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THE FAUNA OF RANCHO LA BREA

PART II. CANIDAE

BY
JOHN C. MERRIAM

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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


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 Leidy\(^1\) 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 Leidy\(^2\) 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:\(^3\)

\(^1\)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 Leidy\(^4\) 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*.

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In 1884 E. D. Cope and J. L. Wortman, in describing the post-Pliocene vertebrates of Indiana, 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, in describing a specimen representing a large fossil wolf from Texas, referred to Leidy's type specimen as representing a distinct species, Canis indiannensis.

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 Allen 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. indiannensis 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 Leidy 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 Merriam to C. indiannensis.

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

The Texas specimen referred to C. indiannensis consisted of portions of an upper dentition, including M1, P2, the canine, and an incisor. It was obtained in the Equus horizon of the Tule Cañon, on Staked Plains of Texas by W. F. Cummins. Cope, 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 Merriam in 1906.

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8 See page 243 of this paper.
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.\footnote{Merriam, J. C., Sunset Magazine, Oct., 1908, p. 172. Also Harper's Weekly, Dec. 18, 1909, p. 11.}

The most recent discovery of remains of *Canis dirus* is that reported by Freudenberg\footnote{Freudenberg, W., Geol. u. Palae. Abh., N.F., Bd. 9, Heft 3, p. 22, 1910.} 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 *Cerus virginianus*, cannot represent other than Pleistocene time.

The Texas specimen described by Cope seems to have occurred at the same horizon as *Mylodon? sodalis*, *Elephas primigenius*, *Equus excelsus*, *E. simplicicus*, *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 *Mylodon*, and is presumably Pleistocene.

The material from Rancho La Brea described in the following paper is
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 Freudenberg 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, Samuel 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 Samuel 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* with reduced deuterocone, M* with greatly reduced hypocone, M, with a small metaconid, P* and P, 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 ionion, 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. 10534, × ½. Fig. 1, lateral view; fig. 2, superior view. Rancho La Brea Beds.
Figs. 3 and 4. *Canis dirus* Leidy. Skull, no. 10834, × ½. 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:

<table>
<thead>
<tr>
<th>Skull</th>
<th>C. dirus(a)</th>
<th>C. pambasileus(b)</th>
<th>C. latrans</th>
</tr>
</thead>
<tbody>
<tr>
<td>Width across palate, measured between outer sides of superior sectorials</td>
<td>38.1%</td>
<td>34%</td>
<td>32%</td>
</tr>
<tr>
<td>Width between most nearly approaching points on upper border of orbits</td>
<td>42.7%</td>
<td>29.8%</td>
<td>16.5%</td>
</tr>
<tr>
<td>Width between postorbital processes of frontals</td>
<td>33.3%</td>
<td>27.2%</td>
<td>24%</td>
</tr>
<tr>
<td>Width across zygomatic arches</td>
<td>62%</td>
<td>55.6%</td>
<td>59.4%</td>
</tr>
</tbody>
</table>

(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 maseteric 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**

