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MEMOIRS
OF THE
UNIVERSITY OF CALIFORNIA

Vol. 1. No. 2

THE FAUNA OF RANCHO LA BREA

PART I. OCCURRENCE

BY
JOHN C. MERRIAM

BERKELEY
THE UNIVERSITY PRESS
1911

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INTRODUCTION

Of the numerous occurrences of animal remains representing prehistoric life on the North American continent, the locality at Rancho La Brea furnishes one of the most nearly complete pictures of the fauna of a given region at a given period that has thus far been obtained. When all of the data have been gathered through intensive study of this field, and when the facts thus assembled have been interpreted, we shall have gone far toward reaching an understanding of the biologic and climatic conditions obtaining in the Los Angeles region during one phase of Pleistocene time. So significant do the results of a study of this fauna appear in relation to the general problem of the Pleistocene, that it seems desirable to bring together the conclusions obtained in work on all phases of the assemblage of life forms here represented.

Since receiving the first specimens from Rancho La Brea, in December, 1905, the Department of Palaeontology at the University of California has been almost continuously engaged in a study of this most alluring field. Some of the results obtained have already been presented in brief papers by J. F. Bovard, L. H. Miller, W. P. Taylor, and the writer. Other articles based on material furnished by the University have been written by Wm. J. Sinclair and by Fordyce Grinnell. The present paper is the first of a series of publications in which it is planned to present in full the results of work on all of the groups represented in the Rancho La Brea fauna. It is not to be presumed that all of the facts relating to any of the groups discussed are yet discovered, and the writing of the last word on the Rancho La Brea fauna will probably fall to investigators of a later generation. It is, however, hoped that at this present stage of progress a considerable number of the principal items of information may be brought together; and that from these we may construct at least the foundation for more extensive work such as naturally follows any initial investigation.

In studying the fauna obtained from the Rancho La Brea Beds the writer has been assisted by many persons who have been interested in the work. Particular acknowledgment is due to Madam Hancock Ross and to Mr. Allan Hancock for their courtesy in permitting the University to carry on its excavations in this interesting field. To Mr. F. M. Anderson and Mr. W. W. Orcutt the writer is indebted for the original information which led to so many discoveries. Mr. Anderson presented his first collection to the University, and Mr. Orcutt permitted the use of his material for study.

Excepting a small part of the expense, which has been met from other funds, the financial support of the work has been generously furnished by Miss Annie M. Alexander, whose personal interest in the progress of the investigation has also been an important factor in the advancement of the work.

Dr. William Bebb of Los Angeles most generously presented to the University the first specimen of the gigantic lion found in the asphalt, and has kindly permitted the use of several important specimens of rodents in his collection.

In the course of the work Dr. Ralph Arnold, Mr. W. W. Orcutt, and Mr. A. E. Preston have greatly assisted in the interpretation of the geologic relations of the asphalt beds.

During the last year's work Mr. L. H. Miller assisted in every way possible in the direction of the excavations, and has contributed a considerable number of valuable specimens to the University. Mr. E. L. Furlong brought together some of the most valuable collections in the first two years of work, and also prepared and mounted many of the specimens. Mr. E. J. Fischer efficiently carried on the work of collection for approximately a year, and has presented several specimens obtained by him before his connection with the University. Dr. C. O. Esterly of Occidental College and Dr. F. C. Clark of the Pacific College of Osteopathy have both assisted very generously through loan and gift to the University of valuable specimens needed for study.

In bringing together such information relating to the Los Angeles asphalt beds as could be obtained from the notes of early explorers, the writer has been much indebted to Professor Frederick J. Teggart and Mr. Porter Garnett for information indicating that the Rancho La Brea locality may have been visited by Gaspar de Portolá.

In connection with the study of special divisions of the fauna considered in later parts of this series of publications, the writer has been grateful for many courtesies extended. Acknowledgment of such services properly appears with a discussion of the materials especially concerned, and is reserved for mention in other parts of the series.

UNIVERSITY OF CALIFORNIA,

May 16, 1911.

Map of region in which the Rancho La Brea Beds are situated. Adapted from U. S. Geological Survey topographic map.

HISTORICAL

The extensive asphalt beds occurring at Rancho La Brea, on the western border of the city of Los Angeles, have been known for many years as one of the most interesting of the numerous bitumen deposits of the state, and have attracted the attention of many investigators concerned with the geology of this region.

The earliest description of bituminous deposits in the Los Angeles region known to the writer is found in the narrative of the Portolá Expedition,¹ written in 1769. In the account of the region traversed, mention is made of springs of pitch, which were observed at a stage in the journey when the party must have been in the vicinity of Rancho La Brea. While it is not possible to make certain of the exact location of the pitch springs described, a study of the route followed gives good reason for suspecting that the locality was actually Rancho La Brea.

Tar pools in the vicinity of Los Angeles were mentioned by Blake² in his geological report included in the Pacific Railroad Survey, though it is not clear that he referred particularly to those at Rancho La Brea. Blake's statement is as follows:

There are several places in the vicinity of the city (Los Angeles) where bituminous or mineral pitch rises from the ground in large quantities. These places are known as tar springs, or pitch springs, and some of them form large ponds or lakes. One of the springs was passed on our way to the city, and was near the outcrop of bituminous shale in the banks of the creek already described. This spring was nothing more than an overflow of the bitumen from a small aperture in the ground, around which it has spread on all sides, so that it covers a circular space about 30 feet in diameter. The accumulated bitumen had hardened by exposure and its outer portions were mingled with sand, so that it was not easy to determine its precise limits. It formed a smooth, hard surface like a pavement, but toward the center it was quite soft and semifluid, like melted pitch. The central portion of the overflow was higher than its margin; and it was evident that all the hard portion had risen in a fluid state and by the heat of the sun had been gradually spread out over the surface; at the same time being constantly exposed to dust, it had become so thoroughly incorporated with it that the compound had all the consistency of an artificial mixture.

¹Diary of Gaspar de Portolá during the California Expedition of 1769-70. Edited by Donald Eugene Smith and Frederick J. Teggart. Publ. Acad. Pacif. Coast Hist., vol. 1, p. 53, October, 1909.—“The 3rd (August 3, 1769), we proceeded for three hours on a good road; to the right of it were extensive swamps of bitumen which is called *chapapote*. We debated whether this substance, which flows melted from underneath the earth, could occasion so many earthquakes.” Also mentioned in Diary of Miguel Costansó, Portolá Expedition of 1769-70. Edited by Frederick J. Teggart. Publ. Acad. Pacif. Coast Hist., vol. 2, p. 183, August, 1911.

²Blake, W. P., Pacific Railway Reports, vol. 5, Geological Report, p. 76, 1857.

In 1865 J. D. Whitney, then state geologist, in writing his report on the general geology of the Los Angeles region, gave a brief discussion³ of the asphalt exposures and tar pools. He referred in his report to the "very large amount of the hardened asphaltum mixed with sand and the bones of cattle and birds which have become entangled in it," but did not state that the remains were those of extinct forms. Whitney's discussion of these beds appears in the succeeding paragraph:

About seven miles due west of Los Angeles is the most important of the numerous tar-springs seen in this vicinity. It is from here that most of the asphaltum used in the town is obtained. Over a space of fifteen or twenty acres, the bituminous material (which when seen by us, in the winter, had exactly the consistency and color of tar) was oozing out of the ground at numerous points. It hardens on exposure to the air, and becomes mixed with sand and dust blown into it, and is then known as "brea." The holes through which the bitumen comes to the surface are not large, few being more than three or four inches in diameter. On removing the tarry substance from the holes, by repeatedly inserting a stick, the empty cavity was very slowly filled up again. At one place there was a pit several yards square, and six or eight feet deep, from which the tar had been taken; but it was filled with water, at the time of our visit, in consequence of late heavy rains. . . . A very large amount of the hardened asphaltum, mixed with sand and the bones of cattle and birds which have become entangled in it, lies scattered over the plain.

As nearly as can be determined, the first published statement in which reference was made to the fossil remains entombed in the asphalt at Rancho La Brea is the following issued by William Denton⁴ in 1875:

The locality is known as Major Hancock's Brea Ranch, and is about eight miles west of Los Angeles, in the valley of the Santa Anna. The bed of asphaltum here covers sixty to eighty acres, and at a depth of thirty feet no bottom has been reached. Thousands of tons have been removed for roofing, paving and combustion, but the supply is almost inexhaustible.

Major Hancock had about twenty-five Chinamen employed in digging out the best of the asphaltum, which is soft enough to agglutinate in the heat of the sun. The material was conveyed to large, open iron boilers, in which it was boiled for twenty-four hours, and then run into sand molds; subsequently it was broken up, for it is quite brittle after being thus boiled, carted for nine miles and shipped to San Francisco, where it was sold for twenty dollars a ton for making asphalt pavement. The bed is about three miles south of the Santa Monica range of mountains, and it appears to lie parallel with them.

Beds of petroleum shale of tertiary age, having in many places a thickness of about two thousand feet, are to be found along the California coast, and at some distance in the interior; they are said, by Professor Whitney, to extend from Cape Mendocino to Los Angeles, a distance of about four hundred and fifty miles. They are exposed in cliffs on the coast near Santa Barbara and Carpinteria, and other places. This shale, there is good reason to believe, is the deposit from which all the asphaltum of California has been derived.

Although this shale is not exposed in the vicinity of the Brea Ranch, it is exposed in various localities at but a short distance, and doubtless underlies the asphaltum deposit, for hundreds of "tar-springs" exist in the vicinity, from which the material is still flowing over the surrounding

³ Whitney, J. D., *Geol. Surv. Calif., Geology*, vol. 1, pp. 174 and 175, 1865.

⁴ Denton, Wm., *Proc. Boston Soc. Nat. Hist.*, vol. 18, p. 185, 1875.

locality, the springs being in some cases elevated, by its deposition around them, several feet above the surrounding level.

Major Hancock presented me with what I found to be a canine tooth of a *Machairodus*, a great saber-toothed feline. It was found at the depth of fifteen feet in the asphaltum. The tooth is nine and a half inches in length, measured along the curve, and the breadth of the crown at the base is an inch and three-quarters, being larger than any tooth of the European *Machairodus*, whose measurement I have been able to find. The crown of the tooth is broken, and its entire length could not have been less, I think, than eleven inches. The tooth from the Val d'Arno, in Italy, referred to by Falconer in his Palaeontological memoirs, measures eight and one-half inches in length, and the breadth of the crown at the base is one and one-half inches, while the tooth found by McEnery in Kent's Hole, England, is six inches in length, and one and one-fifth inches in breadth. The California tooth is closely serrulated on both the concave and convex sides. It seems to have been exposed to the action of the elements for a long time, and contains a number of fractures, some of which have been united by the asphaltum in which it was imbedded.

I obtained a number of teeth of the fossil horse, and bones of the deer, a large bovine animal, the otter, seal, albatross, and other animals. I found near the pit a portion of the right upper jaw of the fossil horse, containing four molar teeth, or three premolars and one true molar. The first premolar is smaller in proportion to the size of the other teeth than those of the recent horse, judging by several with which I have compared it, and smaller than those of the fossil horse of India. It is but one inch in length, and three-quarters of an inch in breadth; but the other three teeth are larger than the average of the recent horse. The *Machairodus* tooth, with several from the fossil horse, were exhibited.

Denton considered the asphalt to be derived from petroleum shales of Tertiary age which were known to be exposed at localities near by, and were presumed to lie beneath the asphalt deposits. Evidence of this was found in the presence in this region of hundreds of tar springs from which the tar was still flowing over the surrounding areas, the springs being in some cases elevated to a height of several feet above the normal level of the ground by deposition of bituminous material.

The first fossil specimen from the asphalt mentioned by Denton is a canine tooth of a large saber-tooth cat, the tooth having been presented to him by Major Hancock. The presumption is therefore that Major Hancock was the first person to take particular notice of the fossil remains in the asphalt.

The saber-tooth canine was stated to have been found at a depth of fifteen feet in the asphaltum, so that no question could arise as to its belonging in the asphalt formation. This tooth was compared with *Machairodus* of Europe, but seemed to represent a larger animal.

Denton also obtained bones and teeth of a fossil horse, and bones considered to represent the deer, a large bovine animal, the otter, seal, albatross, and other animals.

As nearly as can be determined, no other investigator seems to have followed up the work of Denton, which was quite forgotten; and for many years past the great quantities of bones scattered about the refuse heaps, and exposed in the old quarries, have been considered as representing nothing more than

remains of domestic and other animals of this region, which had been trapped in the tar in comparatively recent time.

During the past twenty years the writer has heard frequent mention of bones present in the asphalt deposits, but has always been assured that the remains were unquestionably those of Recent animals, mainly cattle and horses which had been mired in the tar.

So far as the writer has been able to learn, since the discovery by Denton Mr. W. W. Orcutt of Los Angeles was the first person to recognize the remains at Rancho La Brea as evidently fossils, or as belonging to a geological period preceding the present. In December, 1905, Mr. F. M. Anderson visited the Rancho La Brea beds with Mr. Orcutt, and procured a number of fragmentary specimens, including a portion of a saber-tooth skull, several teeth of the great wolf, and a number of dermal ossicles of a ground-sloth. These specimens Mr. Anderson very kindly placed at the writer's disposal. Realizing the importance of the discovery, the locality was visited by the writer, in company with Dr. Ralph Arnold and Mr. A. E. Preston, soon after seeing Mr. Anderson's material. With the assistance of Dr. Arnold and Mr. Preston a small collection of typical specimens was brought together. It was upon this material, together with that presented by Mr. Anderson, that the first descriptions of remains obtained from these deposits were based by the writer.⁵

Some months after the first visit, the field was examined again by the writer under the guidance of Mr. Orcutt, who furnished much valuable information concerning the geologic relations of the region. Regular collecting was begun soon after this, and has been carried on by the University of California since 1906. The total amount of field work aggregates about fifteen months of continuous excavation.

Immediately after the first specimens from Rancho La Brea had been examined by the writer, application was made to the owner of the property for permission to carry on excavations for scientific purposes, and Madam Hancock Ross very graciously allowed the University to take up the work at that time.

⁵ Merriam, J. C., *Science*, n. s., vol. 24, p. 248, 1906. See also Bovard, J. F., *Univ. Calif. Publ. Bull. Dept. Geol.*, vol. 5, p. 157, 1907.

Fig. 1. The lagoon at Rancho La Brea. The surface of the pond is streaked with oil, and gas bubbles are seen escaping through the water. The banks around the lagoon consist to a large extent of asphalt.

Fig. 2. General view looking north toward the Santa Monica Range, and across the region in which the type locality of the Rancho La Brea Beds is situated. The lagoon is situated in the middle ground to the right.

