ON THE AGE DISTRIBUTION OF *SMILODON CALIFORNICUS* BOVARD FROM RANCHO LA BREA

By GEORGE J. MILLER[1]

ABSTRACT: Skulls of over 2100 specimens of *Smilodon californicus* Bovard from the collection of the Los Angeles County Museum of Natural History are studied in an effort to determine the percentages of the various age groups that were trapped in the La Brea Pits. The specimens are arbitrarily classified as Juvenile, Young Adult, Adult, and Aged, using tooth wear and closure of the basioccipital-basisphenoid suture as criteria. The percentages of the four age groups are found to be as follows: 16.6% Juveniles, 23.2% Young Adults, 17.2% Adults, and 8.5% Aged, with 34.5% undetermined. The large number of undetermined, consisting mostly of adults that could not be positively classified as Young Adults, Adults, or Aged, are then classified with the Aged category eliminated, giving the following breakdown: 16.6% Juveniles, 25.7% Young Adults, 56.5% Adults, and 1.2% undetermined. These data show that a cross section of the *Smilodon californicus* population, rather than a preponderance of any one age group, was trapped in the tar pits.

INTRODUCTION

For the past 45 years the Rancho La Brea Fauna has been recognized by paleontologists as the outstanding collection of Pleistocene life available for study (Stock, 1961). Of the many large mammals trapped and preserved in the tar pools, those found in the greatest abundance are *Canis dirus* (the dire wolf), with from 1646 (Marcus, 1960) to 2000 specimens (Stock, 1929a); and *Smilodon californicus* Bovard, (the sabre-tooth cat), with from 1029 (Marcus, 1960) to 1500 specimens (Stock, 1929a). The excellent state of preservation of this material (Stock, 1929b and 1961), together with its abundance, suggests many possibilities for population, variation, extinction, and microevolution studies. In the hope that the information obtained will be of value in the furtherance of the studies mentioned above, the present study attempts to determine the age distribution of *Smilodon californicus* from an examination of the skulls of the animals that were trapped in the tar pits. The term "skull," as used in this paper, denotes any cranial specimen of sufficient completeness to determine the age. *S. californicus* was chosen for this study over *Canis dirus* for convenience only—the *Smilodon* material is more readily accessible. It is hoped that a similar study will be done in the near future on *C. dirus*.

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MATERIAL STUDIED

Skulls and parts of skulls of *Smilodon californicus* from the collection of the Los Angeles County Museum of Natural History were used exclusively in this study. All available catalogued and uncatalogued specimens were examined and taken into consideration (fifty of the 576 catalogued skulls were out on loan and therefore unavailable for study). Out of over 2100 specimens examined, 918 were, for reasons discussed below, found to be suitable for this study.

PROCEDURE

Lack of knowledge of the life span and the rate of maturation of *Smilodon* made it impossible to determine exact age groups, so arbitrary age groups were used (it was not deemed advisable to extrapolate from knowledge of recent carnivores because of the different patterns of tooth wear brought about by *Smilodon's* unique dentition). The age groups were designated as Juvenile, Young Adult, Adult, and Aged.

The Juvenile group includes all skulls with any deciduous dentition or alveoli for deciduous dentition and with no wear on any of the permanent dentition (Figures 1 and 2). This group is probably under-represented because of separation and fragmentation of the soft-boned young skulls with their incompletely sealed sutures (churning, or movement of the petroliferous mass in the tar pits, had a tendency to cause breakage and separation of bones and skeletons as well as cause the phenomenon known as pit wear). Complete skulls of Juveniles are rare (out of 150 Juvenile specimens examined, there were nine complete skulls, and the preparator had wired these together at the sutures as shown in Figure 3); most of the specimens in this age group consist of fragments (Fig. 4). Many skulls and fragments of skulls in this and in other age groups were not used in this study because of the possibility of duplication. When the uncatalogued fragmentary specimens were examined, all pit data were checked, and when a left and right part of an animal of the same age with the same pit data was found only one part of the animal was listed. Although this procedure could cause the elimination of some specimens from the study, any possibility of counting the same animal twice is avoided. As the workers who originally catalogued the fossils from Rancho La Brea are believed to have been extremely accurate (Leslie F. Marcus, 1966, personal communication), this study has not questioned possible duplication of any of the catalogued material.

Skulls with all permanent dentition or alveoli for permanent dentition and no deciduous dentition or alveoli were classified as Young Adults. Other criteria used for this group were: no wear on the incisors, canines, or P3; less than one millimeter of wear on the paracone of the P4 (Figures 5 and 6); and the open basioccipital-basisphenoid suture (Fig. 7). It was observed during the course of this investigation that closure of the basioccipital-

