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THE SABERCAT *SMILODON GRACILIS*
FROM FLORIDA AND A DISCUSSION
OF ITS RELATIONSHIPS
(MAMMALIA, FELIDAE, SMILODONTINI)

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UNIVERSITY OF FLORIDA

GAINESVILLE

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(MAMMALIA, FELIDAE, SMILODONTINI)

ANNALISA BERTA*

ABSTRACT

Dentitions and limbs of the sabercat, *Smilodon gracilis* (Cope 1880), are described from several Florida localities, ranging in age from the late Blancan through the Irvingtonian. These samples provide the largest and best known record of the gracile sabercat. Specimens of *S. gracilis* from Florida are similar to the type material from Port Kennedy Cave, Pennsylvania.

Smilodon gracilis is most closely related to *S. populator* Lund 1842 (junior synonyms include *S. floridanus* Leidy 1889, *S. californicus* Bovard 1907, and *S. fatalis* Leidy 1868, as revised by Slaughter 1963) and is recorded from diverse localities that range in age from the late Irvingtonian through the Rancholabrean in both North and South America. The gracile sabercat is more primitive than *S. populator* in having upper canines only slightly recurved; upper canines and cheek teeth with very finely serrated anterior and posterior margins; P^4 with a well developed protocone; mandible with a large flange, two mental foramina, and a double-rooted P_3 ; less robust limbs and elongate hindfeet. *Smilodon* shares a sister group relationship with *Megantereon*. *S. gracilis* is more derived than *Megantereon* in having incisors enlarged and procumbent, upper canines elongate and robust, P^4 ectoparastyle well developed, and mastoid and glenoid processes enlarged.

Smilodon gracilis shows a trend toward size increase through time. Limb morphology and proportions of smilodontines (including *S. gracilis*) are similar to forest

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felids although these sabercats are usually better sampled at sites where plains and open woodland habitats predominated. Judging from its highly specialized dentition and powerful, short limbs and feet, Smilodon evolved prey capture techniques that relied upon stalking and ambush rather than rapid pursuit.

RESUMEN

Se describen las dentaduras y extremidades del tigre dientes de sable, Smilodon gracilis, provenientes de varias localidades en Florida. Las edades varían entre el Blancano tardío y el Irvingtoniano. Estas muestras constituyen los registros más numerosos y mejor conocidos del tigre dientes de sable. Los especímenes de S. gracilis en Florida son similares al prototipo de la cueva de Port Kennedy Cave (Pennsylvania).

Smilodon gracilis es un pariente cercano de S. populator Lund 1842 (sinónimos recientes incluyen: S. floridanus Leidy 1889, S. californicus Bovard 1907, y S. fatalis Leidy 1868 revisado por Slaughter 1963), el cual ha sido registrado en varias localidades y cuyas edades varían entre el Irvingtoniano tardío y el Rancholabreano, tanto en Norte como Sur América. El tigre dientes de sable es más primitivo que S. populator, ya que presenta los caninos superiores sólo ligeramente curvados; los caninos superiores y molares carecen del margen anterior y posterior poco serrado; el P^4 tiene el protocono bien desarrollado; la mandíbula tiene un reborde grande; dos forámenes y un P^3 de doble raíz; extremidades menos robustas y patas traseras elongadas. Smilodon también está relacionado al género Megantereon. S. gracilis es más avanzado que Megantereon porque tiene incisivos alargados y procumbentes; caninos superiores alargados y robustos; el ectoparaestilo de P^4 bien desarrollado; y los procesos mastoideo y glenoideo alargados.

Smilodon gracilis muestra una tendencia al aumento de tamaño a través del tiempo. La morfología de las extremidades y proporciones generales de los smilodontinidos (incluyendo S. gracilis) son semejantes a las de los felinos de bosques, aunque las muestras de dientes de sable generalmente provienen de sitios con predominancia de llanuras y bosques abiertos. De acuerdo a su dentadura altamente especializada y fuerte, las extremidades y patas cortas, Smilodon desarrolló técnicas de captura de presa en base al asalto y emboscada, en vez de persecución rápida.

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INTRODUCTION

The best known Pleistocene sabercat in North America is the genus *Smilodon* which has been regarded as a member of the tribe Smilodontini together with its close relative *Megantereon* (Kurtén 1963). Smilodontine cats represent the culmination of the sabercat specialization. The upper canines are greatly elongated, slender, and recurved, and how they were used to capture and kill prey has been much discussed (e.g. Simpson 1941, Miller 1969, Emerson and Radinsky 1980). Study of the cranial and postcranial anatomy of these cats has led to interpretations of their probable behavior and ecology (Gonyea 1976). Despite the amount of attention *Smilodon* has commanded in the literature, relatively little is known regarding the systematics and evolution of smilodontine cats.

The sabertooth "tiger," *Smilodon floridanus*, recognized here as a junior synonym of *Smilodon populator*, is best known from the late Pleistocene tar pits at Rancho La Brea, California, where thousands of individuals are represented (Merriam and Stock 1932). *S. populator* has been reported from more than 40 late Irvingtonian and Rancholabrean

localities in Arkansas, California, Florida, Idaho, Louisiana, Mexico, Nebraska, New Mexico, Oregon, Tennessee, Texas, and Utah and also ranged into South America (Kurtén and Anderson 1980).

The gracile sabercat, *Smilodon gracilis*, is less well known. Dental and postcranial remains are reported from the type locality at Port Kennedy Cave, Pennsylvania, and from the following Florida faunas: Santa Fe River IA (Kurtén 1965), Inglis IA (Klein 1971, Webb 1974b), Haile XVA (Robertson 1976), McLeod (this report), Bass Point Waterway No. 1 (Churcher 1984), and El Jobean (Churcher 1984; this report). Since this paper originally went to press, the largest and most complete sample of *Smilodon gracilis* has been recovered from a new locality, Leisey Shell Pit near Ruskin, Florida. A fragmentary lower jaw from Vallecito Creek, California, is here provisionally referred to *Smilodon* cf. *S. gracilis*. *Smilodon gracilis* is considerably smaller than *S. populator* and more slenderly built. The sabers are enlarged but lack strongly serrated edges. A distinct protocone and enlarged ectoparastyle are present on P⁴. The mandibular flange is large, and P₃ is present and usually double rooted. The limbs are short and less robust.

This report describes the Florida record of *Smilodon gracilis*. Previously undescribed material permits a rediagnosis of this species as well as an evaluation of the phylogenetic relationships, stratigraphic distribution, and biogeographic significance of *Smilodon* in North America.

ACKNOWLEDGEMENTS

Richard H. Tedford (American Museum of Natural History) and Gay L. Vostreys and Charles Smart (Academy of Natural Sciences, Philadelphia) kindly allowed use of collections and/or facilities. John S. Waldrop (Timberlane Research Organization), Roy H. Burgess, George Miller, and Ted Downs permitted study of specimens in their collections. Ted Galusha of the Frick Laboratory provided preliminary identification of the undescribed Florida material. Specimen illustrations were expertly drawn by Wendy Zomlefer. Howard Converse prepared specimen casts and radiographs. S. David Webb, William Akerston, Bruce J. MacFadden, C.S. Churcher, Henry Galiano, Robert Hunt, and Earl Manning critically reviewed this manuscript.

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ABBREVIATIONS

The following abbreviations are used for specimens from institutional and private collections: AMNH, Department of Vertebrate Paleontology, The American Museum of Natural History, New York; ANSP, The Academy of Natural Sciences, Philadelphia, Pennsylvania; F:AM, Frick: American Mammals, Department of Vertebrate Paleontology, The American Museum of Natural History, New York; FDT, Florida Diving Tours, Ocala, Florida (private collection); TRO, Timberlane Research Organization, Lake Wales, Florida (private collection); UF, Vertebrate Paleontology Collection, Florida State Museum, Gainesville, Florida.

Other abbreviations are as follows: AP, greatest anteroposterior diameter; C.V., coefficient of variation; e, estimated measurement; N, number of specimens; OR, observed range; SE, standard error; T, greatest transverse diameter; X, mean.

The dental nomenclature used in this paper and illustrated in Figure 1 follows Neff (written communication 1981). The postcranial terminology follows Jayne (1898) and Evans and Christensen (1979). All measurements are in millimeters.

LOCALITIES

Smilodon gracilis is now known from seven localities in Florida (Fig. 2). This sabercat had previously been reported from the first four localities listed below.

SANTA FE RIVER IA.--This river-bottom site in Gilchrist County was discovered by Ben Waller and has produced a mixed collection of Blancan and Rancholabrean fossils (see Webb 1974a).

HAILE XVA.--This fissure fill deposit within the Ocala limestone is located on the property of Parker Brothers Limestone Products near Haile in Alachua County. The site was discovered by P. Kinsey and collected by J. Robertson, S. David Webb, and R. R. Allen (see Robertson 1976).

INGLIS IA.--A sandy fissure fill deposit in Citrus County within the Inglis Member of the Ocala Limestone was exposed during canal dredging operations conducted by the U.S. Army Corps of Engineers. This site was discovered and first collected by Jean Klein and Robert Martin (see Klein 1971, Webb 1974a).

BASS POINT WATERWAY NO. 1.--This locality consists of alternating gravel, silt, and sand forming an *in situ* collecting site in the side of a canal bank near the town of Northport, Sarasota County (Churcher 1984). The stratigraphy and fauna of this locality are presently being studied by paleontologists at the Royal Ontario Museum, Toronto, Canada.

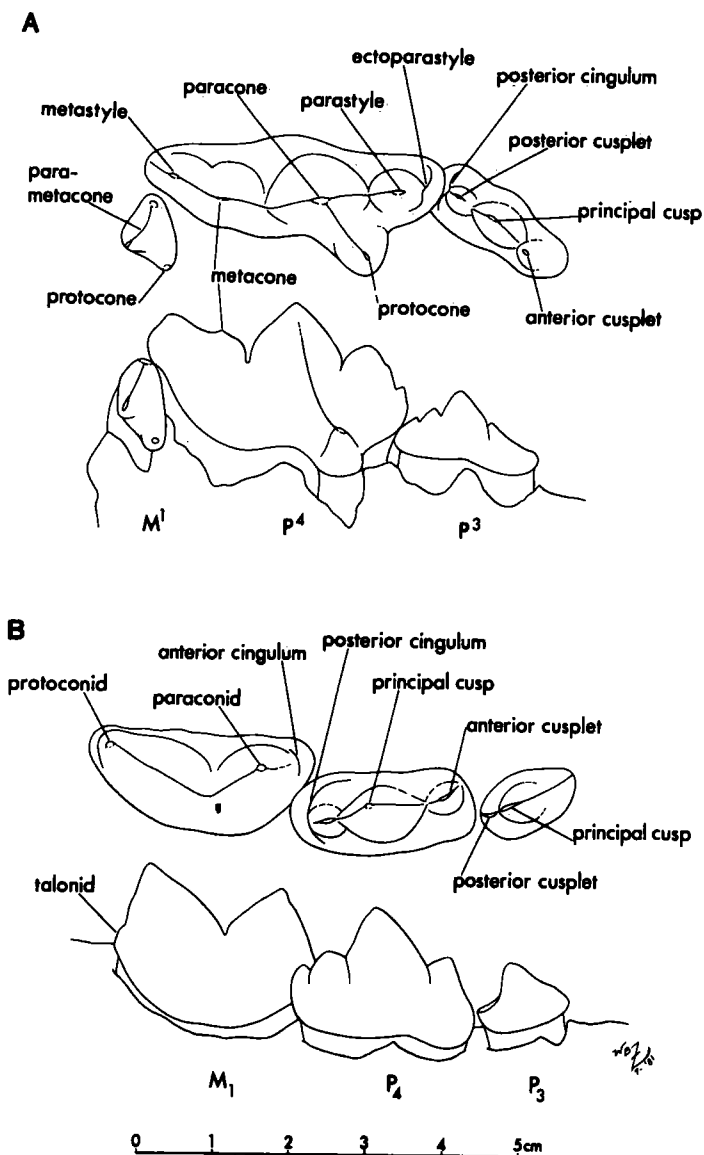


Figure 1. Right Upper (A) and Lower (B) dentition of *Smilodon gracilis* with dental nomenclature used in this study. Upper dentition based on UF 18100 and TRO 1664. Lower dentition based on UF 18102. Anterior is to the right.

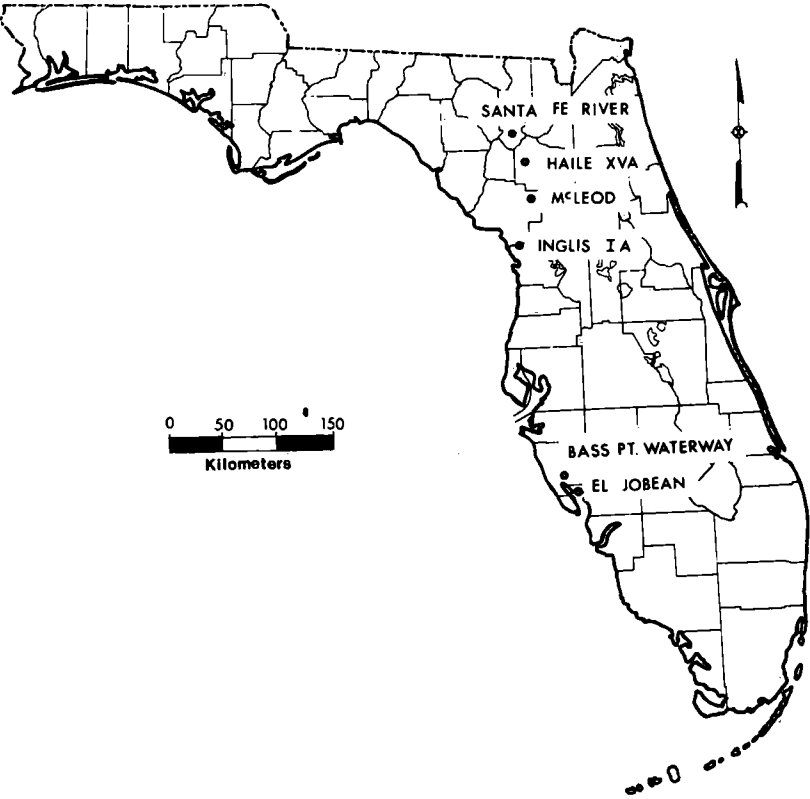


Figure 2 . Smilodon gracilis localities in Florida.

MCLEOD.--A fissure fill deposit, McLeod Limestone Quarry, Smith Pit, Pocket A, approximately 3.3 km. north of Williston, Levy County. This site was discovered and collected by Ted Galusha in 1941.

EL JOBEAN.--Canal spoil dumps near the town of El Jobean, Charlotte County, locality collected by Roy H. Burgess in 1968.

LEISEY SHELL PIT.--A 4-8 cm thick bone bed sandwiched between thick marine shell beds near Ruskin, Hillsborough County. This site was discovered by Frank Garcia and collected by associates of the Tampa Bay Gem and Mineral Society and field parties from the Florida State Museum in 1983 and 1984. The stratigraphy and fauna of this locality are currently being studied by paleontologists at the Florida State Museum. A more detailed study of *Smilodon gracilis* from this locality will be provided in a forthcoming paper (Berta, in prep.).

TAXONOMIC HISTORY OF *SMILODON*

The genus *Smilodon* was established by Lund (1842), who described a single species, *S. populator*, based on material recovered from the Lagoa Santa Caves, Brazil (see Paula Couto 1955). Earlier, Lund (1839) erroneously referred some of this material to *Hyaena neogaea*. Because at the time of the original designation *Hyaena neogaea* was insufficiently defined and no type material was specified, this species is recognized as a *nomen nudum* following Kurtén and Anderson (1980).

The oldest name for a North American *Smilodon* is *Felis* (*Trucifelis*) *fatalis* proposed by Leidy (1868) on the basis of a fragmentary maxilla with P⁴ and the alveolus for M¹ from the "asphalt beds" in Hardin County, Texas. Later, Leidy (1869:366, pl. 28, fig. 10) redescribed and illustrated the specimen under the name *Trucifelis fatalis*. Although Merriam and Stock (1932) and Simpson (1945) recognized *Trucifelis* as a valid subgenus, all later workers have referred this species to *Smilodon* (see Slaughter 1963). The type of *S. fatalis* is similar to *S. gracilis* in its small size, lack of strong serrations, and presence of a protocone. It differs from *S. gracilis* in having a well rounded protocone and a larger ectoparastyle on the upper carnassial. The type of this species is judged too incomplete to provide a specific diagnosis.

Leidy (1889:13-16, pl. 3, fig. 1) described a fragmentary skull lacking teeth from a limestone quarry in Marion County, Florida, as a new species of *Machairodus*, "*M. floridanus*". Beginning with Bovard (1907) all later workers have referred this species to *Smilodon*. Bovard (1907) proposed the species *S. californicus* for the excellent sample from Rancho La Brea, California. He distinguished this species from *S. floridanus* by its shorter muzzle, more posterior position of the posterior nares, and ridges

on the palate (the latter of questionable significance). Merriam and Stock (1932) rejected Bovard's diagnosis and concluded that the principal difference between this species and *S. floridanus* was the orientation of the mastoid process.

Slaughter's (1963) analysis of *Smilodon* supported the conclusion previously developed by Lammers (1959) that *S. californicus* Bovard is a synonym of *S. floridanus* Leidy. Kurten's (1965) study of Florida *Smilodon* led him to synonymize *S. floridanus* with *S. fatalis* and to maintain *S. californicus* as distinct. He distinguished *S. californicus* on the basis of its larger size, broader mastoid region, and "presence of an accessory cuspule on M₁." Webb (1974b), in his evaluation of additional sabercat material from Florida, demonstrated considerable overlap in the ranges of various measurements between these species and thus strengthened the case for synonymy of *S. californicus* with *S. floridanus*. A recent study of North and South American sabercats proposed synonymy of *S. floridanus* with *S. populator* (Berta 1985). *S. populator* can be distinguished from *S. gracilis* on the basis of the following characters: larger size, broadened muzzle, upper canines strongly recurved, upper canines and cheek teeth with strongly serrated anterior and posterior margins, P₄ with very reduced or absent protocone, mandible with reduced flange, single foramen, and P₃ usually absent.

