

## BIOMECHANICAL IMPLICATIONS OF THE VARIATION IN *SMILODON* ECTOCUNEIFORMS FROM RANCHO LA BREA

Christopher A. Shaw and Antonia E. Tejada-Flores<sup>1</sup>

**ABSTRACT.** Of 517 *Smilodon* ectocuneiforms examined from the late Pleistocene Rancho La Brea asphalt deposits, the typically hook-like plantar process is unfused in 23.8 percent. The plantar tuberosity of felid ectocuneiforms develops from a separate center of ossification than that of the main body of the ectocuneiform. Tendons of the *M. tibialis posterior* and *M. peroneus longus*, extensors of the hind limb, interact with the plantar process of the ectocuneiform and affect the development of this bone. The frequency of unfused plantar tuberosities is greater in geologically younger localities at Rancho La Brea and is correlative with an overall increase in *Smilodon* body size. This increase in body mass through time placed greater stress (produced by proportionately more powerful extensor muscles) on the developing plantar process of larger *Smilodon* individuals, preventing fusion to the body of the ectocuneiform. Lever-arm ratios, adjusted for body mass, indicate that *Smilodon* had mechanically more powerful hind limbs than living lions and was able to attack prey by stalking and leaping.

### INTRODUCTION

Osteologically, *Smilodon floridanus* is one of the most completely known extinct species from the late Pleistocene of Rancho La Brea in southern California. Between 1913 and 1915, field parties from the Los Angeles County Museum of Natural History (LACM) excavated extensively in what is now Hancock Park. From 1029 to over 2000 estimated individuals of *Smilodon* are represented in the collections (Marcus, 1960; Miller, 1968) housed at the George C. Page Museum.

In a comparative osteologic study of the felids from Rancho La Brea, Merriam and Stock (1932) noted two morphologic varieties of *Smilodon* ectocuneiforms. The more common variety (Fig. 1A) has a hook-like plantar tuberosity, fused to the body along a broad area; this process is often truncated, the hook being reduced or absent in the less common variety (Fig. 2A). Merriam and Stock (1932) examined 120 ectocuneiforms and found that 70.8 percent bore a well-developed tuberosity. This percentage is 76.2 in our study of 517 specimens. Six of 11 (54.5%) *Smilodon* ectocuneiforms from asphalt deposits of Talara, Peru, have well-de-

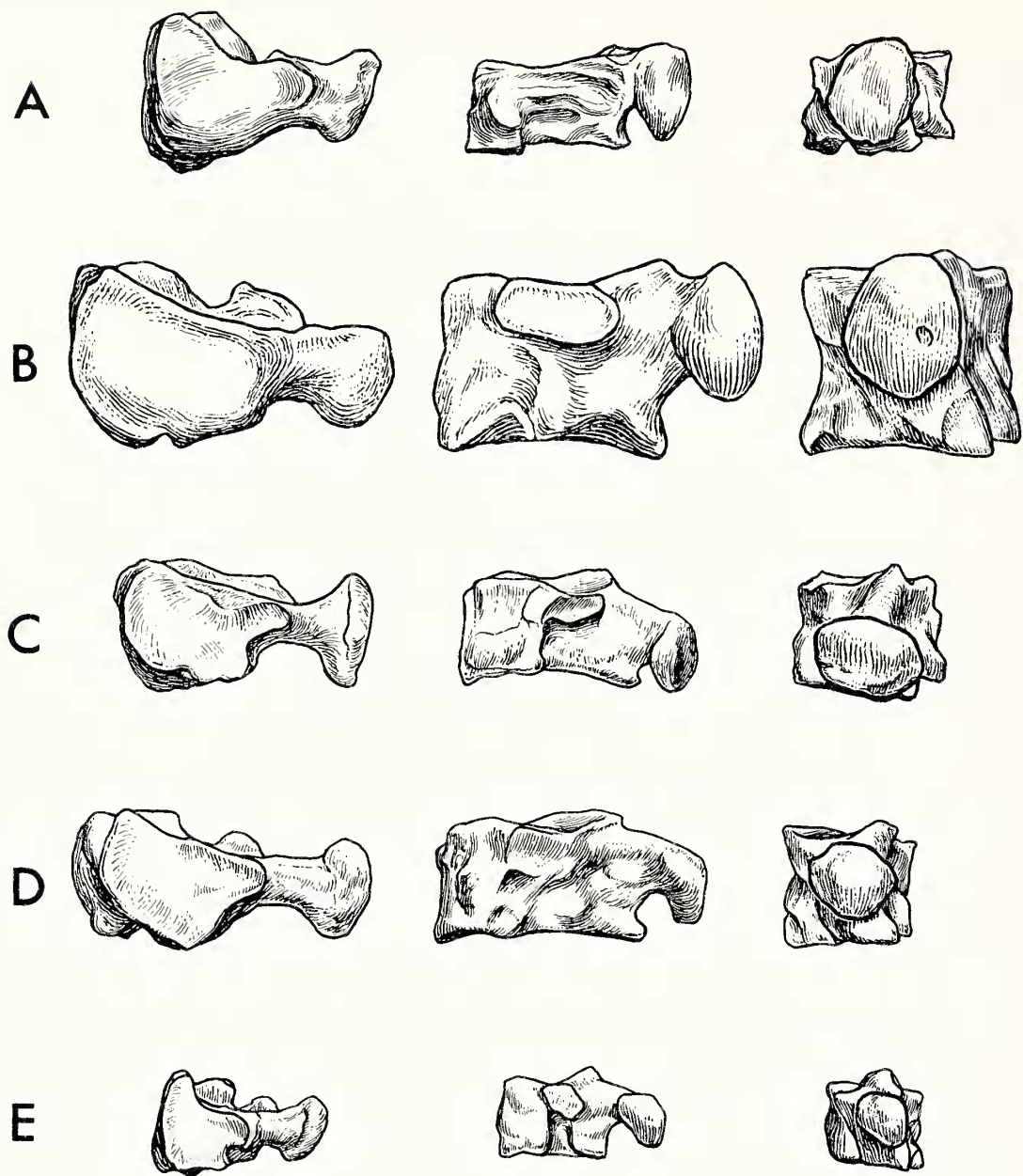
veloped, fused plantar tuberosities (C.S. Churcher, written comm.).