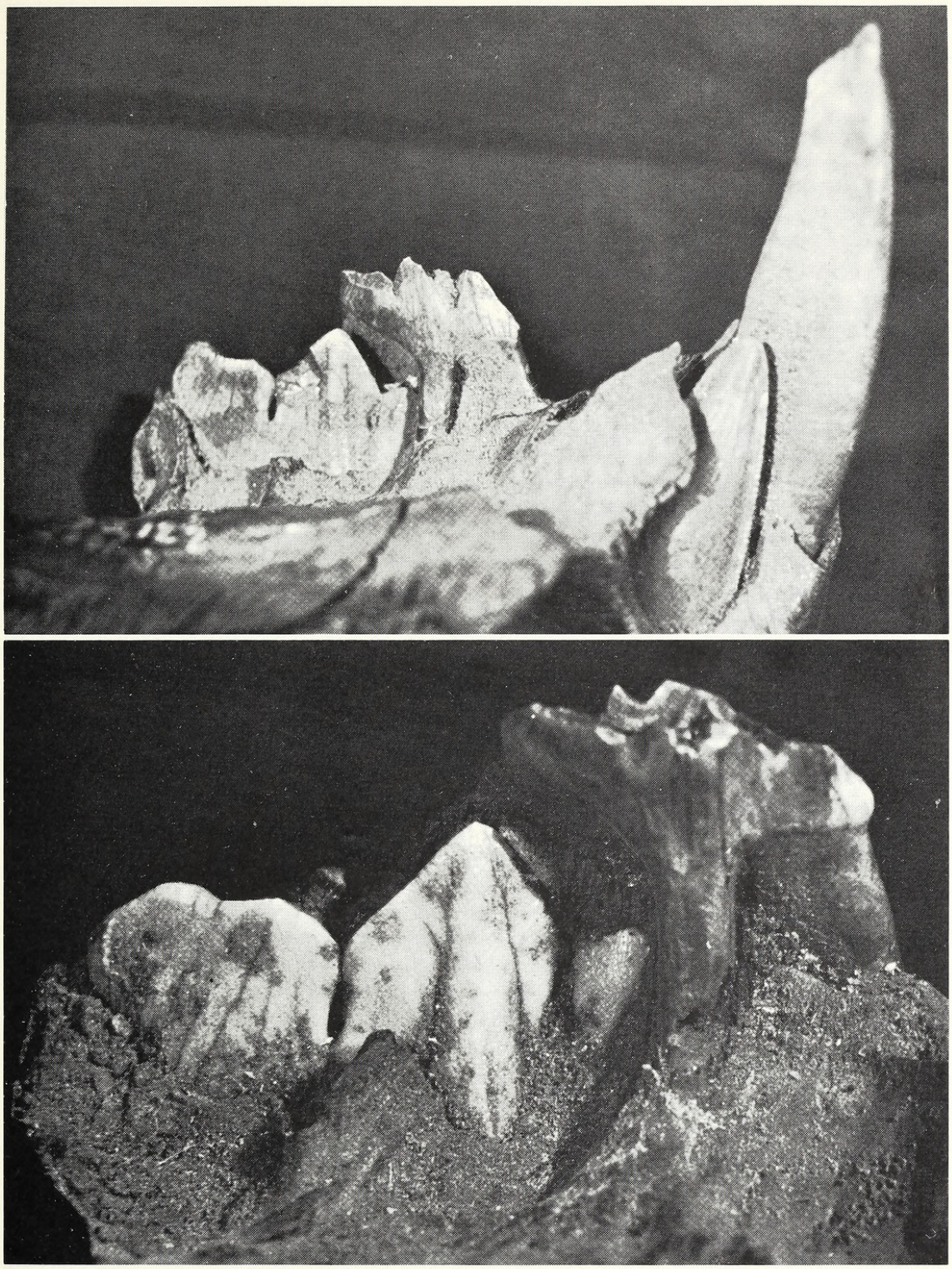


Figure 1. (Upper) *Smilodon californicus* Juvenile. Lingual view of deciduous right C and M3 and right permanent C and P4. Permanent dentition not completely erupted (LACM 2001-30).

Figure 2. (Lower) *Smilodon californicus* Juvenile. Lingual view of deciduous right M3 and permanent right P4. Permanent dentition not completely erupted and showing no wear (LACM 2001-104).

