

PLEISTOCENE AMPHIBIANS AND REPTILES FROM THE LEISEY SHELL PIT, HILLSBOROUGH COUNTY, FLORIDA

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ABSTRACT

Amphibians and reptiles are common among the vertebrate remains recovered from the Leisey Shell Pit. This study was undertaken to document the diversity of these groups and is not a detailed account of all available Leisey specimens. For the sake of completeness, an effort was made to identify every element that could add to the taxonomic list. A total of 20 reptiles and 4 amphibians has been identified from the late early Irvingtonian Leisey 1A and 3A localities. The fossils from the adjacent Leisey 2, which is chronologically mixed (early and late Pleistocene), includes three additional taxa, and these are discussed in the systematic accounts. None of the Leisey sites possesses a diverse herpetofauna, especially compared to Inglis 1A. The Leisey 1A herpetofauna is dominated by three taxa—*Alligator*, *Trachemys*, and *Hesperotestudo*—while Leisey 3A is dominated by aquatic natricine snakes.

RESUMEN

Es común encontrar restos de anfibios y reptiles entre los restos de vertebrados recuperados del depósito de conchuelas de Leisey. Este estudio se llevó a cabo con el objeto de documentar la diversidad de anfibios y reptiles en estos depósitos, sin ser una detallada cuenta de todos los especímenes disponibles para estos depósitos. A bien de ser lo más completo posible, se desarrolló un esfuerzo por identificar cada elemento que pudiera acrecentar la lista taxonómica. Se identificó un total de 20 reptiles y 4 anfibios, provenientes de las localidades Leisey 1A y 3A, pertenecientes al Irvingtoniano temprano. Incluidos en los fósiles encontrados en el depósito adyacente Leisey 2, que se encuentran mezclados cronológicamente (Pleistoceno temprano y tardío), se identificaron tres taxones adicionales, siendo éstos discutidos en la relación sistemática. Ninguno de los sitios Leisey posee una herpetofauna diversa, en especial cuando se la compara con Inglis 1A. La herpetofauna de Leisey 1A es dominada por tres taxones—*Alligator*, *Trachemys* y *Hesperotestudo*—mientras que Leisey 3A es dominada por serpientes acuáticas natricinas.

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INTRODUCTION

Although the fossil record of reptiles and amphibians in Florida has been broadly outlined during the last fifty years of study, several important temporal gaps remain. The record is basically a Neogene one. There are a few scattered records of reptiles from the Eocene limestones that underlie most of Florida and a single Oligocene herpetofauna (I-75) that remains undescribed. The early Miocene fauna is well understood on the basis of Thomas Farm and a series of smaller sites. However, the most serious gap in the herpetofaunal record of Florida exists between those occurrences and the Clarendonian (Love Bone Bed). The Love Bone Bed and a series of other sites document the reptiles and amphibians through the later Miocene into the Pliocene, but there is a second major gap in the record in the Blancan. The herpetofauna of the earliest Pleistocene is well documented by Inglis IA, but until now there has existed a third significant gap in the record, between the earliest Irvingtonian Inglis IA fauna and the numerous Rancholabrean faunas with their abundant reptile and amphibian remains. Thus, the Leisey herpetofauna (late early Irvingtonian, Table 1) fills an important gap in the herpetological fossil record for the State of Florida and the southeastern United States.

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METHODS

The diagnostic features used to identify material have been cited in the species accounts. All measurements are given in millimeters. Terminology for snake vertebrae follows Auffenberg (1963b) and Meylan (1982). Terminology for anuran ilia follows Auffenberg (1956), Tihen (1962), and Lynch (1966); that for the turtle shell follows Zangerl (1969). All specimen numbers refer to the Florida Museum of Natural History (UF) Vertebrate Paleontology Collection.

Abbreviations are: CL, centrum length; NAW, neural arch width; NH, neural spine height; NL, neural spine length; POPR, length of vertebra from front edge of prezygapophyses to rear edge of postzygapophyses; PRPR, width of vertebra to rear edge of prezygapophyses; SCL, straight carapace length; SVL, snout-vent length.

Table 1. Amphibians and reptiles from Leisey 1A, Leisey 3A, and Leisey 2. Taxa followed by one asterisk (*) are earliest known occurrences at Leisey 1A or 3A. Those followed by two asterisks (**) are absent from the modern fauna of Hillsborough Co., Florida. Taxa followed by three asterisks (***) are found only in Leisey 3 (see Morgan and Hulbert this vol.).

Species	Occurrence		
	Irvingtonian		(mixed age?)
	Leisey 1A	Leisey 3A	Leisey 2
<i>Siren</i> sp.	X	X	X
<i>Siren lacertina</i>		X	X
<i>Amphiuma</i> sp.			X
<i>Bufo terrestris</i>	X	X	
cf. <i>Rana</i> sp.	X	X	
<i>Alligator mississippiensis</i>	X	X	X
<i>Ophisaurus compressus</i> *	X	X	
cf. <i>Tropidophis</i> *, **		X	X
<i>Nerodia</i> sp.		X	X
cf. <i>Thamnophis</i> sp.	X	X	X
cf. <i>Nerodia fasciata</i>		X	X
<i>Regina</i> sp.		X	
cf. <i>Regina alleni</i> *		X	
cf. <i>Elaphe obsoleta</i>	X		
<i>Lampropeltis getulus</i>		X	X
<i>Coluber</i> or <i>Masticophis</i>		X	
<i>Drymarchon corais</i>			X
<i>Farancia</i>		X	
cf. <i>Agkistrodon piscivorous</i>	X	X	
cf. <i>Crotalus adamanteus</i>	X		X
<i>Sistrurus miliarius</i>		X	
cf. <i>Caretta caretta</i>	X		
<i>Chelonia mydas</i> ***			
<i>Chelydra serpentina</i> ***			
<i>Macroclemys temminckii</i> **	X	X	X
<i>Hesperotestudo crassiscutata</i> **	X	X	X
<i>Hesperotestudo mlynarskii</i> **	X		
<i>Gopherus polyphemus</i>	X		
<i>Terrapene carolina</i>	X		X
<i>Trachemys scripta</i>	X		X
<i>Pseudemys</i> sp.	X		
<i>Deirochelys reticularia</i>			X
<i>Kinosternon</i> sp.	X	X	
<i>Apalone ferox</i>	X	X	X

SYSTEMATIC PALEONTOLOGY

URODELA

SIRENIDAE

Siren lacertina Linnaeus 1766

Referred Specimens.— Leisey 2: UF 125089, four vertebrae; Leisey 3A: UF 124685, four vertebrae.

The vertebrae are of the form typical of the Sirenidae (Goin and Auffenberg 1955). The centra are amphicoelus, and they have well developed neural spines that are Y-shaped in dorsal view. Ventrally they have well developed central keels with large foramina on either side. These large sirenid vertebrae are referred to *Siren lacertina*, the larger of the two currently recognized living species, on the basis of size alone.

