Geology and Vertebrate Paleontology of Western and Southern North America

Edited By Xiaoming Wang and Lawrence G. Barnes

Contributions in Honor of David P. Whistler

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Fossil dogs (Carnivora, Canidae) from the Sespe and Vaqueros formations in Southern California, with comments on relationships of Phlaocyon taylori

Xiaoming Wang\textsuperscript{1} and Richard H. Tedford\textsuperscript{2}

ABSTRACT. Six species within three subfamilies of Canidae were recovered from the Arikareean through Hemingfordian part of the undifferentiated Sespe/Vaqueros formations as a result of paleontologic resource mitigation activities during Orange County highway construction and landfill programs in Southern California. These can be identified as ?Mesocyon sp., Cynarctoides whistleri sp. nov., Phlaocyon taylori, Desmocyon thomsoni, Metatomartcus canavus, and Leptocyon vulpinus. Canids are generally rare in lower Miocene deposits of Southern California. Of the six species reported herein, only Mesocyon has previously been reported from California. In addition to California, the new species, C. whistleri, also occurs in Texas. Cynarctoides whistleri has a combination of primitive and advanced characters, suggestive of a transitional form that developed in isolation from the main area of evolution for Cynarctoides in the northern Great Plains. The new Phlaocyon material is only the third record of this species known, and it is the first record from outside of Florida. The new California specimen of P. taylori, with its nearly complete upper and lower dentitions, substantially improves our knowledge of, and greatly expands the distribution of this small, hypocarnivorous canid. The coyote- to fox-sized canids Mesocyon, Desmocyon, Metatomartcus, and Leptocyon are also known from the Great Plains, indicating wide distributions for these cursorial forms, whereas the two small, hypocarnivorous canids Cynarctoides and Phlaocyon seem to show regional differentiation, with distributions in Florida, Texas, and Southern California.

INTRODUCTION

Paleontological resource impact mitigation programs associated with the Foothill/Eastern Transportation Corridor toll roads and landfill projects in Orange County, Southern California, during the past 20 years have yielded a substantial collection of vertebrate fossils. More than 4,000 fossil vertebrate specimens, most of them isolated rodent teeth collected via screen washing and heavy-liquid separation techniques, were recovered from more than 100 fossil localities in exposures of the continental Sespe Formation and the undifferentiated Sespe and marine Vaqueros formations in the Santa Ana Mountains and San Joaquin Hills of the northern Peninsular Ranges Province (Whistler and Lander, 2003:fig. 11.1).

Six species belonging to three subfamilies of Canidae were recovered from reddish colored mudstones in terrestrial facies sediments in the Sespe and Vaqueros formations (Arikareean and Hemingfordian). These can be identified as ?Mesocyon sp.; Cynarctoides whistleri sp. nov.; Phlaocyon taylori Hayes, 2000; Desmocyon thomsoni (Matthew, 1907); Metatomartcus canavus (Simpson, 1932); and Leptocyon vulpinus (Matthew, 1907). These new materials fill a large gap in our knowledge of an ecologically diverse group of carnivores from the late Cenozoic of North America.

Of the six canid taxa, only Mesocyon Scott, 1890, was previously known from the early Arikareean of California. The new species of Cynarctoides McGrew, 1938, shows regional differentiation of small, hypocarnivorous taxa in the southern United States. Three specimens of P. taylori from Orange County, with substantial upper and nearly complete lower dentitions, represent the best material for this species, which was previously known only by isolated teeth from Florida. The California specimens of Phlaocyon Matthew, 1899, are also the first records of the species outside of Florida, and they greatly expand the known distribution of this species.

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which produced *Sesapia*, Stock, 1930, a typical early Arikareean oreodont, is near the bottom of the Bowerman Landfill section and below the conglomerate layer, which was used as a marker bed separating early and late Arikareean correlative strata (Whistler and Lander, 2003:figs. 11.2 and 11.3).

The biostratigraphic framework proposed by Whistler and Lander (2003:figs. 2 and 3) was based on a combination of field and faunal correlations, and stratigraphic controls might not be very precise because of the geologic complexities of the landfill property, the long sections often without distinct marker beds, and the limited time available for compiling stratigraphic data during grading. Given the complexity of faulting and the proximity of the six fossil sites included within LACM 6942, one cannot rule out the possibility that these sites might represent more than one stratigraphic horizon.

Of the two fossil canid sites included within LACM 6942, RMW SW 95-1309 was originally considered by D.P. Whistler (personal communication, 2003) to occur in early Arikareean correlative strata below the conglomerate. The other site, RMW TRM 043, was associated with localities LACM 6940 and 6944 that were considered to lie above the conglomerate. However, the *Phlaocyon* lower jaw described here is the only specimen obtained from RMW TRM 043, and lacking an associated fauna from this site, the possibility that TRM 043 might be of early Arikareean age cannot be ruled out.

The locality LC 202, which produced *P. taylori* and *L. vulpinus*, is at the bottom of the local stratigraphic section in the Oso Segment of the Foothill Transportation Corridor (FTC/Oso). This section, which does not contain the conglomerate, is correlated faunally with strata lying above the conglomerate elsewhere in Orange County (Whistler and Lander, 2003:figs. 11.3 and 11.4). Suspected to be a carnivore den, a sample from this site was screen-washed and yielded a small micromammal fauna. Besides the two canids (*P. taylori* and *L. vulpinus*) described here, Whistler and Lander (2003:table 11.2) listed the following micromammals from LC 202: *Herpetotherium* Cope, 1873; *Mioptermophilus* Black, 1963; *Lednymys nematodon* (Cope, 1879); *Schizodontomys* Rensberger, 1973; and "*Nano- tragus ordinatus*? (Matthew, 1907)" (taxa in common from composite list for LC 202 + 205 in Whistler and Lander [2003] and from list in Lander and Whistler [1999]). Of these taxa, the hypertragulid *Nanotragulus* Lull, 1922, is significantly higher crowned than early Arikareean forms, and the heteromyine rodent *Schizodontomys* was listed in the late Arikareean and early Hemingfordian of Southern California (Whistler and Lander, 2003), but its range extends to the
early Arikareean in the High Plains (Korth, 1994; Tedford et al., 2004). The other small mammals, however, have long temporal ranges that extend into early Arikareean time locally and/or regionally.