Slaughter (1963), in a revision of North American *Smilodon*, enlarged the concept of *S. fatalis* and synonymized the following with it: *Smilodontopsis conardi* Brown 1908, *Smilodontopsis troglodytes* Brown 1908, *Smilodon nebraskensis* Matthew 1918, *Smilodon* cf. *S. fatalis* Lull 1921, and *Smilodon trinitensis* Slaughter 1960. He diagnosed *S. fatalis* as follows: "total skull length less than any specimen of *S. californicus*; occiput narrow and triangular, not rounded above; basioccipital lacking well developed vertical keel; inferior canine much reduced with anteroposterior diameter less than 54 percent of the same measurement of P₄; P₄ thin, having a transverse diameter less than 43 percent of the anteroposterior diameter."

As noted by Slaughter (1963), *Smilodon* species are extremely variable. Species synonymized by him under *S. fatalis* fall within the limits of size and individual variation seen in *S. populator* (Berta 1985). Size criteria are not of primary importance in recognition of *Smilodon* species. As Slaughter noted, all *S. fatalis* are not smaller than *S. floridanus*. According to Slaughter, triangular skull occipital regions are characteristic of North American preWisconsin (including late Irvingtonian and early Rancholabrean) *Smilodon*, which he referred to *S. fatalis*. Examination of North and South American *Smilodon* suggests that, while it is generally true that most specimens displaying a triangular occiput are middle Pleistocene (Irvingtonian and Ensenadan), several late Pleistocene (Rancholabrean and Lujanian) specimens were found that exemplified this condition (Berta 1985). It is also possible that the shape of the occiput may reflect sexual

dimorphism, because those specimens that exhibit narrow, triangular occiputs also possess well developed sagittal crests.

Slaughter's diagram showing the relationship between the lower canine and P_4 is plotted in Figure 3 with the addition of North and South American middle and late Pleistocene *Smilodon* (including *S. fatalis* sensu Slaughter 1963, *S. floridanus* Leidy 1889, *S. californicus* Bovard 1907, and *S. populator* Lund 1842). While *S. fatalis* (as revised by Slaughter 1963) does have generally thinner, shorter lower carnassials and canines, additional material demonstrates that several North and South American populations of *S. populator* have measurements whose ranges overlap it. Also apparent in Figure 3 is the fact that these measurements discriminate *Smilodon* chronologically to the extent that the largest specimens of *S. populator* are from late Pleistocene (Rancholabrean and Lujanian) localities. Similarly, late Pleistocene *S. populator* possess larger, broader lower carnassials than do middle Pleistocene (Irvingtonian and Ensenadan) specimens (Fig. 3). No significant differences other than the larger size of late Pleistocene *S. populator* were found. Based on these data I propose including *S. fatalis* (as revised by Slaughter 1963) as a junior synonym of *S. populator*.

In addition to *S. populator* (junior synonyms include *S. floridanus* Leidy 1889, *S. californicus* Bovard 1907, and *S. fatalis* Leidy 1868), a second sabercat species recognized in North America is *S. gracilis*. This species was proposed by Cope (1880:857) on the basis of an upper canine root (ANSP 46) recovered from Port Kennedy Cave, Pennsylvania. Additional cranial and dental material provided the basis for more complete descriptions of this species (Cope 1895, 1899). Examination of ANSP collections demonstrated that several postcranial elements were erroneously referred by Cope (1889) to this species; ANSP 48 (in part) right calcanei and a left distal humerus. These specimens are comparable in size and morphology to the jaguar, *Felis onca*.

Cope (1895) named a second cat, *Uncia mercerii*, based on three premolars. Two of these teeth, a left P_3 and a right P_4 (ANSP 50), are referable to *Smilodon*, and the third tooth may have later been transferred by him to "*Crocota*" *inexpectata* (Gay Vostreys, written communication 1979). Among a large number of postcranial elements catalogued under *S. mercerii* as ANSP 51, only a proximal right metatarsal II and a left metacarpal II are referable to *Smilodon*.

In a third paper Cope (1899) assigned "*U.*" *mercerii* to the genus *Smilodon*, thus recognizing two sabercats from Port Kennedy Cave. He distinguished *S. mercerii* from *S. gracilis* principally by its smaller size and double rooted P_3 . Reevaluation of this material indicates similarity in size (see Tables 1-3) and morphology and supports the synonymy of "*U.*" *mercerii* with *S. gracilis*, as proposed by Kurtén and Anderson (1980). In size and dental and postcranial morphology, *S. gracilis* from Florida resembles the type material from Port Kennedy Cave.

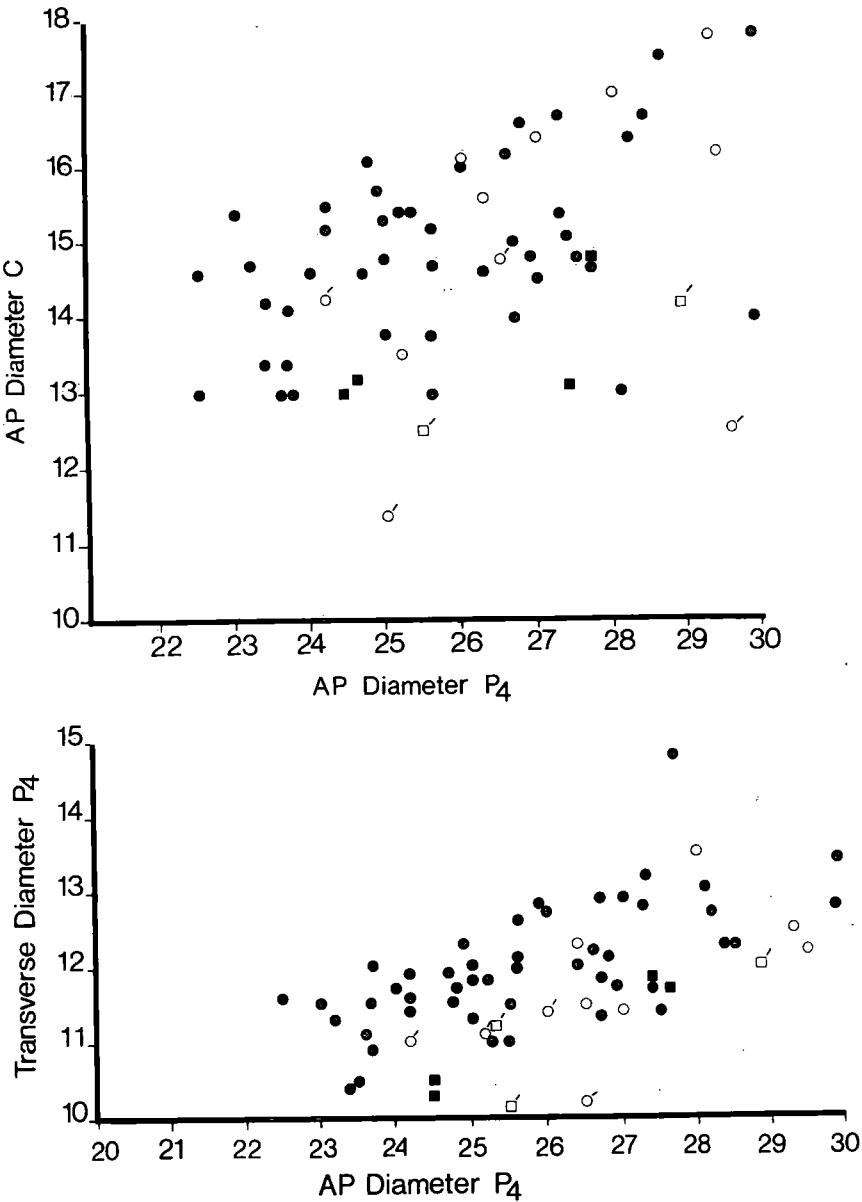


Figure 3. Comparative dental measurements of *Smilodon populator* (North American sample; Merriam and Stock 1932 and additional specimens) (● Rancholabrean), *Smilodon fatalis* (Leidy 1868) (■ = Rancholabrean, □ Irvingtonian), and *Smilodon populator* (South American sample; Berta 1985) (○ = Lujanian, ♂ = Ensenadan).

SYSTEMATIC PALEONTOLOGY

ORDER CARNIVORA BOWDICH 1821
 SUBORDER FELIFORMIA KRETZOI 1945
 SUPERFAMILY Feloidea SIMPSON 1931
 FAMILY FELIDAE GRAY 1821
 SUBFAMILY Machairodontinae GILL 1872
 TRIBE Smilodontini KURTZ 1963
 GENUS *Smilodon* LUND 1842
Smilodon gracilis COPE 1880

Figures 4-18

Smilodon gracilis Cope 1880:857, 1895:448
Machaerodus gracilis Cope 1899:240, pl. XX, fig. 1
Uncia mercerii Cope 1895:448, 1896:392
Smilodon mercerii Cope 1899:245, pl. XX, fig. 2
Smilodon (Smilodontopsis) gracilis Merriam and Stock 1932:15
Smilodontopsis (Machaerodus) gracilis Brown 1908:190
Smilodontopsis (Machaerodus) mercerii Brown 1908:190
Machaerodus? mercerii Matthew 1918:229
Machaerodus? gracilis Matthew 1918:229
Machaerodus gracilis Matthew 1918:229
Machaerodus gracilis Slaughter 1960:490
Machaerodus mercerii Slaughter 1960:490
Megantereon gracilis Martin 1980:149
Ischyrosmilus gracilis Churcher 1984:1

HOLOTYPE.--ANSP 46, root of upper canine.

TYPE LOCALITY.--Port Kennedy Cave, Montgomery County, Pennsylvania.

REVISED DISTRIBUTION AND AGE.--Late Blancan-Late Irvingtonian of Pennsylvania and Florida.

EMENDED DIAGNOSIS.--Differs from *Smilodon populator* in having upper canines only slightly recurved; upper canine teeth with very finely serrated anterior and posterior margins; P⁴ with well developed protocone; mandible with large flange, two mental foramina, double-rooted P₃; less robust limbs and elongate hindfeet. Differs from Old and New World species of *Megantereon* in having incisors enlarged and procumbent; upper

canines elongate and robust; P^4 ectoparastyle well developed; and mastoid and genoid processes enlarged.

REFERRED SPECIMENS.--PORT KENNEDY CAVE, PENNSYLVANIA: ANSP 44, crushed and distorted facial region of skull lacking right M^1 (crown of left upper canine broken and mandible missing right C); ANSP 45, right M^1 in ramal fragment; ANSP 46, left upper canine; ANSP 47, right and left P^4 , left M^1 , left jaw fragment; ANSP 48, right astragalus, proximal ends of metacarpals II and III, ungual phalanx; ANSP 49, right and left rami missing I_1 and P_3 ; ANSP 50, left P^3 , right P_4 ; ANSP 51, proximal end right metatarsal II, left metacarpal II.

FLORIDA.--HAILE XVA: UF 17496, left astragalus, right distal tibia; UF 17498, right metacarpal II, left distal metatarsal II. SANTA FE RIVER IA: FDT 488, right P_4 . INGLIS IA: UF 18097, right premaxillary fragment with C and P^1 alveolus; UF 18098, root fragment of upper canine; UF 12929, UF 12930 upper canine; UF 18100, right maxillary fragment with C alveolus, P^{3-4} - M^1 alveolus; UF 18101, left dP^4 ; UF 18102, partial right ramus with C alveolus, P_{3-4} , M_1 ; UF 18103, posterior one-half of right ramus with P_4 - M_1 ; UF 20065, right ramus with I_3 , C, P_3 alveoli and P_4 - M_1 ; UF 18104, fragment of left ramus with P_3 ; UF 12931, left condyle and angle fragment; UF 18105a, fragmentary left ramus with I_3 , deciduous C alveolus and permanent I and C in crypt, dP_{3-4} ; UF 18105b fragmentary right ramus with dP_3 alveolus, dP_4 ; UF 18105 left dP_4 (2), left and right fragmentary dP_4 's; UF 12930, upper canine fragments; UF 12932 fragmentary right ramus with P_2 alveolus, permanent I_3 and C in crypt; UF 12933 left M_1 ; TRO 1664, right maxillary fragment with P^4 - M^1 ; TRO 1665, left ramus with I_3 , C alveolus, P_{3-4} , M_1 ; UF 69921, axis vertebra; UF 45342, cervical vertebra III; UF 18106, TRO 1670, right humerus; UF 18107, distal one-third (shaft) of right and left humerus; TRO 1669, left humerus missing proximal end; UF 18109, proximal right ulnae (2); UF 18108, left radius; UF 18110, right metacarpal IV (2); UF 12934, left metacarpal II; UF 45409, left metacarpal III; UF 12938, right metacarpal IV; UF 12935, right metacarpal V; UF 18112, proximal right femur; UF 18113, UF 12936, UF 12937, UF 23999, UF 24000, TRO 1668, right calcaneum; TRO 1666, right astragalus; TRO 1667, left astragalus; UF 12939, left metatarsal III; UF 12940, right metatarsal IV. MCLEOD: F:AM 95525, partial left maxillary with C, P^{3-4} ; F:AM 95526, upper canine; F:AM 95522, fragment of right ramus with P_4 - M_1 ; F:AM 95527, right P_4 ; F:AM 95523, right humerus missing proximal end; F:AM 95528, shaft portion of left humerus; F:AM 95524, proximal left ulna; F:AM 69223, proximal left ulna missing olecranon process; F:AM 69220, left radius; F:AM 108538, left scapholunar; F:AM 69249, right metacarpal IV; F:AM 69219, right radius missing proximal end; F:AM 95529, distal two-thirds of left tibia; F:AM 108538, right patella; F:AM 108536, left astragalus; F:AM 95532, F:AM 95533, left calcaneum; F:AM 105838, right cuboid; F:AM 95521, right navicular; F:AM 69241,

right metatarsal III; F:AM 69243, right metatarsal IV; F:AM 95520, proximal right metatarsal IV; F:AM 95531, right metatarsal V; F:AM 95530, right metatarsal IV missing proximal end; F:AM 95535a, left proximal phalanx (forefoot); F:AM 95535b, c, right proximal phalanges (hindfoot); F:AM 108537a, b, c, d, left median phalanges (forefoot). EL JOBEAN: UF 12941, cast of partial left ramus with P_3 alveolus, P_4 - M_1 .

DESCRIPTION OF FLORIDA MATERIAL

DENTITION.--Upper incisors are not represented in the Florida sample studied herein. A partial maxilla, F:AM 95525 from McLeod, preserved the right upper canine as well as P^{3-4} (Fig. 4, Table 1). The canine is elongate, laterally compressed, and slightly recurved anteroposteriorly. The saber differs from that of *Smilodon populator* in being proportionately smaller, shorter, and less curved. Very fine serrations are developed along the anterior and posterior tooth margins and are visible only with the aid of a microscope. The root is only slightly thicker than the alveolar portion of the tooth.

P^3 is preserved in two maxillary fragments, UF 18100 and F:AM 95525 from Inglis IA and McLeod. A very short diastema separates this tooth from the canine. P^3 is elongate, double-rooted, and obliquely positioned in the maxilla. The prominent principal cusp is flanked by a small, medially placed, anterior cusplet and a slightly larger posterior cusplet. A broad cingulum forms the heel of the tooth and contributes to its posterior breadth (Table 1). P^3 is comparable in size and morphology to *Megantereon cultridens*, although late Villafranchian representatives of this species show a trend toward size reduction (see Size Trends).

UF 18100, TRO 1665, and F:AM 95525 all preserve P^4 (Figs. 1, 4, Table 1). This tooth exhibits a well developed sharply pointed protocone and a separate protoconal root, a character *S. gracilis* shares with *Megantereon*. The protocone is anterolingually positioned at a 50° angle relative to the anteroposterior axis of the tooth. The parastyle is large and well developed. A small ectoparastyle is always present. *Megantereon* typically shows weaker development of the ectoparastyle. *S. populator* shows considerable variation in development of the parastyle and ectoparastyle. One specimen from the La Brea sample that lacks the ectoparastyle shows development of a proportionately larger parastyle (Merriam and Stock 1932:48). The metacone forms the long portion of the carnassial blade and is low crowned relative to the paracone. The shearing surface of this tooth is very worn in F:AM 95525, exposing the pulp cavity. Other specimens display prominent circular wear pits and planar wear facets on the lingual surface of the tooth between the protocone and parastyle.

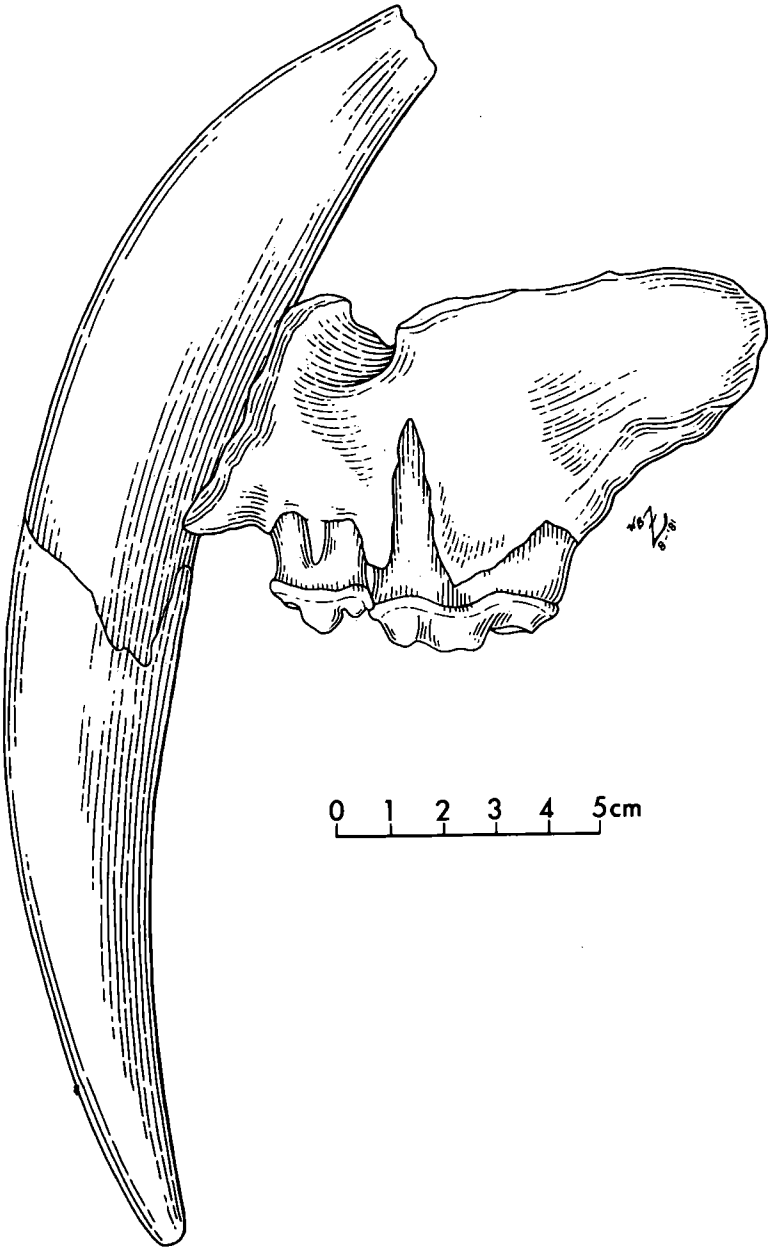


Figure 4. Smilodon gracilis, F:AM 95525 from McLeod, Florida. Lateral view of left maxillary with C, P³⁻⁴

M¹ is preserved in TRO 1664 (Fig. 1, Table 1). The tooth is triangular, transversely elongate, and single rooted most of its length, dividing near the apex of the root. An elongate labial cusp, the parametacone, is developed, as well as a lingual protocone. A large wear facet is present between the parametacone and smaller facets are developed on the anterior and posterior sides of the talon and on the protocone.

