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First Record of the Anuran Family Rhinophrynidae from the Oligocene of Eastern North America

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Abstract.—The anuran family Rhinophrynidae today comprises a single species restricted to southernmost Texas and Central America. Three extinct genera allied to this family are known from the Jurassic (*Rhadinosteus*) and Eocene (*Chelomophrynus*, *Eorhinophrynus*), whereas the sole extant genus *Rhinophrynus* is known from the latest Eocene (Chadronian) of Saskatchewan and the Pleistocene of Mexico. We provide the first records of the Rhinophrynidae from the Oligocene of eastern North America. From two of the oldest terrestrial vertebrate sites on the Florida peninsula (I-75, early Oligocene; Brooksville 2, late Oligocene), we have identified one nearly complete and several partial humeri, two radioulnae, two partial presacral vertebrae, three partial ilia, and one femur that are all referable to the Rhinophrynidae. These specimens are similar in size to the Eocene *Rhinophrynus canadensis*, smaller than the extant *R. dorsalis*, and might be distinguishable from both by features of the ilium and humerus. The presence of rhinophrynids during the Oligocene provides the first indication of change in the anuran fauna on the Florida peninsula during the Cenozoic.

The Florida peninsula in the southeastern United States hosts a rich fauna of frogs and toads (Order Anura) with nearly 30 native species representing five families. In addition to the present-day species, fossils of anurans are known from terrestrial deposits in Florida from the Oligocene, Miocene, Pliocene, and Pleistocene (Table 1). These fossils indicate that each of the extant genera, including *Acris* (Hylidae), *Anaxyrus* (family Bufonidae), *Gastrophryne* (Microhylidae), *Hyla* (or *Dryophytes* following Duellman et al., 2016; Hylidae), *Pseudacris* (Hylidae), *Rana* (Ranidae), and *Scaphiopus* (Scaphiopodidae) has been present on the Florida peninsula for at least the past 18—and possibly past 30—million years (Pratt, 1989; Morgan, 1993; Table 1). Unlike many other vertebrate groups (Hulbert, 2001), there are no definitive examples of anuran families known from the fossil record of Florida that are not represented among its extant species.

Among North American frogs, the family Rhinophrynidae is among the most morphologically distinctive. This family and the Pipidae together comprise the Pipoidea, which originated in the Jurassic and is among the earliest diverging lineages of extant anurans (Cannatella, 2015; Feng et al., 2017). The single extant species *Rhinophrynus dorsalis* is today restricted to southernmost Texas, Mexico, and Central America, where it occurs in semiarid and arid areas with loose soils conducive to digging (Dodd, 2013); it has been reported from the Pleistocene of Mexico (Holman, 1969). In addition, extinct taxa that are more closely related to *Rhinophrynus* than to other pipoid anurans are known from the Mesozoic and Cenozoic of North America, including *Rhadinosteus* from the Jurassic of Utah (Henrici, 1998), *Eorhinophrynus* from the Paleocene of Wyoming (Hecht, 1959; Estes, 1975; Krause, 1980), *Chelomophrynus* from the Eocene of Wyoming (Henrici, 1991; Henrici and Fiorillo, 1993), and the extinct *Rhinophrynus canadensis* from the Eocene of Saskatchewan (Holman, 1963, 1968, 1969, 1972; Roček and Rage, 2000). To date, there are no Mesozoic or Cenozoic records attributed to the Rhinophrynidae *sensu lato* from eastern North America (Henrici, 2016).

We report fossils referable to *Rhinophrynus* from two Oligocene sites in Florida. The majority of the fossils come from Brooksville 2, a site comprised of karst fissure fillings in the Suwanee Limestone near Brooksville, Florida that is one of the earliest terrestrial vertebrate sites in Florida (Arikareean, 26–28 mya; Hayes, 2000). In addition, one humerus comes from the I-75 site (Whitneyean; ~30 mya; Morgan and Czaplewski, 2003) from which several anurans were briefly listed but never described (Patton, 1969; Meylan, 1984; Hulbert, 2001). We provide the first description of any anuran material from the Oligocene of the Florida peninsula and of the Rhinophrynidae from anywhere in eastern North America. In addition to documenting a formerly more widespread distribution of this family, we discuss the first glimpse into possible faunal turnover of anurans on the Florida peninsula during the Cenozoic.

