

THE FOSSIL RECORD OF *ARCTODUS PRISTINUS* (URSIDAE: TREMARCTINAE) IN FLORIDA

Steven D. Emslie¹

ABSTRACT

Cranial and postcranial elements of at least eight individuals of *Arctodus pristinus* (Ursidae: Tremarctinae) are reported from Leisey Shell Pit, an early Irvingtonian vertebrate locality within a marine shell bed. Dental measurements indicate that two distinct sizes, presumably representing males and females, are recognizable in the collection. This bear tentatively is referred from 13 localities in Florida, ranging in age from late Blancan to late Irvingtonian, and is a biochronological indicator for this period. Another tremarctine bear, *Tremarctos floridanus*, so far is known only from Rancholabrean localities in Florida and may have ecologically replaced *A. pristinus*.

RESUMEN

Se reportan elementos craneales y post craneales pertenecientes a por lo menos ocho individuos de *Arctodus pristinus* (Ursidae: Tremarctinae) provenientes del depósito de conchuelas de Leisey, una localidad de vertebrados del Irvingtoniano temprano contenido en una capa de conchuelas marinas. Las mediciones dentales indican la presencia de dos diferentes tamaños, los cuales presumiblemente representan a machos y hembras en la colección. Este oso es tentativamente referido a 13 localidades en Florida, abarcando en edad desde el Blancano tardío hasta el Irvingtoniano tardío, siendo un indicador biocronológico de este período. Otro oso tremarctino, *Tremarctos floridanus*, es conocido hasta ahora sólo para localidades Rancholabreanas en Florida, pudiendo haber reemplazado ecológicamente a *A. pristinus*.

¹ The author is a Courtesy/Curator, Florida Museum of Natural History, University of Florida, P. O. Box 117800, Gainesville FL 32611-7800, U.S.A., and Assistant Professor in the Department Sciences, Western State College, Gunnison CO 81230, U.S.A.

INTRODUCTION

The short-faced bear *Arctodus pristinus* was described by Leidy (1854, 1859) based on a single left m2 from the Ashley River beds, South Carolina. Since that time, although the type specimen apparently was lost, additional material has been reported from Pennsylvania, Maryland, West Virginia, Florida, and Mexico (Kurtén 1967; Kurtén and Anderson 1980; Dalquest and Mooser 1980). All specimens of known age date to the late Blancan through Irvingtonian.

In 1983, shell mining operators at Leisey Shell Pit, Hillsborough County, Florida, uncovered a rich deposit of terrestrial vertebrates within the marine shell beds. The bone layer, designated Leisey Shell Pit 1A, was excavated for over a year by amateur paleontologists and personnel from the Florida Museum of Natural History (FLMNH), Gainesville. Based on associated invertebrate and vertebrate faunas, reversed paleomagnetism and strontium stratigraphy, the deposit is dated to the late early Irvingtonian (Hulbert and Morgan 1989; Webb et al. 1989). Vertebrate remains at the site include cranial and postcranial bones of at least five individuals of *Arctodus pristinus*. These remains are described here; other carnivores from Leisey 1A are reported by Berta (this volume). One bone of *A. pristinus* from Leisey 1B, located stratigraphically below Leisey 1A, two bones from Leisey 1 (from either Leisey 1A or B), and one bone from Leisey 3, located 0.5 km west of Leisey 1A, also are reported. As with Leisey 1A, Leisey 1B and 3 are located within the Bermont Formation and date to the late early Irvingtonian.

ACKNOWLEDGEMENTS

I thank the following people for their assistance with fossil and Recent skeletal material at museums: Phil Angle, Larry Barnes, Sam McLeod, Clayton E. Ray, Charles Smart, and Richard Tedford. Gary S. Morgan provided information on unreported fossil records of *Arctodus* in Florida, and Clayton E. Ray generously provided unpublished information on tremarctine bears. Richard Tedford and Ray commented on an earlier draft of the paper; Morgan and Richard C. Hulbert, Jr., also provided helpful comments and suggestions. Mary Ellen Ahearn provided the photographs.

I also thank the amateur paleontologists of Florida through whose efforts much of the material from Leisey Shell Pit was preserved for scientific study. Those deserving particular recognition are Ralph "Tony" Estevez, Mickey Fowler, Frank A. Garcia, and Eric Hunter. Finally, C. E. "Bud" Leisey, Jr., generously arranged mining operations at Leisey Shell Pit so that vertebrate fossils could be excavated.