Locality LC 166, which produced *D. thomsoni* and *M. canavus*, is in the Santiago Canyon Landfill, a large, ongoing excavation that exposes interbedded dark red sandstone and green and yellow sandstones that are not differentiated between the Sespe or Vaqueros formations and are overlain by marine sandstones of the Topanga Formation. Fossils were recovered by PEAI and RMW personnel, and the resulting fossil assemblage, Santiago Canyon Landfill Local Fauna, is confined to the “Vaqueros” lithofacies (Whistler and Lander, 2003:fig. 11.3, table 11.2). Most of the localities in the Santiago Canyon Landfill produce the Upper OC S/V Fauna, which was postulated to be early Hemingfordian in age mostly on the basis of small mammals (Whistler and Lander, 2003:figs. 11.4 and 11.5).

As discussed herein, *Mesocyon* sp., *P. taylori*, and *L. vulpinus* suggest an early Arikareean age, as determined from their temporal relationships in our systematic studies (Wang, 1994; Wang et al., 1999; Tedford et al., in press), although remains from locality LC 202 possibly indicate a somewhat younger age. *Cynarctoides whistleri* sp. nov., *Desmocyon thomsoni* (Matthew, 1907), and *Metatomarctus canavus* (Simpson, 1932), on the other hand, are from the Hemingfordian part of the section.

**SYSTEMATIC PALEONTOLOGY**

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Canidae Fischer de Waldheim, 1817

Subfamily Hesperocyoninae Martin, 1989

*Mesocyon* Scott, 1890

?*Mesocyon* sp.

**REFERRED SPECIMEN.** LACM 148403, left dentary fragment with broken c–m1, Bee Canyon Landfill locality (= Lower Bowerman Landfill locality of Whistler and Lander [2003] but different from their “Bee Canyon” locality), LACM locality 6942, site RMW SW 95-1309, at the end of Sand Canyon Road, north of the City of Irvine, Orange County, California (see further comments in “Geology, Age, and Associated Fauna” section above).

**COMMENTS.** LACM 148403 is severely crushed and distorted, and most of the teeth suffered considerable damage. Thus, it is not possible to observe many of the morphological features with certainty. The present taxonomic determination is therefore more of an exercise of weighing possibilities rather than a positive identification.

Relatively robust premolars with well-developed posterior accessory cusps and short m1 on LACM 148403 make this specimen unlikely to be a member of the Caninae. It is more difficult, however, to determine whether it belongs to the Hesperocyoninae or Borophaginae. With the exception of two highly derived species of *Phlaocyon* (see Wang et al., 1999), the majority of the late Arikareean and Hemingfordian borophagines are smaller than LACM 148403. That leaves the Hesperocyoninae as a more likely candidate. Within the Hesperocyoninae, *Mesocyon* comes closest to matching the overall morphology of this specimen, and the presence of a metaconid on the m1 rules out *Enhydrocyon* Cope, 1879b, and *Paraenhydrocyon* Wang, 1994.

*Mesocyon* has previously been reported from Arikareean age deposits of Southern California. Stock (1933) described *Mesocyon baileyi* from the Kew Quarry in the Sespe Formation (early Arikareean), a species that was synonymized with *Mesocyon brachyops* by Wang (1994). Walsh and Deméré (1991) reported *Mesocyon* from the Otay Formation (early Arikareean), which was identified more precisely as *Mesocyon coryphaeus* by Wang (1994). The specimen from Orange County is larger and more robust than the Kew Quarry form, and it is more consistent with the size of *M. coryphaeus*.

Subfamily Borophaginae Simpson, 1945

Tribe Phlaocyonini Wang, Tedford, and Taylor, 1999

*Cynarctoides* McGrew, 1938

*Cynarctoides whistleri* new species

Figure 2; Table 1


Figure 2  *Cynarctoides whistleri* sp. nov., OCPC 21796, holotype: A, labial; B, lingual; C, stereophotos of occlusal views.
HOLOTYPE. OCPC 21796, right horizontal ramal fragment with c–m1, field number GC.96.81.52, collected by Gino Calvano of Paleo Environmental Associates on 4 March 1996.

TYPE LOCALITY. OCPC locality 2040, Sec. 23, T4S, R8W, Windy Ridge, Orange County, California. OCPC 2040 is in an interbedded terrestrial and marine, maroon, silty sandstone in the undifferentiated sediments of Sespe or Vaqueros formations in the upper part of the Eastern Transportation Corridor (ETC) Windy Ridge section (Whistler and Lander, 2003:fig. 11.3). The locality is from the ETC Upper Windy Ridge Local Fauna, which belongs to the Upper OC S/V Fauna (Whistler and Lander, 2003: table 11.1, fig. 11.5), early Hemingfordian.

REFERRED SPECIMEN. TMM-BEG 40067-180 (cast AMNH 99659), isolated left m1, from Hidalgo Bluff, Texas A&M Museum locality 47, 5.5 miles (~8.9 km) northwest of Washington on the north side of the Brazos River, Washington County, Texas (Hesse, 1943:166–167). This specimen belongs to the Garvin Gully Fauna in the lower Oakville Formation, and it is middle Hemingfordian.