Materials and Methods

Sampling.—The fossils reported here (Fig. 1) were identified after sorting through anurans isolated after screen-washing matrix from both sites. After comparing these fossils to extant species that are exemplars of all current North American and Caribbean anuran genera, we determined that a subset of these represented a taxon not previously described from the Florida peninsula that we discuss below (Fig. 2). The remainder of the anuran faunas from both the I-75 and Brooksville 2 sites will be described elsewhere. Institutional abbreviations for specimens studied are as follows: CAS, California Academy of Sciences, San Francisco, USA; UF-VP, Division of Vertebrate Paleontology, Florida Museum of Natural History, University of Florida, Gainesville, USA.

CT Scanning.—Following identification, we generated digital three-dimensional models of fossil specimens and comparative material from alcohol-preserved extant specimens using X-ray computed microtomography (CT) at the University of Florida's Nanoscale Research Facility. For this characterization, we used

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TABLE 1. Summary references on fossils of anuran genera native to the Florida peninsula organized by epoch. Note that all toad fossils in Florida have been reported previously as *Bufo*, though we treat them here as the genus *Anaxyrus* that is native to North America.

Family/genus	Epoch	Reference(s)
Bufonidae		
Anaxyrus	Pleistocene	Lynch (1965), Holman (1959, 1978), Meylan (1995)
	Pliocene	Auffenberg (1957), Meylan (2005)
	Miocene	Tihen (1951), Auffenberg (1956), Holman (1967), Webb (1981), Pratt (1989)
	Oligocene	Patton (1969)
Hylidae		
Acris	Pleistocene	Lynch (1965)
	Miocene	Holman (1967), Pratt (1989)
Hyla	Pleistocene	Holman (1959), Lynch (1965)
	Pliocene	Meylan (2005)
	Miocene	Auffenberg (1956), Holman (1967), Webb (1981), Pratt (1989)
Pseudacris	Pleistocene	Lynch (1965)
	Pliocene	Lynch (1964), Wilson (1975)
Microhylidae		
Gastrophryne	Pleistocene	Holman (1958, 1959), Lynch (1965)
	Pliocene	Meylan (2005)
	Miocene	Auffenberg (1956), Holman (1967), Webb (1981)
Ranidae		
Rana	Pleistocene	Holman (1958, 1959, 1978), Lynch (1965), Meylan (1995)
	Pliocene	Auffenberg (1957), Meylan (2005)
	Miocene	Auffenberg (1956), Holman (1967), Webb (1981), Pratt (1989)
Scaphiopodidae		
Scaphiopus	Pleistocene	Holman (1958, 1959, 1978), Lynch (1965)
	Pliocene	Meylan (2005)
	Miocene	Auffenberg (1956), Holman (1967), Webb (1981), Pratt (1989)
	Oligocene	Patton (1969)

a Phoenix v|tome|x M (GE Measurement & Control, Boston, Massachusetts, USA) scanner with a 240-kV X-ray tube and a tungsten target, modifying X-ray generation and detector settings to optimize resolution and contrast (resolution 4.6–78 µm; see Appendix for details). Raw 2D X-ray data were converted to tomograms using the datos|x software v. 2.3 with postprocessing, analyses (including segmentation and measurement), and visualization conducted using VG StudioMax v. 3.2 (Volume Graphics, Heidelberg, Germany). For comparisons, we generated comparable models for two fluid-preserved specimens (CAS-Herp-71766; UF-Herp-13375-4) of *Rhinophrynus dorsalis*, as well as exemplars of other North American taxa (Fig. 2). Our anatomical terminology follows Delfino (2017), Gómez and Turazzini (2016), and Trueb et al. (2011). Tomogram data and mesh files for all fossils and comparative specimens are available via morphosource.org (Appendix Tables 1 and 2), which enables users to view all of the discussed elements in additional views (including material not figured here).

SYSTEMATIC PALEONTOLOGY

Amphibia Linnaeus, 1758
Anura Fischer von Waldheim, 1813
Pipoidea Gray, 1825
Rhinophrynidae Günther, 1859
Rhinophrynus Duméril & Bibron, 1841
Rhinophrynus sp. indet.

Referred Material.—Brooksville 2 Quarry 1A (locality HE003): UF-VP-431013 (right humerus; distal end); 431014 (right proximal ilium; incomplete); 431018–19 (presacral vertebrae); 431020–21 (right humeri; distal end); 431022 (left humerus; distal end); 446628, 446630 (right radioulnae); 446627 (left femur). Brooksville 2 Quarry 1A (locality HE008): 431015 (left proximal ilium; incomplete); 431016 (left proximal ilium; incomplete). I-75 (locality AL018): UF-VP-16714 (right humerus; mostly complete, missing proximal end).

