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Cover image: Hypothetical reconstruction of the extinct salamander *Batrachosauroides* and multiple views of a fossil trunk vertebra (UF 111741) from the Willacoochee Creek Fauna (inset). Illustration by J. R. Bourque.

A LATE MIOCENE OCCURRENCE OF THE EXTINCT SALAMANDER *BATRACHOSAUROIDES* (CAUDATA, BATRACHOSAUROIDIDAE) AND OTHER NEW CAUDATE FOSSILS FROM FLORIDA AND GEORGIA, USA

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ABSTRACT

Two partial vertebrae of the rare, large-bodied, aquatic salamander *Batrachosauroides* are reported from the Upper Miocene Love Bone Bed (late Clarendonian, ~10–9 Ma) Alachua County, Florida. They represent the latest occurrence of *Batrachosauroides* by 2.8–5.8 million years from previous records and are the latest account of the family Batrachosauroididae in the eastern United States, being either younger than or approximately coeval with fossils of *Peratosauroides problematica* from the Clarendonian San Pablo Formation of central California. While most Neogene *Batrachosauroides* in North America are from the warm interval spanning the Late Oligocene Warming (LOW) to the Middle Miocene Climatic Optimum (MMCO), this is the first unequivocal account well after the conclusion of the MMCO suggesting Florida was a post-MMCO refugium during global cooling in the Late Miocene. *Batrachosauroides* vertebrae from the late Hemingfordian Suwannee Springs site (Florida) and the late Barstovian Gragg Mine (southwestern Georgia) are also described. Two other caudate taxa are present at the Love Bone Bed, *Ambystoma* and a mid-sized *Siren* that is the most common amphibian in the Love Bone Bed Local Fauna. The presence and rarity of *Ambystoma* further corroborates the existence of peripheral or seasonal lentic aquatic habitats adjacent to the main lotic body of the Love Bone Bed deposit. Other salamanders from the paleocoastal Gragg Mine Local Fauna include *Notophthalmus* and *Amphiuma* n. sp., aff. *Amphiuma pholeter*. The latter represents the oldest record of the *A. pholeter* lineage and documents its presence in the Gulf Coastal Plain since the Middle Miocene. The Gragg Mine represents a unique interval in the southeast at the conclusion of the MMCO.

Key words: Caudata; *Batrachosauroides*; *Amphiuma*; *Siren*; *Ambystoma*; *Notophthalmus*; Middle Miocene Climatic Optimum

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INTRODUCTION

The family Batrachosauroididae Auffenberg, 1958, is an enigmatic group of large-bodied aquatic salamanders of uncertain phylogenetic affinities and one of the few major clades within Caudata to have gone extinct (Milner, 2000). Batrachosauroidids have been likened to extant *Amphiuma* and *Siren* with regard to morphotype, life history, and habitat preference (Holman, 2006). The previously reported fossil record of batrachosauroidids extends from the Cretaceous of Europe, Asia, and North America to the Late Miocene of North America (Auffenberg, 1961; Estes, 1963, 1969; Naylor, 1981; Sullivan, 1991; Denton and O'Neill, 1998; Holman, 2006; Gardner, 2022). Batrachosauroidids are thought to have dispersed from the western interior of the United States to the Gulf Coastal Plain by the Early Miocene (Taylor and Hesse, 1943; Albright, 1994; Bonett et al., 2013). The oldest species within the genus *Batrachosauroides* Taylor and Hesse, 1943 is *Batrachosauroides gotoi* Estes, 1969 from the lower Eocene (Wasatchian) Golden Valley Formation of South Dakota (Estes, 1988). Neogene occurrences of *Batrachosauroides* include reports from the lowermost Miocene (Arikareean) Toledo Bend locality in eastern Texas (Albright, 1994), and Early Miocene (Hemingfordian 1) Garvin Gully Fauna (includes Hidalgo Bluff locality) of eastern Texas (Auffenberg, 1958; Albright, 1994), Pollack Farm site in Delaware (Weems and George, 2013), and Thomas Farm locality in north central Florida (Estes, 1963). Middle Miocene or early Barstovian (Ba1) occurrences are from the Burkeville Fauna of southeastern Texas, which includes the Moscow site (aka. TMM 31057 and includes 'Site 1' of Polk County, Texas, and Barringer Farm) (Auffenberg, 1958; Holman, 1977) and Point Blank site (aka. TMM 31190; Hinderstein and Boyce, 1977), and Milwhite Gunn Farm Mine (Willacoochee Creek Fauna, Torreya Formation) of the northeastern panhandle of Florida (Bryant, 1991). The previous latest reported occurrences of *Batrachosauroides dissimulans* Taylor and Hesse, 1943 are from the late Barstovian (Ba2) Cold Spring Fauna of Texas (Auffenberg, 1958) (which includes the Fleming Formation of San Jacinto County, the type locality of *B. dissimulans*), Fort Polk Fauna of western Louisiana (Williams, 2009a, 2009b), and Gragg Mine assemblage in southwestern Georgia (Williams, 2009b; Mörs and Hulbert, 2010). The Gragg Mine specimens are described and figured for the first time in the current article. The latest occurring previously reported member of the family is *Peratosauroides problematica* Naylor in Estes, 1981, from the Upper Miocene (Clarendonian) San Pablo Formation of central California (Naylor, 1981; Martín et al., 2012).

Here, we present new fossil records of batrachosauroidid salamanders and accompanying caudate faunas from the southeastern United States, including a late occurrence of *Batrachosauroides* from the Upper Miocene (late Clarendonian, 10–9 Ma) Love Bone Bed, Alachua County, Florida. Previously reported fossils of *Batrachosauroides* from the Early and Middle Miocene of Florida, Georgia, and Texas are also discussed and figured for comparison. Digital models are provided for specimens currently housed in the Division of Vertebrate Paleontology, Florida Museum of Natural History (FLMNH), that have been figured previously as 2-dimensional illustrations or not at all in the literature (see Auffenberg, 1958; Estes, 1963, 1969; Bryant, 1991; Williams, 2009b; Mörs and Hulbert, 2010). Anatomical terminology used in vertebral descriptions follows Gardner (2003).

LOCALITY BACKGROUNDS

We examined *Batrachosauroides* vertebrae from the following four localities in northern Florida and one locality in southernmost Georgia, USA.

Love Bone Bed

The Love Bone Bed is a highly fossiliferous late Clarendonian (10–9 Ma) fluvial deposit in Alachua County, Florida (Fig. 1; Webb et al., 1981; MacFadden and Hulbert, 1990). The diverse vertebrate fauna of about 100 species includes fish (dominated by gar), frogs, snakes, freshwater turtles, land tortoises, alligators, birds, and mammals (Jackson, 1978; Webb et al., 1981; Bourque, 2013,
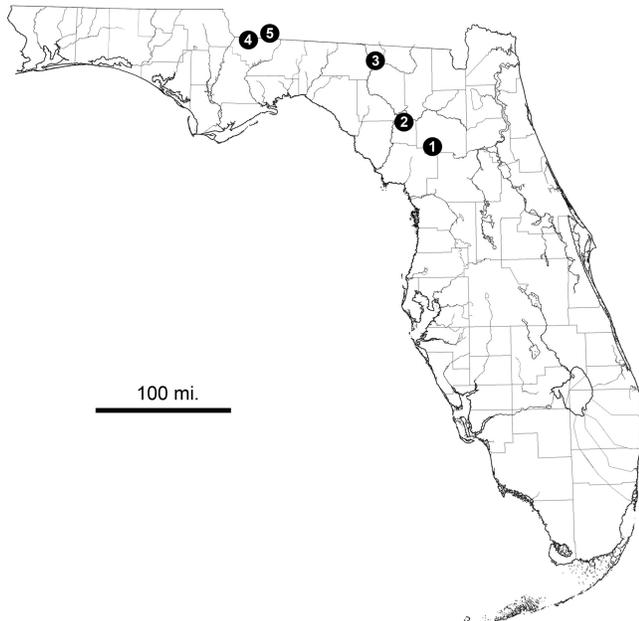
Figure 1. Map of Florida, USA. Black dots indicate Miocene records of *Batrachosauroides* from the following localities: **1**, Love Bone Bed, Alachua Co., FL, late Clarendonian, ~10–9 Ma.; **2**, Thomas Farm, Gilchrist Co., FL, early Hemingfordian, ~18.5–17.5 Ma.; **3**, Suwannee Springs, Hamilton Co., FL, late Hemingfordian, ~17–16 Ma.; **4**, Milwhite Gunn Farm Mine, Gadsen Co., FL, early Barstovian, ~16–15 Ma.; **5**, Gragg Mine, Decatur Co., GA, late Barstovian, ~14.8–14 Ma.

2015; Valdes et al., 2017) and indicates an array of paleoenvironments associated with a subtropical riverine community, such as estuarine, lentic, and flood plain habitats (Webb et al., 1981). Using the relative abundances of individuals belonging to large mammalian herbivore species reported by MacFadden and Hulbert (1990), only about 16% had low-crowned teeth suggesting a browsing diet (e.g., *Tapirus* and *Aepycamelus*, an extinct camelid with a giraffe-like ecology) in more closed habitats. This suggests that the surrounding landscape was predominantly open, relatively dry habitat covered with forbs, grasses, and scattered trees that supported herds of three-toed horses, rhinoceroses, lamine camelids, and gomphothere proboscideans. Webb et al. (1981: p. 537) concluded that whereas the main body of the Love deposit represented a high-energy stream channel, among aquatic spe-

cies, lentic taxa far outnumbered lotic taxa in abundance. However, many of the fish and turtle groups they used to support this hypothesis are common in large, albeit slower moving portions of rivers today. Bourque (2015) noted the relative rarity of turtle taxa such as *Kinosternon notolophus* and a chelydrid that would have inhabited low energy wetlands (e.g., floodplain swamps) adjacent to the Love Bone Bed fluvial system contrasted to the abundance of more fluvial or generalist emydine and trionychid turtles.