Siren sp.

Referred Specimens.— Leisey 1A: UF 84012, 124666, 124688, 124689, four vertebrae; Leisey 2: UF 125090, 3 vertebrae; Leisey 3A: UF 124660, 14 vertebrae; UF 124661, 6 vertebrae; and UF 124665, an atlas.

These vertebrae represent a small sirenid salamander. The smallest Leisey sirenid vertebrae have nearly straight lower margins to their centra. Goin and Auffenberg (1955) suggested that *Siren* can best be distinguished from *Pseudobranchus* by the shape of the lower margin of the centrum. In *Siren intermedia* and *S. lacertina* this margin is straight or nearly so. In *Pseudobranchus* it is distinctly concave. As pointed out by Goin and Auffenberg (1955), the vertebrae of the extant *Siren* species can be distinguished only on the basis of the very large size of some *S. lacertina*. The small size of these vertebrae makes it impossible to identify them to species.

AMPHIUMIDAE

Amphiuma sp.

Referred Specimen.— Leisey 2: UF 124088, one vertebra.

This vertebra is much like those referred to the Sirenidae, being amphicoelus with well developed transverse processes and neural spines. Unlike that of sirenid vertebrae, the neural spine of *Amphiuma* divides distally and is thus T-shaped rather than Y-shaped in dorsal view.

ANURA
BUFONIDAE

Bufo cf. *B. terrestris* (Bonnaterre 1789)

Referred Specimens.— **Leisey 1A:** UF 80773 and 83240, two ilia; **Leisey 3A:** UF 124664, ilium.

These ilia lack a dorsal crest but have a well developed but low dorsal prominence that is directed dorsally. There is no protuberance on the dorsal prominence. This combination of characters distinguishes *Bufo* ilia from those of other anurans. In *Bufo* the ilial prominence is on the dorsal edge of the ilium, and although it may have a roughened area on it, it lacks a protuberance. These ilia strongly suggest those of *Bufo terrestris* in having a low ilial prominence with the anterior and posterior slopes subequal (Tihen 1962).

RANIDAE

cf. *Rana* Linneaus 1758

Referred Specimens.— **Leisey 1A:** UF 124690, ilium; **Leisey 3A:** UF 124662 and 124663, partial right ilia.

These fragmentary ilia show the remains of the large dorsal iliac crest typical of members of this genus. These specimens are too poorly preserved to allow further identification.

CROCODILIA
ALLIGATORIDAE

Alligator mississippiensis (Daudin 1803)

Referred Specimens.— **Leisey 1A:** UF 68908, 68909, 80023, 80143, 80619, 80769, 81136, and 81137, articulars and/or surangulars; UF 68907, 80302, and 80669, dentaries; UF 80075 and 80352, premaxillaries; UF 64388, 68912, and 68942, maxillaries; UF 68943, two parietals; UF 84017, squamosal; UF 81092, jugal; UF 84016, lacrimal; plus many limbs, vertebrae, and osteoderms; **Leisey 3A:** UF 102522, most of a subadult skull and associated right and left mandibles.

Alligator mississippiensis is a very common component of the Leisey fauna. The material listed here is only a sample of the diversity of the isolated elements available. The material referred to this taxon was carefully compared to *Crocodylus acutus*. There are historical records for *C. acutus* less than 50 miles south of Leisey along the Gulf coast in Sarasota County (LeBuff 1957), as well as an unconfirmed Pleistocene record from Citrus County, Florida (Neill 1971). In every case the Leisey elements were identical to *Alligator* and differed significantly from *C. acutus*.

All *Alligator* dentaries from Leisey have very short symphyses, spanning a distance of only two to three alveoli. The symphysis of *C. acutus* is longer, usually four or five alveoli. The surangulars include the posterior portion of a very large mandibular fenestra. In *C. acutus* this fenestra is quite small. In the available articulars the foramen nervi chorda tympani is about one-quarter of the way across the articular condyle as in *Alligator* and not on the medial edge of the articular as in *Crocodylus acutus*. The premaxillae are short and have essentially transverse sutures for the maxillae. These are long and angular in *C. acutus*. Furthermore, in none of these specimens is there evidence of the large dentary teeth of *C. acutus* that pierce the premaxillae. The jugal is more expanded lateral to the orbit than in *C. acutus* and is also concave to flat rather than convex. The lacrimal bone has a broadly opening lacrimal duct, unlike the acute deep opening of this duct in *C. acutus*.

SQUAMATA
LACERTILIA
ANGUIDAE

Ophisaurus compressus Cope 1898

Referred Specimens.— Leisey 1A: UF 84013, a thoracic vertebra; Leisey 3A: UF 124683, a caudal vertebra.

The single thoracic vertebra has a very flat centrum typical of the family Anguidae. The centrum is 2.8 mm long and 1.8 mm wide. The length to width ratio of the vertebral centrum will successfully differentiate the three well known living species of *Ophisaurus* from North America (Meylan 1982, fig. 4; *O. mimicus*, Palmer 1987, not included). The length to width ratio of 1.75 is beyond two standard errors of the mean for the same ratio for 66 body vertebrae of *Ophisaurus attenuatus* and for 99 body vertebrae of *O. ventralis*. It is quite close to the mean for living *O. compressus* (1.74). The caudal vertebrae of *O. compressus* can be distinguished from those of all North American congeners, including the recently described *O. mimicus*, by the presence of a fused fracture plane or autotomy septum. A fused fracture plane is clearly preserved in the Leisey caudal.

SERPENTES
BOIDAE
TROPIDOPHIINAE
cf. *Tropidophis* Bibron 1840
Figure 1, A-E

Referred Specimen.— Leisey 3A: UF 124637, one vertebra.

A single vertebra from the Leisey fauna (Fig. 1) apparently represents a small boid snake of a group that previously is unrecorded from North America north of Mexico. UF 124637 is a small vertebra, with a square centrum ($CL=3.5$, $NAW=3.6$). It is wider across the prezygapophyses ($PRPR=5.2$) than its length from pre- to postzygapophyses ($POPR=4.3$). It has a short neural spine that covers only the posterior half of the neural arch and is very low ($NL=1.6$, $NH=0.6$). The neural arch is slightly depressed; the centrum posteriorly constricted. Accessory processes were present but apparently poorly developed. A weakly projecting hypapophysis extends ventrally from this thoracic vertebra about 0.5 mm along the posterior half of the length of the centrum.

The general shape of the vertebra, particularly the width, and the short neural spine suggest the family Boidae. The small size and development of the hypapophysis suggest the subfamily Tropidophiinae (Bogert 1968a, 1968b; Underwood 1976). The vertebra is most similar to those of *Exiliboa* and some species of *Tropidophis*, especially *T. haetianus* and *T. feicki*.

