Bull. Fla. Mus. Nat. Hist. (2005) 45(4): 171-178

LATE PLIOCENE ANURANS FROM INGLIS 1A, CITRUS COUNTY, FLORIDA

Peter Meylan[1]

On the basis of qualitative osteological characters, six anuran taxa are present in the late Pliocene Inglis 1A Local Fauna, an apparent natural trap in karst Eocene limestone. They are *Scaphiopus holbrookii*, *Gastrophryne carolinensis*, *Hyla cinerea*, *Rana catesbeiana*, *Rana capito*, and *Bufo defensor* n. sp. (that appears to be related to *Bufo terrestris)*. The predominance of adults in the size class distribution of the *Bufo* sample suggests that at least some individuals may have been trapped during migrations to and from breeding sites. Frog species with xeric adaptations dominate the sample, supporting previous theories that the region around the sinkhole that formed the Inglis 1A site was well drained and xeric. Comparison with other known anuran fossils from Florida indicates that the Inglis site is currently the oldest record in Florida of an essentially modern anuran fauna.

Key Words: Pliocene; Florida; Anura; new taxon; *Scaphiopus*; *Gastrophryne*; *Hyla*; *Bufo*; *Rana*

INTRODUCTION

The Pliocene represents a major gap in our knowledge of the fossil anurans of Florida. Pleistocene frogs are known from one late early Irvingtonian locality (Leisey Shell Pit; Meylan 1995) and about a dozen Rancholabrean localities (Brattstrom 1953; Emslie & Morgan 1995; Gut & Ray 1963; Hay 1917; Holman 1958, 1959a, 1959b, 1962, 1978; Lynch 1964, 1965; Tihen 1952; Weigel 1962). Pre-Pliocene anuran faunas from Florida are early Miocene (Thomas Farm, Tihen 1951; Auffenberg 1956) and late Miocene (Haile 6A; Auffenberg 1957). Thus, there remains a gap of about 7 million years between the early late Miocene and late early Pleistocene during which nothing is known about anurans in this state. The “very late Pliocene” record of *Bufo* n. sp. listed in Hulbert (2001:42) is the new species described in this paper.

Anurans from the early Miocene of Thomas Farm are referred to one extinct and five living genera. Three of 12 forms are referred to living species (Tihen 1952; Auffenberg 1956; Hulbert, 2001:41-42). Frogs from the early late Miocene, Haile 6A locality were identified as an extinct new form, *Bufo tiheni*, and *Rana* cf. *pipiens*, the living leopard frog (also reported from Thomas Farm). Pleistocene frog material from Florida, on the other hand, representing 15 species, has all been referred to living genera and species with one exception (*Hyla baderi*, Lynch 1965). Study of collections from the late Blancan of Inglis 1A provides the first opportunity to document a Pliocene frog fauna in Florida, and an opportunity to better document the appearance of the modern frog assemblage.

Inglis 1A is located in Section 9, T. 17 S., R. 16 E., Citrus County, Florida. The site, a sinkhole in the Eocene Inglis Formation that apparently acted as a natural trap, was first discovered in 1967 during excavations for the now defunct Cross Florida Barge Canal. In early January of 1974, about 300 cubic meters of fossiliferous sands were removed from the sinkhole and screened on site by Florida Museum of Natural History staff.

Many fossil sites in north Florida originated as sinkholes and other karst features during different epochs. For this reason stratigraphic superposition data are not applicable. The estimation of the relative age of such sites is instead accomplished by stratigraphic comparison of key taxa in these faunas to faunas of known age. Based on the presence of *Chrysemys platymarginata*, *Titanis walleri*, *Platygonus calcaratus*, and various carnivores, Klein (1971) determined that Inglis 1A represented a late Blancan fauna. A refinement of the chronology of Florida fossil sites by Webb (l974) placed Inglis 1A in the earliest Irvingtonian rather than latest Blancan. Morgan and Hulbert (1995) also treated the site as earliest Irvingtonian, but based on published changes in geologic and geomagnetic polarity time scales, considered

[1]Collegium of Natural Sciences, Eckerd College, 4200 54th Ave. S., St. Petersburg, FL 33711; <meylanpa@eckerd.edu>

the earliest Irvingtonian to be late Pliocene. Although its relative age is unchanged, Inglis 1A is now regarded as latest Blancan rather than earliest Irvingtonian, as the boundary between these two ages is currently defined.

METHODS

In the present study, diagnostic isolated fossil elements of anurans were identified on the basis of qualitative characters. Elements of the pectoral girdle (scapulae) and pelvic girdle (ilia) were found to be most useful (but see Bever, 2005). In addition, a number of other elements, such as the frontoparietals of *Bufo* and the fused sacrococcyx of *Scaphiopus*, were also used.

