FOSSIL CARNIVORES FROM THE LEISEY SHELL PITS, HILLSBOROUGH COUNTY, FLORIDA

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ABSTRACT

Thirteen species of carnivores have been recovered from the Leisey Shell Pits, late early Irvingtonian of Florida. These species include Armbruster's wolf *Canis armbrusteri*, the wolf coyote *Canis edwardii*, the gray fox *Urocyon cinereoargenteus*, the tremarctine bear *Arctodus pristinus*, the gracile sabercat *Smilodon gracilis*, the machairodont *Homotherium* sp., the bobcat *Lynx rufus*, the cheetah-like cat *Miracinonyx inexpectatus*, the raccoon *Procyon lotor*, the long-tailed weasel *Mustela frenata*, the spotted skunk *Spilogale putorius*, the river otter *Lutra canadensis*, and the Caribbean monk seal *Monachus tropicalis*. Of significance, the Leisey carnivore fauna includes (1) the largest, most complete sample of *Smilodon gracilis*, and (2) the first Irvingtonian record from Florida of *Lutra canadensis*. The Leisey carnivores rank with those from Coleman 2A and Inglis IA as the most diverse carnivore faunas known from the Irvingtonian of Florida.

RESUMEN

Se han recuperado trece especies de carnívoros de los depósitos de Conchuelas de Leisey de fines del Irvingtoniano temprano de Florida. Estas especies incluyen el lobo de Armbruster *Canis armbrusteri*, el coyote lobo *Canis edwardii*, el zorro gris *Urocyon cinereoargenteus*, el oso tremarctino *Arctodus pristinus*, el tigre dientes de sable grácil *Smilodon gracilis*, el macairodonte *Homotherium* sp., el lince *Lynx rufus*, el felino tipo guepardo *Miracinonyx inexpectatus*, el mapache *Procyon lotor*, la comadreja de cola larga *Mustela frenata*, el zorrillo moteado *Spilogale putorius*, la nutria de río *Lutra canadensis* y la foca monje del Caribe *Monachus tropicalis*. Significativamente, la fauna de carnívoros de Leisey incluye: (1) La mayor y más completa muestra de *Smilodon gracilis* y (2) el primer registro de *Lutra canadensis* para el Irvingtoniano de Florida. Los carnívoros de Leisey son comparables con los de Coleman 2A e Inglis IA en ser la fauna conocida de carnívoros más diversa del Irvingtoniano de Florida.

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BERTA, A. 1995. Fossil carnivores from theLeisey Shell Pits, Hillsborough County, Florida. Bull. Florida Mus. Nat. Hist. 37 Pt. II(14):463-499.

INTRODUCTION

The Leisey carnivores, a relatively large and diverse sample of well preserved specimens, include cranial, dental, and postcranial remains from six families: Mustelidae, Felidae, Procyonidae, Canidae, Phocidae, and Ursidae. Thirteen species of carnivores are represented with a combined minimum number of 36 individuals (Table 1). In comparison to other Florida Irvingtonian localities Leisey ranks with Inglis 1A and slightly behind Coleman 2A in diversity of carnivores (Webb 1974a: table 2.1; Martin 1974: table 3.1)

At Leisey large carnivores are more numerous and diverse than small carnivores (Table 1). The large carnivores include a large and a small wolf, *Canis armbrusteri* and *C. edwardii*; a tremarctine bear, *Arctodus*; two machairodont cats, *Smilodon* and *Homotherium*; and the cheetah-like cat *Miracinonyx*. The Inglis 1A fauna shares all these taxa, except it has only the small wolf, *C. edwardii*. One additional large carnivore not represented at Leisey but present at Inglis 1A is the hyaena *Chasmaporthetes*. The Coleman 2A large carnivore fauna comprises *C. armbrusteri*, *Arctodus*, and the jaguar, *Panthera onca*.

Small carnivores at Leisey include a fox, *Urocyon*; a raccoon, *Procyon*; a weasel, *Mustela*; a skunk *Spilogale*; an otter, *Lutra*; and a bobcat, *Lynx rufus*. This assemblage is similar to both Inglis 1A and Coleman 2A, although less diverse in lacking the skunks *Conepatus* and *Mephitis*, and unique in the presence of an otter, *Lutra*.

With the exception of the Ursidae (Emslie this volume), representatives of the other five carnivore families will be discussed in this paper. The format for each taxon includes a list of referred specimens, description and/or discussion of this material, and the chronology and stage of evolution of the species as indicated by other occurrences.

The method of measurement for *Smilodon* follows Berta (1987). All measurements are in millimeters (mm) unless indicated otherwise. Abbreviations cited in the tables are as follows: N, number of specimens measured (sample size); X, mean; and OR, observed range.

ACKNOWLEDGEMENTS

I thank Toni Tejada-Flores and Christopher Shaw of the George C. Page Museum for their help in my study of the Rancho La Brea *Smilodon*. I am especially grateful to Toni for measuring specimens in these collections. Ralph (Tony) Estevez, Frank A. Garcia, and James L. Pendergraft donated important specimens to the Florida Museum of Natural History from Leisey 3.

TABLE 1. Species listing and relative abundances of carnivores in the Leisey Shell Pit local fauna.

Leisey carnivores	Minimum number of individuals
Family Canidae	
Canis armbrusteri	3
Canis edwardii	3
Urocyon cinereoargenteus	1
Family Ursidae	
Arctodus pristinus	8
Family Procyonidae	
Procyon lotor	1
Family Mustelidae	
Lutra canadensis	2
Spilogale putorius	1
Mustela frenata	1
Family Felidae	
Lynx rufus	2
Smilodon gracilis	8
Homotherium sp.	3
Miracinonyx inexpectatus	1
Family Phocidae	
Monachus tropicalis	2
TOTAL	36

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich 1821
Family CANIDAE Gray 1821
Canis armbrusteri Gidley 1813

Referred Specimens.— **Leisey 1A**: UF 81654, left maxillary fragment with P4-M1; 81655, right maxillary with M1-2; 81152, right edentulous mandibular ramus; 67091, upper canine; 80662, 81661, left P4; 81656, right P4; 81657, right M1; 81658-81659, right p4; 81660, left m1; 87283, fragment of left mandible with p4. **Leisey 3**: UF 142230, right proximal radius; 132049, right metatarsal IV.

Discussion.— Two large fossil wolves are known from Florida, Armbruster's wolf, *Canis armbrusteri*, and the dire wolf, *Canis dirus* (Berta 1981). The smaller of the two, *C. armbrusteri*, also is known from three other Irvingtonian faunas in Florida, Coleman 2A, McLeod Limerock Mine, and Haile 21A. The Leisey sample of *C. armbrusteri* resembles specimens from Coleman 2A described as *C. lupus* by

Martin (1974). Although *C. armbrusteri* is closely related to gray wolves, it can be distinguished from *C. lupus* by several characters, one of which is apparent among specimens from Leisey, a pronounced buccal cingulum on the M1 (Fig. 1A-B). Comparison of measurements of fossil wolves from the Florida Pleistocene (Martin 1974, table 3.11) with the Leisey sample (Table 2) indicates that the latter sample falls within the size range of Coleman 2A. *C. armbrusteri* is distinctly smaller than either Florida or Rancho La Brea *C. dirus*. The smaller size of *C. armbrusteri*, especially as regards carnassial size, was previously noted and figured by Kurtén and Anderson (1980).

Canis edwardii Gazin 1942

Referred Specimens.– Leisey 1A: UF 67092, posterior skull fragment; 81665, right maxilla with P4-M2; 80372, right premaxilla with I3; 81666, right maxilla with M1-2; 81663, left maxilla with P1-2; 81664, right maxilla with P3; 63667, left mandible with p1-m1; 64399, left mandible with m1; 81670, juvenile right mandible with p3-m1 in crypt; 87291, edentulous maxilla; 81685, edentulous mandible; 67090, 81667, right upper canine; 81682, partial left P3; 80662, left P4; 81668, right P4; 81669, right M1; 81671, right lower canine; 81675, right p2; 81674, right p3; 87285, right m1, 81673, partial right m1; 81672, 87297, left m1; 81677, atlas; 87284, 63671, 87296, axis; 81677, cervical vertebrae; 81127, 81509, 81679, left distal humeri; 81680, right distal radius; 81686, right metacarpal II; 87286, right metacarpal II (juvenile); 87292, left proximal metacarpal II; 87294, right metacarpal III; 87293, 63668, right metacarpal IV; 81219, right distal femur; 67093, 67094, right distal tibiae; 81681, left distal tibia; 63669, right metatarsal III; 63670, right metatarsal IV; 87295, medial phalanx; 87288, 87289, proximal phalanx.

Discussion.– *Canis edwardii* is the best represented canid at Leisey and includes adult and juvenile individuals. In addition to fragmentary maxillae and mandibles, skeletal elements are known. Other Florida Irvingtonian occurrences of this species include Inglis 1A, Haile 21A, and Rigby Shell Pit. This species of small fossil wolf is thought to be related to the red wolf, *Canis rufus* (Tedford pers. comm.). According to Tedford, whose usage is followed here, material referred to *Canis priscolatrans* by Kurtén and Anderson (1980) should be referred to this species.

