DID RANCHO LA BREA LARGE FELIDS (*PANTHERA ATROX* AND *SMILODON FATALIS*) CHANGE IN SIZE OR SHAPE DURING THE LATE PLEISTOCENE?

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Abstract—Previous authors have claimed that the large felids of North America changed in size and shape through the late Pleistocene. We re-examined the two most common felids, the saber-toothed cat *Smilodon fatalis*, and the American lion, *Panthera atrox*, from the Rancho La Brea tar pits in the Page Museum in Los Angeles. We measured large samples (typically 30 to 100 specimens of each element) of several dimensions of the most common bones (typically leg or foot bones) from all the pits with good radiocarbon dates. We analyzed for significance of differences using ANOVA, and used Principal Components Analysis to see if shape changes could be recognized by multivariate analysis of humeri and femora. Even though pollen, plants, snails, and isotopic studies provide evidence of dramatic climatic and vegetational change from the previous interglacial (40 ka-20 ka) to the peak glacial (20 ka-15 ka) to the glacial-interglacial transition (15 ka-10 ka) to the Holocene, none of the felids show any statistically significant differences in size or shape of their bones from one level to the next.

INTRODUCTION

The large felids of Rancho La Brea (RLB) are among the most familiar of all fossils from the late Pleistocene, or Rancholabrean North American Land Mammal Age (NALMA), and subject to much interest and research. The record at RLB provides an excellent sample of the fossils that were trapped in the tar between 35 and 9 ka (Akersten et al., 1983; Stock and Harris, 1992; Friscia et al., 2008). Ever since their description in the classic monograph of Merriam and Stock (1932), scientists have examined many aspects of the evolution and ecology of these RLB cats.

The saber-toothed cat (*Smilodon fatalis*) has been particularly well-studied. Among the early studies of the RLB samples of *S. fatalis* was a paper by Menard (1947), who looked at a selection of metatarsals and metacarpals from different RLB pits, and claimed that they changed in size over time. Menard's data (1947, plate 33) showed that the specimens from Pit 77 are smaller, followed (in increasing order of size) by Pits 4, 3, 61-67, and Pit 13. Menard (1947) measured only the maximum length of these bones, and in most pits had a sample of only 40-60 specimens. No statistical testing was employed, nor were the standard deviations or maximum and minimum size reported.

Critically, the advent of radiocarbon dating (Marcus and Berger, 1984; O'Keefe et al., 2009) has shown that Menard's "sequence" of increasing size through time is incorrect. The smallest specimens do indeed come from the oldest pit (Pit 77, dated at 35,370 years: O'Keefe et al., 2009). However, Menard's "sequence" breaks down after this sample. According to O'Keefe et al. (2009), Pit 3 is 18,593 years in age, Pit 4 is 14,546 years old, Pits 61-67 are 11,581 years old, but Pit 13 is 16,192 years old. The "largest" specimens are actually in the overlapping age ranges of Pits 3 and 4, and significantly older than Pits 61-67, which have smaller specimens. Taking Menard's (1947) old data at face value, they do not show a linear trend through time based on recent radiocarbon dating (Marcus and Berger, 1984; O'Keefe et al., 2009).

Menard's (1947) study of the RLB sample of *Smilodon fatalis* has been cited uncritically ever since as conclusive demonstration of size change in *S. fatalis* (Van Valkenburgh and Sacco, 2002, p. 165). Kurtén (1965) and Berta (1987) also reported size changes in *Smilodon*, but their samples came from the late Pliocene (Blancan NALMA) and the early Pleistocene (Irvingtonian NALMA) *Smilodon gracilis* of Florida, and did not include the last 35,000 years represented by *S. fatalis* at RLB. Kurtén (1965) treated all the RLB specimens as if they were one homogeneous sample. We found that this idea that *Smilodon* gets larger through the late Pleistocene is widespread among Pleistocene paleontologists, as

well as the staff at the Page Museum. As evidence, some people mentioned studies such as Shaw and Tejada-Flores (1985), which does not address size change, but merely a feature of the ectocuneiforms in *Smilodon*. On the other hand, Kurtén and Anderson (1980, p. 191) stated that there was no size change in *Panthera atrox* through the Pleistocene.

With radiocarbon-dated excavations and a larger sample size not available to Menard (1947), the possibility of dimensional and morphological changes in the RLB large felids needs to be re-examined. Of interest here, the last 35,000 years was a period of dramatic climatic changes, from the pre-glacial world 35,000 years ago, to the peak glacial 20,000 years ago, and then through the glacial-interglacial transition from 14,000 to 10,000 years ago and the last 10,000 years of the Holocene. A well-dated climatic record (Warter, 1976; Coltrain et al., 2004; Ward et al., 2005) at RLB was established by terrestrial plants, snails, freshwater mollusks, and isotopic studies. According to deep-sea offshore core samples, the pollen data recovered suggest the vegetation changed from oak-chaparral woodland (59 ka to 24 ka), then it was replaced by a closed-cone coniferous piñon-juniper forest with significant snowfall in the winter at the last glacial maximum (24-14 ka) (Heusser, 1998). During the glacial-interglacial transition (14 ka to 10 ka), the vegetation gradually returned to oak and chaparral with significant alders. In the past 10,000 years of the Holocene, the region was cloaked in the coastal sage scrub vegetation that still lives there today (Heusser, 1998).

If dimensional changes in RLB cats occurred over the past 35,000 years, we would expect them to show some response to the maximum cooling and vegetational change at peak glacial interval some 20,000 years ago. Although not all felids demonstrate Bergmann's rule of larger body size in colder climates of higher latitudes or altitudes, the American puma (*Puma concolor*) does vary in body size by latitude, with the largest in the higher latitudes of North and South America, and the smallest in the tropics (Kurtén, 1973; Agustin Iriarte et al., 1990; Sunquist and Sunquist, 2002). Similarly, among the many subspecies of the tiger (*Panthera tigris*), the largest are the cold-adapted Siberian tigers (227 kg in weight), while the smallest are the tropical subspecies such as the Sumatran tiger (75-140 kg in weight) or the Indochinese tiger (110-140 kg in weight) (Sunquist and Sunquist, 2002). Although Bergmann's rule does not apply to all mammal and bird species (Ashton et al., 2000; Meiri and Dayan, 2003). there are enough examples among large felids with wide geographic ranges that these trends in body size might be expected among Rancho La Brea felids when the climate cooled dramatically at 21 ka. These animals might also show Allen's rule, where colder-climate animals tend to have shorter, more robust limbs and smaller appendages.