Skeletal terminology follows that used by students of anuran paleontology for the last half century including Tihen (1951), Auffenberg (1956), Holman (1959b), Lynch (1971), Tyler (1976), and Menzies et al. (2002). Recent comparative material employed in this study is housed in the Florida Museum of Natural History herpetology collection. The minimum number of individuals was determined for each species by counting the most common right, left, or unpaired element.

SYSTEMATIC PALEONTOLOGY

Family PELOBATIDAE

SCAPHIOPUS HOLBROOKII (Harlan, 1835)

Referred Specimens.—Inglis 1A: UF 222911, 222922-222927, seven right ilia; 222928-222934, seven left ilia; 222912, 222935-222943, 10 sacrococcyges; 222944-222949, six right scapulae; 222913, 222950-222953, five left scapulae.

Discussion.—The presence of the distinctive fused sacrococcyx of *Scaphiopus* (Fig. 1B) and finely textured skull elements to which the skin is coossified establishes the presence of this genus at Inglis 1A. Although fusion of the sacral vertebra to the urostyle occurs as an anomaly in a number of frog genera, among North American anurans it is typical only of the pelobatid genera *Scaphiopus* and *Spea*.

Auffenberg (1956) distinguished the two groups of North American spadefoot toads (treated as the subgenera *Scaphiopus* and *Spea*) on the basis of the ilium. These groups are now treated as genera (Wiens & Titus 1991). In *Scaphiopus*, the protuberance on the ilium is either absent or slightly developed (occurs as a variant in *Spea*). When present, it is located between the dorsal edge of the acetabular fossa and the dorsal margin of the ilium. In *Spea*, the protuberance is ridge-like, and

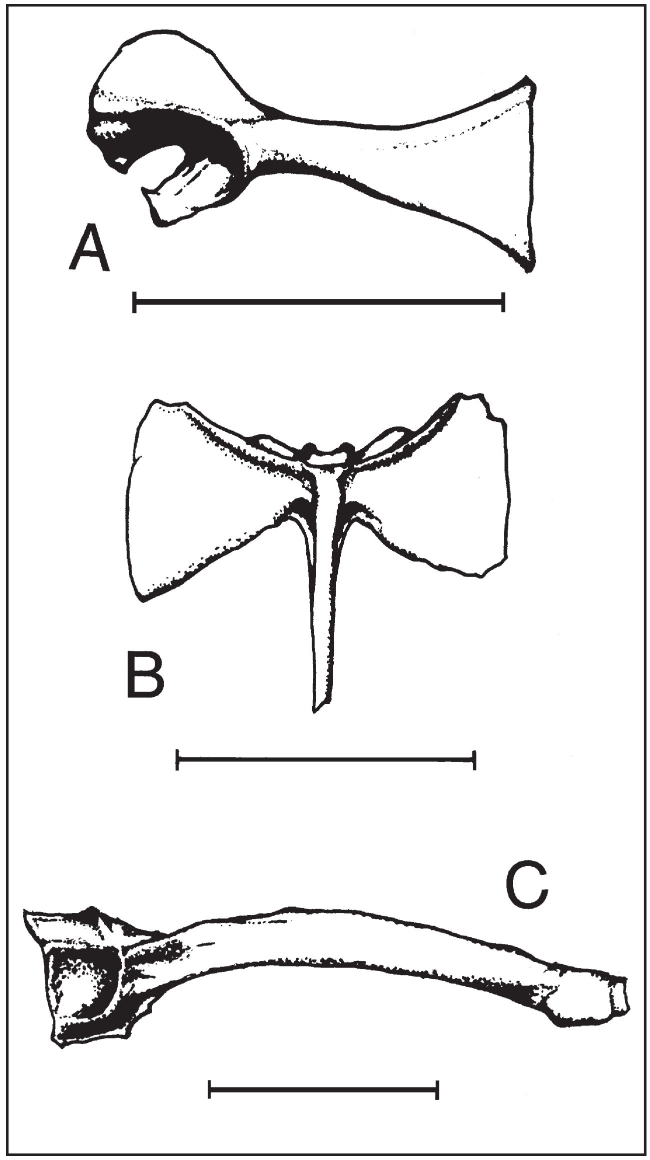

Figure 1. *Scaphiopus holbrookii* from Inglis 1A. A. UF 222913, left scapula in ventral view; B. UF 222912, sacrococcyx in ventral view; C. UF 222911, right ilium in lateral view. Scale = 10 mm.

directed more dorsally, thus contributing to the height of the dorsal acetabular expansion. Twelve ilia present in the Inglis collection have a small prominence located between the dorsal edge of the acetabular fossa and the dorsal edge of the ilium (Fig. 1C). In lateral view the tip of the protuberance protrudes above the dorsal edge of the ilium. This same condition exists in Recent *Scaphiopus holbrookii*.