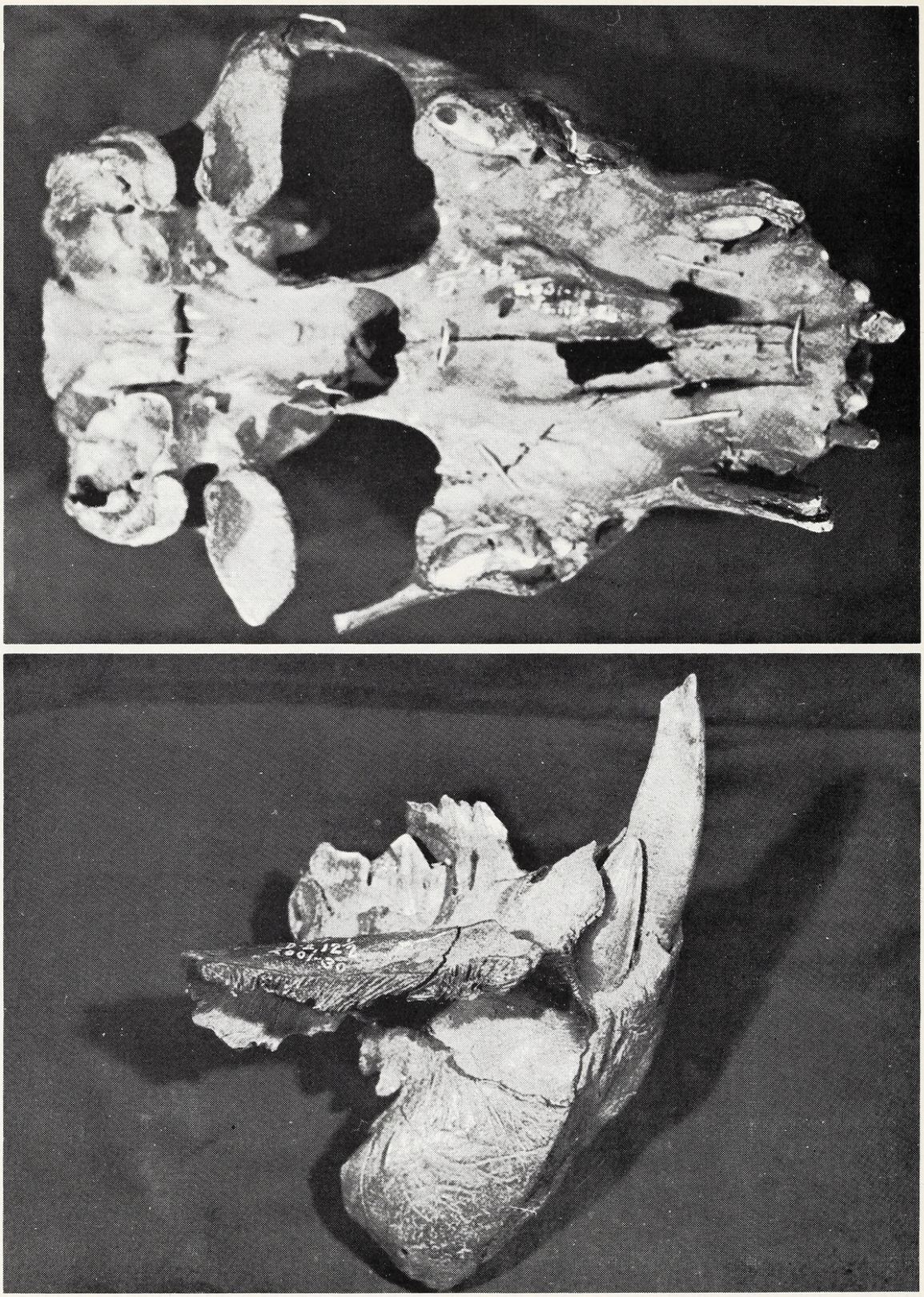


Figure 3 (Upper) *Smilodon californicus* Juvenile. Ventral view of one of the few complete Juvenile skulls recovered from the La Brea Pits (LACM 2001-104).

Figure 4. (Lower) *Smilodon californicus* Juvenile. Typical skull fragment showing upper right permanent and deciduous dentition (LACM 2001-30).

basisphenoid suture coincided with the completion of the emergence of the permanent dentition; therefore, this feature was also used to classify the Young Adults.

Presence of all permanent dentition or alveoli; moderate wear on the canines, incisors, and P3; the paracone and metacone of the P4 worn from one millimeter to one centimeter from the alveolar border (Fig. 8); and the closed basioccipital-basisphenoid suture (Fig. 9) were used as criteria for the Adult grouping.

Extreme wear on all dentition and the P4 worn from one centimeter above the alveolar border to the alveolar border (Fig. 10) were the characteristics used to classify the Aged. Some carnassials were found that were worn through to the pulp cavity as shown in Figure 11. A tooth worn to this extent would not be likely to last much longer so animals with this condition were considered to be near the end of their life span and were therefore classified as Aged.

When a division was made between the Adults and Aged groups, the amount of wear on the P4, unless caused by malocclusion, took precedence over other criteria. Extensive wear was sometimes found on one carnassial and not on the other and was thus considered to be caused by malocclusion rather than by age. Although there are two hypotheses to explain the mode of existence of *Smilodon* (some authorities consider *Smilodon* to have been a fierce predator, whereas others consider him to have been a scavenger or carrion feeder), the carnassial would seem to have been essential to the animal in either case. Another possible cause of extensive wear could be additional use of the carnassials brought about by loss of the canines (Stock, 1961).

Use of closure of the basioccipital-basisphenoid suture as a means of age determination was justified, as discussed above, by the fact that closure was observed to coincide with the emergence of the permanent dentition. Furthermore, the location of the suture at a sturdily constructed area of the skull prevented its opening on Aged specimens that had been subjected to pit churning. Aged skulls were found that had undergone severe strain, with many of the other sutures opened, but still having the basioccipital-basisphenoid suture closed.

RESULTS

Counts taken during this study show that a total of at least 2400 *Smilodon* skulls have been collected from Rancho La Brea, approximately 2100 of these being in the collection of the Los Angeles County Museum of Natural History. This count is somewhat more than that of Stock's (1929) census with 1500 specimens and Marcus' (1960) census with 1029 specimens; however, these censuses were taken using bones other than the skull. The discrepancies may possibly be accounted for by Marcus' (1960)