Among described North American fossils, the Leisey vertebra resembles *Huberophis* from the Eocene of Georgia (Holman 1977). It differs from this species in having a thinner neural spine and a better defined haemal keel. However, the vertebrae are remarkably similar in lateral view. The Leisey specimen also shows some likeness to members of the genus *Geringophis* (Holman 1976, 1982). Two members of this genus of small boids have ventrally expanded haemal keels and neural spines limited to the posterior half of the neural arch. These genera have been placed in the subfamily Erycinae. However, it is possible that they belong to the Tropidophiinae, not the Erycinae.

COLUBRIDAE

NATRICINAE

cf. *Thamnophis* Fitzinger 1843

Referred Specimens.— Leisey 1: UF 84014, 124691, vertebrae; Leisey 2A: UF 125097, two vertebrae; Leisey 3A: UF 124642, one vertebra, UF 124643, two vertebrae, UF 124644, three vertebrae, UF 124680, five vertebrae.

These small vertebrae are long and narrow (the centra are much longer than wide). They have well developed hypapophyses with a long, narrow base. This hypapophysis shape suggests a natricine rather than a viperid snake. The very narrow shape of the centrum suggests a garter snake, rather than a water snake.

Nerodia sp.

Referred Specimens.— Leisey 2: UF 125096, one vertebra; Leisey 3A: UF 124677, three vertebrae.

Nerodia cf. *N. fasciata* (Linneaus 1766)

Referred Specimens.— Leisey 2: UF 125096, one vertebra; Leisey 3A: UF 124646, two vertebrae; UF 124647, seven vertebrae.

These relatively large vertebrae have well-developed, broad hypapophyses and centra that are nearly as wide as long. They appear too large and square to represent *Thamnophis* or *Regina*. The neural spine is about as high as long which is typical of the *Nerodia fasciata/sipedon* complex (see Meylan 1982).

Regina sp.

Referred Specimens.— Leisey 3A: UF 124640, 2 vertebrae, UF 124679, 4 vertebrae.

Regina cf. *R. alleni* (Garman 1874)

Referred Specimens.— Leisey 3A: UF 124641, one vertebra, UF 124678, 2 vertebrae.

Vertebrae representing members of the genus *Regina* can be recognized by their small adult size (30–40 cm SVL), short, sigmoid-shaped hypapophysis and neural spines that overhang anteriorly and posteriorly (Meylan 1982). These vertebrae are larger than those of *Storeria* and *Virginia*, and not as long and narrow as *Thamnophis*. *Regina alleni* is the only member of the genus with long thin accessory processes of the type seen in UF 124641. Another of the vertebrae has a gutter on the dorsal edge of the neural spine, as described by Auffenberg (1963b) for this species.

LAMPROPELTINAE

cf. *Elaphe obsoleta* (Say 1823)

Referred Specimens.— Leisey 1A: UF 83082, a mid-body vertebra; Leisey 3A: UF 124681, one vertebra.

These are essentially perfect mid-dorsal vertebra with square centra and neural arches only slightly wider than long across the zygapophyses. The neural spine is tall and not significantly undercut anteriorly or posteriorly. The haemal keel is narrow and straight. Subcentral ridges are moderately developed. Accessory processes are well developed but not longer than the prezygapophyseal facet. The zygosphenes are nearly as wide as the neural arch; it is straight in dorsal view and roundly convex in anterior view. There are no epizygapophyseal spines.

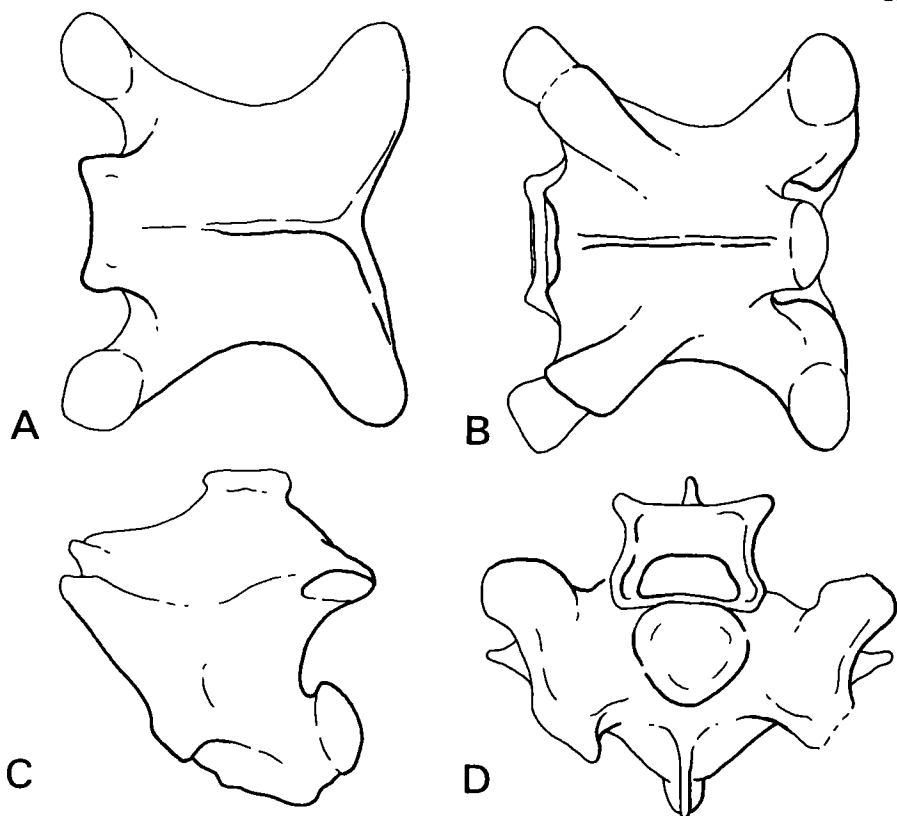


Figure 1. UF 124637, a thoracic vertebra of cf. *Tropidophis* from Leisey 3A, in (A) dorsal, (B) ventral, (C) lateral, and (D) anterior views. Scale bar = 5 mm.

The absence of a hypapophysis, square vertebral centrum, lack of epizygapophyseal spines, and short laterally directed accessory processes suggest that these vertebrae represent one of the constricting colubrids sometimes recognized as the subfamily Lampropeltinae (Smith et al. 1977; Meylan 1982) or tribe Lampropeltini (Dowling and Duellman 1974; Dowling and Fries 1987). The absence of well developed subcentral ridges and the presence of tall neural spines suggest that *Lampropeltis getulus* is not represented. The large size of the vertebrae suggests that one of the other smaller North American *Lampropeltis* is not represented. Although they could represent *Elaphe guttata* or *Pituophis melanolucas*, features of the zygosphenes and neural spine (Meylan 1982) are most like *Elaphe obsoleta*, to which these vertebrae are tentatively referred.

Lampropeltis getula (Linneaus 1766)

Referred Specimens.— Leisey 2: UF 125095, two vertebrae; Leisey 3A: UF 124648, one vertebra.