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Value 1</th>
<th>Value 2</th>
<th>Value 3</th>
<th>Value 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length, anterior end of premaxillaries to posterior end of occipital condyles</td>
<td>282 mm.</td>
<td>267</td>
<td>250</td>
<td>223</td>
</tr>
<tr>
<td>Length, anterior end of premaxillaries to anterior end of posterior nasal openings</td>
<td>155</td>
<td>141</td>
<td>131.5</td>
<td>119</td>
</tr>
<tr>
<td>Width across nose, measured between outer sides of bases of canines</td>
<td>67.3</td>
<td>58.5</td>
<td>52</td>
<td>50.2</td>
</tr>
<tr>
<td>Width, measured between outer sides superior sectorials</td>
<td>107.5</td>
<td>96.2</td>
<td>85</td>
<td>89.5</td>
</tr>
<tr>
<td>Width across zygomatic arches</td>
<td>175 ap</td>
<td>164.5</td>
<td>138.4</td>
<td>134</td>
</tr>
<tr>
<td>Least diameter between superior borders of orbits</td>
<td>64.9</td>
<td>54.1</td>
<td>51</td>
<td>43.2</td>
</tr>
<tr>
<td>Width between postorbital processes of frontals</td>
<td>93.9</td>
<td>77</td>
<td>67.7</td>
<td>64</td>
</tr>
<tr>
<td>Length from a line drawn between posterior borders of glenoid fossae to posterior end of occipital condyles</td>
<td>54</td>
<td>57</td>
<td>52</td>
<td>52</td>
</tr>
<tr>
<td>Length, anterior end of left ramus of mandible to middle of condyle</td>
<td>230 ap</td>
<td>210.5</td>
<td>202</td>
<td>178</td>
</tr>
<tr>
<td>Height of lower jaw measured between summit of coronoid process and inferior side of angle</td>
<td>91.3</td>
<td>87</td>
<td>85.7</td>
<td>82.5</td>
</tr>
<tr>
<td>Height of lower jaw below hypoconid of M₁</td>
<td>39.7</td>
<td>35.3</td>
<td>30.6</td>
<td>29.8</td>
</tr>
<tr>
<td>Height of lower jaw below protoconid of P₁</td>
<td>36.9</td>
<td>32.5</td>
<td>31.9</td>
<td>24.5</td>
</tr>
<tr>
<td>Thickness of lower jaw below protoconid of M₁</td>
<td>20.3</td>
<td>19.3</td>
<td>14.9</td>
<td>16</td>
</tr>
</tbody>
</table>


**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 is not materially different from that in the large modern wolves. On I the basal lobe on the median side is small or wanting and there is a second
minute basal tubercle on the lateral side. \( P^2 \) 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.

\( P^3 \) is sometimes smaller in anteroposterior diameter than \( P^2 \) of the large Recent wolves.

\( P^3 \) 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.

\( M^2 \) 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.

$M^1$ is relatively small compared with the sectorial, and is usually also small compared with $M^1$. 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, $I^1$ being set back at least as far as $I_2$, while the posterior border of $I_3$ is nearly even with the anterior border of $I_1$.

$I_1$ 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. 10854, 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 $C. dirus$.

$P_1$ (figs. 5, 6, and 7) tends to be rather small compared with $P_2$. 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.

P₃ 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 *Temnoceyon*. 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.

P₄ 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.

P₅ is relatively large compared with P₃, but shows almost exactly the same size in relation to M₁ as is seen in the Alaskan *C. pambasilens*. 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 10656 M 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* 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).

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*³ 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*⁴ 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*⁴ 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.