The plantar (posterior) end of truncated ectocuneiforms also exhibits two distinct morphologies. In our sample of 123 specimens, 37 (30.1%) bear a facet (Fig. 2A, right) for apparent articulation with a small nodule of bone, representing the missing plantar process. The remainder have a roughened surface for tendinous or ligamentous attachment similar to that of the fully developed process; furthermore, nine of these specimens (7.3%) exhibit unexplained pathologic bone growth. Four of the five truncated ectocuneiforms from Talara bear a nodular facet (C.S. Churcher, written comm.).

Until recently, the nodule of bone assumed to be associated with the truncated *Smilodon* ectocuneiforms by Merriam and Stock (1932) had not been recognized from Rancho La Brea. Twenty specimens have now been identified in the collections. Seven (LACMHC 10791, 10792, 10795, 10805, 10806, LACMLRP R36931, R51053) are hook-like in shape, identical in morphology to the fused plantar process of complete ectocuneiforms (Fig. 3A); four (LACMHC 10791, 10792, 10805, LACMLRP R36931) bear an articular facet and three do not. The other 13 specimens (LACMHC 10790, 10793, 10794, 10796 through 10803, 10807) do not have an articular facet and are oval and globular in shape. The dorsal (anterior) surface bears an oval rugosity where articulation with or fusion to the body of the ectocuneiform would be expected (Fig. 3B).

Ectocuneiforms of extinct felids (other than *Smilodon*) from Rancho La Brea and those of several extant species from the comparative collections of the American Museum of Natural History, LACM, and the George C. Page Museum (RLB) were examined. Of 40 *Felis atrox* specimens one was truncated; the plantar projection is small and rounded, with a smooth surface texture and no articular facet (Fig. 2C). Small

<sup>1</sup> George C. Page Museum, 5801 Wilshire Boulevard, Los Angeles, California 90036.



2cm

**Figure 1.** Normally developed left ectocuneiforms of *Smilodon* and four species of *Felis*: proximal (left), lateral (center), and plantar (right) views. A. *Smilodon* (LACMHC Q4602). B. *F. atrox* (LACMHC 10788). C. *F. tigris* (RLB 8). D. *F. leo* (LACM M1144). E. *F. concolor* (LACM M1456). Line drawing by Mark Hallett.

samples of extant felid species (*F. leo* (20), *F. tigris* (2), *F. concolor* (6), *F. catus* (4), and *Lynx rufus* (4)) were also examined; only one *F. tigris* ectocuneiform was found to have an unfused plantar process. The prominently hooked plantar tuberosity of this specimen occurs as a separate accessory bone articulated to the body of the ectocuneiform (Figs. 2B

and 3C). The articular facets are large and oval. Furthermore, in this individual, the plantar tuberosity of the ectocuneiform is fused on the left side but not on the right.

It is likely that the plantar process is an ontogenetic center of ossification separate from the main body of the ectocuneiform. Thus far no specific mention of the occurrence of

