A FOSSIL AND ZOOARCHAEOLOGICAL HISTORY OF THE GOPHER TORTOISE (*GOPHERUS POLYPHEMUS*) IN THE SOUTHEASTERN UNITED STATES

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Specimens of fossil gopher tortoises (*Gopherus*) were collected from five late Pliocene, two early Pleistocene, five middle Pleistocene, and 52 late Pleistocene sites in 18 counties in Florida, one county in Georgia, three in South Carolina, and one in Mississippi. Occurrences of fossil *Gopherus polyphemus* in Lowndes County, Mississippi, and Charleston, Colleton, and Horry counties, South Carolina, represent extralimital records outside the current geographic range of the species. The extensive fossil record indicates *G. polyphemus* has been part of the xeric-adapted fauna of the southeastern coastal plain for at least two million years. The majority of the Florida records are from Alachua and Marion counties. This concentration corresponds to the high frequency of late Pleistocene fossil deposits in solution features associated with limestone quarries at Arredondo, Haile, and Reddick. A query of 609 sites in the zooarchaeological database of the Environmental Archaeology laboratory at the Florida Museum of Natural History was made to determine the presence of *G. polyphemus* in 67 archaeological sites from the southeastern United States dating from the latest Pleistocene to the late 19th century. The zooarchaeology collections are heavily weighted in favor of sites from Florida and Georgia. These data are not all inclusive of sites from the Southeast, but present a representative record of the association of this species with humans for nearly 12,000 years. Specimens of *G. polyphemus* from archeological sites are known from 20 Florida counties and one in Georgia.

Key Words: tortoise; *Gopherus polyphemus*; Pleistocene; zooarchaeology; southeastern United States

INTRODUCTION

The fossil and archaeological record for the gopher tortoise, *Gopherus polyphemus*, is extensive but has never been fully reviewed. Hay (1916) named *Gopherus praecedens* based on a left xiphiplastron from the late Pleistocene at Vero (bed 2), Indian River County, Florida. However, Auffenberg (1974) considered this species a synonym of *G. polyphemus*. Other references for fossil records of *G. polyphemus* include Auffenberg (1974), Hay (1917), Holman (1958, 1959, 1995), Holman and Clausen (1984), Hulbert and Pratt (1998), Meylan (1982, 1984, 1995), Weigel (1962), and Young and Laerm (1993).

Gopherus fossils are commonly collected from cave, sinkhole, fluvial, and estuarine deposits in the southeastern United States (Fig. 1). Gopher tortoises also routinely occur in midden deposits and are often mentioned in archaeological site reports (Fig. 2). Native Americans migrated into the southeastern United States near the end of the Pleistocene and apparently lived continuously in this area for at least 12,000 years (Milanich 1994). PaleoIndians probably encountered and foraged on gopher tortoises, as well as extinct tortoises of the genus *Hesperotestudo*. An early archaeological site at Little Salt Spring, Sarasota County, Florida, contained fossils of both *G. polyphemus* and *H. crassiscutata* (Clausen et al. 1979; Holman & Clausen 1984).

The primary purpose of this paper is to review the fossil record of *Gopherus polyphemus* from Florida and the Southeast. It is not our intent to evaluate morphological variability within fossil gopher tortoise populations of the Southeast, or to make taxonomic revisions. The zooarchaeological record presented here is not exhaustive, but provides a representative record of the association of *G. polyphemus* with humans in the region. The late Pliocene samples from the Inglis and Waccasassa sites may represent an undescribed dwarf population of a *Gopherus polyphemus*-like species, but its description lies beyond our present focus. We treat it

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Figure 1. Map of fossil records for Florida. Grey areas represent the county and the number represents the number of sites within a county.

Figure 2. Map of zooarchaeological records for Florida. Grey areas represent the county and the number represents the number of sites within a county.

here as *G.* cf. *polyphemus* because of its general appearance and probable close relationship to the recent species. We consider all late Pliocene and Pleistocene populations from the Southeast to be ecological equivalents of the modern species based on morphological similarities that we consider adaptations for burrowing. The most important conclusion reached here is that *G. polyphemus* has had a long association with the southeastern coastal plain and probably played important roles in southeastern landscape dynamics and human history.

METHODS

Fossil and zooarchaeological materials examined are deposited in following collections: Florida Museum of Natural History's vertebrate paleontology (UF), Florida Geological Survey (UF/FGS), and zooarchaeology (UFea) collections, Charleston Museum (ChM), and United States National Museum (USNM). Specimens in the private collection of Steve and Suzan Hutchens of Old Town, Florida, are designated SSH. We also examined collections at Auburn University, Georgia State College and University at Milledgeville, and the South Carolina State Museum, but failed to find additional material in their collections. Specific locations of sites are maintained in site files at each depository and can be obtained through those listed institutions. Recent material used for comparison was obtained from the Florida Museum of Natural History's herpetological (UFh) and zooarchaeological comparative collections.

Terminology and Measurements

Shell Bone Abbreviations: NUCH, Nuchal; PYG, Pygal; EPI, Epiplastron; ENT, Entoplastron; HYO, Hyoplastron; HYPO, Hypoplastron; and XIPH, Xiphiplastron.

Other Abbreviations: CL, Carapace Length; Ma, millions of years ago; MNI, minimum number of individuals.

Measurements: Measurements are in millimeters (mm). All measurements from external surfaces: HYO length (along midline suture); HYPO length (along midline suture); XIPH length (along midline suture); NUCH greatest length; NUCH width (across front of carapace from suture to suture); CL, carapace length (maximum straight line measurement with calipers). We follow the geologic time scale and faunal ages recommended for Florida by Hulbert (2001).

Table 1. Allometry formula and constants used in carapace length estimate calculations for fossil *Gopherus polyphemus*.

	N	r^2	Intercept (a)	Slope (b)
Nuchal Length	27	0.84	0.79	0.98
Nuchal Width	27	0.88	0.75	1.01
Xiphiplastron Length	26	0.77	0.90	0.89
Hyoplastron Length	26	0.90	1.00	0.75

Carapace Length Regressions

Paleontologists and zooarchaeologists are usually presented with only a portion of an animal skeleton and are unable to measure the whole organism. Fortunately, many skeletal elements scale allometrically with body size (Peters 1983). Allometry reflects the sutural and functional consequences of a change in size or scale among similarly shaped animals (Peters 1983; Schmidt-Nielson 1984; Reitz et al. 1987). Growth is a nonlinear process through ontogeny, and this allometric relationship is described by a mathematical power function $y = a(X^b)$ (Schmidt-Nielson 1984). This is transformed using the common log in order to produce a straight-line regression. The resulting formula is $\log y = a + b(\log X)$ with b as the slope of the line, a the y intercept, x the independent variable (skeletal measurement), and y the dependent variable, the estimated body size (or carapace length).

Table 1 presents the results of the allometric relationship of CL to each of four skeletal elements (NUCH length, NUCH width, HYO length, and XIPH length) that are often well preserved in the fossil record. HYPO length proved unreliable because of the changes in configuration as tortoises mature and, therefore, was not used. The regression constants are based on measurements of 28 modern gopher tortoises from the Florida Museum of Natural History herpetology and environmental archaeology collections. We obtained 109 estimated CLs from 78 separate fossil tortoise elements collected at Inglis 1A and 1C, Coleman 2A, Leisey Shell Pit 1A, Haile 8A, Reddick 1A, and Surprise Cave (Table 2). Each measurement was treated as a separate sample. Measurements (mm), means, standard deviations, and ranges for elements and for estimated CL are presented in Table 2. We did not calculate estimates of CL from any zooarchaeological material.

Diagnostic Characters

Salient morphologic features of the skeletons of the four species of extant gopher tortoises were extensively described by Auffenberg (1975). Data from his study supported two major evolutionary lines within gopher tortoises: the *G. flavomarginatus-polyphemus* and *G. agassizii-berlandieri* groups. The features that distinguish them were reviewed in Bramble (1971), Crumly (1994), and McCord (1997). Bramble (1971, 1982) presented a phenetic analysis for gopher tortoises and erected the genus *Scaptochelys* for the *G. agassizii-berlandieri* group. The name *Scaptochelys* was later suppressed, and an older name, *Xerobates*, suggested as a replacement (Bour & Dubois 1984). Crumly (1994) argued for keeping the two clades in the genus *Gopherus*. McCord (1997, 2002) performed a stratocladistic analysis to evaluate relationships of recent and fossil gopher tortoise species, and his resulting cladogram supported a 2-group arrangement in the genus *Gopherus*. Recent molecular data support the available phenetic and cladistic conclusions and suggest that the two clades have been separated for about 18 million years (Lamb & Lydeard 1994).

For this study, we used a variety of shell features to identify fossil *Gopherus polyphemus*. This method was greatly enhanced by direct comparisons with the extensive recent collections at UF. We relied heavily on the following features to separate *Gopherus* from *Hesperotestudo* and other southeastern fossil turtles: broad EPI beak and shelf, low-domed carapace, thin carapacial and plastral bones, clearly defined scute sulci

Table 2. Measurements (in mm) and descriptive statistics from individual fossil elements of *Gopherus polyphemus* from six sites in Florida.