Locality and Age.—The fossils found at the I-75 site—a sinkhole exposed during highway construction near Gainesville, Florida (Alachua County)—come from the first terrestrial vertebrate site known from the Oligocene of Florida (Hulbert, 2001). The I-75 site is likely from the Whitneyean or earliest Arikareean land mammal ages (~30 mya) as some mammalian taxa restricted to the Arikareean are not present (Hayes, 2000; Morgan and Czaplewski, 2003), making this the oldest terrestrial vertebrate fauna known from the Florida peninsula. Patton (1969) reported both *Bufo* (possibly corresponding to what is now recognized as *Anaxyrus*) and *Scaphiopus* from I-75, and Meylan (1984) also noted that the Ranidae was present (followed by Hulbert, 2001). However, to our knowledge, none of this material has ever been described, figured, or studied further.

The Brooksville site is located near Brooksville, Florida (Hernando County) and is part of the Suwannee Limestone, with at least five clay-filled crevice deposits (Hayes, 2000). The formation lies between the Eocene Ocala limestone to the north and the Miocene Tampa limestone to the south. Based on biochronology, Hayes (2000) dated this site to the Arikareean between 26–28 mya, which was later supported by studies of bats from this site (Czaplewski and Morgan, 2012). The Brooksville 2 local fauna contains a rich diversity of mammals, as well as snakes (Hayes, 2000; Mead, 2013), lizards (Hayes, 2000; Chovanec, 2014), and a kinosternid turtle (Bourque, 2013). In addition, Hayes (2000) reported the presence of three families of anurans, though these were never further identified (simply listed as "Anura: 3 Families present").

Description.—The presacral vertebrae have ectochordal centra and large triangular neural canals (Fig. 1). One vertebra (UF-VP-431019) likely represents the fifth or sixth presacral vertebra (centrum length: 1.4 mm). It has a large and expanded neural arch that extends posteriorly to overlap with the immediately posterior vertebra, as well as prezygapophyses that are immediately dorsal to the transverse processes, which are directed anteriorly. One vertebra (UF-VP-431018) may represent the eighth presacral vertebra that articulates with the sacrum (centrum length: 1.7 mm). As in the last presacral vertebrae of extant *Rhinophrynus dorsalis*, this vertebra has a neural arch that does not extend posteriorly beyond its centrum.

The humeri are robust and exhibit a diaphysis that is slightly bowed dorsally, which is especially clear in the most complete specimen from I-75 (UF-VP-16714). The total preserved length is 10.6 mm, though proximally it lacks the ossified articular surface. The distal humerus has a prominent large round distal condyle (3.3 mm in diameter) that is wider than the width of the

FIG. 1. Osteological comparisons between *Rhinophrynus dorsalis* and fossil *Rhinophrynus* sp. from the Oligocene of Florida. In the center, skeleton of *R. dorsalis* (UF-Herp-13375-4) highlighting elements recovered in the fossil record. Surrounding the skeleton, each element from this recent specimen is to the right of the fossils: (a) right humerus (UF-VP-16714), anterior view; (b) presacral vertebra (UF-VP-431018 compared to presacral V), anterior view; (c) left femur (UF-VP-446627), posterior view; (d) right radioulna (UF-VP-446628), anterior view; (e) presacral vertebra (UF-VP-431019 compared to presacral VIII), anterior view; and (f) right ilium (UF-VP-431014), lateral view. Abbreviations: dae, dorsal acetabular expansion; dc, distal condyle; dp, dorsal protuberance; lc, lateral crest; na, neural arch; ue, ulnar epicondyle; vae, ventral acetabular expansion; vc, ventral crest; vs, ventral sulcus. Scale bars = 2.00 mm.

diaphysis. There is a pronounced cubital fossa proximal to the condyle. A well-developed ulnar epicondyle (entepicondyle) extends to approximately the distal two-thirds of the distal condyle; the radial epicondyle (ectepicondyle) is present but not prominent. There is a weakly developed trochlea between the large distal condyle and the ulnar epicondyle. The ventral crest extends distally beyond the proximodistal midpoint and bears a well-developed medial groove.