GRAGG MINE

Gragg Mine was a fuller's earth clay mine located about 5.6 km southeast of Attapulgus in Decatur County, Georgia (ca. 30.72° N, 84.44° W; Fig. 1). The former mine's location is now fully reclaimed, forested land. In 2004, D. P. Mihalik, who worked for the mining company Engelhard Corporation, informed the FLMNH that he had collected Miocene terrestrial vertebrate fossils on spoil piles in Gragg Mine, including a nearly complete molar of a gomphothere. By this time mining of sediments had stopped and reclamation had begun, thus there was no access to in situ deposits. Mihalik twice led FLMNH field crews in 2004 and 2005 to the Gragg Mine and directed them to the general area where he had found terrestrial fossils. The spoil piles had by then been leveled by heavy equipment and vegetation covered most of the surface. However, several small, exposed areas of brown to tan, sandy clayey sediments were located, which Mihalik confirmed was the fossil-bearing deposit. While surface prospecting did not recover any fossils other than a few small shark and ray teeth, small dark 'specks' in the sediment suggested the presence of microfossils. Bryant (1991) had reported microfossils of amphibians, reptiles, and mammals collected in similar clay mines just 10 km southwest in Gadsden County, Florida. About two metric tons of sediment (dried weight) was collected at Gragg Mine in 2004–2005 and transported to the FLMNH for screenwashing. Gragg Mine is assigned FLMNH VP locality number US018. The only previous mentions of fossils from Gragg Mine were in an

unpublished dissertation (Williams, 2009b) and two sentences in Mörs and Hulbert (2010). This is the first description of the site, collecting methods, overview of the entire fauna, and rationale for its geologic age.

All known macrofossils from Gragg Mine were collected by D. P. Mihalik or his children. Most consist of isolated teeth. He donated a portion of his fossils from Gragg Mine to the FLMNH in 2005 and allowed the others to be molded and casted. The gomphothere molar (UF 216932) is of moderate size, low-crowned, and has a simple, single-trefoiled enamel pattern; it most likely represents the genus *Gomphotherium*. The first appearance datum of *Gomphotherium* in North America is about 14.8 Ma and defines the beginning of the late Barstovian (Tedford et al., 2004; MacFadden et al., 2015). Two species of the hypsodont equid genus *Calippus*, *C. proplacidus* (UF 217573, UF 217583–217584) and *C. circulus* (UF 217582, UF 333980–333981), are present. These are decidedly more advanced than the merychippine-grade equids found in the early Barstovian Willacoochee Creek Fauna of Bryant (1991) and are otherwise only known from late Barstovian faunas in Colorado, Nebraska, Texas, and Florida (Hulbert, 1988). An upper premolar belongs to the large beaver *Amblycastor* (UF 217575, Mörs and Hulbert, 2010), whose last occurrence is from the late Barstovian. Other fossils of large mammals from Gragg Mine belong to taxa that lived during the late Barstovian, but their chronologic ranges extend into older and younger land mammal ages. They include a medial phalanx from a medium-sized felid (UF 217576), a lower premolar of the rhinocerotid *Teleoceras* (UF 217581), and fossils representing three artiodactyl families, Tayassuidae (UF 217577, UF 554595), Camelidae (UF 333982, UF 554602), and Dromomerycidae (UF 217585).

The screenwashed sediment from Gragg Mine produced over 500 fossils of small mammals, mostly isolated teeth with very few partial jaws with one or two teeth. A preliminary estimate of the herpetofauna is 200–300 specimens, but this will likely increase as specimens continue to be catalogued. This is significant as there are no other late Barstovian sites in the southeastern USA with large samples of small vertebrates. Other than the Caudata described here, these specimens have yet to be studied in detail, so their identifications should be regarded as provisional. Fish and snakes are the most abundant non-mammalian constituents, but frogs, salamanders, chelonians, lizards, a crocodilian, and birds are also present. The crocodilian is a small to mid-sized *Alligator* sp. (UF 554927–554928). Chelonians are represented by scant shell fragments and isolated bones of the following: Trionychidae (UF 554920, UF 554925), Kinosternidae (UF 546658, UF 554910, UF 554926), Emydidae (Deirochelyinae) (UF 554922–554924), and Testudinidae (UF 554911–554919).

Not surprisingly, rodents are the most common and diverse group of small mammals, making up about 94% of the sample. At least five families are represented, with a possible sixth. There are two taxa of squirrels, both of small size. The more common is the chipmunk-like *Nototamias* sp. (16 teeth, UF 546996–546998, UF 547033–547045), whereas UF 547032, a lower third molar, is from a gliding squirrel (either *Blackia* or *Sciurion*) previously not known from eastern North America (Godwin, 2008). The extinct family Mylagaulidae is known by a deciduous premolar (UF 546995) and a partial cheek tooth (UF 554690), neither of which is sufficient for generic identification. The extinct geomorph family Jimomyidae is well represented by two genera, *Jimomys* (29 teeth; UF 546931–546939, UF 547046–547063) and *Texomys* (18 teeth; UF 546940–546948, UF 547064–547072). Teeth of the former are relatively higher crowned than named species, and may represent a new species. The majority of the rodent specimens belong to either the Cricetidae (about 27% of all identifiable rodent teeth) or Heteromyidae (about 58%). The former is composed of one or more species of *Copemys* (UF 546913–546930, UF 547073–547139), while the latter likely contains multiple genera (UF 546949–546994, UF 547001–547002) based on variation among the premolars in the sample. All the heteromyid teeth are from small species with brachylophodont to mesodont dentitions. The potential sixth rodent

family in the screenwashed sample is represented by two cheektooth fragments that may belong to a small beaver (Castoridae) such as *Monosaulax* (UF 333978–333979). The non-rodents among the small mammals from Gragg Mine are a possible didelphid marsupial (UF 546903), the hedgehog *Lantanotherium* (UF 546905–546909, UF 547004–547006), two or more shrews (Soricidae; UF 546910–546912, UF 547009), the rabbit *Hypolagus* (UF 554718), and a bat. The latter is known from only a single specimen (UF 547008). It is the most complete dentary in the entire sample and preserves the alveoli for the entire tooth row but retains only the fourth premolar. Spelling of the genus name *Lantanotherium* (as opposed to *Lanthanotherium*) follows McKenna and Bell (1997: p. 277), Gunnell et al. (2008), Furió and Alba (2011), and Crespo et al. (2020).

The make-up of the Gragg Mine small mammal assemblage supports a Middle Miocene, Barstovian age. This is constrained by the first North American occurrence of *Lantanotherium* in the early Barstovian (Gunnell et al., 2008; Korth and Evander, 2016) and the joint last occurrence of *Jimomys* and *Texomys* in the late Barstovian (Flynn et al., 2008). The latest published Miocene records for didelphid marsupials are early Barstovian from coastal Texas and Florida (Slaughter, 1978; Morgan and Pratt, 1988; Hayes, 2005). If the Gragg Mine Local Fauna is late Barstovian and the identification of UF 546903 as a didelphid is confirmed, then it would be the latest North American record for the family prior to the Great American Biotic Interchange. Identification of the Gragg Mine soricids, leporid, heteromyids, and cricetids to the species level and comparisons with those from Barstovian faunas from Florida, Louisiana, Texas, Nebraska, and California are needed for a finer resolution of the chronology of the Gragg Mine Local Fauna. We suggest the early portion of the late Barstovian, ca. 14.8–14.0 Ma, best fits the current data, with primary correlations to the Cold Spring Fauna of Texas, Fort Polk Fauna of western Louisiana, the Keota Fauna of Colorado, and that portion of the Barstow Fauna of southern California collected below the *Hemicyon* Tuff (Tedford et al., 2004).

The paleoenvironment is similar to that hypothesized for the nearby Willacoochee Creek Fauna (Bryant, 1991), and likely represents a coastal, nearshore, deltaic, fluvial deposit with an admixture of marine, freshwater, and terrestrial vertebrates. Fossil deposits in this region of the southeastern United States reflect a transient coastline in the Middle Miocene, farther north than today (Bryant et al., 1992). At 14.8–14.0 Ma, the Gragg Mine deposit is significant in that it represents a coastal plain environment in the southeastern United States at the conclusion and one of the warmest parts of the MMCO, when sea level was close to its highest in the Neogene (Zachos et al., 2001). At this time, Florida was almost entirely submerged with the possible exception of some small islands along the Brooksville Ridge of central Florida and a complex of islands and peninsulas along the border with Georgia and Alabama (Randazzo and Jones, 1997).

MILWHITE GUNN FARM MINE (WILLACOOCHEE CREEK FAUNA)

This locality is one within a complex of mines in Gadsen County, Florida, that comprise the early Barstovian, Middle Miocene, Willacoochee Creek Fauna (Bryant, 1991). The Willacoochee Creek Fauna preserves a diverse array of terrestrial, freshwater, and marine taxa indicative of a coastal deltaic setting. Marine invertebrates were common in the sediments that preserved vertebrate fossils, and marine tetrapods include mysticete and odontocete cetaceans and dugongids (Bryant, 1991). The herpetofauna is diverse and includes a helodermatid lizard, and chelonians that represent the Kinosternidae, Podocnemididae (Pleurodira), small and large Testudinidae, Trionychidae, and Emydidae (Bryant, 1991; Bourque, 2013, 2016). However, a single *Batrachosauroides* vertebra (UF 111741) represents the only amphibian currently known from the fauna (Bryant, 1991).