Late Blancan Inglis 1A	NUCH Length	Estimated CL	NUCH Width	Estimated CL
UF 211285	23.0	133.2	26.6	154.57
UF 211286	20.4	118.42	20.6	119.4
UF 211287	—	—	31.1	181
UF 211288	34.1	195.93	33.3	193.94
UF 211289	32.8	188.6	34.0	198.06
UF 211290	38.0	217.87	43.7	255.50
UF 211291	31.1	179.02	33.9	197.47
UF 211292	36.4	208.87	39.2	228.68
UF 211293	31.1	180.15	31.2	181.59
UF 211294	36.2	207.75	34.5	201
UF 211295	30.6	176.2	31.9	185.71
UF 211296	36.4	208.87	36.1	210.42
UF 211297	31.4	180.71	31.6	183.94
UF 211298	26.2	151.33	30.2	175.71
UF 211323	—	—	32.4	188.65
N=	13	13	15	15
Mean=	31.38	180.53	32.69	190.36
SD=	5.36	30.3	5.2	30.56
Min=	20.4	118.42	20.6	116.4
Max=	38.0	217.87	43.7	225.2

Inglis 1C	NUCH Length	Estimated CL	NUCH Width	Estimated CL
SSH	43.7	249.85	40.1	233.98
SSH	34.6	198.74	35.5	206.89
SSH	40	229.1	39.6	231.03
SSH	42.2	241.44	42.7	249.31
SSH	38.8	222.36	38.7	225.73
SSH	46.2	263.85	43.7	255.2
N=	6	6	6	6
Mean=	40.92	234.22	40.05	233.69
SD=	4.06	22.8	2.94	17.3
Min=	34.6	198.74	35.5	206.89
Max=	46.2	263.85	43.7	255.2

Early-Middle Pleistocene Leisey 1A	XIPH Length	Estimated CL
UF 80458	54	276.59
UF 69394	52.3	268.92
UF 83601	41.3	217.87
N=	3	3
Mean=	49.2	254.43
SD=	6.89	31.9
Min=	41.3	217.87
Max=	54	276.59

Coleman 2A	NUCH Length	Estimated CL	NUCH Width	Estimated CL
UF 13390b	52.2	276.38	50.4	294.75
UF 13390h	62.4	354.23	59.3	347.36
UF 13390c	49.6	282.86	44.9	262.28
UF 13390m	63.1	358.12	59.5	348.55

Table 2. (Cont.)

Coleman 2A	NUCH Length	Estimated CL	NUCH Width	Estimated CL
UF 13390d	53.8	306.31	51.8	303.02
UF 13390e	47.4	270.56	42.9	250.49
UF 13390i	—	—	50.1	292.98
UF 13390l	55.6	316.35	51.3	300.07
UF 13390k	61.4	348.66	—	—
UF 13390j	53	301.85	49.6	290.03
UF 13390f	—	—	44.6	260.51
UF 13390a	—	—	50.2	293.57
N=	9	9	11	11
Mean=	55.39	315.15	50.42	294.87
SD=	5.71	31.82	5.35	31.58
Min=	47.4	270.56	42.9	250.49
Max=	63.1	358.12	59.5	348.55

Coleman 2A	XIPH Length	Estimated CL
UF13391b	55.5	283.41
UF13391a	56.2	286.59
UF13391c	63.5	319.5
UF13397	48.3	250.45
N=	4	4
Mean=	55.88	284.99
SD=	6.21	28.22
Min=	48.3	250.45
Max=	63.5	319.5

Haile 8A	NUCH Length	Estimated CL
UF uncat.	52.3	305.98
UF 9435	52.3	305.98
UF 3254	57.6	337.31
N=	3	3
Mean=	54.07	316.42
SD=	3.06	18.09
Min=	52.3	305.98
Max=	57.76	337.31

Haile 8A	XIPH Length	Estimate CL
UF 3834	49	253.67
UF uncat.	64.2	322.63
UF 3476	49.9	257.82
UF uncat.	46	239.8
UF 3074	49.6	256.44
UF 3071	57.6	292.94
UF 3477	51.9	266.99
UF 2457	62.4	314.57
UF 3786	55.9	285.23
UF 9655	55.4	282.96
UF 3824	59.7	302.42
UF 3823	57.4	292.03
UF 3813	53.5	274.31
UF 9658	55.5	283.41
UF 9591	53.1	272.48
N=	15	15

Table 2. (Cont.)

Haile 8A	XIPH Length	Estimate CL
Mean=	54.74	279.85
SD=	5.08	23.13
Min=	46	239.8
Max=	64.2	322.63

Late Pleistocene Reddick 1A	NUCH Length	Estimated CL	NUCH Width	Estimated CL
UF 2706	70.8	400.9	65.3	382.88
UF 2706	58.0	329.73	55.6	325.48
UF uncat.	29.7	171.12	24.1	139.91
N=	3	3	3	3
Mean=	52.83	300.58	48.33	282.76
SD=	21.03	117.63	21.54	127
Min=	29.7	171.12	24.1	139.91
Max=	70.8	400.9	65.3	382.88

Surprise Cave	NUCH Length	Estimated CL	NUCH Width	Estimated CL
UF 161885	60.8	345.32	60.5	354.46
UF 161674	—	—	50.3	294.16
UF160157	—	—	17.7	102.44
UF161886	—	—	52	304.2
N=	1	1	4	4
Mean=	—	—	45.13	263.82
SD=	—	—	18.82	110.77
Min=	—	—	17.7	102.44
Max=	60.8	345.32	60.5	354.46

Surprise Cave	XIPH Length	Estimated CL
UF 138002	64.5	323.97
UF 161921	50	258.28
UF uncat.	59.7	302.42
UF 150333	66.9	334.68
UF uncat.	50.4	260.11
UF 138060	54.7	279.77
UF 160332	89	431.48
UF 161669	59.6	301.97
N=	8	8
Mean=	61.85	311.59
SD=	12.55	55.73
Min=	50	258.28
Max-	89	431.48

Surprise Cave	HYO Length	Estimated CL
UF uncat.	85	279.94
UF 138001	82.3	273.24
UF 161664	74.1	252.56
UF 160334	87	284.87
UF uncat.	84.2	277.96
N=	5	5
Mean=	82.52	273.24
SD=	5	12.54
Min=	74.1	252.56
Max=	89	284.87

often on raised bone, acute-edged peripherals, bony sulcal spurs developed along the free edge of the peripherals, distinctive shape and size of the XIPH (anal) projections, squarish or broadly rectangular NUCH scale, and obvious bone scar from a vertebral strut on the underside of NUCH.

Bramble (1982) described a suite of unique head, neck, shell, and limb characters that separated *Gopherus flavomarginatus* and *Gopherus polyphemus* from related *Gopherus agassizii* and *Gopherus berlandieri*. Among these features, the ventral strut, which extends from the base of the first dorsal vertebra onto the back of the NUCH, shows as a prominent bone scar on the underside of the NUCH plate in all fossil and recent *G. polyphemus* we examined (Figs. 3-5). Meylan (1982) reported these strut scars in fossil *Gopherus* specimens from the late Pliocene Inglis 1A local fauna (Fig. 3). Strut scars are often 10-15 mm long (greater than 35% of the total width of anterior margin of the NUCH) in a sample of modern and fossil *G. polyphemus* adults. The strut is thought to reinforce the vertebral connection between the neck and body during "head bracing" behavior while tortoises dig with their front legs and stabilize their bodies with the hind legs (Bramble 1978, 1982). This strut (or scar) was present in all *G. flavomarginatus* we examined, but absent or nearly so in large samples (n=40) of modern *G. agassizii* and *G. berlandieri*. Thus, we consider the presence of strut scars as a strong indication that fossil populations dug extensive burrows similar to those associated with modern *G. polyphemus*. We credit Dale R. Jackson who in the early 1970s originally suggested to us the importance of the bone scar character to separate fossil *G. polyphemus* from other Florida fossil turtles. We believe that the extensive encroachment of the strut (and its scar) onto the NUCH is a useful synapomorphy to define *G. flavomarginatus, G. polyphemus*, and other closely related fossil species.

The Zooarchaeological Record

A total of 609 sites in the zooarchaeological database of the Environmental Archaeology laboratory at the Florida Museum of Natural History (UFea) were queried to determine the presence of *Gopherus polyphemus* (Table 4). This database is the largest of its kind presenting a temporal and geographic record of gopher tortoise identified in archaeological sites in the southeastern United States. Due to the heavy focus on Florida archaeology, the UF data are heavily weighted in favor of sites from Florida.