The radioulnae are short (distal epiphysis of ulna to tip of olecranon: 6.5 mm in UF-VP-446628; 4.6 mm in the preserved portion of UF-VP-446630), robust, and wide, with the proximal and distal ends having the same width (approximately 3.0 mm in UF-VP-446628; 2.2 mm in UF-VP-446630). The radioulnae are narrow in lateral view with a distinct ridge extending along the ulna. In dorsal view, the radius and ulna have similar widths and form a broad flat shaft. The longitudinal sulcus on the ventral surface between the radius and ulna is short and deep and associated with three large foramina along the sulcus. Several additional small foramina are present along the midline on the dorsal surface but differ in number between the two fossils. There is also a single large foramen—located within a deep fossa on UF-VP-446628—on the medial surface of the shaft close to the olecranon fossa. A short crest extends along the ventromedial surface of the radius beginning near this large foramen and extending to the distal end of the diaphysis. The olecranon has an "S" shape, with the articular surface corresponding to the ulna being larger than that of the radius.

The ilia from Brooksville 2 have a prominent dorsal acetabular expansion that forms a weak right angle with the base of the iliac shaft. Of the three specimens, UF-VP-431015 preserves the largest portion of the iliac shaft (1.3 mm in height), which appears to be almost straight; the maximum dorsoventral