In all Recent *Scaphiopus* examined, the scapulae were found to have subequal coracoid and clavicle processes. In addition, it was noted that the clavicle processes of these scapulae possess anterior expansions reminiscent of the crests found on the ilia of ranid frogs (Fig. 1A). Eleven scapulae fitting this description are present in the Inglis 1A material. Comparison of these scapulae to Recent skeletons indicates that they are most similar to *Scaphiopus holbrookii*. The two processes mentioned above diverge less in the fossils and in *S. holbrookii* than in other *Scaphiopus* species examined. In addition, the extent of the expansion on the clavicle process in the fossils and in *S. holbrookii* is greater than that observed in other *Scaphiopus*. These features of the scapulae and ilia of the Inglis *Scaphiopus* permit its assignment to the living species *Scaphiopus holbrookii*.

Family BUFONIDAE

***BUFO DEFENSOR* n. sp.**

Holotype Specimen.—Right frontoparietal UF 222916 (Fig. 2B, D).

Referred specimens.—Inglis 1A: UF 222222-222223 two left frontoparietals with fused occipitals; 222224-222439, 215 right ilia; 222915, 222440-222651, 212 left ilia; 222914, 222652-222750, 99 left frontoparietals; 222751-222862, 111 right frontoparietals; 222992-223011, 20 right scapulae; 223012-223029, 18 right scapulae.

Type Locality.—Inglis 1A, Section 9, T. 17 S., R. 16 E., Citrus Co., Florida.

Range.—Known only from the type locality, late Blancan.

Diagnosis.—The frontoparietals of *Bufo defensor* have a larger supraorbital crest than any other New World member of the genus. Although these crests are the same shape as those of *Bufo terrestris*, they are larger and end in a tall hemisphere posteriorly (Fig. 2C-D).

Measurements of the ilia of both species suggest *Bufo defensor* is about one-third larger than *B. terrestris*.

Etymology.—*Bufo defensor* is named for the Florida Defenders of the Environment, a Gainesville-based conservation organization that successfully stopped the building of the Cross Florida Barge Canal, which would have cut into the top of the Floridan Aquifer. It was during excavations for the canal that the type locality was discovered.

Discussion.—The large number of dorsally expanded anuran frontoparietals in the Inglis 1A collection indicates the presence of a toad with large supraorbital crests. Tihen (1962) stated that the frontoparietal is the most useful element for the identification of New World bufonids. An examination of bufonid skeletons (17 species) and figures from Tihen (1962) and Blair (1972) reveals that the crests of the Inglis 1A *Bufo* are much larger than those of any other New World toad, fossil or living. Thus, these frontoparietals and associated elements apparently represent an unnamed species.

The affinities of this toad lie with the *americanus* group of Tihen (1962). In the *calamita* and *valliceps* groups the frontoparietals are always fused to the prootics. This condition is present in only two of 205 frontoparietals from Inglis. Frontoparietal crests are absent in the *boreas* group.

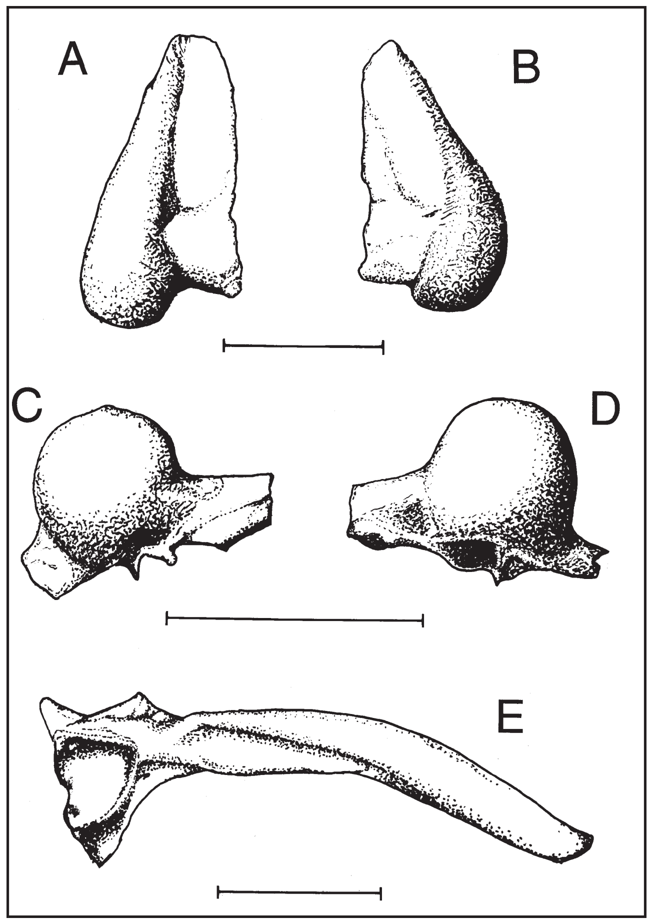

Figure 2. *Bufo defensor* n. sp. from Inglis 1A. A. UF 222914, left frontoparietal in dorsal view; B. UF 222916, holotype right frontoparietal in dorsal view; C. UF 222914; left frontoparietal in posterior view; D. UF 222916, holotype right frontoparietal in posterior view; E. UF 222915, right ilium in lateral view. Scale = 10 mm.