GOPHER TORTOISES AS FOSSILS

Late Pliocene, Florida (2.5-1.8 Ma)

Inglis 1A Local Fauna, Citrus Co.: The Inglis 1A sample includes 17 NUCH (UF 211285-211298, 211323) (Fig. 4), 7 right and 9 left EPI (UF 211324-211339) (Fig. 6), 6 right and 8 left XIPH (UF 211340-211350, 211401-211403), 4 right and 6 left HYO (UF 211405-211414), 1 right and 4 left HYPO (UF 211415-211419), and numerous other shell fragments. No skull material was associated with the sample. We assume a MNI of 17, based on the number of NUCH bones. The sample consists of mostly small individuals with an estimated mean CL of 180.5 (using NUCH length) or 190.4 mm (using NUCH width) (Table 2). Growth annuli are visible on the HYO and HYPO bones. One HYO (UF 211412) has 11 prominent annuli plus the natal plate, suggesting an age of 12 years for this individual, based on known correspondence of annuli to age in modern individuals; a second specimen (UF 211408) shows at least 7 or 8 annuli. The estimated age of Inglis 1A is about 1.9 Ma (Hulbert 2001).

Inglis 1C Local Fauna, Citrus Co.: The UF sample from Inglis 1C includes two partial plastra (both from the left side) and a pair of costals with portions of the lower bridge attached (UF 211421). The most complete specimen in the UF sample is a reconstructed plastron that includes the left HYO and HYPO (UF 211284). These elements together measure 155 mm in length (measured as a straight line from EPI-HYO suture to the HYPO-XIPH suture). We estimate that this specimen originally had a CL of 230 mm based on direct comparison with a similarly-sized contemporary *G. polyphemus* from Alachua County (UFh 39639). The estimated length for this specimen falls within the upper range limits of the Inglis 1A sample. The second plastral specimen is an isolated HYPO (UF 211420)(59.8 mm along the midline suture). The estimated CL of this tortoise may have been larger than UF 211284. Neither of the two HYPO show the curvature associated with male plastral concavities, suggesting that both specimens are females. The plastral elements show growth annuli; however, only the annuli on one HYPO (UF 211284) were distinct enough to be counted (17 plus the natal plate). This suggests an age of 18 years for this specimen, which would make it an adult female by modern standards.

The SSH sample from Inglis 1C includes two anterior parts of the carapace with NUCH and first dorsal vertebrae intact (Figs. 3, 7), 4 isolated NUCH, one partial plastron with both HYO, right side of lower plastron with HYPO and XIPH attached, and numerous carapacial and plastral bones and fragments. The elements are identical to those from Inglis 1A, except the majority of bones are from slightly larger individuals. The Inglis 1A and 1C sites are considered of similar age (Ruez 2001), although 1C may be slightly younger (R. Hulbert pers. comm.).

Inglis 1D Local Fauna, Citrus Co.: The site contained one NUCH and numerous carapace and plastral elements and fragments (SSH). Specimens represent small individuals.

Inglis 1F Local Fauna, Citrus Co.: Gopherus

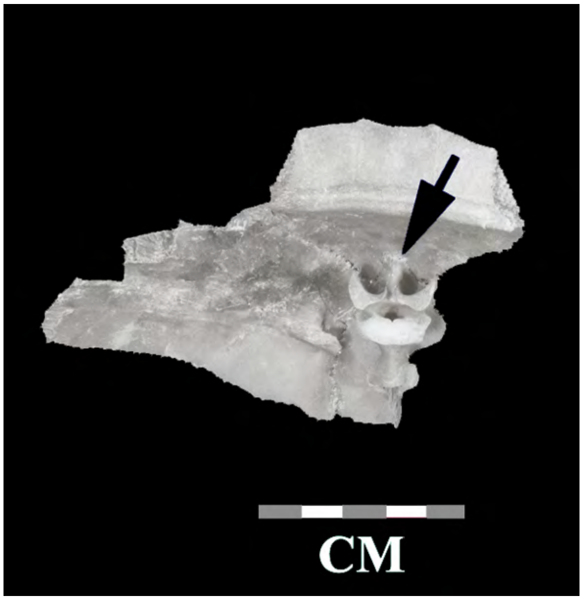

Figure 3. Internal view of the anterior carapace of *Gopherus polyphemus* from Inglis 1C, Citrus Co., Florida. Arrow points to the vertebral strut attached to the posterior edge of the nuchal bone (from the private collection of SSH).

is known from one HYO fragment (SSH).

Waccasassa River 9A Local Fauna, Levy Co.: The sample includes a partial HYPO and several bridge elements (SSH). A late Pliocene age for the Waccasassaa River 9A local fauna is supported by the joint occurrence of *Arctodus pristinus*, *Capromeryx arizonensis*, and *Hemiauchenia gracilis* (UF collection).

Early Pleistocene, Florida (1.8-0.6 Ma)

Leisey Shell Pit 1A Local Fauna, Hillsborough Co.: The Leisey 1A sample of *Gopherus* consists of one partial NUCH (very small) (UF 144309), 12 carapacial elements, one associated pair of EPI (UF 80796), two left and one right HYO, five left and one right XIPH (UF 69394, 80458, 80796, 81063, 83601, 83602), one partial dentary (UF 144598), and one phalanx (UF 144599). Based on XIPH, the MNI of *Gopherus* represented at Leisey is five. Measurements from three left XIPH indicate CLs of 218-277 mm (Table 2). These estimated CLs are greater than those from the late Pliocene samples, but smaller than those from the late Pleistocene or modern samples. The fossils from Leisey 1A are considered to be about 800,000 years younger than those from Inglis.

Haile 21A Local Fauna, Alachua Co.: *Gopherus* is represented by ten partial costals (e.g., UF 63616, 221261, 221851-221854), four neurals (UF 221095, 221303, 221354, 221355), a partial peripheral (UF 221054), and a PYG (UF 221355). Identification as *Gopherus* is based on bone shape and thickness of the specimens.

Middle Pleistocene, Florida (0.6-0.12 Ma)

Tri-Britton Local Fauna, Hendry Co.: The small sample includes one NUCH (UF 209990), several carapacial elements (costal, peripherals, and bridge elements), one right EPI (UF 210862), one ENT (UF

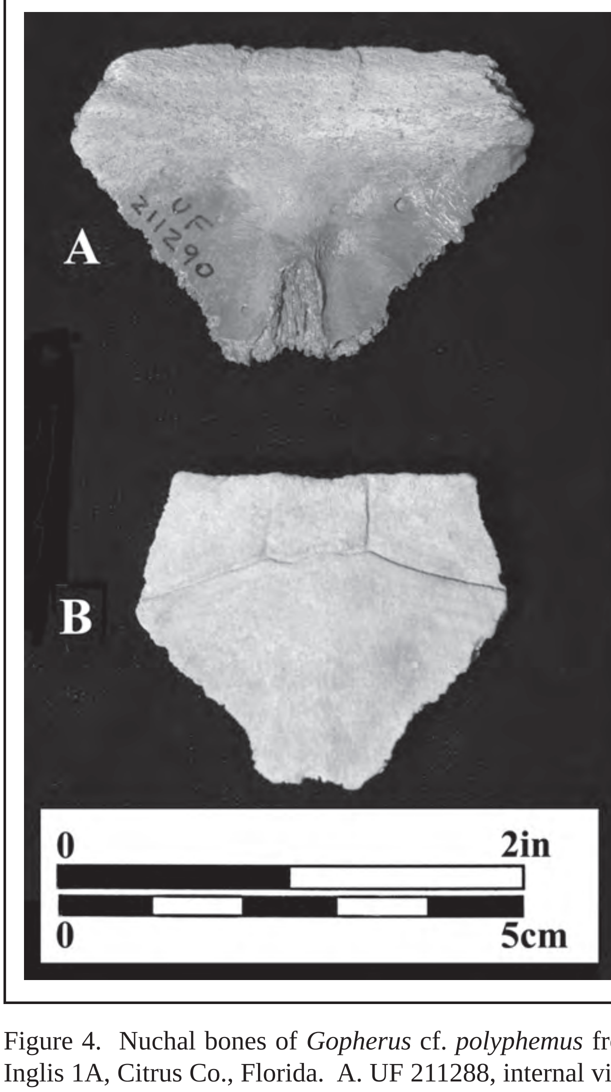

Figure 4. Nuchal bones of *Gopherus* cf. *polyphemus* from Inglis 1A, Citrus Co., Florida. A. UF 211288, internal view (smaller of two). Note the prominent bone scar on the underside of the bone (A) from the attachment of the strut of the first dorsal vertebra. B. UF 211290 showing the shape of the nuchal scute in external view.