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*³.
<table>
<thead>
<tr>
<th>Tooth</th>
<th>Measurement</th>
<th>C. eximius (a)</th>
<th>C. otlus (b)</th>
<th>Type of C.</th>
<th>C. otlus (c)</th>
<th>C. occidentalis (d)</th>
<th>C. otlus (e)</th>
<th>C. otlus (f)</th>
<th>C. otlus (g)</th>
<th>C. miliaris (h)</th>
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</thead>
<tbody>
<tr>
<td>I₁</td>
<td>greatest transverse diameter</td>
<td>7.3</td>
<td>7.5</td>
<td>7.6</td>
<td>7.4</td>
<td>7.0</td>
<td>6.5</td>
<td>7.3</td>
<td>7.0</td>
<td>6.2</td>
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<tr>
<td>C₁</td>
<td>greatest anteroposterior diameter</td>
<td>17.5 mm.</td>
<td>15.5</td>
<td></td>
<td>15.5</td>
<td>14.7</td>
<td>16.8</td>
<td>16.5</td>
<td>19.9</td>
<td>18.2</td>
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<tr>
<td>P₁</td>
<td>greatest anteroposterior diameter</td>
<td>15.4</td>
<td>15.3</td>
<td>13.5</td>
<td>15.5</td>
<td>15.5</td>
<td>16.5</td>
<td>19.9</td>
<td>18.2</td>
<td></td>
</tr>
<tr>
<td>C₂</td>
<td>greatest anteroposterior diameter</td>
<td>16.7</td>
<td>15.8</td>
<td>15.5</td>
<td>15.5</td>
<td>16.5</td>
<td>16.5</td>
<td>19.9</td>
<td>18.2</td>
<td></td>
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<tr>
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<td>greatest anteroposterior diameter</td>
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<td>19.5</td>
<td>16.5</td>
<td>16.5</td>
<td>19.9</td>
<td>18.2</td>
<td>18.2</td>
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<td>35.7</td>
<td>34.5</td>
<td>29.0</td>
<td>32.0</td>
<td>33.7</td>
<td>38.6</td>
<td>32.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M₂</td>
<td>greatest anteroposterior diameter of heel, on outer side</td>
<td>9.2</td>
<td>8.8</td>
<td>8.5</td>
<td>8.5</td>
<td>9.3</td>
<td>7.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M₃</td>
<td>greatest transverse diameter of heel</td>
<td>13.5</td>
<td>13.5</td>
<td>11.5</td>
<td>12.2</td>
<td>12.6</td>
<td>13.7</td>
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<tr>
<td>M₄</td>
<td>greatest transverse diameter of trigonid</td>
<td>14.3</td>
<td>13.6</td>
<td>11.8</td>
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<td></td>
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<tr>
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<td>greatest anteroposterior diameter</td>
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<td>13.5</td>
<td>12.5</td>
<td>12.64</td>
<td>12.5 ap</td>
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<tr>
<td>M₆</td>
<td>greatest anteroposterior diameter of heel, on outer side</td>
<td>4.5</td>
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<td>4.6</td>
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<tr>
<td>P₃</td>
<td>greatest transverse diameter</td>
<td>10.5</td>
<td>10.0</td>
<td>9.0</td>
<td>9.0</td>
<td>9.0</td>
<td>9.1</td>
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</tr>
<tr>
<td>C₇</td>
<td>greatest anteroposterior diameter</td>
<td>12.6</td>
<td>10.5</td>
<td></td>
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<tr>
<td>C₈</td>
<td>greatest anteroposterior diameter at upper edge of enamel</td>
<td>17.0</td>
<td>16.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>P₄</td>
<td>greatest anteroposterior diameter</td>
<td>10.2</td>
<td>9.4</td>
<td>8.5</td>
<td>8.5</td>
<td>8.5</td>
<td>8.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P₅</td>
<td>greatest anteroposterior diameter</td>
<td>16.0</td>
<td>16.2</td>
<td>14.8</td>
<td>15.0</td>
<td>15.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

(a) No. 10824.  
(b) No. 10826.  
(d) No. 115965, U. S. Nat. Mus.  
(e) No. 10828.  
(f) No. 11283.  
(g) No. 11257.  
(h) ap approximate.
C. dirus (c)

Rancho La Brea

C. dirus (O) - Palos Verdes

P3, greatest anteroposterior diameter

18.1

P3, greatest transverse diameter

7.9

P4, greatest anteroposterior diameter

30.7

P4, greatest transverse diameter

15)

P4, greatest transverse diameter across denterocone

16.2

P4, greatest transverse diameter across protocone

13

M3, greatest anteroposterior diameter

13.6

M3, greatest transverse diameter across protocone

10

M3, greatest anteroposterior diameter

15.4

M3, greatest transverse diameter

ap approximate.

* Without posterior enamel.

† Without 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 directly above the apex of the protocone; there seems to have been no denterocone 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 denterocone 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. Dm₃ (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**

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Greatest Anteroposterior Diameter</th>
<th>Greatest Transverse Diameter Across Heel</th>
<th>Greatest Anteroposterior Diameter</th>
<th>Greatest Anteroposterior Diameter</th>
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</thead>
<tbody>
<tr>
<td>Dm₁</td>
<td>8.7 mm</td>
<td>6.6</td>
<td>14.6</td>
<td>10.8</td>
</tr>
<tr>
<td>Dm₂</td>
<td>15.5</td>
<td>10.8</td>
<td>14.6</td>
<td>11.4</td>
</tr>
</tbody>
</table>