DESCRIPTION OF THE TYPE LOCALITY

The fossiliferous asphalt deposits for which the name Rancho La Brea Beds has been used were so designated from their occurrence at Rancho La Brea, on the western side of the city of Los Angeles. The exact situation of the typical locality is as follows: SW $\frac{1}{4}$, sec. 21, T. 1 S, R. 14 W, San Bernardino Base and Meridian. At this place excellent exposures are seen within a radius of a few hundred yards of a small lake near the old Hancock ranch house. The best exposures are found in the banks bordering several extensive open cuts made by Major Hancock many years ago in excavating asphalt for commercial purposes. The lake or lagoon and several small ponds in the vicinity occupy depressions formed in mining asphalt. The work done by Major Hancock in exposing extensive areas of the brea beds, and thus making them easily accessible for examination by geologists and palaeontologists, has been in a large measure contributory to the advancement of our knowledge of this region, as otherwise the fossil-bearing beds might easily have escaped notice.

The Rancho La Brea Beds lie in a wide stretch of slightly rolling country immediately to the south of the abrupt southern slope of the Santa Monica Range. The typical exposures are situated about two and one-half miles from the southern base of the range, and are about two hundred feet below the level from which the mountains rise abruptly.

In the region immediately about the type locality asphalt is exposed in many places, and is evidently only a short distance below the surface over an area at least as large as that in which it actually outcrops. At many points in this region tar springs or seeps pour out considerable quantities of bituminous material. The flow from these seeps is fairly regular in some cases, but at other points more or less irregular exudation occurs through small crater-like vents. The phenomena of extravasation of bituminous products are seen to best advantage in the immediate vicinity of the lagoon or lake, where tar springs and tar seeps are readily discovered. In addition to the outflow of the heavier substances, large quantities of gas may be observed coming up through the water of the lake in great bubbles.

Estimates of the probable extent of the territory in which asphalt beds lie at or near the surface have been made by several persons familiar with this region. The approximations range from about a square mile down to one-fourth of a square mile. The probabilities seem in favor of making the estimate too low rather than too high.

NATURE AND ORIGIN OF THE RANCHO LA BREA BEDS

The formation in which the fossil bones occur at Rancho La Brea is essentially an alluvial accumulation consisting mainly of beds of clay, sand, and asphalt. In some places bedding planes are quite distinctly shown, especially in the clay or sand strata. At other localities the deposit has been irregular or in pockets, and minor local movements of the asphalt or clay masses have possibly increased the irregularity of the beds. The asphalt may occur as a nearly pure bituminous deposit, though it is usually mixed with sand, clay, or other materials. In some places it appears as fairly definite strata, while at other points it has irregularly impregnated beds of sandy or clayey material, and no definite bedding is shown.

The thickness of the asphalt deposits containing bones has not been determined, but these beds probably extend considerably deeper than the lowest levels yet reached. A depth of at least thirty feet is recorded for the work carried on by Major Hancock, and nearly the same horizon has been attained in recent excavations.

The formation in which the asphalt appears has been penetrated by the wells in the Salt Lake Oil Field immediately to the north of the principal brea outcroppings, and seems also to be a part of a series of beds comprising a considerable thickness of sand and clay strata exposed in the hills immediately to the south. The well records of the Salt Lake Field, as described by Arnold,⁶ indicate the presence of Pleistocene strata from fifty to one hundred feet in thickness overlying the Tertiary formations in which the main oil-bearing beds are found. The Pleistocene section penetrated by the oil wells comprises alluvium, clay, coarse sand, gravel, and asphalt, the deposits being apparently all of fresh-water or alluvial origin. Asphalt is well represented down to the bottom of the Pleistocene portion of the section.

The formation exposed in the low, flat ridges immediately to the south of Rancho La Brea is apparently a part of the series represented by the fossil-bearing strata at Rancho La Brea and by the Pleistocene penetrated in the oil wells of the Salt Lake Field. The ridges south of the fossil beds are considerably eroded and terraced, and it is to be presumed that the erosion which is indicated occurred in Pleistocene time. It is therefore probable that the fossiliferous beds now exposed at Rancho La Brea were at one time covered by many feet of strata, which have been removed by erosion inaugurated before the beginning of the Recent epoch.

⁶ Arnold, R., U. S. G. S. Bull. no. 309, p. 187, 1907.

Fig. 1. The locality at which the principal excavation work of the University of California has been carried on. The exposure to the left shows separation of distinct strata. The small white patches in the asphalt represent weathered bones still in the original matrix. Photograph by Ralph Arnold.

Fig. 2. A tar seep. The area in the middle of the seep is very soft. Toward the margins the surface gradually hardens.

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Geologists who have made a study of this region are generally in agreement that the asphalt of Rancho La Brea originates in the shale formations which underlie the Pleistocene beds. According to Arnold, Orentt, and others who have made a special examination of the conditions in the area west of Los Angeles, the Fernando formation, which immediately underlies the Pleistocene beds of the Salt Lake Oil Field, is in this region compressed into a fold, and there are reasons for considering that the crest of this fold is more or less irregularly broken, thus offering an unusual opportunity for the escape of bituminous substances at this place. The seepage of oil and tar has presumably been in progress almost continuously during the whole period of formation of the Rancho La Brea Beds. The asphaltum deposit which has formed represents the residuum left after evaporation of the more volatile portions of the oil. In accordance with slightly varying conditions of deposition, the supply of asphalt has at times been relatively abundant enough to form the greater part of the accumulation; at other times it has sufficed only to make up a small fraction of the material being heaped up in this place.

In the earlier stages of deposition of the Pleistocene formation the quantity of oil reaching the surface would presumably be larger than in the later periods, when the thick accumulation of beds, consisting in part of asphalt, would tend to prevent the escape of bituminous substances coming up from the lower formation. During the later stages of accumulation, as at the present time, it is evident that in addition to slow seepage through the mass, a part of the oil and gas reached the surface through fairly defined channels or pipes. Through passageways of this nature, which are common at Rancho La Brea, the movement of masses of tar may take place spasmodically, the holes being apparently empty at times, and on other occasions discharging voluminously.

The mode of accumulation of the deposit is pretty clearly illustrated by the conditions now obtaining in the vicinity of Rancho La Brea. This region is at the present time a comparatively level country bordered on the northern side by the Santa Monica Range, which rises abruptly to an elevation of about twelve hundred feet above the plain. The lowlands are traversed by a few drainage lines along which detritus is carried from the Santa Monica Range, or from the lower hills, to the east and south. At a number of localities the drainage is so balanced that water easily accumulates to form marshy spots. Tar seepages are common, and lenses of asphalt of irregular shape and thickness are continuously forming.

The relation of the formation containing the mammalian fauna at Rancho La Brea to the marine Pleistocene beds of the San Pedro Series⁷ occurring only a few miles to the south is not as yet entirely clear. From Arnold's investigations it would appear that the alluvial or fresh-water Pleistocene of the

⁷ Arnold, R., Mem. Calif. Acad. Sci., vol. 2, 1903.

Salt Lake Oil Field is nearly continuous with marine beds of upper San Pedro age. As the Rancho La Brea Beds are, so far as known, an alluvial accumulation, they are presumably not perfectly continuous with the marine San Pedro, though an oscillating shore line might cause the interdigitation of marine and alluvial lenses, or estuary conditions might give a gradation from fresh-water to marine beds. That the shore line changed its position somewhat during the deposition of the San Pedro Series is evidenced by the unconformity between the upper and lower members of this series, and by the varying nature of the deposits of the Upper San Pedro. The unconformity between the upper and lower divisions indicates considerable crustal movements.

A suggestion as to the relative age of the Rancho La Brea and San Pedro beds is perhaps to be obtained by consideration of possible relationship of the crustal movements which have affected the two groups of deposits. The series of strata at Rancho La Brea and in the Salt Lake Oil Field is presumably derived in a large measure from erosion of the Santa Monica Range immediately to the north. The abrupt southern slope of this range can hardly be explained on any hypothesis other than that it represents a fault-scarp. In the Salt Lake Oil Field the Pleistocene alluvial beds consist in general of coarser materials below and finer above, showing a gradual adjustment of accumulation to conditions somewhat similar to those obtaining at the present time. Excepting the Recent alluvium, no series of beds later than those in the Pleistocene section penetrated by the oil wells has been observed in the immediate vicinity, and it is to be presumed that these Pleistocene beds represent the accumulation following the last important movement along the fault bordering the southern side of the Santa Monica Range. In view of the fact that the topography of this range is considered to indicate the completion of the faulting movement at no very remote date, it is not improbable that one of the last movements occurred in the period of local changes which were taking place during the deposition of the San Pedro, or at the close of that time. It is true that important movements have occurred in this region of the coast since the deposition of the San Pedro Series, as is evidenced by the prominent coastal terraces which have cut sharply into the San Pedro. Terraces of importance crossing a formation apparently not to be distinguished from the Rancho La Brea Beds have also been referred to as occurring in low hills south of the Salt Lake Oil Field. These movements have, however, been largely of an epeirogenic character. They do not appear to have been accompanied by local faulting, and may not have changed the tectonic relations of the formations at San Pedro and in the vicinity of the Santa Monica Range.

Fig. 1. A pool of asphalt which has come to the surface through a small pipe or channel. The tar has mixed with the soil, so that its boundaries are not readily seen.

Fig. 2. A tar seep coming up through the soil where the ground has been largely occupied by grass and weeds. Puddles and ponds of tar thus formed trap many small animals.

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MODE OF ACCUMULATION OF THE FOSSIL REMAINS

The accumulation of the remains embedded in the fossil beds at Rancho La Brea, as also their assembling in the greater number of the asphalt deposits of southern California, has evidently been controlled by conditions differing largely from those which have produced other kinds of fossil deposits. In the excavation work which has been carried on at Rancho La Brea up to the present time, though a considerable variety of deposits has been encountered, the fossil bones are found to be almost entirely confined to beds which are either pure asphalt or consist of some other material impregnated with tar. When pure sand or clay is present without a tar impregnation there is a conspicuous absence of skeletal remains. While it is possible that some of the impregnated strata may have received their bituminous content since the bones were deposited, the facts of occurrence seem to indicate quite clearly that the presence of tar is the condition which has controlled the accumulation of skeletal remains.

The manner in which tar or asphalt pools may catch unsuspecting animals of all kinds is abundantly illustrated at the present time in many places in California, but nowhere more strikingly than at Rancho La Brea itself, where animals of many kinds have been frequently so firmly entrapped that they died before being discovered, or if found alive were extricated only with the greatest difficulty. As seen at this locality, the tar issuing from springs or from seepages is an exceedingly sticky, tenacious substance which is removed only with the greatest difficulty from the body of any animal with which it may come in contact. Small mammals, birds, or insects running into the soft tar are very quickly rendered helpless by the gummy mass, which binds their feet, and in their struggles soon reaches every part of the body. Around the borders of the pools the tar slowly hardens by evaporation of the lighter constituents until it becomes as solid as an asphalt pavement. Between the hard and the soft portions of the mass there is a very indefinite boundary, the location of which can often be determined only by experiment, and large mammals in many cases run into very tenacious material in this intermediate zone, from which they are unable to extricate themselves. †

Judging from reports of the earliest observers who examined the tar seeps at Rancho La Brea, some of the pools were many feet in diameter in their natural state, and might easily in the course of years have caught a great number of even the largest mammals.

In the natural accumulation of remains at the tar pools through accidental entangling of animals of all kinds, it is to be presumed that a relatively large

percentage of the individuals entombed would consist of young animals with insufficient experience to keep them away from the most dangerous places, or with insufficient strength to extricate themselves. There would also be a relatively large percentage of old, diseased, or maimed individuals that lacked strength to escape when once entangled. In the census of remains that have

Fig. 1. A small area of asphalt in process of excavation, showing the skeletal remains before they had been completely uncovered. In this picture there may be seen the under side of the lower jaw of a horse, considerable parts of the skulls of four saber-tooth cats, four large wolf skulls, two coyote skulls, and many other skeletal parts only imperfectly exposed.

been obtained up to the present time the percentages of quite young, diseased, maimed, and very old individuals are certainly exceptionally large compared with what has been seen by the writer in average collections of remains of similar animals accumulated under other conditions.

In addition to the natural accumulation of animal remains through the entangling of creatures of all kinds by accidental encountering of the tar, it is

apparent from a study of the collections obtained that some extraordinary influence must have brought carnivorous animals of all kinds into contact with the asphalt with relatively greater frequency than other kinds of animals. In all the collections that have been examined the number of carnivorous mammals and birds represented is much greater than that of the other groups. A rough census of the University of California mammal collection from Rancho La Brea shows more representatives of the Carnivora than there are of all the other mammalian orders combined. A similar proportion of carnivorous birds has been noted by Miller^s in the same collections. The number of carnivores represented is entirely out of proportion to the normal number of other animals present in the fauna, and is apparently to be explained by a peculiar process of selection, which may be seen in operation about tar pools at the present time. Whenever an animal of any kind is caught in the tar its struggles and cries naturally attract the attention of carnivorous mammals or birds in the immediate vicinity, and the trapped creature acts as a most efficient lure to bring these predaceous animals into the soft tar with it. It is not improbable that a single small bird or mammal struggling in the tar might be the means of entrapping several carnivores, which in turn would naturally serve to attract still others. The suggestion that struggling animals have served as a nearly continuous lure for Carnivora seems to be the only theory by which we can explain the remarkable entangled masses of carnivore bones which have been entombed in several places. In the first excavations carried on by the University of California a bed of bones was encountered in which the number of saber-tooth and wolf skulls together averaged twenty per cubic yard. More recently in the excavations carried on by Occidental College a nearly circular depression about three feet by six feet in diameter contained thirteen individuals of the saber-tooth, lion, and wolf in a depth of eight feet.

^s Miller, L. H., Univ. Calif. Publ. Bull. Dept. Geol., vol. 5, p. 306, 1909.

STATE OF PRESERVATION AND QUANTITY OF FOSSIL REMAINS

The skeletal remains obtained at Rancho La Brea vary greatly in the state of preservation at different horizons and at different places in the same bed, but in all cases the material seems to be the practically unaltered bone. In most localities the bones are fairly hard and are easily extracted from the matrix. In other places they are very soft and can be removed only with great difficulty. At still other points the enclosing asphalt is very hard and has the appearance of having been exposed to the sun and to weathering action for a long period. In these portions of the beds the bones can be separated satisfactorily only with the aid of chisel and mallet.

As the greater number of the animals entombed in the Rancho La Brea Beds have been entrapped in the tar, it is to be presumed that in a large percentage of cases the major portion of the skeleton has been preserved. Contrary to expectation, connected skeletons are not common. Several factors have evidently combined to scatter the skeletal parts. In most localities the tangled mass of bones shows that the tar at these points remained for a long period soft enough to engulf the bodies of animals, and during this time the struggles of each new victim tended to disturb the skeletons already in the pool. At times when the surface of the asphalt hardened by exposure, such bones as were uncovered may have been broken or perhaps completely destroyed by ungulates tramping over the spot. At all periods during the history of the deposit the viscosity of the asphalt apparently permitted considerable movements in the mass, and the individual bones were moved apart in the viscous layers. These movements would continue after the asphalt beds had been deeply buried by later accumulation, as the pressure of the mass above would at times cause a certain degree of flow in the tar beds.