METHODS

Using digital calipers, we measured only unbroken complete adult specimens. We made measurements of most of the common postcranial bones, including the humeri, femora, patellae, tibiae, astragali, third metacarpals (MCIII) and third metatarsals (MTIII). Data were recorded on Excel spreadsheets, which allowed us to calculate the statistics. Multivariate statistics were calculated using XL Stat.

Radiocarbon dates on the pits follow O'Keefe et al. (2009) and Marcus and Berger (1984) for pits that have not been recently re-dated. Although there was apparently some sexual size dimorphism in the American lions (Wheeler and Jefferson, 2009), but not in *Smilodon fatalis* (Van Valkenburgh and Sacco, 2002), it was not necessary to factor in size due to sexual dimorphism variables as part of this study. Samples were analyzed for normality using the Shapiro-Wilk test, and those samples that were parametric were then analyzed using ANOVA.

RESULTS

Panthera atrox

Basic statistics for all our measurements are given in Table 1. Our plots of the astragali and patellae dimensions through time are shown in Figure 1. As can be seen from the plots, the means of all the different pit samples (large open squares) show no net trends through time, but are stable at approximately the same value from 35 ka to 11 ka. There is no expected increase in body size at the last glacial maximum at 21 ka; in fact, the 21 ka patellar sample is among the smallest in body size (but not the astragalus sample).

To test this visual impression, a Shapiro-Wilk test was performed on all the larger pit samples, and they all proved to be normally distributed. Thus, ANOVA could be used to test for significance of difference between any single pit sample and the overall mean for the entire population. The ANOVA results (Table 2) showed that none of the pit samples of either patellae or astragali was significantly removed from the overall mean at the 95% confidence level. Thus, the *Panthera atrox* samples from Rancho La Brea show no significant changes in size through time, nor are there any samples that are significantly different from the overall mean, even those at 21 ka which might be expected to be larger during the last glacial maximum.

TABLE 1. Basic statistics of *Panthera atrox* bones analyzed in this study.

| Character	Age (ka)	N	Mean	Variance
Patella proximal-distal length	11	32	28.8	4.2
	16	2	26.6	6.5
	18	20	27.1	3.2
	21	5	25.3	7.4
	35	5	25.3	7.7
Patella lateral width	11	32	44.2	14.5
	16	2	44.6	18.0
	18	20	46.3	9.2
	21	5	47.3	5.2
	35	5	46.7	9.3
Patella dorsal-plantar depth	11	32	26.6	5.8
	16	2	27.9	16.8
	18	20	28.4	2.8
	21	5	29.7	1.9
	35	5	29.6	5.3
Astragalus proximal-distal length	11	17	54.1	26.0
	16	3	53.0	3.0
	18	23	54.9	7.9
	21	9	56.3	6.7
	35	6	51.0	22.4
Astragalus lateral width	11	17	64.4	28.5
	16	4	66.0	4.6
	18	23	66.0	6.4
	21	9	66.6	12.5
	35	6	62.3	39.0
Astragalus dorsal-plantar depth	11	17	37.0	10.8
	16	4	38.0	0.6
	18	23	37.2	2.8
	21	9	38.3	2.5
	35	6	35.1	9.3
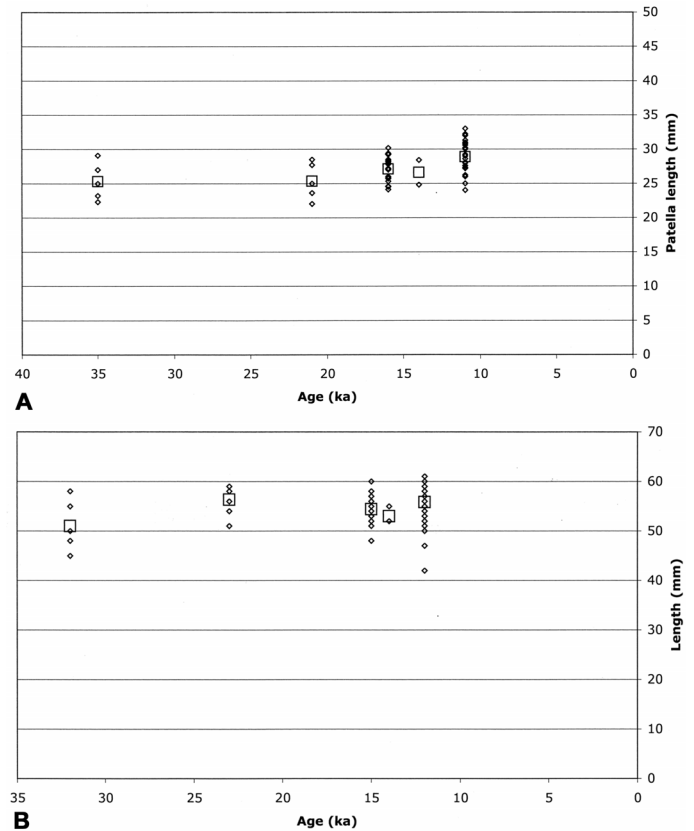
FIGURE 1. Plots of dimensions of *Panthera atrox* bones against the age of the pit sample. Open diamonds indicate individual specimens; open squares are the means for each time interval. **A**, Patellar length. **B**, Astragalus proximal-distal length.

TABLE 2. ANOVA of *Panthera atrox* bones. $F < F_{critical}$ in each case, so the means of each sequential sample are not significantly different from one another at the 0.05 confidence level. Degrees of freedom = 4.

Variable	F	F_{crit}	p	Significant?
Astragalus				
Proximal-distal length	1.87	2.54	0.13	No
Lateral width	1.42	2.54	0.23	No
Dorso-plantar depth	1.74	2.54	0.15	No
Patella				
Proximal-distal length	1.21	2.52	0.00	No
Lateral width	1.88	2.52	0.12	No
Dorso-plantar depth	1.67	2.52	0.00	No

Smilodon fatalis

Similar results were obtained from the much larger sample of *Smilodon fatalis*. Basic statistics of the specimens we measured are given in Table 3. The large number of specimens from numerous well-dated excavations at RLB gives us a clearer sample for our analysis. Visual inspection of the plots of every bone we measured (Figs. 2-3) showed no evidence of size changes through time, nor any significant size increases in the peak glacial interval about 21 ka. For example, linear dimensions of the forelimb elements (Fig. 2) showed no obvious trends in the humerus dimensions (Fig. 2A), and the same lack of trend of the means can be seen in all other humerus measurements (Table 3), and confirmed by ANOVA (Table 4). The lengths of the MCIII are similarly distributed (Fig. 2B, Table 3). Although there seems to be a slight increase in length from 35 ka to 11 ka, as argued by Menard (1947), this difference is not statistically significant (Table 4).