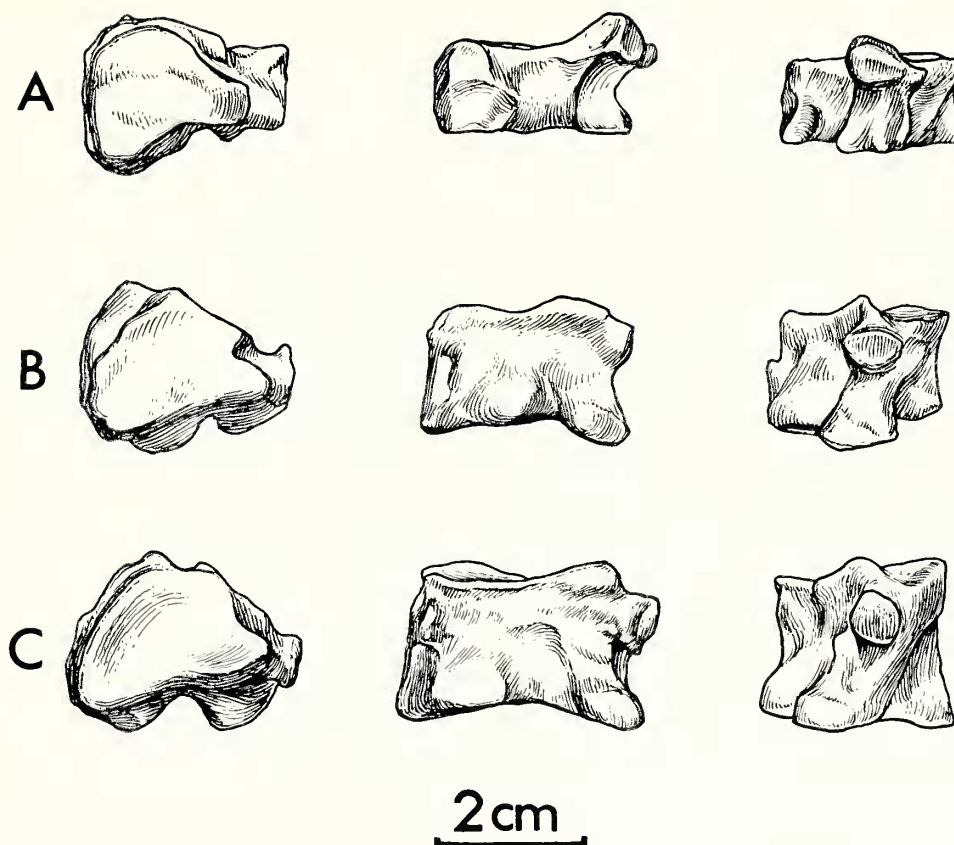


Figure 2. Truncated right ectocuneiforms of *Smilodon* and two species of *Felis*: proximal (left), medial (center), and plantar (right) views. A. *Smilodon* (LACMHC Q4445). B. *F. tigris* (RLB 8). C. *F. atrox* (LACMHC 10789). Line drawing by Mark Hallett.

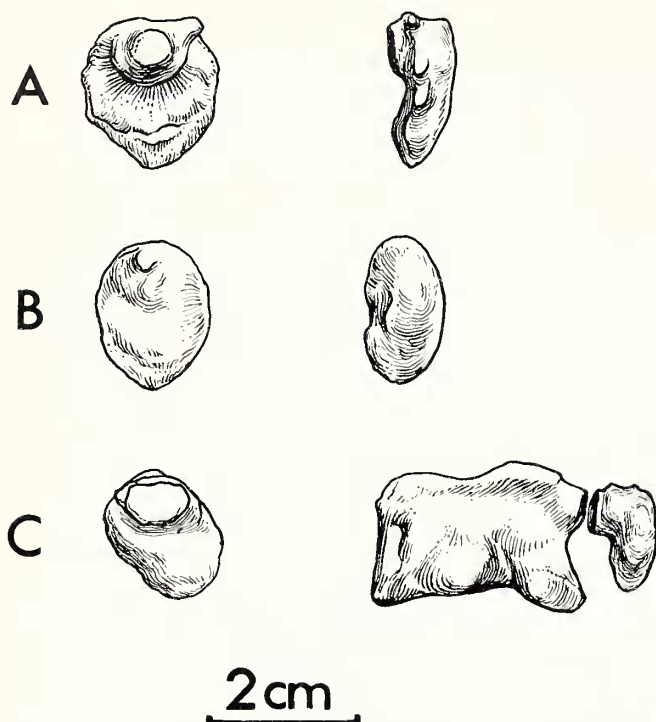
accessory or supernumerary bones associated with the ectocuneiform in mammals has been found in the literature. However, other accessory or supernumerary tarsal elements are apparently common in some mammals (Davis, 1964; Grant and Basmajian, 1965). Two centers of ossification could account for the asymmetry seen in the *F. tigris* individual, with fusion taking place on the left side but not on the right.

#### ANATOMY

Descriptions of *Smilodon* and *Felis atrox* ectocuneiforms are provided by Merriam and Stock (1932). The body of the ectocuneiform in *F. atrox* is very similar to that of all extant felids, but that of *Smilodon* is very different. The proximal surface of the plantar process, between the body and hooked tuberosity, forms a very broad and flat neck in *Smilodon*. This neck consistently equals or exceeds the width of the proximal articular surface nearest the area of fusion to the body (Fig. 1A). In all other felids examined, this neck is medio-laterally constricted and proximo-distally rounded (oval to circular in cross section). It is smooth and flares transversely into the hooked or rounded area of tendon attachment. In the unfused specimen of *F. tigris*, the neck is flared and rugose around the area of articulation. The hook-like character of the plantar tuberosity in *Smilodon*, men-

tioned by Merriam and Stock (1932), is highly developed in *F. tigris*, less developed in *F. leo* and *F. concolor*, and poorly developed in *F. atrox* (Fig. 1). A summary of ectocuneiform measurements is provided in Table 1.