METHODS

Fossil specimens of *Arctodus pristinus*, *A. simus*, and *Tremarctos floridanus* were examined at the Florida Museum of Natural History (UF); the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D. C.; the American Museum of Natural History (AMNH, FAM), New York; the Academy of Natural Sciences (ANSP), Philadelphia; the Natural History Museum of Los Angeles County (LACM); and the University of California Museum of Paleontology (UCMP), Berkeley. Skeletons of *T. ornatus* also were examined at USNM and AMNH. All measurements were taken with vernier and anthropometric calipers. Dental measurements used in this study are self-descriptive; length and width were taken at the base of the enamel of each tooth. Trigonid length of the m1 was taken from the posterior edge of the extra cusp at the lateral border of the trigonid and talonid to the anterior base of the paraconid.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich 1821

Family URSIDAE Gray 1825

Subfamily TREMARCTINAE

Arctodus Leidy 1854

Arctodus pristinus Leidy 1854

Referred Material.— **Leisey 1:** left femur lacking proximal end, UF 129077; left tibia lacking proximal end, UF 129078; left mandible with c1, p2-3, m1 (partial), and m2, Royal Ontario Museum (ROM) 31462. **Leisey 1A:** left I3, UF 81697; right premaxilla with I2, UF 81695; left premaxilla with I1-2, UF 81696; right P4, UF 81739; left P4, UF 81740; two right M1's, UF 81698-81699; right M2, UF 67089; left M2, UF 81741; right i3, UF 87298; right mandible with c1, p4-m2, UF 81693; right mandible with p4-m3, UF 64300; left mandible with c1, p4-m2, UF 81692; left mandible with c1, m1-m3, and right mandible with m1-m3 UF 81694; right metacarpal III, UF 116092. **Leisey 1B:** left humerus lacking proximal end, UF 95882. **Leisey 3:** distal left radius, UF 129079; left metacarpal II, UF 142232. Collectively these specimens represent a minimum of eight individuals.

Description.— Dental and mandibular measurements of this material are provided in Tables 1-2. These specimens display the typical features of Tremarctinae: the presence of an extra lateral cusp on the m1 between the trigonid and talonid, a premasseteric fossa on the mandible (Kurtén and Anderson 1980), and an entepicondylar foramen on the humerus. Characters that most readily distinguish *Arctodus pristinus* from *A. simus* include generally smaller size, relatively narrower cheek teeth, and less crowded anterior lower premolars. Although there is considerable variation in body size in these bears, it is possible to distinguish the two species by measurements and proportions of the teeth (Kurtén 1967).

Many characters of the teeth in *Arctodus pristinus* are identical to *A. simus*, as described by Merriam and Stock (1925). The fossil species "*Ursus (Arctodus) haplodon*," described by Cope (1896) based on material from Port Kennedy Cave, Pennsylvania, now is referred to *A. pristinus* (Kurtén 1967). Cope based his description solely on the m2, however, and did not describe this material in detail. Gidley and Gazin (1938) later referred these specimens to *Arctodus "haplodon*," again limiting their comparisons primarily to the m2. Although Kurtén (1967) completed a thorough quantitative analysis of the dentition of *Arctodus*, including *A. pristinus* from Port Kennedy Cave, the teeth of this species have yet to be described. Description of the dentition of *A. pristinus* from Leisey 1A is presented here. A more detailed comparison and description of this bear from all fossil localities in Florida is beyond the scope of this paper.

The I1-2 (UF 81695-81696) of *Arctodus pristinus* are nearly equal in size and the I3 (UF 81697) is significantly larger. The first two upper incisors are not shovel-shaped, as are the lower incisors, and form a triangular occlusal surface with the anterior edge only slightly higher-crowned than the posterior edge. A shallow groove extends from the base to the crown on the anterior surface, slightly lateral to the midline. The root of I3 is approximately 25% longer than the roots of the first two incisors, and the crown curves laterally. Small wear facets occur near the base of the enamel on the medial surface, where it contacts I2, and on the lateral surface where it is met by c1 during occlusion.

The P4 (UF 81739, 81740) has a shearing surface formed on the medial face of the protocone and metacone. The paracone is small, its unworn crown not extending higher than the trench dividing the paracone and metacone. This tooth has three roots, but those below the metacone and protocone are fused.

The M1 (UF 81698-81699; Fig. 1A and B) has four distinct cusps forming the internal border in the unworn state. With moderate wear, the posterior two of these cusps form a single ridge. The occlusal surface between the equally prominent paracone and metacone and the internal border is crenulated and has a row of three distinct tubercles. The middle tubercle is the largest; the anterior and posterior tubercles connect to the paracone and metacone respectively by small ridges. The antero-internal corner of the tooth has a distinct cingulum giving this area a square shape. Small wear facets occur on the anterior side below the paracone, where it contacts the P4, and on the posterior side where it contacts the M2.