TABLE 3. Basic statistics of *Smilodon fatalis* bones analyzed in this study.

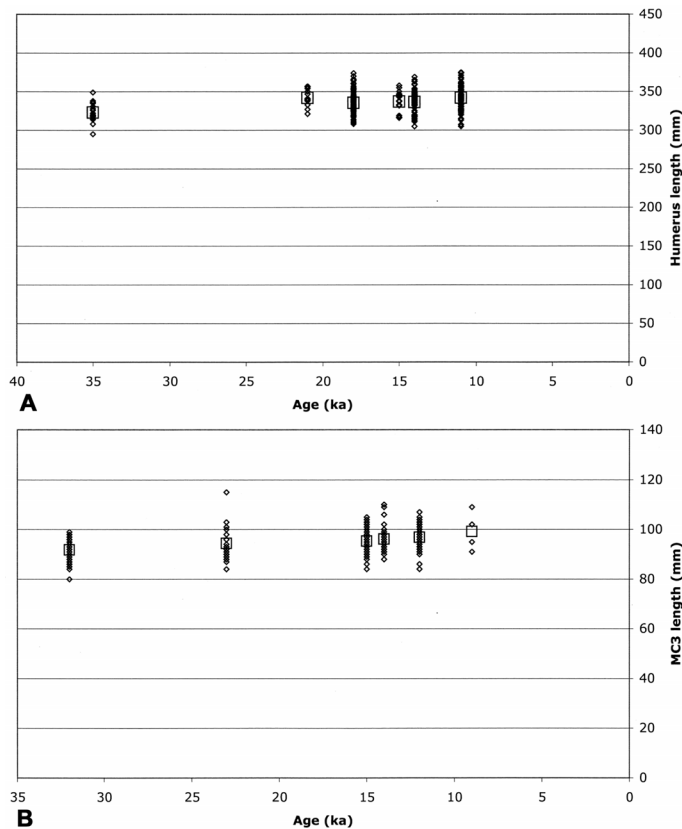| Character	Age (ka)	N	Mean	Variance
MCIII length	11	82	96.8	19.1
	13	4	92.5	62.9
	16	43	96.1	22.4
	18	62	95.7	21.5
	21	24	94.4	44.0
	35	61	91.8	17.8
MCIII midshaft width	11	82	17.2	1.4
	13	4	17.0	0.6
	16	43	16.0	1.8
	18	62	17.3	1.6
	21	24	16.7	2.0
	35	61	16.2	0.8
MCIII midshaft depth	11	82	14.1	0.8
	13	4	14.7	0.9
	16	43	13.4	1.0
	18	62	14.2	1.3
	21	24	14.0	1.2
	35	61	13.8	0.8
MCIII distal width	11	82	25.4	1.7
	13	4	26.2	0.2
	16	43	23.9	4.0
	18	62	25.5	2.8
	21	24	24.4	3.7
	35	61	24.0	1.6
Humerus length	11	79	341.0	317.0
	16	20	337.0	183.2
	18	119	335.8	196.1
	21	12	341.9	130.0
	35	17	323.0	161.5
Humerus proximal width	11	78	80.6	22.7
	16	20	78.2	22.9
	18	100	86.6	80.6
	21	12	80.3	18.7
	35	17	76.6	21.3
Humerus proximal depth	11	78	71.6	15.2
	16	20	69.6	10.6
	18	100	75.2	22.4
	21	12	70.7	11.6
	35	17	67.9	19.3
Humerus midshaft width	11	78	38.6	7.2
	16	20	38.5	7.4
	18	100	44.4	50.1
	21	12	38.5	6.6
	35	17	36.8	6.6
Humerus midshaft depth	11	78	52.6	13.0
	16	20	51.8	17.7
	18	100	44.3	50.7
	21	12	52.3	14.2
	35	17	49.8	14.7
Humerus distal width	11	78	106.7	40.3
	16	20	105.1	21.2
	18	100	105.9	35.9
	21	12	107.3	46.4
	35	17	101.4	38.0
Humerus distal depth	11	78	61.7	17.0
	16	20	61.7	9.9
	18	100	60.8	16.0
	21	12	60.8	8.6
	35	17	56.2	21.3
Femur length	11	196	362.0	230.7
	16	37	356.2	194.4
	18	50	368.7	248.5
	21	8	344.8	481.2
	35	63	348.2	324.8
Femur proximal width	11	193	92.4	21.0
	16	34	93.6	22.7
	18	47	95.1	24.8
	21	5	87.8	18.7
	35	60	92.4	31.2
Femur proximal depth	11	196	48.8	9.3
	16	37	47.1	9.0
	18	50	49.1	7.8
	21	8	46.0	7.4
	35	63	46.7	12.4
Femur midshaft width	11	195	35.7	3.9
	16	37	34.5	5.4
	18	50	36.0	5.5
	21	8	34.2	5.0
	35	63	35.6	4.0
Femur midshaft depth	11	196	32.3	3.7
	16	37	30.7	2.9
	18	50	32.6	4.1
	21	8	30.8	4.1
	35	63	31.1	5.2
Femur distal width	11	196	78.8	12.5
	16	37	75.6	9.7
	18	50	79.2	13.8
	21	8	74.3	23.9
	35	63	77.1	19.3
Femur distal depth	11	196	71.6	14.2
	16	37	69.0	15.2
	18	50	73.8	13.3
	21	8	69.3	17.4
	35	63	71.0	15.1
Patella antero-posterior length	11	102	54.9	15.4
	16	51	52.9	18.2
	18	100	52.2	14.7
	21	30	53.7	14.8
	23	3	50.2	`18.5
	25	6	52.4	8.2
	26	2	53.3	11.0
	29	6	52.3	9.9
	35	51	51.8	14.5
Patella lateral width	11	102	41.7	9.2
	16	51	40.2	8.2
	18	100	39.7	8.0
	21	30	41.3	8.2
	23	3	39.2	13.3
	25	6	42.3	17.6
	26	2	38.4	2.4
	29	6	41.8	6.4
	35	51	40.0	6.6
Patella dorsal-plantar depth	11	102	43.6	4.3
	16	50	44.3	5.7
	18	99	43.0	4.4
	21	30	42.7	4.2
	23	3	43.6	9.3
	25	6	43.1	6.5
	26	2	42.0	2.0
	29	6	43.3	13.4
	35	51	42.7	6.4
Tibia length	11	100	37.2	5.4
	16	48	36.5	5.9
	18	50	36.9	4.0
	21	12	38.2	4.9
	35	50	36.2	5.8
Tibia midshaft width	11	100	28.4	3.8
	16	48	27.3	3.8
	18	50	28.9	4.6
	21	12	29.5	5.3
	35	50	28.9	3.5
Tibia midshaft depth	11	100	28.4	2.8
	16	48	27.3	3.8
	18	50	28.9	4.6
	21	12	29.5	5.3
	35	50	28.9	3.5
Astragalus proximal-distal length	11	102	43.6	4.3
	16	50	44.3	5.7
	18	99	43.0	4.4
	21	30	42.7	4.2
	23	3	43.6	9.3
	25	6	43.1	6.5
	26	2	42.0	2.0
	29	6	43.3	13.4
	35	51	42.7	6.4
Astragalus lateral width	11	102	43.6	4.3
	16	50	44.3	5.7
	18	99	43.0	4.4
	21	30	42.7	4.2
	23	3	43.6	9.3
	25	6	43.1	6.5
	26	2	42.0	2.0
	29	6	43.3	13.4
	35	51	42.7	6.4
Astragalus dorsal-plantar depth	11	102	26.8	4.9
	16	51	25.5	5.2
	18	100	24.6	3.4
	21	30	25.6	4.0
	23	3	23.8	4.3
	25	6	25.7	4.7
	26	2	25.4	3.3
	29	6	25.1	4.5
	35	51	25.5	3.8
MTIII length	11	59	96.2	25.7
	13	4	98.0	4.0
	16	30	96.7	10.4
	18	68	96.3	21.6
	21	23	92.3	24.8
	35	47	92.5	15.4
MTIII midshaft width	11	59	18/8	1.4
	13	4	19/5	0.3
	16	30	17.1	1.7
	18	68	17.9	1.2
	21	23	17.4	1.5
	35	47	17.3	1.0
MTIII midshaft depth	11	59	14.6	0.9
	13	4	14.5	1.0
	16	30	14.1	1.3
	18	68	15.0	0.9
	21	23	14.6	1.2
	35	47	13.7	1.4
MTIII distal width	11	59	23.0	1.8
	13	4	22.5	4.3
	16	30	23.0	1.7
	18	68	23.3	2.6
	21	23	23.0	1.7