The variation observed in *Smilodon* ectocuneiforms may be attributed to muscular forces exerted on this bone. Two muscles interact with the ectocuneiform in modern felids, the *M. tibialis posterior* and the *M. peroneus longus*. These have been reconstructed for *F. atrox* and *Smilodon* (Fig. 4). The *M. tibialis posterior* originates on the entire medial surface of the head of the fibula and between the oblique ridges of the posterior surfaces of the tibia. The muscle ends in a slender flat tendon that passes through the dorsal groove on the medial surface of the tibia, then turns onto the plantar surface of the foot and passes through a groove on the ventral surface of the navicular. It inserts on the posterior surface of the plantar tuberosity of the ectocuneiform and the lateral tuberosity of the navicular. This muscle is an extensor of the foot (Reighard and Jennings, 1951; Crouch, 1969). The *M. peroneus longus*, a flexor of the foot, originates from two areas of the fibula, the lateral surface of the head and the proximal half of the lateral surface. This muscle terminates in a slender tendon which passes through the groove on the lateral surface of the lateral malleolus, then passes through peroneal grooves of the calcaneum, cuboid, and ectocunei-



**Figure 3.** Unfused plantar processes of *Smilodon* and *Felis tigris*: dorsal (left) and medial (right) views. A. *Smilodon* (LACMHC 10791), hooked process with articular facet. B. *Smilodon* (LACMHC 10790), ovoid process without articular facet. C. *F. tigris* (RLB 8). Line drawing by Mark Hallett.

form. Large branches insert on the proximo-posterior bases of the first and fifth metatarsal and slender branches insert similarly on the other metatarsals (Reighard and Jennings, 1951; Crouch, 1969). In addition, the plantar tuberosity of the ectocuneiform serves as the attachment of the plantar navicularicuneiform ligaments (Davis, 1958).

### BIOMECHANICS

Comparison of fore and hind limb size and strength in machairodonts has been discussed by many authors. Schaub (1925) and Bohlin (1940, 1947) assert that the heavily developed fore limbs were not balanced by equally developed hind limbs, therefore, *Smilodon* could not initiate a leaping attack on a prey animal. However, Merriam and Stock (1932) and Simpson (1941) state that the hind limb is weak only relative to the fore limb and that this genus probably began its attack by lunging or leaping.

A more exact comparison can be made by analyzing relative lever-arm ratios in the hind limbs of *Smilodon* and true cats. Any mechanical action can be described by the following equation,

$$F_o = F_i \times L_i / L_o$$

where  $F_o$  = out-force,  $F_i$  = in-force,  $L_i$  = length of the in-lever, and  $L_o$  = length of the out-lever (Hildebrand, 1974).

The out-force, in-lever, and out-lever may be calculated

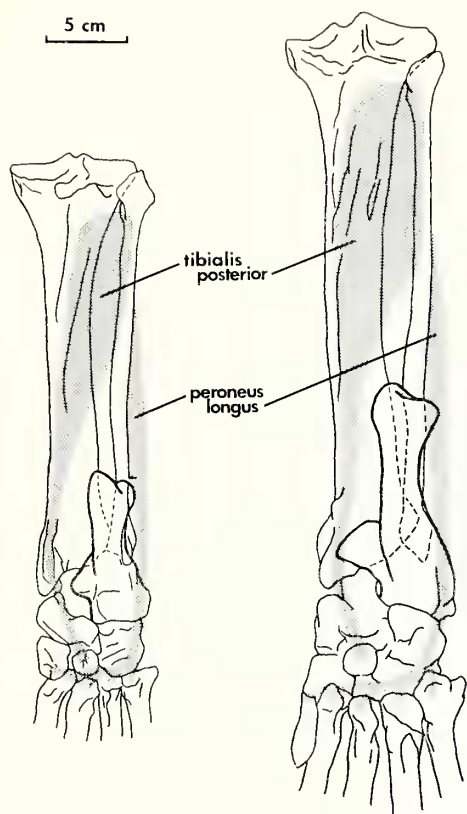
or directly measured for extinct species. The out-force is defined as the resistance (in this case, the body mass of the animal) that must be overcome by a muscular system to obtain momentum. Assuming only the hind limbs are employed to propel the animal forward and each foot bears an equal load,  $F_o$  equals one half of the body mass ( $M/2$ ). Body

**Table 1.** Summary of measurements (in mm) of normally developed (normal) and truncated ectocuneiforms of *Smilodon* and *Felis atrox* from Rancho La Brea. Abbreviations: N = sample size, OR = observed range,  $\bar{x}$  = mean, s = standard deviation, V = coefficient of variation, Dr-Pl = dorso-plantar, Px = proximal, Dt = distal. Measurements taken after Merriam and Stock (1932).

	N	OR	$\bar{x}$	s	V
<i>Smilodon</i>					
Normal					
Dr-Pl depth	182	31.4–45.6	39.0	2.539	6.510
Px-Dt length	187	15.1–23.6	18.8	1.491	7.931
Dt width	184	21.0–28.6	24.7	1.461	5.915
Truncated					
Dr-Pl depth	123	26.8–36.6	31.5	2.013	6.390
Px-Dt length	122	15.1–23.0	17.8	1.461	8.006
Dt width	122	20.8–27.9	25.1	1.384	5.514
<i>Felis atrox</i>					
Normal					
Dr-Pl depth	38	43.6–58.0	51.1	3.589	7.023
Px-Dt length	39	20.6–33.5	26.9	2.297	8.539
Dt width	40	24.1–33.4	29.1	2.236	7.684
Truncated					
Dr-Pl depth	1	33.5			
Px-Dt length	1	23.4			
Dt width	1	26.2			

**Table 2.** Measurements (in mm) of the minimum antero-posterior diameter of *Smilodon* and *Felis atrox* femora. The pits are ranked by order of descending mean weight (in kg) which is calculated using the allometric constants of Alexander et al. (1979). Abbreviations as in Table 1.