The pressure of the rock mass does not seem in general to have distorted the bones greatly. Even the skulls of large animals commonly show comparatively little flattening or twisting. Where one bone has come to rest directly against another, the weaker or softer one is sometimes dented by the harder one; but where the pressure has been exerted through the asphalt above there has usually been change of position rather than change of form.

Judging by the results of excavations carried on up to the present time, the quantity of animal remains entombed in the beds at Rancho La Brea is large. The total area of asphalt in the region, including all of the small outcrops, probably amounts to the larger part of a square mile. A considerable part of this area presumably contains few bones, but fragments are present in a large

Fig. 1. A small pond with tar seeps near the border.

Fig. 2. A tar pool in which two birds had recently been caught. The smaller one, a meadow lark, seen in the lower right-hand corner of the picture, is nearly buried in the tar.

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portion of the beds actually examined. In most of the prominent exposures at Rancho La Brea bones are generally present, though not always abundant. In these localities where any considerable amount of excavation work has been carried on they have usually been discovered in large quantities.

The locality at which the University of California excavations have been carried on has shown a most remarkable mass of skeletal material. During the first stage of the excavations careful count was made of the carnivore specimens obtained, and it appeared that there were thirty or more skulls of *Smilodon californicus*, with fifty or more heads of *Canis indianensis*, in a mass comprising less than four cubic yards. In addition to these skulls there were numerous remains of bison, horse, sloth, coyote, birds, and other forms.

At nearly all points where collecting has been done the skeletal material is somewhat irregularly distributed, and usually appears to be in rather small masses or pockets. The size and shape of these accumulations have presumably been dependent on the nature of the tar pools forming about the vents through which bituminous material has come to the surface.

While it is not safe to make any attempt at an estimate of the quantity of material represented in the whole area of the Rancho La Brea Beds, it is within the limits of probability to say that there are still some thousands of individuals of *Smilodon californicus* and *Canis indianensis* entombed in the deposits of this region. Of other forms the number is also probably very large, though somewhat less than in the case of the Carnivora.

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OF THE
UNIVERSITY OF CALIFORNIA

Vol. 1. No. 2

THE FAUNA OF RANCHO LA BREA

PART II. CANIDAE

BY
JOHN C. MERRIAM

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1912

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INTRODUCTION

Remains of canid forms constitute a large part of the total quantity of fossil remains found in the deposits at Rancho La Brea. Thus far six species have been recognized in the fauna at this locality: these species are, *Canis dirus* Leidy; *Canis occidentalis furlongi* Merriam, J. C.; *Canis milleri* Merriam, J. C.; *Canis ochropus orcutti* Merriam, J. C.; *Canis andersoni* Merriam, J. C.; and *Urocyon californicus* Mearns. Of these forms the great wolf, *Canis dirus*, makes up more than half of the total number of specimens obtained. *C. o. orcutti*, though much rarer than *C. dirus*, is known by a considerable number of specimens. The other species are quite rare.

It is probably true that the species known from the deposits at Rancho La Brea varied to some extent in degree of susceptibility to entanglement in the tar, and therefore that the specimens found represent slightly different percentages of the number of individuals in existence during the period of deposition. It is also probable that some of the forms known were less characteristic of this region than of adjacent territory. There seems, however, little doubt that the proportion of remains of the several species obtained in the asphalt gives a fairly satisfactory approximation of the canid fauna of this region while the beds were accumulating. Though foreshadowing the fauna of the present period in the presence of a gray fox, a coyote, and a timber wolf, the difference between the canid life of this period and that of the present is emphasized in the dominance of the wolves of the *Canis dirus* type, in the presence of the peculiar short-faced *Canis andersoni*, and in the specific or subspecific difference in the coyote and the timber wolf. The gray fox, the only canid of the Rancho La Brea fauna which does not seem to differ distinctly from existing species, is known by very few specimens.

CANIS DIRUS Leidy

Plates 24 to 28; text figures 1 to 26

- Canis primaevus* Leidy. Proc. Acad. Nat. Sc., Philad., 1854, p. 200. Jour. Acad. Nat. Sc., Philad., 1856, ser. 2, vol. 3, p. 167, pl. 17, figs. 11 and 12. (Not *C. primaevus* Hodgson, 1833.)
- Canis dirus* Leidy. Proc. Acad. Nat. Sc., Philad., 1858, p. 21.
- Canis indianensis* Leidy. Jour. Acad. Nat. Sc., Philad., 1869, p. 368.
- Canis indianensis* Leidy. Geol. Surv. Terrs. vol. 1, Fossil Vertebrates, 1873, p. 230, pl. 31, fig. 2.
- Canis mississippiensis* Allen. Am. Jour. Sc., ser. 3, vol. 11, p. 49, 1876.
- Canis lupus*. Cope and Wortman, Indiana Geol. and Nat. Hist., 14th Ann. Rep., part 2, p. 9, 1884.
- Canis indianensis*. Cope, E. D., Jour. Acad. Nat. Sc., Philad., 1895, ser. 2, vol. 9, p. 453, pl. 21, figs. 14 to 16.
- Canis indianensis*. Merriam, J. C., Univ. Calif. Publ. Bull. Dept. Geol., vol. 3, p. 288, 1903.
- Canis indianensis*. Freudenberg, W., Geol. u. Palae. Abh., N. F., Bd. 9, Heft 3, S. 22, 1910.
- Canis indianensis*. Merriam, J. C., Mem. Univ. Calif., vol. 1, no. 2, p. 213, 1911.

Type specimen, an upper jaw with the cheek teeth, now in the collection of the Academy of Sciences, Philadelphia. Type obtained from Pleistocene beds on the Ohio River near Evansville, Indiana.

The forms referred to this species include some of the most remarkable known representatives of the Canidae, and deserve particular mention with reference to structure, geological occurrence, geographic range, and taxonomic position. Up to the time of discovery of the deposits at Rancho La Brea this wolf was known only by very fragmentary remains, and the literature contains no adequate description of any phase of its structure.

Canis dirus is the most abundant and most important of the canids from Rancho La Brea, and was evidently the dominant type of wolf in this region at the time of deposition of the asphalt beds. This species includes the largest individuals of the *Canis* group known from America. Some of the specimens exceed in dimensions all the largest known Recent wolves. Other individuals are considerably smaller than some of the large northern wolves of the present day. The skull is especially large, and the head seems to have been relatively large compared with the limbs. The teeth are very massive, but those regions of the cheek-tooth dentition constructed especially for crushing are relatively small.

The comparatively light limbs and very massive head show that the animal was not as well developed for running as the timber wolves and coyotes. The

massiveness of the dentition without corresponding development of the crushing surface indicates use of the teeth in smashing large bones. The form of the skull suggests that the head was normally held low and was often used in hard pulling and hauling of heavy bodies. The great number of individuals of *C. dirus* found at Rancho La Brea suggests that the wolves of this species sometimes associated themselves in packs, and that groups of considerable size may have assembled to kill isolated ungulates and edentates. Particularly the young, aged, and injured, when they could be separated from their associates, would be the natural prey of the great wolf, but adults in normal strength may also have succumbed to the combined attack of several of these powerful animals.

HISTORY OF LITERATURE ON *CANIS DIRUS*

In 1854 Dr. Joseph Leidy¹ described from deposits occurring on the banks of the Ohio River, a short distance below Evansville, Indiana, a collection of fossil bones including the remains of *Megalonyx jeffersonii*, *Tapirus haysii*, *Equus americanus*, *Bison americanus*, *Cervus virginianus*, and a large wolf. The wolf remains consisted of an almost complete left maxillary containing all but one of the cheek teeth. The species represented seemed to Leidy to vary far enough from any existing form to require a distinct specific designation, and was accordingly described as *Canis primaevus*. Leidy realized that others might fail to recognize the species as distinct, as is indicated in the following statement taken from his paper: "Certain naturalists may regard the fossil as an indication of a variety only of *Canis lupus*, and of the correctness of this view I will not attempt to decide." In 1856 Leidy² figured and redescribed the species under the same name.

In a description of *Canis (Aelurodon) saevus*, published in 1858, Leidy refers to the wolf previously described by him as *Canis primaevus*, as follows:³

"The present extinct species is not so large as the one whose remains have been discovered in association with those of *Megalonyx*, *Tapirus*, *Equus*, etc., on the banks of the Ohio River, Indiana, to which the name of *Canis primaevus* was inadvertently applied (Proc. Acad. Nat. Sc. VII, 200; Jour. Acad. Nat. Sc. iii, 167), and which may now be distinguished by that of *Canis dirus*."

In 1869 Leidy⁴ again referred to the original specimen, which he had described as *Canis primaevus*, and gave to it the name *Canis indianensis*. Apparently Leidy had forgotten the reference to this form under the name of *Canis dirus* in 1858. The name *Canis indianensis* has come to be the designation for this form commonly used in the literature. The writer is indebted to Dr. O. P. Hay for the discovery that Leidy's use of *Canis dirus* for this form preceded its designation as *Canis indianensis*.

¹ Leidy, J., Proc. Acad. Nat. Sc. Philad., vol. 7, p. 200, 1854.

² Leidy, J., Jour. Acad. Nat. Sc. Philad., ser. 2, vol. 3, p. 167, pl. 17, figs. 11 and 12, 1856.

³ Leidy, J., Proc. Acad. Nat. Sc. Philad., p. 21, 1858.

⁴ Leidy, J., Jour. Acad. Nat. Sc. Philad., p. 368, 1869.

In 1884 E. D. Cope and J. L. Wortman, in describing the post-Pliocene vertebrates of Indiana,⁵ reviewed Leidy's description, and after careful consideration of the measurements of the type specimen concluded that it would be impossible to admit this fossil to the rank of a distinct and well-defined species, but it appeared, in their judgment, to be but a variety which has a representative in the mountains of Oregon today.

In 1895 Cope,⁶ in describing a specimen representing a large fossil wolf from Texas, referred to Leidy's type specimen as representing a distinct species, *Canis indianensis*.

Previous to the discovery of *Canis dirus* at Rancho La Brea, excepting the type specimen, the only materials described which had been referred to this form consisted of two specimens from California and one from Texas. Several limb bones described from the lead region of the Upper Mississippi by Allen⁷ represent a form evidently nearer to *C. dirus* than to any other American species, and not separated from it by any characters mentioned in the original description.

The California specimens first referred to *C. indianensis* consisted of a lower jaw which Dr. Lorenzo Yates obtained from a Quaternary deposit in Livermore Valley. The Yates specimen (see fig. 25) was tentatively referred by Leidy⁸ to this species.

In 1903 a fragment of a lower jaw with the canine, the sectorial, and the last premolar, obtained from an asphalt deposit in Tulare County, California, was referred by Merriam⁹ to *C. indianensis*.

A fragment of a lower jaw referred to *C. indianensis* in Sinclair's report on Potter Creek Cave,¹⁰ on a determination by Merriam, possibly represents a timber wolf or another large wolf closely related to this species.¹¹

The Texas specimen referred to *C. indianensis* consisted of portions of an upper dentition, including M¹, P³, the canine, and an incisor. It was obtained in the Equus horizon of the Tule Cañon, on Staked Plains of Texas by W. F. Cuminins. Cope,¹² to whom the specimen was submitted, pointed out some differences between the teeth of this animal and those of Leidy's type, but was inclined to regard it as an individual of the same species.

So far as is known to the writer, the first mention of the occurrence of *Canis dirus* in the deposits of Rancho La Brea appears in the preliminary description of this locality by Merriam¹³ in 1906.

⁵ Cope, E. D., and Wortman, J. L., Indiana Geol. and Nat. Hist., 14th Ann. Rep., part 2, p. 9, 1884.

⁶ Cope, E. D., Jour. Acad. Sc. Philad., ser. 2, vol. 9, p. 453, 1895.

⁷ Allen, J. A., Am. Jour. Sc., ser. 3, vol. 11, p. 49, 1876.

⁸ Leidy, J., Proc. Acad. Sc. Philad., p. 260, 1873; and Geol. Surv. of Terrs., vol. 1, Foss. Verts., p. 230, 1873.

⁹ Merriam, J. C., Univ. Calif. Publ. Bull. Dept. Geol., vol. 3, p. 288, 1903.

¹⁰ Sinclair, W. J., Univ. Calif. Publ. Amer. Arch. Ethn., vol. 2, p. 17, 1904.

¹¹ See page 245 of this paper.

¹² Cope, E. D., Jour. Acad. Sc. Philad., ser. 2, vol. 9, p. 454, 1895.

¹³ Merriam, J. C., Science, n.s., vol. 24, pp. 248-250, Aug., 1906.

Figures of a nearly complete skeleton and of a perfect skull of this species were used in illustration of popular articles published by Merriam in 1908 and 1909.¹⁴

The most recent discovery of remains of *Canis dirus* is that reported by Freudenberg¹⁵ from Tequixquiac, Mexico. At this locality the posterior region of a skull has been found which closely resembles the specimens from Rancho La Brea.

GEOLOGICAL OCCURRENCE AND GEOGRAPHICAL DISTRIBUTION OF *CANIS DIRUS*

The fairly authenticated occurrences of *Canis dirus* known to the writer include Leidy's type specimen from Indiana; the material from the lead region of the Upper Mississippi described by Allen; a specimen from the Sheridan formation of Kansas, now in the American Museum; Cope's specimen from Texas; the California specimens from Livermore Valley, Tulare County, and Rancho La Brea; and the Mexican specimens described by Freudenberg. All of the material referred to *C. dirus* has been obtained from deposits held to be of Pleistocene age. There is reason for believing that the horizons at which these specimens have been found at different localities do not differ greatly, but a discussion of the time relation of these occurrences is best considered in a division of this memoir following a discussion of the fauna.

The collection of remains associated with the type specimen, including, as it does, on the one hand, such extinct forms as *Megalonyx jeffersonii*, *Tapirus haysii*, and *Equus americanus*, and, on the other hand, the Recent *Bison americanus* and *Cervus virginianus*, cannot represent other than Pleistocene time.

The Texas specimen described by Cope seems to have occurred at the same horizon as *Myiodon? sodalis*, *Elephas primigenius*, *Equus excelsus*, *E. semiplicatus*, *E. tau*, *E. major*, *Holomeniscus sulcatus*, and *H. macrocephalus*. This assemblage including the three genera *Equus*, *Elephas* and *Holomeniscus* must be considered as Pleistocene.

The lower jaw which Leidy described from Livermore Valley, California, is presumed to have been associated with a number of remains representing other mammalian forms. This material includes the type specimen of a very large cat, *Felis imperialis*, a bison referred to *Bison latifrons*, and a large camel. The presence of *Bison latifrons* may be considered as evidence of Pleistocene age, though it is uncertain how closely the specimens were associated.

The fragment of a jaw from Tulare County described by Merriam was associated with a portion of the skull of an edentate nearly related to *Myiodon*, and is presumably Pleistocene.