FIGURE 2. Plots of dimensions of *Smilodon fatalis* bones against the age of the pit sample. Open diamonds indicate individual specimens; open squares are the means for each time interval. **A**, Humerus length. **B**, MCIII length.

In the hind limbs, we find the same stasis and lack of any persistent trends (Fig. 3). The linear dimensions of the femora (Table 3, Fig. 3A) fluctuate a bit, but there is no statistically significant trend (Table 4) nor do the largest specimens occur at the last glacial maximum at 21 ka. The linear dimensions of the patellae (which have much larger samples from more pits) show no trend either (Fig. 3B, Table 3), nor do the tibiae (Fig. 3C, Table 3) or astragali (Fig. 3D, Table 3). These samples all proved to be normally distributed by a Shapiro-Wilk test, and ANOVA showed that there were no samples that were significantly removed from the rest of the population at the 95% confidence level (Table 4). Menard (1947) reported size increases from Pit 77 (35 ka) to the younger pits, and there does appear to be a slight increase in our data as well (Fig. 3E). However, these differences are not significant when subjected to analysis by ANOVA (Table 4).

These analyses demonstrate no evidence of significant size change in the linear dimensions of any of the bones we measured. Sometimes, however, there may be changes in shape, such as robustness of the limbs. To address this possibility, we took the midshaft cross-sectional areas of the three main long bones (humerus, femur, tibia) and divided the areas by the lengths to produce a robustness ratio. In all three limbs (Figs. 4A-C), there are no statistically significant trends in robustness. The means fluctuated slightly around the typical value in each plot, but there are no consistent long-term increases or decreases in robustness, nor is there a consistent change in robustness at the peak cooling of the last glacial maximum at 21 ka. If Allen's rule of shorter more robust limbs and other extremities in colder climates applied to these animals, we would expect the most robust specimens in the samples near 21 ka, but there is no evidence of this in our data (Fig. 4).

Multivariate Analysis

Our results show no evidence of significant size or shape changes

through time using basic univariate and bivariate statistics. To explore the possibility of more subtle changes in size or shape through time, we analyzed the two largest limb bones (humerus, femur) with Principal Components Analysis (PCA) to see if any particular size or shape trends emerge from multivariate data sets. All of these samples produced seven variables (Table 3), and there were large sample sizes from most pits, so they were well suited to PCA.

After the PCA was run separately on each pit sample on all seven variables of the humeri and femora, some interesting trends emerged. As is apparent in Table 5 and Figure 5, by far the largest portion of the variability (typically between 55-70% of the variability) loads on Factor 1 or the first principal component (PC1). In most studies like this, the first PC or first factor is usually interpreted to represent the size component of the sample, especially in biological samples that range widely in body size (e.g., juveniles to adults). In this study, all the samples were from adults so there is no juvenile component, but it is apparent that the individual pit samples are still sufficiently variable in size, possibly due to the overlapping ranges of size of males and females. This heavy loading on the first PC/first factor is to be expected in studies such as this. Unfortunately, we cannot directly compare the eigenvalues from these different pit samples and determine whether the differences are statistically significance or not.

For this reason, we adopted the method used by Lewis et al. (2010), and performed ANOVA on the individual scores of each specimen on PC1. Results are shown in Table 6. As with our ANOVA of simple linear variables and robustness ratios, there is no significant difference in the PC1 scores of the samples from the seven different pits. Thus, even more sophisticated methods of teasing out the overall size component from multiple variables confirms what is already apparent in the individual univariate measurements. There are no significant size differences among the five largest pit samples of *Smilodon* dating from 35 ka to 11 ka.