**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, X 1/2. Rancho La Brea Beds.](image16)

![Fig. 17. Canis dirus Leidy. Axis, lateral view, no. 10834, X 1/2. Rancho La Brea Beds.](image17)

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 tuberences 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 tuberences 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 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-
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
epipcondylic 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
evential 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. pam-
basileus, 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. pambasile-
us. Metatarsal II (fig. 23) is slightly narrower trans-
versely at the proximal articular end than in C. pambasileus,
and the angle on the median side of the shaft is less dis-
tinctly marked than in that form. Metatarsal IV, in addi-
tion 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 anter-
oposteriorly in C. dirus than in C. pambasileus and C. occi-
dentalis. It is further characterized by the great promi-

22 23
Figs. 22 and 23. Canis
dirus Leidy. Metatar-
sals, no. 19475, X 15.
Fig. 22, right metatar-
sal five, medial aspect;
fig. 23, right metatar-
sal 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.

<table>
<thead>
<tr>
<th>Element</th>
<th>Measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlas, greatest transverse diameter</td>
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</tr>
<tr>
<td>Axis, greatest anteroposterior diameter of neural spine</td>
<td>73.7</td>
</tr>
<tr>
<td>Scapula, greatest height</td>
<td>291</td>
</tr>
<tr>
<td>Pelvis, greatest length</td>
<td>228</td>
</tr>
<tr>
<td>Humerus, greatest length</td>
<td>240</td>
</tr>
<tr>
<td>Radius, greatest length</td>
<td>220</td>
</tr>
<tr>
<td>Metacarpal four, greatest length</td>
<td>90.5</td>
</tr>
<tr>
<td>Femur, greatest length</td>
<td>260</td>
</tr>
<tr>
<td>Tibia, greatest length</td>
<td>237</td>
</tr>
<tr>
<td>Metatarsal four, greatest length</td>
<td>102.3</td>
</tr>
</tbody>
</table>

**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 the upper 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 M₃. 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 M₁ 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 M₁ 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 M₁ 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 M₁ 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 deutocone as in the California specimens.

The form of P₂ and P₃ 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 P₃. 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 dentocone were very largely developed, and since the hypocone of M₁ is much reduced and the crushing power weak it is not probable that the dentocone of P₃ was unusually developed.

Cope noted that the Texas specimen differed from Leidy’s type in the following particulars: P₃ distinctly longer and the external cingulum weaker; internal root of P₃ extended farther forward; protocone of M₁ less conic than in the type and external cingulum of M₁ 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 M₁, which has carried away the cingulum at this point. If this is the case, the antero-posterior diameter of M₁ would be shortened, and the length of P₃ 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 P₃ has been referred to above by the writer. The slight difference in the degree of lateral compression of the protocone of M₁ 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.
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 M₂. P₄ 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.

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 union region (fig. 24). The last character seems to be practically diagnostic of the C. dirus group. In the large number of speci-

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 Valley\(^{19}\) and the fragment of a lower jaw from Tulare County\(^{20}\), may both presumably be included within the limits of *Canis dirus*. The jaw from Liver-

![Fig. 25. *Canis dirus* Leidy. Right ramus of mandible, \(\times \frac{1}{5}\). Livermore Valley, California. Adapted from Leidy.](image)

![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.](image)

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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**