The vertebrae are referred to the *Lampropeltinae* based on criteria discussed under *Elaphe obsoleta*. The large size and very distinct subcentral ridges of these vertebrae allow their assignment to this species.

COLUBRINAE

Coluber sp. or *Masticophis* sp.

Referred Specimens.— Leisey 3A: UF 124638, two vertebrae, UF 124639, one vertebra, UF 124682, one vertebra.

These vertebrae are much longer than wide and lack hypapophyses. They have long narrow haemal keels and may represent either of these two genera.

Drymarchon corais (Fitzinger 1843)

Referred Specimens.— Leisey 2: UF 125093, two vertebrae.

The vertebrae of *Drymarchon* are immediately recognizable by their large size and the beveled front edge of the neural spine that occurs in most populations (Meylan 1982).

XENODONTINAE

Farancia sp.

Referred Specimens.— Leisey 3A: UF 124645, two vertebrae.

These vertebrae are typical of *Farancia*, being square across the zygapophyses with a markedly depressed neural arch. The accessory processes are short and stout and laterally directed. The haemal keel is strongly developed.

VIPERIDAE

Viperidae gen. et sp. indet.

Referred Specimens.— Leisey 2: UF 125092, one fang; Leisey 3A: UF 124651, three vertebrae.

cf. Agkistrodon piscivorous (Lacépède 1789)

Referred Specimens.— Leisey 1A: UF 86908, five vertebrae; UF 124635, one vertebra, UF 124669, two vertebrae; Leisey 3A: UF 124636, one vertebra.

Agkistrodon piscivorus (Lacépède 1789)

Referred Specimens.— Leisey 1A: UF 124692, one vertebra; Leisey 3A: UF 124687, one vertebra.

cf. Crotalus adamanteus Beauvois 1799

Referred Specimens.— Leisey 1A: UF 84015, 86962, and 124670, three vertebrae; Leisey 2: UF 125091, three vertebrae.

All the above viperid vertebrae are large with thick and strongly developed hypapophyses. The centra are slightly wider than long, and the neural arches are much wider than long measured across the zygapophyses. Such wide vertebrae with thick strongly developed hypapophyses that are not expanded at the base are typical of the Viperidae. Holman (1963) suggested that the absence of pits lateral to the cotyle can be used to assign individual vertebrae to *Crotalus* rather than *Agkistrodon*, but there is some variation in this feature (Meylan 1982). Vertebrae with deep pits are tentatively referred to *Agkistrodon*; those without deep pits are tentatively referred to *Crotalus*. The fang is that of a solenoglyphus snake with only proximal and distal openings.

Sistrurus miliarius (Linnaeus 1766)

Referred Specimens.— Leisey 3A: UF 124676, two vertebrae.

These vertebrae represent very small adult viperid snakes. The neural canal is small relative to cotyle diameter, and they have a long, straight, narrow hypapophysis.

**TESTUDINES
CHELONIIDAE**

cf. Caretta caretta (Linnaeus 1758)

Referred Specimen.— Leisey 1A: UF 82717, a left hyoplastron found in the upper shell bed just above the main bone layer.

This single left hyoplastron represents a cheloniid marine turtle with a very complete plastron. The dermal plastral callosity covers the medial processes of this element all the way to the midline. Based on the configuration of the hyoplastron, the entoplastron was small and elongate, and the hyoplastra met on the midline behind it. The element is 260 mm wide, which is probably too large to be *Lepidochelys*; it is from a more completely ossified plastron than those of either *Chelonia* or *Eretmochelys*.

As UF 82717 was derived from a stratigraphically higher horizon than the main bone layer, it is of younger age and strictly speaking *Caretta* should not be considered a member of the Leisey Shell Pit local fauna. Its probable age is middle to late Pleistocene (Morgan and Hulbert this volume).

Chelonia mydas (Linnaeus 1758)

Referred Specimens.— Leisey 3: UF 124674, a dentary.

The referred dentary has a moderately wide triturating surface with a symphyseal ridge that joins a broad, well developed lingual ridge. At their junction is a large triangular tubercle. *Chelonia*, *Lepidochelys*, and *Eretmochelys* may have a large pyramidal tubercle on the symphysis, but only in *Chelonia* are there deep pits on either side of a well developed symphyseal ridge, a narrow shelf medial to the labial ridge, and a weakly developed symphyseal hook. The dentary represents a small individual (\pm 30 cm SVL) of the size known to frequent inshore waters of Florida's Gulf coast (Carr and Caldwell 1956).

CHELYDRIDAE

Chelydra serpentina (Linnaeus 1758)

Referred Specimens.— Leisey 3: UF 135677, a neural.

The single neural is half-moon-shaped, very wide (almost four times as wide as long), with a very weakly developed midline keel. The neurals of snapping turtles are particularly wide and often lack the regular 6- or 8-sided shapes seen in most turtles. The midline keel is developed too weakly for this element to represent *Macroclemys*.

Macroclemys cf. *M. temmincki* (Troost 1835)

Referred Specimens.— Leisey 1A: UF 84005, a costal fragment; and UF 81198, a peripheral; Leisey 1B: UF 124675, a right dentary; Leisey 2: UF 125099, partial associated shell and skeleton; and uncatalogued parts of two or three individuals; Leisey 3A: UF 116093, a left dentary.

The two dentaries are massive and broad, the two halves of the jaw form a broad symphysis that sweeps gradually upward into a strong, sharp hook. The hook in the dentary of *Chelydra* is much lower (Gaffney 1975, figs. 4 and 5).

The costal is incomplete but shows a triangular, thickened region lateral to its medial edge. This is part of the strong, parasagittal carapacial keels that are typical of *Macroclemys*. The peripheral is about 40 mm long and has a deep pit for insertion of a large rib end. It could represent *Chelydra* or *Macroclemys*. The recent discovery of a snapping turtle in the Blacuan of Florida with a *Chelydra*-like skull but a strongly keeled *Macroclemys*-like shell (Haile 7C; Hulbert et al. 1989) suggests that any assignment of a snapping turtle to genus on the basis of keeled shell fragments alone must be considered tentative. The Leisey records for *Macroclemys* lie far south of its current distribution (Fig. 3; see Discussion).