Among those characters which distinguish *C. edwardii* from *C. rufus* are longer, narrower carnassials (Fig. 1C), and smaller M2 with broad hypocone and weak anterobuccal cingulum (Tedford pers. comm.). Measurements of *C. edwardii* from Leisey are compared with some other Florida occurrences of this species in Table 3. The Leisey *C. edwardii* resembles in size and morphology

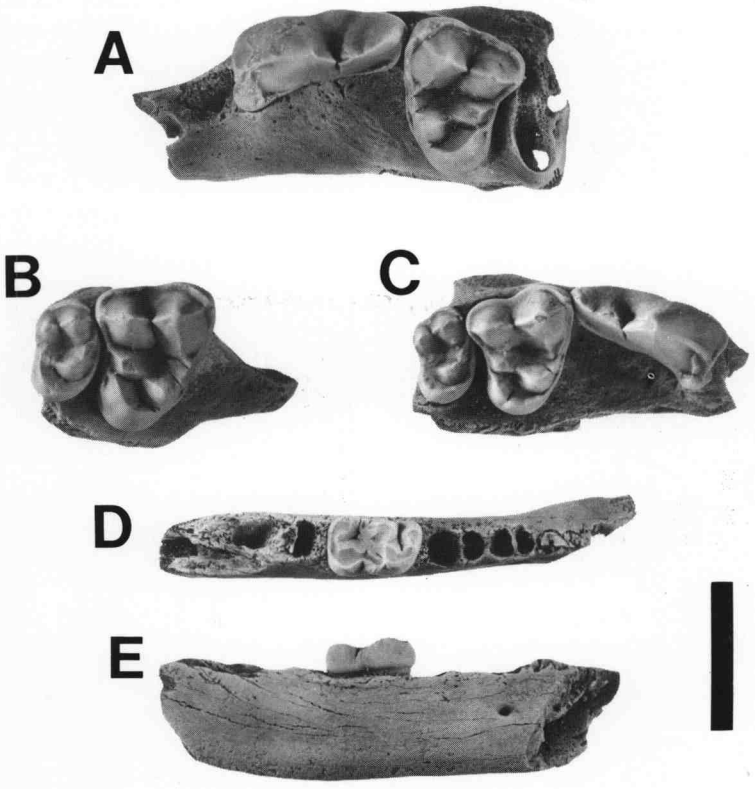

Figure 1. Canidae and Procyonidae from Leisey Shell Pit 1A. (A) *Canis armbrusteri*, UF 81654, occlusal view of left maxilla with P4-M1; (B) *C. armbrusteri*, UF 81655, occlusal view of right maxilla with M1-M2; (C) *C. edwardii*, UF 81665, occlusal view of right maxilla with P4-M2; (D) occlusal and (E) lateral views of *Procyon lotor*, UF 80588, right mandible with m1. Scale bar 20 mm in length.

TABLE 2. Upper tooth measurements of *Canis armbrusteri* from Leisey Shell Pit.

		UF 81654	UF 81655	UF 81656	UF 81657
P4	length	25.4	—	26.3	—
	width	12.2	—	12.1	—
M1	length	16.4	15.9	—	14.5
	width	22.4	22.2	—	20.9
M2	length	—	8.4	—	—
	width	—	13.6	—	—

TABLE 3. Dental and mandibular measurements for *Canis edwardii*.

		Leisey			Haile 21A	Rigby Shell Pit
		N	X	OR	(UF 62561-62562)	(UF 40090-40091)
P4	length	2	21.5	20.5-22.5	22.5	19.0
	width	2	10.3	10.1-10.5	11.4	9.0
M1	length	3	19.3	18.4-20.1	20.0	—
	width	3	14.6	14.5-14.8	14.3	13.5
M2	length	2	12.3	12.2-12.3	12.0	—
	width	2	7.4	6.8-8.0	7.6	—
Depth jaw below middle m1		1	25.8		—	—
p1	length	1	6.1		5.2a	—
	width	1	4.0		—	—
p2	length	1	9.8e		13.1	10.7
	width	-	—		5.4	4.4
p3	length	2	—		14.0	—
	width	2	—		5.7	—
p4	length	1	13.5		14.5	—
	width	1	6.4		7.2	—
m1	length	2	—		24.7	—
	width	2	—		10.5	—

specimens from Haile 21A. Study of skeletal material, including tibiae, femur, radius, cervical vertebrae, and metapodials, referred to this species from Leisey also compared best with the Haile 21A sample.

Urocyon cinereoargenteus (Schreber 1775)

Referred Specimens.– Leisey 1A: UF 81653, right calcaneum.

Discussion.– This specimen agrees in detail with Recent Florida specimens of *Urocyon cinereoargenteus*. Other Florida Irvingtonian records of this species occur at Inglis 1A (Webb 1974a) and Coleman 2A (Martin 1974). Although Martin originally described the Coleman specimens as a new fossil species of gray fox, *U. minicephalus*, I follow Kurtén and Anderson (1980) in recognizing it as a junior synonym of the living gray fox, *U. cinereoargenteus*.

Family PROCYONIDAE Bonaparte 1850
Procyon lotor (Linnaeus 1758)

Referred Specimens.– Leisey 1A: UF 80588, right mandible with posterior crown of p2 and m1. **Leisey 1:** UF 91016, left distal humerus.

Discussion.– The Leisey raccoon is tentatively referred to the modern species *Procyon lotor*. Comparison of Recent specimens indicates that the fossil material differs in its considerably larger size and differing morphology of m1, in which an additional cusp is positioned behind the metaconid (Fig. 1C-D; Table 4). Further study of the fossil material, especially the large Inglis 1A sample, may warrant establishment of a new species (see also Morgan and Hulbert this volume).

This species was previously recorded from a single Florida Irvingtonian fauna, Coleman 2A (Martin 1974). In addition to Leisey, other Florida Irvingtonian faunas that record the presence of *Procyon* are Inglis 1A, Haile 21A, and Haile 16A. The stage of evolution of the Leisey specimen is most similar to that represented by the Inglis jaws.

Table 4. Mandibular and tooth measurements of fossil and Recent *Procyon lotor* from Florida.

	Leisey 1A UF 80588	Coleman 2A UF 13163	Inglis 1A UF 49251	Haile 16A UF 46665	Recent N	Recent X	Recent OR
Toothrow length (p1-m2)	48.0e	39.9	45.7	48.0	5	37.2	36.7-37.6
Depth of mandible below m1	14.8	–	8.5	–	–	–	–
m1 length	12.5	–	12.1	–	5	9.4	9.1-9.5
width	7.7	–	7.7	–	5	6.2	6.0-6.3

Family MUSTELIDAE Swainson 1835
Mustela frenata Lichtenstein 1831

Referred Specimens.– Leisey 3A: UF 95765, right mandible with p4-m1.

Discussion.– This specimen (Fig. 2A) is very similar to the Recent Florida long-tailed weasel, *Mustela frenata*. It is larger than the Devil's Den *M. frenata*, the only other Pleistocene record of this species from Florida (Table 5).

Lutra canadensis (Schreber 1776)

Referred Specimens.-- Leisey 1A: UF 81651, left maxillary with P3; 81652, left M1. **Leisey 3**: UF 124633, left mandible with p3-m1.

Discussion.-- The Leisey otter resembles the fossil species *Lutra parvicuspis* Gidley and Gazin (1933) in its large size (Fig. 2D-E) and P3 with conspicuous posteromedial basin. However, the Leisey specimen differs from *L. parvicuspis* in having a broadly proportioned paracone and metacone (Fig. 2D; Table 6). I follow Kurtén and Anderson (1980) and other workers in synonymizing *L. parvicuspis* with the modern species.

The Leisey occurrence represents the first Irvingtonian record of this species in Florida. Other Irvingtonian occurrences of *L. canadensis* include the slightly younger Cumberland Cave and Port Kennedy Cave faunas of middle Irvingtonian age.

Spilogale putorius (Linnaeus 1758)

Referred Specimens.-- Leisey 3: UF 142229, right mandible with m1.

Discussion.-- The Leisey specimen (Fig 2B-C) compares favorably with a large sample of mandibles from Inglis 1A listed as *Spilogale putorius* by Webb

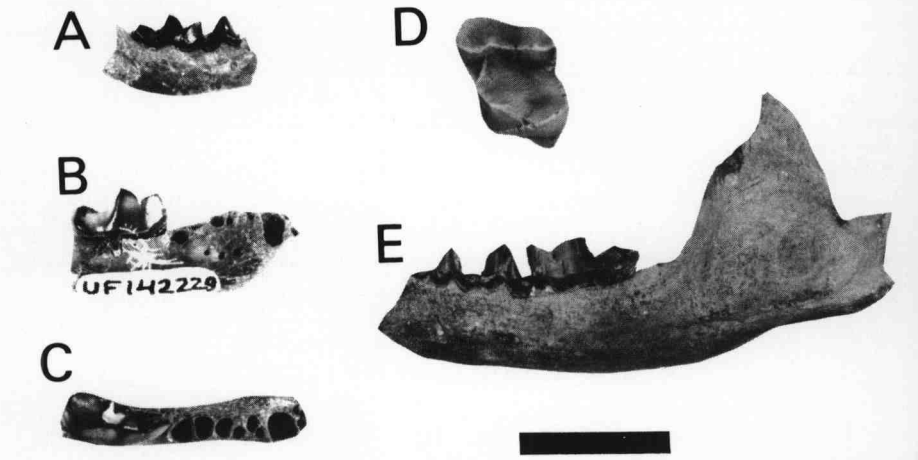

Figure 2. Mustelidae from the Leisey Shell pits. (A) *Mustela frenata*, UF 95765, lateral view, right mandible with p4-m1; (B) lateral and (C) occlusal views, *Spilogale putorius*, UF 142229, right mandible with m1; (D) *Lutra canadensis*, UF 81652, occlusal view, left M1; (E) *L. canadensis*, UF 124633, lateral view, left mandible with p3-m1. Scale bar 14 mm in length for A-C, 16 mm for D, and 20 mm for E.

Table 5. Dental measurements of fossil and Recent *Mustela frenata* from Florida.

		Leisey 3A UF 95765	Devil's Den UF 16542	Recent N	Recent X	Recent OR
p4	length	3.5	–	4	3.4	3.0-3.7
	width	2.0	–	4	1.7	1.5-1.9
m1	length	6.4	5.9	4	5.9	5.1-6.4
	width	2.8	2.2	4	2.3	2.2-2.5

Table 6. Upper tooth measurements of fossil and Recent *Lutra* from Florida.

			Lutra canadensis			*Lutra parvicuspis*[1]		
		UF 81651-81652	N	X	OR	N	X	OR
P3	length	9.0	5	7.6	6.8-8.0	3	7.8	7.5-8.2
	width	5.8	5	5.2	5.0-5.5	3	5.4	5.0-6.0
M1	length	11.7	5	9.4	9.1-9.9	-	-	–
	width	13.6	5	12.2	11.6-12.7	-	-	–

[1] Measurements after Gidley and Gazin (1933).

