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FOSSIL CANIDS FROM THE MEHRTEN FORMATION, LATE CENOZOIC OF NORTHERN CALIFORNIA

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ABSTRACT—The Hemphillian-age Mehrten Formation has yielded several fossil dogs (family Canidae). Initial study had identified all larger canids as *Borophagus secundus* (= *Osteoborus cyonoides*), a bone-crushing borophagine (a diverse subfamily of extinct canids), and all smaller canids as *Canis* cf. *C. davisi*, a canine (a subfamily including all living canids). Later analysis split *B. secundus* into two taxa and reassigned *Canis* cf. *C. davisi* to *Eucyon davisi*, yet omitted fragmentary remains of possible vulpines. Despite this wealth of Mehrten canid materials, a detailed systematic treatment is lacking. More recently, additional specimens have become available, further necessitating a systematic examination of the canids at this site. The present study finds four canid species: two borophagines (*Borophagus parvus* and *B. secundus*) and two canines (*E. davisi* and *Vulpes stenognathus*, newly identified). We support the division of ‘*B. secundus*’ into the smaller *B. parvus* and the larger, more hypercarnivorous *B. secundus* and find two morphotypes within *B. parvus*. A specimen from the Coyote Hill fauna, earliest in the Mehrten sequence, is reassigned to *B. secundus*, extending the temporal range of the species in California into the early Hemphillian. *Borophagus parvus* co-occurs with *B. secundus* only in the lower Modesto Reservoir Member; higher in the sequence, *B. parvus* co-occurs only with canines. Despite the apparent turnover in its co-inhabitants, *B. parvus* exhibits no size change. Given that the characteristics of *B. parvus* and *B. secundus* are intermediate among other *Borophagus*, the Mehrten canids may represent a rapid transition early in the evolution of the *Borophagus* lineage.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

The presence of canids in the Mio-Pliocene Mehrten Formation in the foothills of California’s Sierra Nevada was first recorded over 30 years ago, when Hugh Wagner completed an unpublished Ph.D. dissertation on the geochronology of the Mehrten area, including biostratigraphy and systematics of the extinct faunas (Wagner, 1981). He tentatively identified the Mehrten canids: two of the subfamily Borophaginae, *Osteoborus cyonoides* and *Osteoborus* near *O. cyonoides*, and one of the subfamily Caninae, *Canis* cf. *C. davisi*. Subsequently, Wang et al. (1999) and Tedford et al. (2009) included the Mehrten canids in phylogenetic analyses of Borophaginae and fossil Caninae. Wang et al. (1999) divided Wagner’s *Osteoborus cyonoides* into two species, *Borophagus parvus* and *Borophagus secundus*. Tedford et al. (2009) identified the third canid as *Eucyon davisi* based on a single specimen. Neither of the above synthetic works described or figured the Mehrten canids.

Also present in the Mehrten Formation, but omitted by Wagner’s (1981) dissertation and Tedford et al.’s (2009) monograph, were a

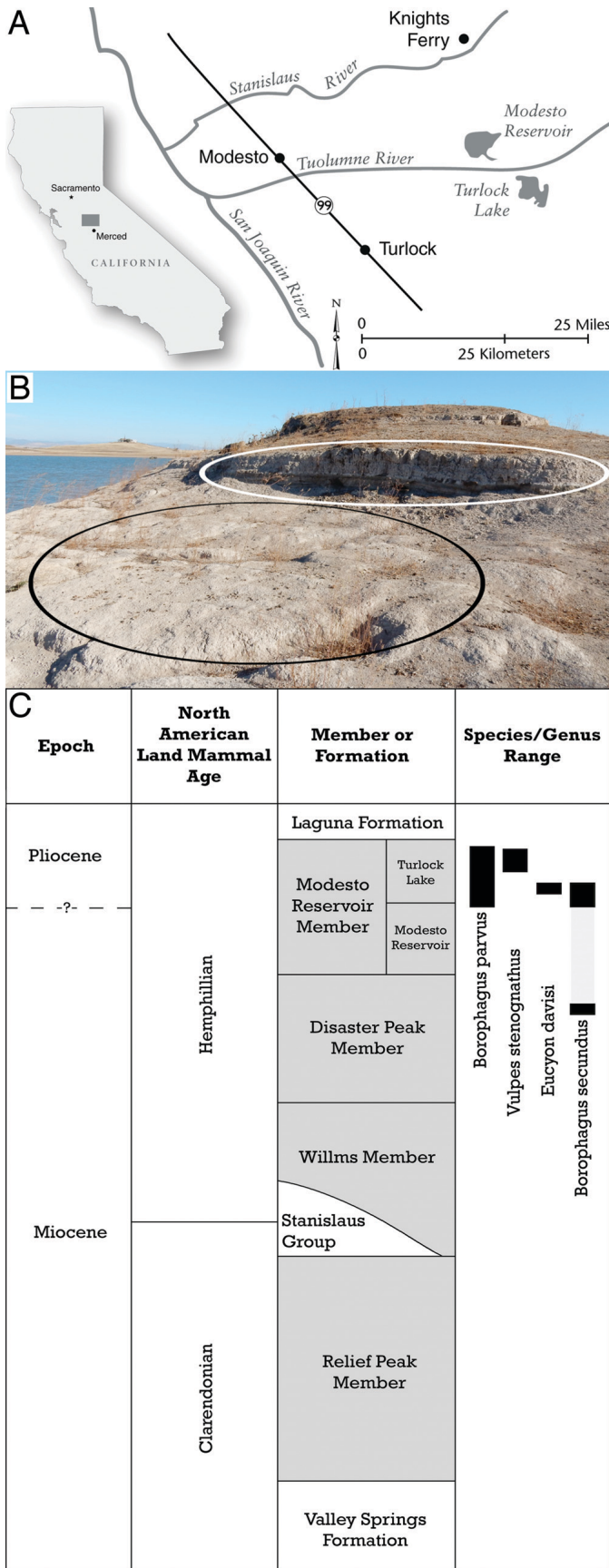
few fragmentary remains that appeared to be a fox, which we identify in the present study as *Vulpes stenognathus*. This newly assigned occurrence—as well as the recent donation of several specimens, including a nearly complete lower jaw of the vulpine, to the University of California Museum of Paleontology by Dennis Garber, collector of most of the Mehrten canid specimens—necessitates a comprehensive description of the canids from this Hemphillian site.