A combination of characters distinguishes *Bufo* ilia from those of other anurans. The ilial prominence is on the dorsal edge of the ilium and lacks a protuberance, although there may be a roughened area on it. The *Bufo* ilia from Inglis (Fig. 2E) strongly suggest those of *Bufo terrestris*. The ilial prominence is low, with either the anterior and posterior slopes subequal or with the anterior slope steeper, sometimes very much so.

The frontoparietal crests of the Inglis toad are similar in shape to those of *Bufo terrestris*. They increase in height posteriorly and end abruptly in a large hemisphere. They are slightly crescent-shaped, with the concave side medial. This similarity in crest shape and ilia suggests that the Inglis toad is closely related to Recent *Bufo terrestris*.

Family HYLIDAE

HYLA CINEREA (Schneider, 1799)

Referred specimens.—Inglis 1A: UF 222921, 222958, two left ilia.

Discussion.—Lynch (1966) noted that fossil tree frogs are comparatively rare. This is certainly true for the Inglis fauna. Only two ilia and two scapulae from Inglis can be assigned to this family.

The ilia of North American members of the genus *Hyla* have a rounded protuberance on the dorsal prominence. This protuberance is usually lateral and does not extend far above the dorsal margin of the prominence (Auffenberg 1956:fig. 3). Specific assignments of hylid ilia have been based on the relative position of the anterior borders of the dorsal protuberance and acetabulum (Lynch 1966), and on the location of the protuberance on the dorsal prominence (Auffenberg 1956). In the Inglis fossils (Fig. 3A), the anterior border of the dorsal prominence is even with the anterior border of the acetabular fossa. A large number of tree frogs, including *H. cinerea*, *H. gratiosa*, *H. squirrela*, *H. versicolor*, and various *Pseudacris*, share this character state (Lynch 1966). In *H. cinerea*, *H. gratiosa* and the Inglis fossils the protuberance covers the dorsal prominence. The ilia of *H. gratiosa* differ from those of *Hyla cinerea* and the Inglis fossils in having the ventral acetabular expansion joining the ilial shaft far anterior to the anterior edge of the dorsal prominence. In *H. cinerea* and the fossils it joins just anterior to this point. Based on these similarities the Inglis hylid is referred to *Hyla cinerea*.

Hylid scapulae are similar in appearance to those of *Scaphiopus*, but they lack the anterior expansion of the clavicle process. It was not possible to identify the two hylid scapulae from Inglis 1A to species.

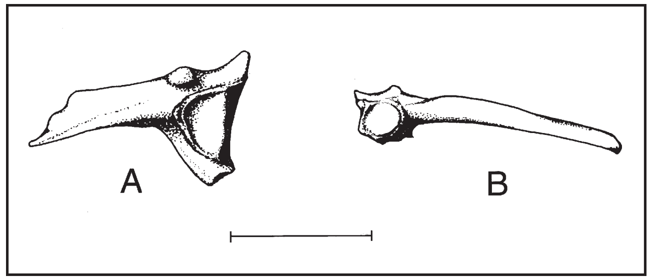

Figure 3. Ilia of hylid and microhylid frogs from Inglis 1A. A. UF 222921, left ilium of *Hyla cinerea* in lateral view; B. UF 222920, right ilium of *Gastrophryne carolinensis* in lateral view. Scale = 5 mm.

Family MICROHYLIDAE

GASTROPHRYNE CAROLINENSIS **(**Holbrook, 1836)

Referred specimens.—Inglis 1A: UF 222920, 222954-222957, five right ilia.

Discussion.—The ilia of *Gastrophryne* can be distinguished from those of other North American frogs by the smooth surface and triangular shape of the dorsal prominence, in combination with the anteriorly produced ventral acetabular expansion (Auffenberg 1956:fig. 2). Five such ilia (Fig 3B) are present in the Inglis material. These ilia are assigned to *G. carolinensis* on the basis of their small size. No other elements were referable to *G. carolinensis*.

Family RANIDAE

RANA CAPITO LeConte, 1855

Referred specimens.—Inglis 1A: UF 222919, 222959-222972 15 right ilia; 222973-222991, 19 left ilia.

RANA CATESBEIANA Shaw, 1802

Referred specimens.—Inglis 1A: UF 222206-222213, eight left ilia; 222918-222221, nine right ilia; 223035-223037 three right scapulae; 222917, 223030-223034 six left scapulae.