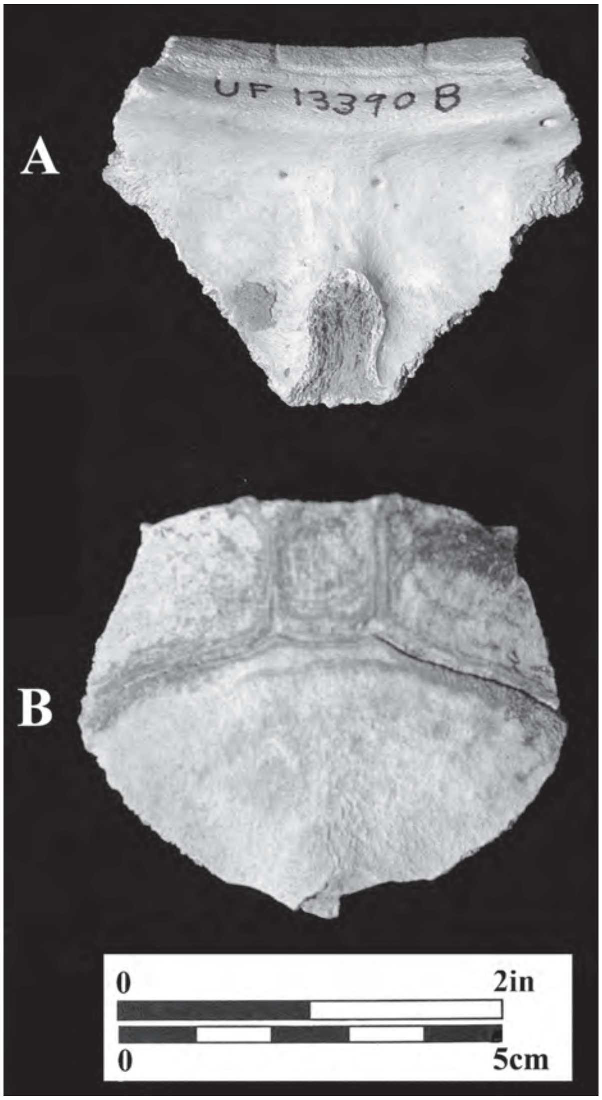

Figure 5. Nuchal bones of *Gopherus polyphemus* from Coleman 2A, Sumter Co., Florida. A. UF 13390B, internal view. Note the bone scar from the ventral strut. B. UF 13390A, showing the shape of the nuchal scute in external view.

208986), two HYPO (UF 209990, 209098), and three XIPH (UF 209098, 209991). No skull material is represented in the sample. The associated mammalian fauna indicates a late Irvingtonian age, ca. 0.3 to 0.5 Ma.

Coleman 2A Local Fauna, Sumter Co.: This large sample includes 13 NUCH (UF 13390) (Fig. 5); five complete EPI (UF 13395a-c, e-f) (Fig. 6); 20 right EPI (UF13392a-t); and 14 left EPI (UF 13394a-m, UF 13395d); 18 PYG (including six with attached suprapygals) (UF 13402); two isolated first suprapygals; two paired XIPH (UF 13391a-b); 18 right XIPH (UF 13391c-e,13397, 13398); and 10 left XIPH (UF 13397, 13398). None of the isolated right and left EPI precisely fitted together, suggesting a MNI of at least 39. No skull material was found in the sample. The estimated CL of tortoises in the Coleman sample ranged from 250-358 mm (Table 2). The associated mammalian fauna indicates a late Irvingtonian age, ca. 0.3 to 0.5 Ma.

Sebastian Canal Local Fauna, Brevard Co.: Gopherus is represented by one peripheral (UF 12989). The associated mammalian fauna indicates a late Irvingtonian age, ca. 0.3 to 0.5 Ma.

Haile 8A Local Fauna, Alachua Co.: The sample from Haile 8A contains one skull (UF 3147), a large number of nearly complete shells (UF 2988, 3127-3131, 3254, 3476-3478, 3786-3790, 3793-3794, 9435, 9575-9582, 51610), 10 isolated NUCH (UF 3024, 3249, 3818, 3835-3839, 9436, 9583), two EPI (UF 9604), a first dorsal vertebra (UF 9604), isolated PYG and suprapygal (UF 19021), XIPH (UF 3791), and assorted fragments (UF 3242, 3257, 9434, 9562, 9565, 9574, 9604, 9673-9675, 9692). There were several neural bones with the first dorsal vertebrae in place. It was obvious that the anterior portion of the vertebrae had been attached to the NUCH in front of the neural. A sample of 28 individuals ranged from 240-337 mm in CL, based on NUCH and XIPH measurements (Table 2). The associated mammalian fauna indicates an early Rancholabrean age, ca. 0.25 Ma.

Late Pleistocene, Florida (120,000-10,000 yr bp)

Fossils of *Gopherus polyphemus* occur in 42 Florida sites of this age (Table 3). We have selected six localities as examples of late Pleistocene sites.

Surprise Cave Local Fauna, Alachua Co.: The large sample consists of seven NUCH (UF 160156-160157, 160208, 160209, 161885-161886, 161674), seven right and three left EPI (UF 160354, 161661-161663, 161914-161917, 161971, uncat.), ten right and six left HYO (UF 138001, 138002, 160334-160335, 161923, 161925, 161664, 161970, uncat.), 12 right and 14 left XIPH (UF 138002, 138060, 138063, 160207, 160332-160333, 160336-160337, 160849, 161669-161670, 161735, 161788-161789, 161919-161922, uncat.), and several hundred shell and internal bone fragments (cat. and uncat. specimens). Two neural bones (UF 160855) have the first cervical vertebrae attached. We estimate a MNI of 14 based on left XIPH, with all being adults except for one very small individual. Estimated CL for a select sample of specimens ranged from 102-431 mm

Table 3. Fauna associates in sites with gopher tortoises. Other fossil tortoise species: *Hesperotestudo (Caudochelys) crassiscutata*, *Hesperotestudo (Hesperotestudo) incisa*, and *Hesperotestudo (Hesperotestudo) mlynarski*. The "Large species" from late Pliocene sites may represent an undescribed species of *Hesperotestudo* with a caudal buckler. An asterisk (*) denotes the presence of two *Hesperotestudo* species associated with gopher tortoises. Habitats: Xeric=Xe, Mesic hardwoods=Me, Pine flatwoods=Pf, Freshwater=Fw, Coastal marine=Cm. Use of parenthesis (Xe) indicates presumed xeric habitat based on the presence of *Gopherus*, but without other supporting associated xeric-adapted taxa. The genus name of *Cnemdipohorus* was recently changed to *Aspidoscelis.*

Sites	County	Other Tortoises	Upland Associates	Habitats
Florida				
Latest Pliocene				
*Inglis 1A	Citrus	Large sp. A *H.* cf. *mlynarskii*	*Rana capito, Geomys, Spilogale, Pituophis, Stilosoma, Heterodon nasicus*	Xe, Me, Pf, Fw
Inglis 1C	Citrus	*H.* cf. *mlynarskii*	*Spilogale*	Xe, Fw
Inglis 1D	Citrus		*Spilogale*	Xe, Fw
Inglis 1F	Citrus	Large sp. A	*Spilogale*	Xe, Fw
*Waccasassa River 9A	Levy	Large sp. A *H.* cf. *mlynarskii*		(Xe), Fw
Early Pleistocene				
*Leisey 1A	Hillsborough	*H.* cf. *crassiscutata* *H.* cf. *mlynarskii*	*Geomys, Podomys*	Xe, Me, Fw, Cm
*Haile 21A	Alachua	*H.* cf. *crassiscutata* *H.* cf. *mlynarskii*	*Podomys*	Xe, Pf, Fw
Middle Pleistocene				
*Haile 8A	Alachua	Large sp. B *H. mlynarskii*	*Geomys*	Xe, Pf, Fw
Sebastian Canal	Brevard	*H. mlynarskii*		(Xe), Fw
*Tri-Britton	Hendry	*H.* cf. *crassiscutata* *H. mlynarskii*		Xe
*LaBelle Highway Pit	Hendry	*H.* cf. *crassiscutata* *H. mlynarskii*		(Xe), Fw
*Coleman 2A	Sumter	*H.* cf. *crassiscutata* *H. mlynarskii*	*Geomys, Spilogale, Pituophis, Heterodon simus, Aspidoscelis, Scaphiopus*	Xe, Me, Pf, Fw
Late Pleistocene				
Arredondo 1A	Alachua	*H. crassiscutata*	*Scaphiopus*	Xe, Me, Fw
Arredondo 1B	Alachua		*Geomys*	Xe, Fw
Arredondo 1C	Alachua	*H. crassiscutata*		(Xe), Fw
*Arredondo 2A	Alachua	*H. crassiscutata* *H. incisa*	*Geomys, Podomys, Scaphiopus, Stilosoma, Heterodon simus*	Xe, Me, Pf, Fw
Haile 1A	Alachua	*H. crassiscutata*		Xe, Fw
Haile 2A	Alachua			(Xe), Fw
Haile 2D	Alachua			(Xe)
Haile 11A	Alachua	*H. incisa*	*Geomys, Podomys*	Xe, Pf

Table 3. (Cont.)