The Mehrten Formation is located east of Modesto, in the northern San Joaquin Valley of California (Fig. 1A). It consists of rhyolitic and andesitic conglomerates and tuffs representing volcanic mudflows and stream, lake, and floodplain deposits shed from the Sierra Nevada Mountains (Fig. 1B). Axelrod (1980) characterized the Turlock Lake flora as a combination of oak woodland-savanna and floodplain assemblages preserved in lacustrine deposits, with aquatic taxa well represented. Comparisons to modern vegetation from nearby regions indicate that the paleoclimate was cooler and wetter (mean annual temperature 15.5°C, mean annual precipitation 635 mm) than modern-day Turlock Lake (mean annual temperature 17.5°C, mean annual precipitation 335 mm). Pleistocene uplift of the Coast Ranges and subsequent rain-shadow effects were suggested to have caused the shift toward a more continental climate (Axelrod, 1980).

Ungulates—equids, rhinocerotids, tayassuids, camelids, cervids, and antilocaprids—are the most abundant fossils from the formation (Wagner, 1981). Also present are giant tusk

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tooth salmon (Sankey et al., 2015) and giant tortoises (Biewer et al., 2016). Carnivorans—felids, ursids, procyonids, mustelids, and canids—are less common. The most abundantly preserved carnivorans are canids, which predominantly come from high in the uppermost unit of the Mehrten Formation, the Modesto Reservoir Member, which is exposed at several Modesto Reservoir and Turlock Lake localities (Fig. 1C). No fossils are documented from the lower levels of this member.

Much of the canid material from the Mehrten Formation is well preserved and abundant, permitting analyses to determine the relationship of the Mehrten canid fauna to other North American fossil canids. Canids arose in North America 40 million years ago and consist of three subfamilies: Hesperocyoninae, the most ancestral radiation; Borophaginae, commonly known as ‘bone-cracking dogs’; and Caninae, the only extant radiation. Hesperocyoninae became extinct in the Barstovian (15 Ma), and only Borophaginae and Caninae are represented in the Hemphillian-age Mehrten Formation. The two species of *Borophagus* in the Mehrten fauna offer insight into the rise of hypercarnivory in this terminal borophagine clade.

Here we present a systematic examination of the Mehrten canids, including previously mentioned specimens as well as recently collected material. In addition, we explore the possibility of sexual dimorphism among the Mehrten borophagines. Lastly, we synthesize available morphometric information regarding other species of *Borophagus* to better understand wider evolutionary trends in the genus during the Mio-Pliocene.

Institutional Abbreviations—LACM, Los Angeles County Museum, Los Angeles, California, U.S.A.; UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.

Anatomical Abbreviations—*l*, length; *m1*, lower first molar; *m1tr*, trigonid of *m1*; *P1–P4*, upper first premolar to fourth premolar, respectively; *p2–p4*, lower second premolar to fourth premolar, respectively; *w*, width.

MATERIAL AND METHODS

All Mehrten canid fossils examined in this study are located at the LACM and the UCMP. Mehrten fossils were examined first hand; measurements of canids from other localities were taken from the literature. All measurements, except those from the literature, were made using Mitutoyo calipers to the nearest 0.01 mm. All information on the stratigraphic levels of each site is from a series of correlated stratigraphic columns in Wagner (1981).

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821

FIGURE 1. **A**, site map of Modesto Reservoir and Turlock Lake. Modesto Reservoir is approximately 32 km east of Modesto, California, and Turlock Lake is about 40 km northeast of Turlock, California. **B**, photo of LACM locality 3917, Cement Goose Pit Island, an exposed unit in the Modesto Reservoir Member. Fossil plant sites (area circled white; Axelrod, 1980) are important reference points to vertebrate sites (area circled black). **C**, stratigraphy of the Mehrten Formation and adjacent formations. Shading indicates members of the Mehrten. Vertical black bars indicate stratigraphic ranges of canids; the gray bar for *B. secundus* signifies a discontinuity in this species’s range through the lower levels of the Modesto Reservoir Member. Modified from Wagner (1981).