The material from Rancho La Brea described in the following paper is

¹⁴ Merriam, J. C., *Sunset Magazine*, Oct., 1908, p. 172. Also *Harper's Weekly*, Dec. 18, 1909, p. 11.

¹⁵ Freudenberg, W., *Geol. u. Palae. Abh.*, N.F., Bd. 9, Heft 3, p. 22, 1910.

associated with a fauna which falls well within the limits of the Pleistocene. A discussion of the definite stage of the Pleistocene represented is deferred to a later chapter, in which the evidence from various sources will be assembled.

The material from the Upper Mississippi region is held to be Pleistocene, and the Sheridan formation in which the Kansas specimen was found is generally considered to represent an early phase of the Pleistocene.

The material described from Mexico by Freudentberg seems to have been derived from the same horizon as the great lion, *Felis atrox*, as is the case at Rancho La Brea, and presumably represents a horizon near that of the Pleistocene of Rancho La Brea.

The known occurrences of *Canis dirus* show that this animal certainly roamed over a large part of the Mississippi Valley; its range extended south into Mexico, and west into middle and southern California. Until we have a more exact determination of the time relations of the beds in which this species is found, it is not possible to be certain as to contemporaneity of the occurrence in all of these regions, but such evidence as is before us indicates that the formations concerned do not differ greatly in age. It is probable that the species was at one time present in all of the regions mentioned, though the earliest and latest occurrences may have differed much in the several regions.

That the range of *Canis dirus* extended considerably beyond the territory marked out by known occurrences is probable, but it is by no means certain that it covered a region as large as that now occupied by wolves of the *C. occidentalis* group. Until we are better acquainted with the correlation problem of the American Pleistocene, it is perhaps unsafe to attach much significance to the possible absence of *C. dirus* from the Pleistocene of Silver Lake, Conard Fissure, Samwel Cave, and Port Kennedy Fissure, and its absence or rarity in Potter Creek Cave. Absence from some of these faunas may be due to difference in age of the beds, but the deposits included in this list represent a wide range of the Pleistocene, and it is not probable that all are so far removed in time from the beds containing *C. dirus* as to have missed completely the life range of that species. Some of the localities, particularly the cave regions, evidently constituted a habitat very different from that of the known occurrences of *C. dirus*, and to this difference in environment the presence or absence of the great wolf may be due in some measure. The faunas of Potter Creek Cave and Samwel Cave in California lived in a hilly or mountainous country covered to a large extent with forest, whereas the Rancho La Brea fauna represents the life of a plain bordering the hills. In view of what is known, the great wolf may be presumed to represent a fauna which ranged mainly over the great plains of an area corresponding approximately to what is now the Sonoran region. What we know of the structure and probable habits of *C. dirus* would be in agreement with such a range, as the animal seems particularly suited for preying upon some of the larger plains mammals.

DIAGNOSTIC CHARACTERS

The largest species of *Canis* known from the faunas of North America. Form and proportions in general near those of the existing timber wolves; head relatively larger and feet relatively smaller than in the large Recent timber wolves of the *Canis pambasileus* type. Skull attaining a length of 310 mm. or more; relatively broad across the palate, frontal region, and zygomatic arches. Sagittal crest high, inion showing an extraordinary backward projection. Posterior extremities of nasal bones extending relatively far back. Nasal processes of frontals relatively short. Postpalatine foramina opposite posterior ends of superior carnassials. Optic foramen and anterior lacerated foramen close together in a common pit. Upper and lower carnassials relatively large and massive. P^4 with reduced deutercone, M^1 with greatly reduced hypocone, M_1 with a small metaconid, P^2 and P_2 often without posterior cusps or tubercles.

SKULL

The skull in this species (figs. 1, 2, 3, and 4) is larger than the cranium of any other wolf known to the writer. The basal length from the anterior end of the premaxillaries to the posterior side of the occipital condyles in one of the large specimens measured (no. 10856) is 282 mm. The total length of the skull projected on the plane of the palate, including the extraordinary backward projection of the inion, may be more than 310 mm. In spite of the great length, the width measured across the palate, between the orbits, across the postorbital processes of the frontals, and across the zygomatic arches, is relatively large, making the skull very massive.

The facial region is characterized by extraordinary backward extension of the nasal bones, which reach a short distance behind a line connecting the most nearly approaching points on the orbits. The nasal processes of the frontals are generally relatively short. In the lateral region of the face an area at the anterior root of the zygomatic arch is generally very sharply depressed and forms a characteristic feature. On the inferior side of the zygomatic arch the attachment of the masseter muscles is very strongly marked, and ends anteriorly on a prominent knob situated at the most inferior point on the suture between the jugal and the maxillary.

The frontal region is relatively broad, the postorbital processes of the frontals being very largely developed. The frontal region shows only a slight median depression, which may be somewhat accentuated toward the nasal and parietal borders of the frontals. The sagittal crest is uniformly high, and is characterized especially by the extraordinary backward extension, which much exceeds that of the other wolves.

Figs. 1 and 2. *Canis dirus* Leidy. Skull, no. 10834, $\times \frac{1}{2}$. Fig. 1, lateral view; fig. 2, superior view. Rancho La Brea Beds.

Figs. 3 and 4. *Canis dirus* Leidy. Skull, no. 10834, $\times \frac{1}{2}$. Fig. 3, posterior view; fig. 4, inferior view. Rancho La Brea Beds.

Percentages of width of the skull at various points in relation to basal length measured from the anterior end of the premaxillaries to the posterior side of the occipital condyles are as follows:

	<i>C. dirus</i> (a)	<i>C. pambasileus</i> (b)	<i>C. latrans</i>
Width across palate, measured between outer sides of superior sectorials	38.1%	34 %	32 %
Width between most nearly approaching points on upper border of orbits	22.7%	20.8%	16.5%
Width between postorbital processes of frontals	33.3%	27.2%	24 %
Width across zygomatic arches	62 %	55.6%	59.4%

(a) No. 10856. All numbers, unless otherwise noted, are from the series of the University of California Collections in Vertebrate Palaeontology.

(b) No. 984, Univ. Calif. Mus. Vert. Zool. From Susitna River, Mt. McKinley region, Alaska. This is according to Elliot (Field Columb. Mus. Publ., Zool. ser., vol. 6, p. 374) the largest Recent species of the North American wolves.

The palate is relatively broad, and the posterior palatine foramina are set relatively far back. The posterior end of the vomer extending backward between the vertical plates of the palatines commonly reaches very slightly beyond the posterior nasal opening. This is in decided contrast to the Recent wolves, in which the broad posterior end of the vomer reaches well beyond the posterior nasal opening. In most of the specimens of *Canis dirus* the posterior nasal opening is relatively wider at the anterior end than in wolves of the *C. occidentalis* type.

The occipito-sphenoidal region of the skull exhibits a tendency to shortening, the distance from the posterior border of the glenoid fossa to the posterior side of the occipital condyles averaging slightly less than in other forms. On the basal occipital the uneven surfaces corresponding to the attachment of the longus capitis muscle are marked by very rough areas which commonly do not extend as far forward as in the timber wolves. In other forms these areas extend forward for a considerable distance anterior to the tympanic bullae. In the space between the tympanic bullae and the anterior end of the inferior notch of the foramen magnum the median ridge extending from the basal occipital to the basal sphenoid is usually relatively prominent and acute, while in the timber wolves it is commonly a low, broad, horizontally truncated ridge.

The posterior aspect of the skull presents in general a very different form from that of the Recent wolves. The two ridges which form the lamboidal crest tend to converge sharply above the occiput, while in most Recent forms they sweep outward rather widely before uniting at the inion. On the other hand, the short processes formed at the lower ends of the transverse ridges and immediately behind the superior side of the posterior root of the zygomatic arches average smaller than in the modern species. In the superior region of the occiput the two lateral depressions in which the attachments of the rectus capitis posticus are situated average extraordinarily deep, and are separated by a narrow ridge which is relatively prominent with reference to the occiput as a whole. The backward projection or overhanging of the inion is extraordinary, as are also the height and thinness of the sagittal crest rising above it in posterior view.

The lower jaw tends to be relatively longer than in most wolves and is also relatively higher and thicker below the inferior carnassial. Although the coronoid process is not unusually high, the masseteric fossa is generally very deep and rough, indicating an unusually strong muscular attachment.

Although the foramina of the skull do not in general vary greatly in form or position from those of the Recent species, certain minor modifications are usually noticeable. The posterior palatine foramina are commonly situated farther back than in the Recent American species, and are nearly opposite the posterior borders of the superior sectorials. The openings of the optic foramen and the anterior lacerated foramen are situated very near together in

an uncommonly deep depression. The foramen ovale and the posterior opening of the alisphenoid canal are also situated very near together, and are usually in a distinct common depression. The situation of these foramina in this species is approximated in some of the Recent wolf species, but the openings are not often so nearly united in the Recent forms as to approach the extreme of variation here.

MEASUREMENTS OF SKULL

	<i>Canis dirus</i> (a)	<i>Canis dirus</i> (b)	<i>Canis pambasileus</i> (c)	<i>Canis milleri</i> (d)
Length, anterior end of premaxillaries to posterior end of occipital condyles	282 mm.	267	250	223
Length, anterior end of premaxillaries to anterior end of posterior nasal openings	155	141	131.5	119
Width across nose, measured between outer sides of bases of canines	67.3	58.5	52	50.2
Width, measured between outer sides superior sectorials	107.5	96.2	85	89.5
Width across zygomatic arches	175 <i>ap</i>	164.5	138.4	134
Least diameter between superior borders of orbits	64.9	54.1	51	43.2
Width between postorbital processes of frontals	93.9	77	67.7	64
Length from a line drawn between posterior borders of glenoid fossae to posterior end of occipital condyles	54	57	52	52
Length, anterior end of left ramus of mandible to middle of condyle	230 <i>ap</i>	210.5	202	178
Height of lower jaw measured between summit of coronoid process and inferior side of angle	91.3	87	85.7	82.5
Height of lower jaw below hypocond of M_1	39.7	35.3	30.6	29.8
Height of lower jaw below protocond of P_3	36.9	32.5	31.9	24.5
Thickness of lower jaw below protocond of M_1	20.3	19.3	14.9	16

(a) No. 10856.

(b) No. 10834.

ap approximate.

(c) No. 984, Univ. Calif. Mus. Vert. Zool.

(d) No. 11257.

PERMANENT DENTITION

Superior Dentition.—The incisors of the upper jaw (fig. 4) are not more noticeably crowded in specimens 10828 and 10856 than in the modern Alaskan wolves.

I^1 is not materially different from that in the large modern wolves. On I^2 the basal lobe on the median side is small or wanting and there is a second

minute basal tubercle on the lateral side. I^3 is not materially different from the corresponding tooth in the modern wolves.

The superior canine seems to be relatively short in anteroposterior diameter at the upper margin of the enamel, its diameter slightly exceeding that of considerably smaller specimens of the Alaskan wolf. The transverse diameter or thickness is relatively large, and the tooth shows a more nearly circular cross-section. The anterointernal enamel ridge usually runs nearly straight up to the margin of the enamel, without turning backward as in Recent Alaskan wolves.

P^1 is sometimes smaller in anteroposterior diameter than P^1 of the large Recent wolves.

P^2 is relatively much smaller compared with the sectorial than in the large Alaskan wolves, the anteroposterior diameter being about one-half that of P^4 . This tooth is frequently almost simple-crowned, as is exemplified in no. 10856, in which there is only the merest trace of a tubercle on the posterior border of the cingulum. In other cases (no. 10893) there is a distinct posterior basal cusp, and behind it a posterior basal tubercle.

P^3 is also relatively small compared with the sectorial. (Ratio of anteroposterior diameter in P^3 and P^4 19:32 in *C. dirus* no. 10856, and 16.5:24.5 in a *C. pambasileus* from Alaska). There is a distinct posterior cusp present, and a very small basal tubercle is usually developed on the posterior border of the cingulum. The small posterior basal tubercle seems to be present more frequently than in the Recent wolves. The protocone is in general not made relatively smaller than in the Recent species through the regular addition of the posterior basal tubercle. The protocone commonly tends to be relatively large anteroposteriorly.

P^4 is relatively large compared with all of the other premolars. The blade is massive, though not much thicker transversely in relation to the size of the skull in general than in the Recent wolves. The deuterocone is usually small, and the root supporting it does not ordinarily project as far toward the median line as in the modern wolves. Though usually distinctly set off from the protocone, the deuterocone is in some cases entirely reduced.

A peculiar feature appearing in quite large percentage of the specimens is found in the development of a sharply angular ridge on the lower side of the cingulum on the outer side of the tritocone. The character of this ridge is in general similar to that of the lower side of the cingulum on the outer side of the upper molars. In one instance (no. 10830) this ridge is very largely developed on the left P^4 , and several distinct, rounded tubercles have arisen upon it. This last instance may possibly be attributed to pathological changes or to injury. It presents an interesting tendency of development, though it may have been stimulated by extraordinary conditions.

M^1 is relatively small both anteroposteriorly and transversely compared

with the carnassial. The most noticeable peculiarity of this tooth is the reduction of the hypocone, which is smaller than in any of the Recent North American wolves. The short ridge of the hypocone never extends forward around the base of the protocone to join an anterior basal ridge as commonly occurs in the Recent wolves. The extreme median side of the hypocone frequently does not extend farther toward the median line than does the base of the protocone. The protocone, paracone, and metacone are not materially different from the corresponding tubercles of the modern wolves, though the bases of the paracone and metacone often tend to be relatively thick transversely. A distinct metaconule is always present and a small protoconule is usually developed.

M² is relatively small compared with the sectorial, and is usually also small compared with M¹. In specimen 10856 its dimensions are practically identical with those of a Recent *C. pambasileus* which has a much smaller skull, and in which the other teeth are smaller. The principal difference between the form of this tooth seen here and that in the Recent wolves is found in the uniformly smaller size of the hypocone. In some instances the anterior end of the hypocone crest does not extend forward as a ridge of the cingulum along the anterior side of the tooth.

Inferior Dentition.—In most specimens observed the incisors are thrown considerably out of alignment by lateral crowding, I² being set back at least as far as I₃, while the posterior border of I₁ is nearly even with the anterior border of I₂.

I₃ has much the same form as in the large Recent Alaskan wolves excepting that the lateral lobe tends to be relatively small.

Fig. 5. *Canis dirus* Leidy. Superior view of inferior premolar and molar series, no. 10834, natural size. Rancho La Brea Beds.

In the inferior canine the sharp anterointernal ridge which marks the enamel of this tooth takes a course somewhat different from that in the Alaskan *C. pambasileus*. In passing forward from the posteroinferior region of the inner face of the tooth it does not rise as rapidly as in the Recent Alaskan wolves, but extends forward to a point near the anterior side of the tooth and only a few millimeters above the base of the enamel before it takes a direct upward course toward the apex of the crown. The angle formed by the sharp upward turning of this ridge is higher up on the side of the tooth, and consequently more obtuse in the Recent Alaskan forms. In a specimen of *C. latrans* from Manitoba this enamel ridge is closely similar to that in *C. dirus*.