DIAGNOSIS OF SPECIES. *Cynarctoides whistleri* is more derived than primitive *Cynarctoides* species, such as *Cynarctoides lemur* (Cope, 1879a), *Cynarctoides roii* (Macdonald, 1963), and *Cynarctoiide harlowi* (Loomis, 1932), in its transversely narrow premolars and high-crowned, cuspidate m1 talonid cusps. Compared with the slightly more derived species of *Cynarctoides luskensis* Wang, Tedford, and Taylor, 1999, and *C. gaunae*, it is also derived in its well-developed protostylid; tall-crowned m1 entoconid and hypoconid, which are of equal height; stronger crista obliqua; and presence of a narrow labial cingulum on m1 trigonid, all of which are characters that become more derived in *C. acridens* (Barbour and Cook, 1914) and *Cynarctoides emryi* Wang, Tedford, and Taylor, 1999. *Cynarctoides whistleri* differs from *C. acridens* and *C. emryi* in its primitive characters, such as m1 entoconid not exceeding hypoconid in height, protostylid and metastylid less well differentiated from the protoconid and metaconid, and less well developed crista obliqua. *Cynarctoides whistleri* has the following autapomorphies: short jaw; short and tall-crowned p2–3 without anterior and posterior accessory cusps, p4 with a very distinct posterior accessory cusp, m1 short and wide, and short m1 trigonid with an obliquely oriented paraconid blade.

ETYMOLOGY. The patronym honors David P. Whistler, curator emeritus of Vertebrate Paleontology at the Natural History Museum of Los Angeles County, for his careful documentation of Southern California vertebrate fossil records and dedicated service during his career in the museum.

DESCRIPTION. OCPC 21796 is a poorly preserved lower jaw from a young adult with fully erupted cheek teeth showing no wear. The horizontal ramus is fragmented into multiple pieces, and much of its ventral border, except a short segment below the p2, is missing. The anterior segment permits a sense of the depth of the dentary (4.5 mm). The horizontal ramus is slender, that is, dorsoventrally shallow and transversely thin, as is characteristic of *Cynarctoides*. The mental foramen is difficult to discern. The dentary posterior to the m1 is mostly missing, and only a partial alveolus for the anterior root of the m2 is present.

The lower canine is slender and recumbent. There is a lingual ridge on the anteromedial face of the tooth, and immediately posterior to it is a shallow groove. An indistinct ridge extends along much of the posterior side of the lower canine. The p1 is single-rooted. Its crown around the apex is preserved, but the basal part is damaged. The p2–4 are double-rooted and lack a cingulum on both lingual and labial sides. The p2 consists of a main cusp and a tiny posterior cingular cusp. The top part of the p2 main cusp is broken. The p3 is well preserved, and it is very high crowned. Besides its large main cusp, a tiny posterior accessory cusp is present, and there is a slight swelling on the anterior border on the p4. The p4 has both an anterior and a posterior cingular cusp, which are of similar sizes and larger than

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<th>C. gaunae</th>
<th>C. acridens</th>
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those on the p3. A prominent posterior accessory cusp projects dorsal half way along the posterior ridge of the p4. The accessory cusp is distinct, high crowned, and of the same height as the m1 paracodon. The p4 main cusp has a slightly procumbent orientation, although part of this might be the result of a slight anterior shift of the main cusps because of postmortem distortion. As a result, the main cusp is slightly procumbent.

The m1 is short, mainly because of its lingually bent paracodon, in contrast to a more longitudinally oriented paracodon in most species of Cynarctoides. The paracodon is approximately half as tall as the protoconid, and it is also significantly lower than the metacodon. The protoconid is the tallest cusp of the tooth. A prominent protostylid is developed on the base of the posterolabial face of the protoconid. Behind the protostylid is a short labial cingulum between the protoconid and hypoconid. The apex of the protostylid is isolated from the main body of the protoconid. The metacodon is also high crowned, and it falls between the protoconid and paracodon in height. At its posterior base is a tiny metastylid immediately in front of a notch between the metacodon and entoconid. The talonid is wide. Both the hypoconid and entoconid have piercing, high-crowned tips and surround a deep talonid basin in the middle. The crown height of the two talonid cusps is about equal. The high, piercing talonid cusps result in deep notches anterior to the cusps, that is, between the metacodon and entoconid and between the protoconid and hypoconid. A small, but distinct, crista obliqua is oriented diagonally and intersects the posterior face of the trigonid just labial to the protoconid–metacodon notch. A small ridge is present posterior to the hypoconid and entoconid along the posterior rim of the talonid.

**COMPARISONS AND DISCUSSION.** Seven species of Cynarctoides were recognized in a revision of the borophagine canids by Wang et al. (1999): *C. lemur, C. roii, C. barlowi, C. luskensis, C. gaunae, C. acridens, and C. emryi*. In recognizing the new species from Southern California, we follow the phylogenetic framework developed by Wang et al. (1999). Within that framework, *C. whistleri* is at a stage of evolution between *C. gaunae* and *C. acridens* in terms of crown heights of m1 hypoconid, entoconid, and protostylid but is much smaller than late Arikareean and early Hemingfordian species of Cynarctoides (Table 1). Furthermore, the lower carnassial is much shorter than those of other contemporaneous species because of a more lingually bent paracodon blade, and it is also transversely wider. This short paracodon blade seems to suggest a more basal position for the California species, in contrast to the more derived cusp morphology on the m1. Associated with the short m1 is a short dentary and short premolars, a character that is absent among species from the Great Plains. The absence of upper teeth, however, prevents us from further analysis of the phylogenetic position of *C. whistleri*. Nevertheless, this combination of primitive and derived dental morphology for *C. whistleri* might suggest a geographic isolation of a southern lineage of Cynarctoides.

In further support of the possibility of geographic differentiation, we have identified a single m1 of early Hemingfordian age from Texas as belonging to *C. whistleri*. An isolated left m1 (TMM-BEG 40067–180, cast AMNH 99659) from the Oakville Formation of Washington County, Texas, was tentatively referred to *C. acridens* by Wang et al. (1999), but with a length of 6.6 mm, this specimen is at the lower end of the size range of the hypodigm of *C. acridens* (Wang et al., 1999:appendix III, table 1). We previously referred this m1 to *C. acridens* because of the stage of development of its protostylid, but it is now more logical to refer it to *C. whistleri*, following the discovery of the Southern Californian form.