Suborder CANIFORMIA Kretzoi, 1943

Infraorder CYNOIDES Flower, 1869

Family CANIDAE Fisher von Waldheim, 1817

Subfamily BOROPHAGINAE Simpson, 1945

Subtribe BOROPHAGINA Wang, Tedford, Taylor, 1999

Genus *BOROPHAGUS* Cope, 1892

BOROPHAGUS PARVUS (Wang, Tedford, and Taylor, 1999) (Figs. 2, 1S–9S)

?*Osteoborus* (Stirton and Vander Hoof, 1933): Stirton, 1939:372, fig. 38.

Osteoborus cyonoides (Martin, 1928): Wagner, 1981:193, figs. 29, 30A.

Stratigraphic Range—Currently known from deposits of late Hemphillian age. *Borophagus parvus* from the Mehrten is limited to its uppermost member, the Modesto Reservoir Member, which is dated to roughly 5 Ma based on correlation to the

Pinole Local Fauna of northern California (Wagner, 1981). The member includes units exposed at Turlock Lake and Modesto Reservoir. *Borophagus parvus* fossils at Turlock Lake are found primarily high in the member but also toward the middle. Fossils are located throughout the lake, with no obvious clustering. At Modesto Reservoir, which stratigraphically underlies Turlock Lake, *B. parvus* is found from only one site in the reservoir's upper reaches, in the middle of the Modesto Reservoir Member.

Geographic Range—Arizona and California.

Referred Material—LACM locality 3908 (UCMP locality V81248); LACM 61650, right partial ramus with p3 alveolus–m3; UCMP 235512, left ramus fragment with p3–m2 broken; LACM 61651, right proximal radius. LACM locality 3909 (UCMP locality V5405): LACM 61690, left ramus with m1–m3; LACM 61691, right ramus with p4–broken–m2 and m3 alveolus; LACM 61692, left ramus with p2–alveolus–m2 and m3 alveolus; LACM 61693, right ramus with p2–alveolus–m1 and m2–m3 alveoli; LACM 61694, right maxillary fragment with C and P2–P3–broken; UCMP 235513, right ramus fragment with p4–broken–m1; UCMP 235514, left dentary with c