(1974a). However, the m1 of the Leisey specimen is slightly larger (anteroposterior length 9.3 mm) than most of the Inglis m1s. Both the Leisey and Inglis specimens are larger than mandibles of the extant spotted skunk from Florida, but are similar in size to those of larger western subspecies of *S. putorius*. Kurtén and Anderson (1980) referred all North American Irvingtonian spotted skunks to *S. putorius*.

Family FELIDAE Gray 1821

Lynx rufus (Schreber 1776)

Referred Specimens.– Leisey 1A: UF 81690, right calcaneum; 81691, metatarsal III; 87300, proximal right ulna; 87299, proximal right metacarpal III.

Leisey 3: UF 124631, left mandible with c, p3-m1; 130012, right proximal humerus; 102668, right distal radius; 130013, left proximal ulna; 102669, left distal femur.

Discussion.– All elements compare well in most features with Recent *Lynx rufus* from Florida (Fig. 3). Differences seen in the Leisey calcaneum are a rounded posterior articular surface and a relatively short shaft. In the modern species the posterior articular surface is nearly triangular, and the shaft is long relative to total length. The Leisey metatarsal differs from Recent specimens of *L. rufus* in having a more extensive proximal posterior projection that is not as broad transversely (Table 7).

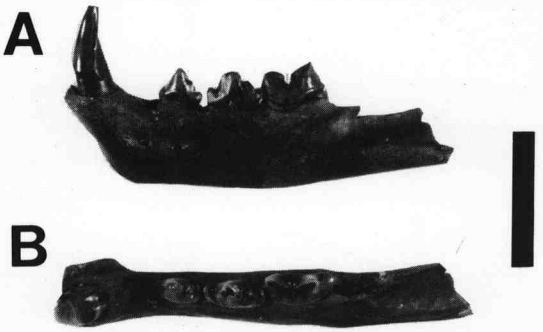

Figure 3. Bobcat (*Lynx rufus*) from Leisey 3. (A) lateral and (B) occlusal views, UF 124631, left mandible with c and p3-m1. Scale bar 20 mm in length.

This species occurs commonly in Florida Rancholabrean faunas and has been recorded previously from two Irvingtonian localities, Inglis 1A and Coleman 2A (Kurtén 1965; Webb 1974a). In his review of small Pleistocene felines of North America, Werderlin (1985) referred all pre-Wisconsin species of *Lynx rufus* (with the exception of the type of *L. r. koakudsi*) to *Lynx rufus calcaratus*. He listed the temporal range of this subspecies as Blancan (Cita Canyon, Texas) to late Sangamonian (Sabertooth Cave, Florida). As Werderlin commented (1985:199), "...it seems possible that these specimens may eventually be referrable to a species distinct from *Lynx rufus* ... this can only be substantiated through discovery of complete skulls, or ... postcranial material that would permit calculation of limb proportions."

Table 7. Measurements of hindlimb elements of fossil and Recent *Lynx rufus* from Florida.

Calcaneum	Leisey 1A UF 81690	Recent N	Recent X	Recent OR
length	36.6	2	39.5	38.0-41.0
width	12.1	2	11.6	9.8-13.4
shaft length	23.0	2	24.8	23.9-25.7

Metatarsal III	Leisey 1A UF 81691	Recent N	Recent X	Recent OR
length	61.4	2	66.2	65.0-67.4
proximal width	8.3	2	9.1	8.6-10.6
proximal depth	10.0	2	11.2	10.5-11.9

Smilodon gracilis (Cope 1880)

Referred Specimens.— Leisey 1A: UF 81700, nearly complete skull with left I2-3, P3-4, M1 and right I1-3, P3-4; 87238, partial skull with P3-4 and complete braincase; 87239, partial skull with left P3-4 and complete braincase; 87242, occipital region of skull; 87240, right mastoid region; 87237, right premaxillary with I1-3; 81714, 87236, left premaxilla with I2-3; 63666, 81617, left premaxilla with I3; 84187, right premaxilla with I3; 83050, right maxilla with P4; 87243, 87245, left maxilla with P3-4; 63652, left maxilla with P4; 87246, right maxilla with P3-4; 80463, edentulous left maxilla fragment; 87241, 87261, left mandible with p4-m1; 81723, nearly complete right mandible with i3-c, p4-m1; 81724, left mandible with c, p3-m1; 86746, nearly complete right mandible; 82529, right mandible with p3-m1; 87258, associated right mandible with p4-m1 and left mandible with p4; 63653, right mandibular ramus with p4; 87275, left mandible with p4; 63655, 63654, 81722, 87244, 80182, 87259, 82251, right upper canines; 86843, 80111, 87276, 84189, left upper canines; 87251, 87260, left I2; 81220, right I1, 87251, 87260, left, I2; 87254, right I2; 80221, left I3; 86692, right fragmentary P4; 67086, 81472, 81017, 83087, left lower canines; 84188, right lower canine; 83088, left p4; 63656, left m1; 63657, partial right m1; 81829, 81726, 81725, 87303, atlas; 67084, 87255, 81507, 67085, 82834, axis; 81828, cervical vertebra; 80028, 2 thoracic vertebrae; 81154, 80162, 81294, 80088,

lumbar vertebrae; 63665, 65397, sacrum; 65074, 81715, 80183, proximal right scapula; 67083, 87304, proximal left scapula; 63659, 81727, 87277, right humerus; 63661, 80184, 67087, right distal humerus; 83581, 81153, 87278, 87307, left humerus; 81371, 81730, 80962, right radius; 81729, left radius; 63663, proximal left radius; 87281, left ulna (distal end missing); 87280, right ulna (proximal and distal end missing); 83429, 63660, 81370, proximal right ulna; 85321, 81728, left ulna; 81221, right innominate; 87256, 87259, associated right and left innominate; 80319, 80087, 80663, 80222, 67082, right partial innominate; 80223, 63664, 81618, 87228, left partial innominate; 67081, 82652, right femur; 87272, proximal left femur; 81732, proximal right tibia; 81731, left tibia; 80917, patella; 87274, proximal left fibula; 67088, distal left fibula; 87259, left astragalus; 87264, left calcaneum; 87267, left. magnum; 87248, left scapholunar; 86963, left pisiform; 87269, left metacarpal III; 87273, left metatarsal IV; 86747, right metacarpal IV; 81712, right metatarsal IV; 86804, right metatarsal V; 87253, 87262, 87247, 88048, proximal phalanx; 81713, 81508, 87263, 81711, 80161, 87270, medial phalanx; 81710, 81295, 87271, 87252, ungual phalanx. **Leisey 3**: UF 142231, proximal two-thirds of right radius.

Description.– The Florida record of *Smilodon gracilis* has been recently reviewed (Berta 1987). The following supplemental description is based on the Leisey sample. Comparisons are made between this sample, previously known material of this species, and the more advanced Rancholabrean species, *Smilodon populator* (Berta 1985).

Skull: *Smilodon gracilis* was described by Cope (1880) largely on the basis of a crushed and distorted skull and mandible. To this can now be added from Leisey a nearly complete skull (UF 81700) and two partial skulls with complete basicrania (UF 87238, 87239).

The Leisey skulls are smaller and more lightly built than *S. populator* (Fig. 4, Table 8). The muzzle is shorter and narrower in this species (Table 8). The anterior narial opening is narrower than in *S. populator* and rises more steeply along its lateral margin owing to relatively less inflated canine tracts. The zygomata are deep and arched with the posterior root of the arch ventrally extended, as is characteristic of the genus. The sagittal crest, although abraded and worn in the most complete specimen, is prominent and elevated above the parietals. The postorbital processes are relatively large, blunt protuberances.

The braincase is posteriorly expanded, and its surface pitted by several large fossae near its junction with the lambdoidal crests. Lambdoidal crests are strongly posteriorly and ventrally directed and enclose a rounded occiput. Several pairs of deep depressions for insertion of the rectus capitus muscles are positioned on either side of the strong vertical keel. The occiput is shorter relative to skull length in this species (Table 8).

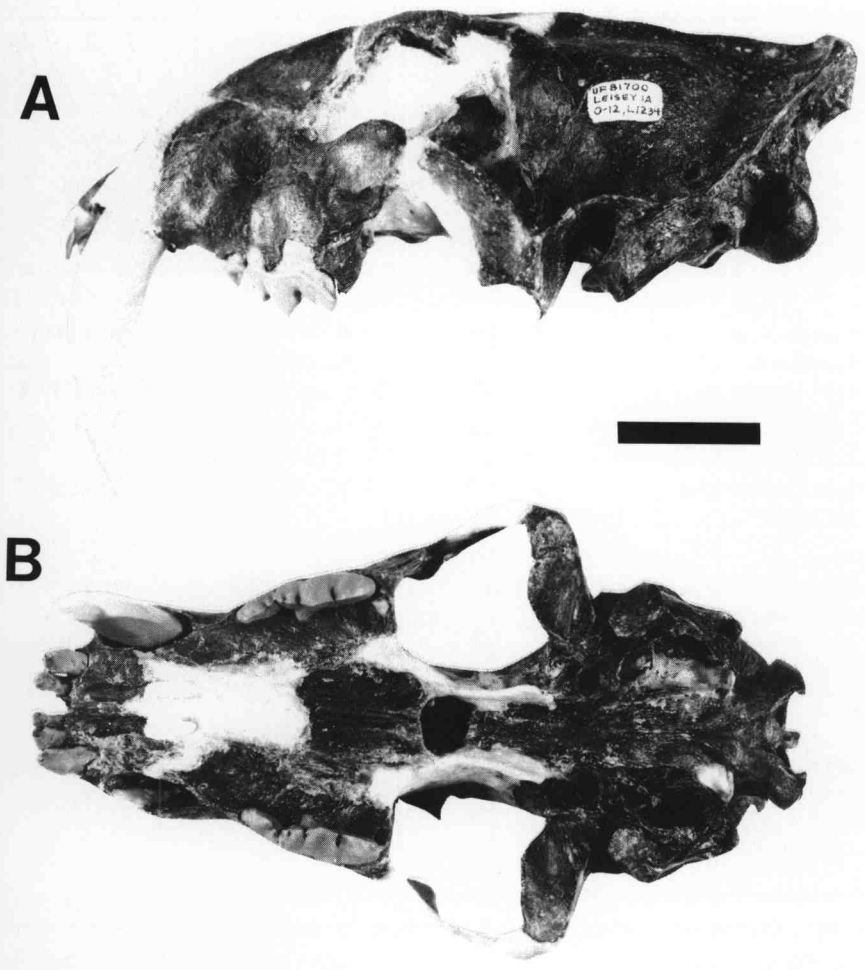

Figure 4. Sabercat skull from Leisey 1A. (A) lateral and (B) ventral views of *Smilodon gracilis*, UF 81700, skull with right and left I2-I3, P3-P4, and right I1. The left canine belongs to a different individual. The teeth were coated for photography. Scale bar 50 mm in length.