P₁ (figs. 5, 6, and 7) tends to be rather small compared with P₂. A faint

indication of an anterior basal tubercle occurs less frequently and is less distinct than in the Alaskan wolves. A faint posterior basal tubercle is present in some instances. Ordinarily both anterior and posterior basal tubercles are absent.

P₂ in most cases shows no trace of either anterior or posterior tubercles, the tooth being as simple in form as the anterior lower premolars of *Temnocyon*. In a few cases, as in specimen 10727 (fig. 7), a well-developed posterior basal cusp is present with a minute posterior basal tubercle situated behind it.

P₃ possesses a distinct posterior cusp, and a minute posterior basal tubercle is sometimes present. The posterior shelf or heel of the cingulum may be prominent and rather sharply turned up on the posterior side, as in the modern wolves; or may, as in no. 10856, be much less distinctly marked, and may slope downward from the posterior basal cusp to the posterior margin of the tooth without exhibiting any upward curvature.

6

7

Figs. 6 and 7. *Canis dirus* Leidy. Lateral view of inferior premolar series. Fig. 6, no. 10834, natural size; fig. 7, no. 10727, natural size. Rancho La Brea Beds.

P₄ is relatively large compared with P₃, but shows almost exactly the same size in relation to M₁ as is seen in the Alaskan *C. pambasileus*. The posterior cusp and posterior basal tubercle are well developed. The posterior portion of the tooth is somewhat wider than the anterior in many cases. The posterior basal tubercle is usually situated on the extreme posterior portion of the cingulum, and its posterior border is the

extreme posterior margin of the tooth. In some cases, as in no. 10727, this tubercle is separated from the posterior border by a distinct notch and another small tubercle is present on the posterior margin of the cingulum.

In M¹, the trigonid portion of the tooth is generally relatively long and massive, or the heel region is relatively short compared with the large Recent wolves of North America. The metaconid is also generally smaller than in the modern species, though not always smaller than in all the Recent varieties. The hypoconid portion of the heel exhibits a tendency toward relatively greater development than the entoconid region. In nearly all specimens three small tubercles have developed in the space between the metaconid and the entoconid. One of these is usually situated on the base of the metaconid, one on the base of the entoconid, and one intermediate between the two. In some cases the number of these secondary tubercles varies above or below three, and their position may also vary somewhat from the situations indicated as most typical.

M₂ and M₃, the tubercular molars, are relatively small both anteroposteriorly

and transversely in comparison with the inferior carnassial. In specimen 10856 M_2 shows an anteroposterior diameter of 12.8 mm., in comparison with 35.7 mm. in the carnassial. In the large Alaskan wolf, *C. pambasileus*, (no. 984, Univ. Calif. Mus. Vert. Zool.) the corresponding dimensions are M_2 , 12 mm.: carnassial 29 mm. In M_3 the relative reduction is still more noticeable, this tooth measuring 7 mm. anteroposteriorly in the *C. pambasileus* specimen and only 6.5 mm. in *C. dirus* (no. 10856). The reduction in M_2 is due in some cases to a noticeable weakness of the heel region. The metaconid of M_2 is in some cases reduced to a small tubercle situated on the side of the nearly central protoconid. In rare cases a small tubercle is present in the paraconid region (fig. 8). As a rule no tubercle is present to represent paraconid or parastylid (fig. 10).

Figs. 8 to 10. *Canis dirus* Leidy. M_2 , superior view, natural size. Fig. 8, no. 19472; fig. 9, no. 19473; fig. 10, no. 19474. Rancho La Brea Beds.

A very large specimen (no. 11281) referred to *C. dirus* presents a number of characters in which the dentition varies slightly from the typical individuals of this species. (See fig. 11). At the same time the principal peculiarities of this specimen are those of the *C. dirus* form. P^4 is exceptionally massive, the transverse diameter of the protocone blade being relatively large. Another even larger upper carnassial with an anteroposterior diameter of 35.2 mm. (no. 12576) is relatively a little thinner transversely. In M^1 of specimen 11281 the hypocone is larger than in any other individual found. It does not, however, reach the relatively large size of the Recent American wolves, nor is the hypocone ridge extended around the anterior side of the protocone as in the wolves of the *C. occidentalis* type. In M^2 also the hypocone is relatively a little larger than in the average of the Rancho La Brea individuals of *C. dirus*. The metacone is also relatively a little larger than in average specimens from this locality, having, as in Leidy's type, nearly the size of the paracone.

Fig. 11 *Canis dirus* Leidy Upper carnassial and upper molars, occlusal view, no. 11281, natural size. Rancho La Brea Beds.

A lower carnassial associated with no. 11281 also indicates an individual of gigantic size. The characters of this tooth are those of the typical *C. dirus*.

Specimen 11281 evidently belongs in the true *C. dirus* group, but represents an exceptionally large form varying from typical individuals in the nature of the hypocone of M^1 .

MEASUREMENTS OF PERMANENT DENTITION

	<i>C. dirus</i> (a) large specimen Rancho La Brea	<i>C. dirus</i> (b) medium specimen Rancho La Brea	Type of <i>C. dirus</i>	<i>C. pambasileus</i> (c) Alaska	<i>C. occidentalis</i> (d) Canada	<i>C. dirus</i> Sheridan formation, Kansas	<i>C. dirus</i> Texas specimen	<i>C. dirus</i> (f) Rancho La Brea	<i>C. milleri</i> (g)
I ₃ , greatest transverse diameter....				7.6					
C, greatest anteroposterior diameter at lower edge of enamel	17.5 mm.			15.5					
P ₁ , greatest anteroposterior diameter	7.7	7.4		7		6.3			
P ₂ , greatest anteroposterior diameter	15.4	15.3		13.5		14.7			
P ₃ , greatest anteroposterior diameter	16.7	15.8		15.5		15.5			16
P ₄ , greatest anteroposterior diameter	20	19.5		16.5	16	19.9			18.2
M ₁ , greatest anteroposterior diameter	35.7	34.5		29	32	33.7		38.6	32
M ₁ , greatest anteroposterior diameter of heel, on outer side.....	9.2	8.8		8.2		8.2		9.3	7.8
M ₁ , greatest transverse diameter of heel	13.5	13		11	12.2	12.6		13.7	12
M ₁ , greatest transverse diameter of trigonid	14.3	13.6		11.8		13.8			13.5
M ₂ , greatest anteroposterior diameter	12.8	13.3		12.3	12.66	12.5ap			12.4
M ₂ , greatest anteroposterior diameter of heel, on outer side.....	4.5	5		4.5					4.6
M ₂ , greatest transverse diameter	10	9.3		10	9	10			9.1
M ₃ , greatest anteroposterior diameter	6.5	7.3		7					5.9
I ¹ , greatest transverse diameter....			7						
I ³ , greatest anteroposterior diameter	12e			10.5					
C, greatest anteroposterior diameter at upper edge of enamel	17			16.2					
P ¹ , greatest anteroposterior diameter	10.2	9.4		8.5					
P ² , greatest anteroposterior diameter	16	16.2	14.8	15					

(a) No. 10856.

(b) No. 10834.

(c) No. 984, Univ. Calif. Mus. Vert. Zool.

(d) No. 115995, U. S. Nat. Mus.

(e) No. 10828.

(f) No. 11282.

(g) No. 11257.

ap approximate.

	<i>C. dirus</i> (a) large specimen Rancho La Brea	<i>C. dirus</i> (b) medium specimen Rancho La Brea	Type of <i>C. dirus</i>	<i>C. pambasileus</i> (c) Alaska	<i>C. occidentalis</i> (d) Canada	<i>C. dirus</i> Sheridan formation Kansas	<i>C. dirus</i> Texas specimen	<i>C. dirus</i> (f) Rancho La Brea	<i>C. milleri</i> (g)
P ³ , greatest anteroposterior diameter	19	18.1	18.2	16.5	17.33		18.5		17.5
P ³ , greatest transverse diameter		7.9	8				8		7.4
P ⁴ , greatest anteroposterior diameter	32	30.7	32 <i>ap</i>	24.5	27			33.8	28.2
P ⁴ , greatest transverse diameter across denterocone	16.2	15	14.5 <i>ap</i>	14	14.5			16.9	15.8
P ⁴ , greatest transverse diameter across protocone	13	13		11				15.3	12.8
M ¹ , greatest anteroposterior diameter	20	18.7	18.5*	17.5			18	20	16.4
M ¹ , greatest transverse diameter	24	23	21.5	22.5	23		21.3	25	20.7
M ¹ , transverse diameter of protocone	13.6		12.6						12.7
M ² , greatest anteroposterior diameter	10	9.2	10	10				10.8	9
M ² , greatest transverse diameter	15.4	14.4	14.9†	14				14.6	12.9

ap approximate.

* Without posterior enamel.

† Without enamel.

MILK DENTITION

The milk dentition is well shown in several specimens. In no. 10831 it presents the following characters: The superior temporary carnassial (figs. 12 and 13) has well-developed cutting blades; the inner root is situated almost

Figs. 12 to 15. *Canis dirus* Leidy. Milk dentition. Figs. 12 and 13, no. 19475, natural size; figs. 14 and 15, no. 19481, natural size. Fig. 12, upper milk carnassial, inner side; fig. 13, upper milk carnassial and tubercular milk molar, occlusal view; fig. 14, lower milk carnassial and preceding tooth, inner side; fig. 15, lower milk carnassial, occlusal view. Rancho La Brea Beds.

directly above the apex of the protocone; there seems to have been no deuterocone present upon the base of the inner root, but there is a minute tubercle on the cingulum a short distance in advance of the base of this root, and nearer the normal position of the deuterocone on the permanent carnassial. In the inferior milk carnassial (figs. 14 and 15) the cutting blades are well-developed

and the metaconid is small; on the heel the entoconid approaches the size of the hypoconid, and the hypoconulid is near the size of the entoconid. Dm_3 (fig. 14) possesses a large posterior cusp. A minute basal tubercle may be present on the anterior side of this tooth.

MEASUREMENTS OF MILK DENTITION

	No. 10831
Dm_3 , greatest anteroposterior diameter	8.7 mm.
Dm_4 , greatest anteroposterior diameter	15.5
Dm_4 , greatest transverse diameter across heel	6.6
Dm^3 , greatest anteroposterior diameter	14.6
Dm^4 , greatest anteroposterior diameter	10.8
Dm^4 , greatest transverse diameter	11.4

VERTEBRAE

Owing to the peculiar occurrence of remains at Rancho La Brea it is very difficult to obtain complete connected skeletons. The viscosity of the asphalt mass in which the bones are entombed has permitted the elements of each individual to move easily in many directions. It has therefore been found very difficult to obtain connected parts such as occasionally appear in most deposits of fossil remains. Particularly exceptional is it to find a vertebral column which is even approximately complete, and in which all of the elements can be recognized as belonging to one specimen and certainly distinct from numberless other skeletons closely packed in the matrix.

For the reasons just given it is difficult to make more certain of the vertebral formula of *Canis dirus* than to learn that the relations of the vertebrae where found in connected portions of the column, and as indicated by the fitting together of the abundant material available, show no indication of a variation in number of vertebrae from that of the modern timber wolves.

Fig. 16. *Canis dirus* Leidy. Atlas, inferior view, no. 10834, $\times \frac{1}{2}$. Rancho La Brea Beds.
Fig. 17. *Canis dirus* Leidy. Axis, lateral view, no. 10834, $\times \frac{1}{2}$. Rancho La Brea Beds.

The *atlas* is rather variable in form, but resembles that of *Canis lupus* in most respects. It differs from that of *C. lupus* mainly in the more common tendency of the transverse processes to take on a triangular form. In *C. lupus*,

and in the wolves generally, the transverse processes of the atlas are broad transversely, and are formed in such a manner as to give each transverse process an approximately quadrate form. In *C. dirus* the lateral margins of the transverse processes are sometimes so truncated that the form tends toward the quadrate; but in many cases the margin, beginning with the anterior notch for the vertebral artery, slopes outward and backward, so that each process tends toward a more nearly triangular form with the apex at the postero-lateral angle. This form of atlas is shown especially well in figure 16.

Compared with the only specimens of *C. occidentalis* available for study, the atlas of *C. dirus* is commonly distinguished; 1) by the much larger opening of the vertebrarterial canal, which perforates the transverse process almost normal to the blade instead of perforating it obliquely; 2) by the much shallower anterior notch for the vertebral artery; 3) by the less marked tendency of the transverse processes to project behind the posterior ends of the facets for articulation with the axis.

The *axis* (fig. 17) is near that of *Canis lupus* in form. In lateral view it tends to be short and relatively high compared with most canids. Seen from below it is relatively wide. It is generally characterized by relatively short transverse processes, which often project little if any behind the posterior end of the centrum. A character which seems generally to appear in the axis of this form is the presence of a shallow notch on each side in the postero-lateral margin of the spine between its postero-superior angle and the small tuberosities just above the posterior zygapophyses. This region of the margin is in most canids without a distinct emargination; there is, however, such a notch in the axis of *C. occidentalis*.

The cervicals from number three to number seven do not differ markedly from those of the modern timber wolves. In number three the low spinal ridge is clearly marked in all specimens examined. The postero-superior tubercles above the postzygapophyses vary considerably in size in different individuals. The anterior and posterior limbs of the transverse processes extend slightly beyond the ends of the centrum. On number five the laterally directed posterior tubercles on the transverse processes are well developed. In number six the anterior side of the blade of each transverse process is commonly rather deeply notched immediately anterior to the base of the process arising laterad of the vertebrarterial canal. The inferior side of number seven is marked by a distinct median ridge.

The *dorsals* do not differ markedly from those of *C. occidentalis*. The first dorsal is usually characterized by a relatively great transverse diameter of the postero-inferior region of the spine, and by the tendency to development of a deep longitudinal groove on this region of the spine. Dorsals three to ten are distinguished from those of some of the other wolves by the absence of notches between the anterior zygapophyses and the anterior border of the trans-

verse processes. The anterior border of the lamina in this region is usually only slightly concave. The small tubercles which commonly appear immediately above the rib-articulation on the transverse processes of the third to the tenth dorsals are commonly rather small compared with those of many canids. On the twelfth and thirteenth dorsals the metapophysial processes are not distinctly separated from the zygapophyses by an antero-median notch as in some other canids, but the inner side of the metapophyses is nearly continuous with the prezygapophysial faces.

The *lumbar*s are closely similar to those of the modern timber wolves. They seem generally to show the same tendency of the inner side of the metapophyses to grade into the inner face of the prezygapophyses shown in the most posterior dorsals.

The *sacrum* varies somewhat in form, being wider posteriorly in some individuals than in others, this difference being possibly due to sex. It does not, however, seem to depart distinctly from the form seen in *Canis lupus*. The posterior extensions of the transverse processes of the last vertebra included in the sacrum commonly extend only a short distance behind the posterior articular face of the centrum, but vary somewhat in this respect. The spines of the posterior vertebrae included in the sacrum are higher than in a specimen of *C. occidentalis* available for comparison.