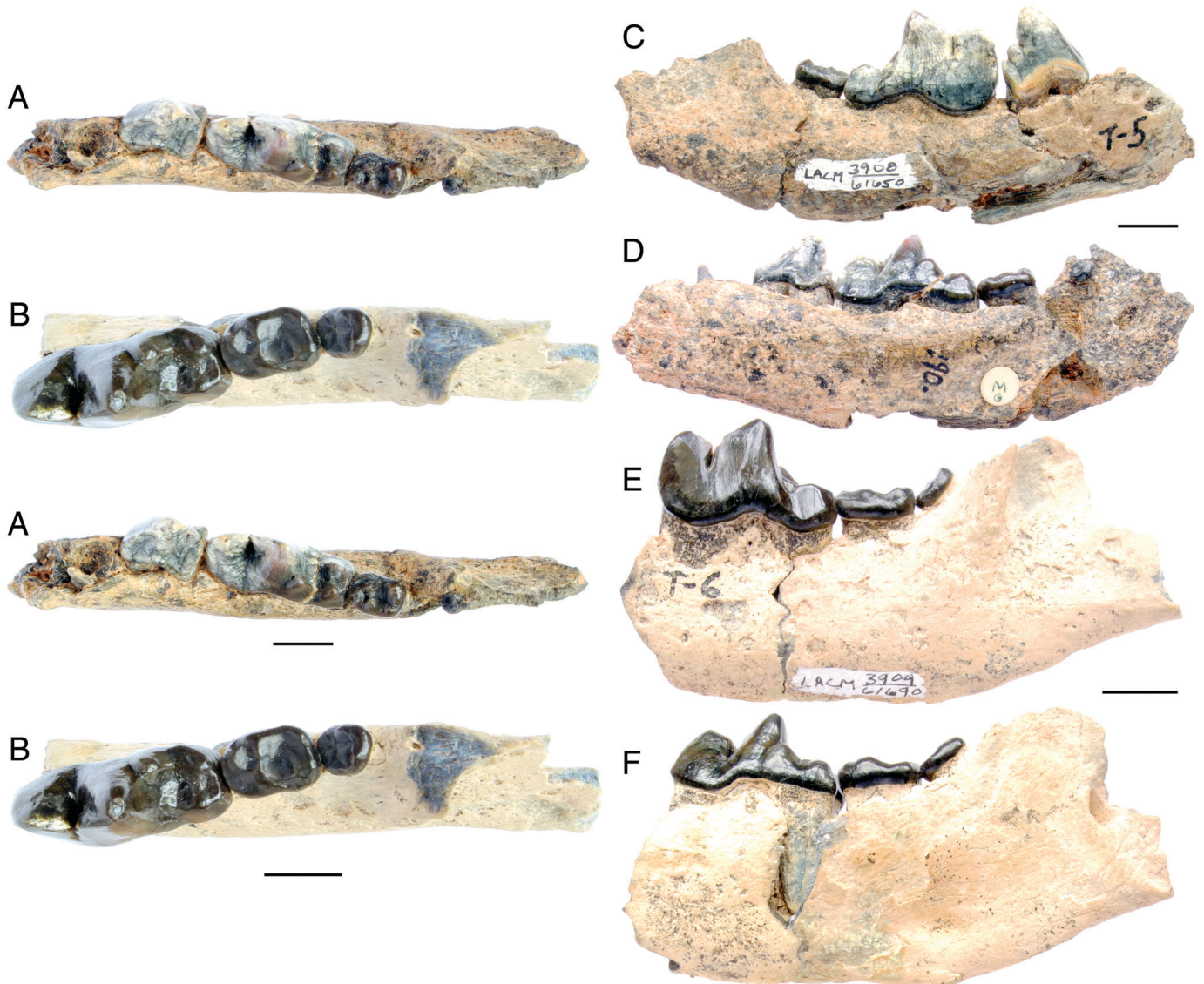


FIGURE 2. LACM 61650 and 61690, right and left dentaries of *Borophagus parvus*. Stereoscopic pairs of occlusal views of **A**, right and **B**, left dentaries; **C**, lateral and **D**, medial views of right dentary; **E**, lateral and **F**, medial views of left dentary. Scale bars equal 10 mm.

alveolus, p2, p3 alveolus, p4–m2, and m3 alveolus. LACM locality 3917 (UCMP locality V6878): LACM 62346, left dentary fragment with c, p2, p3 alveolus, p4 broken, and posterior m1–m3 alveoli; UCMP 235508, right dentary with i1–i3 alveoli, c, p2 alveolus, p3–m1; UCMP 235509, partial left m1, one isolated right c, one isolated right I3, ?associated. LACM locality 3924 (UCMP locality V71137): UCMP 235510, right ramus fragment with p4–m2; LACM 62504, left proximal radius. LACM locality 3925 (UCMP locality V68135): left dentary, ascending ramus fragment. LACM locality 3926: LACM 62519, right ramus with c1, p2–p3 alveoli, and p4–m2; UCMP 44670, left ramus with c1 broken, p2-alveolus–m2, and m3 alveolus; UCMP 65196, right dentary with c, p4–m2. LACM locality 3942: LACM 62696, left ramus with p4–m2; LACM 62697, left ramus with m1; LACM 62698, right ramus with p4; LACM 62701, right M1; LACM 62702, isolated M2. LACM locality 4670: LACM 121534, maxilla fragment with M1. UCMP locality V68134 (LACM locality 3937): UCMP 235515, isolated P2 or P3. UCMP locality V80040: UCMP 124658, maxillary with P4–M2. LACM locality 3950: LACM 62856, proximal left ulna.

Description and Comparison—Most remains of Mehrten *Borophagus parvus* are of teeth and partial jaws. No lower incisors are preserved. Specimens of both right and left lower canines are preserved, bearing an anterolingual and a posterolingual ridge. A small (~2- to 3-mm) diastema lies between c and p2 (p1 is absent in all Mehrten specimens), but no diastema is present behind p2. The p2 is small and round, with a weak lingual cingulum. The p3 is larger, more elongate, and slightly inflated posteriorly but is otherwise very similar in morphology to p2. The p2–p3 are slender and not bulbous, having no accessory cusps but only a posterior cingular cusp produced by an elevated posterior cingulum. The p4 is enlarged relative to p2 and p3, as in other *Borophagus* species. Accessory cusps of the p4 are unequal in size, with the posterior cusp larger; the p4 posterior cingulum is prominent. The cusps on all three lower premolars are aligned along the long axis of each tooth, although in p4 the anterior and posterior accessory cusps are slightly deflected lingually. The m1 has a long shearing trigonid and a short talonid. The trigonid consists almost entirely of paraconid and protoconid; the metaconid is reduced to a posterolingual bump on the trigonid. The talonid is marginally narrower than the trigonid, and the hypoconid and entoconid are equally dominant. A subtle transverse ridge connects the hypoconid and the entoconid, enclosing a small shallow basin in the anterior talonid and partitioning a small, roughly half-circular platform in the posterior talonid. As in the m1, the m2 trigonid is marginally wider than the talonid. The m2 protoconid is smaller than the paraconid and metaconid compared to the relative sizes of the same cusps on m1, whereas the m2 paraconid and metaconid are of equal size to each other as they are on m1. The m2 talonid has a large hypoconid and a low entoconid crest. The m3 is oval, with no distinct cusps and only a low ridge separating the trigonid from the talonid. The ventral outline of the posterior ramus ascends gradually toward the condyloid process.

Borophagus parvus is a small species of *Borophagus*, on average 18% smaller than *B. littoralis* and 20% smaller than *B. secundus* but 14% larger than *B. orc* (body size estimated from m1 length; Van Valkenburgh, 1990). The p1 is absent in California (Mehrten and Pinole Local Fauna) specimens, unlike in most Arizona specimens. The p2 and p3 are more unequal in size than in more derived *Borophagus*, except for *B. secundus* (mean ratio of p2 length to p3 length: *parvus* = 0.85; *secundus* = 0.82; *hilli* = 0.91, *diversidens* = 0.91). Relative to other premolars, p4 is larger than in less derived *Borophagus*. The m1 trigonid is wider relative to m1 length than in *B. pugnator*, about the same proportions as in *B. littoralis*, and narrower than in more derived species of *Borophagus*.