The optic foramen is small, and the large sphenoidal fissure and foramen rotundum are positioned along the lateral side of the alisphenoid. A large bony strut separates the foramen rotundum from the foramen ovale. The foramen ovale is directed ventrally, as in *S. populator*.

Table 8. Comparison of cranial measurements of *Smilodon* from Leisey 1A and Rancho La Brea.

	Smilodon gracilis FLORIDA Leisey 1A		*Smilodon populator*[1] CALIFORNIA Rancho La Brea	
	UF 81700	UF 87239	N	OR
Length, premaxillary–condyles	250	—	25	271.4-344.1
Length, postglenoid cavity–condyles	73.9	73.0	25	83.4-117.8
Greatest width across muzzle at C	70.0	—	25	93.1-117.8
Greatest width across postorbital processes	67.2e	—	25	104.1-130.2
Least width behind postorbital processes	44.8	—	25	52.9- 65.9
Palatal width at C	38.1e	—	25	48.9- 63.0
Palatal width at P4	63.8	—	24	114.7-135.4
Greatest transverse diameter, auditory bulla	36.7	—	25	46.7- 63.9
Greatest width across mastoid processes	98.5	94.3	24	122.0-154.3
Greatest width across condyles	51.5	51.8	25	57.4- 72.3
Minimum distance from occiput-foramen magnum notch	52	—	10	63.3- 90.8*

[1] Measurements following Merriam and Stock (1932) and (*) this study.

The palate is posteriorly broad. Large round embrasure pits are located between P4 and M1 for occlusion with m1. On either side of the midline of the palate are a pair of narrow palatal grooves that extend anteriorly. Lateral to these grooves is a large median trough bounded by another ridge.

The ear region of *S. gracilis* presents more significant differences than other portions of the skull and is discussed in greater detail. The mastoid is not as enlarged relative to the bulla as in *S. populator*, and it does not extend as far anteriorly as in the late Pleistocene species. The paroccipital processes are defined as pointed projections on either side of depressions in the exoccipital. In comparison to *S. populator*, the tubular external auditory meatus forms a more open channel owing to a less expanded mastoid farther separated from the postglenoid process (Fig. 4). The postglenoid foramen is positioned at the base of the postglenoid process near the entrance of the external auditory meatus. It is

variable in size; very reduced in UF 81700, large in UF 87238, and very large in UF 87239. The posterior portion of the postglenoid process is enlarged and extends farther anteriorly than in *S. populator*. In ventral view the mastoid terminates near the level of the glenoid fossa and does not extend medially around the bulla as in most *S. populator*. The mastoid and bulla in *S. gracilis* are farther separated from one another than in *S. populator*. This is especially true for the posterior portion of these elements which remain separate rather than coalescing, as is common in *S. populator*.

The bullae are large and globose. The ventral walls of the bullae are broken in all specimens, exposing the internal structure of the ear, and it is comparable to *S. populator* in structure. The septum dividing the tympanic cavity into a small ectotympanic (tympanic) and large entotympanic (caudal entotympanic of Hunt 1974) is apparent, as is the septum separating the entotympanic into an anterior and posterior chamber. The posterior chamber is much larger and extends into the mastoid process.

Upper Dentition: Judging from the varying stages of tooth wear represented, the Leisey sample includes individuals that ranged in age from young to very old adults. Upper incisors preserved in the skull (UF 81700) and an edentulous maxilla (UF 80463) are arranged transversally in an arc and are very similar in morphology to *S. populator*.

The canine is proportionally smaller, shorter and less curved in *S. gracilis* than in *S. populator* (Fig. 5; Table 9). This tooth is set in the maxilla nearly in line with the cheek toothrow (Fig. 4). The swollen tracts of the canine roots extend to the interorbital constriction. In *S. populator* the canine is medially positioned in the jaw and offset from the cheek toothrow.

Other than the smaller size, P3-4 in the Leisey sample compare well with previous known material (Table 10). Very fine serrations are present along the anterior and posterior tooth margins of P3. P4 presents several distinctive features of *S. gracilis*, a small ectoparastyle, a distinct protocone, and a separate protocone root.

Mandible and Lower Dentition: The mandible and lower dentition of *S. gracilis* are well represented in the Leisey sample and compare favorably in size and morphology with previously known samples (Fig. 6; Table 11). In all Leisey specimens p3 is separated from p4-m1 by a small diastema. In contrast to the variability of p3 seen in other samples of *S. gracilis*, only one specimen of p3 in the Leisey sample, UF 87258, has two distinctly separate roots. In all other specimens p3 is single rooted with a lateral sulcus at crown level dividing the tooth part way down the root and fusing into a single root socket. Since absence of this tooth is common among late Pleistocene *S. populator*, the more common single rooted condition of this tooth in the Leisey sample, as compared with previously

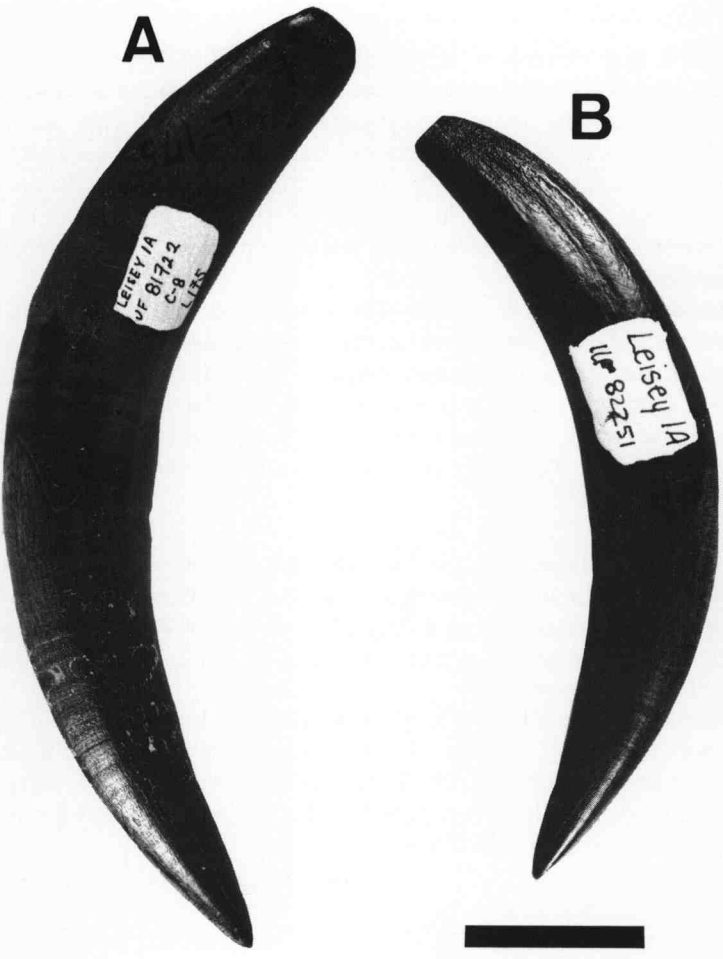

Figure 5. Two *Smilodon gracilis* upper canines from Leisey 1A. (A) UF 81722; (B) UF 82251. Scale bar 30 mm in length.

known samples, is considered evidence of its more advanced stage of evolution. In UF 87258, p4 differs from previously known specimens of this species in lacking an anterior cusplet. Comparison of the length of the lower carnassial indicates that the Leisey sample is intermediate in size between that of Inglis 1A and Port Kennedy specimens (Table 11).

Skeleton: The remainder of the axial skeleton is represented by elements from the major regions of the vertebral column including the cervical, thoracic, and sacral

Table 9. Comparison of upper canine measurements of *Smilodon* from Leisey 1A and Rancho La Brea.

	A-B length[1]	C-D length[2]	Arc[3]
S. gracilis			
FLORIDA			
Leisey 1A			
UF 87244	142.6	44.6	3.197
UF 87122	162.0	52.0	3.114
UF 86692	153.4	52.1	2.943
UF 80111	161.0	53.5	3.012
UF 87276	145.7	47.2	3.086
UF 84189	147.9	44.0	3.361
S. populator[4]			
CALIFORNIA			
Rancho La Brea			
2000-R-48	247.0	72.0	3.430
2000-R-24	225.0	63.0	3.571
2000-L-43	216.0	69.0	3.130
2000-R-21	229.0	68.0	3.367
2000-R-5	226.0	63.0	3.587
2000-R-47	206.0	62.0	3.322
2000-L-16	232.0	66.0	3.515
2000-R-31	234.0	65.0	3.600
2000-L-26	262.0	80.0	3.275
2000-L-2	200.0	58.0	3.448

[1] Total tooth length measured from canine tip to base of root.
[2] Arc length measured normal to enamel margin.
[3] Arc-ratio ab/cd length which approximates curvature of arc.
[4] Measurements based on this study.

vertebrae. With the exception of two cervical vertebrae from Inglis IA, none of these elements was previously known. Other than their smaller size, these elements are virtually indistinguishable from those of *Smilodon populator* (Table 12). Both the atlas and axis display characteristic *Smilodon* features. In the atlas the transverse process extends posteriorly well behind the articulations for the axis. In the axis, the neural spine projects posteriorly behind the posterior zygopophyses. The sacrum is like *S. populator* in having small anterior zygopophyses that do not extend high above the dorsal surface, and a broad dorsal margin lateral to the anterior zygopophyses.

