prior to the late Oligocene. Large temperature drops in the Great Plains could have been a factor in this hypothetical dispersal. However, despite potentially being a warmer climate in Florida, small body size may have been retained, as no large-bodied individuals have yet been recovered at any Oligocene Florida site. This may indicate a lag between the relationships of body size and latitudinal migration. Figure 7 shows dorsal skull length (as a proxy for body size) across the ancestral *Alligator* taxa and Oligocene–Miocene species against global temperatures. The occurrence of UF 422816 is actually smaller than the known *Alligator prenasalis* adults recorded from higher latitudes, but again, sub-adult status cannot be fully ruled out. The position of UF 422816 in time; however, is prior to a significant increase in temperature that precedes the occurrence of the larger *Alligator olseni*, which may have been able to grow larger in these generally warmer temperatures. Meanwhile, *Alligator mcgrewi* retained small size in the presumably cooler latitude of Nebraska at the time. The morphological similarity and potential body size similarity between the Oligocene *Alligator* of Florida and those of the Great Plains indicates a possible faunal affinity between the two regions. Florida has been suggested as a post-Eocene refugium for the turtle *Xenochelys*, which has its latest fossil occurrence at Brooksville 2 and was previously known from the

Eocene of the midwestern United States (Bourque, 2012).

Alternatively, the records of *Alligator* in the Great Plains prior to the new material, combined with the sparse record of Eocene–Oligocene terrestrial deposits in eastern North America, may give an illusion of migration towards the southeast. Thus, it is possible that *Alligator* had a distribution that expanded to coastal areas when they occurred in the Great Plains, and over time climate change resulted in the extirpation of more northern populations. Further fossil material from the southeastern United States may clarify the origin and paleogeography of *Alligator*.

Regardless, the presence of *Alligator* in Florida during the Oligocene increases the antiquity of the genus in southeastern North America by an additional 10–8 million years, so it now has a ca. 26 million-year history in the region. During much of this time, *Alligator* has been the largest predator in its aquatic environment, but this fossil occurrence suggests the possibility that this niche may not have been the ancestral condition for southeastern populations.

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APPENDIX

APPENDIX 1. Additional catalog information about alligatorid specimens included in this study.

Collection	Catalog No	Element	Site	Count (No. of Specimens)	Collection Date
UF	333984	parietal	BROOKSVILLE QUARRY 1E	1	4/12/1994
UF	422817	articular	BROOKSVILLE QUARRY 1	1	1994
UF	425402	dentary, fragment, edentulous	BROOKSVILLE QUARRY 1B	1	09/17/1994
UF	422821	osteoderm	BROOKSVILLE QUARRY 1	1	1994
UF	422822	osteoderm	BROOKSVILLE QUARRY 1	1	1994
UF	422823	osteoderm	BROOKSVILLE QUARRY 1	1	1994
UF	425428	osteoderm	BROOKSVILLE QUARRY 1	1	04/12/1994
UF	424649	osteoderm	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	424656	osteoderm	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	424657	osteoderm	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	424658	osteoderm	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	424666	osteoderm	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	425392	osteoderm	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	425393	osteoderm	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	425394	osteoderm	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	425395	osteoderm	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	425396	osteoderm	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	425397	osteoderm	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	424646	osteoderm	BROOKSVILLE QUARRY 1D	1	04/12/1994
UF	424647	osteoderm	BROOKSVILLE QUARRY 1D	1	04/12/1994
UF	424648	osteoderm	BROOKSVILLE QUARRY 1D	1	04/12/1994
UF	425418	osteoderm	BROOKSVILLE QUARRY 1E	1	1994
UF	425419	osteoderm	BROOKSVILLE QUARRY 1E	1	1994
UF	425432	osteoderm	BROOKSVILLE QUARRY 1E	1	09/17/1994
UF	425423	osteoderm, fragment	BROOKSVILLE QUARRY 1E	1	1994
UF	425411	osteoderm, fragment	BROOKSVILLE QUARRY 1B	22	09/17/1994
UF	425412	osteoderm, fragment	BROOKSVILLE QUARRY 1B	4	04/12/1994
UF	422829	osteoderm, partial	BROOKSVILLE QUARRY 1	1	1994
UF	422827	osteoderm, partial	BROOKSVILLE QUARRY 1	1	1994
UF	422825	osteoderm, partial	BROOKSVILLE QUARRY 1	1	1994
UF	422828	osteoderm, partial	BROOKSVILLE QUARRY 1	1	1994
UF	422826	osteoderm, partial	BROOKSVILLE QUARRY 1	1	1994
UF	422824	osteoderm, partial	BROOKSVILLE QUARRY 1	1	1994
UF	425431	osteoderm, partial	BROOKSVILLE QUARRY 1	1	04/12/1994
UF	425429	osteoderm, partial	BROOKSVILLE QUARRY 1	1	04/12/1994
UF	425430	osteoderm, partial	BROOKSVILLE QUARRY 1	1	04/12/1994
UF	424650	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	424651	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	424652	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	424659	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	05/16/1994