Three right rami; UF 20065, UF 18102, and UF 18103; and one left ramus, TRO 1665, are represented from Inglis IA. A partial left ramus, UF 12941, is known from El Jobean. An additional fragmentary specimen from Inglis IA, UF 12931, preserves the left condyle and a portion of the angle (Fig. 5A, Table 2). TRO 1665 and UF 20065 display enlarged flanges which project ventrally below the rectangular symphysis. In both specimens the flange presents a broadly expanded margin. Among the Port Kennedy specimens, the ventral margin of the flange is noticeably thinner than in the Florida material. One or two large foramina and numerous small foramina perforate the concave anterior surface of the symphysis. Two mental foramina are present on the lateral surface. The smaller, less distinct one is located on the midline of the ramus below the diastema, and a second is positioned several millimeters behind it. A deep masseteric fossa extends to below the posterior root of M₁.

The coronoid process is small and not well developed. The articular surface of the condyle is widest at its medial end. The angle is situated a short distance from the condyle, and its medial surface presents well marked grooves for insertion of the *M. pterygoideus* complex. The medial surface of the ramus bears a shallow groove (Fig. 5B) above the geniohyal depression, which is much better developed in *Megantereon* (Berta and Galiano 1983). In occlusal view (Fig. 5C), behind the canine diastema, the cheek teeth are closely set and the superior border of the mandible containing them is arched laterally.

UF 20065 preserved the I₃ alveolus, which indicates that this tooth was small and transversely compressed (Table 3). The canine is represented only by the alveolus, which suggests that the tooth curved laterally and was obliquely oriented in the jaw. Relative to the upper canine, the corresponding lower tooth was considerably smaller and separated from P₃ by a diastema.

The cheek teeth are rectangular with broadly rounded anterior and posterior margins. P₃ is preserved in a ramal fragment, UF 18104, and in a more complete ramus, UF 18102 (Table 3). It is elongate and double rooted with a smaller anterior root and a single, centrally positioned principal cusp. One specimen shows development of a small posterior cusplet between the principal cusp and the cingular heel. A small diastema is present between P₃₋₄ in all specimens, with the exception of UF 18102. Variation in the morphology of P₃ was noted among the Port Kennedy specimens. In ANSP 44, P₃ is small and single rooted. This same tooth in

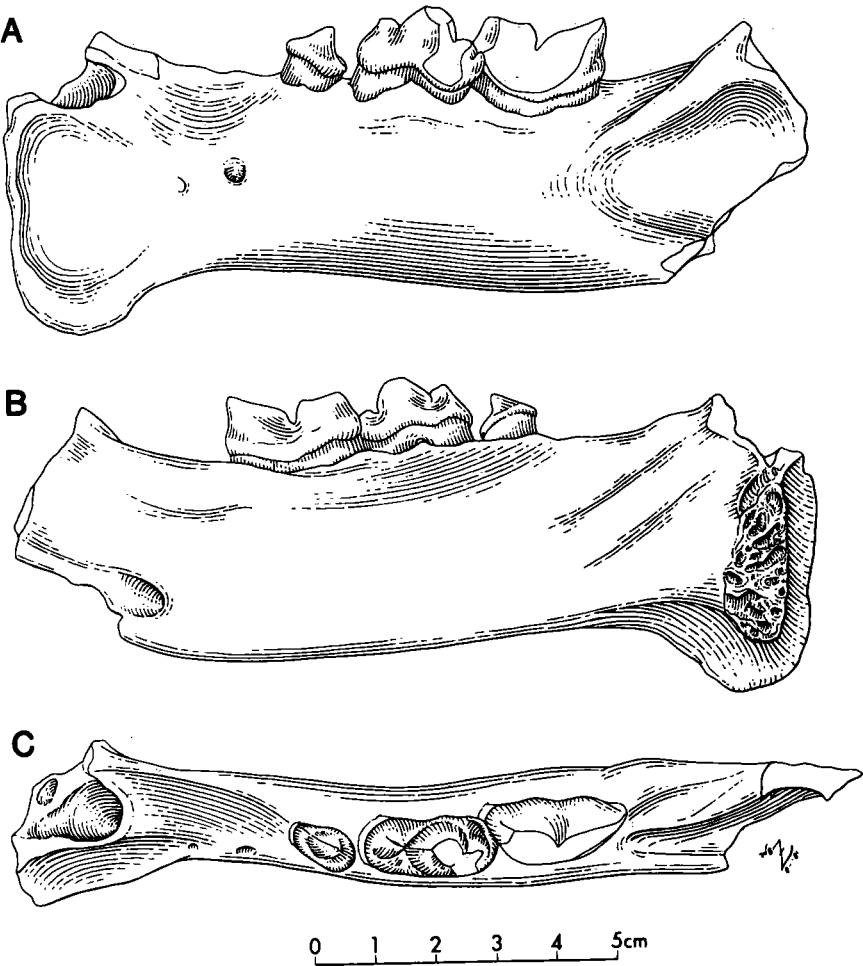


Figure 5. Left ramus, TRO 1665 of Florida *Smilodon gracilis* from Inglis IA. (A) lateral; (B) medial; (C) occlusal views.

ANSP 49, as determined from the alveolus, is similar to the Florida specimens in its larger size and double-rooted condition. Both single- and double-rooted conditions of P_3 are present in *S. populator*, and absence of this tooth is common among late Pleistocene individuals (Berta 1985).

P_4 and M_1 are represented in the following rami: UF 18103, UF 18104, TRO 1665, UF 20065, and UF 12941 from Inglis IA. A specimen from McLeod, F:AM 95522, preserved P_4 - M_1 in a ramal fragment. The principal and accessory cusps of these teeth are inclined posteriorly. P_4 consists of a large principal cusp flanked by subequal anterior and posterior cusplets (Fig. 5, Table 3). The anterior cusplet is medially oriented. Behind the posterior cusplet a strong lingual cingulum forms the heel of the tooth. In *S. populator* this cingulum is less pronounced and a relatively large second posterior cusplet is present. UF 20065 displays small wear facets on the labial surface of the anterior cusplet and the principal cusp. F:AM 95522 has a prominent wear surface developed on the labial side of the principal cusp and the posterior cusplet. The anterior margin of M_1 overlaps the posterior border of P_4 . In M_1 the protoconid blade is longer and taller than the paraconid blade. Pronounced shearing surfaces are present on the labial surfaces of both the paraconid and protoconid blades. A small talonid is developed on the M_1 heel.

Juveniles are represented in the Inglis IA sample by deciduous dentitions. The upper milk dentition is represented by UF 18101, a left dP^3 (Table 4), and several fragmentary canines, UF 12930 and UF 12929.

The milk carnassial, dP^3 , is triangular and three rooted. Principal differences between dP^3 and its replacement in the permanent dentition, P^4 , are its smaller size and cusp orientation. The protocone is well separated from the body of the tooth, and it is oriented perpendicular to the paracone. Relative to the condition seen in adults, the parastyle is medially positioned. A small ectoparastyle is present. Wear surfaces are developed on the superior border of the parastyle-metastyle blade and as a small pit between the protocone and parastyle. In a dP^3 of *Megantereon megantereon* from St. Vallier, France (Viret 1954, pl. 13, fig. 1b) the protocone is in an anterolingual orientation. Another dP^3 in a juvenile *M. megantereon* palate from Puebla de Valverde, Spain (Kurtén and Crusafont-Pairo, 1977:21, fig. 13), differs from the Inglis specimen in its larger size and lack of a protocone.

The lower milk dentition is represented by more material. UF 18105a, a fragmentary left ramus, preserves the deciduous canine alveolus, dP_{3-4} , and a permanent incisor and canine are present in the crypt (Fig. 6, Table 4). A very fragmentary right ramus, UF 18105b, preserves the dP_3 alveolus and dP_4 . UF 12932, a fragment of the symphyseal portion of the right ramus, preserves the P_2 alveolus and the permanent I_3 and C in the crypt. The most complete specimen, UF 18105a, is similar to adult individuals. dP_3 is separated from the canine by a diastema. In the

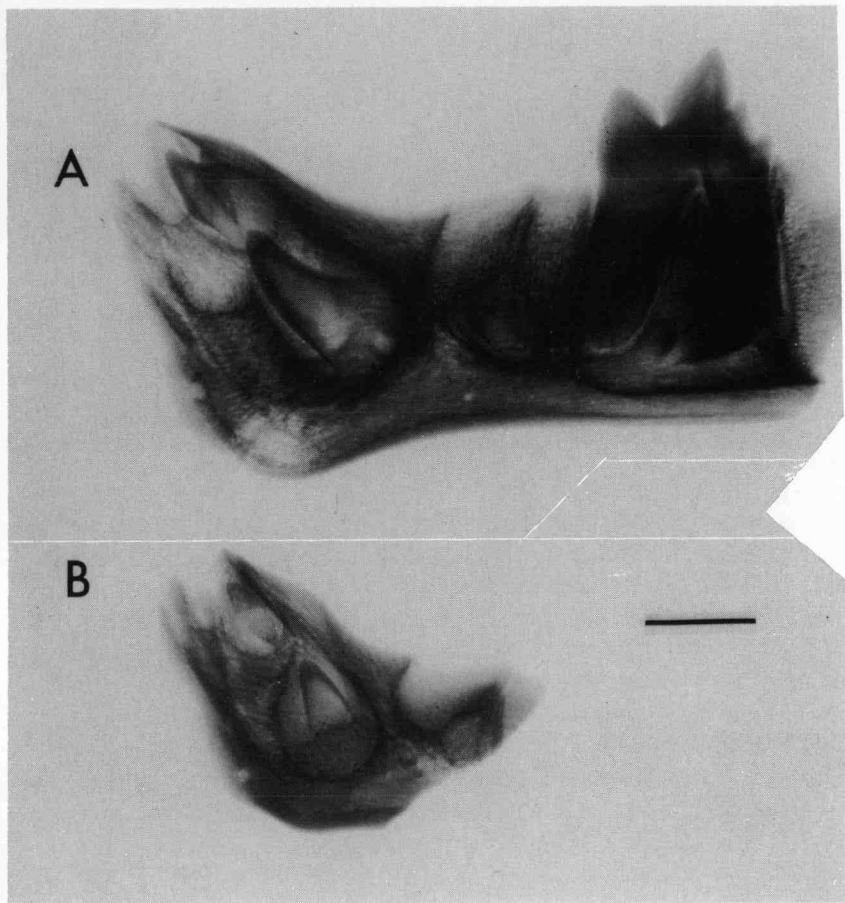


Figure 6. Radiograph of juvenile mandibles and dentition of Florida *Smilodon gracilis* from Inglis IA. (A) lateral view of left ramus, UF 18105a, with deciduous canine alveolus, and permanent I and C in the crypt, dP_{3-4} ; (B) medial view of right ramus, UF 12932, with P_2 alveolus and a permanent I_3 and C in the crypt.

permanent dentition this tooth is replaced by P_2 . dP_3 is double rooted and high crowned with sharp, pointed cusps. As in adults, the principal cusp is flanked by anterior and posterior cusplets. Behind the posterior cusplet, a cingular heel is developed. The sectorial tooth, dP_4 , closely resembles M_1 , but it differs in exhibiting two progressively smaller cusps behind the protoconid. The stage of tooth eruption seen in this specimen compares well with that seen in two juvenile *S. populator* individuals from Rancho La Brea, California (Merriam and Stock 1932, pl. 4, table 11).

Comparison of stages of dental eruption in another machairodont, *Homotherium serum* from Friesenhahn Cave, Texas, suggests that the Florida *S. gracilis* juvenile, UF 18105a, was probably between four and eight months of age at the time of death. This specimen represents an intermediate stage between Stage III and IV in the *Homotherium* eruption sequence characterized by complete eruption of the deciduous dentition and emergence of enamel caps for permanent incisors and canines (Rawn-Schatzinger 1983).

POSTCRANIAL SKELETON.--Much of the skeleton of *Smilodon gracilis* is represented by isolated elements from the McLeod and Inglis IA samples (for individual numbers see Referred Material). The axial skeleton is represented by cervical vertebrae II and III. In the forelimb, the humerus, ulna, radius, scapular, and metacarpals II, III, IV, and V are known; and in the hindlimb, the femur, tibia, patella, astragalus, calcaneum, cuboid, navicular, metatarsals III, IV, and V, and the proximal and median phalanges are represented. These elements are assigned to *S. gracilis* with certainty, because they were collected from sites with dental remains referred to this species and they resemble but are much smaller than specimens referred to *S. populator*. In addition to the machairodont cats, *Megantereon* and *Smilodon populator*, comparisons are made with two true cats, the jaguar, *Felis onca*, and the extinct giant jaguar-like cat, *Felis atrox*. In size and appearance, especially the relative shortness and stockiness of the limbs, the jaguar is a good functional analogue for smilodontine sabercats (see Gonyea 1976).

An axis vertebra, UF 69921, from Inglis IA exhibits a diagnostic feature of the genus, posterior projection of the neural spine. Additionally, the posterior termination of the spine is transversely expanded. In *Felis onca* the neural spine does not extend as far back, and it has a narrower termination. The odontoid process of the Inglis specimen, as is characteristic of *Smilodon*, is relatively shorter and broader than in *Felis onca*.

Cervical vertebra III UF 45342 from Inglis IA possesses two prominent hyperapophyses that project beyond the posterior zygopophyses, as is characteristic of smilodontines. These processes appear as small, rounded tubercles that terminate above the zygopophyses in *F. atrox* and *F. onca*. A depression in the lateral wall of the neural arch in front of the

posterior zygapophysis is present. A similar depression is lacking in *S. populator* and *F. onca*, although small nutrient foramina are seen in this region. Measurements for UF 45342 are as follows: greatest length from ends of anterior zygapophyses to ends of hyperapophyses, 62.0; greatest width across transverse processes, 118.8; greatest depth from posterior border of centrum to top of neural spine, 68.0.

The most abundantly represented skeletal element in the Florida sample of *S. gracilis* is the humerus (Fig. 7, Table 5). Two complete humeri, TRO 1670 and UF 18106, are represented from Inglis IA, and three distal humeri, UF 18107 (2) and F:AM 95523, are known from Inglis IA and McLeod.

In proximal view (Fig. 7A), the medial border of the greater tuberosity bears a smaller tubercle than that of *Felis atrox*, which results in a more open channeled bicapital groove in the sabercat. This tubercle and the greater tuberosity serve as areas of insertion for the anterior part of the *M. pectoralis profundus* which retracts and adducts the forelimb and the *M. supraspinatus* which extends the shoulder joint. In anterior view, the pectoral crest is prominent at the proximal end of the shaft and onto this surface inserts the descending and transverse parts of the *M. pectoralis* complex.

In posterior view (Fig. 7B), the transverse breadth of the distal extremity in smilodontines is especially striking and is reflected in the ratio of humerus length to distal width. Schaub (1925) noted that this ratio in a true felid, *Panthera tigris*, approximated 4.0 compared with a ratio of 3.2 in *Megantereon cultridens*. The same ratio is 3.6 in *S. gracilis* and 3.2 in *S. populator*. The olecranon fossa, which receives the anconeal process of the ulna, is relatively deep in *S. gracilis* and typically transversely broad, although its shape is somewhat variable. In posterior and medial views, the lesser tuberosity is elevated on a distinct pedicel, and a prominent crest marks its medial boundary. It projects medially to a greater degree than in *S. populator* and is most similar to the condition seen in *Megantereon cultridens* (Schaub 1925, fig. 1a). The proximal portion of the shaft in medial view displays a linear roughened area of attachment for the *M. teres major*. A small distally directed nutrient foramen is positioned near the medial border of the shaft above the oblong entepicondylar foramen. The distal extremity of one specimen, TRO 1670, clearly illustrates on the prominent medial epicondyle areas of origin for flexors of the forelimb. Onto the superior broadly rounded projection originates the *M. pronator teres*. Below this prominence are facets for insertion of *M. flexor carpi radialis* and *flexor profundus digitorum* and behind these facets is another for the *M. palmaris longus*.