Discussion.—A long, broad iliac crest is frequently cited as a characteristic of the genus *Rana* (Holman & Schloeder 1991; Meylan 1995). The shape of the posterior edge of the ilial crest serves to distinguish the bullfrogs, *Rana catesbeiana*, *R. grylio*, and *R. hecksheri*, from the smaller ranids, *Rana capito, R. clamitans, R. palustris*, *R. pipiens*, and *R. sylvatica* (Auffenberg 1956). In the bullfrogs this edge slopes off sharply to meet the ilial shaft (Fig. 4A), while in the other group

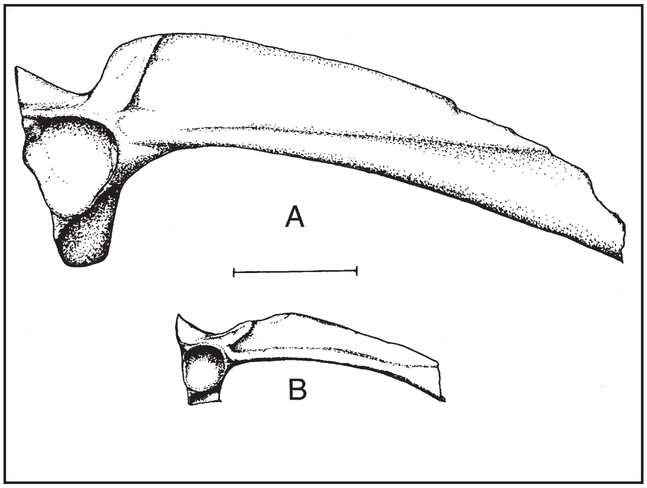

Figure 4. Ilia of ranid frogs from Inglis 1A. A. UF 222918, right ilium of *Rana catesbeiana* in lateral view; B. UF 222919, right ilium of *Rana capito* in lateral view. Scale = 10 mm.

the slope is more gentle (Fig. 4B). In both of these groups the dorsal margin of the ilial crest is a gentle curve until it meets this sloping portion. In *R. capito,* the slope to the ilium forms a smooth curve continuous with the ilial crest.

The Inglis fauna includes two types of ranid ilia. The larger ones are of the bullfrog type, with a steep posterior slope on the ilial crest (Fig 4A). The smaller ones are identical to *Rana capito* in having the entire margin of the ilial crest a single smooth curve (Fig 4B). The only other North American ranid with an ilia crest similar to *R. capito* is *Rana virgatipes*. In this species only the subadults have a continuously curved margin on the dorsal crest. Adults are more similar to the *Rana pipiens* group with an angle present in the outline of the ilial crest where it begins the descent to the ilial shaft. Thus, the Inglis ranid ilia exhibiting a smoothly curved margin to their ilial crest are best assigned to *Rana capito*. The larger ilia cannot be distinguished from those of either *Rana catesbeiana* or *Rana grylio*. The assignment of the Inglis bullfrog to *R. catesbeiana* is made on the basis of the scapulae.

Ranid scapulae differ from those of other North American frogs in their large size and in the relationship of the clavicle and coracoid processes. All ranid scapulae when examined in ventrolateral view have the coracoid process lying almost entirely behind the larger clavicle process (Fig. 5B). Close examination of size of the scapula and morphology of these two processes suggest that two types of ranid scapulae can be recognized in the Inglis collection. The larger one has a clavicle process that is larger and a more convex medial margin. The smaller one has a smaller clavicle process with a less convex medial margin. I have assumed that the large ranid scapulae represent the same species as the large bullfrog ilia. The smaller scapulae can be assigned to *Rana capito*, to which they are very similar.

The shape of the articular surface of the coracoid process can distinguish the scapulae of the bullfrogs *Rana catesbeiana* and *Rana grylio*. In *R. grylio* this surface is elliptical; while in *R. catesbeiana* it is more crescent-shaped, being flat on one side. The bullfrog scapulae from Inglis are more similar to those of *R. catesbeiana* than to those of *R. grylio*. Thus, the Inglis bullfrog is assigned to the former.

DISCUSSION

Paleoecology

The Inglis site probably represents a coastal savanna fauna (Webb 1978). Klein (1971) found that most of the large mammals present in the fauna are species that would be expected to inhabit a scrub-grassland ecotone. However, he noted the presence of tapir and capybara as evidence of mesic habitats. Although he did not discuss rodents in detail, he noted the presence of *Sigmodon* and *Lepus alleni* (the latter now restricted to more arid situations west of the eastern Gulf of Mexico), both of which live in fairly dry grassy regions. He also mentioned the presence of *Geomys*, the pocket gopher, which is restricted to well-drained soil by its burrowing habits.