Table 10. Measurements of upper dentition of *Smilodon*.

	I1		I2		I3		P3		P4		M1	
	L	W	L	W	L	W	L	W	L	W	L	W
S. gracilis												
FLORIDA												
(Leisey)												
UF 87242	7.3	-	8.6	-	10.5	-	-	-	-	-		
UF 87243	-	-	-	-	-	-	14.0	6.2	31.3	11.9		
UF 87246	-	-	-	-	-	-	13.5	6.3	31.6	11.4		
UF 87238	-	-	-	-	-	-	15.3	7.4	32.4	14.3		
UF 81700	7.5	7.9	10.0	9.0	10.7	10.9	14.7	7.2	32.0	13.9		
(Inglis IA[1])	-	-	-	-	-	-	15.9	7.1	32.0-	11.8e-		
(McLeod)	-	-	-	-	-	-	16.5	7.8	33.7e	12.9(2)	5.1	7.5e
(Bass Point Waterway) I[2]					8.5-	10.1-	16.2-	7.0-	30.4	11.5e	-	-
(El Jobean Pit[2])					9.1(2)	10.2(2)	17.0(2)	7.4(2)	34.2	11.9e		
							17.3	7.1	30.5	12.7		
PENNSYLVANIA							15.4-	6.5-	32.0-	11.8-		
(Port Kennedy[1])	7.5	5.4	8.7	7.4	10.3	9.0	16.0(2)	7.2(2)	33.7(2)	12.9(2)	8.4	4.7
S. populator												
FLORIDA												
(Ichetucknee[3])												
UF 3470	-	-	-	-	-	-	-	-	41.1	16.0	-	-
(Melbourne[3])												
USNM	-	-	-	-	-	-	-	-	35.7	-	-	-
CALIFORNIA												
(Rancho La Brea[4])												
Minimum	-	5.0	-	7.6	-	11.0	15.0	8.4	37.5	14.2	-	-
Maximum (N=25)	-	7.6	-	9.7	-	13.0	19.7	10.6	46.0	19.9	-	-

[1] Measurements following Berta (1987).
[2] Measurements following Churcher (1985).
[3] Measurements following Kurten (1965).
[4] Measurements following Merriam and Stock (1932).

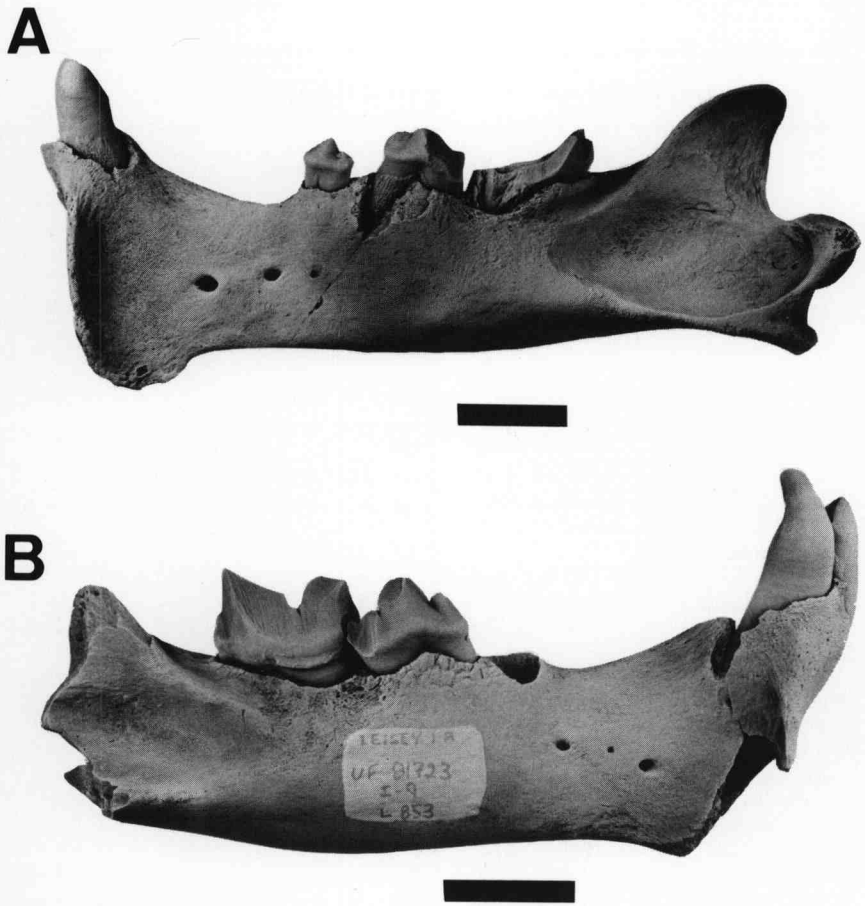

Figure 6. Mandibles of *Smilodon gracilis* from Leisey 1A in lateral view. (A) UF 81724, left mandible with c and p3-m1; (B) UF 81723, right mandible with i3, c, and p4-m1. Specimens coated for photography. Scale bars 20 mm in length.

The scapula is not represented by any complete specimens; only the articular end is preserved. The lateral border of the glenoid fossa below the base of the spine is incised by a prominent notch, as in *S. populator*, that is lacking or very small in *Panthera onca*. Also, the glenoid fossa is narrow transversely at the cranial border (Table 13).

As was true for previously known Florida samples of *S. gracilis*, the humerus is abundantly represented at Leisey. In most dimensions this element is larger than the humeri in the Inglis 1A sample, although considerably smaller than those of the McLeod sample (Table 14). The proximal end of the humerus is

Table 11. Measurements of mandibular rami and lower dentition of *Smilodon*.

	Smilodon gracilis						
	FLORIDA						
	Leisey 1A						Inglis 1A[1]
	UF 81724	UF 87258	UF 81723	UF 82529	UF 81723	UF 87241	
Greatest depth, flange	55.6e	52.5e	-	-	-	-	52.8
Least depth ramus below diastema	28.2	26.2	27.8	29.0	29.3	28.1	26.4-29.3(3)
Width ramus at diastema	11.0	11.5	11.6	11.3	11.5	11.6	11.0-11.7e(3)
Width ramus at m1	15.4	15.2	16.8	15.2	15.2	17.3	14.2-15.9(4)
Mandibular toothrow length	54.0	55.3	50.4e	54.3	54.5	54.5	48.6-51.9(4)
Height, angle-coronoid	54.1	-	-	-	-	-	-
Length, symphysis-condyle	149.5e	-	-	-	-	-	-
c length	10.2	-	10.5	-	10.0	-	9.3e-11.3e(2)
width	-	-	-	-	7.5	-	7.1e-8.3e(2)
p3 length	9.5	-	-	9.0	9.4	-	8.1e-12.0(4)
width	5.0	-	-	5.0	5.3	-	5.1e-6.1(4)
p4 length	-	19.0	18.7e	18.7	-	-	18.2-20.3(4)
width	-	8.9	8.1	9.0e	-	-	7.8-8.5(4)
m1 length	-	23.6	23.0	23.7	-	-	20.8-23.0(5)
width	-	10.7	10.0	-	-	-	9.4-10.0(5)

characterized by an open channeled bicipital groove. The lateral profile is diagnostic of *Smilodon* in having the junction of the greater tuberosity and the anterior border of the shaft nearly orthogonal, whereas in true cats these surfaces form arcuate connections. The distal end is broad relative to total length (Fig. 7A); the ratio of length to distal width ranges from 3.5 to 4.0. By comparison, this same ratio approximates 3.2 in *Smilodon populator*, 3.2 in *Megantereon cultridens*, and 4.0 in *Panthera tigris*. The supracondyloid ridge displays several well developed muscle scars for the origin of extensors of the forelimb and manus.

Table 11 Extended

Smilodon gracilis			*Smilodon populator*			
FLORIDA		PENNSYL-VANIA	FLORIDA			CALI-FORNIA
El Jobean	Bass Point Waterway I[2]	Port Kennedy[1]	Ichetucknee[3]	Aucilla River[4]	Hog Creek[4]	Rancho La Brea[5]
-	-	50.7e-65.0(3)	-	-	-	
26.4e	-	30.3-31.7e(3)	29.6-30.4(2)	30.8	28.4	27.3-38.7
11.7e	-	11.8-13.3e(3)	-	-	-	-
15.5e	-	15.4e-17.3e(3)	-	-	-	-
-	-	57.5-59.0e(3)	-	-	-	48.3-60.9
-	-	-	55.5-67.3(2)	-	-	58.0-76.3
-	-	-	171-197(2)	-	-	178.3-230.0
-	-	7.0e-11.2(3)	14.4	13.8	13.4e	13.0-16.6
-	-	7.2-7.6(3)	9.8	9.5	11.9e	9.7-12.2
12.0e	-	10.6e-11.5e(2)	-	-	-	6.5-10.2
4.6e	-	4.0e-4.3e(2)	-	-	-	5.7-7.1
19.5	-	20.0-20.4(4)	25.0-27.0(2)	25.0	23.4	23.2-27.7
8.0	8.8	8.4-9.5(4)	10.8-12.8(2)	11.3	10.4	10.9-14.6
21.3	23.0a	22.0-25.2(3)	27.5-30.0(2)	25.4	27.0	25.0-32.1
9.7	10.0a	9.8-10.5(3)	12.9-14.5(2)	12.4	13.2	12.4-17.6

[1] Measurements following Berta (1987).
[2] Measurements following Churcher (1985).
[3] Measurements following Kurtén (1965).
[4] Measurements following Webb (1974b).
[5] Measurements following Merriam and Stock (1932).

Except for its larger size, the ulna agrees closely with those previously described from Inglis 1A and McLeod (Table 15). It is relatively short with a robust shaft and a broad distal end. In anterior view (Fig. 7B), a large ovate scar

Table 12. Measurements of atlas and axis vertebrae and sacrum of *Smilodon*.