In regard to the question of shape differences, PCA has often been used as a method to tease out differences in shape that are not apparent by simple inspection of univariate or bivariate data. Given that the second factor/PC2 explains only 9-15% of the total variability (Table 5), the second factor/PC2 may not be a significant indicator of shape change. Nonetheless, we studied the factor loadings for all the variables. As shown in Figure 6, circular plots of F1 vs. F2 in the humeri show no consistent trends among which variables loaded most heavily on PC2/F2. Only variable 3 (midshaft width) was divergent on the F2 axis in the samples from 11 ka, 16 ka, 18 ka, but not 14 ka, 21 ka, or 35 ka. Nor does variable 4 (midshaft depth) diverge at all from the other variables, so this does not seem to correspond to simple midshaft robustness (consistent with our data plotted in Fig. 4). Variable 1 (humerus proximal width) is slightly separated from the rest at 16 ka and 18 ka, but in no other pit sample. None of the remaining five variables separate from the rest of the cluster on the F2 axis more than once. Thus, there are no obvious trends in shape change in the humeri in the F2/PC2.

Likewise, there are occasional examples of variables that stand out from the main cluster in the femora (Fig. 7), but no consistent trends through the pits in sequence. For example, variable 6 (distal antero-posterior length) stands out at 11 ka, 35 ka, and possibly at 18 ka, but at no other time, while variable 2 (proximal antero-posterior length of the femur) stands out at 21 ka, but at no other time. The same information can be gleaned from tables of factor loadings on the variables, but these will not be reprinted here since they are redundant of the plots in Figs. 6 and 7.

In summary, multivariate analysis revealed no trends that were not already apparent in the univariate and bivariate analyses. Size of the humeri and femora (as represented by the eigenvalues of the first PC/first factor) showed no real differences from one pit to the next, and this was confirmed by ANOVA of individual scores of each variable on PC1. No consistent shape differences (e.g., robustness) were detected by simple ratios (Fig. 4), and we found no consistent shape differences in the
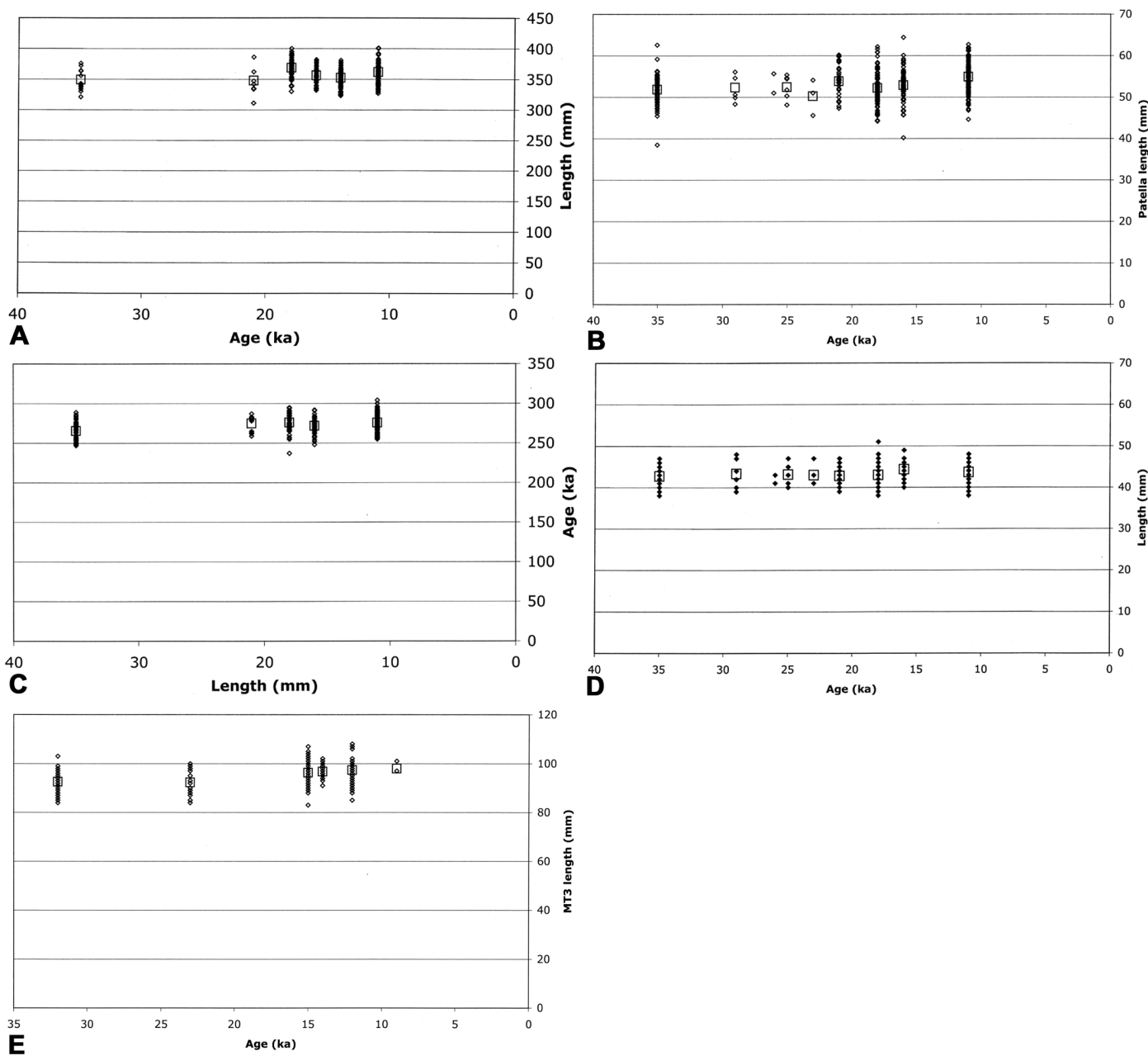
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FIGURE 3. Plots of dimensions of *Smilodon fatalis* bones against the age of the pit sample. Open diamonds indicate individual specimens; open squares are the means for each time interval. **A**, Femur length. **B**, Patella antero-posterior length. **C**, Tibia length. **D**, Astragalus length. **E**, MTIII length.