The M2 (UF 81741, 67089; Fig. 1C and D) has a prominent paracone and slightly less prominent metacone. The breadth at the metacone can be equal to or slightly less than the breadth at the paracone. Posterior to the metacone, the tooth tapers significantly. The occlusal surface is greatly crenulated and a small cingulum occurs on the antero-internal corner of the tooth. A small wear facet is present on the anterior side where it abuts the M1. This tooth was found to be highly variable in modern *Tremarctos ornatus*. In the Leisey specimens, variations are apparent as well: UF 81741 has a relatively longer "heel" and the tooth tapers more abruptly than in UF 67089.

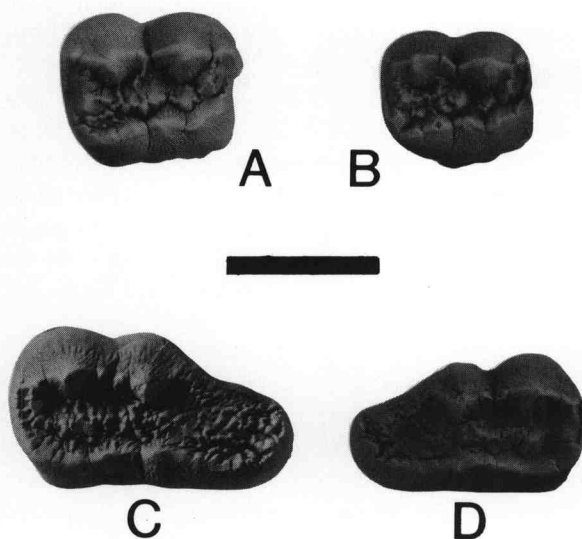


Figure 1. Upper cheek teeth of *Arctodus pristinus* from Leisey Shell Pit 1A showing specimens probably from males (left) and females (right). (A) UF 81698, RM1; (B) UF 81699, RM1; (C) UF 81741, LM2; (D) UF 67089, RM2. Scale 1X, Bar=2 cm.

The i3 (UF 87298) is distinctly shovel-shaped and has a prominent lateral flange. The canine (UF 81692-816933; Fig. 2) is heavily rooted and broadest at the base of the enamel. A distinct ridge extends from the apex of the crown to the base on the antero-internal border, and a shorter and less distinct ridge is found at the postero-internal border.

The p4 (UF 64300, 81692-81693; Figs. 2-3) is robust, with a single prominent cusp. In the unworn condition, this cusp is much lower than the apex of the unworn paraconid of m1. The posterior side contacts the base of the m1. This tooth has two fused roots.

The m1 (UF 64300, 81692-81694; Figs. 2-3) has a high paraconid and protoconid that form a weak, lateral shearing surface. With moderate wear, the shearing surface is lost and the paraconid and protoconid wear flat. The trigonid is divided from the talonid by a prominent metaconid medially, and a small extra cusp laterally that is lost with moderate wear. The talonid is expanded laterally forming a large crushing platform with the trigonid of m2.