SUWANNEE SPRINGS

Little has been published about this road cut locality on US 129 just north of the Suwannee River in Hamilton County, Florida (Fig. 1; see Frailey, 1978; Tedford and Hunter, 1984; Bourque,

2013, 2016). It exposes the Lower Miocene Marks Head Formation (sensu Scott, 1988). Its age is approximately 17–16 Ma (late Hemingfordian) based largely on the presence of the horse *Merychippus gunteri* (Bourque, 2013). The herpetofauna consists of a small alligatorid, *Thecachampsa*, two testudinids (a small and mid-sized species), podocnemidid side-necked turtles (Pleurodira), and one of the oldest records of the mud turtle *Kinosternon* (Bourque, 2013; Bourque, 2016). *Batrachosauroides* is represented by two partial vertebrae (described below).

Thomas Farm

Thomas Farm is a paleosinkhole ephemeral pond deposit in Gilchrist County, Florida. Vertebrate fossils are found in alternating beds of gray clay and calcareous sand or boulders (Simpson, 1932; Olsen, 1962; Pratt, 1990). Fossils of both large and small vertebrates are present in large numbers, with a total species richness in excess of 100. An early Hemingfordian age (He1) is indicated by the combined presence of the bear *Phoberocyon*, the mustelid *Leptarctus*, the rhinocerotids *Menoceras* and *Floridaceras*, and the canids *Metatomarctus* and *Euoplocyon* (Tedford et al., 2004). This differs from the age of Thomas Farm shown in the correlation chart in Tedford et al. (2004: fig. 6.2), that has it ranging over about one million years from the later third of the He1 through the first third of the He2. This duration is likely at least two orders of magnitude too long. As noted by Tedford et al. (2004: p. 213), there are major differences in He1 and He2 faunas, with 31 mammalian genera first appearing in the He2. Of these, only one, the sciurid *Petauristodon*, is known from Thomas Farm. However, the first appearance of *Petauristodon* is now known to have occurred earlier than the He2 (Whistler and Lander, 2003; MacFadden et al., 2014). Furthermore, fossils of the presumptive He2 taxon *Petauristodon* occur in the same or lower beds at Thomas Farm as the He1 taxa *Menoceras* and *Floridaceras* (see Appendix 1). So, there is no longer reason to assign any portion of Thomas Farm to the He2. There is an extensive literature on fossils from Thomas Farm that was most recently summarized by Morgan and Czaplewski (2023).

Despite the fact that thousands of fossils have been collected at Thomas Farm since its discovery in 1931, only a single specimen of *Batrachosauroides* (an atlas vertebra, UF 7802) has been found, and that specimen was previously described by Estes (1963, 1969, 1981). The scarcity of *Batrachosauroides* suggests that it was either uncommon at this ancient small pond or that the single atlas was potentially brought to the site from another wetland by a predator (e.g., raptor or other bird of prey) or scavenger before final deposition.

MATERIALS AND METHODS

High-resolution Computed Tomography (CT) scanning was performed on 20 vertebrae using the UF Nanoscale Research Facility's Phoenix V|tome|X M dual tube CT system. Samples were suspended in cotton-filled polyethylene tubes and scanned as a sequential batch using the Datos|X A software (Waygate Technologies, Skaneateles, NY, USA). Scanning parameters were modified to maximize resolution, contrast and signal to noise (see Appendix 2). Radiographs were converted to tomograms using Datos|X R (Waygate Technologies, Skaneateles, NY, USA), using the edge enhancement, ROI filter, and inline median modules. The resulting datasets were segmented, visualized, and analyzed in VGStudioMax 2023.2 (Volume Graphics, Heidelberg Germany). Tomogram stacks and stereolithography mesh files are available to download from www.Morphosource.org (see Appendix 2 for DOI links).

Institutional Abbreviations

FLMNH, Florida Museum of Natural History, University of Florida, Gainesville, Florida; **TMM**, Texas Vertebrate Paleontology Collection, Jackson School Museum of Earth History, University of Texas at Austin, Austin, Texas; **UF**, Division of Vertebrate Paleontology, Florida Museum of Natural History, University of Florida, Gainesville, Florida; **UF/H**, Division of Herpetology, Florida

Figure 2. Trunk vertebrae of *Batrachosauroides* sp. from the late Clarendonian Love Bone Bed, Florida. **A**, UF 293802 and **B**, UF 546455 (subadult). Aspects from left to right: anterior, left lateral, posterior, right lateral, dorsal, and ventral.

Museum of Natural History, University of Florida, Gainesville, Florida. **UF/TRO**, formerly part of the Timberlane Research Organization Collection, Lake Wales, Florida, now housed at the Division of Vertebrate Paleontology, Florida Museum of Natural History, Gainesville, Florida.

Fossil Caudate Specimens Examined

    Batrachosauroides sp.: UF 293802, UF 546455 (Love Bone Bed, FL), UF/TRO 546528–546529 (Suwannee Springs, FL), UF 2013 (Moscow locality, Burkeville Fauna, TX; see also Auffenberg, 1958: fig. 2), UF 7802 (Thomas Farm, FL; see also Estes, 1963: fig. 2 lower right), UF 111741 (Milwhite Gunn Farm Mine, FL; see also Bryant, 1991: fig. 5A–B), UF 217589, UF 546635, UF 546653–546656 (Gragg Mine, GA); *Ambystoma* sp.: UF 546456–546458 (Love Bone Bed, FL); *Siren* sp.: UF 403843–403867, UF 546459–546470, UF 546853 (Love Bone Bed, FL); *Siren simpsoni*: UF 2767 (Haile 6A); *Pseudobranchus* sp.: UF 2768 (Haile 6A); *Amphiuma* n. sp., aff. *A. pholeter*: UF 546636–546641, UF 546652 (Gragg Mine, GA); *Notophthalmus* sp.: UF 546642–546651 (Gragg Mine, GA). Numerous extant salamander skeletons used for comparisons are housed in the Division of Herpetology, FLMNH.

SYSTEMATIC PALEONTOLOGY

Subclass LISSAMPHIBIA Haeckel, 1866
Order CAUDATA Scopoli, 1777
Family BATRACHOSAUROIDIDAE Auffenberg, 1958
Genus *BATRACHOSAUROIDES* Taylor and Hesse, 1943

    Type Species.—*Batrachosauroides dissimulans*, holotype TMM 10038-2234, skull and jaws only (Taylor and Hesse, 1943) from the late Barstovian Cold Spring Fauna of eastern Texas. The holotype was reported missing for nearly four decades (Estes, 1969; Holman, 2006); however, has since been located and is currently housed at TMM under the revised catalog number TMM 10038-2234 (ex-TAM 2234) (J. C. Sagebiel, TMM, pers. comm.). Auffenberg (1958) attributed vertebrae collected from "the same bed as that of the type skull", as well as vertebrae from similarly aged localities in the region (now considered part of the early Barstovian Burkeville Fauna), to *B. dissimulans* and provided an amended diagnosis for the species (p. 172–173). Estes (1981: p. 30) subsequently provided a differential diagnosis to distinguish *B. dissimulans* from the Eocene species *Batrachosauroides gotoi*.
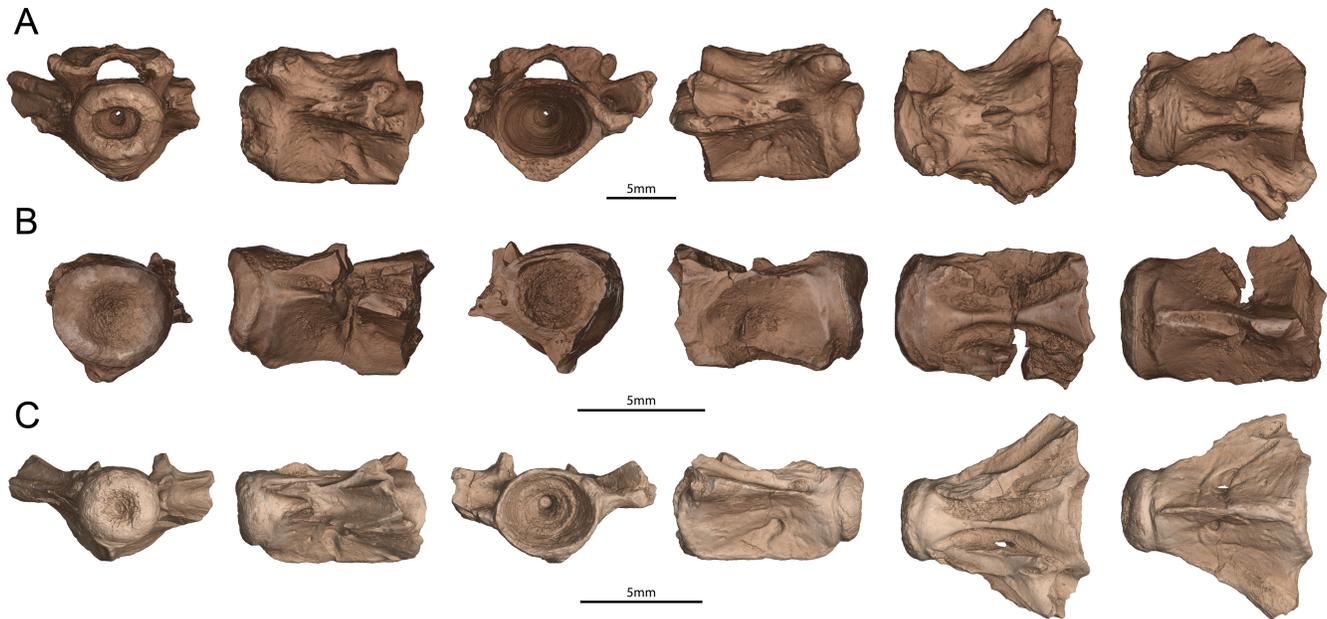
Figure 3. Trunk vertebrae of *Batrachosauroides* sp. from the late Barstovian Gragg Mine, Georgia. **A**, UF 217589; **B**, UF 546635; and **C**, UF 546653. Aspects from left to right: anterior, left lateral, posterior, right lateral, dorsal, and ventral.