	N	OR	$\bar{x}$	s	$\bar{x}$ weight
<i>Smilodon</i>					
Pit					
3	121	27.4–36.6	31.9	1.921	154.3
61/67	92	25.4–36.6	31.5	1.851	149.0
4	78	27.7–35.1	30.8	1.636	139.9
77	61	26.0–33.6	30.5	2.003	136.2
13	36	26.2–32.9	30.4	1.461	134.9
Total sample	415	25.4–36.9	31.3	1.947	146.3
<i>Felis atrox</i>					
Total sample	23	30.8–43.7	35.1	3.450	201.2



**Figure 4.** Posterior view of distal hind limb showing the origin and insertion of the *M. tibialis posterior* and *M. peroneus longus* in *Smilodon* (left) and *Felis atrox* (right). Illustration by Mark Hallett.

mass was calculated from the minimum antero-posterior femur midshaft diameter of *Smilodon* and *F. atrox* (Table 2) using the allometric constants of Alexander et al. (1979). Lengths of the in-lever (distal end of calcaneum to calcaneal pivot at tibia,  $L_i$ ) and out-lever (calcaneal pivot to end of metatarsal III,  $L_o$ ) were calculated from mean lengths of the calcaneum, navicular, ectocuneiform, and metatarsal III for *Smilodon*, *Felis atrox*, and *F. leo* (Tables 3 and 4).

The in-force is produced by contraction of extensors of the lower hind limb and will approximate the minimum amount of contractile force required to overcome the inertia of the body mass. These muscles include the *M. gastrocnemius*, *M. soleus*, *M. plantaris*, *M. peroneus brevis*, and *M. tibialis posterior*. The large *M. gastrocnemius* arises from the patella and femoral sesamoids and inserts on the distal calcaneum. The *M. plantaris* has a similar origin but crosses the tuber calcis to insert on the plantar aponeurosis of the foot. The other muscles originate along portions of the tibia and/or fibula and insert on the distal calcaneum (*M. soleus*) or on palmar areas of the foot. Using the mechanical equation above,  $F_i$  was calculated for *Smilodon*, *Felis atrox*, and *F. leo* (Table 4).

The out-force will become greater as the in-force or in-lever length is increased or as the out-lever length is decreased. The mean lever ratio ( $L_i/L_o$ ) is nearly equal in *Felis*

*atrox* and *F. leo*. Because the  $L_o$  of *Smilodon* has been appreciably shortened and the  $L_i$  lengthened, this ratio is proportionately much greater, increasing the potential out-force capability of hind foot extension. Adjusting for allometric differences in mass ( $M$ ) between comparable species by using  $M/2 = F_o$  and solving the mechanical equation gives the minimum amounts of in-force ( $F_i$ ) necessary to overcome inertia. The smaller the value  $F_i$ , the more powerful the muscular contraction; the larger the value of  $F_i$ , the more rapid the

**Table 3.** Proximo-distal length measurements (in mm) of hind foot elements of *Smilodon*, *Felis atrox*, and *F. leo*. Statistics on metatarsal III of *Smilodon* taken from Menard (1947). Abbreviations: Pv-Dt = pivot to distal, \* = approximately. Other abbreviations as in Table 1.

	N	OR	$\bar{x}$	s	V
<i>Smilodon</i>					
Calcaneum					
Total length	50	84.6–101.5	93.5	3.628	3.879
Pv–Dt length	50	20.8–28.8	24.4	1.999	8.188
Navicular	30	16.6–21.5	18.6	1.198	6.429
Ectocuneiform	187	15.1–23.6	18.8	1.491	7.931
Metatarsal III	759	*85–112	97.8	*4.7	*4.8
<i>Felis atrox</i>					
Calcaneum					
Total length	56	108.0–140.4	125.3	7.792	6.219
Pv–Dt length	56	34.1–48.9	40.9	3.579	8.744
Navicular	54	15.9–20.7	18.5	1.321	7.140
Ectocuneiform	39	20.6–33.5	26.9	2.297	8.539
Metatarsal III	49	132.0–157.8	145.7	7.292	5.004
<i>Felis leo</i>					
Calcaneum					
Total length	20	90.9–114.9	103.5	6.736	6.508
Pv–Dt length	20	28.9–37.7	34.0	2.708	7.965
Navicular	20	14.1–18.2	15.8	1.151	7.287
Ectocuneiform	19	18.7–23.0	21.1	1.259	5.969
Metatarsal III	19	112.4–139.0	126.8	8.107	6.393

**Table 4.** Lever-arm statistics used to determine relative hind limb lever strength between *Smilodon*, *Felis leo*, and *F. atrox* where  $F_o = F_i \times L_i/L_o$ . Abbreviations:  $\bar{x}$  = mean,  $L_i$  = in-lever,  $L_o$  = out-lever,  $M$  = mass,  $F_o$  = out-force,  $F_i$  = in-force. Weight of *F. leo* from Schaller (1972).