Species of Cynarctoides have a long geologic time span of approximately 15 million years from early Arikareean to early Barstovian and, with the exception of *C. lemur* from the John Day Formation of Oregon and *C. acridens* from the Barstow Formation of Southern California, they are generally not found in the western coastal states. Despite the long chronologic range for the genus Cynarctoides, it displays its maximum diversity only in the late Arikareean and early Hemingfordian. *Cynarctoides whistleri*, the first reported occurrence of the genus in Hemingfordian strata of California, offers an opportunity to study the transitional morphology within the Cynarctoides lineage and permits a study of regional differentiation in the southern United States.

Cynarctoides is a highly unusual canid that demonstrates one of the few developments of secondary herbivory by carnivores. The terminal species, *C. emryi*, developed modestly selenodont upper and lower molars, similar to those in primitive artiodactyls, that are unique among North American carnivores. A rare parallel is seen among the Miocene lophocyonine viverrids of Europe (Fejfar and Schmidt-Kittler, 1984, 1987; Koufos et al., 1994). The less derived species of Cynarctoides developed tendencies toward ever more piercing cusp morphology that parallel dental features of insectivores. Cynarctoides whistleri appears to be a transitional species between the primitive forms (such as *C. lemur, C. luskensis, C. gaunae*) and the more derived species (*C. acridens* and *C. emryi*). In a clade of hypocarnivorous canids, it is perhaps not surprising to find this additional diversity in a more coastal (and possibly wooded) habitat in Southern California.
Phlaocyon Matthew, 1899

Phlaocyon taylori Hayes, 2000
Figures 3 and 4; Table 2

HOLOTYPE. UF 163524, an isolated left m1, Brooksville 2 Local Fauna, Hernando County, Florida (Hayes, 2000).

REFERRED SPECIMENS. LACM 148401, complete left horizontal ramus with c–m3, Bee Canyon Landfill locality (= Bowerman Landfill locality of Whistler and Lander [2003] but different from their “Bee Canyon” locality), LACM locality 6942, site RMW TRM 043, at the end of Sand Canyon Road, north of the City of Irvine, Orange County, California; LC 9112, left maxillary fragment with P4 and posterior root of P3, FTC/Oso locality, LC locality 202 (LC fossil site number GC 9781-167), Orange County, California; and LC 9114, maxillary fragment with right P4–M1, FTC/Oso locality, LC locality 202 (see further comments in “Geology, Age, and Associated Fauna” section above). See Hayes (2000) for additional referred specimens from Florida, except UF 163741, which is presently excluded from the hypodigm.

EMENDED DIAGNOSIS OF SPECIES. Well-developed P4 anterior cingulum, large protocone on P4, lingual cingulum enlarged to form precursor of hypocone; large upper molars relative to P4, transversely short M1–2, accessory cuspule of metaconules in M1–2; horizontal ramus slender; protostylid variably present on m1–2.

DESCRIPTION. The palate fragments are too poorly preserved to determine much of their morphology. The P4 is represented by two specimens (LC 9112 and LC 9114). These two teeth are nearly identical in size and shape (Table 2). The P4 in LC 9112 is better preserved and suffers from less wear. The overall proportions of the P4 are short and broad, which is characteristic of all Phlaocyon. There is a broad labial cingulum throughout the length of the
Figure 4  Lower jaw and teeth of *Phlaocyon taylori* Hayes, 2000, from California and Florida: A–B, left jaw, LACM 148401: A, medial view; B, lateral view; C, occlusal view of left lower teeth, LACM 148401; D, left m3, UF 163716; E, right m2 (reversed), UF 163511; F, left m1, UF 163524, holotype; G, right p4 (reversed), UF 163720. Upper scale is for A and B, and lower scale is for C–G.
tooth (more so in LC 9112 than in LC 9114), although its lower boundary on the labial surfaces of the paracone and metastyle is not very distinct. The lingual cingulum is also well developed. The anterior part of the tooth is swollen to such an extent that it fills up the space posterior to the protocone. This swelling is too worn on both specimens to permit recognition of a hypocone, although a wear facet (created by occlusion with the lower carnassial blade) indicates the possible existence of such a cusp. The anterior cingulum at the base of the paracone is slightly elevated, suggesting a rudimentary parastyle. The P4 protocone is very large, conical, and anterior to the anterior border of the paracone. There is no cingulum surrounding the protocone.

The upper molars represented by LC 9114 are extremely worn. The M1 has a quadrate outline—anteroposteriorly long and transversely short—contrasting with the more transversely elongated outlines occurring in basal borophagines. A narrow labial cingulum and a much reduced parastyle are in contrast with those of the hesperocyonines. The paracone and metacone are nearly equal in size and positioned rather labially because of the narrow labial cingulum. Heavy wear in the lingual cusps prevents observation of the cusp patterns. The internal cingulum narrows anterolingual to the protocone. The M2 protocone is very large, conical, and anterior to the anterior border of the paracone. There is no cingulum surrounding the protocone.

The upper teeth are little worn, with only the tip of the lower canine showing signs of slight wear, and the other cheek teeth unworn. No incisor is preserved. The lower canine is recumbent, and it has an oval cross section throughout its length. There is no anterior or posterior ridge, and the enamel surface is free of wrinkles or ornamentation. There is no lingual cingulum, although a slight swelling is present in its place. The p1 is single-rooted and single-cusped. It is slightly procumbent with a much longer posterior ridge than the anterior ridge. There is no sign of an anterior or posterior cingular or accessory cusp. The p2 is double-rooted. Its main cusp is broken at the apex. As in the p1, the posterior ridge on the main cusp is considerably longer than the anterior ridge. In contrast to the p1, however, there is a slight swelling at the anterior base of the main cusp, although this swelling is not yet a

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The dentary is known from a nearly complete left horizontal ramus (LACM 148401), which is extensively fractured but otherwise suffers little distortion. The horizontal ramus is shallow, with a depth of 7.5 mm below the m1. It has a nearly uniform depth through much of its length and tapers slightly anterior to the p3. There are two mental foramina: one between p1 and p2 and another between p2 and p3. The coronoid process of the dentary is rather erect, with a straight anterior border and a rounded dorsal border. The masseteric fossa is well delineated anteriorly and ventrally. The mandibular condyle is positioned on a plane dorsal to the occlusal surface of lower cheek teeth. The angular process is broken. The mandibular symphysis is long, reaching as far posteriorly as the middle of the p2.