TESTUDINIDAE

Hesperotestudo Williams 1950

Bramble (1971) questioned the naturalness of the genus *Geochelone* as used by Williams (1950), Loveridge and Williams (1957), and Auffenberg (1974). He felt that it included taxa that were ancestral to gopher tortoises (*Gopherus*) as well as living *Geochelone*. Further studies of these taxa (Crumly 1982, 1984) support Bramble's contention. Crumly (1984) identified the presence of a lateral surangular process as an important derived feature suggesting monophyly of advanced tortoises, including all living species of *Geochelone* (the type is the living species, *Geochelone elegans* Schopff 1792) and such genera as *Testudo*, *Indotestudo*, and *Malacochersus*. This process is unknown among North American fossil forms. The current trend towards the restriction of scientific names to monophyletic groups would suggest that the application of the name *Geochelone* to any North American tortoise would be inappropriate, since it would make *Geochelone* paraphyletic. Bramble (1971) and Auffenberg (1974) have clearly indicated that the name *Hesperotestudo* (usually used as a subgenus) applies to those North American tortoises in which the dermal ossicles are extremely well developed and the proximal caudal vertebrae have expanded lateral processes. Preston (1979) previously applied this name at the generic level in his review of late Pleistocene turtles from the mid-continental United States. The North American forms currently referred to *Geochelone* should be called *Hesperotestudo* in order to promote a better understanding of the interrelationships among land tortoises.

It has long been suggested that there are two lineages of *Hesperotestudo* in the Pleistocene of Florida. These lineages have been separated on the basis of size, the development of the caudal buckler, the visibility of growth rings, depth of the anal notch, and other details of shell morphology (Auffenberg 1963a, 1988).

Using these criteria, these large (subgenus *Caudochelys*) and small (subgenus *Hesperotestudo*) lines can be recognized in the Leisey fauna.

Hesperotestudo (Caudochelys) crassiscutata (Leidy 1889)

Figure 2

Referred Specimens.— **Leisey 1A:** UF 64395, parts of five costals; UF 65005, peripheral; 80593, much of a plastron (510 mm midline length); - UF 84300, epiplastron; UF 65052, 65053, 65054, 68928, partial plastra; UF 80676, entoplastron; UF 80593, 83602, 84007, 84066, 84299, 84301, 84311, isolated xiphiplastra; UF 81925, nuchal; UF 64396, 68933, 81480, 68919, femora; UF 84024, 84025, armor; UF 64398, 65051, 88126, caudal vertebrae; **Leisey 2:** UF 125065, left epiplastron; UF 125064, neural; **Leisey 3:** UF 130008, proximal humerus; **Leisey 3A:** UF 102513, a very large humerus.

The name *Hesperotestudo crassiscutata* is based on *Testudo crassiscutata* Leidy from the Pleistocene of Florida. Although this lineage of large land tortoises has been traced from the Miocene through the Pleistocene of Florida (Auffenberg 1963a), no species other than *H. crassiscutata* has been described from the Pleistocene of Florida, and it seems likely that this is the species represented by most of the *Hesperotestudo* material in the fauna.

Hesperotestudo cf. *H. mlynarskii* (Auffenberg 1988)

Referred Specimens.— **Leisey 1A:** UF 80675, much of a plastron with parts of a carapace; UF 80897, 81132, epiplastra; UF 80351, entoplastron; UF 80166, 80361, hyoplastra; UF 83090, xiphiplastron; UF 80461, nuchal; UF 83091, pygal; **Leisey 2:** UF 142235, left epiplastron (may represent this species or *H. incisa*).

Hesperotestudo mlynarskii was recently described from the late Irvingtonian Coleman 2A locality in Sumter County, Florida (Auffenberg 1988). It is considered to differ from Rancholabrean *H. incisa* in part by having a shallower anal notch (Auffenberg 1988, fig. 3). A single small xiphiplastron (UF 83090) falls in the range of variation known for *H. mlynarskii* and well below that known for *H. incisa*. It is based on this single element that the Leisey representative of the *turgida*-complex tortoise is tentatively referred to this recently described form.

Gopherus polyphemus (Daudin 1803)

Referred Specimens.— **Leisey 1A:** UF 80559, 80796, and 81485, epiplastra; UF 64394, 68939, 80363, 80458, 81007, 81063, xiphiplastra; UF 68900, nuchal; UF 82605, two peripherals; UF 84302, pygal.

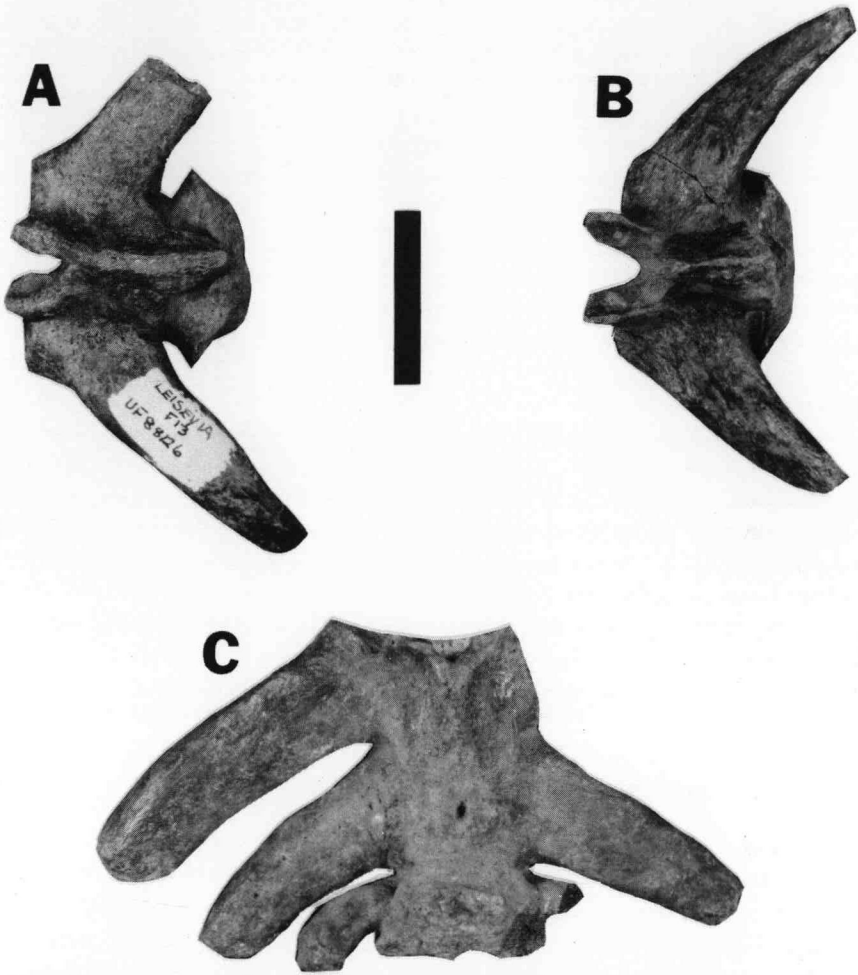


Figure 2. UF 64398, 65051, and 88126, caudal vertebrae from a large *Hesperotestudo* cf. *H. crassiscutata*. These vertebrae all show the broad flat transverse processes of the caudal vertebrae which appear to be diagnostic for the genus. Scale bar = 30 mm for A and B, 20 mm for C.

The nuchal of *Gopherus* is the most immediately identifiable element. This genus is unique among testudinoids in having a ventral strut on the nuchal against which the neural spine of the first thoracic abuts (Bramble 1982). This structure is evident in the nuchal (UF 68900) from Leisey.