	<i>Smilodon</i>	<i>Felis leo</i>	<i>Felis atrox</i>
$\bar{x} L_i$ (mm)	69.1	69.5	84.4
$\bar{x} L_o$ (mm)	159.6	197.7	232.9
ratio $\bar{x} L_i/\bar{x} L_o$	0.43	0.35	0.36
$\bar{x} M/2$ (kg) (= $F_o$ )	72.9	81.0	100.6
minimum $F_i$	169.5	231.4	279.4

**Table 5.** Ectocuneiform samples and radiocarbon dates on bone collagen from Pits 3, 4, 13, 61/67, and 77. The sites from Rancho La Brea are ranked from oldest to youngest. Specimen data from Talara, Peru, provided by C.S. Churcher (written comm.) and radiocarbon dates from Churcher (1966). Abbreviations: Lt = left, Rt = right, % = percent of sample from the site. Other abbreviations as in Table 1.

Pit	Total N	Normal				Truncated				OR dates	
		N	%	Lt	Rt	N	%	Lt	Rt		
77	169	157	92.9	81	76	12	7.1	6	6	3	28,200–33,100
4	44	32	72.7	16	16	12	27.3	6	6	12	13,500–36,000
3	141	80	56.7	40	40	61	43.3	31	30	9	12,650–21,400
13	33	30	90.9	16	14	3	9.1	2	1	4	14,310–15,360
61/67	56	36	64.3	17	19	20	35.7	14	6	5	11,130–13,600
Other pits	74	64	79.7	37	22	15	20.3	7	8	—	—
Total sample	517	394	76.2	207	187	123	23.8	66	57	33	11,130–36,000
Talara	11	6	54.5	3	3	5	45.5	2	3	4	13,616–14,418

muscular contraction. Of the three species examined (Table 4), *Smilodon* exhibits the smallest  $F_1$ , indicating a more powerful hind limb than *F. atrox* and *F. leo*. Obviously, *Felis leo* is adept at running, leaping and in-place wrestling when pursuing prey. *Smilodon*, with an even more powerful foot leverage system and less body mass, was able to propel itself more powerfully than living lions. The robust forelimbs of *Smilodon* appear to be yet more powerfully organized and constructed than the hind. Therefore, although the hind limb is “weaker” than the fore limb as Schaub (1925) and Bohlin (1940, 1947) state, and proportioned differently than in most true cats (as argued by Merriam and Stock, 1932, and by Simpson, 1941), both are clearly more powerful appendages than those of large living cats. In addition, the minimum  $F_1$  (Table 4) shows that the La Brea lion (*F. atrox*) had a disproportionately weaker (read “speedier”) foot leverage system for its body mass than the smaller modern lion (*F. leo*). Thus in the La Brea ecosystem, the roles of large felids were played by the smaller, more powerfully legged sabertooth and the larger, speedier-legged lion.

### CHANGES THROUGH TIME

Morphologic change during Pleistocene time is documented in many mammalian lineages. In some taxa (e.g., *Felis onca*), size is the main difference between fossil and living forms (Kurten, 1973). Many felid taxa exhibit a gradual overall size reduction throughout the Pleistocene; in contrast, the size of *Smilodon* increased (Kurten, 1965).

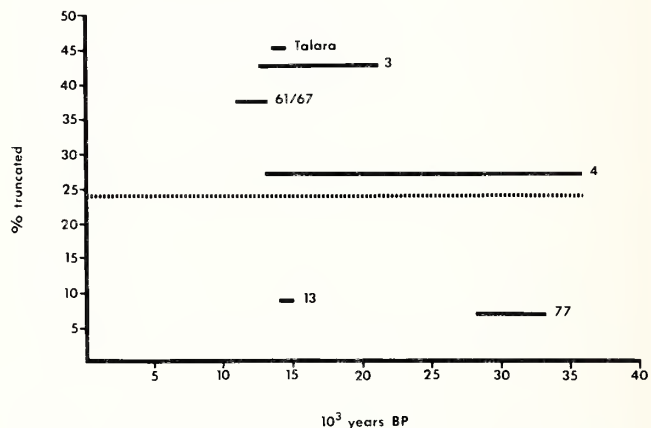
Samples of *Smilodon* ectocuneiforms are available from

**Table 6.** Chi-square values comparing frequencies of normally developed and truncated *Smilodon* ectocuneiforms from five pits at Rancho La Brea. \* =  $P < 0.05$ , \*\* =  $P < 0.01$ . Probabilities interpolated from Zar (1974).

Pit	3	61/67	4	13
61/67	0.36			
4	**	*		
13	**	**	**	
77	**	**	**	0.45

several radiocarbon dated localities (pits) at Rancho La Brea. Most sites accumulated fossil specimens within one or two brief, definable periods spanning about 3000 years or less. These are fairly evenly spaced between 11,000 and 36,000 years B.P. (Akersten et al., 1983; Marcus and Berger, 1984). The most reliable radiocarbon dates from Rancho La Brea are those measured on bone collagen (Ho et al., 1969; Akersten et al., 1983). In many instances collagen dates can be reliably correlated with stratigraphic depth within a single pit. Specimens from Pits 3, 4, 13, 61/67, and 77 have been radiocarbon dated and these sites contained the largest samples of ectocuneiforms (Table 5).