Atlas	Greatest Anterior Width	Greatest Posterior Width	Greatest Length	Height
S. gracilis				
(Leisey)				
UF 81725	53.6	-	56.7	23.1
UF 81726	54.2	52.0	55.4	25.4
UF 81829	52.5	54.5	59.9	-
S. populator				
(Rancho La Brea[1])				
OR (N=10)	72.7-88.5	70.1-88.4	69.8-86.0	46.0-56.7

Axis	Greatest Length	Depth Centrum	Greatest Anterior Width	Greatest Posterior Width	Height
S. gracilis					
(Leisey)					
UF 67084	76.8	-	54.6	-	41.5
UF 82834	74.5	15.1	51.6	41.7	-
UF 87255	75.0	18.1	51.3	39.4	37.9
UF 81507	73.0	-	52.8	-	-
UF 67085	-	-	55.6	-	-
S. populator					
(Rancho La Brea[1])					
OR (N=10)	86.9-108.5	21.1-31.9	63.6-84.2	45.1-71.5	81.4-103.3

Sacrum	Greatest Length	Greatest Anterior Width	Depth, Anterior Centrum
S. gracilis			
(Leisey)			
UF 63665	55.4	72.7	8.5
UF 65397	56.7	72.5	9.6
S. populator			
(Arredondo[2])			
UF 2562	126.0	93.0	24.0
(Rancho La Brea[1])			
OR (N=10)	76.2-90.6	77.0-110.5	23.0-33.9

[1] Measurements following Merriam and Stock (1932).
[2] Measurements following Kurtén (1965).

Table 13. Measurements of scapula and pelvis of *Smilodon*.

Scapula	Greatest Width, Glenoid Cavity	Greatest Length, Glenoid Cavity	Least Width, Neck
S. gracilis			
(Leisey)			
UF 80183	29.5	40.3	40.6
UF 81715	30.7	41.7	45.0
UF 67083	30.9	39.4	45.0
UF 65074	-	40.5	-
S. populator			
(Arredondo[1])			
UF 2562	-	-	58.1
(Rancho La Brea[2])			
OR (N=10)	40.8-57.9	67.0-87.1	55.1-76.4

Pelvis	Length	Greatest Depth, Ilium	Acetabulum Diameter
S. gracilis			
(Leisey)			
UF 81221	239.0	22.5	33.4
UF 67083	-	22.1	33.5
S. populator			
(Arredondo[1])			
UF 2562	300.0a	70.0	45.5
(Rancho La Brea[2])			
OR (N=10)	283a-368	73.8-94.0	44.3-54.8

[1] Measurements following Kurtén (1965).
[2] Measurements following Merriam and Stock (1932).

on the shaft provides an area of origin for carpal and digital flexor, M. flexor profundus digitorum. The broad olecranon process of this species resembles *S. populator* as does the proximally and laterally directed coronoid process that is distinctly distally directed in true cats.

The radius also resembles that of previously described samples. The short, slightly curved shaft is relatively slender in comparison with *S. populator* (Fig. 7C-D; Table 15).

The pelvis of *S. gracilis* is known only from Leisey. Except for its smaller size and slender proportions, it is very similar to *S. populator* (Table 13). The ilium differs from those of *Panthera onca* and other true cats in having a more prominent inferior iliac spine that is positioned further dorsally on the crest of the ilium creating a sharper ridge (Fig. 8).

Table 14. Measurements of the humerus of *Smilodon*.

	Length	Prox. Depth	Prox. Width	Shaft Depth	Shaft Width	Distal Depth	Distal Width	Least Depth
S. gracilis (Leisey)								
UF 87250	256	71.7	52.3	–	–	41.4	67.7	23.7
UF 87249	235e	64.2	–	33.8	21.0	–	–	20.6
UF 87277	238	65.5	53.0	32.7	21.9	38.3	65.3	19.7
UF 83581	253	68.0	55.2	31.0	22.1	37.7	63.5	20.6
UF 81727	257	71.6	55.4	31.6	23.5	51.9	69.5	21.8
UF 87307	245	69.5	52.9	33.5	24.1	37.5	70.1	22.1
UF 63659	232	66.6	46.7	28.0	20.5	38.8	65.7	21.2
UF 87278	258	69.8	58.3	33.6	23.5	42.5	69.1	22.0
UF 81153	236	66.6	51.3	28.8	19.9	38.1	66.4	21.1
(Inglis IA[1])								
OR	237(1)	68.5-74.3(2)	48.5-55.3(2)	31.8-37.5(5)	20.7-24.7(5)	38.3-42.7(3)	66.6-76.1(3)	20.5-21.1(3)
(McLeod[1])								
OR	–	–	–	40.5-41.7(2)	25.6-26.3(2)	44.7(1)	–	–
S. populator								
(Arredondo[2])								
UF 2562	307	94.6	67.3	–	29.0	–	96.9	–
(Rancho La Brea[3])								
OR	309-385	92.0-118.2	75.4-92.4	–	32.2-41.7	–	98.7-128.3	–

[1] Measurements following Berta (1987).
[2] Measurements following Kurtén (1965).
[3] Measurements following Merriam and Stock (1932).

In the only known patella of *S. gracilis* from Leisey, the distal end is prolonged owing to ossification of a small portion of the patellar ligament. In this specimen, UF 80917, the greatest proximodistal diameter of this element measures 23.2 mm, and the greatest transverse width measures 36.7 mm. By contrast, a patella from McLeod is considerably deeper proximodistally, these dimensions measure 41.9 mm and 34.8 mm, respectively.

The femur from Leisey is very similar to that from Inglis 1A (Table 16). This element is shorter and more slender at both ends than that of *S. populator* (Fig. 9A). Several structural peculiarities of the proximal end distinguish *S. gracilis* from *P. onca*. In *S. gracilis* a tuberosity is apparent on the anterior rim of the

Figure 7. Forelimb elements of *Smilodon gracilis* from Leisey 1A. (A) UF 81727, right humerus in anterior view; (B) UF 81728, left ulna in anterior view, (C) anterior and (D) posterior views of UF 81730, right radius. Scale bar 50 mm in length.

intertrochanteric fossa; *P. onca* lacks this tuberosity. The proximal end of the femur in *S. gracilis* is further characterized by a more medial position of the lesser trochanter. In distal view, the intercondylar notch is more deeply incised than that of *P. onca*.

Table 15. Measurements of the ulnae and radii of *Smilodon*.

Ulna	Length	Olecranon Process Width	Olecranon Process Depth	Sigmoid Notch Width	Coronoid Process Width	Shaft Width	Shaft Depth	Distal Width
S. gracilis (Leisey)								
UF 85231	237	27.5	30.7	27.8	45.5	28.2	14.4	24.6
UF 81728	–	26.9	39.2	51.4	29.5	17.4	–	
UF 63660	–	–	36.1	–	–	–	–	–
UF 83429	–	24.9	31.8	32.4	47.5	–	–	–
	–	26.0	33.2	29.5	47.6	28.1	16.4	–
(Inglis IA[1])								
UF 18109	–	21.8	33.0	26.5	41.5	42.6	12.7	27.9
(McLeod[1])								
F:AM 95524	–	26.1	31.6	29.7	50.2	47.5	13.8	30.5
S. populator								
(Arredondo[2])								
UF 2562	310.3	–	46.7	63.2				
(Rancho La Brea[3])								
OR (N=10)	287-372	–	41.5-60.2	57.3-78.8	–	–	–	19.1-33.8

Radius	Length	Prox. Long Diameter	Prox. Short Diameter	Shaft Width	Shaft Depth	Distal Long Diameter	Distal Short Diameter
S. gracilis (Leisey)							
UF 81730	185	26.5	20.3	22.1	13.1	40.1	26.3
UF 81729	185	26.3	20.4	21.9	12.9	39.3	25.4
UF 81371	209	29.0	22.6	23.2	12.0	41.3	26.1
(McLeod[1])							
OR	–	35.2(1)	27.8(1)	23.6-26.4(2)	15.4-16.1(2)	45.6-49.7(2)	31.3-32.0(2)
S. populator							
(Arredondo[2])							
UF 2562	240e	42.8	33.2	26.5	18.5		
(Rancho La Brea[3])							
OR (N=10)	235-295	41.3-55.5	32.2-44.0	26.0-38.8	16.5-24.6		

1 Measurements following Berta (1987).
2 Measurements following Kurtén (1965).
3 Measurements following Merriam and Stock (1932).

Figure 8. Lateral view of UF 81221, right innominate of *Smilodon gracilis* from Leisey 1A. Scale bar 30 mm in length.

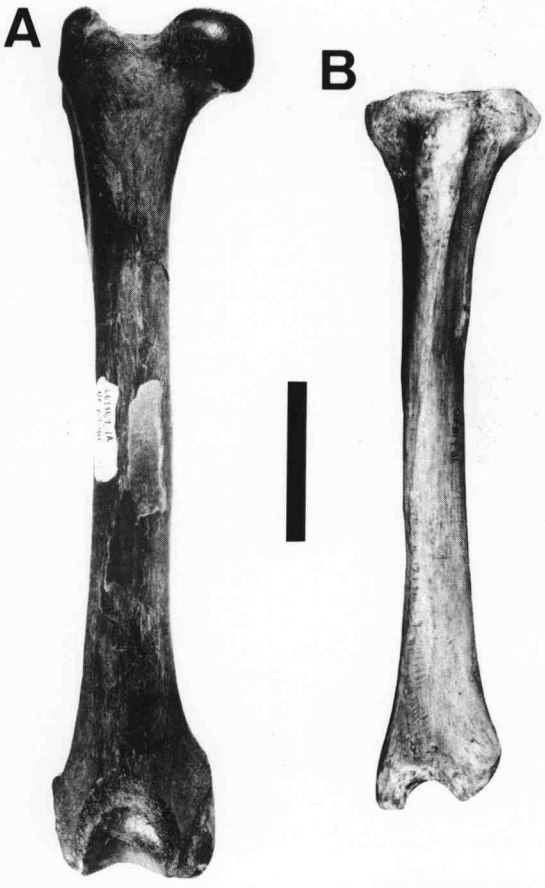

Figure 9. Hindlimb elements of *Smilodon gracilis* from Leisey 1A. (A) UF 67081, right femur in anterior veiw; (B) UF 81731, left tibia in anterior view. Scale bar 50 mm in length.