Sites	County	Other Tortoises	Upland Associates	Habitats
*Haile 12A	Alachua	*H. crassiscutata* *H. incisa*		(Xe), Pf
Haile 13C	Alachua	*H. crassiscutata*	*Geomys*	Xe
*Haile 14A	Alachua	*H. crassiscutata* *H. incisa*	*Spilogale, Stilosoma, Aspidoscelis*	Xe, Pf, Fw
High Springs 1A	Alachua			(Xe)
Hornsby Springs	Alachua	*H. crassiscutata*		(Xe). Fw
Kanapaha 1C	Alachua	*H. crassiscutata*		(Xe), Fw
Surprise Cave	Alachua	*H. crassiscutata*		(Xe), Pf, Fw
Wades Cave	Alachua		*Geomys*	Xe, Pf
Melbourne	Brevard	*H. crassiscutata*		(Xe)
Bone Cave	Citrus	*H. crassiscutata*		(Xe), Fw
Lecanto 2A	Citrus	*H. crassiscutata*	*Geomys, Thomomys, Podomys, Scaphiopus*	Xe, Me, Pf, Fw
Sabertooth Cave	Citrus			
Ichetucknee River	Columbia	*H. crassiscutata*	*Spilogale*	Xe
Santa Fe 1	Columbia			
Santa Fe 2	Columbia	*H. crassiscutata*	*Geomys*	Xe, Fw
Santa Fe 8	Columbia	*H. crassiscutata*		(Xe), Fw
Monkey Jungle	Dade		*Podomys*	Xe, Me
Nocatee	Desota			(Xe), Fw
*Jacksonville Beach	Duval	*H. crassiscutata* *H. incisa*		(Xe), Fw, Cm
Vero	Indian River	*H. crassiscutata*	*Geomys, Peromyscus polionotus, Pituophis*	Xe, Fw, Cm
*Devils Den	Levy	*H. crassiscutata* *H. incisa*	*Geomys, Podomys, Spilogale, Pituophis, Heterodon simus, Scaphiopus*	Xe
Waccasassa 5A	Levy	*H. crassiscutata*		(Xe)
Williston 3A	Levy			
Withlacoochee 7A	Levy			
Eickelberger Cave	Marion		*Geomys, Pituophis*	Xe, Me, Fw
Kendrick 1A	Marion		*Geomys, Spilogale*	Xe, Fw
Medford Cave	Marion	*H. crassiscutata*	*Geomys, Heterodon simus*	Xe, Me, Fw
*Reddick 1A	Marion	*H. crassiscutata* *H. incisa*	*Geomys, Podomys,Pituophis, Aspidoscelis*	Xe. Me, Fw
Reddick 1B	Marion	*H. crassiscutata*	*Pituophis, Heterodon simus, Scaphiopus*	Xe, Me, Fw
Reddick 1C	Marion			(Xe), Me, Fw
Reddick 1D	Marion	*H. crassiscutata*		(Xe), Fw
Reddick 1X	Marion			(Xe)
Pratt Whitney Canal	Palm Beach	*H. crassiscutata*		(Xe), Fw
Seminole Field	Pinellas			(Xe), Fw

Table 3. (Cont.)

Sites	County	Other Tortoises	Upland Associates	Habitats
Little Salt Springs	Sarasota	*H. crassiscutata*		
*Wilson Quarry	St. Johns	*H. crassiscutata*		(Xe), Fw,
		H. incisa		Cm
Aucilla 3J	Taylor	*H. crassiscutata*		(Xe), Cm
St. Marks River	Wakulla	*H. incisa*	*Geomys*	Xe, Fw, Cm
Georgia				
Late Pleistocene				
Savannah	Chatham			(Xe)
Isle of Hope				
	Chatham	*H. crassiscutata*	*Pituophis*	Xe, Pf,
		H. incisa		Fw, Cm
Mississippi				
Late Pleistocene				
Catalpa Creek				
	Lowndes	*H. crassiscutata*		(Xe), Fw
South Carolina				
Late Pleistocene				
Charleston	Charleston			
Edisto Beach	Edisto	*H. crassiscutata*		(Xe)
Myrtle Beach	Horry			(Xe)

(based on XIPH, HYO, NUCH lengths and widths).

Bone Cave Local Fauna, Citrus Co.: The substantial sample includes 2 large NUCH (UF uncat.), 4 left and 3 right EPI (UF 6534, uncat.), 2 left XIPH (UF 6534, uncat.), one femur (UF 2256), a neural with attached first dorsal vertebra (UF uncat.), one anterior plastron with EPI (eroded) and ENT (UF2100), and many shell fragments (UF 6519, 6534, uncat.).

Lecanto 2A Local Fauna., Citrus Co.: The sample includes one NUCH (UF 128231), two HYO and three peripherals (UF 128241-128245), a maxilla (UF 128235), and a series of cervical vertebrae, leg bones, and girdle pieces (UF 128294, 128230, 128238-128244).

Monkey Jungle Hammock Local Fauna, Dade Co.: One shell fragment (UF18708) is available. This Dade County site lies near Cutler Ridge, which is the southernmost locality for recent colonies on the Atlantic Coast.

Reddick 1A Local Fauna, Marion Co.: The sample consists of a skull (UF 2401), three NUCH (UF 2461, 2706), EPI (UF 19066), XIPH (UF 19052), various other shell fragments (UF 2457, 2527, 2529, 2637, 2706) and a series of phalanges (UF 112190-112196). Carapacial fragments (UF 2527, 2529, 2706) are from large individuals.

Wilson Quarry Local Fauna, St. Johns Co.: One peripheral (UF 11598) was found in a cemented marine shell hash associated with the Anastasia Formation, indicating a inshore origin, with the tortoise possibly originating from the dune strand along a former coast line. Modern *G. polyphemus* currently occupy these habitats along the Atlantic coast, where they often live in large colonies.

Late Pleistocene, Georgia

Fragments of several fossil gopher tortoises have been found in coastal sites in Chatham County. A Charleston Museum specimen (ChMPV-1538) was probably picked from spoil piles along the Intracoastal Waterway (Al Sanders, Charleston Museum, pers. comm.). The Isle of Hope site lies “seaward (east) of the Pamlico barrier island complex." The vertebrate fauna is associated with estuarine and neritic species of mollusks (Hulbert & Pratt 1998). The Isle of Hope fauna includes recent, as well as extinct, vertebrate taxa (e.g., *Hesperotestudo crassiscutata, H. incisa, Equus, Mammut,* and *Mammuthus*). Several scenarios on the possible depositional origin of this local fauna were discussed by Hulbert and Pratt (1998).

Late Pleistocene, Mississippi

There is only one record of fossil *Gopherus* from Mississippi. This specimen is a water-worn XIPH from Catalpa Creek, near Columbus, Lowndes County (UF 23834). The site lies 190 km north of the nearest contemporary locality for *Gopherus* in Mississippi (Wayne County), and 160 km northwest of the closest site in Alabama (Choctaw County). The specimen was collected in a stream deposit along with a number of other turtle species, including *Hesperotestudo crassiscutata* and the freshwater *Macrochelys temminckii*.

Late Pleistocene, South Carolina

Three fossil deposits, all late Pleistocene, contain remains of *Gopherus polyphemus*: Edisto Island (Charleston and Colleton counties.)(ChMVP-1537, 6414), and the Intracoastal Waterway site near Myrtle Beach (Horry County) (ChMPV-1539). The Horry County record was previously reported by Auffenberg and Franz (1978e, shown as star on range map). A fourth record for *G. polyphemus* was taken from an archaeological site near Myrtle Beach, where human transport may have been involved in its occurrence there (Jim Knight, South Carolina State Museum, Columbia, pers. comm.). The Charleston area and the Horry County sites lay 50 and 245 km, respectively, northeast of the most northern locations of extant populations in Hampton and Jasper counties (Auffenberg & Franz 1982). Surprisingly, no *Gopherus* specimens are reported from the productive Ardis or Camelot sites (Jim Knight, pers. comm.). Both of these sites sample time periods when *Gopherus* was common in Florida.

FOSSIL DISTRIBUTION AND THE ENVIRONMENT

The fossil record for *Gopherus polyphemus* consists of 58 occurrences in Florida and six in three other southeastern states (Table 3). The fossil and zooarchaeological record is discontinuous during Plio-Pleistocene and Holocene times. All of the Florida fossil sites are restricted to the peninsula (east of Apalachicola River). Sites older than late Pleistocene account for only 20% of the sample and are limited to Alachua, Brevard, Citrus, Hendry, Hillsborough, Levy, and Sumter counties, Florida (Table 3). The oldest fossils are from Inglis 1A, 1C, 1D, and 1F in Citrus County, and Waccasassa River 9A in Levy County, Florida. We have yet to locate specimens from older late Blancan sites (ca. 2-2.5 Ma) in Florida, such as Haile 7C, Macasphalt Shell Pit, and Haile 15A. All of the Florida and Georgia records occur within the modern range of *G. polyphemus*. Records from Mississippi and South Carolina are extralimital, indicating a slightly more northerly distribution in the southeastern coastal plain in the late Pleistocene. The scarcity of *Gopherus* fossils from the early and middle Pleistocene may reflect a paucity of suitable habitats during this period, or simply the smaller pool of sites that represent these ages. Conversely, their abundance in late Pleistocene faunas might indicate a time of expansion of xeric upland habitats and/or larger populations of tortoises.