The epiplastra and xiphiplastra are like those of other tortoises in having gular and anal projections. However, these elements, as well as the peripherals

and pygal thought to represent this species, are too large to represent *Hesperotestudo mlynarskii* and too thin to represent *H. crassiscuttata* of this size.

EMYDIDAE

Terrapene carolina (Linnaeus 1758)

Referred Specimens.— Leisey 1A: UF 80022, most of the anterior lobe of the plastron; UF 80898, partial carapace; UF 81027, the central portion of the posterior lobe of a plastron; UF 82441, parts of a shell; UF 83709, parts of both hyoplastra with hinge; UF 85405, much of a carapace; Leisey 2: UF 125066 and 125067, partial carapaces; UF 125068 and 125069, partial plastra; UF 125070, ilium.

All the shell material exhibits fusion between the elements. A hinge between the hyo- and hypoplastra is evident in the preserved plastra, and the bridge peripherals were not sutured to the plastron. Several of these specimens represent large box turtles, up to approximately 230 mm straight carapace length. The posterior peripherals are not extremely recurved, and there is a prominent dorsal keel in UF 80898 and 85405.

There can be no doubt that this material represents a box turtle of the genus *Terrapene*. The peaked shape of the shell and presence of a dorsal keel suggests that *T. ornata* is not represented. Although it is comparable in size, it does not have the strongly flared posterior peripherals that are typical of *Terrapene carolina putnami* or *T. c. major* (Milstead 1969). It has the well developed dorsal keel of *T. c. bauri*, but it appears to represent a form somewhat larger than this subspecies, therefore it is referred simply to *Terrapene carolina*.

Trachemys scripta (Schoepff 1792)

Referred Specimens.— This taxon is abundant throughout Leisey 1A and also is present in Leisey 2. It is represented in the UF collection by hundreds of isolated elements, as well as several partial shells. Leisey 1A: UF 81146, 81488, 82440, and 82612.

This material represents a moderately large emydid with a primitive neural pattern (4<6<6<6<6<6<6), short rib heads, plastral buttresses reaching costals one and five and inframarginal series divided by contact between marginal and plastral scales. All the carapacial elements are covered by elongate rugosities. There is well developed nuchal scute underlap, and the posterior peripherals are doubly scalloped, but not recurved as in *T. idahoensis* (Jackson 1988). The epiplastra have a straight anterior edge that is perpendicular to the midline and has a small anterior denticle at its lateral extreme. The gular scutes overlap the epiplastron for well over one-half of their dorsal length (56-98%, mean = 70.4% ±

12.8; $N = 11$ epiplastral). The entoplastra are slightly wider than long ($L/W = 0.86 \pm 0.06$, $N = 9$).

The sculpturing of the carapacial elements and the degree of nuchal scute underlap and gular scute overlap is typical of *Trachemys scripta*. The referred epiplastra are unlike those of the *Pseudemys floridana* and *P. rubriventris* groups which are smoothly rounded anteriorly, lack a well developed denticle, and have much shorter gular scute overlap.

Pseudemys sp.

Referred Specimens.— Leisey 1A: UF 82758, an epiplastron; Leisey 3: UF 135681, left hyoplastron.

This single emydid epiplastron is unlike that of *Trachemys* in having a smoothly rounded anterior margin and very short scute overlap. It could represent either a *P. floridana* or *P. rubriventris* group member.

Deirochelys sp.

Referred Specimens.— Leisey 2: UF 125071, partial costal; UF 125072, partial peripheral.

Jackson (1978) described the diagnostic lateral displacement of the ribheads in this taxon which allows identification of isolated costals. The weak ornamentation, typical of *Deirochelys*, is seen in both the costal and peripheral.

Kinosternon sp.

Referred Specimens.— Leisey 1A: UF 84920, a nuchal, Leisey 2: UF 125073, nuchal; UF 125081, 125082, two hyoplastron; UF 125083-125086, four hypoplastra; UF 125075-125077, three costals; UF 125074, one neural; UF 125078-125080, three peripherals; UF 125087, one epiplastron, Leisey 3A: UF 124652, a partial nuchal; UF 124684, the left half of a dentary.

The plastral elements of *Kinosternon* can be recognized by their small size, presence of hinged joints and absence of dorsally projecting plastral buttresses on the hyo- and hypoplastra. The width of the plastral elements suggests that *Kinosternon* rather than *Sternotherus* is present. The nuchals have a very narrow area covered by marginal scutes, a very small nuchal scute, and broad coverage by the first costal scutes.

TRIONYCHIDAE

Apalone ferox (Schneider 1783)

Referred Specimens.— **Leisey 1A:** UF 80549, 80662, two costals; UF 81005, epiplastron; UF 81006, nuchal; UF 81031, xiphiplastron; UF 81032, fused hyo- hypoplastra; UF 81064, costal; UF 81091, 81100, two epiplastra; UF 81101, two costals; UF 81141, costal; UF 81763, first left costal; UF 83078, left maxilla; UF 83437, right maxilla; UF 83720, fused hyo-hypoplastra; UF 83843, fused first and second neurals; UF 83859, fused hyo-hypoplastra; UF 83860, right hypoplastron; UF 84004, 7th costal; UF 84022, left humerus; UF 84023, cervical five or six; **Leisey 2:** UF 125060, a skull; UF 125062, fused hyo-hypoplastron; UF 125098, a pleural; UF 125063, a humerus; UF 125061, a neural; **Leisey 3:** UF 135682-135684, partial hyo-hypoplastron; **Leisey 3A:** UF 102468, 142236, and 142237, partial costals.

Apalone ferox is the only living New World softshell in which the hyo- and hypoplastra are normally fused to one another in the adults. Only one small unfused trionychid hypoplastron was found in this fauna. At least three other fused hyo-hypoplastra were collected. Other features of this trionychid material is consistent with this identification (Meylan 1987). The other two living North American forms, *A. spinifera* and *A. mutica*, have callosities on the epiplastra as adults. Three adult epiplastra from Leisey (UF 81005, 81091, and 81100) lack such callosities. The seventh costal (UF 84004) has rib attachments for thoracic vertebrae seven and eight fused to it, indicating that the eighth costal was fused with the seventh. This occurs only in the subtribe Platypeltini, to which *A. ferox* belongs. Furthermore, the maxillae (UF 83078 and 83437) belong to the same individual and reveal that the maxillae met above the premaxillae, as in all softshells, but did not meet on the midline of the palate, which is also a derived feature of this subtribe.

DISCUSSION

The herpetofauna from Leisey differs little from that of Hillsborough County, Florida, today (Table 1). It is essentially modern. Only the two species of *Hesperotestudo* are now extinct. Two other elements of the fauna, *Macrolemys* and the tropidophine snake, are no longer found in this area.