It is not easy to make certain of the form of the tail and of the number of vertebrae included in it; so far as can be determined, the number of *caudals* did not vary distinctly from that in *C. occidentalis*. The size of the tail as indicated by the form of the posterior region of the sacrum was not very different from that of the modern timber wolves. The individual caudal centra are not found to differ in form from those of the timber wolves.

No peculiar characters are noted in the elements of the rib-basket and sternum.

EXTREMITIES AND ARCHES

The form and proportions of the limbs in *Canis dirus* show that it was an animal constructed on much the same lines as the timber wolves, though somewhat heavier, with the limbs lighter in relation to the head. It was probably slower-footed than the modern forms.

Anterior Arch and Limbs.—The *scapula* varies somewhat in the series of specimens available, but is in general hardly to be distinguished from that of *Canis lupus* or *C. occidentalis*, excepting in its larger size. The region of the infraspinous fossa is commonly very wide, and the area for attachment of the *teres major* is distinctly marked.

The *humerus* is a massive bone compared with that commonly seen in the Canidae. The deltoid ridge and the tuberosities are usually very strongly developed. The *ulna* and *radius* are both heavy elements. The *ulna* is not dis-

tinguished from that of the timber wolves by any sharply-marked characters. The head of the radius is, in general, relatively thick anteroposteriorly in correspondence to the anteroposterior thickness of the massive distal end of the humerus. On the distal end of the radius there is commonly only a faint groove for the tendon of the extensor ossis metacarpi pollicis, whereas in many modern wolves and coyotes this groove and the tubercle above it are clearly marked. The small size of the groove possibly indicates weakness of the extensor muscle of the thumb. A similarly shallow groove has been noted on one radius of a specimen of *C. occidentalis*.

Study of a large series of specimens of *C. dirus* indicates that the feet are not relatively as heavy as in the large timber wolf, *C. pambasileus*. The mesopodial elements of the average specimens are of about the same size as those of a specimen of *C. pambasileus* in which the skull is somewhat smaller than in the average of *C. dirus*. Compared with the same skeleton of *C. pambasileus*, the average specimen of *C. dirus* has absolutely smaller metapodial and phalangeal elements.

In the *manus* of *C. dirus*, excepting minor differences, the form of the elements generally resembles that of the modern wolves quite closely. Among the carpals, the scapholunar seems commonly to be distinguished by the shorter transverse diameter of the medial facet of the distal side upon which the trapezoid articulates. This would seem to indicate a smaller transverse diameter of the trapezoid and a corresponding narrowing of the head of metacarpal two. It has not, however, been noted that either of these elements is markedly narrowed. The metacarpals in some cases have the shaft relatively wide anteroposteriorly in *C. dirus*. In metacarpal four the anterior medial facet at the proximal end is developed as a relatively long downwardly extended surface marked by a gentle elevation at about the middle of its length. In *C. pambasileus* this facet is shorter vertically, and the protuberance is much more prominent. In some of the other canid forms, as in the domestic dog and in the coyote, this facet does not reach as far down on the shaft.

So far as can be determined, the *pollex* is not larger, and is probably on the average smaller, than in the timber wolves. The finding of skeletons in which the elements are associated is very uncommon at Rancho La Brea, and it has been especially difficult to make certain of the association of the smaller elements of the limbs. The suggestion that the pollex was small is based on the fact that the average of the specimens of metacarpal one in the collection is relatively small, this evidence being supported by that of the small groove for the tendon of the extensor ossis metacarpi pollicis, and the small, short facet for the trapezoid.

The average of the phalangeal elements of the anterior limb in the collection is smaller than in a large specimen of *C. pambasileus*. The terminal phal-

anges have stout, gently curved claw-cores, and are extended inferiorly as strong subungular processes.

Posterior Arch and Limbs.—The *pelvic arch* is closely similar to that of the timber wolves. In the posterior extremities the *femur* (fig. 18) varies considerably in the weight of the shaft, being in some cases heavier than in the timber wolves. The tibia is commonly very massive. In the femur the greater trochanter is always large in adult animals, and may project upward to a point almost level with the proximal side of the head. The smaller troch-

Fig. 18. *Canis dirus* Leidy. Femur, posterior view, no. 10540, $\times \frac{1}{2}$. Rancho La Brea Beds.
Figs. 19 to 21. *Canis dirus* Leidy. Tibia, no. 19482, $\times \frac{1}{2}$. Fig. 19, anterior side; fig. 20, medial view; fig. 21, superior view. Rancho La Brea Beds.

anter and the spiral line below it are always well developed. The tubercle on the postero-lateral region of the shaft just above the popliteal surface is usually clearly marked, and is sometimes very large. Frequently the external epicondylar line passing through this tubercle is extended as a long, narrow sharp-edged ridge.

The *tibia* (figs. 19, 20, and 21) is usually characterized by a very prominent cnemial crest which fades out inferiorly in the lower portion of the upper third of this element. No peculiar characters are noted in the *fibula*.

The *astragalus* has much the same form as in *Canis pambasileus*, excepting in the vertical diameter of the neck. The distal face for articulation with the navicular is transversely elongated in *C. dirus* to such an extent that the long diameter is about one-third greater than the short or vertical diameter. In *C. pambasileus* the neck and head are thicker, and the terminal face for articulation with the navicular is more nearly round.

In the *calcaneum* the distal face for articulation with the cuboid tends to be a little narrower transversely and more nearly quadrate in form in *C. pambasileus* than in *C. dirus*. The *cuboid* is a little narrower transversely in proportion to its length, and the distal face for articulation with metatarsals four and five somewhat narrower in *C. dirus* than in *C. pambasileus*. Corresponding to the form of the head of the astragalus the *navicular* is relatively narrow anteroposteriorly or vertically in *C. dirus*. It is also noted that in this species the small posterior facet which meets the calcaneum is relatively larger than in *C. pambasileus*. The cuneiform elements are not materially different from those of the modern wolves.

The *metatarsals*, like the metacarpals, are relatively somewhat shorter in the average specimen of *C. dirus* than in *C. pambasileus*, though large specimens are present which exceed the largest measurements known in the latter form. The metatarsals of *C. dirus*, even where shorter absolutely than in *C. pambasileus*, are distinctly wider anteroposteriorly in the upper half of the shaft. Metatarsal I of *C. dirus* does not appear to show any noteworthy difference from that of the modern wolves. It is at least as large relatively as in *C. pambasileus*. Metatarsal II (fig. 23) is slightly narrower transversely at the proximal articular end than in *C. pambasileus*, and the angle on the median side of the shaft is less distinctly marked than in that form. Metatarsal IV, in addition to the greater anteroposterior width of the shaft, shows a sharper anteromedian angle in the middle third of the shaft. Metatarsal V (fig. 22) is very distinctly wider anteroposteriorly in *C. dirus* than in *C. pambasileus* and *C. occidentalis*. It is further characterized by the great promi-

Figs. 22 and 23. *Canis dirus* Leidy. Metatarsals, no. 19475, $\times \frac{1}{2}$. Fig. 22, right metatarsal five, medial aspect; fig. 23, right metatarsal two, lateral aspect. Rancho La Brea Beds.

nence of the tuberosity external to the proximal articular facet; in this character it is, however, not distinctly different from *C. occidentalis*.

As nearly as can be determined, relatively small size of the proximal phalanges obtains in the hind feet, as in the anterior extremities.

MEASUREMENTS OF IMPORTANT SKELETAL PARTS

The following measurements are taken from skeletal elements representing individuals of relatively large size. It is not certain that any two of the elements chosen represent the same individual.

Atlas, greatest transverse diameter	120.5 mm.
Axis, greatest anteroposterior diameter of neural spine	73.7
Scapula, greatest height	201
Pelvis, greatest length	228
Humerus, greatest length	240
Radius, greatest length	220
Metacarpal four, greatest length	90.5
Femur, greatest length	260
Tibia, greatest length	237
Metatarsal four, greatest length	102.3

COMPARISON OF RANCHO LA BREA SPECIMENS WITH PREVIOUSLY KNOWN MATERIAL

Comparison with the Type Specimen.—In order to fix the systematic position of the California species satisfactorily it was considered of the utmost importance to make a comparison with Leidy's type specimen. Mr. Witmer Stone of the Philadelphia Academy of Natural Sciences responded most cordially to a request for the loan of the original specimen, making it possible to compare the California collection with the type.

As a result of the comparison of the type with a large number of the specimens from the asphalt deposits, there appears to be no essential difference between the Indiana and the California forms. Such differences as exist are hardly greater than the minor individual differences among California specimens evidently representing one species.

In the type specimen (pl. 25, fig. 3) the form of M^1 , the most important tooth of the upper dentition, differs from that of the other wolves and resembles the California specimens in the extreme reduction of the hypocone. The form of this tooth is in general similar in the Indiana and California forms. If any difference is noticeable, it is in the slightly wider bases of the paracone and the metacone, and in the distinctly concave posterior border of the average California specimen. Numerous individuals are present in the California collection in which the outer pair of tubercles does not show a broader base than in Leidy's type. The posterior border of most of the California specimens is generally rather sharply concave immediately behind the depression for the reception of the hypoconid of M_1 . In the type the posterior border is very

slightly concave at this point. In the type specimen the enamel has been almost entirely broken away from the outer and posterior sides of the metacone; and as the extension of the cingulum around the postero-external angle of the tooth is largely removed, the border appears unnaturally straight. In a few California specimens the posterior border is almost as straight with the postero-external portion of the cingulum present as it now appears in the type specimen with the enamel absent from this region.

In the type specimen the cingulum of the anterior side of the paracone of M^1 appears relatively weak owing to the breaking away of the enamel immediately above the lower border of the cingulum. Judging from its sharp inferior ridge, the cingulum in this region was fully as strongly developed originally as in the Rancho La Brea specimens.

In Leidy's description attention is called to the greater abruptness of the external portion of the basal ridge or cingulum than in the Recent wolves. In the type specimen the external portion of the cingulum of M^1 is marked by a fairly sharp ridge extending along the base of the paracone. This ridge is better developed than in most of the large modern wolves, and the inferior side of that portion of the cingulum bordering the posterior part of the base of the paracone forms a somewhat sharper ridge than in the average of the Rancho La Brea specimens. In some of the California specimens, however, the form and strength of the external cingulum correspond quite closely to what we see in the type.

The form of M^2 in the type does not differ materially from that in the California specimens. The anterior end of the hypocone is extended around the inner and anterior side of the protocone, whereas in many of the California specimens it is interrupted on the antero-internal region of the tooth. There are, however, a number of individuals from Rancho La Brea in which precisely the relations shown here are exhibited. In this tooth the metacone appears to approach the size of the paracone rather more closely than in most of the California specimens. The enamel being removed from both tubercles, it would be unsafe to accept the relative dimensions as certainly representing the true external form. Moreover, some of the Rancho La Brea specimens show practically the same relative dimensions of paracone and metacone as appear in M^2 of the type specimen.

The superior carnassial of the type is badly broken, and shows nothing of the protocone blade. The antero-internal root does not extend far in toward the median line, indicating a small deuterocone as in the California specimens.

The form of P^2 and P^3 of the type is closely similar to that of the California specimens. The extraordinarily strong internal cingula and the strong antero-internal ridges which Leidy mentions as occurring on these teeth in the type are noticed also in most of the Rancho La Brea specimens.

The form of the maxillary bone of the type is not noticeably different from that in the California species, excepting that the superior border of the infra-

orbital foramen is situated a little lower than in the larger specimens from Rancho La Brea.

Comparison with Cope's Texas Specimen.—The material which Cope described from the Texas Pleistocene includes very little on which to base a comparison. Fortunately the first upper molar (pl. 25, fig. 5), which is the most characteristic tooth in the whole dental series of *C. dirus*, is represented. The dimensions of this tooth, as nearly as can be determined from Cope's figure of the specimen, are near to those of the type and to those of the California specimens. The general form of the tooth is clearly similar to that of both the type and the California material in the essential characters. The hypocone is greatly reduced, and the protocone is of moderate size, while the paracone and metacone are rather large. According to Cope's description and figure, the alveolus of the antero-internal root of the superior carnassial extends far forward so that its anterior border overlaps the posterior third of P^3 . Such a form in this root has not been exactly duplicated in the California material, although it is suggested in one specimen. If it is normal it would probably constitute a valid character distinguishing the Texas form. It is conceivable that the form of root seen here is abnormal. It seems quite unnecessary unless the deuterocone were very largely developed, and since the hypocone of M^1 is much reduced and the crushing power weak it is not probable that the deuterocone of P^4 was unusually developed.

Cope noted that the Texas specimen differed from Leidy's type in the following particulars: P^3 distinctly longer and the external cingulum weaker; internal root of P^4 extended farther forward; protocone of M^1 less conic than in the type and external cingulum of M^1 weaker. He suggested that the difference in the external cingula might be due to age, and was inclined to consider the two individuals as representing the same species.

In Cope's figure of the Texas specimen¹⁶ there is a suggestion of a break at the postero-external angle of M^1 , which has carried away the cingulum at this point. If this is the case, the anteroposterior diameter of M^1 would be shortened, and the length of P^3 would appear relatively large. The character of the external cingulum is found to be quite variable in the Rancho La Brea series of specimens. The nature of the antero-internal root of P^4 has been referred to above by the writer. The slight difference in the degree of lateral compression of the protocone of M^1 is fully equalled among the individuals of the Rancho La Brea series.

So far as evidence is available, there seems to be good reason for considering the California and Texas forms as closely related, if not identical species.

Comparison with Material from Sheridan Formation.—A specimen in the collections of the American Museum which was obtained in the Sheridan formation of Kansas evidently represents *Canis dirus*. It consists of a lower jaw

¹⁶ Cope, E. D., Jour. Acad. Sc. Philad., ser. 2, vol. 9, pl. 21, fig. 15, 1895.

(no. 10391 Amer. Mus. Nat. Hist.) with well worn dentition. Measurements of the mandible and dentition correspond closely with those of average specimens of *C. dirus* from Rancho La Brea, as is shown in the table of measurements on page 232. The mandible is exceptionally high and thick as in *C. dirus*. The massive sectorial is indistinguishable in form from that of *C. dirus*, as is also M_2 . P_4 is noticeably large compared with the corresponding tooth in *C. occidentalis*, and in this respect resembles *C. dirus*. The Sheridan Beds are presumed to represent an early phase of the Pleistocene.

Comparison with Material from the Valley of Mexico.—Of considerable interest in connection with a study of the distribution of the American Pleistocene fauna is the occurrence in the Valley of Mexico of remains indistinguishable from the specimens of *Canis dirus* from Rancho La Brea.

Fig. 24. *Canis dirus* Leidy. Posterior portion of a cranium, $\times \frac{1}{2}$. Tequixquiac, Mexico. Adapted from Freudenberg.