The lower teeth are little worn, with only the tip of the lower canine showing signs of slight wear, and the other cheek teeth unworn. No incisor is preserved. The lower canine is recumbent, and it has an oval cross section throughout its length. There is no anterior or posterior ridge, and the enamel surface is free of wrinkles or ornamentation. There is no lingual cingulum, although a slight swelling is present in its place. The p1 is single-rooted and single-cusped. It is slightly procumbent with a much longer posterior ridge than the anterior ridge. There is no sign of an anterior or posterior cingular or accessory cusp. The p2 is double-rooted. Its main cusp is broken at the apex. As in the p1, the posterior ridge on the main cusp is considerably longer than the anterior ridge. In contrast to the p1, however, there is a slight swelling at the anterior base of the main cusp, although this swelling is not yet a

Table 2  Dental measurements (mm) of Phlaocyon taylori Hayes, 2000, and P. achoros (Frailey, 1979) (those for P. achoros are from Wang et al. [1999]).

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<tr>
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<td>m1 length</td>
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<td>m1 Trigonid width</td>
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<tr>
<td>m1 Talonid width</td>
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<td>m2 length</td>
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</tr>
<tr>
<td>m2 width</td>
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</table>

The dentary is known from a nearly complete left horizontal ramus (LACM 148401), which is extensively fractured but otherwise suffers little distortion. The horizontal ramus is shallow, with a depth of 7.5 mm below the m1. It has a nearly uniform depth through much of its length and tapers slightly anterior to the p3. There are two mental foramina: one between p1 and p2 and another between p2 and p3. The coronoid process of the dentary is rather erect, with a straight anterior border and a rounded dorsal border. The masseteric fossa is well delineated anteriorly and ventrally. The mandibular condyle is positioned on a plane dorsal to the occlusal surface of lower cheek teeth. The angular process is broken. The mandibular symphysis is long, reaching as far posteriorly as the middle of the p2.

The lower teeth are little worn, with only the tip of the lower canine showing signs of slight wear, and the other cheek teeth unworn. No incisor is preserved. The lower canine is recumbent, and it has an oval cross section throughout its length. There is no anterior or posterior ridge, and the enamel surface is free of wrinkles or ornamentation. There is no lingual cingulum, although a slight swelling is present in its place. The p1 is single-rooted and single-cusped. It is slightly procumbent with a much longer posterior ridge than the anterior ridge. There is no sign of an anterior or posterior cingular or accessory cusp. The p2 is double-rooted. Its main cusp is broken at the apex. As in the p1, the posterior ridge on the main cusp is considerably longer than the anterior ridge. In contrast to the p1, however, there is a slight swelling at the anterior base of the main cusp, although this swelling is not yet a
An exceptionally small, re-
P. taylori & P. taylori lacks the narrow and elongated premolars
(such Phlaocyon C. lemur Science Series 41 Wang and Tedford: Canids of Southern California
m1, and it is ridgelike and oriented anteroposte-
small basin. The hypoconid is similar to that on
and a small entoconid; the two cusps enclose a
bicusp talonid is formed by a large hypoconid
protostylid. The talonid is basined, surrounded by
lingual cingulum on P4, a better developed
posterior talon (shelf) is present. Along the apical
portion of the posterior ridge there is a vague
notch in contrast to a distinct notch on the p4.
The p4 has a well-developed posterior accessory
cusp delineated by the aforementioned notch.
This accessory cusp is rather tall, exceeding half
the height of the main cusp, and it is positioned
labially off center in occlusal view. The accessory
cusp is also swollen somewhat more toward the
labial side. A tiny anterior cingular cusp is present
on p4. The posterior cingulum is well developed,
and it is elevated slightly at its posterior end to
indicate a tiny posterior cingular cusp. The
anterior and posterior cingula are not continuous
around the main body of the tooth.
The m1 is relatively short and wide. The
trigonid is short because of its lingually bent
shearing blade. The protoconid is the largest and
tallest cusp in the trigonid. The paraconid bends
sharply lingually from the protoconid blade, such
that the apex of the paraconid is set near the
lingual border of the trigonid. The metaconid is
set slightly posterior to the protoconid. It is
strongly developed and taller than the paraconid.
A small metastylid is present at the base of the
posterior ridge of the metaconid, but there is no
protostylid. The talonid is basined, surrounded by
a larger and lower hypoconid and a smaller and
taller entoconid. The hypoconid is ridgelike, and
it extends anteriorly to the posterior base of the
trigonid. The posterior ridge of the hypoconid
bends lingually and tapers toward the talonid
basin. The entoconid is significantly taller than
the hypoconid. Its anterior ridge is cut off by a
sharp notch between the entoconid and metasty-
lid. There is a tiny hypoconulid at the posterior
end of the talonid, which is not tall enough to
surround the talonid basin, that is, the basin is
open posteriorly. There is no lingual cingulum
surrounding either the trigonid or the talonid. An
indistinct labial cingulum is present around the
carnassial notch, and there is also a short
cingulum between the trigonid and talonid.
The m2 is relatively large. The paraconid is
absent and its position is indicated by a low shelf
anterior to the protoconid. The metaconid is
much larger and taller than the protoconid, but,
unlike the m1, it does not have a metastylid. The
apex of the metaconid is slightly posterior to that
of the protoconid. The protoconid is centrally
located, and posterolateral to it is a small
protostylid at the base of the protoconid. The
bicusp talonid is formed by a large hypoconid
and a small entoconid; the two cusps enclose a
small basin. The hypoconid is similar to that on
m1, and it is ridgelike and oriented anteroposte-
riorly. The entoconid is of the same height as the
hypoconid, and it is positioned on the poster-
olinguar corner of the tooth. As on the m1, there
is a notch between the metaconid and entoconid.
There is no lingual cingulum. A labial cingulum is
present at the anterolabial corner of the tooth.
The m3 is a small, circular tooth with very low
cusps. There are two indistinct cusps on both
lingual and labial borders of the tooth.
COMPARISONS. An exceptionally small, re-
duced M1 paraastyle, and basined talonid on the
m1 indicate that this specimen (LACM 148401)
does not belong to the subfamily Hesperocyonini-
nae (see Wang, 1994). Although its shallow
horizontal ramus might suggest relationships to
early members of the subfamily Caninae, such as
Leptocyon Matthew, 1918, the teeth show no
characteristics of that subfamily. Phlaocyon
taylori lacks the narrow and elongated premolars
and a long, longitudinally oriented, shearing
blade on the upper and lower carnassials—
derived characters that are typically present in
members of the Caninae (Tedford et al., 1995).
Within the subfamily Borophaginae, early
forms are dominated by the hypocarnivorous
tribe Phlaocyonini, which is defined by a single
derived character: a protostylid on the lower
molars (Wang et al., 1999). This feature is weakly
present in LACM 148401. Of the two genera
within the Phlaocyonini, basal Cynarctoides (such as C. lemur) further shares with the present taxon
a slender horizontal ramus. However, the Cali-
ifornia form resembles species within the genus
Phlaocyon, as indicated by a number of shared
derived characters: short and stout premolars,
reduced P4 relative to size of upper molars, large
and anteriorly located protocone of P4, enlarged
lingual cingulum of P4 that tends to form a
hypocone, quadrate (transversely short) upper
molars, and a wide m1 talonid.
Hayes (2000) recently described P. taylori on
the basis of 37 isolated teeth from the Brooksville
2 Local Fauna in central Florida and two referred
teeth (a canine and a p4) from the Cow House
Slough Local Fauna in southern Florida. The
California form falls within the proportions and
size range of P. taylori (Fig. 5), which is the
smallest known species of Phlaocyon. Although
the California material generally compares favor-
ably with the Florida counterparts, there are a
few minor differences. In general, the Florida
lototypic specimens tend to have a less expanded
lingual cingulum on P4, a better developed
protostylid (especially on the m1), and a more
distinct metastylid (entoconulid) on m1 (Figs. 3
and 4). These differences are likely the result of
intraspecific variation over a wide geographic
area and differences in stage of evolution between
samples of different ages (see further comments
below). The associated lower teeth of LACM
148401 also permit recognition of a misidentified
lower canine (UF 163741) in Hayes’ original hypodigm. This canine has numerous fine grooves along the shaft that are completely absent in LACM 148401. Other known Phlaocyon specimens also lack such fine grooves.