TABLE 4. ANOVA of *Smilodon fatalis* bones. $F < F_{critical}$ in each case, so the means of each sequential sample are not significantly different from one another at the 0.05 confidence level. Degrees of freedom = 5.

| Variable	F	F_{crit}	p	Significant?
Humerus				
Length	1.50	2.40	0.00	No
Proximal width	1.54	2.41	0.00	No
Proximal depth	1.88	2.41	0.00	No
Midshaft width	1.97	2.41	0.00	No
Midshaft depth	1.82	2.41	0.00	No
Distal width	2.05	2.41	0.02	No
Distal depth	0.70	2.41	0.00	No
MCIII				
Length	1.45	2.25	0.00	No
Midshaft width	1.02	2.25	0.00	No
Midshaft depth	1.97	2.25	0.01	No
Distal width	1.23	2.25	0.00	No
Femur				
Length	1.66	2.39	0.00	No
Proximal width	1.82	2.39	0.00	No
Proximal depth	0.88	2.39	0.00	No
Midshaft width	1.96	2.39	0.00	No
Midshaft depth	1.75	2.39	0.00	No
Distal width	1.02	2.39	0.00	No
Distal depth	1.95	2.39	0.00	No
Patella				
Proximal-distal length	1.32	1.96	0.00	No
Lateral width	1.26	1.96	0.00	No
Dorso-plantar depth	1.77	1.96	0.00	No
Tibia				
Length	1.97	2.41	0.00	No
Midshaft width	0.58	2.41	0.00	No
Midshaft depth	2.14	2.41	0.01	No
MTIII				
Length	1.63	2.25	0.00	No
Midshaft width	1.77	2.25	0.00	No
Midshaft depth	1.22	2.25	0.00	No
Distal width	0.47	2.25	0.79	No
Astragalus				
Proximal-distal length	1.52	1.96	0.01	No
Lateral width	1.27	2.12	0.26	No
Dorso-plantar depth	1.13	2.12	0.00	No
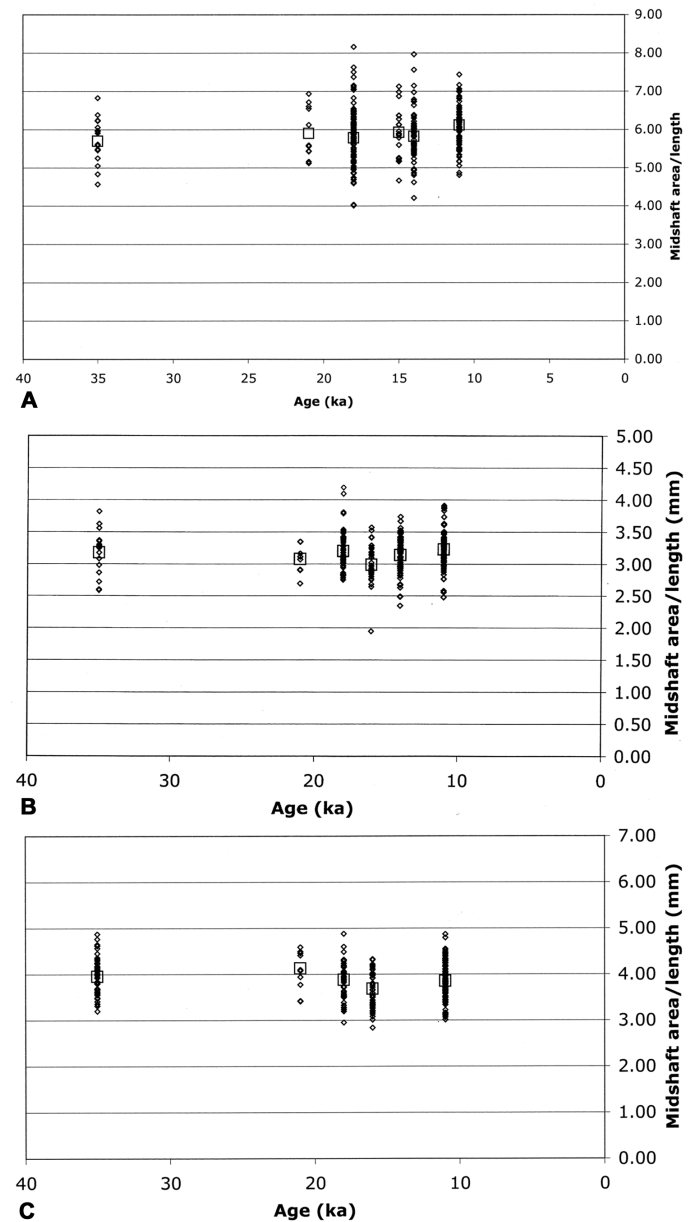
FIGURE 4. Plots of robustness ratios of the major limb bones of *Smilodon fatalis*, as measured by the ratios of the midshaft area divided by the length of each bone. Symbols as in Fig. 1. **A**, Humerus. **B**, Femur. **C**, Tibia.

TABLE 5. Multivariate statistics of *Smilodon fatalis* humeri and femora. "F1, F2…F7" are the seven factors in the PCA. "% Variability" shows how much of the total variability is accounted for by each factor.

HUMERI

	Pit Age (ka)	N	F1	F2	F3	F4	F5	F6	F7
Eigenvalue	11	34	4.36	1.11	0.46	0.33	0.29	0.24	0.17
% Variability			62.40	15.98	6.64	4.77	4.22	3.48	2.49
Eigenvalue	14	57	4.27	0.87	0.64	0.44	0.29	0.27	0.19
% Variability			61.05	12.56	9.24	6.30	4.21	3.86	2.76
Eigenvalue	16	20	3.95	1.04	0.88	0.51	0.29	0.21	0.09
% Variability			56.52	14.95	12.61	7.27	4.23	3.04	1.34
Eigenvalue	18	100	3.29	1.93	0.53	0.42	0.38	0.23	0.19
% Variability			47.02	27.69	7.69	6.01	5.50	3.33	2.73
Eigenvalue	21	12	4.65	1.24	0.57	0.29	0.14	0.05	0.02
% Variability			66.52	17.80	8.20	4.22	2.08	0.81	0.33
Eigenvalue	35	17	4.89	0.76	0.59	0.33	0.24	0.12	0.03
% Variability			69.23	10.91	8.42	4.76	3.60	1.81	0.55