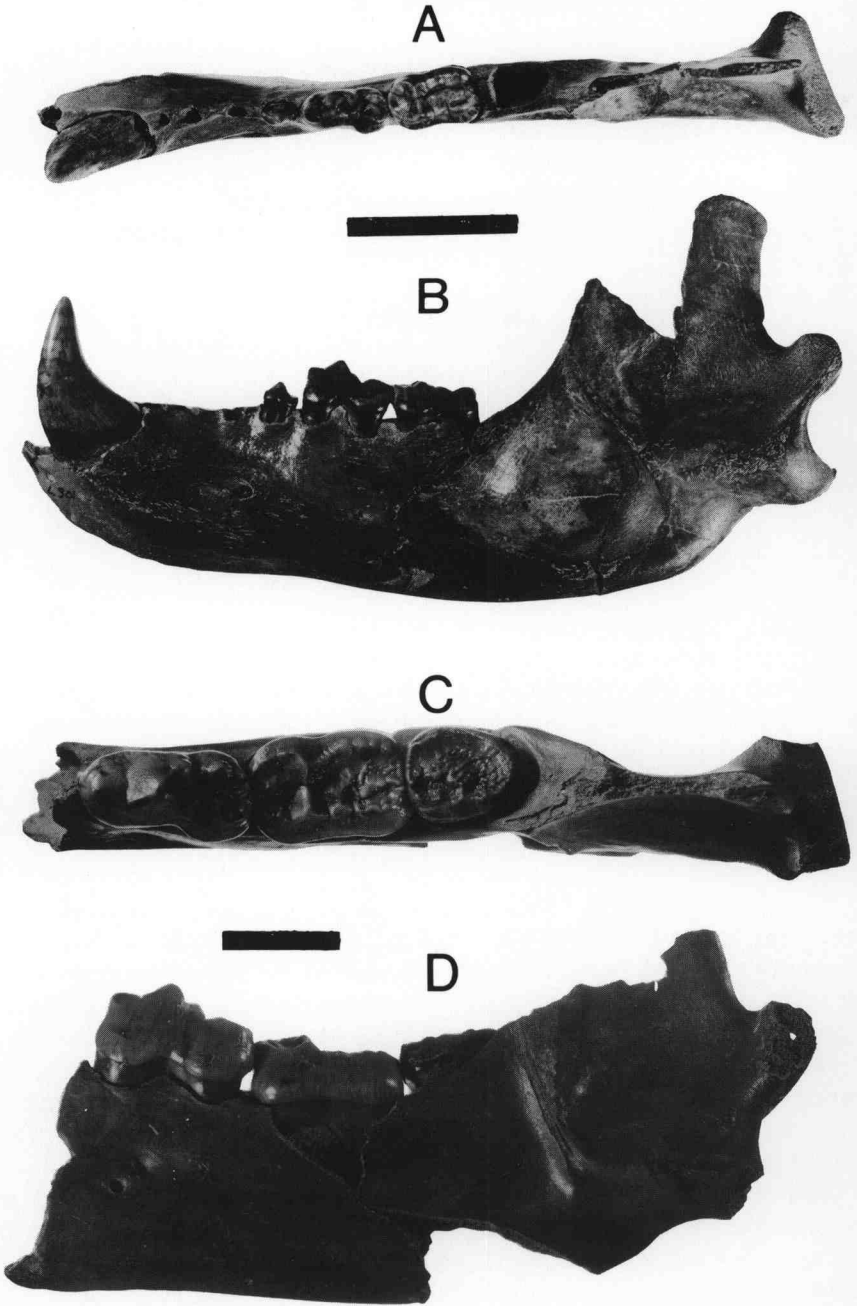


Figure 2. Left mandible, UF 81692, in occlusal (A) and lateral views (B) and left mandible, UF 81694, in occlusal (C) and lateral views (D) of *Arctodus pristinus* from Leisey Shell Pit 1A. Scale at top .44X, bar=5 cm; bottom .75X, bar=2 cm.