Besides the above-mentioned misidentification of an upper canine, the rest of the Florida hypodigm for *P. taylori* appears to be correctly assigned. Although isolated teeth represent all of the Brooksville 2 Local Fauna *Phlaocyon* material collected by screen washing, the small pockets of the fissure-fill deposits from which the collections came seem to indicate that the Florida *Phlaocyon* teeth probably represent a relatively uniform sample of limited geographic and chronologic distribution (Hayes, 2000). By comparison, the California material might come from somewhat different horizons, as shown in the slight morphological disparity between the upper and lower teeth. For example, compared with the Florida material, the upper teeth (LC 9112 and LC 9114) from California show a broader P4, usually a derived character in *Phlaocyon*, whereas the California lower teeth (LACM 148401) have a weaker development of the protostylids on lower molars, a more primitive feature. Such variation
Table 3  Data matrix (12 taxa and 26 characters) for cladistic analysis of species of Phlaocyon. Coding for P. taylori is based on composite materials from Florida and California and, for other taxa, follows Wang et al. (1999). Certain characters (e.g., size and proportions of premolars) are probably not fully independent within the Phlaocyon clade, but remain separately coded because they often vary independently within the Borophaginae as a whole. Character numbers (in parentheses) and polarities are as follows (see Wang et al. [1999] for detailed descriptions of individual characters): (1) rostrum length, 0 = unshortened, 1 = shortened; (2) frontal sinus, 0 = absent, 1 = present; (3) zygomatic scar, 0 = wide, 1 = narrow; (4) I3 size, 0 = small, 1 = enlarged; (5) canine crown lateral groove, 0 = absent, 1 = present; (6) premolar cusplets, 0 = well developed, 1 = reduced; (7) premolar high crowned, 0 = no, 1 = yes; (8) premolars shortened, 0 = no, 1 = yes; (9) premolar width, 0 = narrow; 1 = widened; (10) upper molar enlargement, 0 = no, 1 = yes; (11) P4 protocone, 0 = small, 1 = large; (12) P4 paraconule, 0 = absent, 1 = weakly developed; (13) P4 lingual cingulum, 0 = narrow, 1 = widened, 2 = formation of hypocone; (14) M1 shape, 0 = transversely wide, 1 = transversely narrow; (15) M1 metaconule, 0 = small, 1 = large, 2 = extra labial cuspule; (16) M1 internal cingulum, 0 = ridgelike, 1 = conical (to form a hypocone); (17) M1 paraconule, 0 = absent or weak, 1 = distinct; (18) M2 internal cingulum, 0 = ridgelike, 1 = cusplike; (19) M2 metaconule, 0 = isolated, 1 = connected to posterior cingulum; (20) P1, 0 = present, 1 = absent; (21) m1 protostylid, 0 = absent, 1 = small, 2 = large; (22) m1 talonid cusps, 0 = crestlike, 1 = conical, 2 = with transverse cristids; (23) m1 talonid, 0 = narrow, 1 = widened; (24) m2 enlargement, 0 = not enlarged, 1 = enlarged; (25) m2 reduction, 0 = not reduced, 1 = reduced; (26) m2 protostylid, 0 = absent, 1 = small, 2 = large.