The lateral profile of the greater tuberosity (Fig. 7C) is diagnostic in smilodontines. The juncture of the greater tuberosity and the anterior border of the shaft is nearly orthogonal in *Smilodon* and *Megantereon*

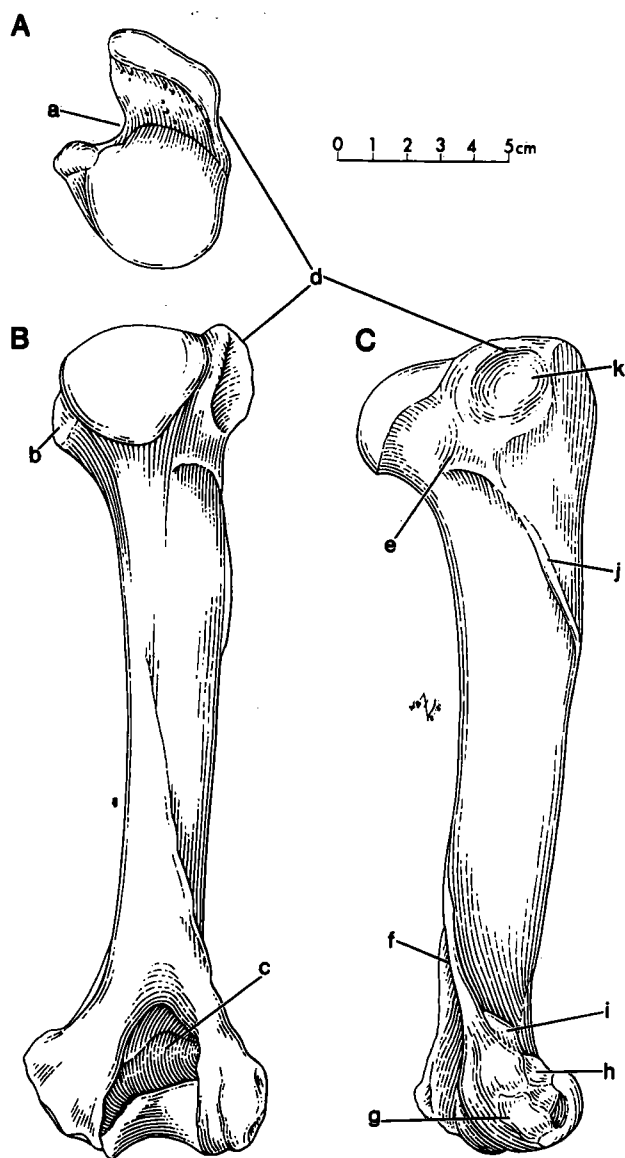


Figure 7. Right humerus, UF 18106, of Florida Smilodon gracilis from Inglis IA. (A) proximal; (B) posterior; (C) lateral views. (a) bicipital groove, (b) lesser tuberosity, (c) olecranon fossa, (d) greater tuberosity, (e) for insertion of M. teres minor, (f) supracondylar crest, (g) for insertion of lateral ligament, (h) for origin of M. extensor carpi radialis and M. extensor communis digitorum, (j) deltoid crest, (k) for insertion of M. infraspinatus.

(Schaub 1925), while in true cats these surfaces form an arcuate connection. The depression for insertion of *M. infraspinatus* is at the same level as the head of the humerus in both smilodontines and *F. onca*. The position of the insertion of this muscle relative to the head of the humerus has the effect of increasing the abductor function, and because the insertion is not parallel to the sagittal plane of this element, the rotary function is increased. Below that is a rugose quadrate area for insertion of the *M. teres minor*, well defined in all *S. gracilis* and similar to the degree of development in *F. onca*. By comparison, the *M. teres* scar in *S. populator* is smaller and not well developed. As the action of this muscle is one of flexion and abduction of the forelimb, the gracile saber cat was probably capable of greater forelimb mobility than the late Pleistocene species. The deltoid crest originates below the infraspinatus depression and extends anteriorly as a well developed ridge to its junction with the pectoral ridge (see Fig. 7C). The deltoid crest is the most prominent feature of the lateral surface of the shaft in both *S. gracilis* and *S. populator* and provides insertion for the *M. deltoideus*. One specimen, TRO 1670, exhibits an irregular bony growth on the anterolateral surface of the shaft, perhaps the result of a secondary calcification within a tendon. The posterolateral border of the shaft forms a sharp crest, the supracondyloid ridge from which originate muscles that act to rotate and extend the forelimb. The *M. supinator* originates on the proximal portion of this ridge. Near the distal end of the ridge is a prominent, ovate muscle scar which probably afforded attachment for the *Mm. extensor carpi radialis* and *extensor communis digitorum*. Below this elongate facet is a small, short area of origin for the *M. extensor digitorum lateralis*. The lateral ligament inserts below this onto the distal surface of the lateral epicondyle.

Two proximal left ulnae, F:AM 95524 and F:AM 69223 (without olecranon process), and two right ulnae, UF 18109, are represented from McLeod and Inglis 1A (Fig. 8, Table 6). In proximal view, the olecranon process is quadrate and broader than in true cats. The posterior surface is the area of insertion for the scapular head of the *M. triceps*. As noted by Merriam and Stock (1932:115), the broadened olecranon process among smilodontines also furnishes a longer area of insertion for the posterior humeral head of the *M. triceps*. There are significant differences in the degree of development of the lateral and medial margins of the olecranon fossa in both *S. gracilis* and *F. onca* (Fig. 8B). Among these cats, the high, strongly developed lateral margin affords a broader area of insertion for the lateral head of the *M. triceps* than does the lower, less developed medial margin where the medial head of the *M. triceps* inserts. By comparison, in *S. populator* the lateral margin is heavy but not as prominently developed relative to the medial margin. Because the *M. triceps* functions to extend the elbow joint, its stronger degree of development in *S. gracilis* provides

further evidence of increased flexibility and more powerful extension of the forelimb in this sabercat.

The coronoid process is directed proximally and laterally, not distally as in true cats (Fig. 8A). The distal two-thirds of the shaft is represented only by F:AM 69223. In lateral view, a longitudinal muscle scar for origin of the ulnar head of the *M. flexor profundus digitorum* is positioned on the medial margin. As illustrated in this view, the posterior margin of the proximal end in both *Smilodon* and *Megantereon* (Schaub 1925) displays a relatively straight edge in contrast to the strongly curved margin exhibited by true cats.

Both a right and a left radius, F:AM 69219 and F:AM 69220, are known from McLeod and a left radius, UF 18108, is represented from Inglis IA (Fig. 9, Table 6). In contrast to true cats, the short diameter (transverse width) of the head is greater and provides a broader articulating surface for the humerus. In lateral view, the margin of the articular surface is slightly rounded and noticeably downturned.

On the anterior surface of the shaft (Fig. 9A) a slight swelling is developed for insertion of the *M. supinator* which acts to rotate the forelimb. This facet appears flattened and less prominent in *S. populator* and *F. onca*. In this view the distal end presents a concave surface for articulation with the scapholunar. Its medial one-half is anteroposteriorly broader than in true cats.

On the posterior surface (Fig. 9B) positioned a short distance below the head is a prominent linear, ovate swelling, the bicipital tuberosity. Below this tuberosity is a roughened area of origin for the *M. abductor pollicis longus*. In this view, the oblique line which rises from the lower one-third of the tuberosity and passes from the proximal lateral margin across the posterior surface to an insertion point on the medial margin is well defined on F:AM 69219. This broad area, defined by the oblique line and the medial margin, suggests development of a large flexor of the forepaw, the *M. flexor digitorum profundus*. Below the insertion point of this muscle on the medial margin is a prominent roughened area for insertion of the *M. pronator teres*.

The shaft is short and slightly curved and in comparison with *S. populator*, relatively slender. Medially positioned on the distal extremity is the wedge shaped, anteromedially broad styloid process. The distal end of this surface bears three distinct grooves for extensors of the forepaw. The most medial groove is deep and lodges the tendon of *M. abductor pollicis longus*. The middle groove, the largest and shallowest, contains the tendon of the *M. extensor carpi radialis*. The most lateral groove, which is broad and shallow when compared with true cats, holds the tendon of the *M. extensor digitorum communis*.

A left scapholunar, F:AM 108538 (Fig. 10), has a rectangular and anteroposteriorly convex proximal surface. The ulnar half is broadly

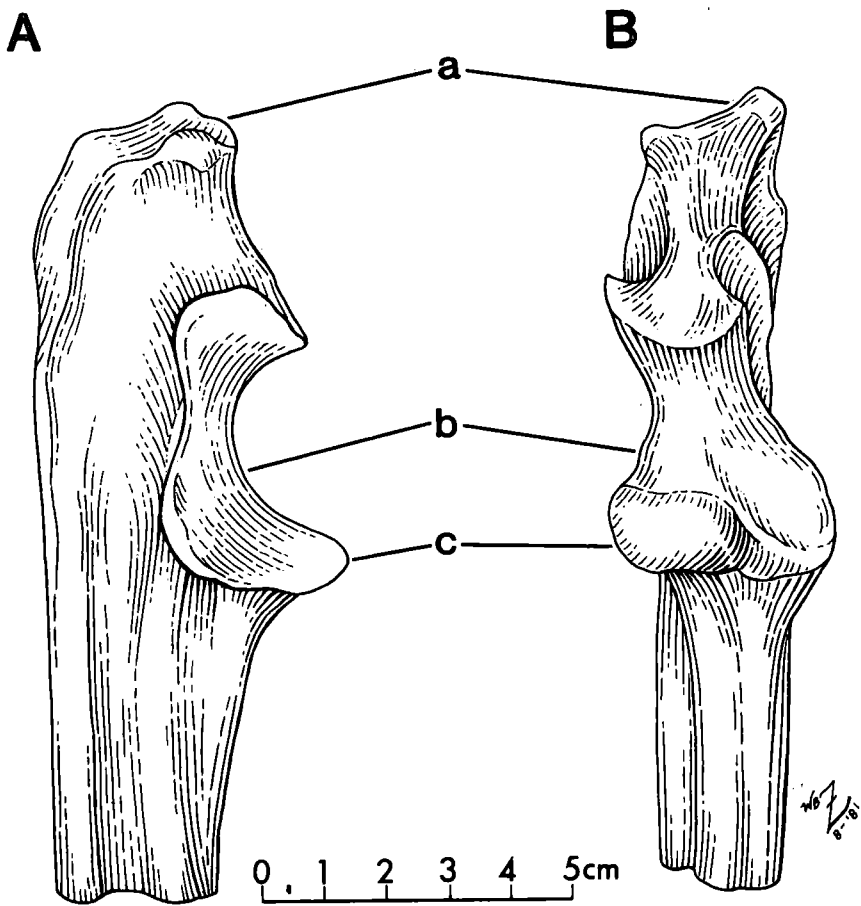


Figure 8. Right ulna, UF 18109, of Florida *Smilodon gracilis* from Inglis IA. (A) lateral; (B) anterior views. (a) olecranon process, (b) trochlear notch (c) coronoid process.

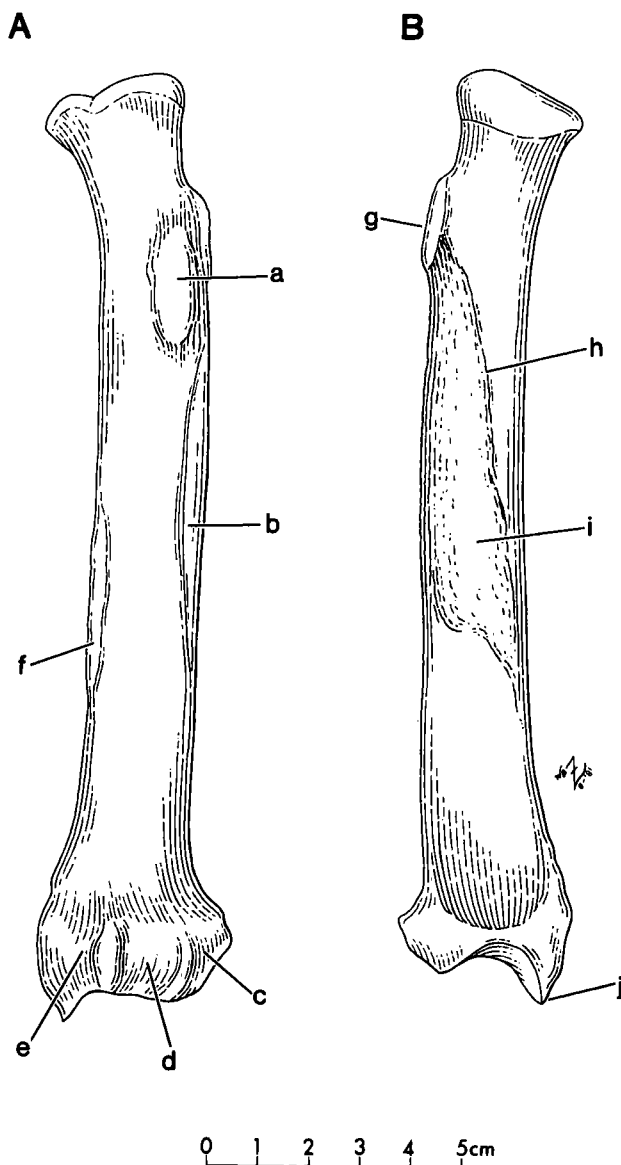


Figure 9. Left radius, F:AM 69220, of Smilodon gracilis from McLeod. (A) anterior; (B) posterior views. (a) for insertion of M. supinator; (b) for origin of M. abductor pollicis longus, (c) for insertion of M. extensor digitorum communis, (d) for insertion of M. extensor carpi radialis, (e) for insertion of M. abductor pollicis longus, (f) for insertion of M. pronator teres, (g) bicipital tuberosity, (h) oblique line, (i) for insertion of M. flexor digitorum profundus, (j) styloid process.

rounded, whereas the radial half is elevated to a sharp crest that is continuous with projection of this element into a distinct proximal process (Fig. 10A).

In anterior view, the depth of the element toward the ulnar side is less than in true cats. The ulnar border presents three emarginations which are the edges of the articular cavities for the unciform, magnum, and trapezoid. On the proximal process is positioned a triangular facet for articulation with the sesamoid. In posterior view, this element appears nearly rectangular. The surface is flat except for the proximal process where a deep groove is present for passage of the tendon of the *M. flexor carpi radialis* which is responsible for flexion of the wrist. In lateral view, the crescentic facet for the unciform is narrow anteroposteriorly and does not show an increase in width toward the radial side as in true cats.

Four irregularly shaped facets which articulate with the distal carpals are conspicuous in distal view (Fig. 10B). The smallest of these facets is that for the sesamoid. Behind this facet is that for the trapezium and trapezoid which are separated by a ridge. The trapezoid facet in *S. gracilis* is broader mediolaterally and extends farther toward the posterior border than in *S. populator*. Separating the trapezoid from the deep concavity for the magnum is a small pit which provides a point of insertion for a ligament. The magnum facet passes laterally into the distal-facing crescentic unciform facet. Measurements for F:AM 108538 are as follows: anteroposterior diameter, 34.8; transverse diameter, 44.7; proximodistal diameter, 25.7.

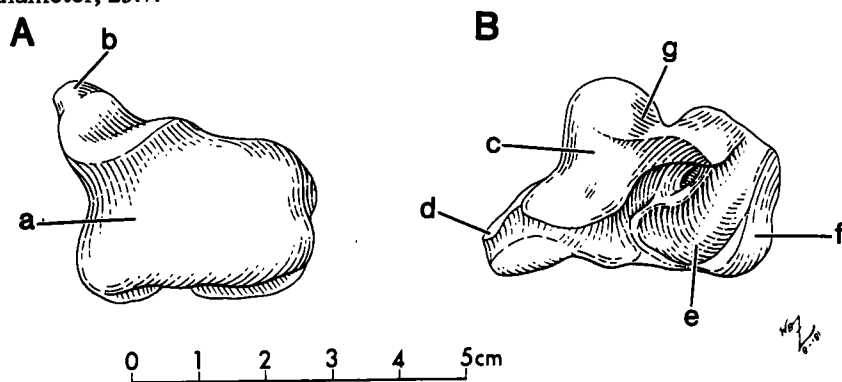


Figure 10. Left scapholunar, F:AM 108538, of Florida *Smilodon gracilis* from McLeod. (A) proximal; (B) distal views. (a) for articulation with radius, (b) proximal process, (c) for articulation with trapezium, (d) for articulation with sesamoid, (e) for articulation with magnum, (f) for articulation with unciform, (g) for articulation with trapezoid.

The metacarpals are relatively short and robust in comparison with those of a similar sized true cat. Both a right (UF 17498) and a left (UF 12934) metacarpal II are represented from Haile XVA and Inglis IA (Fig. 11A, B, Table 7). The proximal surface that articulates with the distal end of the trapezoid lacks the strongly triangular shape seen in true cats. In anterior view (Fig. 11A), the oblique groove for the radial artery is prominent. Medially, the swelling for insertion of the tendon of the *M. extensor carpi radialis*, which functions to extend and abduct the forepaw, is more pronounced than in true cats. In medial view (Fig. 11B), the facet for the trapezium is elongate proximodistally and elevated above the remaining part of the anterior facet accentuating the strong depression adjacent to it. A similar projection of the trapezium was noted by Vrba (1981) in *Megantereon whitei* from Kromdraai, South Africa. In true cats, projection of the trapezium only slightly interrupts the general concavity of the surface. In lateral view, the shape of the metacarpal facet is broad and elongate proximodistally, as is characteristic of the genus. A facet for the magnum is lacking.

A left metacarpal III, UF 45409, is known from Inglis IA (Fig. 11C, D, Table 7). The proximal surface which articulates with the magnum is broadly concave. Along its lateral border is a rectangular facet for the unciform. Presence of this facet is diagnostic in smilodontines and *F. onca*. A deep, broad notch defines the medial border of the proximal surface in contrast to the acute, shallow notch in *F. atrox* and *F. onca*. In medial view, the anterior facet for metacarpal II is flat, and it has a more nearly longitudinal axis in contrast to the oblique axis in *Felis atrox* and *F. onca*. In lateral view (Fig. 11D), above the broad concavity for articulation with metacarpal IV, is the uniform facet. Below this concavity is a roughened area for origin of the *M. interosseous*.

Metacarpal IV is represented by UF 18110 and F:AM 69249 from Inglis IA and McLeod (Fig. 11E, F, Table 7). As is characteristic of the genus, the posterior side of the proximal end is not as broad as in true cats. The anterior border is notched near the middle. In anterior view (Fig. 11E), a diagnostic feature of this genus is apparent. The unciform surface forms a sharp angle with the plane of the surface for metacarpal III. In *F. onca* this angle is less prominent, and in *F. atrox* no sharp distinction between these surfaces exists. In medial view, a notch is present in the convex articulating surface for metacarpal III. Below this surface the shaft is slightly roughened for ligament attachments.