The m1 retains a small metaconid, and the talonid is wider relative to m1 length than in all other *Borophagus*. The talonid is well defined, with equally sized hypoconid and entoconid, unlike in later *Borophagus* that move toward trenchant talonids. The m2 is shorter than m1 and retains a well-developed metaconid.

A morphological cline is present among Mehrten *B. parvus*. Individuals on the more robust end have heavy dental wear and broad and deep jaws ($n = 5$; average breadth between m1 and m2 = 12.68 ± 0.59 mm; average depth between m1 and m2 = 27.17 ± 0.64 mm), whereas more gracile individuals have slight dental wear and slender and shallow jaws ($n = 7$; average breadth between m1 and m2 = 11.32 ± 0.74 mm; average depth between m1 and m2 = 23.7 ± 1.19 mm). In occlusal view, the tooth row is more convex among the more robust individuals, with the apex at the laterally offset p4, which is slightly imbricated with the m1. In contrast, more gracile individuals have a tooth row that is straighter in occlusal view. The bone in more gracile individuals also tends to wear away to a much lesser degree along the labial side of the tooth roots than in more robust individuals.

BOROPHAGUS SECUNDUS (Matthew and Cook, 1909) (Figs. 3, 10S)

- Aelurodon saevus secundus* Matthew and Cook, 1909:372, fig. 3. Matthew, 1918:185.
Hyaenognathus direptor Matthew, 1924:100, fig. 20. Vander Hoof, 1931:18. Stirton and Vander Hoof, 1933:177.
Hyaenognathus cyonoides Martin, 1928:235, figs. 1–3.
Borophagus cyonoides (Martin): Matthew and Stirton, 1930:173, pls. 21–33; Vander Hoof, 1931:19; Reed and Longnecker, 1932:66.
Borophagus secundus (Matthew and Cook): Vander Hoof, 1931:18; Wang et al., 1999.
Osteoborus cyonoides (Martin): Stirton and Vander Hoof, 1933:177; Savage, 1941:694, pl. 1, fig. 10; McGrew, 1944:75, fig. 25; Dalquest, 1969:5; Dalquest, 1983:20; Richey, 1979:107; Harrison, 1983:15, figs. 8, 9; Webb and Perrigo, 1984:241; Munthe, 1998:137; Miller and Carranza-Castañeda, 1998:546.
Osteoborus secundus (Matthew and Cook): Stirton and Vander Hoof, 1933:178; Skinner et al., 1977:358; Vander Hoof and Gregory, 1940:158; Richey, 1979:114; Munthe, 1998:137.
Osteoborus cf. *cyonoides* (Martin): Hesse, 1936:59; Webb and Perrigo, 1984:247, fig. 10.
Amphicyon sp. Olson and McGrew, 1941:1236, pl. 4, figs. E, F.
Osteoborus sp. Macdonald, 1959:877.
Borophagus sp. Cook and Macdonald, 1962:563.
Osteoborus direptor (Matthew): Richey, 1979:107; Munthe, 1998:137.
Osteoborus near *O. cyonoides* (Martin): Wagner, 1981:201, fig. 30.

Stratigraphic Range—Currently known from deposits of early to late Hemphillian age. *Borophagus secundus* in the Mehrten is known from only three sites: at Turlock Lake, Modesto Reservoir, and Coyote Hill. The Coyote Hill locality is much lower in the Mehrten stratigraphy than any of the other canid localities discussed here and is part of the older Disaster Peak Member. *Borophagus secundus* co-occurs with *B. parvus* at Modesto Reservoir, in the middle of the section, and is at the same stratigraphic level as *B. parvus* at Turlock Lake. These are the only two stratigraphic levels where the two species co-occur.

Geographic Range—Kansas, Oklahoma, Texas, New Mexico, California, Mexico, Honduras, and El Salvador.