<table>
<thead>
<tr>
<th></th>
<th>No. 18854, large specimen, Rancho La Brea</th>
<th>No. 18824, median specimen, Rancho La Brea</th>
<th>Livermore Valley specimen</th>
<th>Tulare County specimen</th>
<th>Kansas specimen, Sheridan, Wash.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of lower jaw from condyle to anterior side of canine</td>
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<td>204</td>
<td>200.0 mm.</td>
<td>...</td>
<td>198</td>
</tr>
<tr>
<td>Depth of lower jaw at condyle</td>
<td>48</td>
<td>44</td>
<td>44.1</td>
<td>...</td>
<td>43</td>
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<tr>
<td>Depth of lower jaw at M&lt;sub&gt;2&lt;/sub&gt;</td>
<td>39.7</td>
<td>37</td>
<td>37.5</td>
<td>42</td>
<td>39.5&lt;sub&gt;ap&lt;/sub&gt;</td>
</tr>
<tr>
<td>Length from posterior side of M&lt;sub&gt;2&lt;/sub&gt; to anterior side of canine</td>
<td>148</td>
<td>137.7</td>
<td>137.5</td>
<td>...</td>
<td>133&lt;sub&gt;ap&lt;/sub&gt;</td>
</tr>
<tr>
<td>Length of inferior molar and premolar series</td>
<td>119.5</td>
<td>113</td>
<td>112.5</td>
<td>...</td>
<td>110&lt;sub&gt;ap&lt;/sub&gt;</td>
</tr>
<tr>
<td>Anteroposterior diameter of inferior canine</td>
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<td>16.5</td>
<td>17.5</td>
<td>13</td>
<td>...</td>
</tr>
<tr>
<td>M&lt;sub&gt;1&lt;/sub&gt; anteroposterior diameter</td>
<td>35.7</td>
<td>34.5</td>
<td>34.1</td>
<td>35</td>
<td>33.7</td>
</tr>
</tbody>
</table>

<sub><sup>ap</sup> approximate.</sub>

A fragment of a large wolf jaw (no. 5018) obtained in the Pleistocene deposits of Potter Creek Cave, Shasta County, California<sup>21</sup> 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.

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### Comparative Measurements

<table>
<thead>
<tr>
<th></th>
<th>Dolores Creek Cave</th>
<th>Coelodonta transversa, Recent</th>
<th>Coelodonta transversa, Recent</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>M</strong>&lt;sub&gt;1&lt;/sub&gt;, greatest anteroposterior diameter</td>
<td>ap33 mm.</td>
<td>35.7</td>
<td>32</td>
</tr>
<tr>
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<td>9.5</td>
<td>13.5</td>
<td>11.4</td>
</tr>
<tr>
<td><strong>P</strong>&lt;sub&gt;4&lt;/sub&gt;, greatest anteroposterior diameter</td>
<td>15.3</td>
<td>20</td>
<td>19.8</td>
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<tr>
<td><strong>P</strong>&lt;sub&gt;4&lt;/sub&gt;, greatest transverse diameter</td>
<td>7.3</td>
<td>10.5</td>
<td>9.3</td>
</tr>
<tr>
<td><strong>P</strong>&lt;sub&gt;2&lt;/sub&gt;, greatest anteroposterior diameter</td>
<td>13.2</td>
<td>16.7</td>
<td>15.8</td>
</tr>
<tr>
<td><strong>P</strong>&lt;sub&gt;2&lt;/sub&gt;, greatest anteroposterior diameter</td>
<td>12.3</td>
<td>15.4</td>
<td>15</td>
</tr>
</tbody>
</table>

*ap* approximate.

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

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. P1 and M1 especially heavy. M1 (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. P2 with a distinct posterior cusp. M1 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. P4 and M3 are much larger in proportion to the size of the skull than in any of the true timber wolves. P4 greatly exceeds the relative dimensions in typical C. occidentalis. In the general form and massiveness of P4, 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, X 1/2. Fig. 27, lateral view; fig. 28, superior view. Rancho La Brea Beds.
MERRIAM: THE FAUNA OF RANCHO LA BREA.

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Figs. 29 and 30. *Canis milleri* Merriam, J. C. Skull, no. 11257, × ½. 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.

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 relatively 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


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, × 1/5; fig. 32b, M1 and M2, occlusal view, natural size; fig. 32c, portion of lower jaw with molars, × 1/2. Rancho La Brea Beds.](image-url)

longi* differ from *C. dirus* particularly in the form of M1 (figs. 32a and 32b). This tooth is relatively wide transversely, the inner lobe is relatively narrow anteroposteriorly, and the hypocone is relatively large. The hypocone 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 hypocone 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 M₂ 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 M₁ 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. M₂ is in this specimen of the narrow form with small metacone and hypocone. P₃ differs from the corresponding tooth of *C. dirus* in being very narrow instead of wide pos-

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Figs. 33a and 33b. *Canis occidentalis furiongi* Merriam, J. C. No. 19792, × ½. 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 M° 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. P° is, however, much heavier than in the modern wolves and resembles closely P° 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*. 