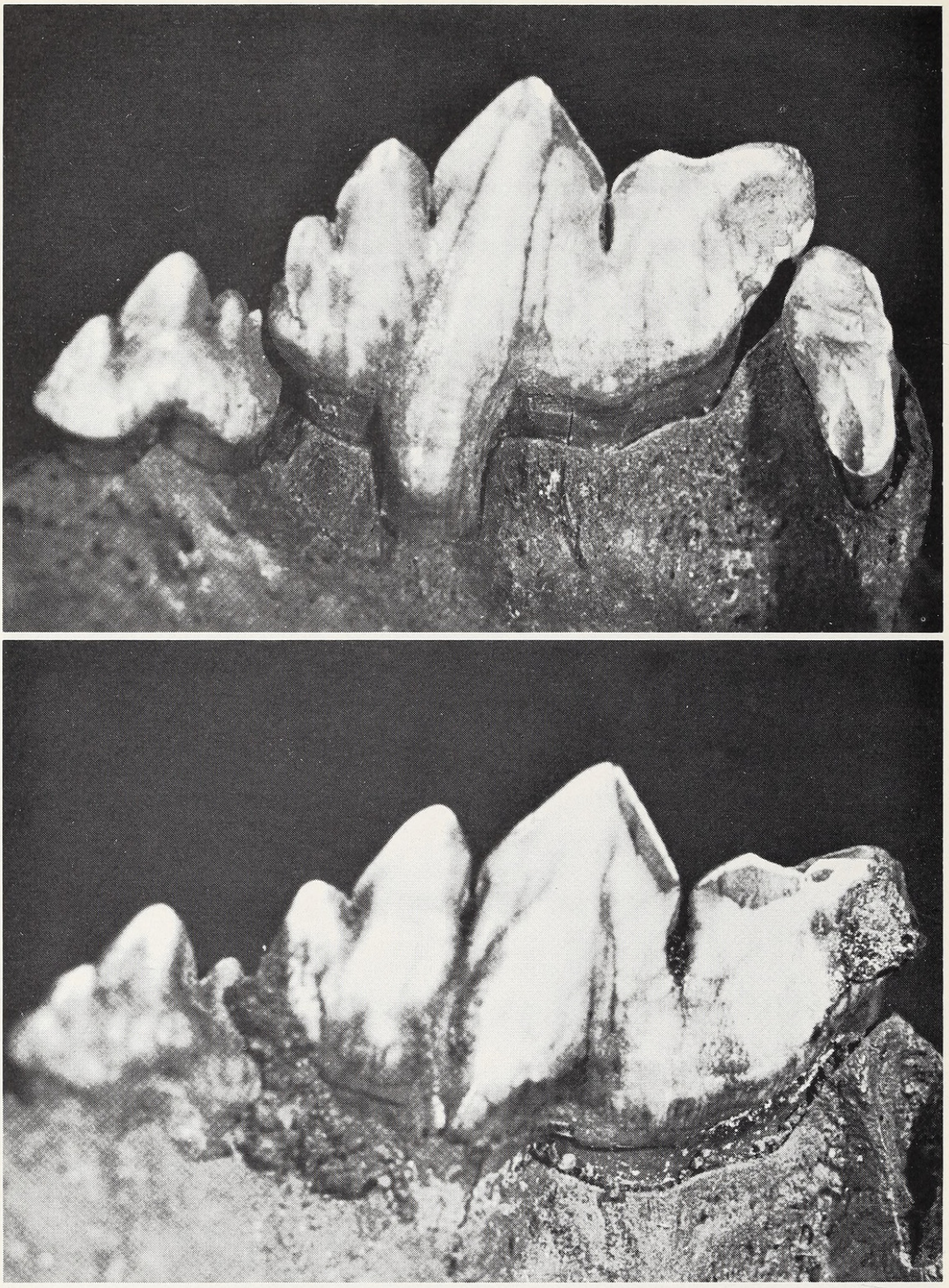


Figure 5. (Upper) *Smilodon californicus* Young Adult. Lingual view of permanent left P3, P4, and M1 showing less than one millimeter of wear on the paracone of the P4 (LACM 2001-101).

Figure 6 (Lower) *Smilodon californicus.* Young Adult. Lingual view of permanent left P3 and P4 showing one millimeter of wear on the paracone of the P4 (LACM 2001-290).

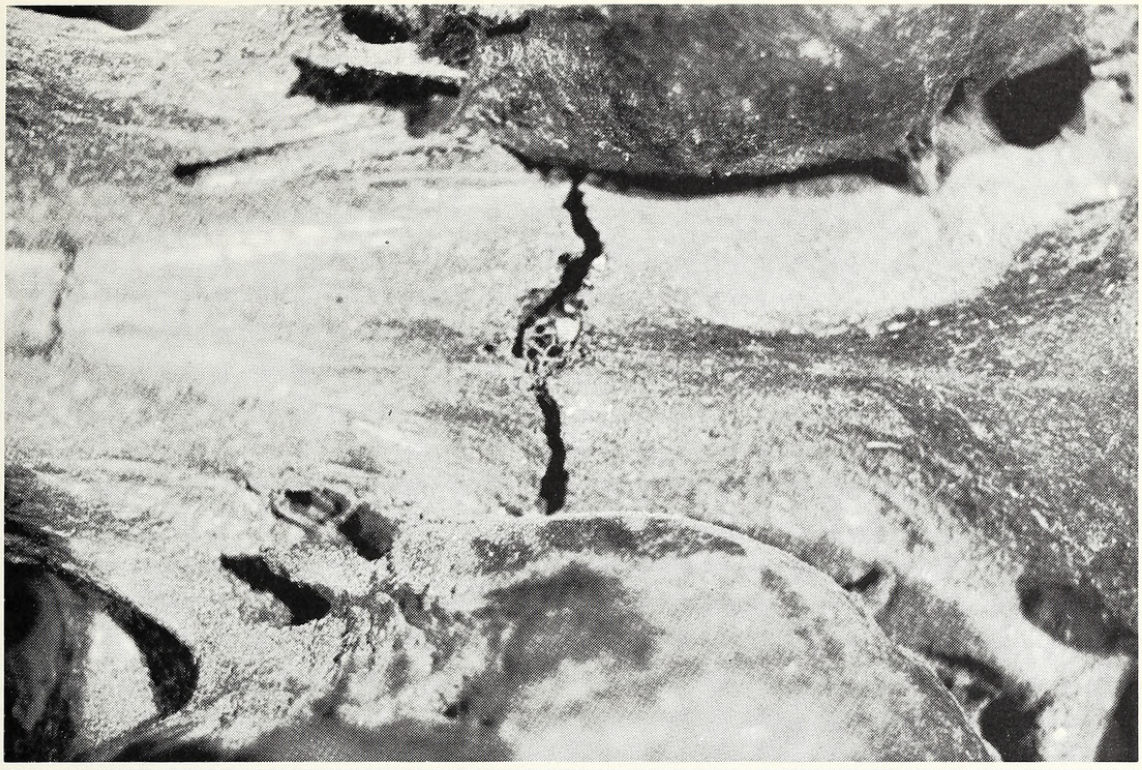
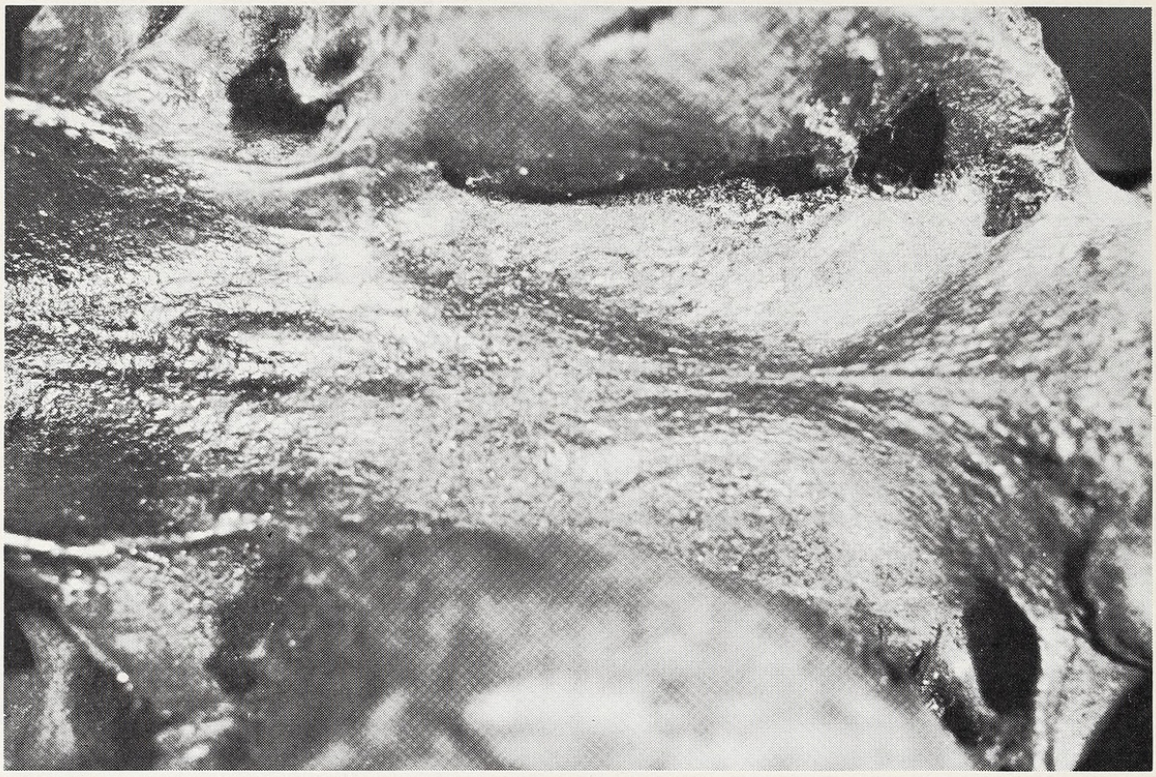