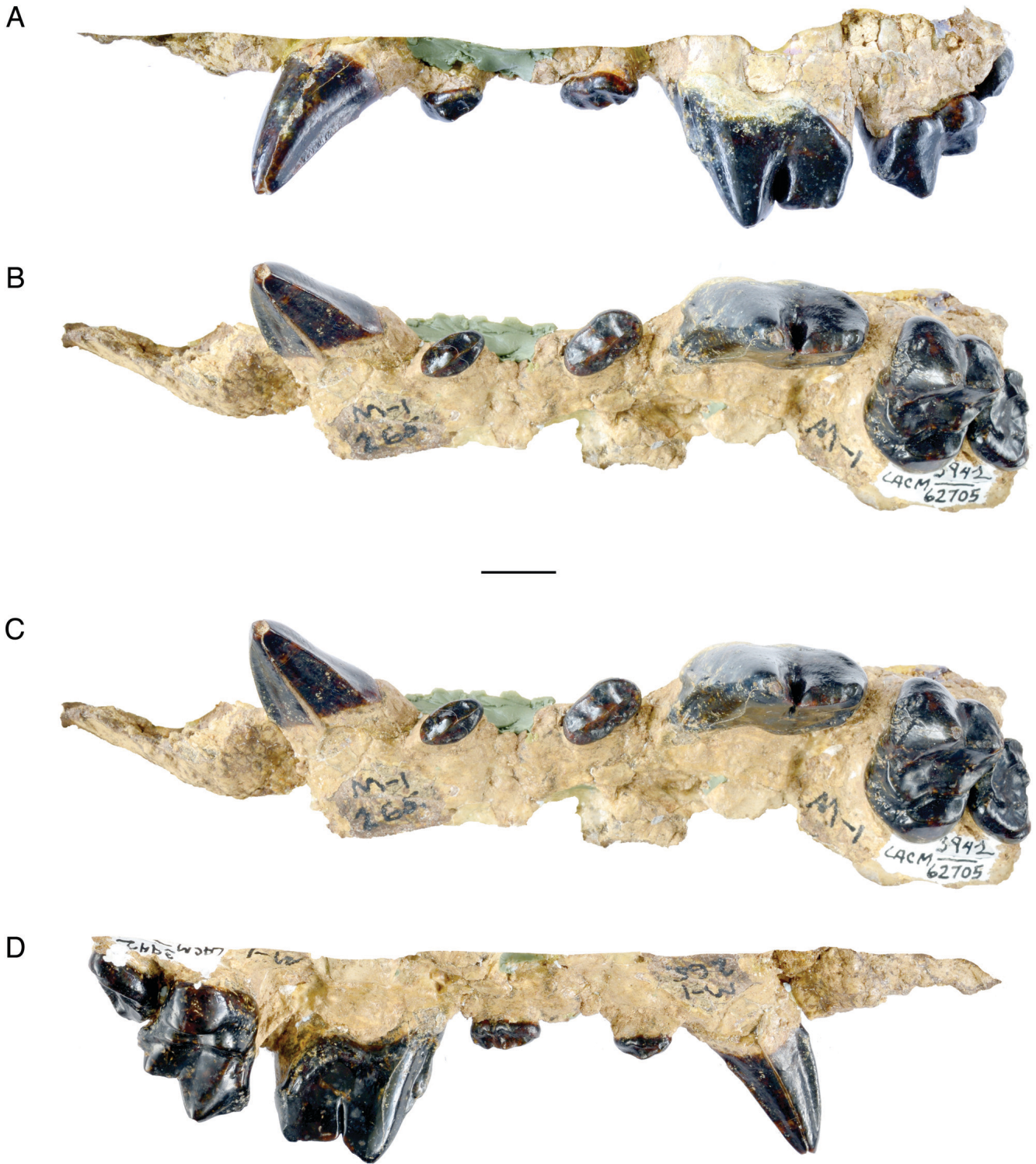


FIGURE 3. LACM 62705, left maxillary fragment of *Borophagus secundus*. **A**, lateral view of left maxilla; **B**, **C**, stereoscopic pair of occlusal view of left maxilla; **D**, medial view of left maxilla. Scale bar equals 10 mm.

Referred Material—LACM locality 3914: LACM 61931, maxilla fragment with M1–M2. LACM locality 3942: LACM 62705, left partial premaxilla–maxilla with C1 and P1, P3–M2. UCMP locality V65711: UCMP 235516, isolated I3. UCMP locality V72005: UCMP 97982, dentary fragment with p4.

Description and Comparison—*Borophagus secundus* is known from the Mehrten Formation mainly by remains of the upper jaw. An isolated I3 is present, pointed (not spatulate) in shape and with a relatively straight (not procumbent) root. The two accessory cusps on the I3 form posterolateral