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MERRIAM: THE FAUNA OF RANCHO LA BREA. 253
### Measurements of Dentition and Skull

<table>
<thead>
<tr>
<th></th>
<th>No. 10838</th>
<th>No. 10733</th>
<th>No. 10733</th>
<th>C. diors (c)</th>
<th>C. milleri (b)</th>
<th>C. ornata (a)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rancho La Brea</td>
<td>Rancho La Brea</td>
<td>Rancho La Brea</td>
<td>Rancho La Brea</td>
<td>Rancho La Brea</td>
<td>Rancho La Brea</td>
</tr>
<tr>
<td>Length, posterior side of superior canine to posterior side of M²</td>
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<td>...</td>
<td>115.5</td>
<td>86</td>
<td>91</td>
</tr>
<tr>
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<td>48.5</td>
<td>...</td>
<td>54</td>
<td>47.7</td>
<td>46</td>
</tr>
<tr>
<td>P¹, anteroposterior diameter</td>
<td>23.6</td>
<td>26.8</td>
<td>24</td>
<td>30.7</td>
<td>28.2</td>
<td>25.5</td>
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<tr>
<td>M³, anteroposterior diameter along outer border</td>
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<td>17.2</td>
<td>15.5</td>
<td>18.8</td>
<td>17</td>
<td>17.4</td>
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<tr>
<td>M³, greatest transverse diameter</td>
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<td>18</td>
<td>23</td>
<td>20.7</td>
<td>19.4</td>
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<td>7.9</td>
<td>8.2</td>
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<td>8.5</td>
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<td>M², greatest transverse diameter</td>
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<td>10.5</td>
<td>14.4</td>
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<tr>
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<td>39.6</td>
<td>37.7</td>
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<td>Width, from outer side of alveolus of P¹ to median line</td>
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<td>...</td>
<td>27.5</td>
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<td>M₁, anteroposterior diameter</td>
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<td>28.3</td>
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<tr>
<td>M₁, thickness measured across protoconid</td>
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<td>...</td>
<td>13.6</td>
<td>13.5</td>
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<td>M₂, anteroposterior diameter</td>
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<td>...</td>
<td>...</td>
<td>13.3</td>
<td>12.4</td>
<td>11.7</td>
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</table>

(a) No. 10834  
(b) No. 11257  
(c) No. 1308, U. S. Nat. Mus.
CANIS OCHROPUS ORCUTTI Merriam, J. C.

Text figures 34 to 40


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.

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-
particularly 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). $M'$ tends also to be somewhat heavier than in the typical $C. ochropus$, and in this respect

![Figures 36a and 36b](image_url)

more nearly approaches the typical $C. latrans$. In $M$, 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 $M'$. $M^2$ 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.

![Figures 37, 38, and 39](image_url)
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 \textit{C. ochropus}. It is not impossible that two forms, typical \textit{C. ochropus} and \textit{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 \textit{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 \textit{C. ochropus orcutti} for the group more truthfully represents the facts than would designation as typical \textit{C. ochropus}. With a much larger series of specimens available it is possible that a further separation of the coyotes would be possible.
MERRIAM: THE FAUNA OF RANCHO LA BREA.