Table 16. Measurements of femur, tibia, and fibula of *Smilodon*.

	Length	Prox. Width	Prox. Depth	Shaft Width	Shaft Depth	Distal Width	Distal Depth	Weight[1] (kg)
Femur								
S. gracilis (Leisey)								
UF 67081	279	65.7	–	23.7	26.0	54.4	50.2	87
UF 82652	274	63.8	–	20.5	23.4	53.5	53.3	67
(Inglis IA)								
UF 18112	–	67.4	38.0	31.7	28.4	–	–	111
S. populator								
(Arredondo)								
UF 2562	334	86.0	–	30.5	28.0	71.5	66.5	–
(Rancho La Brea)								
OR (N=10)	317-408	82.7-108.8	–	30.1-40.5	26.8-35.4	65.2-90.2	63.9-80.3	155
Tibia								
S. gracilis (Leisey)								
UF 81731	226	56.6	57.3	20.8	24.2	40.5	28.0	
UF 81732	–	54.2	56.0	–	–	–	–	
(Haile XVA)								
UF 17496	–	–	–	22.6	20.2	41.9e	29.5	
(McLeod)								
F:AM 95529	–	–	–	20.8	33.0	44.3	32.8	
S. populator								
(Arredondo)								
UF 2562	252	77.4	–	24.5	–	51.7	–	
(Rancho La Brea)								
OR (N=10)	239-305	72.5-90.4	–	25.1-33.0	–	45.0-63.3	–	
Fibula								
S. gracilis (Leisey)								
UF 67088	–	–	–	–	–	21.5	13.4	
S. populator								
(Rancho La Brea)								
OR (N=10)	212.7-265.0	32.5-45.9	–	9.4-15.3	9.2-11.9	–	17.2-26.8	

[1] Calculations based on Shaw and Tejada-Flores (1985: Table 2).

Table 17. Measurements of metacarpal II, III, and IV of *Smilodon*.

	Length	Prox. Width	Prox. Depth	Shaft Width	Shaft Depth	Distal Width	Distal Depth
Metacarpal II							
S. gracilis (Leisey)							
UF 86752	67.5	18.7	18.8	10.7	10.8	16.2	15.6
(Haile XVA)	74.9	18.8	22.0	13.3	13.0	21.0	18.2
(Inglis IA)	75.0	18.8	22.3	12.0	11.4	17.9	17.2
(Port Kennedy)	70.9	15.9-	19.5-	11.9	11.8	18.7	13.0
OR		17.5(2)	22.9(2)				
Metacarpal III							
S. gracilis (Leisey)							
UF 87269	82.2	18.6	–	–	–	–	–
(Port Kennedy)	–	20.9	18.9	10.6	10.1	17.5	15.4
	–	–	20.6	–	–	–	–
S. populator							
(Reddick)							
UF 2537	100.0	26.0	24.6	17.4	–	25.6	–
(Rancho La Brea)							
OR (N=77)	83.0-	24.2-	22.8-	14.5-	–	22.4-	–
	110.0	30.7	29.2	20.0		29.4	
Metacarpal IV							
S. gracilis (Leisey)							
UF 86747	71.2	14.7	15.4	9.5	10.9	14.8	15.6
(Inglis IA)	77.5	16.7	19.4	10.7	10.2	16.8	16.8
(McLeod)	83.7	19.4	20.6	11.8	–	20.1	18.0
S. populator							
(Reddick)							
UF 2537	93.0	23.2	23.8	14.0	–	22.4	–
(Rancho La Brea)							
OR (N=733)	79.0-	18.9-	20.6-	12.3-	–	19.6-	–
	107.0	26.6	27.4	16.0		24.6	

The tibia of this species at Leisey is complete. The proximal end differs from that of *S. populator* in the sharper projection of the posterior border of the lateral condyle (Fig. 9B). In posterior view, the distal end exhibits a stepped posterior margin with well developed grooves for Mm. flexor hallucis longus, flexor digitorum longus, and tibialis caudalis.

Table 18. Measurements of metatarsal IV and V of *Smilodon*.

	Length	Prox. Width	Prox. Depth	Shaft Width	Shaft Depth	Distal Width	Distal Depth
Metatarsal IV							
S. gracilis (Leisey)							
UF 81712	88.2	15.8	19.9	10.3	12.0	15.1	14.2
UF 87273	88.4	15.0	19.1	9.5	11.0	14.7	15.3
(Inglis IA)	89.5	17.6	21.8	11.2	12.3	16.3	15.5
(McLeod)	91.6	20.3	24.7	11.6-13.4(2)	12.5-14.5(2)	17.9-18.0(2)	16.0-16.8(2)
S. populator (Reddick)							
UF 2537 (Arredondo)	101.0	–	28.0	15.6	–	21.5	–
UF 2562 (Rancho La Brea)	96.0	–	26.3	14.1	–	20.2	–
OR (N=748)	84.0-114.0	16.1-19.9	25.8-17.0	13.0-25.2	–	18.5 25.2	– –
Metatarsal V							
S. gracilis (Leisey)							
UF 81709	77.4	15.6	15.2	8.1	8.5	8.5	13.0
(McLeod)	79.4	23.7	18.5	9.9	11.7	15.0	15.9
S. populator (Arredondo)							
UF 2562 (Rancho La Brea)	78.0	–	24.5	12.1	–	17.1	–
OR (N=722)	71.0-95.0	–	24.5-28.6	10.5-13.8	–	17.1 21.6	–

The fibula, previously unknown for this species is similar to that of *S. populator* but smaller (Table 16). It differs from that of *P. onca* in having a less prominent projection of the lateral malleolus.

The metatarsals, like the metacarpals, are relatively short relative to total limb lengths (Tables 17, 18). The metatarsals are longer and more slenderly proportioned than the metacarpals, as was previously noted for this species (Berta 1987). Metacarpal II differs from Inglis 1A and Haile 15A specimens in lacking a prominent projection of the facet for the trapezium above the articular surface;

however, it shows a *Smilodon*-like sharp depression in this surface. *Panthera onca* differs in having a more gently concave articular surface.

Comparison of limb lengths of *S. gracilis* from Leisey indicate that this sample was intermediate in size between Inglis 1A and McLeod/Port Kennedy samples (Tables 14-18). The limbs of *S. gracilis* and *S. populator* were similarly proportioned (Table 19) and support the interpretation of *Smilodon* as a short limbed, robust machairodont with especially powerful forelimbs. Body mass calculations (see Shaw and Tejada-Flores 1985) indicate that *S. gracilis* averaged one-third smaller than *S. populator*.

Discussion.– *Smilodon gracilis* is by far the most abundantly represented carnivore at Leisey. In addition, the Leisey sample is the largest and best known record of the gracile sabercat.

Cope's (1880, 1895, 1899) original description of *S. gracilis* was based on fragmentary material from Port Kennedy Cave (middle Irvingtonian fide Lundelius et al. 1987). This species is much better represented from Florida faunas and has been documented from the late Blancan Haile 15A, Santa Fe River 1A, Bass Point Waterway and El Jobean faunas, and the Irvingtonian Inglis 1A and McLeod faunas (Berta 1987; Churcher 1984). The Leisey and Haile 21A occurrences now can be added to these Irvingtonian records.

The gracile sabercat from Leisey shows several characters not seen in the very early Irvingtonian Inglis 1A sample--larger size, typically a single-rooted p3, and reduced p3. The later Irvingtonian occurrences of *S. gracilis* from Port Kennedy Cave and McLeod show most significantly further increase in size. Based on the preceding discussion, the stage of evolution of *S. gracilis* at Leisey is intermediate between that of Inglis 1A and Port Kennedy/McLeod specimens, and supports a late early Irvingtonian age for the Leisey fauna.

Homotherium sp.

Referred Specimens.– **Leisey 1**: UF 95764, right I2. **Leisey 1A**: UF 81738, deciduous incisor; 81733, left m1; 84841, distal right humerus; 63662, left femur.

Discussion.– Machairodont cats are in need of revision. Because of the uncertainty regarding machairodont taxonomy (e.g., see Berta and Galiano 1983), formal diagnosis of these few specimens from Leisey must await description of a larger, better preserved sample (skull and skeleton) of this same cat from Haile 21A.

The deciduous incisor has a compressed crown and a single basal cuspule erupted on the lingual tooth margin. Serrations are present along the mesial and

Table 19. Limb proportions in *Smilodon* (based on mean values for lengths of limb elements in mm).

	S. gracilis	*S. populator*[1]
Humerus	244.5(8)	344.9(10)
Radius	194.0(3)	265.7(10)
Metacarpal II	72.1(4)	90.1(676)
Femur	276.5(2)	367.7(10)
Tibia	226.0	273.6(10)
Metatarsal II	89.4(4)	99.0(766)
Humerus X 100/H+R+Mtc	47.9	49.2
Radius X 100/H+R+Mtc	38.0	37.9
Mtc X 100/H+R+Mtc	14.1	12.8
Femur X 100/F+T+Mtt	46.7	49.7
Tibia X 100/F+T+Mtt	38.2	37.0
Mt X 100/F+T+Mtt	15.1	13.4

[1] Measurements following Merriam and Stock (1932)

distal margins. The tip of the crown and serrations on the distal side are worn away. The root is partially formed and the apical root foramen is open. This specimen indicates the presence of a very young juvenile at Leisey. Comparisons with juvenile *Dinobastis* from Friesenhahn Cave described by Rawn-Schatzinger (1983) suggests that this individual represents Stage II of the eruption sequence.

An isolated I2 referred to this genus compares favorably in size and morphology with the Haile 21A specimen (Table 20). Prominent basal cusps with serrated medial and lateral margins are positioned on either side of the central cusp.

The lower carnassial, larger than Reddick 1A or Friesenhahn machairodonts, compares best with the Haile 21A homothere. The tooth enamel is crenulate, and coarse serrations are present along the sides of the paraconid and protoconid blades (Fig. 10B).