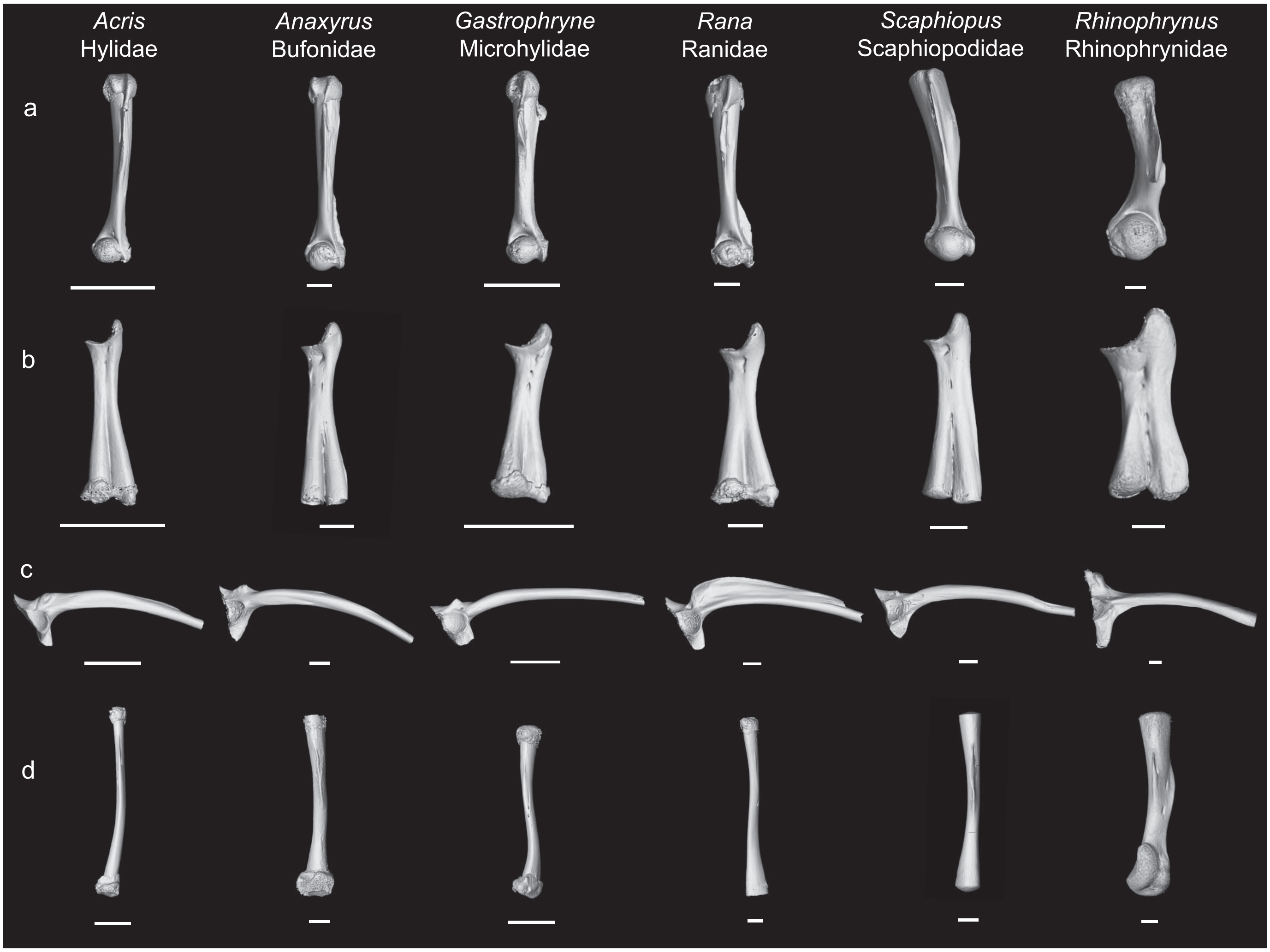

FIG. 2. Osteological comparison of anuran genera native today to the southeastern United States and frequently recovered in the fossil record of Florida. (a) Right humerus (anterior view), (b) right radioulna (anterior view), (c) right ilium (lateral view), and (d) left femur (posterior view). Species samples include *Acris gryllus* (UF-Herp-107362), *Anaxyrus terrestris* (UF-Herp-3170), *Gastrophryne carolinensis* (UF-Herp-110645), *Rana clamitans* (UF-Herp-76511), *Scaphiopus holbrookii* (UF-Herp-9620), and *Rhinophrynus dorsalis* (UF-Herp-13375-4). Scale bars = 2.00 mm.

dimension of UF-VP-431015 is 6.7 mm (maximum acetabulum dimension: 2.7 mm). The ventral acetabular expansion is not preserved completely in any of these specimens (Fig. 1). The dorsal protuberance is bulbous and located at the anteriormost extent of the dorsal acetabular expansion, which is best preserved on UF-VP-431014, but does not project dorsally beyond the margins of the dorsal acetabular expansion; the maximum dorsoventral dimension of UF-VP-431014 is 5.2 mm (maximum acetabulum dimension: 2.6 mm). The posterior margin of the ilium articulating with the ischium is straight, and the medial surface lacks a tubercle.

The femur is robust, short (7.0 mm in length), and bowed posteriorly. The epiphyseal surface that articulates with the pelvis is not preserved. The diaphysis has a well-developed lateral crest that extends from the diaphysis proximally, reaching its maximum height proximally and terminating 1.3 mm from the proximal head. An oval foramen is located next to the distal end of the lateral crest. Ventrally, an additional crest extends from the distal femur toward the proximal head, and is most pronounced at the middle. Two foramina are located along this auxiliary crest; the larger is found at the distal end of the crest and the smaller at the ventral edge, creating a small canal along its base. Additional smaller foramina are located dorsally along the diaphysis. Distally, the femur has a distinctive distal condyle that articulates with the tibiofibula. This distal condyle is ovoid in shape and surrounded by small foramina along the dorsal, ventral, and posterior surfaces of the diaphysis. In addition, the articular surface of the distal condyle bears distinct articular surfaces extending both posteriorly and posteroventrally.

Remarks.—These specimens all likely represent postmetamorphic individuals because neural arches are fused to the centra, and the distal condyles of the humeri are well ossified and fully synostosed to the diaphyses. However, the lack of a fully ossified proximal articular cartilage may indicate that at least UF-VP-16714 does not represent a fully mature adult. Further, the specimens from Brooksville and I-75 tend to be smaller than elements found in adult specimens of the extant *Rhinophrynus dorsalis* (Table 2), which reach 50–90-mm snout–vent length as adults (Dodd, 2013).

Comparisons.—The skeletal elements reported here are clearly distinguishable from those of other taxa in North America, including bufonids, hylids, microhylids, and ranids (Fig. 2). The limb elements of *Rhinophrynus* are all distinguishable from other

TABLE 2. Comparison of measurements between fossil specimens of *Rhinophrynus* cited in the text to skeletal elements from two preserved specimens of *R. dorsalis*. For comparisons to the fossils, the right humerus and radioulna and left femur was measured for *R. dorsalis*. Measurements in millimeters.

	Fossils	CAS-Herp-71766	UF-Herp-13375-4
Snout–vent length	–	31.2	65.8
Humerus length	10.6	10.7	17.6
Radioulna length	6.5	7.2	11.4
Femur length	7.0	13.8	22.2
Ilium shaft height	1.3	1.2	2.1
Acetabulum height	2.7 / 2.6	2.6	3.1
Vertebral length, PS V	1.4	1.6	3.2
Vertebral length, PS VIII	1.7	1.6	3.4

genera by being stout with prominent crests and articular surfaces. The humerus of *Rhinophrynus* has a large distal condyle relative to the length of the bone and thick, curved diaphysis bearing a prominent crest. The radioulna similarly has wide distal articular surfaces relative to its total length. Likewise, the femur of *Rhinophrynus* has relatively large distal articular surfaces, a curved diaphysis, prominent crests, and, uniquely among the taxa considered here, a distal articular surface that extends well onto the posteroventral surface of the diaphysis. The ilium is readily distinguished by a narrow iliac shaft and a tall, angular dorsal acetabular expansion. The vertebrae of *Rhinophrynus* consistently have ectochordal centra (Fig. 1; Cannatella, 1982) because of the lack of fusion of the centrum to the intervertebral disc (Walker, 1938).