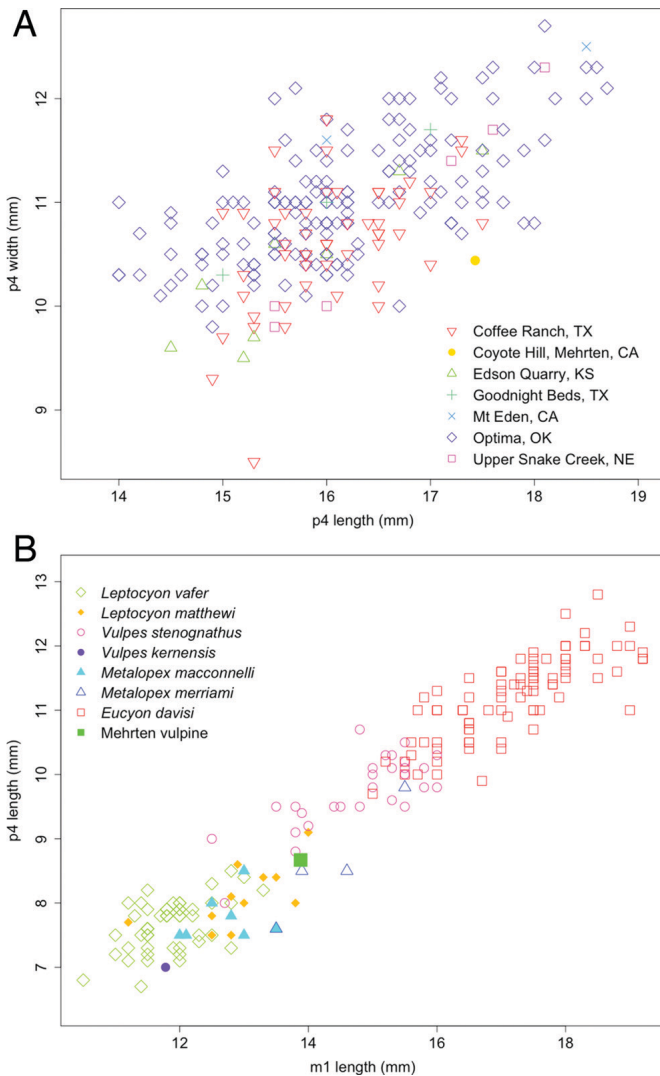


FIGURE 4. Bivariate plots of dental measurements. **A**, p4 width against p4 length for populations of *Borophagus secundus*. UCMP 97982, the Coyote Hill p4, represented by a yellow circle, is narrow given its length, but both its length and width fall within the range of all other *B. secundus* p4 length and width. **B**, p4 length against m1 length for species of small-bodied fossil canines. UCMP 235505, the Mehrten vulpine, represented by a green square, is in the lower size range of *Vulpes stenognathus*.

ridges along the base of the tooth. One upper canine is present, with a distinct ridge marking both the anterior and posterior face of the tooth. The cheek teeth are lightly worn, and cusp patterns are well preserved. The cheek teeth are tightly packed. There is no diastema in front of or behind the P1, and both P1 and P3 are imbricated, with anterior ends slanting mid-sagittally. P1's widest point occurs at its main cusp, located slightly anteriorly. P1's single anterior and posterior accessory cusps are arranged on the tooth's central ridge. P2 is not preserved. The P3 also has two accessory cusps, one anterior and one posterior to the main cusp. The posterior accessory cusp is separated from the main cusp by a small notch and is distinct from the posterior cingulum; the cingulum makes the posterior of the tooth its widest point. The P4 is a very large and robust tooth with a wide shearing blade. Its protocone is extremely reduced, forming only a small anteromedial corner of the tooth. A large parastyle is present on the P4, connected to the protocone by a ridge, as

is typical of advanced Borophagina (Baskin, 1980). Of the labial cusps on the P4, the parastyle is the lowest and the paracone is the tallest; the paracone shows slight wear at the tip. A cingulum extends along the base of the P4, from the posterior edge of the tooth along the lingual side, ending at about the level of the carnassial notch. The M1 is enlarged to a similar degree as the P4; however, the M1 protocone and hypocone are reduced to small crests, and a labial cingulum is not prominent. The M2 is present and quite reduced in size compared to the M1, with most cusps reduced to ridges. A ridge connects the paracone and metacone, and another one connects the protocone and hypocone.

Borophagus secundus is larger than *B. parvus* and about the same size as *B. pugnator* but smaller than more derived species of *Borophagus*. The paracone is significantly taller than the metastyle on P4 and taller than the metacone on M1. Cusps on upper non-carnassial premolars are aligned along the long axis of each tooth; accessory cusps are not deflected laterally. Occlusal outlines of upper non-carnassial premolars are oval and narrow. The difference in size between P4 and M1 in *B. secundus*, as measured by length and width, is smaller than in *B. orc* but larger than in *B. pugnator*.

The single p4 from the Coyote Hill fauna (UCMP 97982), formerly classified as *Osteoborus* near *O. cyonoides* (Wagner, 1981), is here assigned to *B. secundus*. Morphologically, it resembles both *B. parvus* and *B. secundus* in the inflation of the posterior cingulum into roughly squared-off posterolabial and posterolingual corners (Fig. 10S). The Coyote Hill p4 fits well within the range of p4 length of other California (Mt. Eden fauna) *B. secundus*, although it is narrower (Fig. 4A). *Borophagus secundus* at Mt. Eden is, however, more robust than the bulk of *B. secundus* elsewhere: for instance at Coffee Ranch, Texas. In comparison to Coffee Ranch *B. secundus*, the Coyote Hill p4 is still narrow given its length, but both its length and width fall within the range of Coffee Ranch *B. secundus* p4 length and width (Fig. 4A). The Coyote Hill p4 extends the temporal range of *B. secundus* in California into the Early Hemphillian.

Subfamily CANINAE Gill, 1872

Tribe VULPINI Hemprich and Ehrenberg, 1832

Genus *VULPES* Frisch, 1775

VULPES STENOGNATHUS (Savage, 1941)

(Figs. 5, 11S)

Leptocyon cf. *vafer* (Leidy): Cook and Macdonald, 1962:562.

Stratigraphic Range—Currently known from deposits of late Clarendonian to late Hemphillian age. *Vulpes* fossils in the Mehrten have been found from only two sites at Turlock Lake, high in the section. They co-occur with *B. parvus* at one site; the other site is at a stratigraphic level slightly lower than the first.

Geographic Range—Arizona, California, Colorado, Florida, Nebraska, Nevada, New Mexico, Oklahoma, Oregon, Texas, and northern Mexico.

Referred Material—LACM locality 3917 (UCMP locality V6878): LACM 62331, left edentulous maxillary fragment; LACM 62332, right P2–P3; LACM 62333, canine; LACM 62334, canine; LACM 62335, p3; LACM 62336, right edentulous dentary fragment with m1–m3 alveoli; LACM 62337, edentulous dentary fragment with m1 alveolus; LACM 62338, left edentulous dentary fragment with p4–m3 alveoli; UCMP 235505, left dentary with c, p1 alveolus, p2 broken, p3–m2, and m3 alveolus. LACM locality 3922 (UCMP locality V5836): UCMP 235504, left maxillary fragment with M1–M2.