BATRACHOSAUROIDES sp.
(Figs. 2–4)

Locality and Age.—Love Bone Bed, Alachua County, Florida; Alachua Formation, late Clarendonian (Cl3), Late Miocene, 10–9 Ma (Webb et al., 1981; Tedford et al., 2004).
Referred Specimens.—UF 293802 and UF 546455, partial trunk vertebrae (Fig. 2).

Locality and Age.—Gragg Mine, Decatur County, Georgia; Middle Miocene, Barstovian (Ba2), 14.8–14 Ma (refined age presented here; see also Mörs and Hulbert, 2010).
Referred Specimens.—UF 217589, UF 546635, UF 546653–546656, partial trunk vertebrae (Fig. 3).

Locality and Age.—Milwhite Gunn Farm Mine, Gadsen County, Florida; Torreya Formation, Middle Miocene, Barstovian (Ba1), ~16–15 Ma (Bryant, 1991).
Referred Specimen.—UF 111741, trunk vertebra (Fig. 4E). Previously figured as line illustration in Bryant (1991: fig. 5A–B).

Locality and Age.—Suwannee Springs, Hamilton County, Florida; Marks Head Formation, Early Miocene, Hemingfordian (He2), ~17–16 Ma (Frailey, 1978; Tedford and Hunter, 1984; Bourque, 2013).
Referred Specimens.—UF/TRO 546528–546529 (Fig. 4B–C).

Locality and Age.—Thomas Farm, Gilchrist County, Florida; Early Miocene, Hemingfordian (He1), ~18.5–17.5 Ma (Morgan and Czaplewski, 2023).
Referred Specimen.—UF 7802 (Fig. 4A). Previously figured as a stippled illustration in Estes (1963: fig. 2 lower right).

Remarks.—*Batrachosauroides* specimens from localities in the southeastern Gulf Coastal Plain (Florida and Georgia) are not identified to the species level here. These fossils consist of isolated and mostly incomplete vertebrae, whereas the holotype of *Batrachosauroides dissimulans* is a cranio-dental specimen (Taylor and Hesse, 1943). While Auffenberg (1958) attributed vertebrae from the Burkeville Fauna (Texas) to the
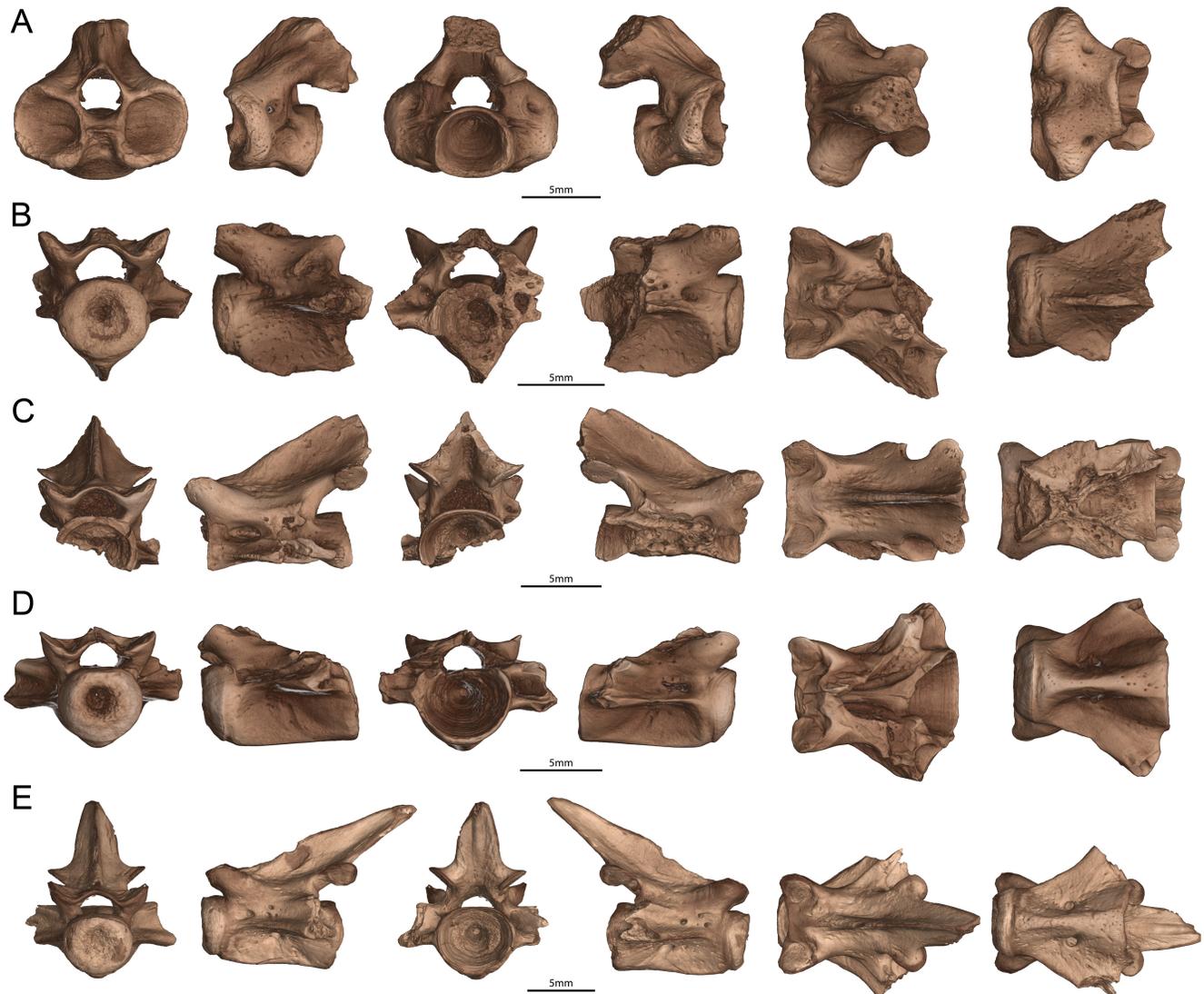
Figure 4. Vertebrae of *Batrachosauroides* sp. **A**, UF 7802, atlas from Thomas Farm, Florida (see also Estes, 1963: fig. 2 lower right). **B**, UF/TRO 546528 and **C**, UF/TRO 546529 trunk vertebrae from Suwannee Springs, Florida. **D**, UF 2013 trunk vertebra from the Moscow locality (Burkeville Fauna), Texas (see also Auffenberg, 1958: fig. 2). **E**, UF 111741 trunk vertebra from the Milwhite Gunn Farm Mine (Willacoochee Creek Fauna), Florida (see also Bryant, 1991: fig. 5A–B). Aspects from left to right: anterior, left lateral, posterior, right lateral, dorsal, and ventral.

species *B. dissimulans* under the assumption that they were collected from the same deposit and general area, our current understanding is that those Burkeville vertebrae are at least one million years older than the type specimen from Cold Spring (Texas). Similarly, Bryant (1991) attributed a nearly complete trunk vertebra (UF 111741) from the Milwhite Gunn Farm Mine to the species *B. dissimulans*, which is approximately one million or more years older than Cold Spring. Ad-

ditionally, Estes (1963, 1969, 1981) attributed the only known *Batrachosauroides* specimen from Thomas Farm (an atlas, UF 7802) to the species *B. dissimulans*; however, that account is the oldest record from Florida and ~3.5 million years older than the type locality at Cold Spring. Furthermore, UF 7802 is notably larger than most trunk vertebrae from younger deposits in Florida. A single *Batrachosauroides* vertebra (UF 217589) previously referred to the species *B. dissimulans* from

the Gragg Mine (Mörs and Hulbert, 2010) was not identified to the species level based on any specific characters according to RCH; however, the Gragg Mine specimens are essentially contemporaneous with the type of *B. dissimulans* from the Cold Spring Fauna. Given the extensive time span that *Batrachosauroides* was present in the Gulf Coastal Plain (~23–9 Ma) and the absence of cranial fossils to compare to the holotype, it is possible that more than a single species was present in the region during the Miocene. Therefore, we prefer to be taxonomically conservative and open to the possibility of undocumented diversity within *Batrachosauroides*.