The snakes indicate similar ecological conditions. Most of the fossil material represents xerically adapted

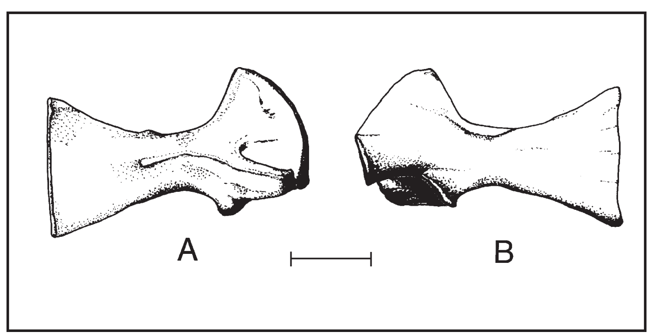

Figure 5. Scapula of *Rana catesbeiana* from Inglis 1A. UF 222917, left scapula in (A) dorsal and (B) ventral views. Scale = 5 mm.

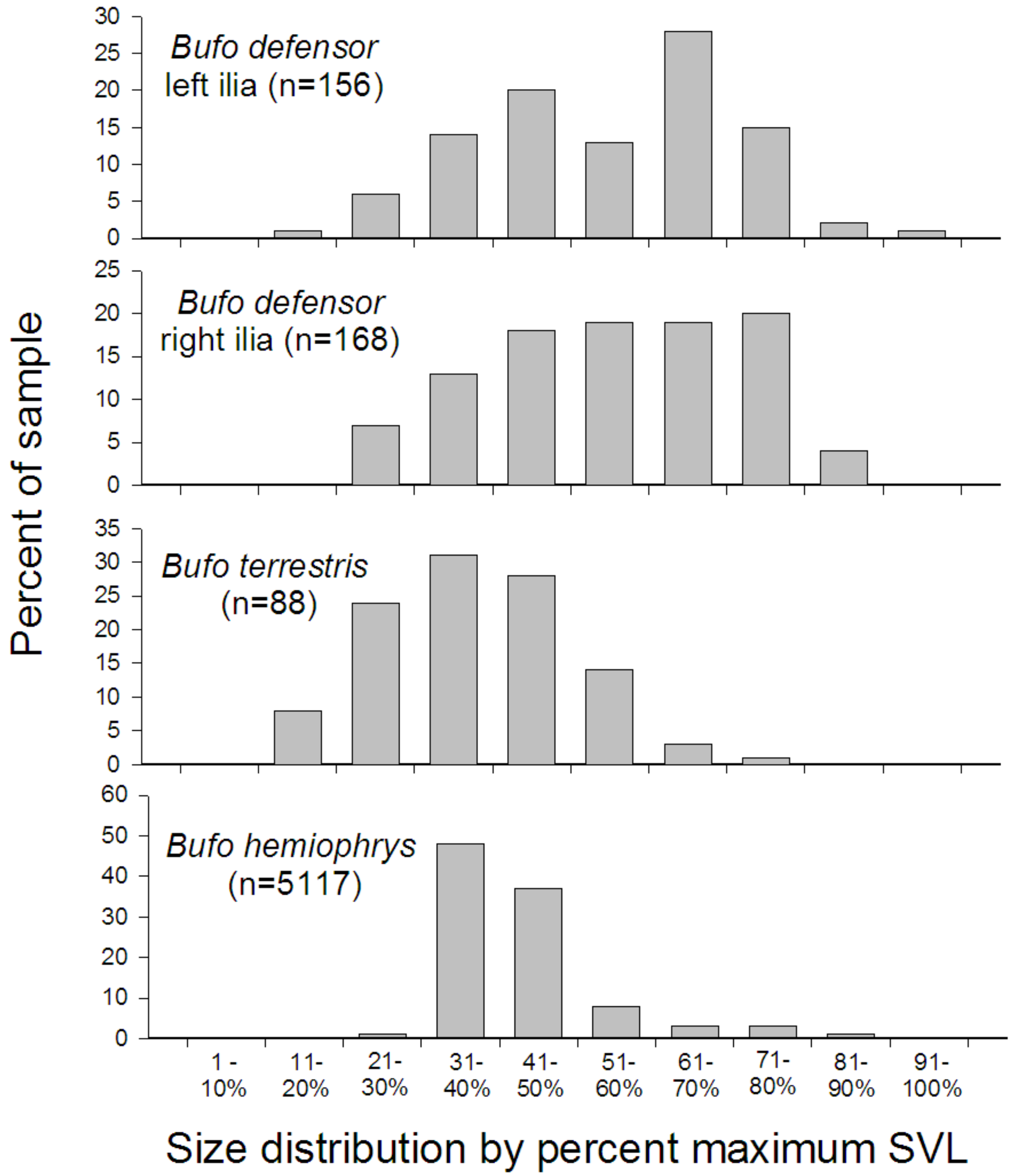

Figure 6. Size distributions of samples of three toads. The size distribution of the extinct toad, *Bufo defensor* from the late Pliocene of Inglis 1A (two separate estimates) is compared to that for two living toads: *Bufo terrestris* from the Ocala National Forest, Florida, and *Bufo hemiophrys* from northwestern Minnesota. Each size distribution is given as percent of the total sample made up by representatives of deciles of maximum body size for each species.

genera such as *Crotalus*, *Masticophis*, *Coluber*, *Pituophis*, and *Heterodon*. Very little material represents mesically adapted genera such as *Nerodia* and *Thamnophis* (Meylan 1982). Similarly, the presence of the amphisbaenian *Rhineura* at the site (Meylan 1982) indicates well-drained soil, typical of a xeric community.