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**Referred Specimen.** LC 7658, crushed cranial fragments with left and right bullae, erupting left P2, broken dP3, complete dP4, House Slough local faunas in the middle Arikareean. In a recent synthesis, Tedford et al. (2004) put the Brooksville 2 and Buda local faunas within their “Ar2” between 26 and 23 Ma. Being a small, hypocarnivorous carnivoran in the Arikareean, Phlaocyon is one of the earliest canids to occupy an ecological space similar to that of modern procyonids, as suggested long ago by Wortman and Matthew (1899), who pointed out the striking dental similarities between Phlaocyon and procyonids. As do living raccoons, the small Phlaocyon in the Arikareean of Florida might have preferred wooded areas in accord with its omnivorous diet. Presence of such forms in Southern California might suggest the existence of similar habitats at that time.

**Tribe Borophagini** (Simpson, 1945) Wang, Tedford, and Taylor, 1999

**Desmocyon** Wang, Tedford, and Taylor, 1999

**Desmocyon thomsoni** (Matthew, 1907)  
Figure 7A and 7B; Table 4

**Referred Specimen.** LC 7658, crushed cranial fragments with left and right bullae, erupting left P2, broken dP3, complete dP4,
M1, and erupting right P4–M1. Field No. GC 93.24.22, in SE Borrow Site of the Santiago Canyon Landfill locality, LC locality 166, Orange County, California. Undifferentiated Sespe or Vaqueros formations, Hemingfordian age. Collected by Gino Galvano on 8 January 1993 (see further comments in "Geology, Age, and Associated Fauna" section above).

**DESCRIPTION.** Much of the cranium is too crushed and fragmented to be described. Part of the skull roof is preserved and shows a smooth surface with a sagittal crest, probably as a result of immaturity as indicated by its deciduous teeth. The two bullae are preserved, but they are extensively distorted.

The dp3 preserves only the posterior portion of the shearing blade behind the deciduous carnassial notch. Its anterior and lingual roots indicate its anteriorly expanded paracone and lingually positioned protocone, as is typical of deciduous carnassials of canids. The dp4 is completely preserved and suffers moderate wear in its talon basin. A triangular outline for the tooth is typical of deciduous P4s of canids. The paracone and metacone are about equal in size, and they are more marginally located and more toward the anterior and posterior corners of the tooth, respectively, than is the case for the permanent M1. The parastyle is very reduced but a metastyle is well developed posterior to the metacone and being almost as long as the metacone. The protocone is also very marginally located toward the lingual border, which leaves a large, shallow talon basin that shows appreciable wear against the hypoconid of the dp4. A very indistinct protoconule and metaconule are present, which are also somewhat worn. There is no lingual cingulum surrounding the protocone, as is present on the adult dentition (M1).

The left P4 is presumably still unerupted in the palate dorsal to the dp3–4. The right P4 is in a similar stage of eruption, but the dp4 is mostly missing, permitting the P4 to be fully exposed. The P4 is un worn. The paracone reclines backward and has two prominent, sharp ridges that originate from the base of the tooth. A larger
ridge is on the anterior face of the paracone and ends near the apex of the paracone. A smaller ridge immediately lingual to the anterior ridge terminates about midway along the paracone; it is connected to the base of the protocone. The anterior ridge widens at the base to form a triangular facet facing anteriorly, as is typical for mesocarnivorous borophagines. This triangular facet is very weakly notched toward the ventral tip, indicating the formation of a small parastyle. The conical P4 protocone is retracted slightly toward the main body of the paracone; thus, it might appear to be slightly less salient than it originally was. A distinct lingual cingulum is present along the entire length of the lingual border of the tooth.

The left and right M1s are perfectly preserved. Although fully erupted, they have suffered no discernable wear. The sizes and heights of the metacone and paracone are almost identical, although the paracone has a more prominent lingual ridge near its base. The protocone is about the same size and height as the paracone, followed posteriorly by a slightly smaller metaconule. The lingual cingulum (hypocone) surrounds the protocone and metaconule, although the anterior segment tapers off along the anterior facet of the protocone. There are indistinct notches along the crest of the lingual cingulum.

Table 4   Dental measurements (mm) of *Desmocyon thomsoni* (Matthew, 1907) from Southern California, the holotype from South Dakota, and the means of specimens from South Dakota, Wyoming, Nebraska, Oregon, and New Mexico after Wang et al. (1999:appendix III).

<table>
<thead>
<tr>
<th></th>
<th>Southern California</th>
<th>South Dakota</th>
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<td>dP3 width</td>
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<td>M1 width</td>
<td>12.2</td>
<td>12.8</td>
<td>11.89</td>
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* Estimated.
Table 5  Dental measurements (mm) of *Metatomarctus caninus* (Simpson, 1932) from Southern California and the means of specimens from Florida, Delaware, Nebraska, Wyoming, and New Mexico after Wang et al. (1999:appendix III).

<table>
<thead>
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<th>Southern California</th>
<th>Eastern North America</th>
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<td>LC 7692</td>
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COMPARISONS. The dental morphology of LC 7658 is that of a typical mesocarnivorous borophagine, with a reduced parastyle, a well-developed metaconule, and a lingual cingulum that surrounds the entire protocone and metacone. The dimensions of the P4 in LC 7658 are similar to those of *Paratomarctus kelloggii* (Merriam, 1911), but the M1 lacks the corresponding enlargement in a hypocarnivorous form such as the latter. Although LC 7658 is also comparable in size to *Microtomonarctus conferta* (Matthew, 1918), its lack of a fully developed parastyle on the P4 is in sharp contrast to the presence of this structure in *M. conferta*. Furthermore, the M1s in *M. conferta* tend to be more quadrate than in the somewhat transversely elongated outline in LC 7658.

Within the paraphyletic genus *Desmocyon*, *Desmocyon matthewi* Wang, Tedford, and Taylor, 1999, also has similar dental dimensions to LC 7658. *Desmocyon matthewi* is mainly diagnosed on the basis of slightly more derived cranial morphology (domed forehead and connection of the premaxillary and frontal) and a transverse cistid between hypoconid and entoconid of the m1, characters that are not preserved on LC 7658. Our decision to assign this specimen to *D. thomsoni* is thus somewhat arbitrary, and it is mainly based on the slightly smaller size of the latter, which is more consistent with LC 7658.