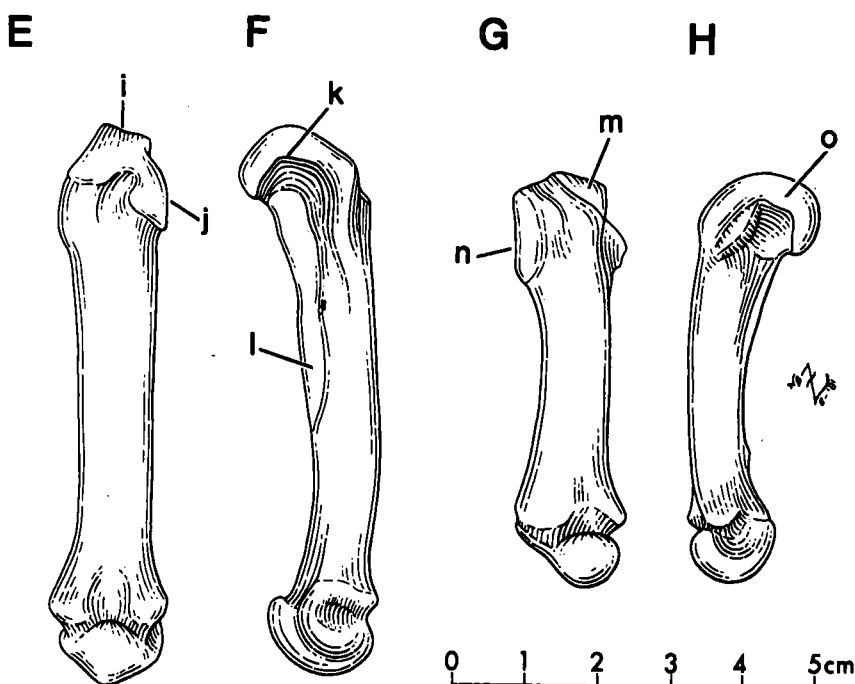
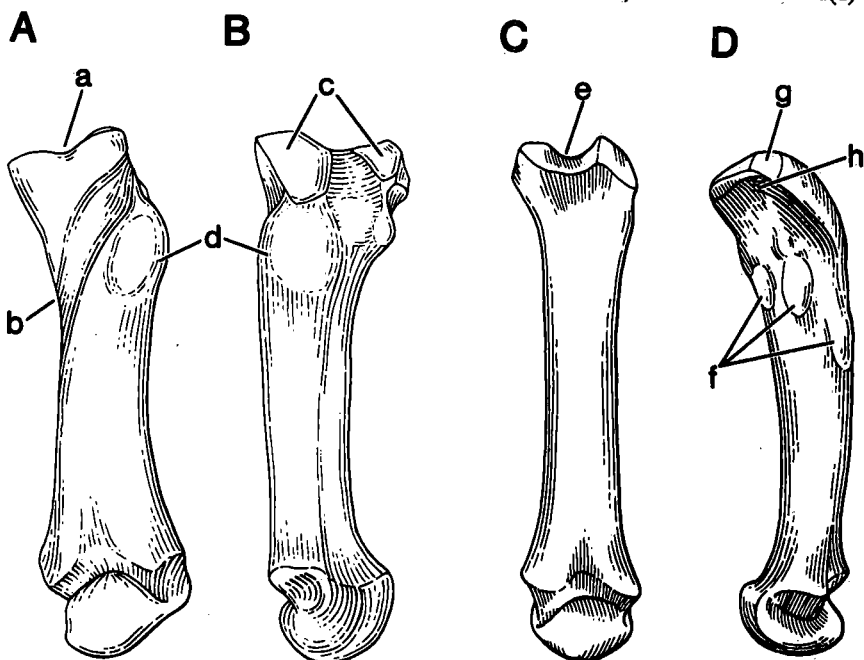
In lateral view (Fig. 11F), the articular surface for metacarpal V is prominent. Perhaps the most useful character separating this species from *S. populator* is the structure of the palmar hook. In *S. gracilis* the hook is flattened at the base. In *S. populator* it is bulbous and projects ventrally from the base. Extending from the proximal border of the hook to the

medial portion of the shaft is a prominent roughened area for origin of the *M. interosseus*.

UF 12935, a right metacarpal V from Inglis IA, is particularly short and robust (Fig. 11G, H; Table 7). The rounded proximal surface which articulates with the unciform is broad. Its curved lateral border (Fig. 11G) passes onto the roughened tuberosity of the proximal end. Onto this tuberosity attach ligaments and the *M. extensor carpi ulnaris* which functions to extend and abduct the forepaw. In medial view (Fig. 11H), the notch which incises the margin of the articulating facet for metacarpal IV is broad rather than narrow as in true cats. The posterior side forms a prominent hook. The shaft is flattened posteriorly and the median border of the distal end is sharply keeled.

A proximal right femur, UF 18112, is represented from Inglis IA (Fig. 12, Table 8). In proximal and posterior views (Fig. 12B), the head is hemispherical and at the same elevation as the pyramid-shaped greater trochanter. The greater trochanter is medially inclined relative to the anteroposterior axis of the shaft. The posterior surface serves as a broad area of attachment for extensors of the hip, the *Mm. gluteus, medius, minimus*, and *pyriformis*. The trochanteric fossa is large, though not as broad anteroposteriorly as in *S. populator*. True cats are usually distinguished in having a narrow, more restricted fossa. As is characteristic of smilodontines, a rounded prominent tuberosity is positioned between the head and the trochanteric fossa (see Fig. 12A, B). This tuberosity is less developed in true cats. The large lesser trochanter is directly below the tuberosity, a more medial position than in true cats. The tendon of the combined *M. psoas* and *iliacus*, extensors of the hip, insert on its apex. The posterior intertrochanteric crest which separates the fossa from the greater trochanter appears transversely rounded rather than flattened and angular as in true cats. On the upper part of this crest are areas of insertion for the *M. gluteus medius* and, below that for the *M. quadratus femoris*. Also apparent in posterior view (Fig. 12B) is the anterior intertrochanteric line which extends from the neck obliquely to its junction with the linea aspera below the lesser trochanter. It marks the upper border of the area of origin for *M. vastus externus*, an extensor of the hip joint.

A right patella, F:AM 108538, is represented from McLeod (Fig. 12). Most of the posterior surface is occupied by a concavo-convex articular facet for the trochlea of the femur (Fig. 12C). The distal end is broadly rounded. In lateral view (Fig. 12D), the anterior surface, which bears longitudinal striae, is strongly arched at its proximal end, becoming gently convex distally. The great proximal depth of this element is a diagnostic generic character. Measurements for F:AM 108538 are as follows: greatest anteroposterior diameter, 22.0; greatest transverse width, 34.8; greatest proximodistal diameter, 41.9.



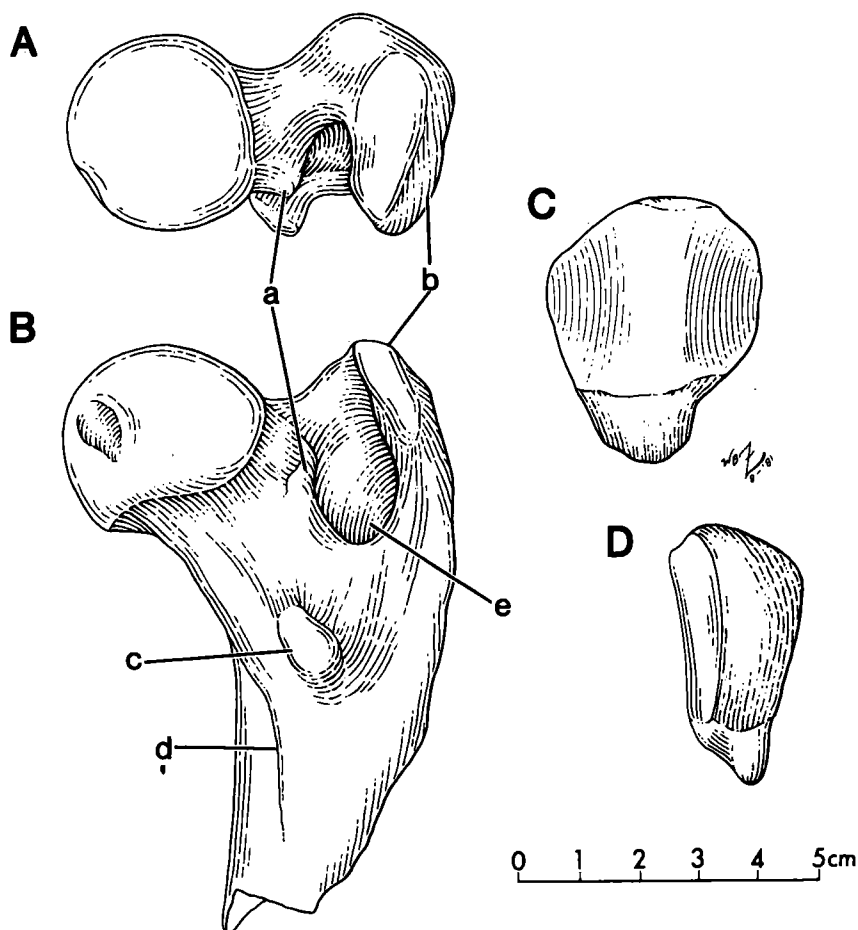


Figure 12. Right proximal femur, UF 18112, of Florida Smilodon gracilis from Inglis IA. (A) proximal; (B) posterior views. (a) prominent tuberosity, (b) greater trochanter, (c) lesser trochanter, (d) anterior intertrochanteric line, (e) intertrochanteric fossa. Right patella, F:AM 108538, of Florida Smilodon gracilis from McLeod. (C) posterior; (D) lateral views.

Figure 11. Right metacarpal II, UF 17498, of Florida Smilodon gracilis from Haile XVA. (A) anterior; (B) medial views. (a) for articulation with trapezoid, (b) radial artery, (c) for articulation with trapezium, (d) for insertion of M. extensor carpi radialis. Left metacarpal III, UF 45409, from Inglis IA. (C) anterior; (D) lateral views. (e) for articulation with magnum, (f) for origin of M. interosseo, (g) for articulation with unciform, (h) for articulation with metacarpal IV. Right metacarpal IV, UF 18110, of Florida Smilodon gracilis from Inglis IA. (E) anterior; (F) lateral views. (i) for articulation with unciform, (j) for articulation with metacarpal III, (k) for articulation with metacarpal V, (l) for origin of M. interosseo. Right metacarpal V, UF 12935, of Florida Smilodon gracilis from Inglis IA. (G) anterior; (H) medial views. (m) for articulation with unciform, (n) for insertion of M. extensor carpi ulnaris, (o) for articulation with metacarpal IV.

A right and a left distal tibia, UF 17496 and F:AM 95529, are represented from Haile XVA and McLeod (Fig. 13, Table 8). In anterior view (Fig. 13A), a relatively shallow notch defines the medial border of the distal extremity in contrast to the much deeper notch developed in true cats.

In posterior and medial views (Fig. 13B, C), the shaft of F:AM 95529 displays a strong vertical keel. This portion of the shaft is typically only slightly convex. Distally, the shaft is noticeably flattened as in *S. populator*. The medial malleolus in *Smilodon* and *Megantereon cultridens* projects farther distally than in true cats. Also noted in posterior view is a large, well defined deep groove on the medial malleolus for the tendon of *M. tibialis caudalis*, which is responsible for extension of the tarsus and outward rotation of the foot. A prominent ridge separates the course of the medial tendon of the *M. flexor digitorum longus* from the lateral tendon of the *M. flexor hallucis longus*, which function as flexors of the tarsus and extensors of the digits. In distal view, as is characteristic of smilodontines, the articular surface for the astragalus is anteroposteriorly broad. A triangular facet for articulation with the fibula exists on the extreme posterolateral corner of the element.

One right astragalus, TRO 1666, and three left astragali, UF 17496, TRO 1667, and F:AM 108536, are known from Inglis IA, Haile XVA, and McLeod (Fig. 14, Table 9). In anterior view (Fig. 14A), this element is characteristic of smilodontines and *F. onca* in having a short, broad neck and a shallowly grooved trochlea. The anteromedial border of the head extends farther distally on the neck than in true cats. A similar observation was noted by Schaub (1925) for *Megantereon cultridens*. The shape of the head is flattened and less hemispherical among smilodontines in comparison with true cats.

In posterior view (Fig. 14B), are two articular facets for the calcaneum. The sustentacular facet is connected by a narrow strip to the navicular facet in this species and *F. onca*. Between these facets is a small ovoid pit for attachment of a ligament. In *S. populator* a much broader connection between these facets is developed. In the extinct cat *F. atrox* and the Recent cats *F. leo* and *P. trigris*, these facets are separate articular facets, and the ligamental pit is deeper. A deep, oblique groove separates these articular surfaces from the astragalocalcaneal facet on the lateral half of the element. An astragalar foramen, present in three specimens in the distal portion of the groove, is absent in true cats.

Four right calcanei; TRO 1668, F:AM 95534, F:AM 95532, and UF 24000; and four left calcanei; F:AM 95533, UF 12936, UF 12937, UF 18113, and UF 23999; are known from Inglis IA and McLeod (Fig. 15, Table 10). In anterior view (Fig. 15A) the most diagnostic feature is apparent, the orientation of the sustentacular and navicular facets relative to the cuboid border. In *F. atrox*, these facets are well separated from one another. In *S. populator*, these facets are adjacent and their articular surfaces broadly

joined. In *S. gracilis* and *F. onca*, a narrow articular strip connects these facets. The large, concave astragalocalcaneal facet in *Smilodon* usually does not encroach upon the short, robust calcaneal tuber as far as in true cats. A prominent groove for transmission of the tendon of the *M. peroneus longus*,

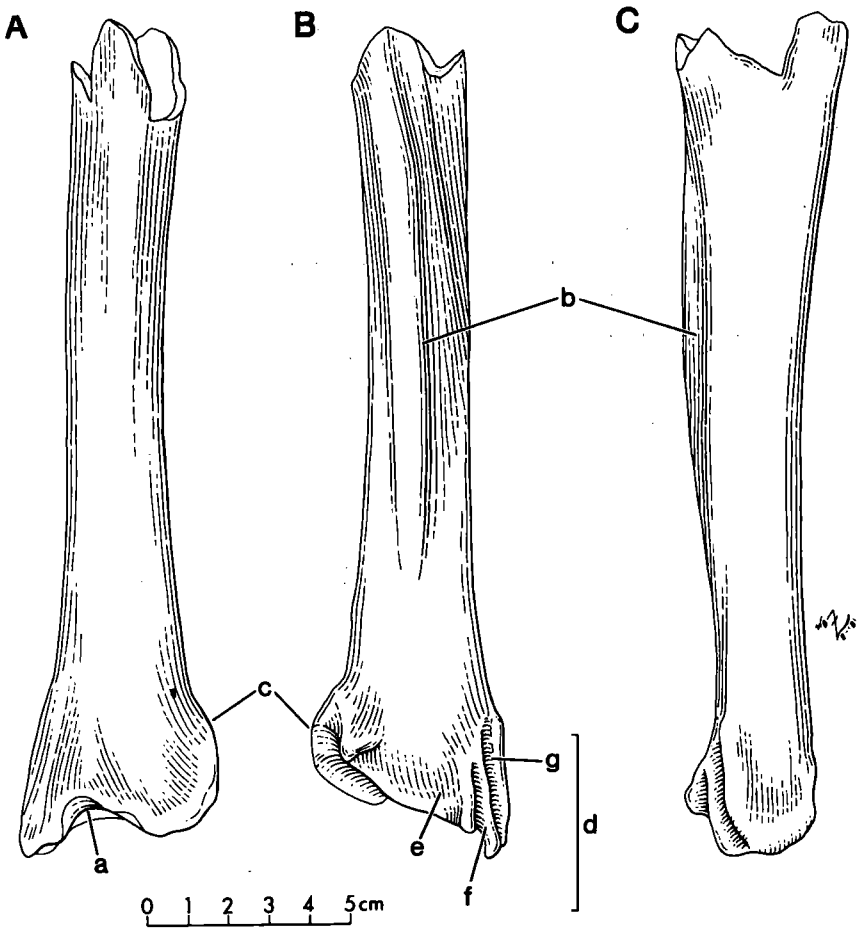


Figure 13. Left distal tibia, F:AM 95529, of Florida *Smilodon gracilis* from McLeod. (A) anterior; (B) posterior, and (C) medial views. (a) shallow notch, (b) keel, (c) lateral malleolus, (d) medial malleolus, (e) for origin of *M. flexor hallucis longus*, (f) for origin of *M. flexor digitorum longus*, (g) for origin of *M. tibialis caudalis*.

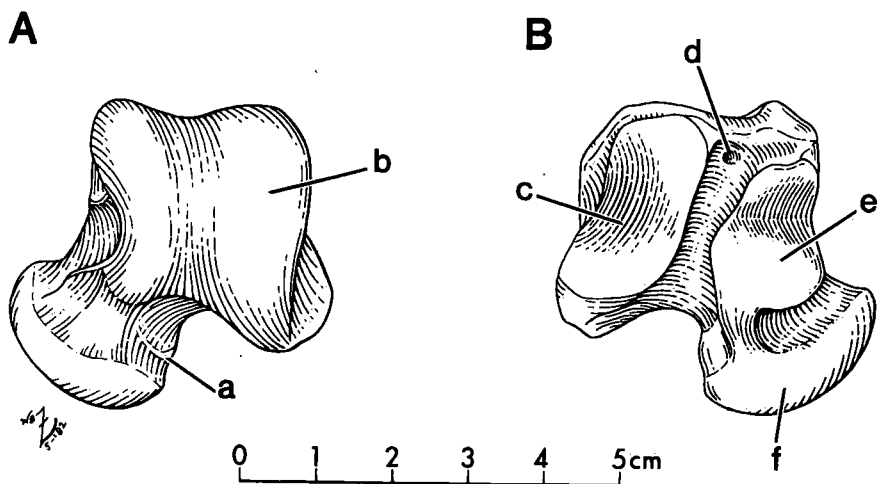


Figure 14. Left astragalus, F:AM 17496, of Florida Smilodon gracilis from Haile XVA. (A) anterior; (B) posterior views. (a) neck, (b) tibial trochlea, (c) astragalocalcaneal facet, (d) astragalar foramen, (e) sustentacular facet, (f) navicular facet.