The evidence from the anurans corroborates these other data and further indicates that the Inglis fauna represents a xerically adapted community. The anuran fauna also suggests that some permanent water was present near the Inglis site, but it was probably a sinkhole pond rather then a marsh or swamp.

A minimum of 270 individual anurans were preserved in the Inglis fauna. Of these, 258 are from xerophyllic species. Their xeric adaptations consist mainly of behavioral avoidance of desiccation. *Gastrophryne*, *Bufo*, and *Scaphiopus* avoid desiccation by digging burrows of their own, while *Rana capito* accomplishes this same end in Florida by inhabiting gopher tortoise burrows. The only Inglis species that require mesic or hydric habitats are *Hyla cinerea* and *Rana catesbeiana*. The remains of large *R. catesbeiana* in the Inglis fauna is an indication that some permanent water was close to the Inglis site during its formation.

A consideration of the size classes of *Bufo* preserved in the Inglis fauna suggests that individuals of this genus were trapped in the sinkhole as they were migrating to or from breeding sites. This may be true for some of the other anurans as well, but small sample sizes preclude testing.

A size class distribution for the Inglis fossil *Bufo* was made possible by determining the relationship of snout-vent length (SVL) to acetabular fossa height (AFH) for a composite of 17 individuals representing six species of *Bufo*. The relationship was found to be linear, AFH=0.0413 (SVL) + 0.774 (r=0.905). Using this equation a snout-vent length corresponding to 156 left and 168 right fossil ilia was determined. Population size distribution, by deciles of maximum snout-vent length for the two sets of Inglis fossil ilia (right and left), was compared to size distributions for Recent *Bufo terrestris* and *Bufo hemiophrys* populations (Fig. 6). The *Bufo terrestris* sample was obtained from 88 individuals can-trapped in the Ocala National Forest, Marion County, Florida, during 1976 and 1977. The *Bufo hemiophrys* data are extracted from a large sample collected in northwestern Minnesota (Tester & Breckenridge 1964:fig. 2). Both of these samples consist of resident populations rather than breeding aggregations.

In the Inglis samples, a majority of the toads are larger than one-half the maximum size. For the two Recent populations the majority of toads are between one-third and one-half maximum size. Thus, the Inglis sample includes more mature toads than would be expected in a resident population of *Bufo*. This suggests that the Inglis sample does not represent a local resident population. Although the presence of numerous small individuals indicates that a local population existed in proximity to the site, the preponderance of adults suggests that numerous mature individuals were trapped during migrations to and from breeding sites.

Faunal Relationships

The six anuran species present in the Inglis 1A fauna are either extant or closely related to extant species. A large majority are xeric adapted. An older anuran fauna from the Miocene Thomas Farm locality consists of at least 11 taxa, nine of which are extinct. Among these is *Proacris*, a now extinct genus. The Thomas Farm frog fauna includes mostly hylids and ranids (9 of 12 taxa), which can be considered more mesophylic rather than xerophilic forms.

Between the early Miocene and late Pliocene the anuran fauna of Florida approached its modern state. If the Inglis fauna is representative of Florida in the latest Blancan, it suggests that at least the xeric elements of Florida's modern frog fauna were well established by that time.

ACKNOWLEDGEMENTS

This paper was originally written in 1978 for a "Biology of Amphibians" course taught by Marty Crump. Dave Webb read and commented on the paper at that time and encouraged me to put it into shape for publication. My apology to Dave for taking so long. The paper has also benefited from reviews by Walt Auffenberg, J. Alan Holman, and Dick Franz; preparation for publication has been supported by Eckerd College. Roberta McKendry retyped the manuscript; Ryan Argo prepared the skeletal illustrations.

LITERATURE CITED

Auffenberg, W. 1956. Remarks on some Miocene anurans from Florida, with a description of a new species of *Hyla*. Breviora, 52:1-11.

Auffenberg, W. 1957. A new species of *Bufo* from the Pliocene of Florida. Quarterly Journal of the Florida Academy of Sciences, 20(1):14-20.

Bever, G.S. 2005. Variation in the ilium of North American *Bufo* (Lissamphibia: Anura) and its implications for species-level identification of fragmentary anuran fossils. Journal of Vertebrate Paleontology, 25:548-560.

Blair, W. F. 1972. Evolution in the Genus *Bufo*. University of Texas Press, Austin, 459 p.