FEMORA

	Pit Age (ka)	N	F1	F2	F3	F4	F5	F6	F7
Eigenvalue	11	74	4.37	0.73	0.66	0.44	0.38	0.23	0.15
% Variability			62.55	10.47	9.53	6.30	5.51	3.35	2.26
Eigenvalue	14	76	4.61	0.65	0.57	0.43	0.30	0.24	0.16
% Variability			65.97	9.30	8.19	6.23	4.39	3.52	2.36
Eigenvalue	16	36	4.52	0.91	0.62	0.29	0.28	0.23	0.12
% Variability			65.68	13.01	8.90	4.21	4.06	3.37	1.84
Eigenvalue	18	50	4.85	0.61	0.56	0.37	0.22	0.19	0.17
% Variability			69.38	8.77	8.07	5.33	3.16	2.73	2.54
Eigenvalue	21	8	5.13	0.65	0.56	0.38	0.20	0.03	0.01
% Variability			73.34	9.40	8.07	5.47	2.96	0.54	0.20
Eigenvalue	35	16	4.88	0.62	0.52	0.47	0.25	0.13	0.09
% Variability			69.81	8.95	7.53	6.73	3.62	1.94	1.39

TABLE 6. ANOVA of individual factor scores of the first PC/first factor of each observation *Smilodon fatalis* bones. $F < F_{critical}$ in each case, so the means of each sequential sample are not significantly different from one another at the 0.05 confidence level. Degrees of freedom = 5.

Variable	F	F_{crit}	p	Significant?
Humerus factor scores	0.492	2.252	0.781	No
Femur factor scores	0.154	2.249	0.978	No

multivariate analyses of these bones as well.