Collection	Catalog No	Element	Site	Count (No. of Specimens)	Collection Date
UF	424660	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	424661	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	424662	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	424663	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	424664	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	424665	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	05/16/1994
UF	425398	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	425399	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	425400	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	425401	osteoderm, partial	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	425406	osteoderm, partial	BROOKSVILLE QUARRY 1B	1	09/17/1994
UF	425407	osteoderm, partial	BROOKSVILLE QUARRY 1B	1	09/17/1994
UF	425408	osteoderm, partial	BROOKSVILLE QUARRY 1B	1	09/17/1994
UF	425409	osteoderm, partial	BROOKSVILLE QUARRY 1B	1	09/17/1994
UF	425410	osteoderm, partial	BROOKSVILLE QUARRY 1B	1	09/17/1994
UF	425413	osteoderm, partial	BROOKSVILLE QUARRY 1B	1	04/12/1994
UF	425417	osteoderm, partial	BROOKSVILLE QUARRY 1C	1	09/17/1994
UF	425420	osteoderm, partial	BROOKSVILLE QUARRY 1E	1	1994
UF	425421	osteoderm, partial	BROOKSVILLE QUARRY 1E	1	1994
UF	425422	osteoderm, partial	BROOKSVILLE QUARRY 1E	1	1994
UF	425433	osteoderm, partial	BROOKSVILLE QUARRY 1E	1	09/17/1994
UF	425434	osteoderm, partial	BROOKSVILLE QUARRY 1E	1	09/17/1994
UF	424655	phalanx, distal	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	425405	phalanx, distal	BROOKSVILLE QUARRY 1B	1	09/17/1994
UF	422816	premaxilla, edentulous	BROOKSVILLE QUARRY 1E	1	09/17/1994
UF	425424	skull element, fragment	BROOKSVILLE QUARRY 1E	1	1994
UF	422819	tooth	BROOKSVILLE QUARRY 1	1	1994
UF	422820	tooth	BROOKSVILLE QUARRY 1	1	1994
UF	422818	tooth	BROOKSVILLE QUARRY 1	1	1994
UF	425426	tooth	BROOKSVILLE QUARRY 1	1	04/12/1994
UF	425427	tooth	BROOKSVILLE QUARRY 1	1	04/12/1994
UF	425425	tooth	BROOKSVILLE QUARRY 1	1	04/12/1994
UF	425403	tooth	BROOKSVILLE QUARRY 1B	1	09/17/1994
UF	425404	tooth	BROOKSVILLE QUARRY 1B	1	09/17/1994
UF	425414	tooth	BROOKSVILLE QUARRY 1B	1	04/12/1994
UF	425415	tooth	BROOKSVILLE QUARRY 1B	1	04/12/1994
UF	425416	tooth	BROOKSVILLE QUARRY 1B	1	04/12/1994
UF	424654	tooth, crown	BROOKSVILLE QUARRY 1A	1	04/12/1994
UF	425435	vertebra, caudal	BROOKSVILLE QUARRY 1E	1	09/17/1994
UF	424653	vertebra, neural arch and neural spine	BROOKSVILLE QUARRY 1A	1	04/12/1994
UD	16729	osteoderm, partial	I-75	1	1966-1967
UF	424638	caudal vertebra	LIVE OAK (=SB-1A)	1	10/14/1984
UF	424637	caudal vertebra	LIVE OAK (=SB-1A)	1	10/14/1984
UF	424633	osteoderm	LIVE OAK (=SB-1A)	1	10/16/1983

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UF	424634	osteoderm	LIVE OAK (=SB-1A)	1	10/16/1983
UF	424635	osteoderm	LIVE OAK (=SB-1A)	1	10/14/1984
UF	424636	osteoderm	LIVE OAK (=SB-1A)	1	10/14/1984
UF	424639	tooth	LIVE OAK (=SB-1A)	1	10/14/1984
UF	424640	tooth, crown	LIVE OAK (=SB-1A)	1	10/14/1984
UF	424641	tooth, crown	LIVE OAK (=SB-1A)	1	10/14/1984