Figure 7. (Upper) *Smilodon californicus* Young Adult. Ventral view of skull showing basioccipital-basisphenoid suture not closed (LACM 2001-101).

Figure 8. (Lower) *Smilodon californicus* Adult. Lingual view of permanent left P3 and P4 showing more than one millimeter of wear on the paracone and metacone of the P4 (LACM 2001-250).



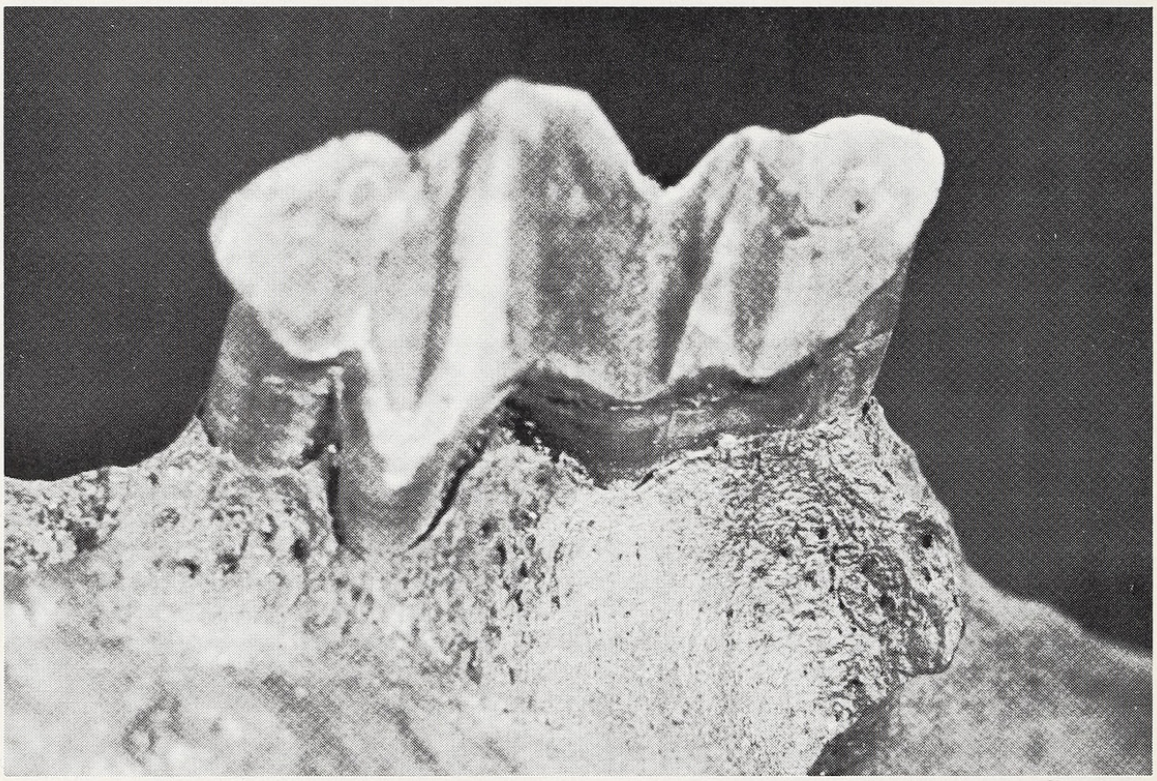


Figure 9. (Upper) *Smilodon californicus* Adult. Ventral view of skull showing basi-occipital-basisphenoid suture closed (LACM 2001-96).