At present *Macrolemys* is found no farther south than the drainage of the Suwannee River (Fig. 3). However, there is evidence that it was found throughout much of peninsular Florida in the early Pleistocene (Table 2). The most likely explanation for the marked reduction in the range of *Macrolemys* during the Pleistocene is the drowning of its riverine habitats by marine transgressions

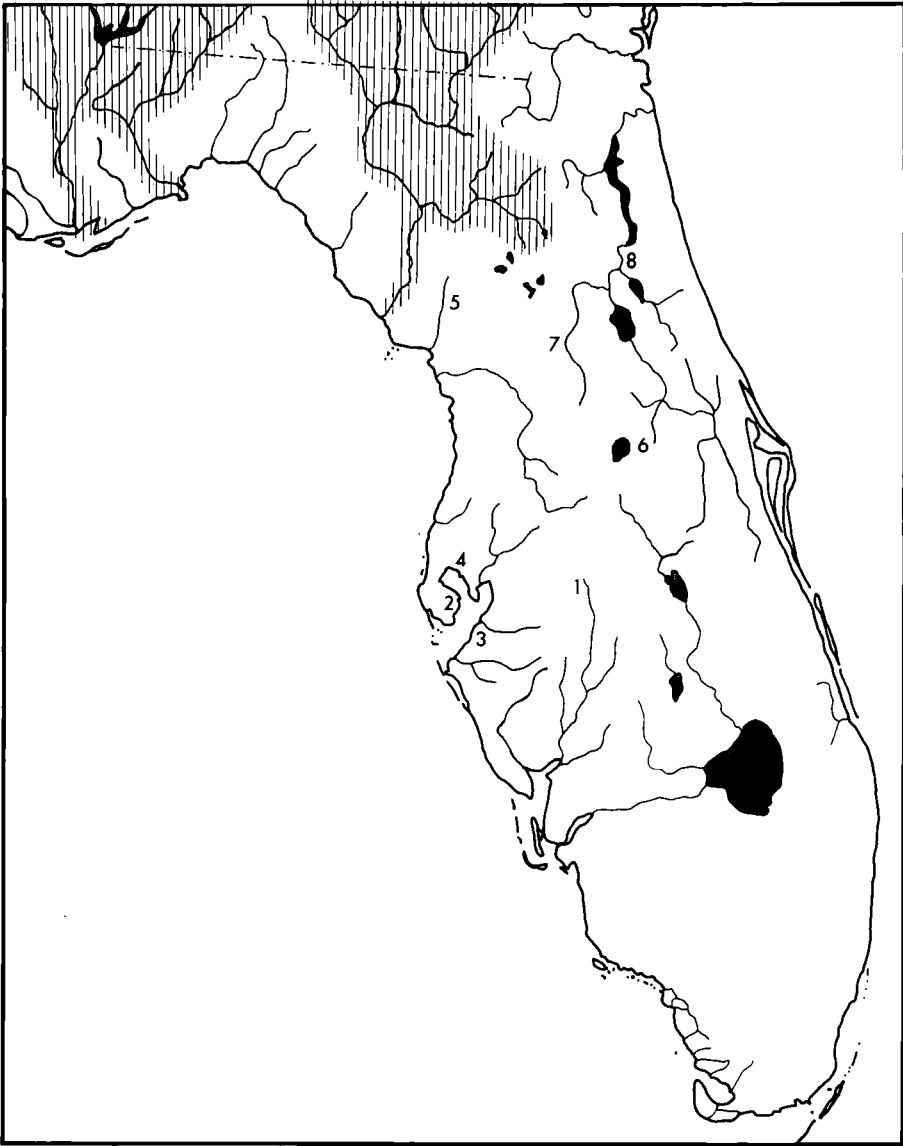


Figure 3. Recent range and fossil occurrences for *Macroclémys temminckii* in Florida. The Recent range of this species is crosshatched. Fossil localities from which this species has been recovered are: (1) Ft. Green Mine 13, (2) St. Petersburg Times, (3) Leisey Shell Pit, (4) Oldsmar 1, (5) Wekiva Spring, (6) Rock Springs, (7) Oklawaha I, and (8) Buzzard Island. The age, material collected, museum number, river drainage, and other details of these occurrences are given in Table 2.

Table 2. Records from peninsular Florida for fossil *Macroclmys temmincki* outside of its modern range.*

Locality	Land Mammal Age	Catalogue No.	Element	River drainage	Max. el. (in m)
Ft. Green Mine 13 Polk Co.	Hemphillian	UF 55829 UF 58055 UF 90367	pygals neurals	Peace	40
St. Petersburg Times Pinellas Co.	late Blancan	UF 69683-69690	peripherals	—	15
Lelsey Shell Pit Hillsborough Co.	Irvingtonian	UF 84005, 81198 124675, 116093	costal, peripherals, dentaries	Little Manatee	38
Oldsmar 1 Pinellas Co.	early Rancholabrean	UF 135629	shell	—	3
Wekiva Spring Levy Co.	Rancholabrean	UF 2508 UF 9852	mandible epiplastra, peripherals	Wekiva	19
Lelsey 2	Rancholabrean	UF 125099	partial skeleton	Little Manatee	38
Rock Springs Orange Co.	Rancholabrean	UF 135685	bridge peripheral	St. Johns	20
Oklawaha 1	Rancholabrean	UF 135686, 135688 135689, 135687	dentary, peripheral peripheral, neural	St. Johns	20
Buzzard Island St. Johns River near San Mateo	Rancholabrean	UF 137924	dentary	St. Johns	20

* Specimens from Macasphalt (= Warren Brothers) Shell Pit, West Palm Beach Site, and Port Charlotte are considered to represent large *Chelydra serpentina*. Hay's (1908) report of four peripherals "probably from Peace Creek beds" is not included.

Table 3. Preferred habitats of extant species in the Leisey 1A herpetofauna. The number of elements representing each taxon is listed below the Florida plant communities in which each species is found regularly. Data are largely from Carr (1940).

	Longleaf pine ¹	Xeric hammock ²	Mesic hammock	Flatwoods	Lentic waters ³	Lotic waters ⁴
<i>Siren</i> sp.				4		
<i>Bufo terrestris</i>	1	1	1	1	1	
cf. <i>Rana</i>	1	1	1	1	1	1
<i>Alligator mississippiensis</i>						19+
<i>Ophisaurus compressus</i>		1				
cf. <i>Thamnophis</i>			2	2	2	
cf. <i>Elaphe obsoleta</i>		1				
cf. <i>Agkistrodon piscivorous</i>			9	9	9	
cf. <i>Crotalus adamanteus</i>	3	3	3	3		
<i>Macroclemys temminckii</i>						2
<i>Gopherus polyphemus</i>	13	13				
<i>Terrapene carolina</i>		6	6	6		
<i>Trachemys scripta</i>					100+	
<i>Pseudemys</i>					1	1
<i>Kinosternon</i>						1
<i>Apalone ferox</i>					23+	
Total for Habitat	18	26	22	26	137+	24+

1 = high pine

2 = upland hammock

3 = swamps, ponds

4 = rivers

(Pritchard 1989). Webb (1974) pointed out that the ecological requirements of certain species make them particularly susceptible to changes in sea level and thus useful in identifying eustatic changes in Florida. *Macroclemys temminckii* falls into this category. It is restricted to the main channels of rivers and streams and apparently moves overland infrequently. This species would be eliminated from any basin that was completely submerged by saltwater during a major transgression.