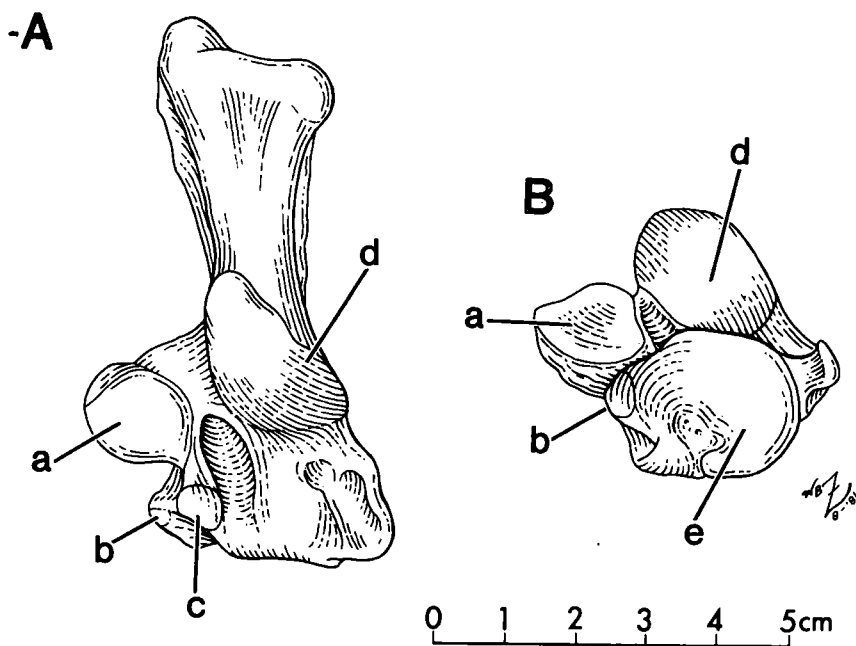


Figure 15. Left calcaneum, F:AM 95533, of Florida Smilodon gracilis from McLeod. (A) anterior; (B) distal views. (a) sustentacular facet, (b) navicular facet, (c) astragalar facet, (d) astragalocalcaneal facet, (e) cuboid facet.

which functions in eversion and abduction of the foot, is positioned on the lateral margin of the calcaneal tuber. This groove is present, although less well developed, in true cats with the exception of the jaguar. The sustentaculum is elevated only a short distance above the distal end, a diagnostic feature of smilodontines. The proximal portion of this element in lateral view is marked by a distinct pit for insertion of the external lateral ligament. At the distal end a deep groove, which transmits the tendon of the *M. peroneus longus*, crosses the lateral surface. In distal view (Fig. 15B), the articular surface for the cuboid is distinctly concave and pierced by numerous foramina. A small triangular facet for the navicular, absent in true cats, is usually present on its medial margin.

A right cuboid, F:AM 105838, from McLeod (Fig. 16) has a roughly rectangular proximal surface with nearly straight dorsal and medial margins (Fig. 16A). The posterior border is emarginate to a greater degree than in true cats. This surface is slightly convex and articulates with the distal end of the calcaneum. In medial view (Fig. 16B), the navicular facet occupies the dorsoplantar corner of the cuboid. In this specimen two facets provide articulation for the ectocuneiform. As noted by Jayne (1898), these facets are subject to variation; in both *Smilodon* and true cats they are joined together in a single crescentic facet which, in *Smilodon*, is positioned farther distally than in true cats. Also illustrated in this view is the shorter proximodistal diameter of the element when compared with true cats.

In posterior view the cuboid is divided into two parts by an oblique groove which provides passage for the tendon of the *M. peroneus longus*. Proximal to this groove is a prominent tuberosity on which flexors of the digits originate, the *Mm. adductor indicis*, *adductor digiti minimi*, and the *opponens digiti minimi*. Medial to the tuberosity is a concavity roughened for the insertion of a ligament. A characteristic of the genus is seen on the distal face of the cuboid; the articular facet for metatarsal IV is smaller than this same facet in true cats. The facet for metatarsal V in *Smilodon* is larger than the same facet in true cats. Measurements for F:AM 105838 are as follows: anteroposterior diameter, 23.7; transverse diameter, 25.2; proximodistal diameter, 24.5. In a right navicular, F:AM 95521, from McLeod (Fig. 16), most of the proximal surface is occupied by the concave, oblong facet for the distal end of the astragalus (Fig. 16C). This facet is slightly deeper than in true cats.

In lateral view (Fig. 16D), another unique generic character is visible. In addition to the presence of a triangular, flat facet for articulation with the cuboid, a small, convex facet for the calcaneum is positioned proximal to the former facet. The calcaneal facet is absent among true cats.

The proximal plantar tuberosity is more strongly developed than in *Smilodon populator*. The medial side presents no articular facets and is oblong and convex.

The rectangular distal surface displays rounded margins. The posterolateral portion is roughened for attachment of interosseous ligaments, and the remainder of the surface is occupied by articular facets for the cuneiform bones. The largest facet, for the ectocuneiform occupies the dorsolateral portion of the element. It is not as broad dorsolaterally as in true cats, and the dorsolateral margin is angular rather than broadly rounded. A deep pit for insertion of a ligament exists posteromedially. A small round facet for articulation with the proximal surface of the ectocuneiform separates this pit from the medial margin. Dorsal to this facet is a slightly larger facet, which articulates with the proximal surface of the mesocuneiform. Measurements for F:AM 95521 are as follows: anteroposterior diameter, 37.3; transverse diameter, 26.0.

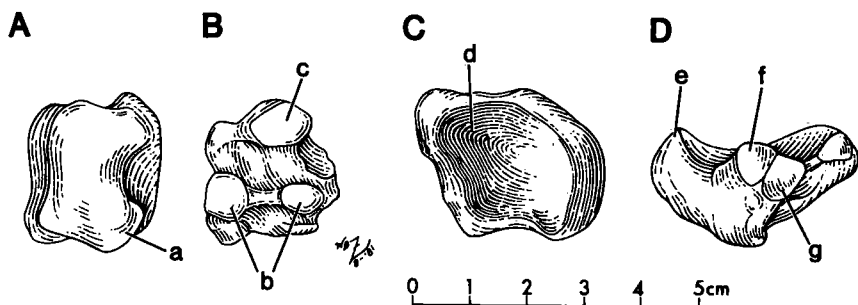
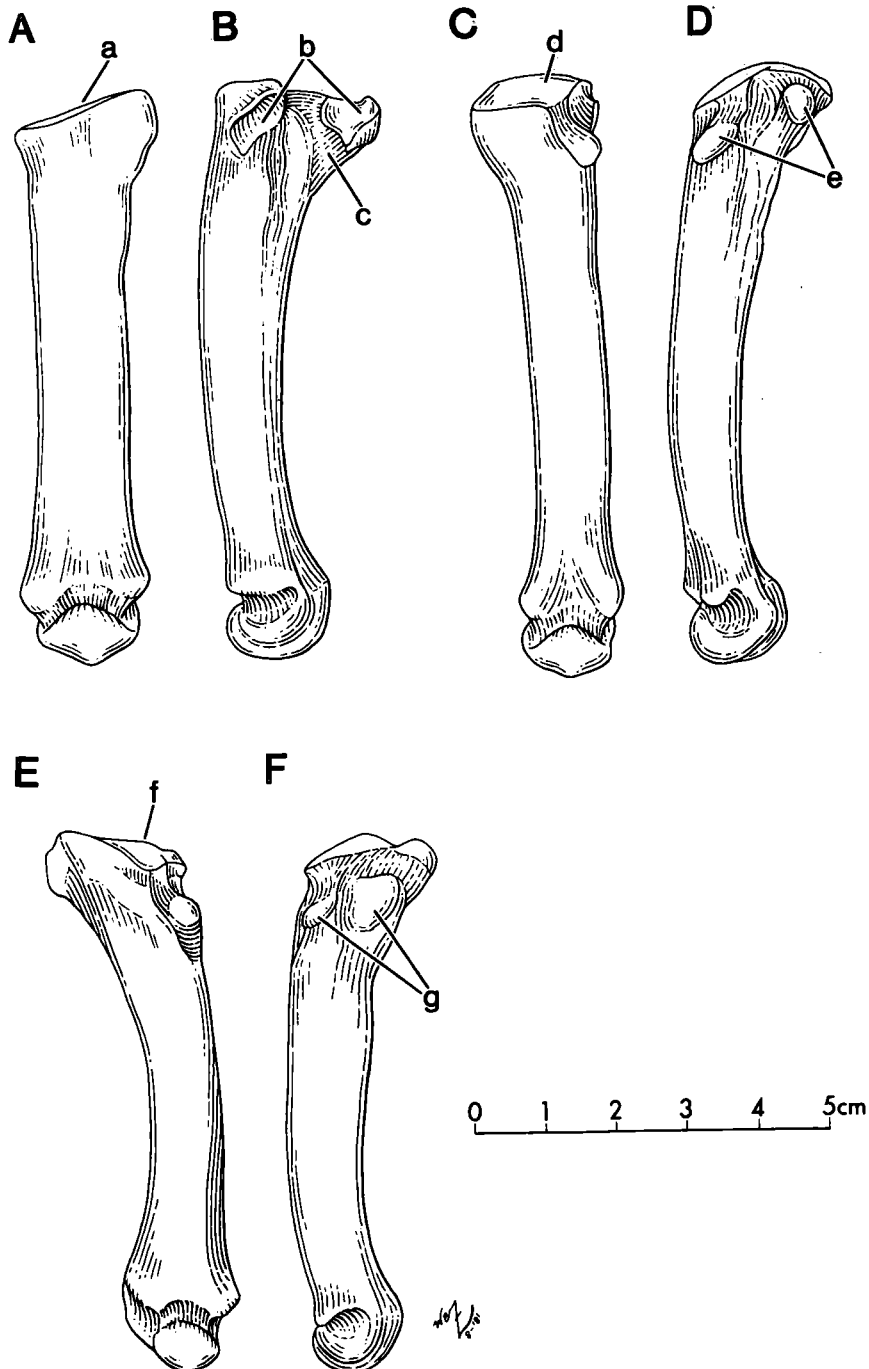


Figure 16. Right cuboid, F:AM 105838, of Florida *Smilodon gracilis* from McLeod. (A) proximal; (B) medial views. Anterior is to the left. (a) for articulation with calcaneum, (b) for articulation with ectocuneiform, (c) for articulation with navicular. Right navicular, F:AM 95521, of Florida *Smilodon gracilis* from McLeod. (C) proximal; (D) lateral views. Anterior is to the left. (d) for articulation with astragalus, (e) proximal plantar tuberosity, (f) for articulation with calcaneum, (g) for articulation with cuboid.

Figure 17. Left metatarsal III, UF 12939, of Florida *Smilodon gracilis* from McLeod. (A) anterior; (B) lateral views. (a) articulation with ectocuneiform, (b) for articulation with metatarsal IV, (c) for insertion of ligament. Right metatarsal IV, UF 12940, of Florida *Smilodon gracilis* from Inglis IA. (C) anterior; (D) medial views. (d) for articulation with metatarsal III. Right metatarsal V, F:AM 95531, of Florida *Smilodon gracilis* from McLeod. (E) anterior; (F) medial views. (f) proximal tuberosity for articulation with cuboid, (g) for articulation with metatarsal IV.



As is true of the metacarpals, the metatarsals are relatively short and robust. Metatarsal III (UF 12939, F:AM 69241) is represented from Inglis IA and McLeod (Fig. 17A, B, Table 11). The proximal surface is T-shaped and the arm extends posteriorly. The posterior portion of the arm is transversely broader and shorter than in true cats. In anterior view (Fig. 17A), the proximal surface, which articulates with the ectocuneiform, is nearly flat and slopes medially.

In medial view, two facets which articulate with metatarsal II are separated by a groove. The posterior facet is obliquely oriented, whereas in true cats the axis is longitudinal. Below these facets on the shaft are roughened areas for insertion of ligaments binding this element to metatarsal II. In lateral view (Fig. 17B), are positioned two facets which articulate with metatarsal IV. As is characteristic of the genus, the larger posterior facet extends farther ventrally and proximally, forming a broad surface of attachment. Below these facets are prominent rugosities for ligament attachments. The medullary foramen is proximally positioned on the shaft.

Metatarsal IV (UF 12940, F:AM 95530, and F:AM 69243) is known from Inglis IA and McLeod (Fig. 17C, D, Table 11). The proximal surface for articulation with the cuboid is rectangular and less extensive than in true cats (Fig. 17, Table 11). The proximal surface for articulation with the cuboid is rectangular and less extensive than in true cats (Fig. 17C). In *Smilodon* the posterior tuberosity extends for a considerable distance behind the posterior margin of the cuboid facet.

In medial view (Fig. 17D), at the proximal end, is an ovoid anterior facet and a rectangular posterior facet for articulation with metatarsal V. These facets are separated from one another by a groove. In lateral view one large posterior facet and a small anterior facet, both rectangular, provide articulation surfaces for metatarsal III. In *S. gracilis* the posterior facet is considerably smaller in the anteroposterior dimension. The anterior facet is situated on a distinct pedicel and separated from the posterior tuberosity. Below the posterior facet is a linear roughened area for origin of the *M. interosseous*.

A right metatarsal V, F:AM 95531, is represented from McLeod (Fig. 17, Table 11). The proximal surface is triangular. The anterior view (Fig. 17E) is characteristic of the genus: the proximal tuberosity is not flattened and elongate as in true cats, rather it is rounded and shortened proximodistally. In *S. populator* this tuberosity is less pronounced. A notch is present along its posterior margin. The stoutness of the shaft and its degree of curvature are well illustrated in this view. In medial view (Fig. 17F), two facets for articulation with metatarsal IV are positioned below the flattened articular facet for the distal end of cuboid. In *S. gracilis*, the separation between the cuboid facet and the posterior metatarsal IV facet is

sharp and angular. In *S. populator*, these two facets, although separated by a sharp ridge, are broadly convex. Below the posterior articular facet is a prominent tendon scar.

Of the three proximal phalanges represented from McLeod, F:AM 95535a is assigned to the second digit of the left forepaw; F:AM 95535b and F:AM 95535c are assigned to the second and third digits of the right hindpaw, respectively (Fig. 18 A-F, Table 12). These assignments are based on relative size, degree of curvature, and shape of the proximal surface of the element. In posterior view, the lateral and medial sides of the shaft of all proximal phalanges are marked near their distal ends by ovate roughened tendon scars. F:AM 95535a displays an arcuate anterior border on the proximal surface and a narrowly incised posterior border. The shaft is arched lateromedially. F:AM 95535b exhibits an arcuate border that gives way to a sharply angular posteromedial border on the proximal surface. The posterior surface is broadly notched which, along with the greater transverse width of the shaft, identifies this element as belonging to the hindpaw. F:AM 95535c displays an arcuate anterior border and a narrowly notched posterior border. The shaft is flattened lateromedially, distinguishing it from F:AM 95535a.

Four middle phalanges are represented from McLeod, F:AM 108537a, F:AM 108537b, F:AM 108537c, and F:AM 108537d, are assigned to the second, third, fourth, and fifth digits of the left forepaw. The proximal surface of all middle phalanges is triangular with concave facets for articulation with the trochlea of the proximal phalanges. The medial border of the shaft in F:AM 108537a is strongly curved. Arthritic lipping is displayed on the proximolateral extremity of the shaft. F:AM 108537c is similar in structure, although somewhat larger, than F:AM 108537b and shows arthritic lipping on the distal portion of the shaft and articular head. F:AM 108537d displays a curved median border and a deeply concave shaft proximodistally.

ADAPTATIONS

Smilodon gracilis is characterized by the presence of large, slightly recurved upper canines with long sharp-edged blades that lack strong serrations. Most traditional reconstructions show sabercats as active predators killing large prey by stabbing with their elongate canines into the back of the head or the nape of the neck. As demonstrated in a functional analysis of sabertooth jaw mechanics, it is more likely that the throat or neck was the target area where "one slash could sever critical blood vessels and result in rapid death" (Emerson and Radinsky 1980:308). As Martin (1980) suggested, sabercats were probably unable to tear flesh directly from

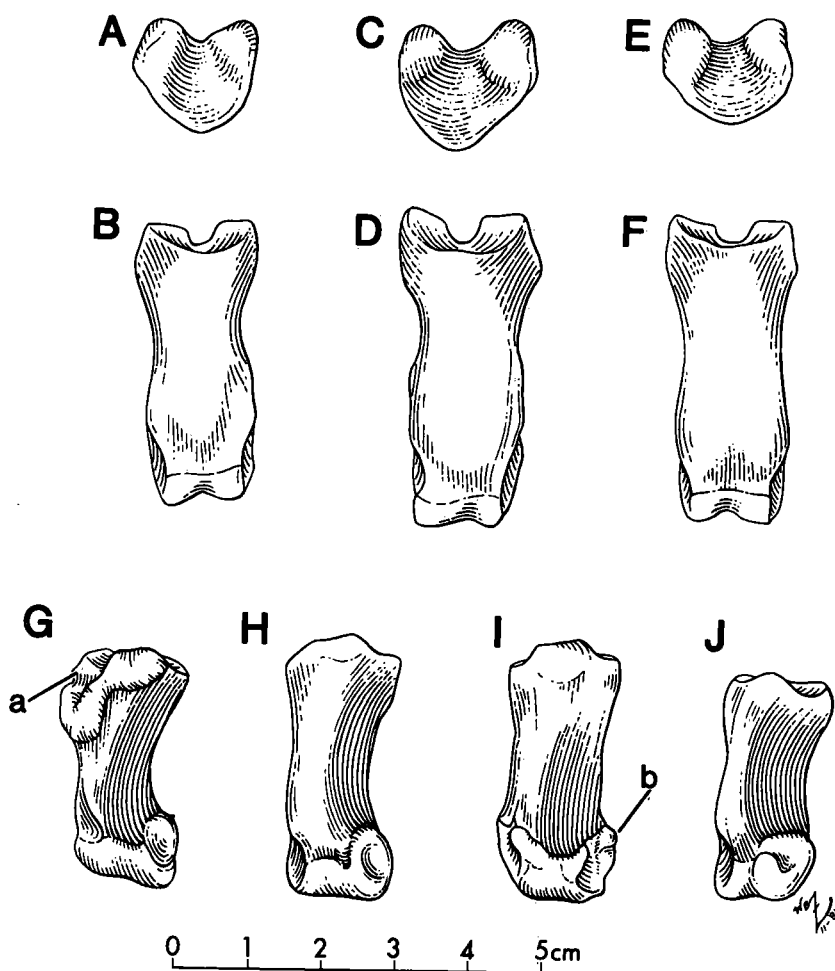


Figure 18. Left proximal phalanx (digit II, forefoot) F:AM 95535a, of Florida *Smilodon gracilis* from McLeod. (A) proximal; (B) anterior views. Right proximal phalanx (digit II, hindfoot) F:AM 95535b, of Florida *Smilodon gracilis* from McLeod. (C) proximal; (D) anterior views. Right proximal phalanx (digit III, hindfoot) F:AM 95535c, of Florida *Smilodon gracilis* from McLeod. (E) proximal; (F) anterior views. Left medial phalanx (digit II, hindfoot) F:AM 108537a of Florida *Smilodon gracilis* from McLeod. (G) anterior view. (a) arthritic lippling. Left medial phalanx (digit III, hindfoot) F:AM 108537b, of Florida *Smilodon gracilis* from McLeod. (H) anterior view. Left medial phalanx (digit IV, hindfoot) F:AM 108537c, of Florida *Smilodon gracilis* from McLeod. (b) arthritic lippling. Left medial phalanx (digit V, hindfoot) F:AM 108537d, of Florida *Smilodon gracilis* from McLeod. (J) anterior view.

the bone, as do other carnivores, because the upper canines would get in the way. Food was probably taken in to the side of the mouth, an operation perhaps facilitated by the incisors. Both upper and lower incisors of sabercats are prognathous, sharply pointed, and recurved, and they probably served to pull flesh away from the bone. Once in the mouth, food was processed by elongate shearing blades of the highly modified cheek teeth. The mandible, with its relatively large flange, served as protection for the sabers, as noted by Kurtén (1963) who interpreted reduction of the flange in *S. populator* to be the result of the saber biting outside the lower lip.