In comparison to other North American taxa, the ilia, vertebrae, humeri, femur, and radioulnae preserved from Brooksville 2 and I-75 all strongly resemble those of the extant *Rhinophrynus dorsalis* (Holman, 1963; Estes, 1975) and the extinct *R. canadensis* (Holman, 1963, 2003). There are notable differences between *Rhinophrynus* and the extinct rhinophrynid genera *Rhadinosteus* Henrici, 1998, *Eorhynophrynus* Estes, 1975, and *Chelomophrynus* Henrici, 1991, especially in the humerus, ilium, and femur. *Rhinophrynus* differs from *Rhadinosteus* by having a humerus with a rounded distal condyle and similarly developed ent- and ectepicondyles as well as a femur with well-developed crests (Henrici, 1998). It differs from *Chelomophrynus* by having a femur that is not dorsoventrally flattened distally, an ilium with a straighter iliac shaft that lacks lateral keel and a more excavated ventral acetabular expansion (Holman, 2003); while not depicted in Henrici (1991), the humerus of *Chelomophrynus* does have developed ventral and lateral crests separated by a medial groove (A. Henrici, pers. comm.). Last, *Rhinophrynus* differs from *Eorhinophrynus* in having a humerus with a less extensive lateral crest and lacking a medial ventral crest that descends towards the distal condyle (Estes, 1975).

The Florida material can be differentiated from the ilia of both *R. dorsalis* and *R. canadensis* by having a dorsal protuberance that does not project prominently beyond the dorsal extent of the dorsal acetabular expansion. Although the ventral acetabular expansion is not preserved in the Florida material, the preacetabular region is similar to *R. dorsalis* by being wider relative to the acetabulum than in *R. canadensis*. The Brooksville femur is less robust than the two extant specimens and has a less-developed ventral crest, which in the extant specimens extends from the distal epiphysis to the middle part of the diaphysis. The posteroventral surface of the distal condyle is more developed in the extant *R. dorsalis* than in the fossil. The preserved portions of the humeri are generally similar between *R. canadensis* and the Florida material by having a prominent ulnar epicondyle, potentially more so than in *R. dorsalis*, though the trochlea between the large distal condyle and the ulnar epicondyle appears more well developed in the Florida material (see fig. 25 in Holman, 2003). The shaft of the radioulnae from Brooksville is narrower in lateral view than in *R. dorsalis* and also has an ulnar process of the olecranon that is more elongated. Although other skeletal elements are referred to *R. canadensis* by Holman (1963, 2003), including radioulnae, tibiofibulae, and vertebrae, because these have not been figured, are only briefly described, and none of the type or referred material can be located today (Holman, 2003; R. McKellar, pers. comm.), further comparisons with the Florida material are not possible.

DISCUSSION

The fossils from Oligocene Brooksville 2 and I-75 are the first example of an anuran family known from fossils in peninsular Florida that is not represented among its modern species. Taken together with the extinct *R. canadensis* from the Eocene of Saskatchewan (Holman, 1963), this record indicates a larger distribution for the genus *Rhinophrynus* during the early Cenozoic. Because modern *R. dorsalis* occupies arid or semiarid regions and there are no known rhinophrynids from the Miocene, Pliocene, or Pleistocene, this Oligocene record of *Rhinophrynus* in Florida suggests turnover in the anuran fauna associated with climatic cooling and progressive aridification extending from the Oligocene through the Miocene to the present (Böhme, 2003; Anderson et al., 2011; Hansen et al., 2013). Although the Oligocene reptile faunas of Florida from sites such as I-75, White Springs 1A and 3B, and Brooksville 2 remain incompletely documented, it is clear these include taxa such as typhlopid and boid snakes (Patton, 1969; Morgan, 1989; Mead, 2013; Mead and Schubert, 2013) and the kinosternid turtle *Xenochelys* (Bourque, 2013) that later disappeared from Florida. It also remains unclear whether squamate families documented from the Miocene Thomas Farm site such as Helodermatidae and Xantusiidae (Estes, 1963; Hulbert, 1992, 2001; Bhullar and Smith, 2008) might have been present in the Oligocene as well. Because of the climatic changes from the Oligocene through Miocene and the fact that many genera of amphibians and reptiles appear in the fossil record for the first time in the Oligocene (Hutchison, 1992), the fossil record of the Florida provides a valuable window into origins and transitions in the North American herpetofauna.