Modern populations of *Gopherus polyphemus* are associated with upland longleaf pine (*Pinus palustris*)-oak uplands, dry oak-pine hammocks, scrubby pine flatwoods, and sand pine (*Pinus clausa*)-scrub oak ridges in the Southeast (Auffenberg & Franz 1982). Gopher tortoises also occur in ruderal settings, such as gardens, pastures, lawns, old fields, and road sides. Fire is demonstrably the most important natural force in the maintenance of modern gopher tortoise colonies and their xerophytic habitats. Fire acts to reduce the densities of woody species, remove leaf litter, and open the tree canopy (Myers 1994), which fosters light penetration and the growth of herbaceous forage species as well as creating areas of open soil used by tortoises for nesting. Often these fire-dominated pine forests have an open, savanna-like appearance with a continuous grassy and herbaceous low understory.

We contend that pre-Columbian populations of gopher tortoises are similarly predisposed to droughty habitats and that they with other xeric-adapted specialists common in Pleistocene deposits, e.g., *Geomys, Spilogale, Podomys, Peromyscus* (*polionotus*), *Pituophis, Heterodon* (*nasicus/simus*), *Stilosoma, Aspidoscellis* (=*Cnemidophorus*), *Scaphiopus*, and *Rana* (*capito*), are strong signatures for the presence of xerophytic pine landscapes in the Southeast in the past. We further suggest that these prehistoric habitats are similar, if not identical, to modern upland habitats and that frequent fires that regulate them today influenced them in the past. This implies, then, that contem-

Table 4. The presence of *Gopherus polyphemus* in Zooarchaeological Assemblages from Florida and Georgia.

FLMNH Accession #	Site Name	Site Designation #	Cultural period and Date Years BP	State	County
x	Litle Salt Spring	8So18	Late Pleistocene — ca. 11500 BP	Florida	Sarasota
x	Cutler Fossil Site	8DA2001	Early Archaic — ca. 8500	Florida	Dade
0019	Tick Is.	8VO24	Middle Archaic — 7000-5000 BP	Florida	Volusia
0572	Lake Monroe Outlet Midden	8VO53	Middle Archaic — 7000-5000 BP	Florida	Volusia
0224	Palmer-Taylor	8SE18	Middle Archaic — 7000-5000 BP	Florida	
0025	Summer Haven	8SJ46	Late Archaic — 5000-2500 BP	Florida	St. Johns
0172	Boca Weir	8PB56	Late Archaic — 5000-2500 BP	Florida	Palm Beach
0447	Useppa Is.	8LL51	Late Archaic — 5000-2500 BP	Florida	Lee
0448	Horrs Is.	8CR209	Late Archaic — 5000-2500 BP	Florida	Collier
0462	Cresent Beach Midden	8SJ43	Late Archaic — 5000-2500 BP	Florida	St. Johns
0587	Enclave Site	8PA1139	Late Archaic — 5000-2500 BP	Florida	Pasco
0296	Bay West Immokalee Archaic	8CR200	Archaic	Florida	Collier
0021	Cotton	8VO83	Archaic	Florida	Volusia
0160	Ft. Center	8GL13	ca. 2800—450 BP	Florida	Glades
0465	Piney Point 1	8NA3	ca. 2500-1650 BP	Florida	Nassau
0224a	Alderman	8Vo135	St. Johns I - II — ca. 2400-1100 BP	Florida	Volusia
0511	Deer Island Causeway Site	8LA512	St. Johns I - ca. 2400-1800 BP	Florida	Lake
0188	Wightman Site	8L54	Glades I — ca. 2250-1850 BP	Florida	
0108	Key Marco	8Cr107	ca. 2350 BP	Florida	Collier
0179	Cumberland Is.	9Cam12 + 9Cam13	Deptford — ca. 2450 BP	Georgia	Camden
0599	Brickell Point	8DA12	Glades I — ca. 1950-1600 BP	Florida	Dade
0254	Granada Site	8DA11	Glades I — ca. 1950-1450 BP	Florida	Dade
0294	Hontoon Is.	8VO202	St. Johns — ca. 1950 BP	Florida	Volusia
0131	Alexander Spring Bath House		St. Johns II a — ca. 1850-450 BP	Florida	
0254	Granada Site	8DA11	Glades II — ca. 1450-750 BP	Florida	Dade
0142	Black Creek 1	8DA85	Glades II — ca. 1200-750 BP	Florida	Dade
0018	Jungerman	8BR136	St. Johns I — ca. 1200-640 BP	Florida	Brevard
0020	Goodman	8DU66A	St. Johns I — ca. 1200-640 BP	Florida	Duval
0107	Palm Coast	8Fl15	St. Johns I — ca. 1200-640 BP	Florida	Flagler
0024	Boynton Inlet	8 PB54	Glades II - III — ca. 1200-430 BP	Florida	Palm Beach
0254	Granada Site	8DA11	Glades II - III — ca. 1200-431 BP	Florida	Dade
0556	Remnant Mound (Shaw's Point)	8MA-7	Manasota — ca. 1055-540 BP	Florida	Manatee
0312	Jacksonville Electric Authority	8DU634/8DU669	Savannah — ca. 950-550 BP	Florida	Duval
0163	Maximo Point	8PI31	ca. 950-250 BP	Florida	
0254	Granada Site	8DA11	Glades IIIb — ca. 600-450 BP	Florida	Dade
0113	Melton	8A169	ca. 750-550 BP	Florida	Alachua
0294	Hontoon Is.	8VO202	St. Johns — ca. 450 BP	Florida	Volusia
0326 (429)	Fig Spring's	8CO1	ca. 450 BP	Florida	Columbia
0221	Baptizing Spr.	8Su65	Historic — ca. 400-300 BP	Florida	Suwanee
0222	Arrivas House	8SJ46	Historic — ca. 400-300 BP	Florida	St. Johns
0242	Palm Row	8SA 36-4	Historic — ca. 375-150 BP	Florida	St. Johns
0283	Ximenez-Fatio 19th C	8SA 34-2	Historic — ca. 375-150 BP	Florida	St. Johns
0518	DeBurgo-Pellicer	SA 7-7	Historic — ca. 375-150 BP	Florida	St. Johns
0583	Ximenez-Fatio	SA34-2	Historic — ca. 375-150 BP	Florida	St. Johns
0451	St. Francis Barracks	8 SA42A	Historic — ca. 350-300 BP	Florida	St. Johns
0220	DeLeon	8SA26-1	Historic — ca. 300-present BP	Florida	St. Johns
0267	Useppa	8LL51	Historic — ca. 300 BP	Florida	Lee

Table 4. (Cont.)

FLMNH Accession #	Site Name	Site Designation #	Cultural period and Date Years BP	State	County
0584	Segui/Kirby-Smith	SA34-3	Historic — ca. 200-100 BP	Florida	St. Johns
0191	De Hita House	8SA7-4	Historic — ca. 230-187 BP	Florida	St. Johns
0227	De Mesa (Old Spanish Inn)	8SA 7-6	Historic — ca. 200-100 BP	Florida	St. Johns
0230	Acosta	SA 13-5	Historic — ca. 200-100 BP	Florida	St. Johns
0234	De la Cruz	8SA 16-23	Historic — ca. 200-100 BP	Florida	St. Johns
0315	Ft. Matanzas 1980 exc.	FOMA	Historic — ca. 200 BP	Florida	St. Johns
0243b	Kings Bay: Kings Bay	9CAM171	St. Simons - Historic Plantation	Georgia	Camden
0243c	Kings Bay: Plantation Site	9CAM172	Historic Plantation — ca. 200 BP	Georgia	Camden
0243d	Kings Bay	9CAM173	Historic Plantation	Georgia	Camden
0243e	Kings Bay: Marianna Plantation	9CAM174	Historic Plantation	Georgia	Camden
0381	Sugar House	9Cam205	Historic - ca. 150 BP	Georgia	Camden
0422	Christ Church	8Es49	Historic — ca. 187-168 BP	Florida	Escambia
0430	Br. Commanding Officer's	8Es1150	Historic — ca. 187-168 BP	Florida	Escambia
0243h	Kings Bay: Araminta Sowerby Site	9CAM178	Historic ca. 150 BP	Georgia	Camden
0313	Kingsley Plantation	8DU108	Historic — ca. 130-50 BP	Florida	Duval
0569	Segui/Kirby-Smith	SA34-3	Historic — ca. 200-100 BP	Florida	St. Johns
0266	Castillo	St. Augustine	Historic	Florida	St. Johns

porary longleaf pine-dominated scrubby flatwoods and sandhill, dry pine-oak hammocks, and sand pine-scrub oak ridge habitats have existed in the Southeast for at least two million years, the clock for modern *G. polyphemus* beginning with the fossils at Inglis and Waccasassa River.