The frequency of normally developed (versus truncated) ectocuneiforms is distinct in each of these five sites (Table 5). The chi-square values show significant differences between all sites except between Pits 3 and 61/67 and between 13 and 77 (Table 6). In addition, pits in which high frequency of truncation is observed are roughly correlative to younger radiocarbon horizons (Table 5 and Fig. 5) and increased body mass (Table 2). As observed, Pits 3 and 61/67, with high



**Figure 5.** Change in frequency of *Smilodon* ectocuneiform truncation through time of the samples from five localities at Rancho La Brea and one from Talara, Peru. Dotted line represents the mean ectocuneiform truncation for the total sample from Rancho La Brea.

truncation frequencies, are of relatively young radiocarbon age and contain *Smilodon* with the largest mean body size. The small sample of comparable age from Talara (Table 5) also has a high frequency of ectocuneiform truncation. The sample from Pit 4 was accumulated throughout the time span represented at Rancho La Brea and, as expected, the ectocuneiform truncation frequency and mean body mass are most similar to the entire sample (Tables 5 and 6). Pit 77, which contains animals with relatively small body mass and low ectocuneiform truncation frequency, is one of the oldest sites of fossil accumulation; *Smilodon* body mass and truncation frequency is similar in Pit 13, although radiocarbon dates indicate it to be a much younger deposit, comparable in age to Pits 3 and 61/67.

The similarity between Pits 13 and 77 is unexpected. Radiocarbon dates of specimens from these pits do not appear inaccurate (Marcus, pers. comm.). The sample of *Smilodon* from Pit 13 is the least variable in observed range and standard deviation of all samples from Rancho La Brea (Tables 2 and 5; Menard, 1947). Its temporal range is also the most restricted, only spanning approximately 1000 years of accumulation (Table 5). Furthermore, the body mass calculations (Table 2) indicate a depositional episode biased toward the entrapment of small individuals. When excavating Pit 13, Wyman (1914) remarked that the *Smilodon* materials "appear to average small as compared to those from other pits," which is consistent with the low frequency of ectocuneiform truncation and the small body mass measured from femoral diameters. Thus, the low frequency of ectocuneiform truncation in Pit 13 near the terminal Pleistocene is due to an accumulation bias selectively entrapping small individuals of *Smilodon*.

## DISCUSSION

Several factors may have contributed to the observed increase in frequency of plantar process truncation in *Smilodon* ectocuneiforms from Rancho La Brea. An important consideration is the effect of allometric increase of muscle and tendon size through time and the increased stress in the relatively small area of insertion on (and interaction around) the plantar tuberosity. As the *M. tibialis posterior* and *M. peroneus longus* became more massive, so did their tendons. The area of insertion of the *M. tibialis posterior* on normally developed ectocuneiforms is about equal in *Smilodon* and *Felis atrox* (a considerably larger animal); similarly, the groove for the *M. peroneus longus* is the same absolute size in both taxa (Figs. 1A and 1E). These features imply that both muscles in each taxon were of comparable size. However, the proximo-distal length of the ectocuneiform is much shorter in *Smilodon* (Table 1) and the neck connecting the plantar process is flattened and less robust. If the plantar process and body of the ectocuneiform were ontogenetically two centers of ossification, movement of a large *M. peroneus longus* tendon and the contraction of a powerful *M. tibialis posterior* would tend to continually pull the plantar process away from the body, preventing fusion. When two centers of ossification develop close together, an articular facet forms in the area

of syndesmotic attachment between the bone surfaces (Fig. 3A); if they ossify further apart the ovoid plantar process (Fig. 3B) would likely function as a sesamoid within the *M. tibialis posterior* tendon. With increase of *Smilodon* body mass through time, the increased muscular stress on the plantar process of the ectocuneiform could explain the observed lower frequency of fusion between these centers of ossification.

It is interesting to note that the Felidae possess the most robust plantar tuberosity of all living mammals. Within this family, its degree of development is roughly negatively associated with cursorial behavior. It is characteristic that less cursorial felids have a large *M. tibialis posterior* (Ginsberg, 1961) and a robust plantar process with a pronounced hook for its insertion (e.g., *Felis tigris*, *F. onca*); the most cursorial felid (*Acinonyx*) has a reduced *M. tibialis posterior* and a reduced plantar process, very similar to canids. *F. leo* and *F. atrox* fall between these extremes. Morphologically, the plantar process of *Smilodon* is most like that of *F. tigris* and *F. onca*.

Of the large living cats, *Felis onca* is most similar to *Smilodon* in limb proportions (Gonyea, 1976a). Though digitigrade, both taxa share several features of the hind limb (short, stocky tibia and fibula, large *M. tibialis posterior*, and short, slightly splayed metatarsals) characteristic of plantigrade carnivores (Ginsberg, 1961). Ginsberg (1961) noted that *F. onca* rarely employs a "rapid pursuit phase" in prey capture, but usually leaps with a single bound, overpowering its victim; he suggests identical predatory behavior in machairodonts. Gonyea (1976b) stated that *Smilodon* probably used ambush and stalking techniques to capture prey, immobilizing it with the powerful front limbs. Similar limb proportions between *Felis onca* and *Smilodon* have been interpreted as indicative of habitat (Gonyea, 1976b); this similarity, however, is more likely to reflect a common prey capture technique. This is supported by the *Smilodon* limb mechanics presented here.