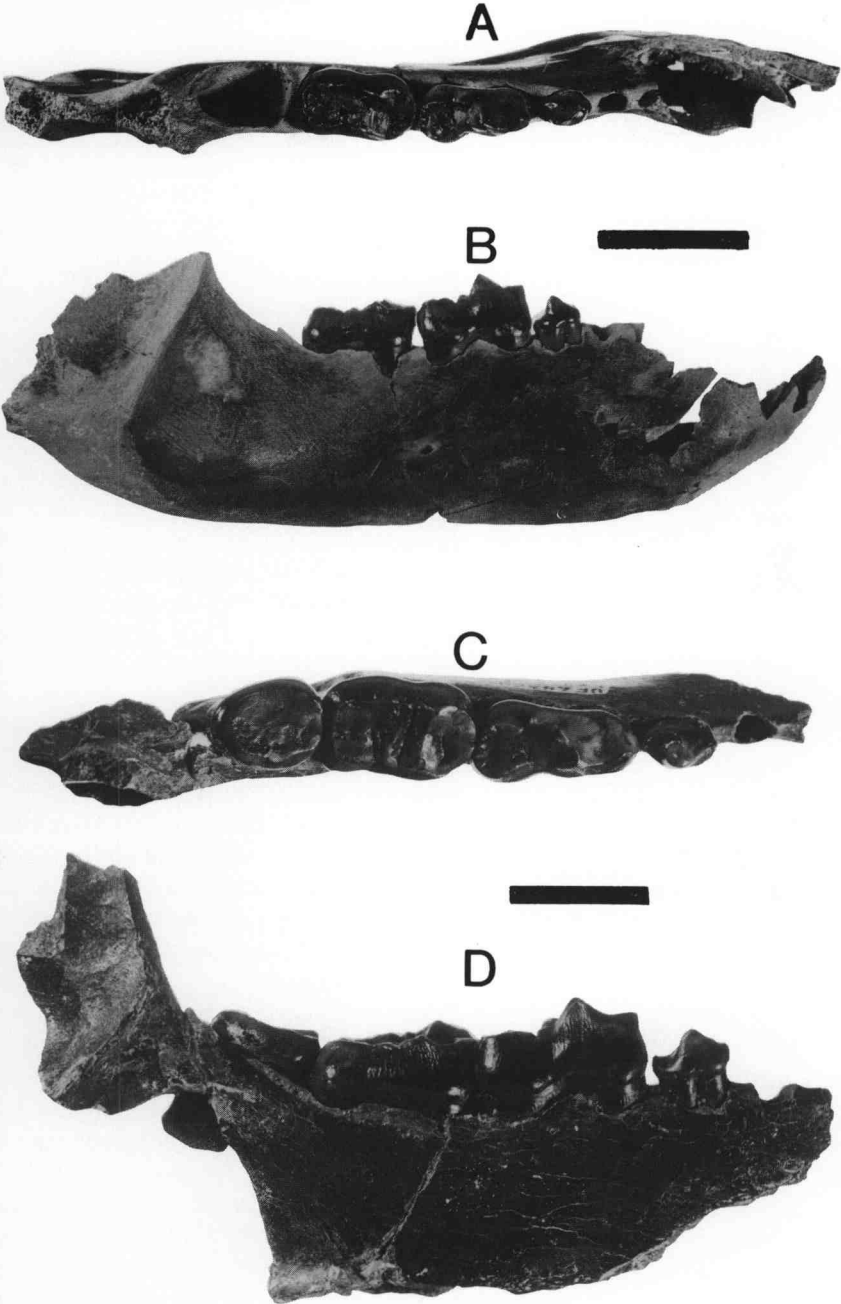


Figure 3. Right mandible, UF 81693, in occlusal (A) and lateral (B) views and right mandible, UF 64300 in occlusal (C) and lateral (D) views of *Arctodus pristinus* from Leisey Shell Pit 1A. Scale at top .62X, bar=3 cm; bottom .9X, bar=2 cm.

Table 1. Dental measurements (mm) of *Arctodus pristinus* from Leisey Shell Pit 1A.

Specimen	Length	Greatest width	Anterior width	Central width
P4 UF 81739	17.5	13.2		
UF 81740	20.5	16.0		
M1 UF 81698	25.1	21.8		
UF 81699	20.6	17.7		
M2 UF 67089	33.0		19.6	17.7
UF 81741	39.0		22.5	20.7

The m2 (UF 64300, 81692-81694; Figs. 2-3) is usually broader anteriorly but the shape of this tooth is variable, and it can be equally broad or broader posteriorly (see also Cope 1896 and Kurtén 1967). The most prominent cusp is the metaconid which is connected transversely with the protoconid by a distinct, trenchant ridge. This ridge divides the short, basin-shaped trigonid from the long talonid. Two oblique tubercles occur in the talonid and are lost with moderate wear; the anterior tubercle is connected to the lingual border of the crown by a small ridge.

The m3 (UF 64300, 81694; Figs. 2-3) also varies in shape but is usually broadest anteriorly and tapers posteriorly giving the tooth an oval shape. The protoconid is the most prominent cusp, and the occlusal surface is crenulated.

The nearly complete mandible (UF 81692; Fig. 2A and B), has alveoli for i1-3 that are considerably crowded so that i2 has been pushed posterior to i1 and i3. The anterior premolars, however, are well-spaced with the greatest diastema occurring between p2 and p3. The premasseteric fossa is moderately developed. The condyloid process, viewed laterally, is located high above the occlusal surfaces of the cheek teeth, and a prominent and robust angular process extends only slightly posterior to the posterior border of the condyloid process. A large mental foramen occurs at the midline of the ramus, below the anterior root of p4. The cheek teeth are fully erupted and have light wear.

The paired mandibles, UF 81694 (Fig. 2C and D), are from the largest individual represented in the sample. The cheek teeth have light to moderate wear, and the premasseteric fossa is weakly developed. This fossa seems to form with age; it was observed to be poorly developed in subadults of the living spectacled bear, *Tremarctos ornatus*, but completely developed in adults. The condyloid process, viewed laterally, is only slightly higher than the occlusal surfaces of the cheek teeth, and the angular process is missing.

The right mandible (UF 81693, Fig. 3A and B) and left mandible (ROM 31462) are from young individuals. The cheek teeth are fully erupted with light

Table 2. Mandibular measurements (mm) of *Arctodus pristinus* from Leisey Shell Pit 1A. Depth at diastema is taken between p2 and p3.

Specimen	Length c1-m3	Depth at diastema	Length	Width	Ant. Width	Post. Width	Trig. Length
UF 81693	123.3	43.6					
p4			10.7	6.8			
m1			24.8		10.5	13.0	16.5
m2			23.5		15.2	15.1	
UF 64300							
p4			11.3	6.8			
m1			25.0		10.6	13.1	16.0
m2			22.6		15.5	15.0	
m3			16.1	13.5			
UF 81692	149.5	48.8	241.0				
c1				17.5			
p4			11.1	7.3			
m1			27.0		11.4	14.3	18.0
m2			26.5		17.5	17.7	
UF 81694							
c1				17.3			
m1			29.5		13.2	16.0	20.5
m2			28.0		18.7	19.0	
m3			21.5	16.4			

wear, and the premasseteric fossae are weakly developed. The canines are unworn, and the root is incompletely ossified and fragmented in UF 81693. The coronoid and angular processes are missing in both specimens.