Most Florida sites with *Gopherus* include other herpetological species. Many of these taxa show a propensity for specific habitat specialization. For example, Meylan (1982, 1984) listed 47 species (one salamander, 6 frogs, 7 turtles, 5 lizards, one amphisbaenid, 26 snakes, and the alligator) from the two-million-year-old Inglis 1A site. All of these species are present in modern Florida habitats except for seven extinct taxa and three extralimital species (*Gerrhonotus* sp., *Liochlorophis vernalis*, and *Heterodon nasicus*). By grouping these faunal elements, Meylan concluded that six modern Florida habitat types were represented at Inglis in the late Pliocene: longleaf pine, xeric hammocks, mesophytic hammocks, pine flatwoods, wetlands (swamps, marshes, and ponds), and rivers. He described the landscape as follows: "...the herpetofauna, other vertebrates, and sedimentary context suggest a mixed habitat of mature longleaf pine with xeric hammock interspersed. Xeric hammock would be expected in the depressions characteristic of a karst topography. That one or more of these depressions contained water at least seasonally..." (Meylan 1982:67).

Following Meylan's lead, we evaluated each of the Florida fossil sites that contained gopher tortoises (Table 3). We assumed that all 58 Florida sites had a xeric component based on the presence of gopher tortoises; 27 of these sites also included other xeric-adapted amphibians (*Scaphiopus holbrookii, Rana capito)*, reptiles *(Aspidoscelis sexlineatus, Heterodon nasicus/ simus, Pituophis melanoleucus, Stilosoma extenuatum)*, and mammals *(Geomys pinetis, Podomys* sp., *Peromyscus polionotus*, and *Spilogale putorius*). Freshwater taxa were represented in 38 sites. Most of the aquatic taxa (e.g., *Amphiuma, Alligator, Trachemys, Pseudemys, Nerodia*, etc.) are characteristic of marsh and weedy pond habitats, most of which can be found in small wetlands in upland areas. Pine flatwoods and mesic (woodlands) taxa were found at 10 and 12 sites, respectively; coastal (estuarine) species occurred in only 6 sites. The presence of *Rana capito* at Inglis 1C and *Podomys* sp. at Leisey Shell Pit 1A and Haile 21A indicate that the typical commensal fauna associated with the burrows of modern gopher tortoises was already established by the late Pliocene and early Pleistocene, at least in Florida.

All of the Plio-Pleistocene populations of *Gopherus* in Florida lived with elements of the extinct megafauna. Forty of the *Gopherus* sites include one or two extinct tortoise species in the genus *Hesperotestudo* (4 of 5 late Pliocene sites, 2 of 2 early Pleistocene sites, 5 of 5 middle Pleistocene sites, and 30 of 46 late Pleistocene sites) (Table 3). *Gopherus* was also found in association with *Hesperotestudo* at Isle of Hope (Georgia), Catalpa Creek (Mississippi), and Edisto Beach (South Carolina).

One of the values of biotic reconstruction is that it provides an ecological framework in which to insert populations of extinct taxa. Examination of Table 3 shows that 20 Florida sites with *Gopherus* and *Hesperotestudo* had strong xeric species signatures (multiple upland species associates). Nine sites with *Hesperotestudo* had only terrestrial species represented in their faunas; 30 sites had a mixture of terrestrial plus freshwater species, which presumably meant that water was close by (habitat assessment not available for Little Salt Spring site). The presence of freshwater appears to be the most important correlate that favors the presence of *Hesperotestudo* at any given sites. This is also true for many modern tortoise species, which are known to congregate at wet places. The relationship with water sources would assure proper water balance, water storage, and thermoregulation in more mesic-adapted tortoise species. The local distributions of modern gopher tortoise populations are not known to track wetlands, probably because of their fossorial life style, which help them mitigate water and temperature stresses.

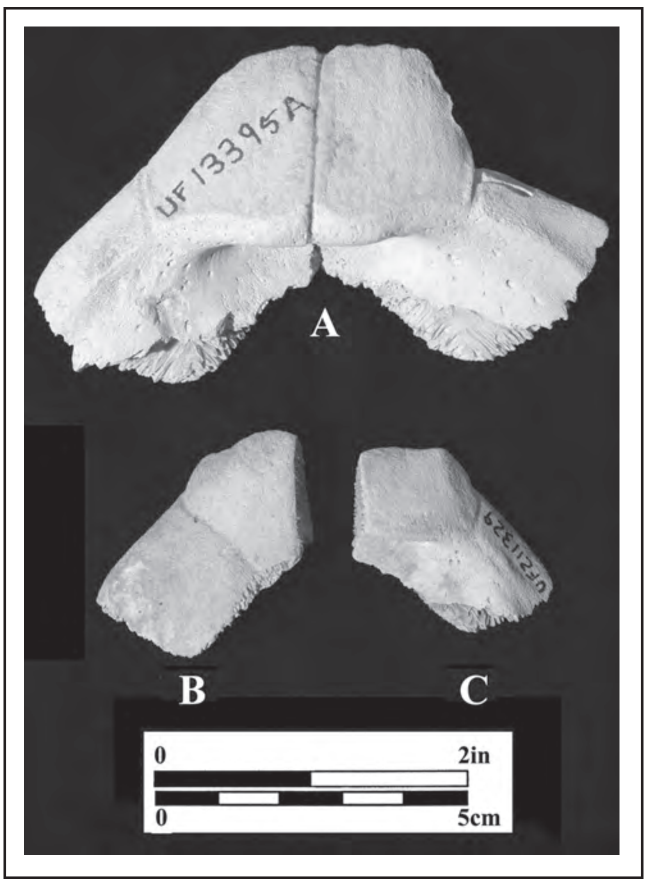

Figure 6. Epiplastra of *Gopherus polyphemus*. A. UF 13395A, Coleman 2A, Sumter Co., Florida. Complete EPI showing prominent gular projection, deep excavation, and prominent lip. B. UF 211330, Inglis 1A, Citrus Co., Florida. Right EPI. C. UF 211329, Inglis 1A, Citrus Co., Florida. Right EPI (underside).

Figure 7. Dorsal view of the anterior carapace of *Gopherus* cf. *polyphemus* from Inglis 1C, Citrus Co., Florida (from the private collection of SSH), showing the nuchal bone, first three neural bones, first three pairs of costals, and associated peripheral bones. This is the most complete specimen from the Inglis series.

WERE GOPHER TORTOISES LARGER IN THE PAST?

Based on 109 measurements of 78 fossil shell elements, we estimate CLs for fossil gopher tortoises ranged from 102 mm at Surprise Cave to more than 400 mm at Reddick 1A and Surprise Cave (Table 2). Demographic studies of modern *Gopherus polyphemus* reported adult sizes (as CL) of 230-341, 238-368 mm (Auffenberg & Iverson 1979) and 232-291, 242-307, and 245-272 mm (Diemer 1992) for north Florida populations; and 335 mm (max. adult CL) (Landers et al 1982) for southwest Georgia. Auffenberg and Iverson (1979) and Diemer and Moore (1994) indicated 226 and 232 mm CL and 10-15 and 14-18 years, respectively, for the minimum sizes and ages of females at first reproduction for north Florida populations; Landers et al. (1982) listed 250-265 mm and 19-21 years for southwest Georgia females. Size at hatching is 49-52 mm CL (RF, pers. observ.). The largest CLs recorded for extant populations of this species are 368 mm (Conant & Collins 1998), 380 mm for a female from Citrus County, Florida (R. Ashton, pers. comm.), and 387 mm from Martin County, Florida (Timmerman & Roberts 1994).

The largest fossils from Reddick 1A (401 mm based on NUCH length) and Surprise Cave (431 mm based on XIPH length) exceed the known maximum carapacial limits of modern *G. polyphemus*. Estimated CLs for 29 individual measurements from Reddick 1A, Coleman 2A, Haile 8A, and Surprise Cave are 300 mm or greater. A complete plastron, labeled as *Gopherus praecedens* (USNM 11999) from Melbourne, Brevard County, Florida, measured 335 mm along the midline suture (and 360 mm TL) indicating a CL of at least 360 mm. Mean CLs of samples from Coleman 2A (315 mm based on NUCH length), Haile 8A (316 mm based NUCH width), Reddick 1A (301 mm based NUCH length), and Surprise Cave (312 mm based on XIPH length) are 300 mm or greater. These data suggest that *G. polyphemus* frequently attained larger body sizes during the Pleistocene than in most modern populations today. Many of these Pleistocene individuals rivaled or exceeded the maximum sizes known for modern *G. flavomarginatus* (371 mm CL listed in Legler & Webb 1961), which is considered the largest living species of *Gopherus*.