Any attempt to determine the extent of transgression necessary to flood any late Neogene or Pleistocene river basins in Florida is complicated by the observation that the northern part of the peninsula may have been uplifted 36–41 m during the Pleistocene (Opdyke et al. 1984). Thus, the paleoelevation of the basins for which we have records of *Macroclemys* (Table 2) cannot be determined accurately. It is, nevertheless, possible to make some observations about the past distribution of *Macroclemys* in Florida.

A late Miocene low sea level stand between 6.7 and 5.2 Ma (Haq et al. 1987) would be the best explanation for the expansion of this turtle's range into peninsular Florida. Low sea level would have promoted downstream coalescence of major rivers and streams on the Gulf Coast. This regression would explain the Hemphillian record from Polk County, which is in the Peace River drainage. A subsequent transgression and high sea level stand between 5.2 and 3.0 Ma would have eliminated all southern peninsular *Macrolemys* populations. Following this major early Pliocene sea level rise subsequent regressions apparently were sufficient to allow *Macrolemys* to re-enter a number of drainage systems along the west coast of Florida (such as the Wekiva and Little Manatee rivers) but, as far as is known, not sufficient to allow the re-establishment of this species in the Peace River drainage.

Transgressions during the Pleistocene may have been responsible for the extinction of *Macrolemys* from some of the lower elevation drainages (Oldsmar, Wekiva). However, no transgression that would be sufficient to cause extinction of the Leisey population (Little Manatee River) is known (Haq et al. 1987).

It is interesting that during the Rancholabrean, *Macrolemys* occurred in the St. Johns and Oklawaha rivers (Table 2). It is absent from this system today and could have been eliminated only by a sea level rise of about 20 m.

Paleoecology.— Since only two of the 26 taxa found in the herpetofauna of Leisey 1A and 3A are extinct, accurate reconstruction of the paleoenvironment of these sites is feasible. If we assume that the habitat requirements of the members of the herpetofauna have not changed significantly in the last 1.5 million years, then habitat reconstruction is affected most seriously by problems of transportation, sorting, and sampling. The sampling is admittedly biased, because many elements of the most common species (*Alligator*, *Trachemys*, *Hesperotestudo*, *Apalone*) were not studied and do not appear under referred specimens. However, as large samples of each are reported, and they dominate the reconstruction of the paleoenvironment, it seems unlikely that a complete treatment of all material would change the outcome reported here. Transportation and sorting also are not likely to be serious problems. Disarticulated shells of individual turtles were found in adjacent squares in many cases at Leisey 1A (Pratt and Hulbert this volume), and many articulated skeletons were found at Leisey 3A. These associations and the absence of water-worn fossils suggest that the faunas are largely autochthonous.

I have followed the methodology employed in Meylan (1982), where the number of occurrences for each taxon is scored for each of six major habitat types in which it occurs commonly (Tables 3 and 4). In this case the absolute number of elements rather than a minimum number of individuals is used. Across the bottom of each table the number of times that a species common to a given habitat type occurs in the Leisey 1A and 3A faunas is summed.

Table 4. Preferred habitats of extant species in the Leisey 3A herpetofauna. The number of elements representing each taxon is listed below the Florida plant communities in which each species is regularly found. Data are largely from Carr (1940).

	Longleaf pine ¹	Xeric hammock ²	Mesic hammock	Flatwoods	Lentic waters ³	Lotic waters ⁴
<i>Siren</i> sp.					21	
<i>Siren lacertina</i>					4	
<i>Bufo terrestris</i>	1	1	1	1	1	
cf. <i>Rana</i>	2	2	2	2	2	2
<i>Alligator mississippiensis</i>					15+	
<i>Ophisaurus compressus</i>		1				
cf. <i>Thamnophis</i>			11	11	11	
cf. <i>Nerodia</i>					3	
cf. <i>Nerodia fasciata</i>					9	
cf. <i>Regina</i>					6	
cf. <i>Regina alleni</i>					3	
cf. <i>Elaphe obsoleta</i>		1				
<i>Lampropeltis getulus</i>				1	1	
<i>Coluber</i> or <i>Masticophis</i>	4	4	4	4	4	
<i>Farancia</i>					4	
cf. <i>Agkistrodon piscivorus</i>			2	2	2	
<i>Sistrurus miliarius</i>	2	2		2		
<i>Macroclemys temminckii</i>					1	
<i>Apalone ferox</i>				1		
<i>Kinosternon</i>				2		
Total for Habitat	9	10	20	26	87+	2

1 = high pine

2 = upland hammock

3 = swamps, ponds

4 = rivers

5 This is an articulated skull with mandibles.

For both sites, species that are typical of lentic freshwater systems predominate. However, there is a clear difference between the two sites. In Leisey 1A *Trachemys scripta*, *Apalone ferox*, and *Alligator mississippiensis* are the most common species in the fauna. These are all freshwater species that can be found in a variety of habitats. They are generally not abundant in large rivers but require open water. In Leisey 3A the most common species are *Siren*, *Thamnophis*, *Nerodia*, and *Regina*. Again, these are all forms associated with lentic freshwater systems. However, none is an open water species. Two species that normally require some open water (*Alligator* and *Apalone*) are represented (this is an artifact of curation, not actual rarity). Thus, Leisey 3A is more likely representative of a slough filled with emergent vegetation, while Leisey 1A was probably assembled in

a body of open water such as an oxbow lake or a pond. Both sites contain the lotic species *Macroclemys temmincki* and, therefore, probably were connected to a permanent river, at least periodically.

It is also clear that upland species are more abundant in Leisey 1A than in Leisey 3A. *Gopherus*, *Terrapene*, and *Crotalus* are found in the former but not in the latter. Furthermore, the two species of *Hesperotestudo* (not included in Tables 3 and 4) are common in Leisey 1A (see species accounts) but represented by a single humerus in Leisey 3A. Thus, Leisey must have been adjacent to an upland community, most likely high pine or xeric hammock, to account for the large number of highly terrestrial turtles.

Two species of Florida's Recent herpetofauna, *Regina alleni* and *Ophisaurus compressus*, are reported from Leisey and predate any previous reports. Of the three species of glass lizards found in peninsular Florida, *O. ventralis* and *O. attenuatus* are described from localities predating Leisey. The only previous report of *O. compressus* is from the Rancholabrean of Haile 2B (Auffenberg 1955).

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