In comparison with true cats, limbs and feet of the gracile sabercat reflect differences in form and extent of articular areas, muscle attachment sites, and relative proportions of the elements themselves. Modifications of smilodontine felids over true cats were in the direction of power and flexibility rather than speed.

The importance of the anterior limbs in grasping and holding prey in sabercats is evident when one considers the lateral forces that occurred on the canines during the stabbing of struggling prey. The forelimb of the gracile sabercat was capable of considerable range of motion and movement. The abductor function of the limbs was increased as judged from the broad lateral epicondyle and associated musculature and the well developed *M. teres* scar on the humerus.

Both *S. gracilis* and *F. onca* have an olecranon process with a larger lateral margin relative to that of the medial margin. According to Gonyea (1978), among forest adapted felids (e.g. clouded leopard, *Neofelis nebulosa*, and jaguar, *Felis onca*) a large lateral olecranon is correlated with a large lateral *M. triceps*, which permits greater mediolateral rotation at the elbow joint in these cats. The increased supinator-pronator ability of the saber cat forelimb is further reflected in the laterally positioned larger radial notch which permitted medial rotation of the wrist during flexion.

Gonyea (1978) correlated shape and position of the olecranon fossa with habitat preference in a functional study of felid forelimb anatomy. He demonstrated a greater olecranon angle among those carnivores in which motion about the humero-ulnar joint is not restricted in the mediolateral plane. Felids that were exclusively forest dwellers were found to have a high inclination of the olecranon fossa. The inclination of the olecranon fossa relative to the longitudinal axis in *S. gracilis* (N=4) varies between 23° and 27°. This high value suggests that the Florida gracile sabercat was forest adapted.

Smilodontine felids exemplify the digitigrade posture characteristic of true cats; however, both *Smilodon* and *Felis onca* display several features of the hindlimbs and feet that are more characteristic of plantigrade felids (including *Hoplophoneus*, *Eusmilus*, and *Sansanomilus*; see Ginsburg 1961). Plantigrade features shared by *Smilodon* and *F. onca* include relatively short, stocky limbs, broad area of insertion on the tibia for the *M. tibialis caudalis*, development of a large groove on the short calcaneal tuber for passage of the *M. peroneus longus*, and short metapodials which, when articulated, tend to spread out in a fan. These features strongly suggest a de-emphasis upon cursoriality and an increase in power and flexibility among these sabercats.

The hindfeet of *S. gracilis* are significantly larger than the forefeet (Tables 7 and 12). A similar proportional relationship exists between the fore- and hindfeet of *Megantereon cultridens* (Schaub 1925:256). In contrast, *S. populator* exhibits more equally proportioned feet (Merriam and Stock 1932, tables 55-61 and 80-86). The fore and hindfeet of sabercats were equipped with retractile claws which may have enhanced prey immobilization and facilitated an accurate canine strike.

Unfortunately the limbs of *S. gracilis* are incomplete and do not permit the computation of limb ratios. It has been shown by Gonyea (1976) that the short, robust limbs and body proportions of *S. populator* are similar to those of modern felids that inhabit forested environments. However, this species seems to be better represented in plains and woodland habitats (e.g. Rancho La Brea). One of the best known samples of the gracile sabercat, that from Inglis IA, provides additional evidence for occurrence of this taxon in open habitats. Gonyea suggested that the success of *Smilodon* in low structured habitats may have been a function of its sociality and group hunting efforts.

The dental and postcranial anatomy of smilodontine felids suggests that they evolved hunting strategies that relied upon stalking and ambush rather than rapid pursuit. Limb morphology suggests that they were forest adapted, although they are better sampled from plains and woodland habitats.

SIZE TRENDS

Faunal comparisons of tooth and postcranial measurements between the late Blancan (El Jobean), early Irvingtonian (Inglis IA), and late Irvingtonian (Port Kennedy, McLeod) localities indicate that late Irvingtonian specimens average larger and suggest a trend toward size increase for the gracile sabercat. Kurten (1968) and Kurten and Crusafont-Pairo (1977) observed a similar increase in size among Eurasian *Megantereon* during the Villafranchian (Tables 13, 14). It is also apparent from these data that *S. gracilis* was a larger animal than *Megantereon*.

The upper canines of late Irvingtonian *S. gracilis* are significantly larger and broader than those of late Villafranchian *Megantereon cultridens*, although sexual dimorphism probably accounts for some of this variation. A fragmentary upper canine referred to *S. populator* from Conard Fissure (late Irvingtonian) is slightly larger than the late Irvingtonian *S. gracilis*. P^3 in late Villafranchian *M. cultridens* shows a tendency toward reduction in size when compared with early Villafranchian specimens, although a parallel trend was not observed among *S. gracilis* (Table 13).

The lesser size variability of M_1 makes it particularly sensitive to evolutionary increase in body size in mammalian species (Gingerich 1974). The larger M_1 of both late Irvingtonian *S. gracilis* and late Villafranchian *M. cultridens*, relative to earlier specimens of each species, provides the best evidence for an increase in size of these sabercats through time. The more derived species, *S. populator*, is significantly larger than either *S. gracilis* or *M. cultridens*, as demonstrated by comparison of tooth and body measurements (Tables 13, 14).

PHYLOGENETIC RELATIONSHIPS

Recently Churcher (1984) proposed recognition of *Smilodon gracilis* as a junior synonym of species described under *Ischyrosmilus*, which he referred to the tribe Smilodontini. This hypothesis differs fundamentally from the hypothesis of machairodont relationships presented by Berta and Galiano (1983) and from the views presented here. A comprehensive systematic revision of the machairodont Felidae is necessary to fully resolve these differences. Although such a revision is clearly beyond the scope of this paper, the following discussion will provide a preliminary rebuttal of Churcher's proposal.

Central to Churcher's systematic hypothesis is his statement that "All characteristics given by Merriam for species of the genus *Ischyrosmilus*, except variation in size, are descriptive and accurately diagnose Port

Kennedy [and Florida] *Smilodon gracilis*." Merriam's (1918) description of *Ischyrosmilus* is as follows: "mandible massive, flange clearly marked, relatively wide anteriorly, slightly wider than in *Smilodon*, not as strongly developed as in *Machaerodus* but shorter than in *Smilodon*. P_3 very small, with only one root. P_4 with single cusp or incipient division of this cusp." Examination of both the Port Kennedy and Florida sabercat material shows that they bear little resemblance to Merriam's description. As Churcher (1984:20) commented, "...the mandibles of *S. gracilis* and *S. mercerii* are more slender and lightly built than are those of *S. floridanus* ..." and, as he adds later, "the flanges...are thinner." Length of the diastema may be of questionable value as it appears to vary to some degree with the age of the individual (Merriam and Stock 1932, pl. 4). The reduction in size of P_3 is not diagnostic of *Ischyrosmilus*, because it is also seen in *Smilodon* and *Megantereon*. Churcher's (1984, Fig. 1) photograph shows that P_4 is not single cusped but rather consists of a principal cusp flanked by a posterior cusplet and a strong lingual cingulum that forms the tooth heel.

Churcher (1984) compared the Port Kennedy type material of *Smilodon gracilis* with the Rancho La Brea and Talara, Ecuador, late Pleistocene *Smilodon* and concluded that these sabercats represented different genera, although he noted their similar morphology and slightly overlapping measurements. Apart from their smaller size and more gracile proportions, the most distinctive features of the Port Kennedy sabercat noted by Churcher include finer serrations on the canine, the absence of a protocone (despite the presence of a protoradix) on P^4 , and a well developed mandibular flange. The condition of the protocone on P^4 is probably variable, as is shown in the larger sample of *S. gracilis* from both Inglis IA and Leisey Shell Pit in which a small isolated protocone supported by a large root is regularly present. The well developed serrations on the canines and the reduced mandibular flange diagnostic of *S. populator* are more reasonably considered species level differences that would be expected in the transition from *S. gracilis* to *S. populator*. In short, Churcher's (1984) taxonomic proposal does not seem necessary, although his view of machairodont systematics deserves further testing.

Berta and Galiano (1983) rejected *Ischyrosmilus* as a useful taxon and referred the genotype *Ischyrosmilus ischyurus* to the genus *Dinobastis*. The following suite of characters diagnose *Dinobastis*: mandibular flange with a strongly rectangular symphyseal margin, angular process long and bulbous, deeply excavated masseteric fossa, single mental foramen on flange, and shorter, dagger-like upper canines. This cat is known from Irvingtonian through Rancholabrean deposits in North America. The largest, most complete sample is from Friesenhahn Cave in Texas (Meade 1961), although considerable undescribed material from near Fairbanks, Alaska, exists in the Frick collection (AMNH).

Other recognized species of *Ischyrosmilus*, *I. crusafonti*, *I. johnsoni*, and *I. idahoensis*, were reassigned to *Homotherium* by Berta and Galiano (1983). *Homotherium* differs from *Dinobastis* in the following features: mandibular flange with an angled symphyseal margin, angular process prominent but not bulbous, shallow masseteric fossa, and long, strongly recurved saber-like upper canines. *Homotherium* is well known in Asia; in North America it occurs in Blancan sites in California (Asphalto), Idaho (Fromans Ferry), Texas (Cita Canyon and Channing), and Nebraska (Broadwater).

The relationship between *Homotherium*, *Dinobastis*, and other machairodonts was discussed by Berta and Galiano (1983). They recognized three tribes within the Machairodontinae: Metailurini, Machairodontini, and Smilodontini. These three tribes share primitively the following characters: upper canines elongate and laterally compressed, upper incisors enlarged, P^4 parastyle enlarged, P^3 and $P^{3/3-4}$ with strong anterior and posterior accessory cusps, robust rectangular symphysis, and reduced coronoid process. *Dinobastis*, *Homotherium*, and *Machairodus* were included in the Machairodontini. They can be distinguished from genera in the more derived Smilodontini by the following characters: deeper more massive mandibles, elongate mastoid process ventrally directed and not closely appressed to the glenoid process, upper incisors arranged in a broad arc, shorter flatter upper canines, long narrow carnassials, serrated margins on P_4-M_1 , M_1 with small talonid heel, and long limbs with slender proportions.

Smilodon and *Megantereon* comprise the tribe Smilodontini, sister group of all other machairodonts. A summary of the cladistic relationships of *Smilodon* and related taxa is presented in Figure 19. The close relationship between *Smilodon* and *Megantereon* has been recognized by various authors (Schaub 1925; Thenius 1967; Kurtén 1963, 1968; Repenning 1967; Schultz and Martin 1970; Beaumont 1978; and Martin 1980). Martin (1980) referred *S. gracilis* (sic) to *Megantereon* on the basis of the following similarities: lack of serrations on upper canines, relatively large mandibular flange, and a large P_3 . These similarities represent shared primitive characters and cannot be used to support a close phylogenetic relationship between these taxa. Berta and Galiano (1983) proposed a closer relationship of *S. gracilis* to *S. populator* than to *Megantereon*.

Megantereon and *Smilodon* share the following derived characters (Fig. 19, point 1): (a) upper canines elongate, laterally compressed, and recurved; (b) long postcanine diastema; (c) P^4 with reduced protocone, ectoparastyle enlarged, and anteriorly directed; (d) glenoid process enlarged; (e) prominent postorbital processes; (f) well developed supraoccipital crest; (g) lower canines reduced; (h) $P^{2/2}$ lost; (i) $P^{3/3}$

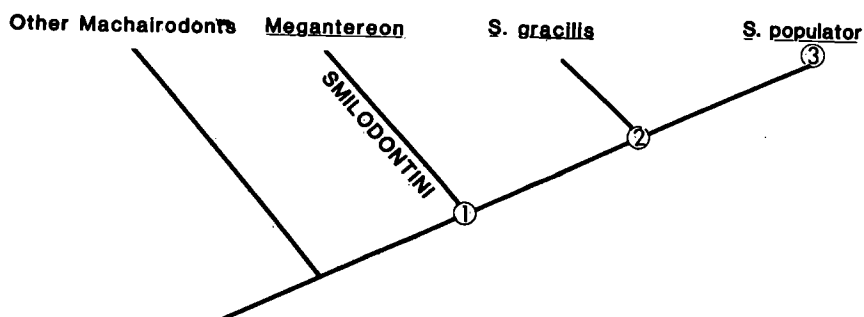
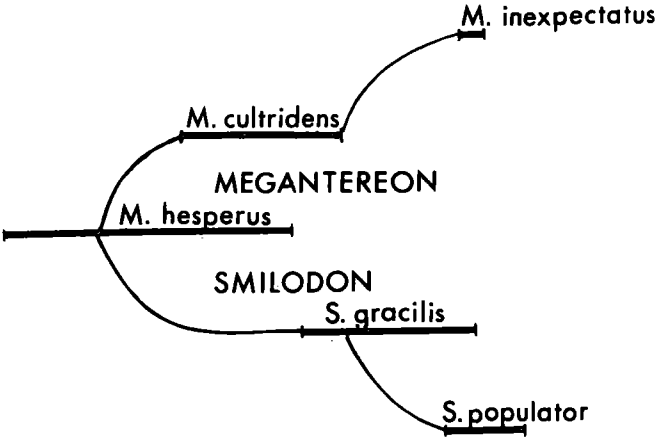


Figure 19. Cladogram expressing relationships among the Smilodontini. Numbers refer to shared derived characters explained in text.

Figure 20. Phylogram expressing relationships among the Smilodontini plotted against geologic time. Vertical bars represent approximate geochronologic occurrence of a particular taxon. Lines express relationships. Geologic time scale follows Berggren and Van Couvering, 1974. Correlation of North American and European mammal ages are slightly modified from Fejfar (1976) and Repenning (in press).

M p	Y	b	6
Epochs			
European L.M. Ages		No. American L.M. Ages	
Steinheim.		Ranchol.	
Biharian		Irvington.	
Villafranchian		Blancan	
Ruscinian		Hemphillian	
PLEIST.		PLIOCENE	
1		4	
2		5	
3		6	
MIOCENE			



reduced; (j) coronoid process reduced; (k) mandibular flange; (l) limbs and feet short and stocky; and (m) shortened tail. *Smilodon* differs from *Megantereon* in the following characters (Fig. 19, point 2): (a) incisors enlarged and procumbent; (b) upper canines further elongated and robust; (c) glenoid process greatly enlarged; (d) mastoid process enlarged; (e) P^3 reduced, sometimes with single or fused roots; (f) P^4 ectoparastyle further enlarged; and (g) mandibular flange reduced.

The *Smilodon* lineage is comprised of two species. Within this species group a morphocline is recognized from *S. gracilis* to *S. populator*. *S. gracilis* can be viewed as a transitional taxon separable from *S. populator* largely by its lack of characters. *S. populator* is distinguished from *S. gracilis* on the basis of the following characters (Fig. 19, point 3): (a) larger size; (b) upper canines more strongly recurved; (c) upper canines and cheek teeth with strongly serrated anterior and posterior margins; (d) P^4 with reduced protocone; (e) broadened muzzle; (f) mandible with single large mental foramen; (g) P_3 usually absent; and (h) mandibular flange greatly reduced.

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

Figure 20 summarizes the phylogenetic relationships of *Smilodon* and *Megantereon* plotted against geologic time. The oldest record of *Megantereon* is *M. hesperus* from the late Hemphillian Upper Bone Valley Formation of Florida (Berta and Galiano 1983). This species ranged into central and western North America during the middle Blancan. Old World records of *Megantereon* indicate that the genus first appeared in Eurasia and Africa somewhat later, during the early Villafranchian. At least one species, *M. inexpectatus*, survived into early Biharian at Choukoutien.