The right mandible (UF 64300, Fig. 3C and D) is from a small adult, and the cheek teeth have moderate wear. The premasseteric fossa is mostly missing but appears to be weakly developed.

Quantitatively, the teeth of *Arctodus pristinus* from Leisey 1A fall into two size classes presumably representing males and females (see Fig. 1 and Tables 1-2). Unfortunately, the sample size from Leisey 1A is too small to be meaningful, or to illustrate graphically. UF 81698, 81740-81741, 81692, and 81694 are from large individuals or males; UF 81699, 67089, 81739 and 64300 are from small

individuals or females. All measurements fall within the size range, or smaller, than measurements of *A. pristinus* given by Kurtén (1967).

DISCUSSION

Arctodus pristinus is now known from 13 localities in Florida (Fig. 4). Because material from most of these localities has not been reported or described, identification remains tentative. The material ranges in age from late Blancan and early Irvingtonian (Sante Fe River 1, Webb 1974; Kissimmee River, Morgan and Hulbert this volume; Inglis 1A, Klein 1971; Speaker Carr 1981) to latest Irvingtonian (Coleman 2A; Ritchie 1980). The species is incorrectly reported from the Waccasassa River (Rancholabrean) by Webb (1974) and Kurtén and Anderson (1980); the material is actually *Tremarctos floridanus*. These records indicate that *A. pristinus* is restricted to late Pliocene to middle Pleistocene localities in Florida and is a biochronological indicator for the late Blancan through Irvingtonian.

A single left M2 (UF 10700) from Sante Fe River 1, Gilchrist County, and a left I3 (UF 51248) from Kissimmee River, Okeechobee County, are so far the earliest records of *Arctodus* from Florida. These localities all date to the late Blancan (Morgan and Hulbert this volume). UF 10700 is similar in most features to UF 67089 and 81741 from Leisey 1A, and given the amount of morphologic variation that is apparent in this tooth (see above), it probably represents *A. pristinus*. UF 51248 is nearly identical to a left I3 (UF 81697) from Leisey 1A.

A nearly complete left mandible with c1 and m1-3 (cast of specimen, UF 40089) from Rigby Shell Pit, Sarasota County, is very similar to UF 81692 in size, and in spacing of alveoli for anterior premolars and incisors. A partial right M1 (UF 124534), a right i3 (UF 60852), and fragmentary shafts of an ulna (UF 40092) and a radius (UF 40093) also are known from this site. A partial palate with left I2, right and left C1, and right and left P4-M2 (UF 136072) was collected at Bass Point Waterway in North Port, Sarasota County. This specimen compares well with UF 81739, 81699, and 67089 but is slightly larger in size. A fragmentary right premaxilla (UF 19403) from Port Charlotte, Charlotte County, also is from a large individual. A proximal left metatarsal V (UF 17331) is known from Crystal River Power Plant, Citrus County. Material from McLeod Limerock Mine, Levy County, includes a right maxilla with P4-M2 (FAM 117477), a right m2 (FAM 117478), a left M2, a left m3, 5 incisors, and a fragment of a canine (FAM uncat.), all of which compare well with the material from Leisey 1A. Only a single right m1 (UF 124536) is known from Apollo Beach, Hillsborough County, and it is similar in size and characters to UF 81692 from Leisey 1A.

Florida records reported by Kurtén and Anderson (1980) include Coleman 2A, Sumter County, and Sebastian Canal, Brevard County. Only a single isolated tooth is known from each of these localities: a left M1 (UF 12363) from the