Referral of a distal humerus to this genus is suggested by its similarity to the Haile 21A machairodont and is distinct from *Smilodon*, the only other large felid represented at Leisey. This element differs from *Smilodon* in being larger and more robust. In addition, the shaft at the level of the entepicondylar foramen is broader and flatter mediolaterally, the supracondylar ridge is not as strongly developed, and the distal end is narrower posteromedially (Table 21).

A femur also referred to *Homotherium* from Leisey, although considerably smaller, agrees well with the Haile 21A homothere. It differs from *Smilodon* in numerous features, including lack of a prominent tuberosity between the head and

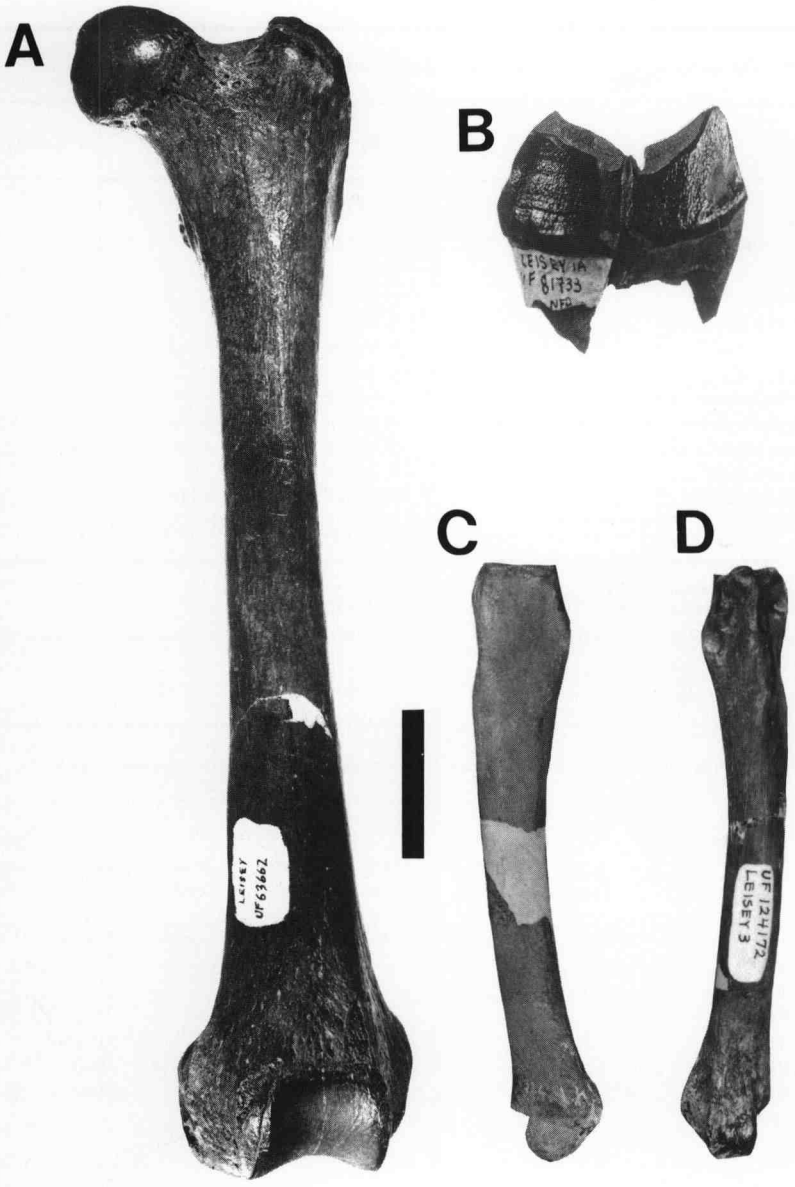

Figure 10. *Homotherium* and *Miracinonyx* from the Leisey Shell Pits. (A-B) *Homotherium* sp., (C-D) *Miracinonyx inexpectatus*. (A) UF 63662, left femur in anterior view; (B) UF 81733, left m1 in lateral view; (C) anterior and (D) posterior views of UF 124172, right metatarsal II. Scale bar 35 mm in length for A, 20 mm for B, and 30 mm for C-D.

Table 20. Comparative measurements of teeth of *Homotherium* sp. and related felids.

	Length	Width	Lpcd	Lpad
I2				
Homotherium sp.				
Leisey	13.6	12.6	–	–
Dinobastis serus				
Friesenhahn[1]	–	11.5-12.0	–	–
m1				
Homotherium sp.				
Leisey	33.9	14.4	16.7e	12.4
Haile 21A	34.1	15.7	15.2	13.5
Dinobastis serus				
Reddick 1A[2]	28.5	11.1	15.0	–
Friesenhahn	25.6-30.6	10.2-12.8	13.6-15.4	–

[1] Measurements follow Meade (1961).
[2] Measurements follow Waldrop (1974), Lpcd=length of protoconid, Lpad=length of paraconid.

Table 21. Comparative measurements of humeri and femora of *Homotherium* sp. and related felids.

	Length	Prox. Width	Prox. Depth	Shaft Width	Shaft Depth	Distal Width	Least Distal Depth
Humerus							
Homotherium sp.							
Leisey		–	–	–	–	75.0	28.5
Haile 21A	361	82	106	–	–	105.0	–
Inglis 1A	302e	–	91	–	–	84.0	–
Dinobastis serus Friesenhahn (OR, N = 4)	340-358	72-76	92-104	–	–	83-84	30-31
Femur							
Homotherium sp.							
Leisey	318	79.0	–	28.4	26.0	64.5	65.5
Haile 21A	381	104.0	–	–	–	83.0	–
Dinobastis serus Friesenhahn (OR, N = 5)	338-353	89.2-95.7	41.0-42.8	30.0-31.3	27.3-28.8		

greater trochanter; lesser trochanter more medial in position; intertrochanteric fossa larger anteroposteriorly, forming a broad shelf that extends from the lesser trochanter to the fossa; and finally, distal condyles situated closer together (Fig. 10A).

Prior to this record, *Homotherium* was reported from Florida and for the first time from eastern North America from the early Irvingtonian Inglis 1A site (Webb 1974a) and from the Rancholabrean Reddick 1A site (Waldrop 1974). Identity of the Reddick 1A machairodont, of which more material is now available, as *Homotherium* rather than *Dinobastis* is questioned here and must await further systematic study. In any case, although comparable elements are not available for the Leisey sample in size and morphology, this same machairodont from Haile 21A can be readily distinguished from the Reddick 1A cat in having longer upper canines and P4 with a distinct protocone supported by a root.

Miracinonyx inexpectatus (Cope 1895)

Referred Specimen.– Leisey 3: UF 124172, right metatarsal II.

Discussion.– The late Blancan and Irvingtonian cheetah-like cat *Miracinonyx inexpectatus* only very recently has been reported from Florida by Van Valkenburgh et al. (1990), who identified a mandible, metatarsal IV, and several additional unspecified postcranial elements from Inglis 1A. The Inglis sample also includes a metatarsal II (UF 45471) that compares very closely in size and morphological features with the metatarsal II from Leisey (Fig. 10C-D). Both the Leisey and Inglis metatarsals are referred to *M. inexpectatus* based on their large size and striking elongation. Measurements of the Leisey specimen are very similar to those of a metatarsal II of *M. inexpectatus* (Table 22) from the middle Irvingtonian Hamilton Cave, West Virginia (Van Valkenburgh et al. 1990).

Table 22. Measurements of the metatarsal II of *Miracinonyx inexpectatus* from Leisey Shell Pit, Inglis 1A, and Hamilton Cave. Abbreviations and measurements for Hamilton Cave specimen are from Van Valkenburgh et al. (1990).

	Leisey UF 124172	Inglis UF 45471	Hamilton Cave USNM 401092
Total length (L)	120.6	112.0	120.1
Proximal breadth (BP)	15.7	14.8	12.5
Proximal depth (APP)	23.0	22.8	22.3
Midshaft diameter (BS)	11.8	11.7	10.5
Distal breadth (BD)	17.8	17.6	18.4

Family PHOCIDAE Gray 1825
Monachus tropicalis (Gray 1850)

Referred Specimens.– Leisey 1A: UF 81734, right upper first postcanine tooth; 80499, p3.

Discussion.– The upper postcanine tooth agrees in detail with a specimen of the modern species *Monachus tropicalis* from a Florida archaeological site, (Malabar, South Indian Field, Brevard Co.). Measurements for UF 81734 are: greatest length, 11.75 mm, greatest width, 8.3 mm. A second tooth, a well worn and poorly preserved right p3 is tentatively referred to this species.

The only other well documented Florida Irvingtonian occurrence of this species is a fragmentary left mandible with m2 from Rigby Shell Pit (UF 36456).

SUMMARY

The Leisey carnivores are among the most diverse Florida Irvingtonian assemblages known, second only to the Coleman 2A fauna. Thirteen species represent a minimum number of 36 individuals. The largest, most complete sample of the sabercat *Smilodon gracilis* is from this locality and adds considerably to our knowledge of the species. The Leisey sample provides evidence for the gradual increase in size of *S. gracilis* during the Irvingtonian. Based on the stage of evolution of this species an age intermediate between Inglis 1A and McLeod is supported for the Leisey fauna. Another machairodont cat, *Homotherium*, less well known from Florida, is also recorded from this fauna. A large and a small wolf, *Canis armbrusteri* and *C. edwardii* respectively, as well as the tremarctine bear *Arctodus pristinus* are additional large carnivores represented at Leisey. *Canis edwardii*, the second most abundant carnivore, is represented by skeletal material as well as fragmentary maxillae and mandibles. In addition to the above mentioned large terrestrial carnivores, a single pinniped is recorded, the Caribbean Monk Seal *Monachus tropicalis*.

Among the small carnivores recorded from Leisey, the occurrence of the otter *Lutra canadensis* is significant as it represents the first Irvingtonian record from Florida of this species. Other small carnivores recorded include the fox *Urocyon cineroargenteus*, the raccoon *Procyon lotor*, the long-tailed weasel *Mustela frenata*, the spotted skunk *Spilogale putorius*, and the bobcat *Lynx rufus*.

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