## ACKNOWLEDGMENTS

We thank C.S. Churcher for providing data on those specimens from Talara, Peru, that are housed at the Royal Ontario Museum. George L. Callison contributed much time and advice on the biomechanical aspects of this study. Comparative material of *Felis leo* was made available by Daniel H. Russell of the American Museum of Natural History. William A. Akersten, David E. Fortsch, John M. Harris, George T. Jefferson, Leslie F. Marcus, and James P. Quinn read the manuscript critically. Partial support of this research was provided by the Los Angeles County Museum of Natural History Foundation.

## LITERATURE CITED

- Akersten, W.A., C.A. Shaw, and G.T. Jefferson. 1983. Rancho La Brea: status and future. *Paleobiology* 9(3):211-17.
- Alexander, R.McN., A.S. Jayes, G.M.O. Maloij, and E.M. Wathuta. 1979. Allometry of the limb bones of mam-

- mals from shrews (*Sorex*) to elephant (*Loxodonta*). *Journal of Zoology* 189:305–14.
- Bohlin, B. 1940. Food habit of the machaerodonts, with special regard to *Smilodon*. *Bulletin of the Geological Institute of Uppsala* 28:156–74.
- . 1947. The sabre-toothed tigers once more. *Bulletin of the Geological Institute of Uppsala* 32:11–20.
- Churcher, C.S. 1966. The insect fauna from the Talara tar-seeps, Peru. *Canadian Journal of Zoology* 44:985–93.
- Crouch, J.E. 1969. *Text-atlas of cat anatomy*. Philadelphia: Lea and Fediger, 399 pp.
- Davis, D.D. 1958. Tarsal ligaments of the spectacled bear. *Fieldiana: Zoology* 39(13):91–105.
- . 1964. The giant panda, a morphological study of evolutionary mechanisms. *Fieldiana: Zoology* 3:1–339.
- Ginsburg, L. 1961. Plantigradie et digitigradie chez les Carnivores Fissipèdes. *Mammalia* 25(1):1–21.
- Gonyea, W.J. 1976a. Adaptive differences in the body proportions of large felids. *Acta Anatomica* 96:81–96.
- . 1976b. The behavioral implications of saber-toothed felid morphology. *Paleobiology* 2:332–42.
- Grant, J.C.B., and J.V. Basmajian. 1965. *Grant's method of anatomy*. Baltimore: The Williams & Wilkins Company, 777 pp.
- Hildebrand, M. 1974. *Analysis of vertebrate structure*. New York: John Wiley & Sons, 710 pp.
- Ho, T.Y., L.F. Marcus, and R. Berger. 1969. Radiocarbon dating of petroleum-impregnated bone from tar pits at Rancho La Brea, California. *Science* 164:1051–52.
- Kurten, B. 1965. The Pleistocene Felidae of Florida. *Bulletin of the Florida State Museum* 9:215–73.
- . 1973. Pleistocene jaguars in North America. *Commentationes Biologicae Societas Scientiarum Fennica* 62: 1–23.
- Marcus, L.F. 1960. *A census of the abundant large Pleistocene mammals from Rancho La Brea*. Contributions in Science, no. 38, 11 pp. Natural History Museum of Los Angeles County.
- Marcus, L.F., and R. Berger. 1984. The significance of radiocarbon dates for Rancho La Brea. Pages 159–83 in *Quaternary extinctions*, ed. P. Martin and R. Klein. Tucson: University of Arizona Press.
- Menard, H.W., Jr. 1947. Measurements in length of the metapodials of *Smilodon*. Original Data, Archives, George C. Page Museum, Los Angeles, California.
- Merriam, J.C., and C. Stock. 1932. *The Felidae of Rancho La Brea*. Carnegie Institution of Washington Publication no. 422, 231 pp.
- Miller, G.J. 1968. *On the age distribution of Smilodon californicus Bovard from Rancho La Brea*. Contributions in Science, no. 131, 17 pp. Natural History Museum of Los Angeles County.
- Reighard, J., and H.S. Jennings. 1951. *Anatomy of the cat*. New York: Henry Holt and Company, 498 pp.
- Schaller, G.B. 1972. *The Serengeti lion*. Chicago: University of Chicago Press, 480 pp.
- Schaub, S. 1925. Ueber die Osteologie von *Machaerodus cultridens* Cuvier. *Eclogae Geologicae Helveticae* 19(1): 255–66.
- Simpson, G.G. 1941. The function of saber-like canines in carnivorous mammals. *American Museum Novitates* 1130:1–12.
- Wyman, L.E. 1914. Field notes, Rancho La Brea. Archives, George C. Page Museum, Los Angeles, California.
- Zar, J.H. 1974. *Biostatistical analysis*. New Jersey: Prentice-Hall, Inc., 620 pp.

Accepted 26 October 1984.