Previous research makes clear that other anuran genera previously identified from the fossil record of Florida should be treated with caution. Based on a single ilium from Thomas Farm, an early Miocene site, Holman (1961) described *Proacris*, which he referred to the Hylidae. However, both Sanchíz (1998) and Roček and Rage (2000) questioned whether *Proacris* is distinct from *Acris* or *Pseudacris*, both of which have been rarely reported in the fossil record of Florida. Holman (1967) reported *Acris* from Thomas Farm, the same Miocene site as *Proacris*, based on a fragmentary ilium; the genus is also known from the Pleistocene of Florida (Lynch, 1965). To date, the genus *Pseudacris* has been reported only from the Pleistocene of Florida (Lynch, 1965; Wilson, 1975). Early on, Lynch (1966) discussed the difficulties in using features such as the position of the dorsal protuberance relative to the acetabulum to discriminate among hylid taxa including *Pseudacris* and *Acris*. In this light, the extinct genus *Proacris* should be considered *incertae sedis* in the Hylidae.

Two other records of anuran genera from Thomas Farm have been called into doubt by later workers. First, Holman (1964) reported *Leptodactylus* (family Leptodactylidae) from Thomas Farm. Lynch (1971) later referred this material to *Rana*, which is well known from this site (Tihen, 1951; Auffenberg, 1956, 1957; Holman, 1964). In addition, Holman (1967) reported *Eleutherodactylus* (family Eleutherodactylidae) from Thomas Farm, based on a single ilium, but this too has been considered doubtful (Pratt, 1986; Hulbert, 1992). Although it is certainly within the realm of possibility that both Eleutherodactylidae and Leptodactylidae could be found in the fossil record of the Florida peninsula, rigorous study of additional material in the context of a broader taxonomic sampling is needed.

The anuran fauna of the Oligocene of peninsular Florida remains poorly explored. In addition to the I-75 and Brooksville sites (Patton, 1969; this study), anuran fossils have been reported from the Arikareean White Springs site (Morgan, 1989) though never described further. Ongoing research on fossils from these and other Oligocene sites reveals a wealth of anuran material (M. Vallejo-Pareja and D. C. Blackburn, unpubl. data). This period of time is especially interesting for North America in the context of recent time-calibrated molecular phylogenies (e.g., Li et al., 2015; Yuan et al., 2016; Feng et al., 2017; Hutter et al., 2017). At least based on the historical biogeography of extant genera in North America, we might expect to find taxa such as *Gastrophryne*, *Rana*, and *Hyla*. Whereas bufonids such as *Anaxyrus* may have originated later, time-calibrated molecular phylogenies suggest an earlier origin to the Caribbean *Peltophryne* (Alonso et al., 2012), which conceivably could turn up in the fossil record of Florida. Connections between the Miocene or Oligocene amphibians and reptiles from the Florida peninsula and the present-day fauna of the Greater Antilles have been repeatedly posited, including for *Eleutherodactylus* (Goin, 1958; Holman, 1967; but see Hulbert, 1992), "*Bufo*" *praevis* (Tihen, 1962), xantusiid and gekkotan lizards, and iguanians referable to families such as Dactyloidae, Iguanidae, and Leiocephalidae (Estes, 1963; Meylan, 1982, 1984; Chovanec, 2014). Further, as our description of *Rhinophrynus* demonstrates, both extant and extinct genera not currently found in eastern North America might have previously existed on the Florida peninsula. Thorough study of anurans from Oligocene sites on the Florida peninsula may provide important insights into the assembly of the eastern North American frog fauna and its relationship with Caribbean anurans.

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Supplementary Data

Supplementary data associated with this article can be found online at http://dx.doi.org/10.1670/19-044.s1.

APPENDIX TABLE 1. Taxonomy and digital object identifiers (DOI) of images of preserved specimens used for comparison. All specimens are complete skeletons and no photographs used a filter. DOIs in MorphoSource repository correspond to TIFF stacks (upper) and STL (lower) image files for each specimen.