The recent investigations of Freudenberg¹⁷ have shown the existence in Mexico of a varied mammalian fauna, which resembles in many respects the Pleistocene fauna of the California region. Included in the assemblage are several specimens of a large wolf. Photographs and a cast of the best preserved specimen¹⁸ which Dr. Freudenberg very kindly placed at the writer's disposal represent an animal which does not appear to be specifically distinguishable from the Rancho La Brea form of *C. dirus*. No remains of the dentition of the Mexican type seem to have been obtained, so that a fully satisfactory determination of the characters is not possible, but the close relationship of the forms is evident from such comparisons as can be made. Especially noticeable are the similarity in size, in the form of the occipital region, and in the nature of the overhanging inion region (fig. 24). The last character seems to be practically diagnostic of the *C. dirus* group. In the large number of speci-

¹⁷ Freudenberg, W., Geol. u. Palae. Abh., N.F., Bd. 9, Heft 3, 1910. Die Säugethierfauna des Pliocäns und Postpliocäns von Mexico.

¹⁸ See Freudenberg, *ibid.*, Taf. 6, figs. 2, 3, 4.

mens available in the collections from Rancho La Brea the individuals unquestionably included in the species referred to *C. dirus* show considerable range of size and form. The Mexican species falls well within the range of variation of the Rancho La Brea specimens. The marked angle in the forehead of the Mexican specimen, formed by the sharp downward slope of the fronto-maxillary region above the orbit, is matched by the contour of the skull in several specimens representing old individuals from Rancho La Brea.

Comparison with Previously Described Californian Material.—The specimens already described from California, comprising the mandible from Livermore Valley¹⁹ and the fragment of a lower jaw from Tulare County²⁰, may both presumably be included within the limits of *Canis dirus*. The jaw from Liver-

Fig. 25. *Canis dirus* Leidy. Right ramus of mandible, $\times \frac{1}{2}$. Livermore Valley, California. Adapted from Leidy.

more Valley (fig. 25), as shown by the table of measurements below, is closely similar in dimensions to specimens from Rancho La Brea. The specimen from Tulare County (fig. 26) seemed to show a somewhat heavier jaw than the

Fig. 26. *Canis dirus* Leidy. A portion of the left ramus of the mandible, $\times \frac{3}{4}$. Oil Springs, Oil Cañon, Tulare County, California.

¹⁹ Leidy, J., Geol. Surv. Terrs., vol. i, Foss. Verts, p. 230, 1873.

²⁰ Merriam, J. C., Univ. Calif. Publ. Bull. Dept. Geol., vol. 3, no. 14, p. 288, 1903.

individuals from Rancho La Brea. This may have been due in part to crushing, as the specimen was much broken. The measurement of the canine is much smaller than that in the larger individuals from Rancho La Brea, but was evidently taken somewhat higher up on the cone of the tooth. Considering the amount of variation known in the specimens at Rancho La Brea, there seems to be good reason for including both the Livermore Valley and Tulare County specimens in the group of *Canis dirus*.

COMPARATIVE MEASUREMENTS

	No. 10856, large specimen, Rancho La Brea	No. 10834, medium specimen, Rancho La Brea	Livermore Valley specimen	Tulare County specimen	Kansas specimen, Sheridan Beds
Length of lower jaw from condyle to anterior side of canine	219 _{ap}	204	200. mm.		198
Depth of lower jaw at condyle	48	44	44.1		43
Depth of lower jaw at M ₁	39.7	37	37.5	42	39.5 _{ap}
Length from posterior side of M ₃ to anterior side of canine	148	137.7	137.5		133 _{ap}
Length of inferior molar and pre- molar series	119.5	113	112.5		110 _{ap}
Anteroposterior diameter of in- ferior canine	17.5	16.5	17.5	13	
M ₁ , anteroposterior diameter	35.7	34.5	34.1	35	33.7

_{ap} approximate.

A fragment of a large wolf jaw (no. 5018) obtained in the Pleistocene deposits of Potter Creek Cave, Shasta County, California²¹ shows some of the characters of *Canis dirus*, as is indicated in the table of measurements below. The inferior carnassial is larger than that of the Recent wolves, but the heel is much narrower than in the typical *C. dirus*, and the inferior premolars are relatively very small. The only specimen known is so fragmentary that final judgment as to its affinities should probably be withheld until better material can be obtained, but there does not seem to be sufficient evidence available to warrant definite separation of the Potter Creek form from the group of *C. occidentalis*.

²¹ Univ. Calif. Publ. Am. Arch. Ethn., vol. 2, no. 1, p. 17, 1904.

COMPARATIVE MEASUREMENTS

	No. 5018 Potter Creek Cave specimen	No. 10856 <i>C. dirus</i> Rancho La Brea	No. 10727 <i>C. dirus</i> Rancho La Brea	<i>C. occidentalis</i> , Recent (a)	<i>C. pambasilus</i> , Recent (b)
M ₁ , greatest anteroposterior diameter	<i>ap</i> 33 mm.	35.7	32	32	29.7
M ₁ , transverse diameter of heel	9.5	13.5	11.4		10
P ₄ , greatest anteroposterior diameter	15.3	20	19.8	16	16.5
P ₄ , greatest transverse diameter	7.3	10.5	9.3	8.5	7.7
P ₃ , greatest anteroposterior diameter	13.2	16.7	15.8		14.6
P ₂ , greatest anteroposterior diameter	12.3	15.4	15		12.5

ap approximate.

(a) No. 115995 U. S. Nat. Mus.

(b) No. 8321. Calif. Mus. Vert. Zool.

CANIS MILLERI, N. Sp.

Text figures 27 to 31

Type specimen, a skull with lower jaw, no. 11257, University of California Collections in Vertebrate Palaeontology. Found four feet below the surface in the asphalt deposits at Rancho La Brea. The species is named in honor of Dr. L. H. Miller, whose assistance in furthering the investigations at Rancho La Brea has been greatly appreciated by the writer.

Skull and dentition (figs. 27, 28, 29, 30, and 31) intermediate between *Canis occidentalis* and *C. dirus*. Characters differing from those of *C. dirus* as follows: Skull much smaller. Nasals narrower posteriorly. Nasal processes of frontals broader and extending much farther forward. Fronto-facial region relatively flat, and postorbital processes of frontals small. Sagittal crest low. Overhang of inion relatively small. Sharp median ridge of occiput wanting. Posterior palatine foramina relatively far forward. Lower jaw slightly narrower anteriorly than in typical *C. dirus*. Teeth relatively large, P^4 and M_1 especially heavy. M^1 (fig. 31) with unusually large hypocone, which extends around the antero-internal region of the protocone, and is connected with a low shelf of the cingulum on the anterior side of the tooth. P_2 with a distinct posterior cusp. M_1 relatively large.

The skull of *Canis milleri* differs markedly from that of *C. occidentalis* in its greater width, especially in the palate, and in the much more massive dentition. P^4 and M^1 are much larger in proportion to the size of the skull than in any of the true timber wolves. P^4 greatly exceeds the relative dimensions in typical *C. occidentalis*. In the general form and massiveness of P^4 , this species closely approaches *C. dirus*, from which it is, however, clearly separated by other characters as indicated above. The nearest approach to the assemblage of characters seen in *C. milleri* is found in *C. occidentalis furlongi*. From this form *C. milleri* is distinguished by greater width of skull, especially in the palatine region; greater interorbital width of the frontal region; shorter and wider nasals; longer nasal processes of the frontals; somewhat heavier upper carnassials; and wider inner lobes of the upper molars.

The form seen in skull no. 11257 was at first considered as probably representing a young female of *Canis dirus*, the peculiar assemblage of characters observed being in part such as might occur in young individuals of this sex. Careful analysis of the collection does not, however, support this view.

Figs. 27 and 28. *Canis milleri* Merriam, J. C. Skull, no. 11257, $\times \frac{1}{2}$. Fig. 27, lateral view; fig. 28, superior view. Rancho La Brea Beds.

Figs. 29 and 30. *Canis milleri* Merriam, J. C. Skull, no. 11257, $\times \frac{1}{2}$. Fig. 29, posterior view; fig. 30, inferior view. Rancho La Brea Beds.

A study of between forty and fifty skulls of *C. dirus* shows no other specimen exhibiting the characters seen here, though there are available well-preserved specimens representing all stages of development, from forms with milk dentition to very aged individuals with teeth nearly worn away. In the collection of specimens unquestionably referred to *C. dirus* there is much variation in many of the characters, particularly in size, and there is reason to believe that among the adults a number of the lighter skulls with weaker muscle attachments represent females. It is, to say the least, highly improbable that skull no. 11257 represents the only female in this collection. That the characters of youth added to those of sex are competent to extend the range of form in *C. dirus* so far as to reach the assemblage of characters seen in specimen no. 11257 seems also improbable. This skull is that of a young adult much beyond the stage of development of many *C. dirus* specimens in which the typical characters of the species are strongly expressed. Moreover, the variation in form of the nasals and nasal processes of the frontals is just opposite to that which would be expected in youthful animals. In all young specimens the nasal processes of the frontals are exceptionally short, while in

no. 11257 they are larger than in any other individuals, including those of advanced age.

Fig. 31. *Canis milleri* Merriam, J. C.
Superior carnassial and superior
molars, oclusal view, no. 11257,
natural size. Rancho La Brea
Beds.

The Miller wolf was an animal about as large as the modern timber wolf, but with a relatively shorter and heavier head. It is to be presumed that the living animal differed very noticeably from the dire wolf in size and in general contour of the body. Of the Miller wolf as yet we know with certainty only the skull. The species was evidently a rela-

tively rare form at Rancho La Brea, but may have been much more common in other regions at the time this deposit was forming.

For measurements of *Canis milleri* see table of comparative measurements of skull, p. 227, and dentition, p. 232.

CANIS OCCIDENTALIS FURLONGI Merriam, J. C.

Text figures 32a to 33b

Canis occidentalis furlongi Merriam, J. C. Univ. Calif. Publ. Bull. Dept. Geol., vol. 5, p. 393, 1910.

There are in the collections from Rancho La Brea several fragmentary specimens representing a wolf species near *Canis occidentalis*. One of these specimens was made the type of a new subspecies in the publication cited above. The type material of the Rancho La Brea form when compared with typical *C. occidentalis* exhibits a tendency to relative narrowness of the nose, the superior carnassial tends to be relatively massive, and the second upper molar seems relatively narrow anteroposteriorly.

The Rancho La Brea specimens originally referred to *C. occidentalis fur-*

Figs. 32a to 32c. *Canis occidentalis furlongi* Merriam, J. C. No. 11283. Fig. 32a, portion of the skull with dentition, inferior aspect, $\times \frac{1}{2}$; fig. 32b, M^1 and M^2 , occlusal view, natural size; fig. 32c, portion of lower jaw with molars, $\times \frac{1}{2}$. Rancho La Brea Beds.

longi differ from *C. dirus* particularly in the form of M^1 (figs. 32a and 32b). This tooth is relatively wide transversely, the inner lobe is relatively narrow anteroposteriorly, and the hypoecone is relatively large. The hypoecone has approximately the size and form seen in average specimens of wolves in the *C. occidentalis* group, and as in that species the anterior end of the hypoecone ridge swings forward around the anterior side of the protocone instead of being interrupted as in *C. dirus*.

In a fragment of a mandible (fig. 32c) accompanying the upper jaw specimen most clearly resembling *C. occidentalis*, the carnassial shows a metaconid even weaker than that of *C. dirus*, while the entoconid is slightly larger than in average *C. dirus* specimens. On M_2 the protoconid seems slightly smaller and the heel region relatively larger than in *C. dirus*, though the metaconid is small compared with the protoconid. The proportions of the talonid region with reference to the trigonid are much as in *C. occidentalis*.

In one of the small specimens (no. 10733) of the *C. occidentalis* type from Rancho La Brea the hypocone of M^1 is rather small, though larger than in the typical *C. dirus*, and the anterior extension of the hypocone ridge around the anterior side of the protocone is barely interrupted. M^2 is in this specimen of the narrow form with small metacone and hypocone. P^3 differs from the corresponding tooth of *C. dirus* in being very narrow instead of wide pos-

Figs. 33a and 33b. *Canis occidentalis furlongi* Merriam, J. C. No. 19792, $\times \frac{1}{2}$. Fig. 33a, skull superior view; fig. 33b, skull inferior view. Rancho La Brea Beds.

teriorly, and in the almost entire absence of a posterior basal tubercle behind the posterior cusp. The portion of the palatine region present seems to narrow anteriorly. This specimen varies in some respects toward *C. dirus*, but the size, general form, and especially the proportions of M¹ indicate that it belongs with the group of individuals referred to *C. occidentalis furlongi* rather than to *C. dirus* or to *C. milleri*.

A small wolf skull, no. 19792, of the *C. occidentalis* type, obtained at Rancho La Brea by Dr. L. H. Miller, resembles *C. occidentalis furlongi* in the characters of the upper molars, and is referred to that form. This specimen (figs. 33a and 33b) differs widely from *C. dirus*, and in most characters in which it differs from *C. dirus*, it resembles *C. occidentalis*. The skull is much smaller than in *C. dirus*, and is also relatively narrower. The nasal bones are long and narrow. The postorbital processes of the frontals are small, the sagittal crest is low, and the inion does not show the extraordinary overhang so characteristic of *C. dirus*. The posterior narial opening is narrow at the anterior end, instead of flaring as is commonly seen in *C. dirus*. The posterior palatine foramina are situated relatively far forward as in *C. occidentalis*. The molars are of the *C. occidentalis* form. P⁴ is, however, much heavier than in the modern wolves and resembles closely P⁴ of *C. milleri*. In the northern wolves of the *C. pambasileus* type the upper carnassial may be quite massive, but falls considerably below the stage of development seen in this form.

Although there is a noticeable variation in the size of the teeth in the Rancho La Brea specimens referred to *C. occidentalis furlongi*, this material seems to represent a single form which differs from the modern gray wolves at least to the extent of subspecific variation.

This wolf type was evidently relatively rare compared with *C. dirus*, and was much less common than the coyotes in this particular region. From what is known of the distribution of wolves of the *C. occidentalis* type it is doubtful whether they have ever been relatively abundant in the region of southwestern United States, as *C. dirus* was certainly the dominant species through a considerable part of Pleistocene time, and the coyote group has apparently been the most abundantly represented canid type since the disappearance of *C. dirus*.