DESCRIPTION AND COMPARISONS

Love Bone Bed Specimens

Two partial trunk vertebrae are known from the Love Bone Bed. UF 293802 is a partial opisthocoelous trunk vertebra of a large-bodied salamander (Fig. 2A). From what is preserved, it measures 12.14 mm in total length, 9.59 mm long along the centrum, 10.67 mm wide, and 11.82 mm tall. Its broken and polished preservation implies that it endured sedimentary abrasion and transport (commonly observed on many specimens from this site). The anterior condyle head, right margin of the posterior cotyle, posteriormost end of the neural spine, postzygapophyses, and transverse or rib-bearing processes are not preserved. Although the ossified condyle head is missing, the preserved condyle base is laterally compressed making it ovoid or taller than wide in anterior outline. The preserved basal most portion of the left transverse processes suggests those were bifurcate in life.

Dorsally, there is a distinct neural crest that would have extended to the posteriorly elongate neural spine in life. The neural spine is broken along the plane of the postzygapophyses. The transverse surface of the neural spine break is relatively broad indicating that the neural spine would have extended well posterior to the vertebral centrum as is typical for the family. Like other *Batrachosauroides* vertebrae examined, it lacks basapophyses. The vertebrarterial canal ter-

minates anteriorly just below the prezygapophyses and adjacent to the anterior condyle, and posteriorly below the postzygapophyses and adjacent to the posterior cotyle. The vertebrarterial canals are distinctly visible in anterior aspect in that they protrude laterally from the centrum. There is a prominent subcentral keel that extends the length of the centrum, from the anterior condyle to the posterior cotyle. This keel is constricted medially and broadest anteriorly and posteriorly. Approximately midway along the base of the subcentral keel is a pair of subcentral foramina. The prezygapophyses are upwardly oriented at a ~45° angle. The upper margin of the neural canal is highly vaulted.

UF 546455 is a partial opisthocoelous vertebral centrum of a subadult (Fig. 2B). Its identification as a subadult is due to its small size and broad width of the notochordal canal. The centrum length is ~4.4 mm and it is 4.26 mm tall anteriorly. The paired prezygapophyses are preserved and upwardly oriented at greater than a 45° angle. The neural canal is highly arched. A strong, straight subcentral keel is present with a subcentral foramen preserved on the left side. The neural spine and postzygapophyses are not preserved. The left transverse processes are only basally preserved and were likely bifurcate in life.

Gragg Mine Specimens

Six fragmentary trunk vertebral centra of *Batrachosauroides* are known from the Gragg Mine. UF 217589 (Fig. 3A) is a relatively complete opisthocoelous centrum with the right prezygapophysis preserved. The neural spine and postzygapophyses are missing. It is the largest specimen from the Gragg Mine, 13.21 mm long at the centrum and 9.91 mm tall anteriorly. The anterior condyle is well ossified. The posterior cotyle is preserved but chipped along the bottom margin. The prezygapophyses are upwardly oriented approximately at a 45° angle. The neural canal is highly arched medially as with other *Batrachosauroides* trunk vertebrae. The transverse processes are missing but basally preserved on the right side and were likely bifurcate. A strong, straight subcentral keel

is present with paired subcentral foramina located on either side. UF 546635 (Fig. 3B) is a relatively complete centrum with complete condyle and cotyle with a chipped outer margin. The centrum is 8.14 mm long. The subcentral keel and foramina are preserved but the former is chipped. UF 546653 (Fig. 3C) is the second-most complete specimen in preserving the anterior condyle and posterior cotyle and the centrum is 7.91 mm long. The condyle is well ossified with a pinhole sized notochordal canal externally. The subcentral keel is straight with paired subcentral foramina positioned medially at the base of the keel. The paired vertebrarterial canals are preserved. UF 546654–546656 (not figured) are isolated fragments of the anterior portions of centra with condyles preserved.

MILWHITE GUNN FARM MINE SPECIMEN

A single opisthocoelous trunk vertebra (UF 111741) (Fig. 4E) is known from this mine locality and the entire Willacoochee Creek Fauna. It is one of the most complete trunk vertebrae of *Batrachosauroides* in southeastern North America in missing only the posteriormost tip of the neural spine and distal ends of the transverse processes. Measurements were previously provided by Bryant (1991) and are as follows: centrum length (CL), 11.1 mm; centrum width at narrowest portion of zygapophyseal ridges (CW), 6.3 mm; centrum height at anterior margin (CH), 4.6 mm; and neural arch height above centrum (NH), 8.2 mm. Our measurements differ only slightly and are as follows: CL, 10.93 mm; CW, 5.38; CH, 4.73 mm; NH, 7.6 mm. The prezygapophyses and postzygapophyses are inclined at approximately a 45° angle. The subcentral keel is relatively straight in lateral view, with paired subcentral foramina positioned medially at the base of the keel. The anterior condyle is well ossified, has a deep concavity at the center, and the notochordal canal is enclosed indicating the specimen is that of an adult. The neural spine is elongate and extends ~2.98 mm posterior to the centrum at the margin of the posterior cotyle; however, the neural spine would have been more extensive in life given the distal tip is missing on the fossil. A tall, thin me-

dial crest is preserved that runs the length of the neural spine.

SUWANNEE SPRINGS SPECIMENS

Two partial trunk vertebrae are known from Suwannee Springs. UF/TRO 546528 (Fig. 4B) is the partial anterior portion of a vertebra. The prezygapophyses are inclined at approximately a 45° angle from the centrum. The neural canal is highly vaulted medially between the prezygapophyses. The anterior condyle is well ossified and the notochordal canal is enclosed externally. The centrum is tall ventrally with a pronounced subcentral keel. The anterior terminus of the vertebrarterial canal is positioned well forward on the centrum and under the main portion of the prezygapophyses similar to the specimens from the Love Bone Bed. The anteriormost portion of the neural spine is preserved between the prezygapophyses and is broad and thick.

UF/TRO 546529 (Fig. 4C) is a partial vertebra that preserves most of the dorsal half. It is 11.97 mm long from the pre- to postzygapophyses. It was opisthocoelous in life, but the condyle is broken and missing. The prezygapophyses are inclined at approximately a 45° angle, and the neural canal is highly vaulted medially between the prezygapophyses. The dorsal crest is mostly preserved and is tall anteriorly, where it begins at the posterior portion of the prezygapophyses, and the postzygapophyses extend posteriorly well beyond the posterior cotyle margin of the centrum similar to UF 111741 (Fig. 4E).

THOMAS FARM SPECIMEN

A single atlas vertebra (UF 7802) (Fig. 4A) represents the only record of *Batrachosauroides* from Thomas Farm, and the oldest record of a batrachosauroidid from Florida. The atlas is relatively large compared to other *Batrachosauroides* vertebrae from Florida. UF 7802 was previously described by Estes (1963, 1969, 1981). Measurements from Estes (1963) are as follows: intercotylar maximum width (MW), 14.3 mm; and maximum centrum length (ML), 7.5 mm. Our measurements are nearly identical: MW, 14.2 mm; and ML,

~7.2–7.7 mm. As stated by Estes (1963), the atlas is robust and well ossified, and the posterior portion of the neural spine is missing but would have extended posteriorly well past the centrum. The postzygapophyses are oriented at slightly less than a 45° angle and extend posteriorly ~3.5 mm past the posteriormost margin of the posterior cotyle of the centrum.

Comparisons

In most aspects, UF 293802 and UF 546455 (Fig. 2) from the Late Miocene Love Bone Bed are very similar to *Batrachosauroides* trunk vertebrae from other localities examined for this study. However, the centrum of UF 293802 is more laterally compressed (dorso-ventrally elongate) and the subcentral keel ventrally taller than the Middle Miocene *Batrachosauroides* vertebra UF 217589 (Fig. 3A) from the Gragg Mine, UF 111741 (Fig. 4E) from the Milwhite Gunn Farm Mine, and UF 2013 (Fig. 4D) from the Moscow locality in Texas. It is unclear if this is a diagnostic character of a new species, or perhaps this feature is variable throughout the vertebral column and signifies a particular region of the body. The prezygapophyses are more anteriorly extensive in UF 111741 than in UF 293802, but these seem eroded in the latter. Notably, the anterior terminus of the vertebrarterial canal is situated more anteriorly in UF 293802, UF 546455, UF/TRO 546528, and UF/TRO 546529 than in UF 111741 and UF 217589, where the terminus is situated near the posterior base of the prezygapophyses in the latter two specimens. The vertebrarterial canals are wide anteriorly and protrude laterally so they are distinctly visible in anterior view in UF 293802 and UF 217589, perhaps indicating these are from a similar body region. The Love Bone Bed specimens are approximately contemporaneous or younger than another batrachosauroidid, *Peratosauroides problematica* from central California (Naylor, 1981). However, *P. problematica* was described as having amphicoelous vertebrae in contrast to the Love Bone Bed vertebrae (and all specimens from the eastern United States) which differ in having opisthocoelous vertebrae.