Brattstrom, B. H. 1953. Records of Pleistocene reptiles and amphibians from Florida. Quarterly Journal of the Florida Academy of Sciences, 16(4):243-248.

Emslie, S. D., & G. S. Morgan. 1995. Taphonomy of a late Pleistocene carnivore den, Dade County, Florida. Pp. 65-83 *in* D. W. Steadman & J. I. Mead (eds.), Late Quaternary Environments and Deep History: a Tribute to Paul S. Martin. Mammoth Site of Hot Springs, South Dakota, Scientific Papers, Vol. 3.

Gut, H. J., & C. E. Ray. 1963. The Pleistocene vertebrate fauna of Reddick, Florida. Quarterly Journal of the Florida Academy of Sciences, 26:315-328.

Hay, O. P. 1917. Vertebrata mostly from stratum no.3 at Vero, Florida, together with descriptions of new species. Annual Report Florida State Geological Survey, 9:43-68.

Holman, J. A. 1958. The Pleistocene herpetofauna of Sabertooth Cave, Citrus Co., Florida. Copeia, 1958(4):276-280.

Holman, J. A. 1959a. A Pleistocene herpetofauna near Orange Lake, Florida. Herpetologica, 15(3):121-125.

Holman, J. A. 1959b. Amphibians and reptiles from the Pleistocene (Illinoian) of Wil1iston, Florida. Copeia, 1959(2):96-102.

Holman, J. A. 1962. Additional Records of Florida Pleistocene amphibians and reptiles. Herpetologica, 18(2):115-119.

Holman, J. A. 1978. The late Pleistocene herpetofauna of Devil's Den sinkhole Levy Co., Florida. Herpetologica, 34:228-237.

Holman, J. A., & M. E. Schloeder. 1991. Fossil herpetofauna of the Lisco C quarries (Pliocene: early Blancan) of Nebraska. Transactions of the Nebraska Academy of Sciences, 18:19-29.

Hulbert, R. C. 2001. Checklist of Florida's fossil vertebrates. Pp. 34-74 *in* R. C. Hulbert (ed.), The Fossil Vertebrates of Florida. University Press of Florida, Gainesville.

Klein, J. G. 1971. The ferungulates of the Inglis 1A local fauna, early Pleistocene of Florida. M.Sc. Thesis, University of Florida, Gainesville, 115 p.

Lynch, J. D. 1964. Additional hylid and leptodactylid remains from the Pleistocene of Texas and Florida. Herpetologica, 20(2):141-142.

Lynch, J. D. 1965. The Pleistocene amphibians from pit II Arredondo, Florida. Copeia, 1965(1):72-77.

Lynch, J. D. 1966. Additional treefrogs (Hylidae) from the North American Pleistocene. Annals of Carnegie Museum, 11:265-271.

Lynch, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. Miscellaneous Publications of the University of Kansas Museum of Natural History, 53:1-238.

Menzies, J. I., L. Russell, M. J. Tyler, & M. J. Mountain. 2002. Fossil frogs from the central highlands of Papua New Guinea. Alcheringia, 26:341-351.

Meylan, P. A. 1982. The squamate reptiles of the Inglis 1A Fauna (Irvingtonian: Citrus County, Florida). Bulletin of the Florida State Museum, Biological Sciences, 27(3):1-85.

Meylan, P. A. 1995. Pleistocene amphibians and reptiles from the Leisey Shell Pit, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History 37(9):273-297.

Morgan, G. S., & R. C. Hulbert, Jr. 1995. Overview of the Geology and Vertebrate Biochronology of the Leisey Shell Pit Local Fauna, Hillsborough County, Florida. Bulletin of the Florida Museum of Natural History, 37(1):1-92.

Tester, J. R., & W. J. Breckenridge. 1964. Population dynamics of the Manitoba toad, *Bufo hemiophrys*, in northwestern Minnesota. Ecology, 45:592-601.

Tihen, J. A. 1951. Anuran remains from the Miocene of Florida, with the description of a new species of Bufo. Copeia, 1951:230-235.

Tihen, J. A. 1952. *Rana grylio* from the Pleistocene of Florida. Herpetologica, 8:107.

Tihen, J. A. 1962. A review of New World fossil bufonids. American Midland Naturalist, 68(1):1-50.

Tyler, M. J. 1976. Comparative osteology of the pelvic girdle of Australian frogs and description of a new fossil genus. Transactions of the Royal Society of South Australia, 100:3-14.

Webb, S. D., ed. 1974. The Pleistocene Mammals of Florida. University of Florida Press, Gainesville, 270 p.

Webb, S. D. 1978. A history of savanna vertebrates in the New World. Part II: South America and the great interchange. Annual Review of Ecology and Systematics, 9:393-426.

Weigel, R. D. 1962. Fossil vertebrates of Vero, Florida. Florida Geological Survey Special Publication, 10:1-59.