MEASUREMENTS OF DENTITION AND SKULL

	No. 11283 Rancho La Brea	No. 19792 Rancho La Brea	No. 10733 Rancho La Brea	<i>C. dirus</i> (a) Rancho La Brea	<i>C. milleri</i> (b) Rancho La Brea	<i>C. occidentalis</i> (c) Recent
Length, posterior side of superior canine to posterior side of M ²	81.5 mm.	87		115.5	86	91
Length, anterior side of P ⁴ to posterior side M ²	44.7	48.5		54	47.7	46
P ⁴ , anteroposterior diameter	23.6	26.8	24	30.7	28.2	25.5
M ¹ , anteroposterior diameter along outer border	16	17.2	15.5	18.8	17	17.4
M ¹ , greatest transverse diameter	19.3	21.5	18	23	20.7	19.4
M ² , anteroposterior diameter along outer border	8	7.9	8.2	9.2	9	8.5
M ² , greatest transverse diameter	10.8	13.5	10.5	14.4	12.9	12.3
Width, from outer side of alveolus of M ¹ to median line	39	39.6	37.7	46.5	41.8	38.3
Width, from outer side of alveolus of P ¹ to median line	18	20.2		27.5	22.5	19.5
M ₁ , anteroposterior diameter	27			34.5	32	28.3
M ₁ , thickness measured across protoconid	11.5			13.6	13.5	11
M ₂ , anteroposterior diameter	11.5			13.3	12.4	11.7

(a) No. 10834

(b) No. 11257

(c) No. 1308. U. S. Nat. Mus.

CANIS OCHROPUS ORCUTTI Merriam, J. C.

Text figures 34 to 40

Canis orcutti Merriam, J. C., Univ. Calif. Publ. Bull. Dept. Geol. vol. 5, p. 391, 1910.

Type specimen, no. 10842, University of California Collections in Vertebrate Palaeontology. From the asphalt beds of Rancho La Brea, California.

The specimens referred to this form are next in number to those representing *Canis dirus* in the beds at Rancho La Brea, but are relatively rare compared with remains of that species. Though several factors may have tended to keep the number of coyotes entangled in the asphalt down to a percentage of the whole population somewhat less than in the case of the great wolves, it is probable that the smallness of the number of coyotes recovered is due mainly to an absolutely much smaller representation of these forms in this region during the time of accumulation of the asphalt beds.

It is hardly to be presumed that coyotes would avoid the flat land bordering the hills to such an extent as to reduce the percentage of individuals entangled much below that in the case of *C. dirus*, though this might be true of the timber wolves. The principal factors which may have contributed to keep down the percentage of coyotes captured by the asphalt seem to be, nature of the lure attracting wolves, mode of hunting, and possible difference in intelligent recognition of the danger encountered. Most of the carnivores engulfed in the tar have been captured in one of three ways: by accidental crossing of soft tar pools, by the lure of water pools in association with tar springs, and by the lure of entangled animals which might serve as food. Accidents under the first two heads would occur with about the same frequency in the two groups of wolves unless in one of them a grade of intelligence was developed which enabled the individuals to obtain a relatively better knowledge of danger signs. Whether the coyote was the more intelligent animal is not easily determined. It did, however, possess a relatively larger, though absolutely smaller, brain. It is not improbable that its sight, hearing, and smell were more acute than in the great wolf. If this be true, there is reason to suspect that the coyote would more readily perceive and avoid a danger not unusual in this region.

The third factor, lure of animals, is the only one of the three which seems to have significance worth more than passing mention in this connection. Judging from such evidence as we have, it seems probable that the great wolves were powerful enough to prey upon animals of considerable size, that they were so constructed as to make the tearing apart of large animals fairly

easy work, and that they were numerous enough to make hunting in packs a natural method of attack. The coyotes evidently preyed upon small mammals and birds, and hunted alone or in small groups. In all of the asphalt collections brought together thus far the number of individuals representing the larger mammals has been unexpectedly great compared with that of the smaller forms, and the number of birds which would naturally serve as food for coyotes is also small. It may therefore be true that the lure for large wolves was exceptionally good. It is to be noted, however, that even compared with a small number of individuals representing the smaller mammals the number of coyotes is small. It seems therefore possible to explain the number of coyotes present either on the supposition that, owing to much superior intelligence, out of a large number relatively few succumbed to accidental encountering of the tar, or to the attraction of living bait, or on the theory that the number of coyotes in the region was absolutely very much smaller than that of the great wolves. The latter view seems to give the principal reason for the small representation.

Figs. 34 and 35. *Canis ochropus orcutti* Merriam, J. C. Skull, no. 10842, $\times \frac{1}{2}$. Fig. 34, lateral view; fig. 35, posterior view. Rancho La Brea Beds.

This subspecies is closely related to *Canis ochropus* now living in southern California. The skulls of *Canis ochropus orcutti* average somewhat larger than in the living *C. ochropus*, and are noticeably broader across the palate and zygomatic arches (figs. 34, 35, and 40). The mandible is considerably higher, par-

ticularly below the molars, and is also thicker transversely than in the living form of this region. The dimensions of the teeth do not vary greatly from the living species excepting in the thickness of both the upper and lower carnassials, which are heavier in the fossil form (figs. 36a and 36b). M^1 tends also to be somewhat heavier than in the typical *C. ochropus*, and in this respect

Figs. 36a and 36b. *Canis ochropus orcutti* Merriam, J. C. Fig. 36a, superior carnassial and molars, occlusal view, no. 19791, natural size; fig. 36b, inferior cheek-tooth dentition, occlusal view, no. 10842, $\times \frac{1}{2}$. Rancho La Brea Beds.

more nearly approaches the typical *C. latrans*. In M_1 the metaconid seems to be slightly less prominent medially than in the typical *C. ochropus*, possibly owing to the greater thickness of the trigonid blade in the fossil form.

The form from Rancho La Brea differs from the typical *C. latrans* and resembles the type of *C. ochropus* in the relatively narrow anteroposterior diameter of M^1 . M^2 is sometimes smaller than in either the typical *latrans* or the typical *ochropus* form.

A skeleton of this species which has been assembled from parts of separate individuals shows little difference from that of the living *C. ochropus* of this region. It is evident that the coyote of Rancho La Brea was a slender-legged creature, and was swift-footed like its living relative.

Fig. 37. *Canis ochropus orcutti* Merriam, J. C. Inferior view of atlas, no. 10842, $\times \frac{1}{2}$. Rancho La Brea Beds.
 Fig. 38. *Canis ochropus orcutti* Merriam, J. C. Lateral view of axis, no. 10842, $\times \frac{1}{2}$. Rancho La Brea Beds.
 Fig. 39. *Canis ochropus orcutti* Merriam, J. C. Metatarsus, $\times \frac{1}{2}$. Rancho La Brea Beds.

In the collection of canid forms from Rancho La Brea there are a number of fragmentary specimens representing parts of the cranium of small coyotes which are hardly to be distinguished from the corresponding regions in the skull of typical *C. ochropus*. It is not impossible that two forms, typical *C. ochropus* and *C. ochropus orcutti*, were present. It is also possible that all of the forms of Rancho La Brea should be included in one variety which should go under the name of the living *ochropus*. From such material as is available the writer is, however, inclined to believe that the Rancho La Brea form differs somewhat from the living type; and if all of the individuals are to be included in one subspecies, the use of the name *C. ochropus orcutti* for the group more truthfully represents the facts than would designation as typical *C. ochropus*. With a much larger series of specimens available it is possible that a further separation of the coyotes would be possible.

MEASUREMENTS OF SKULL AND DENTITION

	C. o. oreutti (a) large specimen Rancho La Brea	C. o. oreutti (b) small specimen Rancho La Brea	C. ochropus (c) large Recent specimen	C. latrans (d) Recent	C. andersoni (e) type specimen Rancho La Brea
Length from anterior end of premaxillaries to posterior side of occipital condyles....	197.5mm.	188.5	192	179.5	166.1
Width across zygomatic arches		108	104	106.8	91
Width between outer sides of tritocones of P ⁴		65	57	58.9	56
Least width between superior borders of orbits		38	35.4	29.6	31.9
Width between postorbital processes of frontals		55	53.5	44	38.2
Length, posterior side of superior canine to posterior side of M ²		80.5	80	72.6	64.5 <i>ap</i>
Length, anterior side of P ⁴ to posterior side of M ²		37.3	38.7	38.7	36.5 <i>ap</i>
P ³ , anteroposterior diameter		13.3	13.2	13.2	
P ⁴ , anteroposterior diameter		21.2	20.8	21	20
P ⁴ , thickness across protocone		8.5	7.5	7.7	7.8
M ¹ , anteroposterior diameter measured along outer border		13.3	12.8	14	
M ¹ , greatest transverse diameter		16	16	16.2	
M ² , anteroposterior diameter measured along outer border		7.3	8	7.5	
M ² , greatest transverse diameter		10.5	11.3	11.5	
		No. 11278	C. ochro- pus (c)	C. lat- rans (d)	
Length, anterior end of left ramus of mandible to middle of posterior side of condyles		145.5mm.	149	140	
Height of mandible below posterior side of P ₂		17	16.3	17.4	
Height of mandible below posterior side of M ₁		22.5	19.4	20.9	
Thickness of mandible below protoconid of M ₁		11.8	10	9.6	
Length, posterior side inferior canine to posterior side of M ₂		85	85	77.5	
P ₃ , anteroposterior diameter		11.7	11.5	12.5	
P ₃ , greatest transverse diameter		4.8	4.5	4.8	
M ₁ , anteroposterior diameter		22.9	22.2	22.5	
M ₁ , greatest transverse diameter of trigonid		9.5	8.1	8.3	
M ₂ , anteroposterior diameter		9.8	9.8	9.8	

(a) No. 12264.

(b) No. 10842.

(c) No. 651, Univ. Calif. Mus. Vert. Zool.

(d) No. 10993.

(e) No. 12249.

ap approximate.

CANIS ANDERSONI Merriam, J. C.

Text figures 41 and 42

Canis andersoni Merriam, J. C., Univ. Calif. Publ. Bull. Dept. Geol., vol. 5, p. 393, 1910.

Type specimen no. 12249, University of California Collections in Vertebrate Palaeontology. From the asphalt beds of Rancho La Brea, California.

A single specimen in the collections from Rancho La Brea represents a short-headed, coyote-like wolf quite different from any form known to the writer. The skull (figs. 41 and 42) is about as broad as that of *Canis ochropus* but is relatively very short, with a relatively short and broad muzzle. This difference is noticeable also in comparison with the typical *C. latrans*. Though

Fig. 40. *Canis ochropus orcutti* Merriam, J. C. Superior view of skull, no. 12264, $\times \frac{1}{2}$. Rancho La Brea Beds.

Figs. 41 and 42. *Canis andersoni* Merriam, J. C. Skull, no. 12249, $\times \frac{1}{2}$. Fig. 41, superior view; fig. 42, inferior view. Rancho La Brea Beds.

this specimen represents a young individual, the permanent dentition had been complete and there is no reason to believe that the form and proportions of the skull would have changed materially in later life. Of the dentition only the superior carnassials have been preserved. These teeth have approximately the size of those in *C. ochropus*, but appear slightly thicker. A number of minor differences between this specimen and typical representatives of the known coyotes may have specific or subspecific value, but their estimation is not possible with any degree of satisfaction when only one specimen is available for comparison.

It is to be hoped that other material representing this form may be obtained so that some conception of the outlines of the body may be possible.

MEASUREMENTS OF SKULL AND DENTITION

No. 12249

Length from anterior end of premaxillaries to posterior side of occipital condyles	166.1 mm.
Width across zygomatic arches	91
Width between outer sides of tritococones of P ⁴	56
Least width between superior borders of orbits	31.9
Width between postorbital processes of frontals	38.2
Length, posterior side of superior canine to posterior side of M ²	64.5 <i>ap</i>
Length, anterior side of P ⁴ to posterior side of M ²	36.5 <i>ap</i>
P ⁴ , anteroposterior diameter	20
P ⁴ , thickness across protocone	7.8

ap approximate.

UROCYON CALIFORNICUS Mearns

Text figure 43

A finely preserved skull (fig. 43), no. 12263, represents a form almost identical with the existing *Urocyon californicus* of southern California. As is indicated in the table of measurements below, the dimensions are very close to those of two Recent specimens from the San Jacinto region not far distant. It is interesting to note that this form has survived to the present day with less modification than the other canid types.

Fig. 43. *Urocyon californicus* Mearns. Superior view of skull, no. 12263, $\times \frac{1}{2}$. Rancho La Brea Beds.

Portions of the lower jaw and dentition of a form evidently representing this species are also known from Rancho La Brea.

MEASUREMENTS OF SKULL AND DENTITION

	No. 12263 Rancho La Brea	No. 2324a Recent	No. 2316a Recent
Length of skull, anterior end of premaxillaries to posterior side occipital condyles	119.3 mm.	118.7	122.8
Width across zygomatic arches	68.2	64.4	67.6
Least width between superior borders of orbits	23.8	22.5	26
Width of palate between inner borders of second upper molars	17	15.8	18.4
Length of superior dental series from anterior side of canine alveolus to posterior side of M ²	52.2	52.5	53.2
Length from anterior side of P ⁴ to posterior side of M ²	22.3	22.5	22.3
P ⁴ , anteroposterior diameter along outer border	9.9	10	
M ² , anteroposterior diameter along outer border	7.5	8.4	7.7
M ¹ , greatest transverse diameter	10.6	11.4	10.5
M ² , anteroposterior diameter along outer border	5.4	6	5.6
M ² , greatest transverse diameter	7.9	8.2	7.4

a Univ. Calif. Mus. Vert. Zool.

Date of issue, October 25, 1912.

PLATE 24.

EXPLANATION OF PLATE 24

Fig. 1. *Canis dirus* Leidy. Skeleton approximately one-seventh natural size. Rancho La Brea Beds.

Fig. 2. *Canis ochropus orcutti* Merriam, J. C. Skeleton approximately one-seventh natural size. Rancho La Brea Beds.

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PLATE 25.

EXPLANATION OF PLATE 25

Canis dirus Leidy

- Fig. 1. Skull, no. 10834, lateral view, $\times \frac{3}{5}$. Rancho La Brea Beds.
Fig. 2. Skull, no. 19796, inferior view, $\times \frac{3}{5}$. Rancho La Brea Beds.
Fig. 3. M^1 and M^2 of the type specimen, natural size.
Fig. 4. M^1 and M^2 of specimen no. 10856, natural size. Rancho La Brea Beds.
Fig. 5. P^3 and M^1 of the Texas specimen described by Cope, natural size.

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PLATE 26.

EXPLANATION OF PLATE 26

Canis dirus Leidy. Rancho La Brea Beds

Figures three-fifths natural size

Fig. 1. Skull, no. 12266, superior view.

Fig. 2. Skull of unusual relative breadth, no. 19796, superior view.

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PLATE 27.

EXPLANATION OF PLATE 27
Canis dirus Leidy. Rancho La Brea Beds

Figures three-fifths natural size

Fig. 1. Scapula, outer side, no. 12963.

Fig. 2. Pelvis, outer side, no. 19377.

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PLATE 28.

EXPLANATION OF PLATE 28

Canis dirus Leidy. Rancho La Brea Beds

Figures approximately three-fifths natural size

- Fig. 1. Humerus, anterior view.
- Fig. 2. Ulna, lateral view.
- Fig. 3. Radius, anterior view.
- Fig. 4. Femur, anterior view.
- Fig. 5. Tibia, anterior view.

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