This is the first report of this species in California. Neither species of *Desmocyon* has previously been recorded in California, although the smaller and more primitive *D. thomsoni* is more widespread and has a longer geologic range than *D. matthewi* (see Wang et al., 1999). *Desmocyon thomsoni* is present in the John Day Formation of Oregon, but it is represented by only a maxillary fragment with M1–2 (AMNH 7238).

Metatomarctus Wang, Tedford, and Taylor, 1999

Metatomarctus caninus (Simpson, 1932) Figure 7C; Table 5

REFERRED SPECIMEN. LC 7692, isolated left M1, field No. GC 93.24.121, collected by Gino Galvano on 13 May 1993, in SE Borrow Site of the Santiago Canyon Landfill locality, LC locality 166, Orange County, California. Undifferentiated sediments of Sespe or Vaqueros formations, Hemingfordian age. (see further comments in “Geology, Age, and Associated Fauna” section above).

DESCRIPTION. LC 7692 suffers from breakage across the middle, resulting in a small gap (missing enamel) near the posterior end of the break. The paracone in LC 7692 is slightly larger and taller than the metacone, and the protocone is slightly larger than the metacone. A labial cingulum is well developed along the entire length of the paracone–metacone. The lingual cingulum (hypocone) surrounds both the protocone and metacone. The cingulum has a transversely broad base and occupies a much larger area than the protocone and metacone combined. The cingulum is also taller than the protocone.

COMPARISONS. LC 7692 is clearly a borophagine canid because of its large metacone, reduced parastyle area, and a rather anteriorly located lingual cingulum (hypocone), characters that are in contrast to the much reduced metaconules, large parastyles, and posteriorly located lingual cingulum in hesperocyonines (Wang, 1994). Among medium-sized mesocarnivorous borophagines, LC 7692 compares best with *M. caninus* in size, overall proportions (transversely long), and a thickened lingual cingulum, although caution needs to be exercised when identifying such meager material. A larger size (by 15%), more transversely elongated proportion, and a broader lingual cingulum are features that easily distinguish LC 6792 from *D. thomsoni* from the same locality (LC loc. 166).

Subfamily Caninae

Fischer de Waldheim, 1817

Leptocyon Matthew, 1918

*Leptocyon vulpinus* (Matthew, 1907) Figure 8; Table 6

REFERRED SPECIMEN. LC 9113, maxillary fragment with left P4–M1, FTC/Oso locality, LC locality 202, 33°36′03″N, 117°36′52″W, Orange County, California (see further comments in “Geology, Age, and Associated Fauna” section above).

DESCRIPTION. The maxillary fragment preserves the floor of the orbit and the ventral border of the infraorbital canal. The P4 is slender and elongated. Only a small anterior cingulum is present. There is no labial cingulum, whereas the lingual cingulum is weakly developed and restricted to the posterior half of the tooth. A distinct protocone is located anterior to the anterior border of the paracone, such that the apex of the protocone is at the same level as the anterior border of the paracone. The protocone is conical without a surrounding cingulum. The
The paracone has a faint anterior ridge leading to the anterior cingulum.

The M1 is labiolingually narrow. The para-style area is reduced, such that the labial cingulum has a uniform width around both the paracone and metacone. The paracone is slightly larger than the metacone, and these two cusps are connected by a ridge. The protocone is crestlike. Wear on the preprotocrista makes the paraconule indistinct, whereas the metaconule is still clearly visible, which expands lingually from the postprotocrista. The internal cingulum is narrow and surrounds the protocone. The anterior segment is much thinner than the medial segment. The internal cingulum is also divided by a small notch at a level just posterior to the protocone.

The M2 is represented by the anterior labial and lingual alveoli, which indicate that the M2 is not enlarged.

COMPARISONS. Among early canids, LC 9113 is easily distinguishable from members of the Hesperocyoninae by its anteriorly located P4 protocone, reduced parastyle on the M1, narrow lingual cingulum of M1 that does not swell posterolingually, and a distinct metaconule. These characters indicate that LC 9113 belongs to the Borophaginae–Caninae clade. Morphological differences between basal borophagines and canines are subtle, and for lack of more diagnostic teeth, LC 9113 is here placed with the Caninae mainly on the basis of dental proportions: a transversely narrow and elongated P4 and transversely elongated M1.

Late Oligocene and middle Miocene basal Caninae are represented by a series of small fox-sized forms in the genus Leptocyon (Tedford et al., 1995, in press). Among early Leptocyon of Arikareean and Hemingfordian age, LC 9113 falls within the size range of *L. vulpinus* (Table 6). A noticeable difference is the anteroposteriorly short M1 in LC 9113, here tentatively interpreted as a geographic variation. Following Matthew’s (1907) original description of *Notocyon vulpinus* from the “Lower Rosebud” beds of South Dakota, the holotype had remained the only specimen of this species to include upper teeth, prior to the present description of LC 9113.

CONCLUSIONS

1. Six species of fossil dogs, representing three subfamilies of Canidae were collected from Southern California during paleontologic resource mitigation activities. These can be identified as *Mesocyon* sp., *Cynarctoides* whistleri sp. nov., *Phtacynon* taylori, Desmocyon thomsoni, Metatomarctus canavus, and *Leptocyon vulpinus* from the Arikareean through Hemingfordian parts of sediments referred to as the undifferentiated Sespe/Vaqueros formations.

2. We name the new species, *C. whistleri*, from California and Texas. Its combination of primitive and derived characters indicates that it is a transitional form, probably in isolation from the main theater of evolution for *Cynarctoides* in the northern Great Plains.

3. The specimen that we identify as *P. taylori* is the first record of this species outside of Florida, and the Southern California material substantially improves our knowledge of this small canid.

4. The coyote- to fox-sized canids Mesocyon, Desmocyon, Metatomarctus, and Leptocyon were previously known from the Great Plains, and their presence in California indicates wider distributions for these cursorial forms.
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LITERATURE CITED


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