Figure 10. (Lower) *Smilodon californicus* Aged. Lingual view of permanent left P4 showing tooth worn down to within one centimeter of the alveolar border (LACM 2001-102).

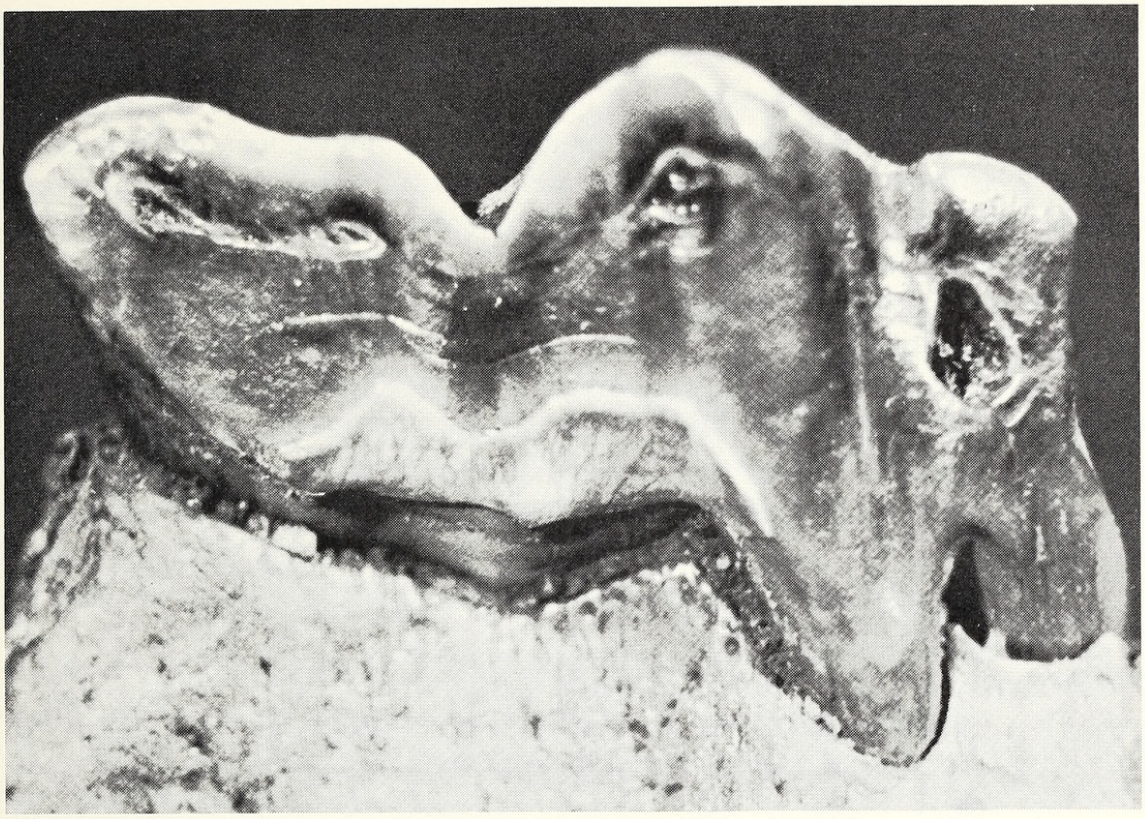


Figure 11. Smilodon californicus Aged. Lingual view of permanent right P4 showing tooth worn through to the pulp cavity (LACM 2001-297).

Selection Hypothesis, in which he suggests the possibility of selective preservation and of selective collection. The Rancho La Brea field notes show that during excavation of the pits a great many specimens were discarded as being too poorly preserved to merit retention (Wyman, 1913). Many collectors have a tendency to be more selective when collecting a rich deposit than they would be under more normal circumstances and it seems that the La Brea collectors were affected by this human weakness. There are 576 catalogued skulls in the Los Angeles County Museum of Natural History collection, 50 of which were out on loan and thus not studied; 342 uncatalogued but identifiable; and over 1350 uncatalogued fragmentary specimens which were not suitable for this study, making a total of at least 2100 specimens in the Los Angeles County Museum collection. A recent census of the collection at the University of California at Berkeley (John E. Mawby, 1966 personal communication) showed 111 skulls and fragments of skulls (an additional 62 fragmentary specimens in this collection are probable duplications). Many skulls from the Berkeley collection have been loaned or traded; it is probable that the collection originally contained at least 200 skulls. Data were not available on the smaller collections made by Occidental College, Los Angeles High School, and other institutions. If these

smaller collections are disregarded, there is a total of at least 2100 skulls, 918 or 43.7% of which were suitable for or available for and used in this study. It must be emphasized that the 2100 skulls include many fragments and thus may give an exaggerated picture of the number of animals represented. It is quite probable that many of these fragments are from the same animal. This probable variable, as mentioned above, was taken into account in this investigation.