Measurements of Skull and Dentition

<table>
<thead>
<tr>
<th>Measurements</th>
<th>C. ochrospilus (c)</th>
<th>C. ochrospilus (d)</th>
<th>C. latrans (c)</th>
<th>C. latrans (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length from anterior end of premaxillaries to posterior side of occipital condyles</td>
<td>197.5 mm.</td>
<td>188.5</td>
<td>192</td>
<td>179.5</td>
</tr>
<tr>
<td>Width across zygomatic arches</td>
<td>108</td>
<td>104</td>
<td>106.8</td>
<td>91</td>
</tr>
<tr>
<td>Width between outer sides of tritocones of P4</td>
<td>65</td>
<td>57</td>
<td>59.9</td>
<td>56</td>
</tr>
<tr>
<td>Least width between superior borders of orbits</td>
<td>38</td>
<td>35.4</td>
<td>29.6</td>
<td>31.9</td>
</tr>
<tr>
<td>Width between postorbital processes of frontals</td>
<td>55</td>
<td>53.5</td>
<td>44</td>
<td>38.2</td>
</tr>
<tr>
<td>Length, posterior side of superior canine to posterior side of M2</td>
<td>80.5</td>
<td>80</td>
<td>72.6</td>
<td>64.5 ap</td>
</tr>
<tr>
<td>Length, anterior side of P4 to posterior side of M2</td>
<td>37.3</td>
<td>38.7</td>
<td>38.7</td>
<td>36.5 ap</td>
</tr>
<tr>
<td>P3, anteroposterior diameter</td>
<td>13.3</td>
<td>12.2</td>
<td>12.2</td>
<td>12.2</td>
</tr>
<tr>
<td>P4, anteroposterior diameter</td>
<td>21.2</td>
<td>20.8</td>
<td>21</td>
<td>20</td>
</tr>
<tr>
<td>P4, thickness across protocone</td>
<td>8.5</td>
<td>7.5</td>
<td>7.7</td>
<td>7.8</td>
</tr>
<tr>
<td>M1, anteroposterior diameter measured along outer border</td>
<td>13.3</td>
<td>12.8</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>M2, greatest transverse diameter</td>
<td>16</td>
<td>16</td>
<td>16.2</td>
<td>16.2</td>
</tr>
<tr>
<td>M2, anteroposterior diameter measured along outer border</td>
<td>7.3</td>
<td>8</td>
<td>7.5</td>
<td>7.5</td>
</tr>
<tr>
<td>M2, greatest transverse diameter</td>
<td>10.5</td>
<td>11.3</td>
<td>11.5</td>
<td>11.5</td>
</tr>
<tr>
<td>Length, anterior end of left ramus of mandible to middle of posterior side of condyles</td>
<td>145.5 mm.</td>
<td>149</td>
<td>140</td>
<td></td>
</tr>
<tr>
<td>Height of mandible below posterior side of P2</td>
<td>17</td>
<td>16.3</td>
<td>17.4</td>
<td></td>
</tr>
<tr>
<td>Height of mandible below posterior side of M1</td>
<td>22.5</td>
<td>19.4</td>
<td>20.9</td>
<td></td>
</tr>
<tr>
<td>Thickness of mandible below protoconid of M1</td>
<td>11.8</td>
<td>10</td>
<td>9.6</td>
<td></td>
</tr>
<tr>
<td>Length, posterior side inferior canine to posterior side of M1</td>
<td>85</td>
<td>85</td>
<td>77.5</td>
<td></td>
</tr>
<tr>
<td>P3, anteroposterior diameter</td>
<td>11.7</td>
<td>11.5</td>
<td>12.5</td>
<td></td>
</tr>
<tr>
<td>P4, greatest transverse diameter</td>
<td>4.8</td>
<td>4.5</td>
<td>4.8</td>
<td></td>
</tr>
<tr>
<td>M1, anteroposterior diameter</td>
<td>22.9</td>
<td>22.2</td>
<td>22.5</td>
<td></td>
</tr>
<tr>
<td>M2, greatest transverse diameter of trigonid</td>
<td>9.5</td>
<td>8.1</td>
<td>8.3</td>
<td></td>
</tr>
<tr>
<td>M2, anteroposterior diameter</td>
<td>9.8</td>
<td>9.8</td>
<td>9.8</td>
<td></td>
</tr>
</tbody>
</table>

No. 11278

C. ochrospilus (c) C. latrans (d)

(a) No. 10934.
(b) No. 10849.
(d) No. 10093.
(e) No. 10249.

ap approximate.
CANIS ANDERSONI Merriam, J. C.