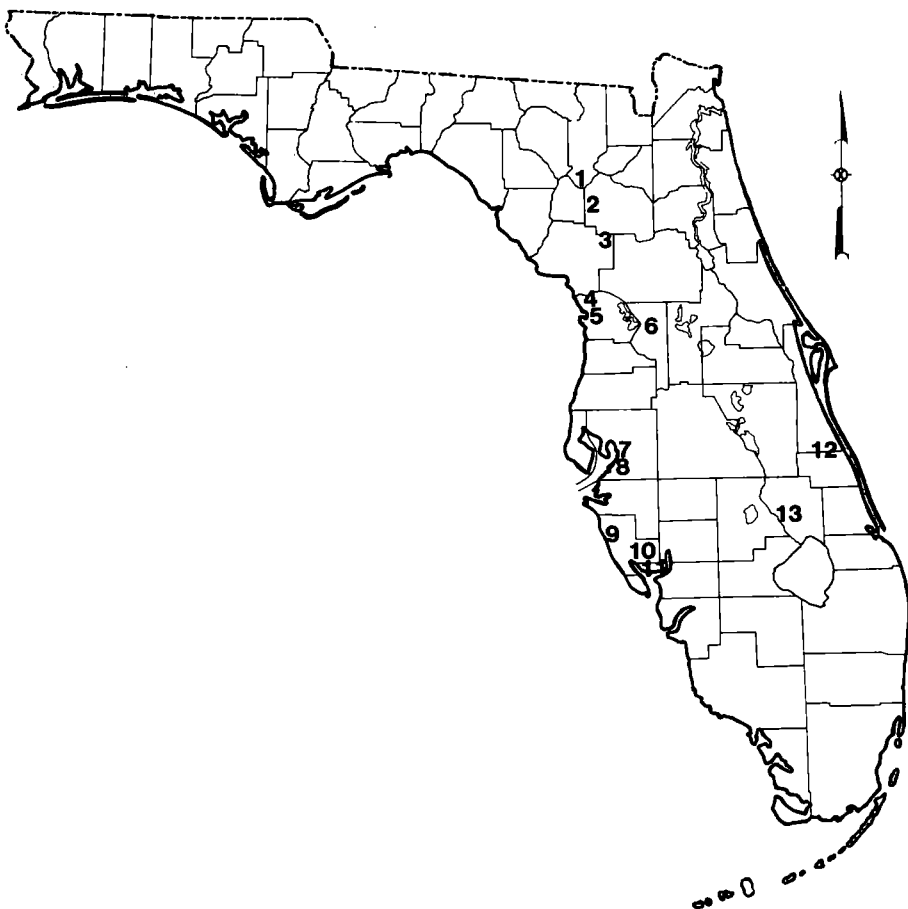


Figure 4. Vertebrate localities in Florida from which remains of *Arctodus pristinus* have been identified. (1) Sante Fe River 1, Gilchrist County; (2) Haile 16A, Alachua County; (3) McLeod Limerock Mine, Levy County; (4) Inglis 1A, Citrus County; (5) Crystal River, Citrus County; (6) Coleman 2A, Sumter County; (7) Apollo Beach, Hillsborough County; (8) Leisey Shell Pit, Hillsborough County; (9) Rigby Shell Pit, Sarasota County; (10) Bass Point Waterway, Sarasota County; (11) Port Charlotte, Charlotte County; (12) Sebastian Canal, Brevard County; (13) Kissimmee River, Okeechobee County.

former, and a right m2 (UF 19402) from the latter. These specimens are nearly identical in size and characters to UF 81698 and 81694, respectively, from Leisey 1A and consequently may represent male individuals. Other material from Florida is more extensive and includes 17 cranial and 106 postcranial elements of at least 5 individuals from Haile 16A, Alachua County, and 4 cranial and 21 postcranial

bones of at least 2 individuals from Inglis 1A, Citrus County. The specimens from Inglis include a braincase and auditory region of the skull previously unknown for *Arctodus pristinus*.

By far the largest sample of dentition of *Arctodus pristinus* is from Port Kennedy Cave, Pennsylvania, which Cope (1896) estimated to represent at least 36 individuals. Kurtén (1967) completed a quantitative analysis of this material in comparison to *A. simus* and found that these species could be distinguished by measurements and proportions of the teeth, despite a large variation in body size. An examination of the Port Kennedy material indicated no major differences with that from Leisey 1A.

A crushed right mandible (USNM 8005) of *Arctodus pristinus* from Cumberland Cave, Maryland, lacks all teeth except a fragmentary i3, canine, and fragmentary m2. The alveoli of i1-2, with i3, are spaced similarly to those of UF 81692. Morphological features of the canine and m2 are identical to the Leisey material. A left maxilla with M1-2, formerly at Princeton (PU 18794) and now at Yale, was not examined. A complete right and left tibia (USNM 8180), apparently from one individual, also are known from this cave.

A right mandible of *Arctodus pristinus* from Aguascalientes, Mexico, was not available for comparison but is discussed by Dalquest and Mooser (1980). This specimen has all teeth except the p1-3 and p4; dental measurements provided by these authors are compatible with Kurtén's (1967) measurements for this species. The mental foramen is positioned slightly more rostral than in UF 81692, and the largest diastema is between p3 and p4 instead of p2 and p3. The depth of the ramus at this latter diastema is greater in the Mexican specimen (57 mm) than in UF 81692-81693 (Table 2). A crushed skull and jaws (FAM 98969) and fragmentary skeletal elements from the Irvingtonian locality at Stout's Ranch, Seward County, Kansas, may represent a large *A. pristinus* (R. Tedford pers. comm.). The specimen is similar in size to small individuals of *A. simus*, and has a relatively longer m1 (30.0 mm) compared to *A. pristinus* from Leisey 1A, but the lower premolars are well-spaced. If it does represent *A. pristinus*, it extends the geographic range of this species into the midwestern U. S.