CONCLUSIONS

There have been claims in the literature that large felids (particularly *Smilodon fatalis*) from Rancho La Brea changed in size or shape in the late Pleistocene. We examined these claims by measuring multiple dimensions of many of the common limb elements (humeri, MCIII in the forelimb; the femur, patella, tibia, astragalus, and MTIII in the hind limb) from every pit with good radiocarbon dates and large sample sizes. Simple univariate plots of the linear dimensions these bones over time showed no evidence of significant size changes, as established by ANOVA. This is true even during the last glacial maximum at 21 ka, when larger body size would be expected as a response to colder climates (Bergmann's rule) or shorter, more robust limbs might be anticipated (Allen's rule). Robustness of the limbs (midshaft cross-sectional area divided by length) showed no changes through time. Finally, principal components analysis isolated a size dimension in the first PC/first factor (which accounted for 55-75% of the variation), but ANOVA of these data showed that there was no significant change through time. The second and third principal components, which accounted for only a few percent of the variation, showed no consistent trends on any one variable over more than a few pits. Thus, there is no evidence from any data that *Panthera atrox* and *Smilodon fatalis* showed any significant size or shape change from 35 ka to 11 ka.
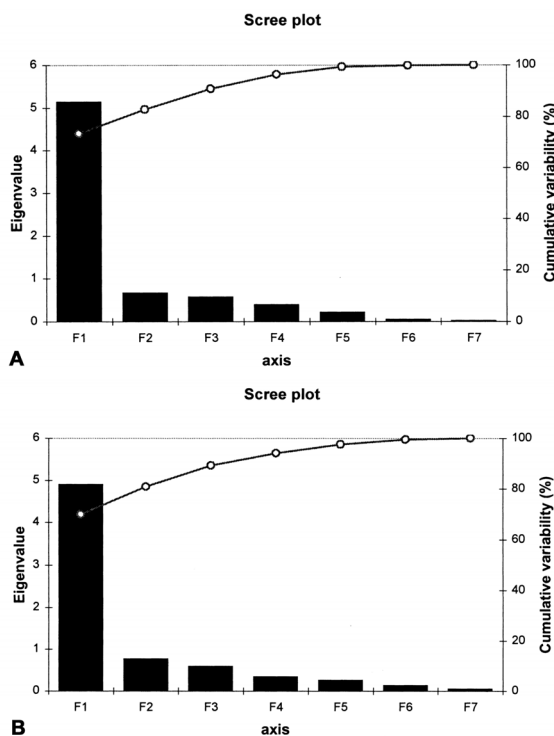
FIGURE 5. Typical scree plots of the eigenvalues for each factor, showing the loadings on each as a percentage of the total. In most samples, the first factor ("F1") accounts for 55-75% of the variation, and none of the remaining factors account for more than 10-15% of the total variation.
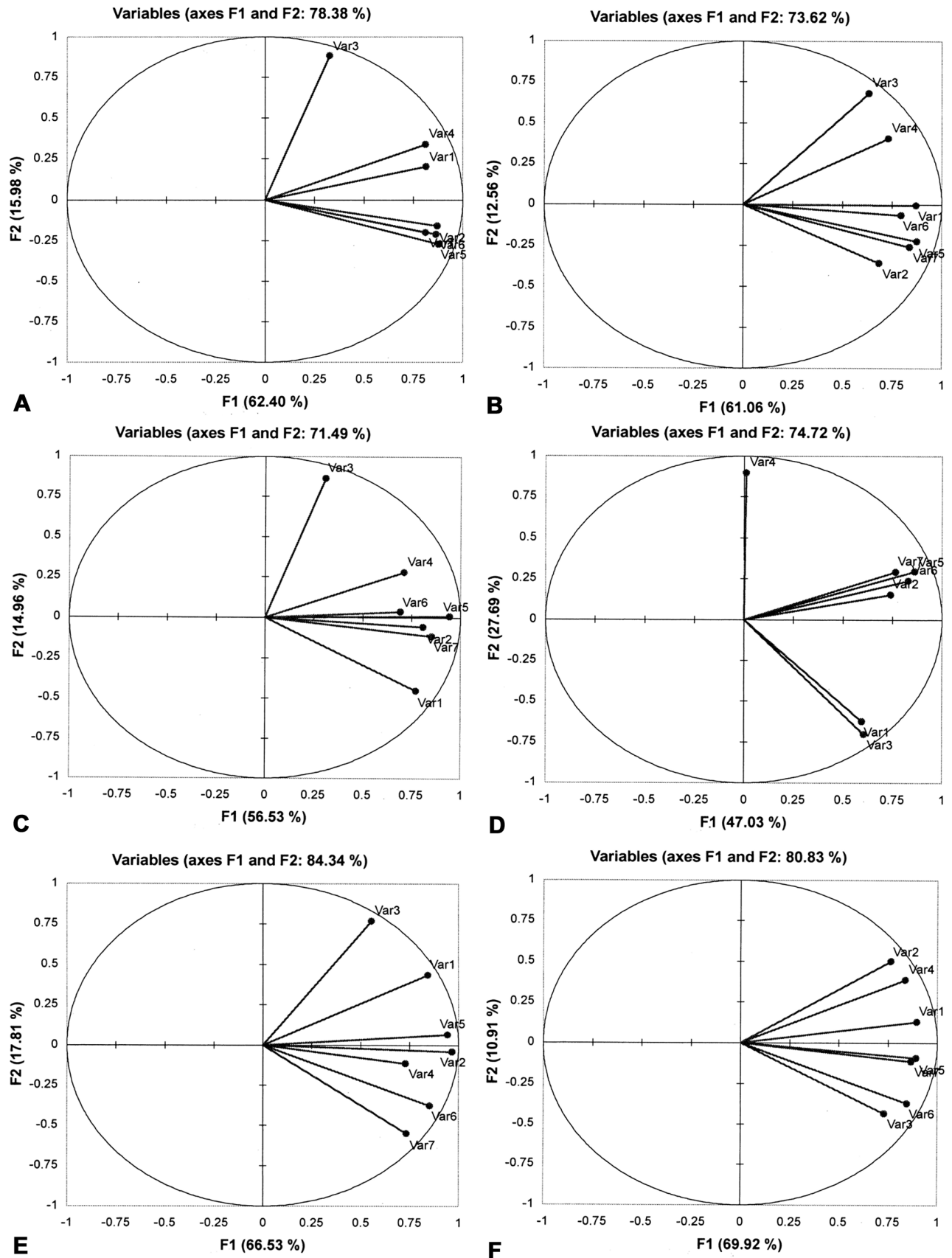
FIGURE 6. Circular plots of the humerus variables plotted against the F1 and F2 axes, showing which variables diverge most from the main cluster on the F2 axis. Variables coded as follows: Var1 = Proximal width; Var2 = Proximal depth; Var3 = Midshaft width; Var4 = Midshaft depth; Var5 = Distal width; Var6 = Distal depth; Var7 = Maximum length. **A**, 35 ka sample. **B**, 21 ka sample. **C**, 18 ka sample. **D**, 16 ka sample. **E**, 14 ka sample. **F**, 11 ka sample.
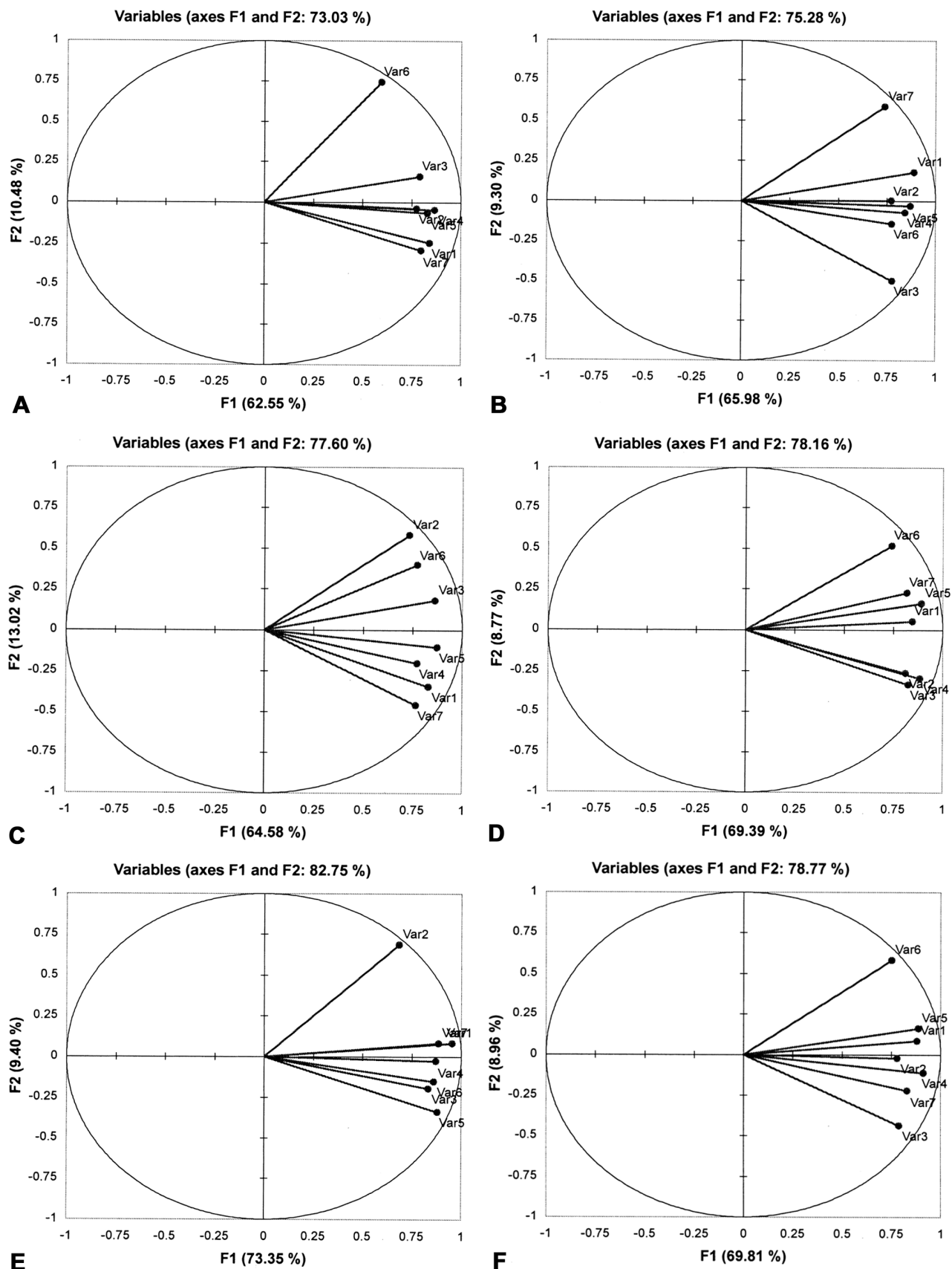
FIGURE 7. Circular plots of the femur variables plotted against the F1 and F2 axes, showing which variables diverge most from the main cluster on the F2 axis. Variables coded as in Figure 6. **A**, 35 ka sample. **B**, 21 ka sample. **C**, 18 ka sample. **D**, 16 ka sample. **E**, 14 ka sample. **F**, 11 ka sample.

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