The entire sample from Inglis 1A and Inglis 1C contains only small individuals, most falling near or below the minimum size for sexual maturity expressed in modern female *Gopherus polyphemus* (Table 2). Samples from Inglis 1D, 1F, and Waccasassa River 9A (SSH) also consist of smaller individuals. Together, these samples suggest a small body size for all late Pliocene populations of *Gopherus* in Florida. Several explanations are possible to explain this size discrepancy: (1) the samples represent a yet unrecognized species or subspecies of small gopher tortoises, (2) some physical attribute of the site caused the selective preservation of only small individuals, or (3) certain ecological factors, such as selective predation, disease, several years of successful recruitment, or some catastrophic event, caused a temporary shift in the size (and age) structure of the population. Any of these scenarios are possible. The first scenario has the greatest merit given the smaller body sizes of the entire late Pliocene gopher tortoise sample. It remains possible that this population could eventually be recognized as distinct upon a more comprehensive review (see above). The second scenario is more remote since faunal samples include extinct large tortoises (*Hesperotestudo)* and other megafaunal species. The ecological scenario remains plausible, although the causal agent is not readily apparent. This last explanation also implies that the samples were deposited during a very short time period.

GOPHER TORTOISES IN THE ARCHAEOLOGICAL RECORD

Zooarchaeological Data

The temporal and geographic distribution of *Gopherus polyphemus* in the zooarchaeological record of Florida and Georgia is presented in Table 4 and Figure 2. We identified 67 dateable sites from 20 Florida counties and one county in Georgia containing *Gopherus polyphemus* remains. This accounts for approximately 12,000 years of human history and human culture in varying stages of complexity; from fisher, hunter, and gatherers to the 19th Century.

Late Pleistocene: The first humans arrived in southeastern North America during the late Pleistocene, ca. 12,000 yrBP. The climate was cooler and drier and the late Pleistocene sea was well below its current level (Davis 1997; Randazo & Jones 1997). It is for this latter reason that most of the zooarchaeological record of these earliest people is difficult to document. Most of their living sites were inundated by the rising Holocene sea, taking with it well preserved and intact midden deposits. Some late Pleistocene sites are found along Florida's rivers and springs. The zooarchaeological evidence of these locations tends to be rare relative to other archaeological periods, thus making their documentation difficult. Little Salt Spring represents one such site that contains the remains of gopher tortoise and

Hesperotestudo crassiscutata (Clausen et al. 1979; Holman & Clausen 1984). It is unclear if these animals were the remains of subsistence resources or whether they were animals living around the site when humans occupied the region. Nonetheless, Little Salt Spring appears to be the only locality in which the gopher tortoise is found in association with late Pleistocene period humans.

Early Archaic Period (10,000-8,000 BP): The early Archaic period residents of the southeastern United States faced a rapidly changing environment. The climate was still cooler and dryer, and sea level lower than at present (Davis 1997). By the time the Cutler fossil (Table 4; Fig. 2) site was occupied by early Archaic people, the Pleistocene megafauna (e.g., mammoth, mastodon, giant sloth, and *Hesperotestudo crassiscutata*) was extinct. Humans were subsisting on smaller animals, and gopher tortoises were among the zooarchaeological remains identified from the Cutler site (Table 4; Fig. 2).

Middle Archaic Period (8,000-7,000 BP): The archaeology of Florida indicates that humans had become more sedentary and their populations more numerous by the middle Archaic period (Russo 1991). Fishing, shellfishing, and gathering were the primary subsistence activities, while hunting of upland game was of secondary importance. Gopher tortoise remains are represented in two middle Archaic period sites along the St. Johns River and one site in southwest Florida (Table 4; Fig. 2).

Late Archaic Period (5,000-2,500 BP): Environmental conditions of the late Archaic Period had approached modern conditions. Permanent settlements continued to be established and human populations continued to grow. By ca. 4,000 BP, fiber-tempered ceramics were invented along the coast of the southeastern United States. Subsistence practices resembled those established in the middle Archaic period. Gopher tortoise remains are known from six zooarchaeological assemblages in six Florida counties (Table 4; Fig. 2)

Woodland and Mississippian Period to European Contact (2,800-450 BP): Table 4 and Figure 2 presents a list with remains known from 24 sites in 13 Florida and Georgia counties. These data show that gopher tortoises were clearly represented by a temporally and geographically diverse group of archaeological cultures. Nonetheless, aquatic (marine and freshwater) resources were the focus of these people, whereas upland game, such as gopher tortoise, was of secondary importance.

Historic Period in Florida and Georgia (ca. A.D. 1513 – 19th Century): The date A.D. 1513 marks the discovery of Florida by Juan Ponce de Leon and represents the start of European colonization of southeastern North America. The subsistence record from Florida and Georgia show a clear association of gopher tortoises with historic Native American people, early Spanish and British colonists, and plantations of the 18th and 19th centuries (Table 4; Fig. 2).

THE ASSOCIATION OF GOPHER TORTOISES AND HUMANS

As we indicated above, gopher tortoises are xeric habitat specialists. Fire is the most important natural variable in the maintenance of their populations. However, the appearance of humans near the end of the Pleistocene presented another important variable that affected and continues to affect gopher tortoise populations. It is known that pronounced anthropogenic alteration of the environment may occur with the incursion of pre-industrial peoples into a region (Rambo 1985; Redford 1990; Steadman 1995; Quitmyer & Jones 2000; Wing 2001). Such changes in the environment may not necessarily be a consequence of cultural complexity, but rather the interaction of human behavior with the environment. The rudiments of environmental degradation probably appeared earlier in human history than most scientists have realized (Jackson et al. 2000). Jackson et al. (2000) suggested that the deleterious effect on various aspects of the environment have been a prolonged phenomenon that started with pre-industrial people.

Habitat destruction has had a clear influence on modern gopher tortoise populations, while in some cases gopher tortoise habitat can be created by human disturbances of the environment, such as in gardens, pastures, lawns, old-fields, and roadsides (Auffenberg & Franz 1982). Linares (1976) reported a similar pattern for the American tropics where there is a positive correlation in the zooarchaeological record between the appearance of pre-Columbian gardening and the increased frequency of animals that are attracted to garden plots where they were hunted and consumed.

The mid-Holocene archaeological record of the southeastern United States indicates that humans were giving up their mobile hunter-gatherer strategies for a sedentary lifestyle (Russo 1991; Quitmyer et al. 1997). The zooarchaeological evidence shows that the adoption of a sedentary life style along the coastal plain was supported by the exploitation of marine and aquatic resources (Reitz & Quitmyer 1988; Reitz & Wing 1999; Quitmyer & Massaro 1999; Quitmyer 2001, 2002). Sedentism would have contributed to greater disturbance of local environments. Gopher tortoise remains in the zooarchaeological record of most post mid-Holocene sites is typically a minor component of the overall midden assemblages (Larson 1980), a pattern that does not appear to change for nearly 12,000 years of human history. One explanation for their low numbers in faunal assemblages is that gopher tortoises were only opportunistically exploited during the course of everyday subsistence activity (Larson 1980). It is also possible that gopher tortoise habitat was created by disturbance around human living sites (e.g., reduction of fuel woods and land clearing). These scenarios remain a subject of further research, but it is clear that there has been an association of humans and gopher tortoises since the end of the Pleistocene (Table 4).

CONCLUSIONS

The data for 64 fossil and 67 zooarchaeological sites show that *Gopherus polyphemus* has been part of the southeastern coastal plain fauna for about two million years. This tortoise first appeared in the Inglis and Waccasassa 9A local faunas in the late Pliocene. Its fossils are known from relatively few sites in the early and middle Pleistocene. The samples are more numerous in the late Pleistocene. We contend that gopher tortoises and other associated xeric-adapted species found in these sites are strong signatures for the presence of longleaf pine sandhills, oak-pine hammocks, and sand pine-scrub oak ridges during the late Pliocene and Pleistocene. Presumably, as in the case today, frequent fires strongly influenced the aspect and species composition of these pine landscapes. The fossil record also indicates that gopher tortoises lived with extinct portions of the Pleistocene megafauna, including extinct tortoises of the genus *Hesperotestudo*. Gopher tortoises and *Hesperotestudo* occurred together at 42 (68%) (Florida + other states) fossil sites. The record also suggests that earliest populations of gopher tortoises were relatively smaller than the middle-late Pleistocene or extant populations. The largest individuals in the Pleistocene samples rivaled or exceeded the CLs of their extant Mexican relative, *Gopherus flavomarginatus*, which traditionally has been thought to be larger.

Near the end of the Pleistocene, humans entered the landscape of the southeastern United States, and this corresponds to the extinction of a variety of animals such as the horse, mammoth, mastodon, and tortoises of the genus *Hesperotestudo*. The zooarchaeological records from Georgia and Florida show that humans and gopher tortoises have remained in associated with each other for 12,000 years. The data indicate that during this time gopher tortoises represented a regular food item, albeit a minor one. The development of agriculture within native American cultures may have led to increased gopher tortoise populations accompanying disturbance from forest clearing, crop planting, and abandonment of food plots.

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