DISCUSSION

Batrachosauroides and Warm Paleoclimate

Batrachosauroidids are one of the few major caudate groups to have gone extinct (Milner, 2000), and their extinction is likely correlated with climatic shifts, specifically with global cooling in the Late Miocene. Previous accounts of batrachosauroidids in North America are from intervals when globally warm mean annual temperatures (MATs) are hypothesized to have been much warmer than today (Zachos et al., 2001; Woodburne, 2004) (Fig. 5). *Batrachosauroides* was most common in the Southeastern Coastal Plain (Williams, 2009b; Bonett et al., 2013) from the interval that spans the Late Oligocene Warming (LOW) to the Middle Miocene Climatic Optimum (MMCO), a period of global climate change marked by megathermal temperatures at the onset (during LOW) and conclusion (during MMCO) of this warming event (Zachos et al., 2001). It was thought that *Batrachosauroides* did not survive long past the MMCO as summarized by Bonett et al. (2013: fig. 3). Records from the late Barstovian (Ba2) Fort Polk Formation of western Louisiana (Williams, 2009a, 2009b) and Gragg Mine of southwestern Georgia are from the conclusion of the MMCO and at the onset of global cooling (Zachos et al., 2001; Woodburne, 2004). The record from the Love Bone Bed is one of the latest reports of Batrachosauroididae and the latest of *Batrachosauroides*. This implies that in the southeastern United States, Florida was a likely post-MMCO refugium for these salamanders during the Late Miocene, which were previously more common and well-distributed across the Gulf and Atlantic coastal plains during the warmer Early and Middle Miocene (Taylor and Hesse, 1943; Auffenberg, 1958; Estes, 1963, 1969; Holman, 1977; Hinderstein and Boyce, 1977; Bryant, 1991; Albright, 1994; Mörs and Hulbert, 2010). The record from the Love Bone Bed is also one of the most southern occurrences of the family, and the most southern occurrence of *Batrachosauroides*, albeit not by much. At the time of the Love Bone Bed deposition, global MATs would have been much cooler than those experienced from the LOW to the
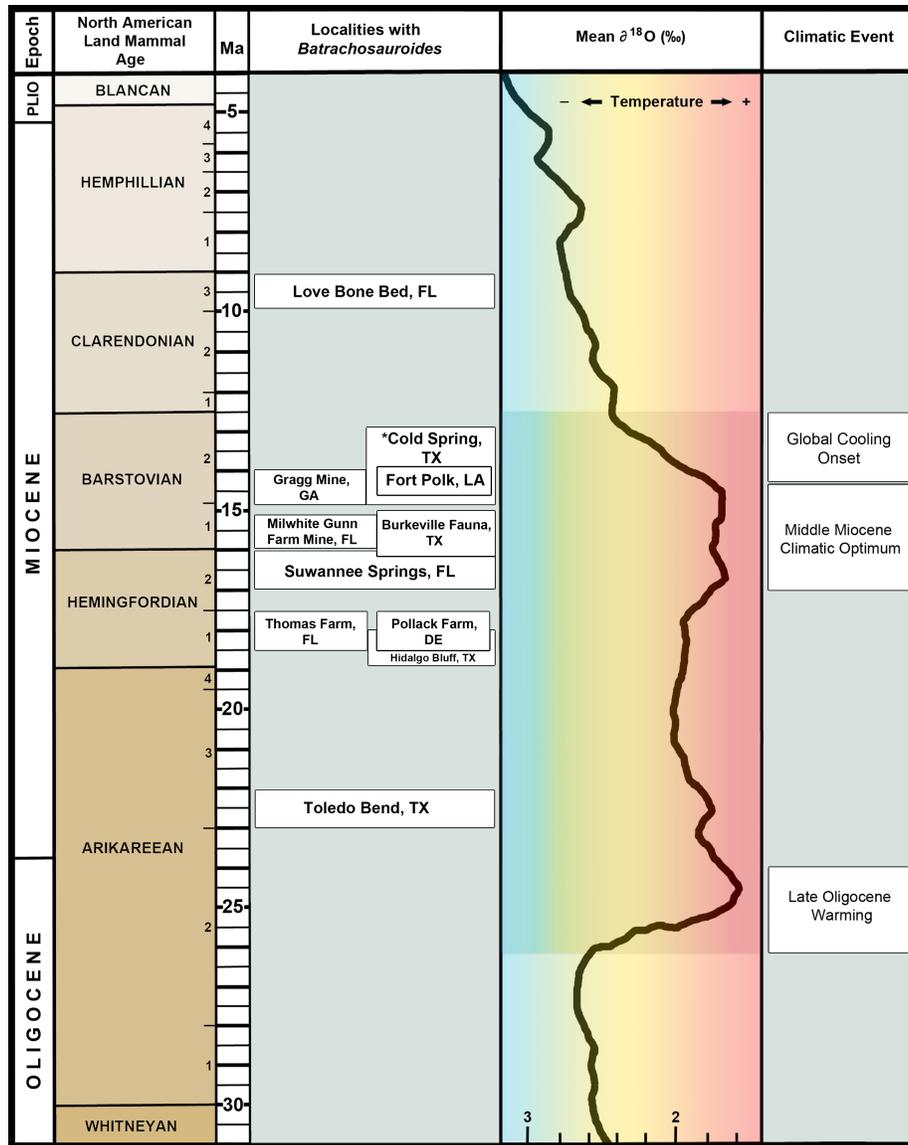
Figure 5. Correlation timeline comparing known localities and faunas with *Batrachosauroides* fossils in the Gulf and Atlantic coastal plains to global temperature shifts (Zachos et al., 2001; modified from Tedford et al., 2004). Previously published *Batrachosauroides* records from the following (bottom to top): Toledo Bend (Albright, 1994); Pollack Farm (Weems and George, 2013); Hidalgo Bluff (aka. TMM 40067; part of Garvin Gully Fauna) (Albright, 1994); Thomas Farm (Estes, 1963); Burkeville Fauna, which includes Moscow (aka. TMM 31057 and includes 'Site 1' of Polk County, TX, and Barringer Farm, TX) (Auffenberg, 1958) and Point Blank site (aka. TMM 31190; Hinderstein and Boyce, 1977); Milwhite Gunn Farm Mine, Willacoochee Creek Fauna (Bryant, 1991); Gragg Mine (Mörs and Hulbert, 2010; age range amended here); Cold Spring Fauna (Auffenberg, 1958); Fort Polk Fauna (Williams, 2009a, 2009b). Asterisk (*****) indicates type occurrence of *Batrachosauroides dissimulans*. Darkened portion of temperature gradient indicates warm interval bracketed by the Late Oligocene Warming (LOW) and the conclusion phase of the Middle Miocene Climatic Optimum (MMCO) and the onset of global cooling at approximately the Barstovian-Clarendonian NALMA boundary. All previous records of the species *B. dissimulans* or *B.* aff. *dissimulans* fall within this interval.

MMCO, and similar to those last experienced in the late Oligocene, just prior to the LOW (Zachos et al., 2001). This is significant when considering there are no *Batrachosauroides* fossils known from the Oligocene and their last pre-Oligocene occurrence was from the early Eocene (Wasatchian) of

North Dakota with *Batrachosauroides gotoi* (Estes, 1981; Holman, 2006; Williams, 2009b) during the Greenhouse World (Zachos et al., 2001). It is unclear if batrachosauroidids made it to warmer lower latitudes in continental North America, such as Mexico or Central America, by the Oligocene and then emigrated north to the Gulf and Atlantic coastal plains when MATs were more favorable from the LOW to the MMCO. In addition to *Batrachosauroides*, an increasing number of Greenhouse World and xeric-associated reptiles and amphibians made a relatively brief appearance in the southeastern United States from the interval just prior to LOW through the MMCO, such as *Xenochelys floridensis* (Bourque, 2013), Kinosterninae gen. et sp. nov. (Bourque, 2015; fig. 10), podocnemidid pleurodire turtles (Bourque, 2016), dermatemydid turtles (Albright, 1994), helodermatid and xantusiid lizards (Bryant, 1991; Hayes, 2000; Hulbert, 2001; Bhullar and Smith, 2008; Bourque, 2013), a rhinophrynid frog (Blackburn et al., 2019), and dwarf alligatorids (Bourque, 2013; Hastings et al., 2023). These accounts further support the southeastern United States, in particular Florida, as a post-Eocene, late Oligocene to Middle Miocene refugium for exceptionally warm or tropically adapted reptiles and amphibians. Despite the fact that the account of *Batrachosauroides* from Love Bone Bed is well after the MMCO, the presence and commonality of co-occurring ectothermic, presumably warm-adapted, vertebrates such as giant tortoises and two different crocodilian taxa suggests a warm climate with mild winters in north-central Florida.

The rarity of batrachosauroidids from the Love Bone Bed is notable in that many thousands of macro- and microfossils comprising a multitude of different taxa were collected from the site during its excavation (Webb et al., 1981; over 45,000 cataloged specimens in the FLMNH Vertebrate Paleontology collection as of 6/11/2023). This suggests that *Batrachosauroides* was exceptionally rare in the Late Miocene of Florida, and/or that it preferred peripheral habitats adjacent to the main lotic deposit of the Love Bone Bed. The tumbled preservation of UF 293802 suggests

that it was fluvially transported before final burial, perhaps having originated from a more still-water habitat, such as a floodplain swamp or an oxbow in the river. However, its color and preservation resemble that of other Love Bone Bed fossils, so it is unlikely that the specimen was reworked from a stratigraphically older deposit. Many *Siren* fossil vertebrae from the Love Bone Bed exhibit a similar preservation and despite there being hundreds of specimens, pristine representatives are rarer than worn and polished ones. Using extant *Siren* and *Amphiuma* as modern analogs like other workers have proposed (Holman, 2006), it is probable that *Batrachosauroides* preferred slower moving portions of rivers and still, vegetated wetlands.