CONCLUSIONS

Arctodus pristinus is now known from 13 late Pliocene and early Pleistocene localities in Florida. The sample from Leisey Shell Pit adds to the growing list of records, and to our understanding of this species. A closely related species, *Tremarctos floridanus*, also is well-known from Florida from at least 19 sites (it is incorrectly reported from Inglis 1A and Withlacoochee River 7A by Webb [1974] and Kurtén and Anderson [1980]). All known-age specimens date to the late Pleistocene (Rancholabrean) and do not coincide with the presence of *A. pristinus* within the state. It is possible that *T. floridanus* was an ecological replacement of

A. pristinus. Both species, as well as *A. simus* from western North America, were probably largely herbivorous (Kurtén 1966, 1967; Kurtén and Anderson 1980; Emslie and Czaplewski 1985), much like the extant spectacled bear, *T. ornatus*, in South America (Peyton 1980). *T. floridanus* is known, however, from early Irvingtonian and Blancan localities in western North America (Kurtén and Anderson 1980) and may yet be found in similar-aged sites in Florida.

Material of *Arctodus pristinus* in Florida exhibits not only sexual dimorphism, but also differences in morphologic features that probably represent temporal and geographic variation. Considerable sexual variation was observed in 16 skeletons of *T. ornatus* at USNM: males are usually larger and have a large sagittal crest, whereas females are smaller and have a reduced or no sagittal crest. In addition, the features of the dentition can be quite variable, particularly the M2. Study of these variations is needed prior to further systematic work with fossil tremarctines.

LITERATURE CITED

- Cope, E. D. 1896. New and little known Mammalia from the Port Kennedy bone deposit. *Proc. Acad. Nat. Sci. Philadelphia* 48:378-394.
- Dalquest, W. W., and O. Mooser. 1980. *Arctodus pristinus* Leidy in the Pleistocene of Aguascalientes, Mexico. *J. Mamm.* 61 (4):724-725.
- Emslie, S. D., and N. Czaplewski. 1985. A new record of giant short-faced bear *Arctodus simus* from western North America, with a re-evaluation of its paleobiology. *Contrib. Sci. Nat. Hist. Mus. Los Angeles Co.* 371:1-12.
- Gidley, J. W., and C. L. Gazin. 1938. The Pleistocene vertebrate fauna from Cumberland Cave, Maryland. *U. S. Natl. Mus. Bull.* 171:1-99.
- Hulbert, R. C., Jr., and G. S. Morgan. 1989. Stratigraphy, paleoecology, and vertebrate fauna of the Leisey Shell Pit Local Fauna, early Pleistocene (Irvingtonian) of southwestern Florida. *Pap. Florida Paleon.* 2:1-19.
- Klein, J. 1971. Fossil mammals from Inglis 1A, late Blancan of Citrus County, Florida. M. S. Thesis, Univ. Florida, Gainesville.
- Kurtén, B. 1966. Pleistocene bears of North America 1. Genus *Tremarctos*, spectacled bears. *Acta Zoologica Fennica* 115:1-120.
- _____. 1967. Pleistocene bears of North America 2. Genus *Arctodus*, short-faced bears. *Acta Zoologica Fennica* 117:1-60.
- _____, and E. Anderson. 1980. Pleistocene Mammals of North America. Columbia Univ. Press, New York.
- Leidy, J. 1854. Remarks on *Sus americanus* or *Harlanus americanus* and on other extinct mammals. *Proc. Acad. Nat. Sci. Philadelphia* 7:89-90.
- _____. 1859. Description of vertebrate fossils. Pp. 99-122 in F. S. Holmes, ed. *Post-Pleistocene Fossils of South-Carolina*. Russell and Jones, Charleston.
- Merriam, J. C., and C. Stock. 1925. Relationships and structure of the short-faced bear, *Arctotherium*, from the Pleistocene of California. *Carnegie Inst. Washington Publ.* No. 347:1-35.
- Peyton, B. 1980. Ecology, distribution, and food habits of spectacled bears, *Tremarctos ornatus*, in Peru. *J. Mamm.* 61:639-652.
- Ritchie, T. L. 1980. Two mid-Pleistocene avifaunas from Coleman, Florida. *Bull. Florida State Mus., Biol. Sci.* 26 (1):1-36.
- Speaker Carr, G. E. 1981. An early Pleistocene avifauna from Inglis, Florida. Ph.D. diss., Univ. Florida, Gainesville.
- Webb, S. D. 1974. Chronology of Florida Pleistocene mammals. Pp. 5-31 in S. D. Webb, ed. *Pleistocene Mammals of Florida*. Univ. Presses Florida, Gainesville.

- _____, G. S. Morgan, R. C. Hulbert, Jr., D. S. Jones, B. J. MacFadden, and P. A. Mueller. 1989. Geochronology of a rich early Pleistocene vertebrate fauna, Leisey Shell Pit, Tampa Bay, Florida. *Quat. Res.* 32:96-110.