Taxon	Family	Accession number	Voxel size (mm)	Voltage (kV)/ amperage (µA)	Watts	Exposure time (s)	Projections	DOI
Anaxyrus terrestris	Bufonidae	UF-H-3170-1	0.03225349	100/200	20	0.200098	1,500	doi:10.17602/M2/M11377 doi:10.17620/M2/M11374
Acris gryllus	Hylidae	UF-H-107362	0.02702997	90/200	18	0.200098	2,000	doi:10.17602/M2/M20033 doi:10.17620/M2/M20037
Gastrophryne carolinensis	Microhylidae	UF-H-110645	0.02906136	90/200	18	0.200098	2,000	doi:10.17602/M2/M25067 doi:10.17620/M2/M20081
Rana clamitans	Ranidae	UF-H-76511	0.04749801	90/200	18	0.200098	1,800	doi:10.17602/M2/M20098 doi:10.17620/M2/M20064
Rhinophrynus dorsalis	Rhinophrynidae	CAS-H-71766	0.02721782	125/150	18.75	0.200098	1,700	doi:10.17602/M2/M48893 doi:10.17620/M2/M16302
Rhinophrynus dorsalis	Rhinophrynidae	UF-H-13375-4	0.06257171	120/150	18	0.333096	1,300	doi:10.17602/M2/M71249 doi:10.17620/M2/M71185
Scaphiopus holbrookii	Scaphiopodidae	UF-H-9620	0.0781306	70/200	14	0.200098	960	doi:10.17602/M2/M22642 doi:10.17620/M2/M22641

APPENDIX TABLE 2. Descriptions and digital object identifiers (DOI) of images of fossil specimens. All specimens are from *Rhinophrynus* sp. (family Rhinophrynidae) with projection averaging of 3. Digital object identifiers in MorphoSource repository correspond to TIFF stacks (upper) and STL (lower) image files for each specimen.

Accession number	Fossil element	Voxel size (mm)	Voltage (kV)/ amperage (µA)	Watts	Exposure time (s)	Filter	Projections	DOI
UF-VP-16714	Right humerus	0.00684892	80/140	11.2	0.200098	None	2,200	doi:10.17602/M2/M57068 doi:10.17620/M2/M57414
UF-VP-431013	Right humerus	0.03595345	150/400	60	0.5	0.1 mm Cu	2,250	doi:10.17620/M2/M57077 doi:10.17620/M2/M57407
UF-VP-431014	Right proximal ilium	0.02844607	120/200	24	0.2	0.1 mm Cu	2,200	doi:10.17602/M2/M57067 doi:10.17620/M2/M57501
UF-VP-431015	Left proximal ilium	0.00531234	80/200	16	0.2	None	2,200	doi:10.17602/M2/M57078 doi:10.17620/M2/M57768
UF-VP-431016	Left proximal ilium	0.03302707	150/400	60	0.5	0.1 mm Cu	2,250	doi:10.17602/M2/M57079 doi:10.17620/M2/M57080
UF-VP-431018	Presacral vertebra	0.02844607	120/200	24	0.2	0.1 mm Cu	2,200	doi:10.17602/M2/M57069 doi:10.17620/M2/M57769
UF-VP-431019	Presacral vertebra	0.00625492	80/140	11.2	0.2	None	2,200	doi:10.17602/M2/M57072 doi:10.17620/M2/M57073
UF-VP-431020	Right humerus	0.04264243	80/150	12	0.333	0.1 mm Cu	1,600	doi:10.17602/M2/M57081 doi:10.17620/M2/M57082
UF-VP-431021	Right humerus	0.02898126	80/150	12	0.333	0.1 mm Cu	2,200	doi:10.17602/M2/M57083 doi:10.17620/M2/M57084
UF-VP-431022	Left humerus	0.00458233	80/140	11.2	0.2	None	2,200	doi:10.17602/M2/M57070 doi:10.17620/M2/M57071
UF-VP-446627	Left femur	0.00531234	80/200	16	0.2	None	2,200	doi:10.17602/M2/M71041 doi:10.17620/M2/M71172
UF-VP-446628	Right radioulna	0.00531234	80/200	16	0.2	None	2,200	doi:10.17602/M2/M71042 doi:10.17620/M2/M71170
UF-VP-446630	Right radioulna	0.00605054	80/200	16	0.2	None	2,200	doi:10.17602/M2/M71039 doi:10.17620/M2/M71040