OTHER CAUDATES FROM THE LOVE BONE BED

Caudates from the Love Bone Bed are numerically dominated by vertebrae of a medium-sized *Siren* sp. (UF 403843–403867, UF 546459–546470, and numerous uncatalogued specimens), first reported by Webb et al. (1981) (Fig. 6A–C). The *Siren* likely represents an extinct species but compares well in approximate size and general morphology to living *Siren intermedia* examined (UF/H 158868). None approaches the large body size of extant *Siren lacertina*. The largest vertebrae are approximately the same size as the extinct *Siren simpsoni* from the Late Miocene (late Hemphillian) Haile 6A locality, Alachua County, Florida (Goin and Auffenberg, 1955). Although both have a relatively tall neural spine, *S. simpsoni* differs from the Love *Siren* in having a more laterally pronounced and very straight interzygapophyseal ridge when viewed in lateral aspect, whereas the interzygapophyseal ridge is less pronounced and curved down at the transverse process in the Love *Siren*. Two sirenids, *Siren simpsoni* and *Pseudobranchus* sp. (e.g., UF 2768), co-occur at Haile 6A. We compared some extremely small sirenid fossil vertebrae collected at the Love Bone Bed to the extant dwarf sirens, *Pseudobranchus striatus* and *Pseudobranchus axanthus*. These resemble *P. striatus* and *P. axanthus* in having a slightly concave (in lateral aspect)
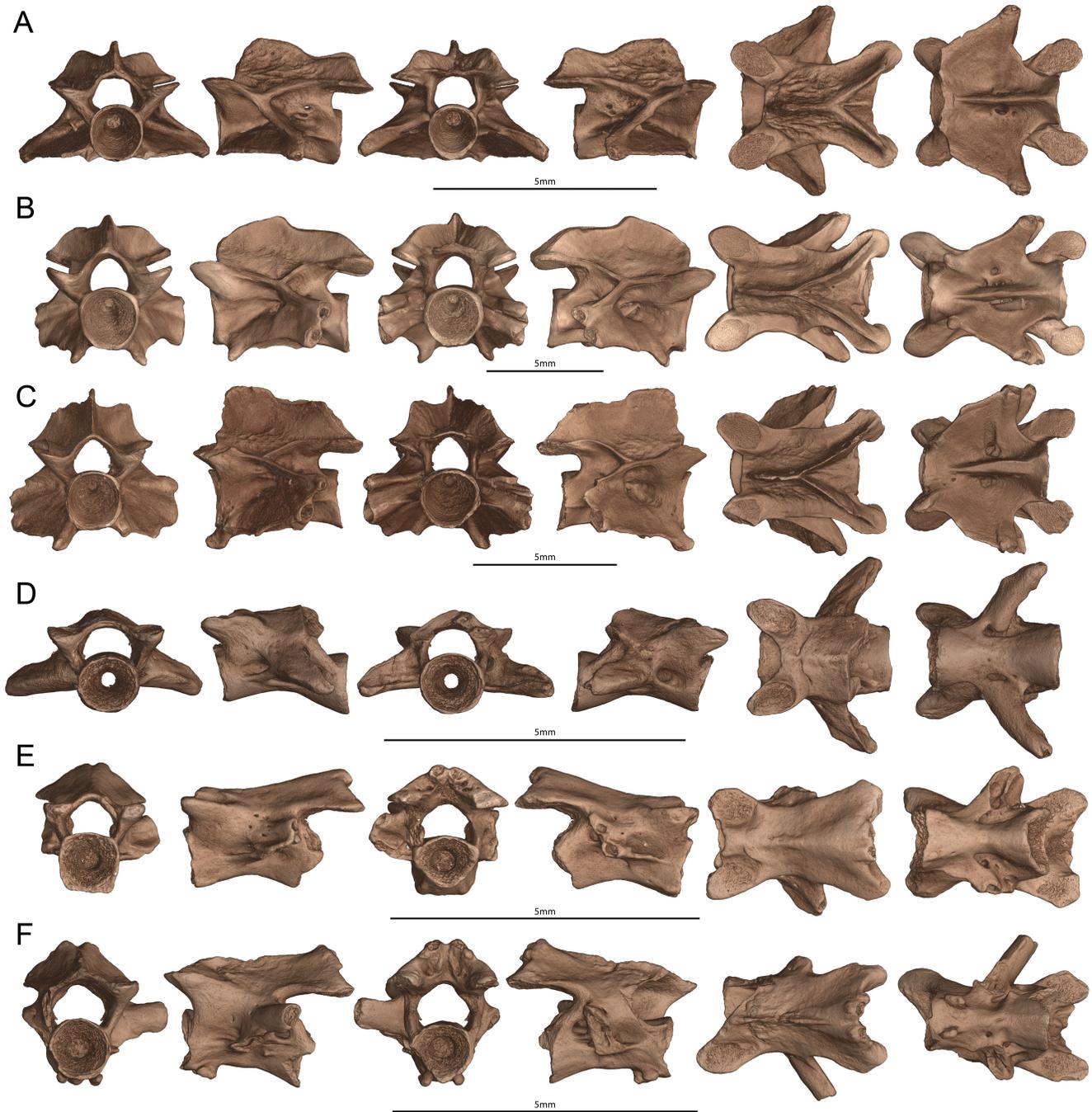
Figure 6. Caudate trunk vertebrae from the Love Bone Bed, Florida. **A–C**, *Siren* sp., represented by **A**, UF 546459; **B**, UF 546462; and **C**, UF 546464. **D–F**, *Ambystoma* sp., represented by **D**, UF 546456; **E**, UF 546457; and **F**, UF 546458. Aspects from left to right: anterior, left lateral, posterior, right lateral, dorsal, and ventral.

subcentral keel (Goin and Auffenberg, 1955) and a very low dorsal crest (e.g., UF 546469–546470, and UF 546853); however, they more closely resemble *Siren intermedia* in overall height to width proportions (vertebrae of *Siren* are taller whereas

those of *Pseudobranchus* more compressed and therefore elongate in appearance), in having a more prominently ridged subcentral keel, in lacking a pronounced lateral constriction posterior to the transverse processes in dorsal-ventral aspect
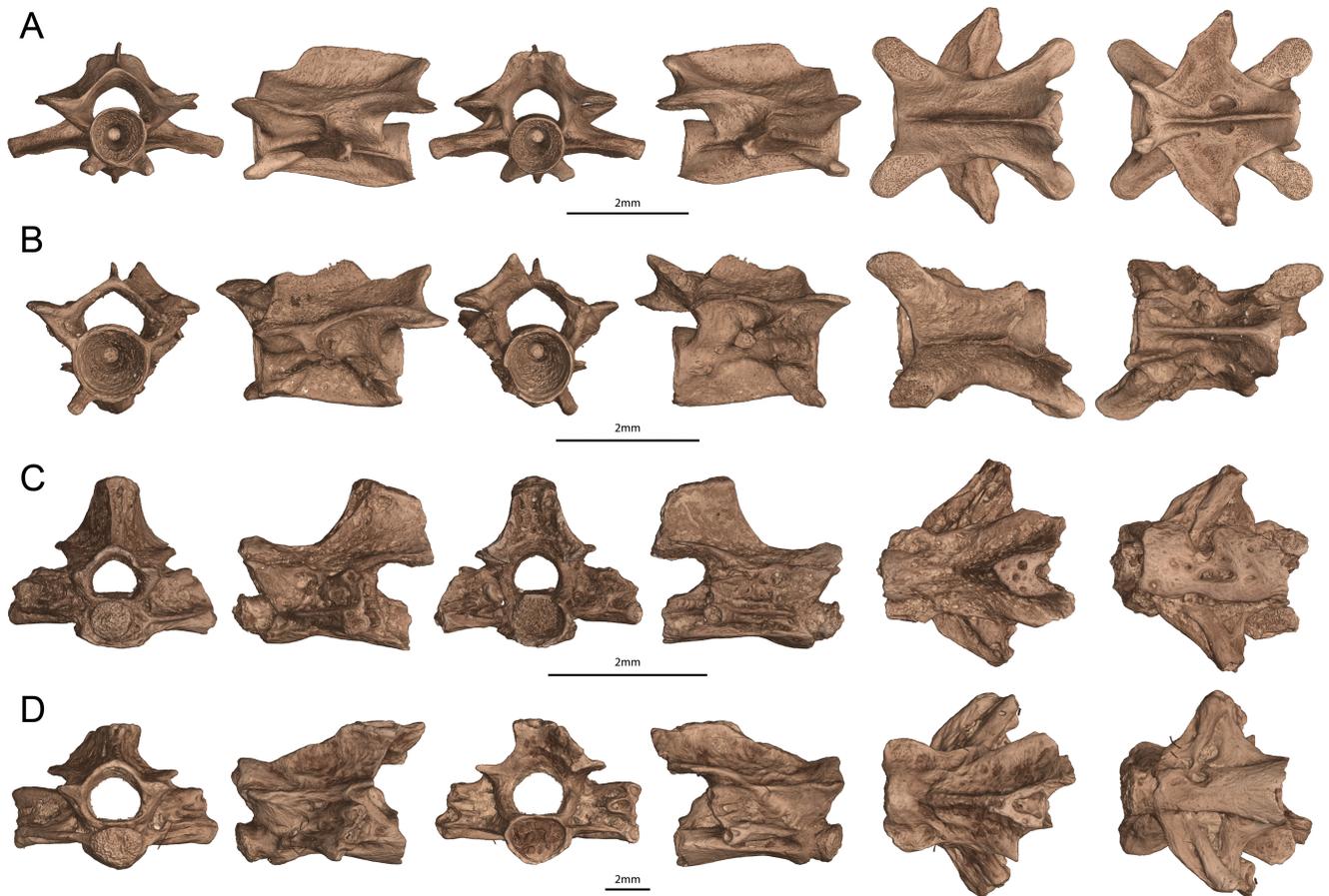
Figure 7. Caudate trunk vertebrae from the Gragg Mine, Georgia (**B–D**). **A**, UF/H 152951, Recent *Amphiuma pholeter* compared to **B**, UF 546636, *Amphiuma* n. sp., aff. *A. pholeter*. *Notophthalmus* sp., represented by **C**, UF 546644 and **D**, UF 546643. Aspects from left to right: anterior, left lateral, posterior, right lateral, dorsal, and ventral.