Table 1 shows a breakdown of the data obtained into four age groups: Juvenile, Young Adult, Adult, and Aged, with an undetermined group consisting of 11 Juveniles, 24 Juvenile or Young Adult fragments, and 283 Adults. Because the 11 Juveniles are possible duplications, they are not included in the classification. The 283 Adults could not be classified as Adults or Aged because of their poor condition—too many teeth missing in some, and difficulty in distinguishing between age and pit wear in others; however, they could all be positively identified as mature adults by closure

TABLE 1
FREQUENCY IN NUMBER AND PERCENT OF INDIVIDUALS OF EACH AGE GROUP

Age Group	*Frequency in Number of Individuals*	*Percent of Individuals*
Juveniles	150	16.6
Young Adults	213	23.2
Adults	158	17.2
Aged	79	8.5
Undetermined	318	34.5
Totals	918	100.0

TABLE 2
FREQUENCY IN NUMBER AND PERCENT OF INDIVIDUALS OF EACH AGE GROUP (THREE AGE GROUPS)

Age Group	*Frequency in Number of Individuals*	*Percent of Individuals*
Juveniles	150	16.6
Young Adults	237	25.7
Adults	520	56.5
Undetermined	11	1.2
Totals	918	100.0

of the basioccipital-basisphenoid suture. Although Table 1 shows a good age distribution, 34.5% of the animals studied remain unclassified. It was therefore decided for purposes of comparison to combine the Adults and the Aged and to include the 283 undetermined Adults under the heading of Adults, and to place the 24 fragmentary young specimens under the Young Adult heading to give the results shown in Table 2. The decision to place the 24 young animals in the Young Adult grouping was made by using either tooth wear or closure of the basioccipital-basisphenoid suture as criteria instead of using both as was done in Table 1.

In Table 3 the distribution of the four age groups is shown for the most heavily populated pits. The percentage distribution of the same data is shown in Table 4. The data from Tables 3 and 4 were combined into three age

TABLE 3
FREQUENCY OF SKULLS OF EACH AGE GROUP
IN THE MOST HEAVILY POPULATED PITS
(FOUR AGE GROUPS)

	Pit Number						
	3	61-67	4	77	13	60	2
Age Group							
Juveniles	61	23	24	7	9	4	4
Young Adults	56	44	19	7	4	0	3
Adults	65	62	26	4	1	3	2
Aged	27	33	15	1	1	0	1
Undetermined	136	95	26	44	43	11	6
Totals	345	257	110	63	58	18	16

TABLE 4
PERCENT OF SKULLS OF EACH AGE GROUP
IN THE MOST HEAVILY POPULATED PITS
(FOUR AGE GROUPS)

	Pit Number						
	3	61-67	4	77	13	60	2
Age Group							
Juveniles	17.6	9.0	21.8	11.1	15.5	22.2	25.0
Young Adults	16.2	17.1	17.2	11.1	6.9	0.0	18.8
Adults	18.9	24.1	23.7	6.3	1.7	16.7	12.5
Aged	7.9	12.8	13.6	1.6	1.7	0.0	6.2
Undetermined	39.4	37.0	23.7	69.9	74.2	61.1	37.5

groups (Juvenile, Young Adult, and Adult) in the same manner as described above (the specimens under the undetermined heading were all classified except for the 11 doubtful Juveniles) to give the distribution of the animals in the seven most heavily populated pits as seen in Tables 5 and 6. A total of 867 specimens was used in the pit breakdown, which made a smaller sampling than was used in the over-all distribution because the smaller pits were not included and because skulls without pit data were necessarily eliminated. The data for Pit 61 and Pit 67 were combined because these two pits were actually "one large pit" (Marcus, 1960).

TABLE 5
FREQUENCY OF SKULLS OF EACH AGE GROUP
IN THE MOST HEAVILY POPULATED PITS
(THREE AGE GROUPS)

	Pit Number						
	3	61-67	4	77	13	60	2
Age Group							
Juveniles	68	27	25	7	9	5	4
Young Adults	91	69	22	17	12	0	5
Adults	177	161	63	39	37	13	5
Undetermined	9	0	0	0	0	0	2
Totals	345	257	110	63	58	18	16

TABLE 6
PERCENT OF SKULLS OF EACH AGE GROUP
IN THE MOST HEAVILY POPULATED PITS
(THREE AGE GROUPS)

	Pit Number						
	3	61-67	4	77	13	60	2
Age Group							
Juveniles	19.3	10.5	22.7	11.1	15.5	27.8	25.0
Young Adults	26.5	26.8	20.0	27.0	20.7	0.0	31.3
Adults	51.6	62.7	57.3	61.9	63.8	72.2	31.3
Undetermined	2.6	0.0	0.0	0.0	0.0	0.0	12.4

DISCUSSIONS AND CONCLUSIONS

It is believed that the use of the two different age distributions (Juvenile, Young Adult, Adult, and Aged as opposed to Juvenile, Young Adult,

and Adult), gives a more thorough view of the data than does a single breakdown. Both breakdowns are considered to be of value in that the four-class grouping gives a more detailed picture of the distribution, whereas the three-class grouping includes a larger sampling. It may be noted that the three-class grouping, "youth, middle life, and old age," was favored by Kurtén (1954).

The most likely place for deviation is in the Juvenile category, wherein poor preservation of young animals would result in a low count. The possibility of increased fecundity (Merriam and Stock, 1932) would, however, have a tendency to partially offset this factor. It has been hypothesized that animals on the verge of extinction, undergoing a population decrease, experience an increase in fecundity as a natural compensatory mechanism. This phenomenon may be compared to a similar condition that may be observed on a smaller scale in living populations today during so-called "good years." In a time of drought or other adverse climatic conditions litter size and populations decrease. When environmental conditions improve and the food supply becomes abundant an increase in fecundity may be observed. Favorable conditions would have a tendency to occur when the population is reduced, as the environment would then be more able to meet the needs of the smaller population. There is also the possibility that younger animals with their greater vigor would be better able to avoid being trapped or to escape after being trapped. However, it would seem that the lack of experience of such animals coupled with their youthful exuberance would tend to lead them into more trouble, thus increasing the probability of their blundering into the tar pools. The net result would thus probably be a mutual cancellation of these two factors.

Two possibilities of discrepancies in the division of the Adult and Aged exist because some animals show excessive tooth wear for their age (Kurtén, 1954); and because of difficulty in distinguishing between pit wear and age. Combining these two groups into the Adult grouping, as was done in Tables 2, 5, and 6, eliminated this problem.