During the late Blancan, the genus *Smilodon* evolved in North America. *S. gracilis* is recorded from the following Florida late Blancan faunas: Haile XVA (Webb 1974a, Robertson 1976), Santa Fe River IA (Kurtén 1965), and Bass Point Waterway No. 1 (Churcher 1984) (Fig. 1). The age assignment for these faunas is supported by the presence of *Nannippus phlegon* (Robertson 1976, MacFadden and Waldrop 1980; Churcher 1984), a Blancan "index fossil." The El Jobean record of *S. gracilis* may also represent a late Blancan occurrence of this taxon. Unfortunately, no additional fauna was collected from this locality (Burgess, written communication 1981). *S. gracilis* is best represented in eastern North America in the early Irvingtonian of Florida at Inglis IA (Klein 1971, Webb 1974b), Leisey Shell Pit, and at Port Kennedy Cave, Pennsylvania, the type locality. The Inglis IA fauna can be considered equivalent in age to the Curtis Ranch fauna which Lindsay et al. (1975) assigned to the Matuyama Polarity Chron, approximately 1.9 mybp. In addition to *S. gracilis*, the

following mammalian taxa are common to both faunas: *Chasmaporthetes ossifragus*, *Canis edwardii*, *Platygonus bicalcaratus*, *Capromeryx arizonensis*, and an advanced *Ondatra* cf. *O. idahoensis*. The Port Kennedy Cave fauna resembles that of Conard Fissure and Cumberland Cave, which are probably Kansan in age. A slightly older age, Aftonian or early Kansan, is suggested for Port Kennedy by the presence of *S. gracilis* and *Ursus americanus*, more advanced than their late Blancan predecessors (Kurtén and Anderson 1980). The stage of evolution of *Neofiber* at McLeod supports a late Kansan or early Yarmouthian age for the fauna (Frazier 1977). A fragmentary lower jaw here referred to *Smilodon* cf. *S. gracilis* was collected from the late Blancan/early Irvingtonian Palm Springs Formation, Vallecito Creek, California. The Vallecito section spans an interval from 0.8 to 1.5 mybp and has been correlated with the Blanco and Curtis Ranch faunas (Kurtén and Anderson 1980). Kurtén (1967) referred a lower jaw from Rancholabrean deposits as Valsequillo, near Puebla, Mexico, to *Smilodon* cf. *S. gracilis*. However, lack of diagnostic *S. gracilis* characters; mandible with large flange, two mental foramina, and a double rooted P_3 , suggests that this specimen may represent *S. populator*. According to R. Graham (pers. comm. 1983), a fragmentary astragalus, atlas, and lumbar vertebra from this same locality support a less specific identification as *Smilodon* sp.

The derived species, *Smilodon populator*, also apparently evolved in North America during the late Irvingtonian and extended its range southward through Mexico and Central America into South America. Remains of *Smilodon* (probably *S. populator*) are documented from Pleistocene deposits in Chapala and Valle de Puebla, Mexico (Ferrusquia 1979) and Hormiguero, El Salvador (Stirton and Gealey 1943). In South America, middle and late Pleistocene (Ensenadan-Lujanian) localities record the presence of *S. populator* in Argentina, Bolivia, Brazil, Ecuador, Peru, and Uruguay (Berta 1985). This broad extension in the geographic range of *S. populator* is not surprising, especially when one considers the equally broad present-day ranges of the puma (*Felis concolor*) in the New World and the lion (*Felis leo*) in the Old World. As in North America, *Smilodon* became extinct in South America at the end of the Pleistocene.

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Table 1. Measurements of the upper dentition of *Smilodon gracilis*.

	I ¹		I ²		I ³		C		P ³		P ⁴		M ₁	
	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T
Port Kennedy PA														
ANSP 50									15.4	7.2				
ANSP 47							26.8	13.3			32.0	12.9		
ANSP 47													8.4	4.7
ANSP 46							25.9	13.1						
ANSP 44	7.5	5.4	8.7	7.4	10.3	9.0	35.5	15.2	16.0	6.5	33.7e	11.8e		
Florida														
Inglis IA														
UF 18099							16.5e	9.3e						
UF 12927							14.3e	8.2e						
UF 18100									15.9	7.1	30.3	13.3	5.1e	7.5e
UF 12928							14.2e	8.0e						
TRO 1664											31.0	13.2		
McLeod														
F:AM 95525							29.7	14.2	16.5	7.8	30.4e	11.5e		
F:AM 95526							31.4	14.4e						

Table 2. Measurements of mandibular rami of *Smilodon gracilis*.

	Florida						Pennsylvania	
	UF 20065	UF 18102	UF 18103	UF 12931	UF 12941	TRO 1665	ANSP 49 ^r	ANSP 49 ^l
Greatest depth, flange ^x	52.8							50.7e
Least depth ramus below diastema	26.4	29.4			26.4e	29.3	30.3	31.5
Depth ramus below M ₁ ⁺		28.6	28.4		27.5e	30.1	32.3	32.4
Width ramus at diastema	11.3	11.0			11.7e	11.6	12.0	11.8
Width ramus at M ₁	14.5	14.6	15.9		15.5e	14.2	16.3	17.3e
Mandibular tooththrow length (P ₃ -M ₁)	49.8	51.9			54.5	48.6	57.5	57.5
Height, angle-condyle				29.6				59.3e

x, measured from superior border of symphysis to base of flange; +, measured on the medial side below M₁; r, right; l, left

Table 3. Measurements of the lower dentition of *Smilodon gracilis*.

	I ₁		I ₂		I ₃		C		P ₃		P ₄		M ₁	
	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T	AP	T
Port Kennedy PA														
ANSP 44	5.3	3.7	7.1	5.0	8.2	7.5	7.0e	7.3			20.4	9.5	25.2	10.5
ANSP 49 ^r			6.3	4.8	7.7	6.2	10.1	7.6	11.5e	4.3e	20.3	8.5	22.0	9.8
ANSP 49 ^l			6.1	5.0	8.0	5.9	11.2	7.2	10.6e	4.0e	20.2	8.5	22.5	10.0
ANSP 50											20.0	8.4		
Florida														
Inglis IA														
UF 18102							11.3e	7.1e	11.0	6.1	20.3	8.5	23.0	10.0
UF 20065					5.6e	3.0e	9.3e	8.3e	8.1e	5.3e	18.2	7.8	20.8	9.4
UF 18103											19.0	8.0	20.8	9.7
UF 12933													21.4	7.7
UF 18104									12.0	6.0				
TRO 1665									10.1	6.0	18.8	8.3	20.9	10.0
Santa Fe River IA														
FDT 488											22.2	9.5		
McLeod														
F:AM 95522											21.8e	8.9	24.7e	9.7e
F:AM 95527											22.0	9.3		
El Jobean														
UF 12941									12.0e	4.6e	19.5	8.0	21.3	9.7

r, right; l, left

Table 4. Comparative measurements of deciduous P⁴, mandible, and lower dentition of *Smilodon gracilis* and *S. populator*.

	<i>S. gracilis</i> , Florida		<i>S. populator</i> ¹ , California	
	UF 18105a	UF 18105b	2002-R-6	2002-R-781
Least depth of ramus below diastema	19.3		20.6	26.2
Depth ramus below dP ₄	22.4	12.0	28.2	32.0
Width ramus below dP ₄	21.8	11.0	15.5	17.4
Greatest depth flange	30.9			
<i>S. gracilis</i>				
	UF 18105a	UF 18105c	UF 18105d	UF 18105b
dP ₃ AP---	11.7			
T---	4.8			
dP ₄ AP---	15.2	14.1	10.1	10.1
T---	5.2	5.3	4.8	3.6
UF 18101				
dP ₃ AP---	20.3			
T---	13.7			

¹ Measurements from Merriam and Stock (1932)

Table 5. Measurements of the humerus of *Smilodon gracilis* from Florida.

	Greatest Length	Proximal Depth	Proximal Width	Shaft Depth ⁺	Shaft Width ⁺	Distal Depth	Distal Width	Least Depth ^x
Inglis IA								
UF 18106	237.0	68.5	48.8	36.8	21.7	38.3	66.6	20.5
UF 18107 ^r				32.6	24.6			
UF 18107 ^l				31.8	20.7			
TRO 1669				32.9	23.0	42.7	70.1	20.6
TRO 1670		74.3	55.3	37.5	24.7	42.3	76.1	21.1
McLeod								
F:AM 95523				41.7	26.3	44.7		
F:AM 95528				40.5	25.6			

⁺, measured at junction of deltoid and pectoral crests; ^x, measured at middle of trochlea; r, right; l, left.

Table 6. Measurements of the ulnae and radii of *Smilodon gracilis* from Florida.

Ulna	Olecranon Process Width	Olecranon Process Depth	Sigmoid Notch Width	Coronoid Process Width ⁺	Shaft Width ^x	Shaft Width ^x	Distal Width
Inglis IA							
UF 18109	21.8	33.0	26.5	41.5	42.6	12.7	27.9
McLeod							
F:AM 95524	26.1	31.6	29.7	50.2	47.5	13.8	30.5

Radius	Greatest Length	Proximal Long Diameter	Proximal Short Diameter	Shaft Width ⁺	Shaft Depth ⁺	Distal Long Diameter	Distal Short Diameter
McLeod							
F:AM 69220		35.2	27.8	26.4	16.1	45.6	32.0
F:AM 69219				23.6	15.4	49.7	31.3
Inglis IA							
UF 18108	162.6e	28.5	21.2	26.3	12.8		

⁺ measured from shaft to coronoid process, maximum anteroposterior diameter
^x measured at base of ulnar tuberosity
^e measured above *M. pronator teres* scar

Table 7. Measurements of metacarpals II, III, IV, and V of *Smilodon gracilis*.

	Greatest Length	Proximal Width	Proximal Depth	Shaft Width	Shaft Depth	Distal Width	Distal Depth
<u>Metacarpal II</u>							
Port Kennedy PA							
ANSP 51	70.9	15.9	19.5	11.9	11.8	18.7	13.0
ANSP 48		17.5	22.9				
Florida							
Inglis IA							
UF 12934	75.0	18.8	22.3	12.0	11.4	17.9	17.2
Haile XVA							
UF 17498	74.9	18.8	22.0	13.3	13.0	21.0	18.2
<u>Metacarpal III</u>							
Port Kennedy PA							
ANSP 48		20.9	20.6				
Florida							
Inglis IA							
UF 45409	73.0	17.9	17.5	10.5	10.7	16.7	14.9
<u>Metacarpal IV</u>							
Florida							
Inglis IA							
UF 12938	76.4	16.2	18.0	10.9	10.2	15.6	14.7
UF 18110	77.5	16.7	19.4	10.7	10.2	16.8	16.8
McLeod							
F:AM 69249	83.7	19.4	20.6	11.8	11.8	20.1	18.0
<u>Metacarpal V</u>							
Florida							
Inglis IA							
UF 12935	58.9	16.3	17.3	9.7	9.7	15.9	14.0

Table 8. Measurements of the femur and tibiae of *Smilodon gracilis* from Florida.

	Greatest Length	Proximal Width	Proximal Depth	Shaft Width ⁺	Shaft Depth ⁺	Distal Width	Distal Depth
Femur							
Inglis IA							
UF 18112		67.4	38.0	31.7	28.4		
Tibia							
Haile XVA							
UF 17496				22.6	20.2	41.9e	29.4
McLeod							
F:AM 95529				20.8	33.0	44.3	32.8

⁺, femur measured at base of lesser trochanter; tibia measured at middle of shaft

Table 9. Measurements of the astragali of *Smilodon gracilis*.

	Greatest Length	Width	Head, Transverse Diameter	Head, Anteroposterior Diameter	Neck, Transverse Diameter
Port Kennedy PA					
ANSP 48	42.4	37.9	24.7	17.8	19.7
Florida					
Inglis IA					
UF 17496	41.8	37.0	25.6	17.4	20.2
TRO 1666	39.5	36.2	24.3	16.4e	17.0e
TRO 1667	37.6	40.4	23.0	15.2	18.0
McLeod					
F:AM 108536	46.7	41.1	28.2	18.9	20.7

Table 10. Measurements of the calcanei of *Smilodon gracilis* from Florida.

	Greatest Length	Width ⁺	Distal Width ^x	Sustentacular Facet [*]
Inglis IA				
UF 18113	68.4	31.3	20.9	21.7
UF 2399	66.1	31.3	27.6	23.0
UF 24000	69.0	30.7	22.8	24.5
UF 12936	72.9	32.9	30.2	26.0
UF 12937	60.1e	25.4e		
TRO 1668	65.6	29.7	25.3	22.2
McLeod				
F:AM 95534	72.2	37.5	30.8	77.7
F:AM 95532	71.5	38.4	33.6	24.0
F:AM 95333	78.5	36.2	34.9	24.6

⁺, greatest width across astragalar facets

^x, greatest width across cuboid surface

^{*}, least depth of sustentacular facet, measured normal to distal margin and to edge of facet

Table 11. Measurements of metatarsal III, IV, and V of *Smilodon gracilis* from Florida.

	Greatest Length	Proximal Width	Proximal Depth	Shaft Width	Shaft Depth	Distal Width	Distal Depth
Metatarsal III							
Inglis IA							
UF 12939	84.2	21.1	25.7	13.7	12.0	19.1	15.5
McLeod							
F:AM 69241	90.7	22.2e	28.3	14.1	12.7	20.3	17.6
Metatarsal IV							
Inglis IA							
UF 12940	89.5	17.6	21.8	11.2	12.3	16.3	15.5
McLeod							
F:AM 69243	91.6	20.3	24.7	13.4	14.5	18.0	16.8
F:AM 95530				11.6	12.5	17.9	16.0
Metatarsal V							
McLeod							
F:AM 95531	79.4	23.7	18.5	9.9	11.7	15.0	15.9

Table 12. Measurements of proximal and middle phalanges of *Smilodon gracilis* from McLeod in Florida.

	Length	Proximal Width	Proximal Depth	Distal Width
Proximal Phalanges				
F:AM 95535a	38.2	16.6	17.5	13.8
F:AM 95535b	42.3	19.2	19.7	14.5
F:AM 95535c	40.5	18.0	15.0	13.9
Middle Phalanges				
F:AM 108357a	32.5	15.5	13.6	14.0
F:AM 108357b	35.9	15.8	13.1	14.2
F:AM 108357c	34.9	15.2	13.0	16.0
F:AM 108357d	30.2	15.0	12.9	13.7

Table 13. Measurements (mm) and statistics for *Smilodon gracilis*, *S. populator*, and *Megantereon cultridens*.

Tooth	Dimension	N	$\bar{X} \pm SE$	OR	CV
<i>Smilodon gracilis</i>					
Early Irvingtonian					
C	AP				
	T				
P ³	AP	1	15.9		
	T	1	7.1		
M ₁	AP	6	21.4±0.34	20.8-21.4	3.9
	T	6	9.8±0.09	9.4- 9.7	2.2
Late Irvingtonian					
C	AP	5	29.9±1.72	25.9-35.5	12.8
	T	5	14.0±0.38	13.1-15.2	6.1
P ³	AP	3	16.0±0.32	15.4-16.5	3.4
	T	3	7.2±0.38	6.5- 7.8	9.0
M ₁	AP	4	23.6±0.79	22.0-25.2	6.7
	T	4	10.0±0.18	9.7-10.5	3.5
<i>S. populator</i> ¹					
Late Irvingtonian					
C	AP	1	31.3		
	T	1	13.8		
P ³	AP				
	T				
M ₁	AP	2	28.3	27.0-29.5	
	T	2	13.8	12.6-15.0	
<i>Megantereon cultridens</i> ²					
Early Villafranchian					
C	AP	8	19.9±0.62	18.7-22.8	8.8
	T	8	11.0±0.30	9.9-12.0	7.8
P ³	AP	8	15.1±0.24	14.3-15.8	4.6
	T	8	6.8±0.17	6.2- 7.4	6.9
M ₁	AP	4	18.9±0.23	18.4-19.4	2.4
	T	4	9.2±0.20	8.7- 9.7	4.5
Late Villafranchian					
C	AP	5	24.1±0.30	23.2-24.9	2.8
	T	5	12.4±0.44	11.6-13.8	7.8
P ³	AP	3	14.5±1.26	12.6-16.9	15.2
	T	3	7.2±0.66	6.3- 8.5	15.7
M ₁	AP	10	21.1±0.67	17.4-24.0	10.0
	T	9	10.2±0.32	8.7-11.3	9.4

¹ measurements from Churcher 1984² Late Irvingtonian: Conard Fissure

measurements from Kurtén and Crusafont-Pairo 1977

Early Villafranchian: Perrier, St. Vallier, Puebla
de Valverde

Late Villafranchian: Seneze, Olivola, Valdarno

Table 14. Fore- and hindfoot measurements (mm) and statistics for *Smilodon gracilis*, *S. populator*, and *Megantereon whitei*.

Element	Dimension	N	$\overline{X} \pm SE$	OR	CV
<i>Smilodon gracilis</i>					
Early Irvingtonian					
Metacarpal II	Length	2	75.0	76.4-77.5	
	Distal				
Calcaneum	Width	2	19.4	15.6-16.8	
	Length	5	68.4 \pm 1.7	63.4-73.9	5.7
Astragalus	Width	6	30.2 \pm 1.1	25.4-32.9	8.5
	Length	3	39.6 \pm 1.2	39.5-41.8	5.3
Metatarsal IV	Width	3	37.9 \pm 1.3	36.2-37.6	5.9
	Length	1	89.5		
	Width	1	17.6		
Late Irvingtonian					
Metacarpal II	Length	1	70.9		
	Distal				
Calcaneum	Width	1	18.7		
	Length	3	78.1 \pm 0.20	77.8-78.5	0.45
Astragalus	Width	3	37.4 \pm 0.64	36.2-38.4	3.0
	Length	2	44.6	42.4-46.7	
Metatarsal IV	Width	2	39.5	37.9-41.1	
	Length	1	91.6		
	Width	1	20.3		
<i>S. populator</i> ¹					
Late Irvingtonian					
Metacarpal II	Length				
	Distal				
Calcaneum	Width	1	20.2		
	Length	1	84.4		
Astragalus	Width	1	48.7		
	Length	3	46.0 \pm 1.1	44.3-47.7	4.1
Metatarsal IV	Width	3	45.5 \pm 1.9	42.2-48.8	7.8
	Length				
	Width	1	21.6		
<i>Megantereon whitei</i> ²					
Late Villafranchian					
Metacarpal II	Length		63.0		
	Distal				
Calcaneum	Width		15.2		
	Length	1	72.0e		
Astragalus	Width				
	Length	1	43.0e		
Metatarsal IV	Width				
	Length	1	80.0		
	Distal				
	Width	1	14.5		

¹ measurements from Churcher 1984

Late Irvingtonian: Conard Fissure

² measurements from Vrba 1981

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