(*P. striatus* has a constricted vertebral waist), and in having a well-developed continuous interzygapophyseal ridge (*P. striatus* lacks a defined ridge centrally on the vertebra). Given that the oldest described *Pseudobranchus* fossils are *Pseudobranchus vetustus* from the Late Miocene (early Hemphillian 1) of north-central Florida (Goin and Auffenberg, 1955), it would not be unexpected to find older Miocene fossils with polymorphisms or a unique suite of shared features between the two living genera as seen in some specimens from the Love Bone Bed sample.

Mole salamanders of the genus *Ambystoma* are extremely rare and previously unreported, represented by only three vertebral specimens (UF 546456–546458; Fig. 6D–F). These trunk vertebrae compare well with those of extant *Ambystoma maculatum* and *Ambystoma opacum* examined in being amphicoelous, stoutly proportioned, having tiny anterior basapophyses or subtle basapophyseal crests, a narrowly spaced notch at the bifurcate crest of the neural spine (vs. a more widely spaced notch in plethodontids), and a relatively broad centrum ventrally. The rarity of ambystomatids and batrachosauroidids at the Love Bone Bed further corroborates the presence of low energy water bodies adjacent to the main river body as suggested by Webb et al. (1981: p. 537) and Bourque (2015). The majority of living ambystomatids are terrestrial and require ephemeral or lentic to sluggish fish-free water bodies for breeding (Petranka, 1998). Given that the Love Bone Bed was lotic and predatory fish were the most common fossils found there, the main stream body of the deposit would

have been inhospitable for these salamanders. This suggests that the *Ambystoma* vertebrae were either transported from a nearby peripheral habitat or that an individual *Ambystoma* would on occasion enter the river system.

OTHER CAUDATES FROM THE GRAGG MINE

Salamanders from the Gragg Mine include *Batrachosauroides* (described above), a small-bodied *Amphiuma*, and *Notophthalmus*, the latter of which is the most abundant caudate in the fauna. All are represented by isolated vertebrae. The trunk vertebrae of the *Amphiuma* (Fig. 7B) compare favorably with those of extant *Amphiuma pholeter* (Fig. 7A) in their extremely small size, very low neural spine, and widely spaced but prominent anterior basapophyses. However, the fossils most likely represent a new species of the pan-*pholeter* lineage in having a more defined interzygapophyseal ridge that is taller at the postzygapophyses than in extant *A. pholeter* examined, e.g., UF/H 152951 (Fig. 7A). This record is significant in that relatively little is known about extant *A. pholeter* and nothing has been previously published about its fossil record. It is understudied and seldom encountered, has a restricted geographic range along the northeast border of the Gulf of Mexico Coastal Plain that includes the region where the Gragg fossils were collected, and is somewhat habitat specific preferring deep liquid muck in floodplains of streams and rivers (Petranka, 1998; Bonett et al., 2009). Phylogenetically, *A. pholeter* has been recovered as basal to other living amphiumas (Karlin and Means, 1994) or more recently as sister to *Amphiuma means* (Bonett et al., 2009). These fossils place the pan-*pholeter* lineage in the region for at least the past 14.8–14 million years. The fossil vertebrae of *Notophthalmus* (Fig. 7C–D) require further study and comparisons to previously named Miocene species that include *Notophthalmus crassus* (Hemingfordian, Batesland Formation, South Dakota) (Tihen, 1974), *Notophthalmus robustus* (Hemingfordian, Thomas Farm, Florida) (Estes, 1963), and *Notophthalmus slaughteri* (early Barstovian, Trinity River Local Fauna, Texas) (Holman, 1966).

SYMPATRY OF AQUATIC LONG-BODIED SALAMANDERS

In discussing sympatry of aquatic long-bodied salamanders, the Gragg Mine caudate fauna is unusual for the southeastern Gulf Coastal Plain in that an amphiumid is present and a sirenid is not, most often the opposite holds true, or these genera co-occur in Miocene and other later Cenozoic deposits (JRB pers. observ.). It also represents one of the few co-occurrences of an amphiumid with *Batrachosauroides*. Other co-occurrences of amphiumids and batrachosauroidids are from the early Barstovian Moscow site, Polk County, Texas, and Arikareean 3 Toledo Bend locality in Newton County, Texas (Auffenberg, 1958; Albright, 1994; Holman, 1977; Holman, 2006). The Moscow site additionally preserved the co-occurrence of these two families and sirenids (Holman, 1977). Both the oldest and latest records of *Batrachosauroides* in Florida are from localities where *Batrachosauroides* co-occurs with *Siren*. Thomas Farm preserves the occurrence of *Batrachosauroides* and the species *Siren hesterna* (Goin and Auffenberg, 1955; Estes, 1963), and the Love Bone Bed preserves a co-occurrence of *Batrachosauroides* and a currently undescribed species of *Siren*.

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AUTHOR CONTRIBUTIONS

JRB designed the project and drafted the manuscript; ELS produced CT scans, drafted associated methods, Appendix 2, and specimen figures; and RCH drafted Appendix 1, most of the background for the Gragg Mine and Thomas Farm localities, and their revised age estimates based on mammalian biochronology. All authors edited the manuscript.

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Appendix 1: Table showing stratigraphic distribution of *Floridaceras*, *Menoceras*, and *Petauristodon* fossils recovered during 1981–1985 excavations at Thomas Farm. Units correspond to those of Pratt (1990); those without fossils of any of the three taxa are omitted. None of these taxa are particularly abundant at the site, so their absence in any particular stratum is not surprising. This is especially true for the absence of the two rhinos in Unit 15, as this bed contained relatively few fossils of larger taxa (Pratt, 1990). The stratigraphic distributions contradict the chronologic ranges given by Tedford et al. (2004) that would require all records of *Petauristodon* to be from units above those with either of the two rhinos.

Unit number	*Floridaceras*	*Menoceras*	*Petauristodon*
15			UF 90351*
7	UF 176197	UF 176195	
6	UF 156149*		
5			UF 90361
4	UF 185709*		
2	UF 176199		UF 90353
1	UF 204153	UF 204154	

*More than a single specimen found in this unit.

Appendix 2: Table with high-resolution CT data and scan hyperlinks. UF specimens displayed using Darwin Core Triplet identifier scheme.

Specimen ID	Species	Collection locality	Voxel resolution (mm)	voltage (kV)	current (µA)	Detector capture (mS)	projection number	Filter	MorphoSource DOI
UF:UF:111741	*Batrachosauroides* sp.	Milwhite Gunn Farm Mine, FL	0.02189503	100	250	200.098	1000	0.1 mm Cu	10.17602/M2/M572777
UF:UF:2013	*Batrachosauroides* sp.	Moscow locality, Burkeville Fauna, TX	0.03025475	100	250	200.098	800	0.1 mm Cu	10.17602/M2/M572776
UF:UF:217589	*Batrachosauroides* sp.	Gragg Mine, GA	0.03025475	100	250	200.098	800	0.1 mm Cu	10.17602/M2/M572789
UF:UF:293802	*Batrachosauroides* sp.	Love Bone Bed, FL	0.02189503	100	250	200.098	1000	0.1 mm Cu	10.17602/M2/M572791
UF:UF:546455	*Batrachosauroides* sp.	Love Bone Bed, FL	0.00506056	80	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572804
UF:UF:546456	*Ambystoma* sp.	Love Bone Bed, FL	0.00272016	60	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572805
UF:UF:546457	*Ambystoma* sp.	Love Bone Bed, FL	0.00338695	60	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572818
UF:UF:546458	*Ambystoma* sp.	Love Bone Bed, FL	0.00319958	60	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572819
UF:UF:546459	*Siren* sp.	Love Bone Bed, FL	0.00304426	60	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572833
UF:UF:546462	*Siren* sp.	Love Bone Bed, FL	0.00552109	80	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572834
UF:UF:546464	*Siren* sp.	Love Bone Bed, FL	0.00403291	80	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572847
UF:UF:546635	*Batrachosauroides* sp.	Gragg Mine, GA	0.0050589	80	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572848
UF:UF:546636	*Amphiuma* sp.	Gragg Mine, GA	0.00296423	60	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572861
UF:UF:546643	*Notophthalmus* sp.	Gragg Mine, GA	0.0018126	60	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572862
UF:UF:546644	*Notophthalmus* sp.	Gragg Mine, GA	0.00212803	60	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572875
UF:UF:546653	*Batrachosauroides* sp.	Gragg Mine, GA	0.00506048	80	200	250.097	2000	0.1 mm Cu	10.17602/M2/M572876
UF:UF:7802	*Batrachosauroides* sp.	Thomas Farm, FL	0.03025475	100	250	200.098	800	0.1 mm Cu	10.17602/M2/M572889
UF:UF/TRO:546528	*Batrachosauroides* sp.	Suwannee Springs, FL	0.01578675	80	200	250.097	1800	Al 0.3 mm	10.17602/M2/M572890
UF:UF/TRO:546529	*Batrachosauroides* sp.	Suwannee Springs, FL	0.01578675	80	200	250.097	1800	Al 0.3 mm	10.17602/M2/M572901
UF:Herp:152951	*Amphiuma pholeter*	Liberty County, FL	0.00296427	60	200	250.097	2000	none	10.17602/M2/M572627