Selective preservation and collection (Marcus, 1960) is a possible variable that could not be controlled at this late date.

The age distribution in Table 1 clearly shows that a cross section of the *Smilodon* population was trapped and preserved in the La Brea Pits, rather than a majority of any one age group. Table 1 also shows that there are a sufficient number of specimens from each age group for population, variation, extinction, and microevolutionary studies (it should be recognized that until dating of this material has been accomplished, the collection represents a population over an indefinite period of time). These data also show that at least 8.5% of the *Smilodon* population reached old age.

The need for age dating of the La Brea collection has long been recognized (Howard 1960, Stock 1961); however, very little has been done.

Although work is now in progress on the dating of animal remains and some information has been obtained, all published material to date has been from analyses of wood samples. A "wood sample" from an unidentified pit was dated as 16,325 + or − 2000 years B. P. (Before Present) (Douglas 1952). Howard (1962) commented on the questionable value of this dating because of the lack of proper data on the specimen and because of the method used. Stock (1961) referred to the La Brea fauna as "late middle Pleistocene" and "late Pleistocene." Howard (1960) reported dating of a tree from Pit 3 as 14,500 B. P. + or − 200 years. As Howard observed, "The dating of the tree from pit 3 undoubtedly could apply as well to the fossil bones of the extinct animals . . . . ." It is also possible that the bones found stratigraphically below the tree roots are even older (Hildegarde Howard, 1967, personal communication). However, this is an isolated case. The fortuitous circumstance of a tree rooted in amongst the bones occurred only in one pit. This was the state of things as of 1962. Recent radio-carbon dating by Berger and Libby (1966) has extended the time range for Rancho La Brea considerably as shown below:

Pit 4,	5 foot depth	33,700 + or − 1600 years B. P.
Pit 9,	8½ foot depth	13,300 + or − 160 years B. P.
Pit 9,	16 foot depth	> 40,000 years B. P.
Pit 16,	6½ foot depth	> 40,000 years B. P.
Pit 16,	12 foot depth	> 40,000 years B. P.
Pit 77,	no record of depth	37,000 + or − 2660 years B. P.

Although this gives a much better perspective of the age of some of the pits, this work was also done on wood samples, and any correlation between the wood and the bones is open to question. Due to pit churning the correlation between bones found in any one pit at the same depth and in the same grid may also be questioned. Berger and Libby (1966) also report a date of 23,300 + or − 510 years B. P. for cypress wood and 32,350 + or − 1400 years B. P. for leaves of California live oak from the University of California at Berkeley collection of Rancho La Brea material. Axelrod (1966) used these data for an analysis of the Rancho La Brea flora in which he was able to show that "at least two widely different communities" were "entombed in the tar pits at different times, and under wholly different climatic conditions." Recent (July, 1966) unpublished dating of *Canis dirus* humeri by Geochron Labs., Inc. showed a specimen from Pit 3 at a depth of 22 to 25 feet to have an age of 9860 + or − 550 C-14 years B. P., and a specimen from Pit 16 at 8 to 12 feet to have an age of 10,710 + or − 320 C-14 years B. P. This dating was, however, on carbonate, as it was found to be impractical to date the collagen because of contamination by petroleum and other organic compounds such as paint. (Paint was used by the original curators to label the bone.) New collagen extraction methods

now being developed promise to overcome this difficulty. There is, therefore, still a need for an extensive dating of bone. As will be suggested below, two of the pits may be considered as representative of the over-all distribution of *Smilodon* from La Brea. Possibly the most valuable procedure would thus be to date all of one element from one of the more prevalent animals such as *Smilodon californicus* or *Canis dirus* for one of the more representative pits. As Berger and Libby (1966) show Pit 4 to be one of the oldest pits and Pit 4 will be suggested below to be one of the representative pits, it might be most useful to do this work on Pit 4, although Pit 3 should also be considered as one of the representative pits.

Although Tables 1 and 2 show a larger proportion of Adults than of Juveniles, if the Juvenile and Young Adults are combined and then compared with the adults, a ratio of approximately 56 adults to 42 young is obtained. Without taking into consideration the poor preservation chances of young animals, this ratio is reasonably close to the age distribution (58 adults to 40 young) found in recent living populations of *Panthera (Felis) leo* (Guggisberg, 1963), the only recent large cat for which age distribution data were available. A chi-square test for deviation on these data based on the methods of Simpson, Roe and Lewontin (1960) showed a P value of .7 or no significant deviation from the expected. It may be argued that any comparison between *Smilodon* and the African lion is not necessarily pertinent but there are no data on populations of any size of large carnivores, either fossil or living, available.

The frequency of skulls from the four age groups (Juvenile, Young Adult, Adult, and Aged) in the most heavily populated pits (Tables 3 and 4) shows Pit 3 and Pit 4 to have an age distribution very close to that of all the pits combined (Table 1). Pit 3 and Pit 4 may thus possibly be representative of the Rancho La Brea *Smilodon* population, so either of these two pits could be utilized in a population study instead of studying the entire collection. Although similar frequencies being found in similar or related populations may not necessarily mean that the populations are identical (Leslie F. Marcus, 1967, personal communication), the fact that the age distributions are so nearly alike would seem to justify taking full advantage of the similarities.

The breakdown of the data into three age groups (Juvenile, Young Adult, and Adult) also shows the age distribution of *Smilodon* from Pit 3 and Pit 4 to be in close agreement with the distribution of the entire *Smilodon* collection (Tables 2, 5, and 6).

The conclusion is therefore made that the Rancho La Brea population of *Smilodon californicus,* as represented by the collection of the Los Angeles County Museum of Natural History, is a valid cross section of a population in time and as such, is excellent material for studies of population, variation, extinction, microevolution, and other related paleontological problems.

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