Text figures 41 and 42


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

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Fig. 40. *Canis ochropus ochratus* Merriam, J. C. Superior view of skull, no. 12264, × 1/4. Rancho La Brea Beds.

Figs. 41 and 42. *Canis andersoni* Merriam, J. C. Skull, no. 12249, × 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**

<table>
<thead>
<tr>
<th>Measurement Description</th>
<th>No. 12249</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length from anterior end of premaxillaries to posterior side of occipital condyles</td>
<td>166.1 mm.</td>
</tr>
<tr>
<td>Width across zygomatic arches</td>
<td>91</td>
</tr>
<tr>
<td>Width between outer sides of tritocones of P4</td>
<td>56</td>
</tr>
<tr>
<td>Least width between superior borders of orbits</td>
<td>31.9</td>
</tr>
<tr>
<td>Width between postorbital processes of frontals</td>
<td>38.2</td>
</tr>
<tr>
<td>Length, posterior side of superior canine to posterior side of M3</td>
<td>64.5 ap</td>
</tr>
<tr>
<td>Length, anterior side of P4 to posterior side of M3</td>
<td>36.5 ap</td>
</tr>
<tr>
<td>P4, anteroposterior diameter</td>
<td>20</td>
</tr>
<tr>
<td>P4, thickness across protocone</td>
<td>7.8</td>
</tr>
</tbody>
</table>

*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.

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

<table>
<thead>
<tr>
<th></th>
<th>No. 12263 Rancho La Brea</th>
<th>No. 2324a Recent</th>
<th>No. 2316a Recent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of skull, anterior end of premaxillaries to posterior side occipital condyles</td>
<td>119.3 mm.</td>
<td>118.7</td>
<td>122.8</td>
</tr>
<tr>
<td>Width across zygomatic arches</td>
<td>68.2</td>
<td>64.4</td>
<td>67.6</td>
</tr>
<tr>
<td>Least width between superior borders of orbits</td>
<td>23.8</td>
<td>22.5</td>
<td>26</td>
</tr>
<tr>
<td>Width of palate between inner borders of second upper molars</td>
<td>17</td>
<td>15.8</td>
<td>18.4</td>
</tr>
<tr>
<td>Length of superior dental series from anterior side of canine alveolus to posterior side of M2</td>
<td>52.2</td>
<td>52.5</td>
<td>53.2</td>
</tr>
<tr>
<td>Length from anterior side of P4 to posterior side of M2</td>
<td>22.3</td>
<td>22.5</td>
<td>22.3</td>
</tr>
<tr>
<td>P4, anteroposterior diameter along outer border</td>
<td>9.9</td>
<td>10</td>
<td>.....</td>
</tr>
<tr>
<td>M3, anteroposterior diameter along outer border</td>
<td>7.5</td>
<td>8.4</td>
<td>7.7</td>
</tr>
<tr>
<td>M3, greatest transverse diameter</td>
<td>10.6</td>
<td>11.4</td>
<td>10.5</td>
</tr>
<tr>
<td>M4, anteroposterior diameter along outer border</td>
<td>5.4</td>
<td>6</td>
<td>5.6</td>
</tr>
<tr>
<td>M4, greatest transverse diameter</td>
<td>7.9</td>
<td>8.2</td>
<td>7.4</td>
</tr>
</tbody>
</table>


Date of issue, October 25, 1912.
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.
PLATE 25.
EXPLANATION OF PLATE 25

*Canis dirus* Leidy

Fig. 1. Skull, no. 10834, lateral view, × 3/5. Rancho La Brea Beds.

Fig. 2. Skull, no. 19796, inferior view, × 3/5. Rancho La Brea Beds.

Fig. 3. M1 and M2 of the type specimen, natural size.

Fig. 4. M1 and M2 of specimen no. 10856, natural size. Rancho La Brea Beds.

Fig. 5. P3 and M1 of the Texas specimen described by Cope, natural size.
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.
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.
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.