Description and Comparison—Most vulpine specimens from the Mehrten Formation are edentulous and very fragmentary. However, one well-preserved left dentary (UCMP 235505;

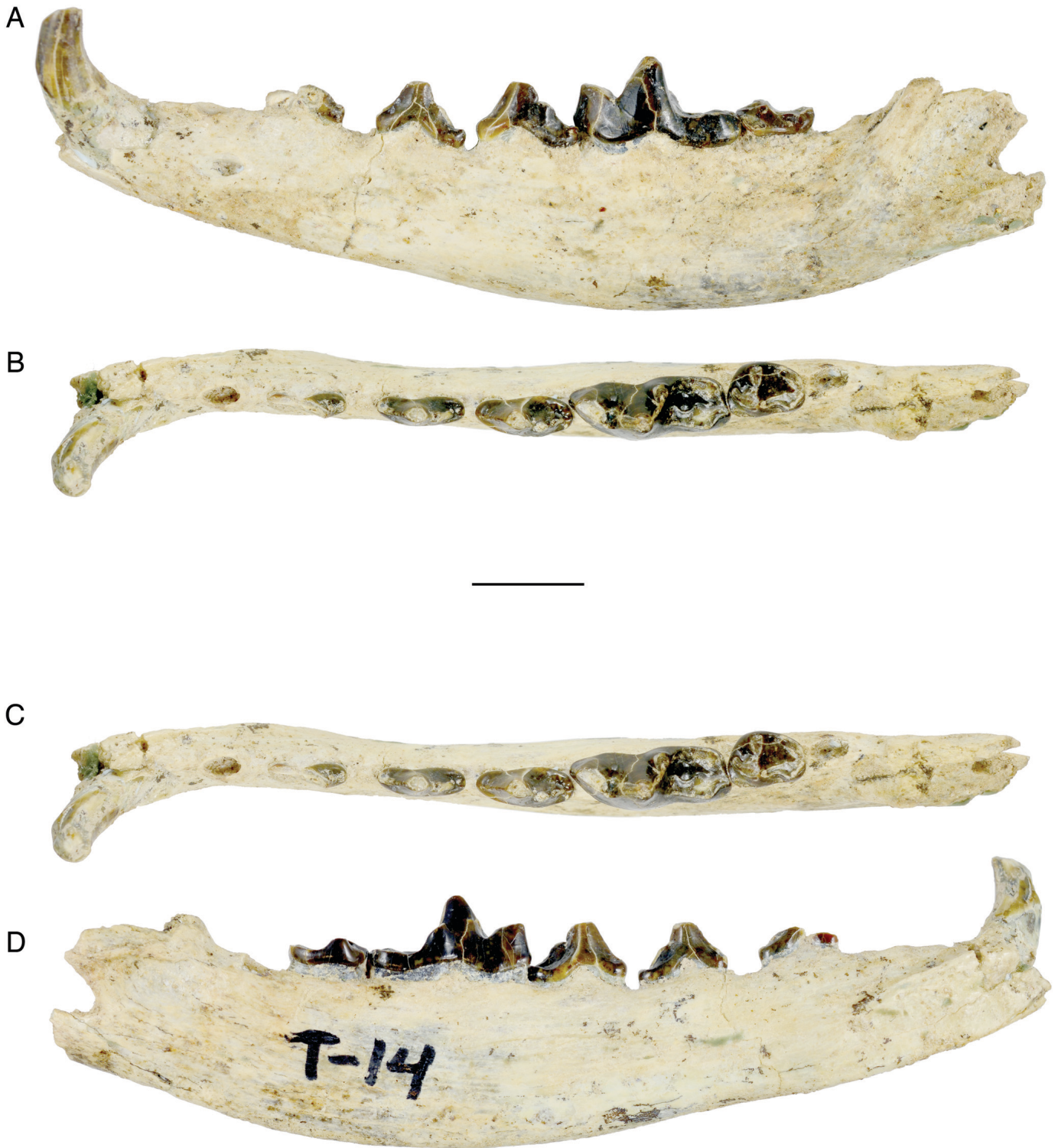


FIGURE 5. UCMP 235505, left dentary of *Vulpes stenognathus*. **A**, lateral view of left dentary; **B**, **C**, stereoscopic pair of occlusal view of left dentary; **D**, medial view of left dentary. Scale bar equals 10 mm.

Fig. 5) retains most of the lower teeth. The mandibular symphysis is elongated, extending posteroventrally down the length of the ramus body from the rostral border of the canine to the level of the p2. The dentary has a diastema (~3.1 mm) between c and p1; a ridge divides the diastema into a medial and a lateral portion. One mental foramen is

present, positioned halfway down the depth of the ramus between p1 and p2. The p1 is missing, represented only by the alveolus. The p2 is broken but apparently elongate and with no basal cingulum. The p3 is larger than p2, with a slight posterolingual widening, no anterior accessory cusp, and a distinct posterior accessory cusp. The p4 is larger than p3,

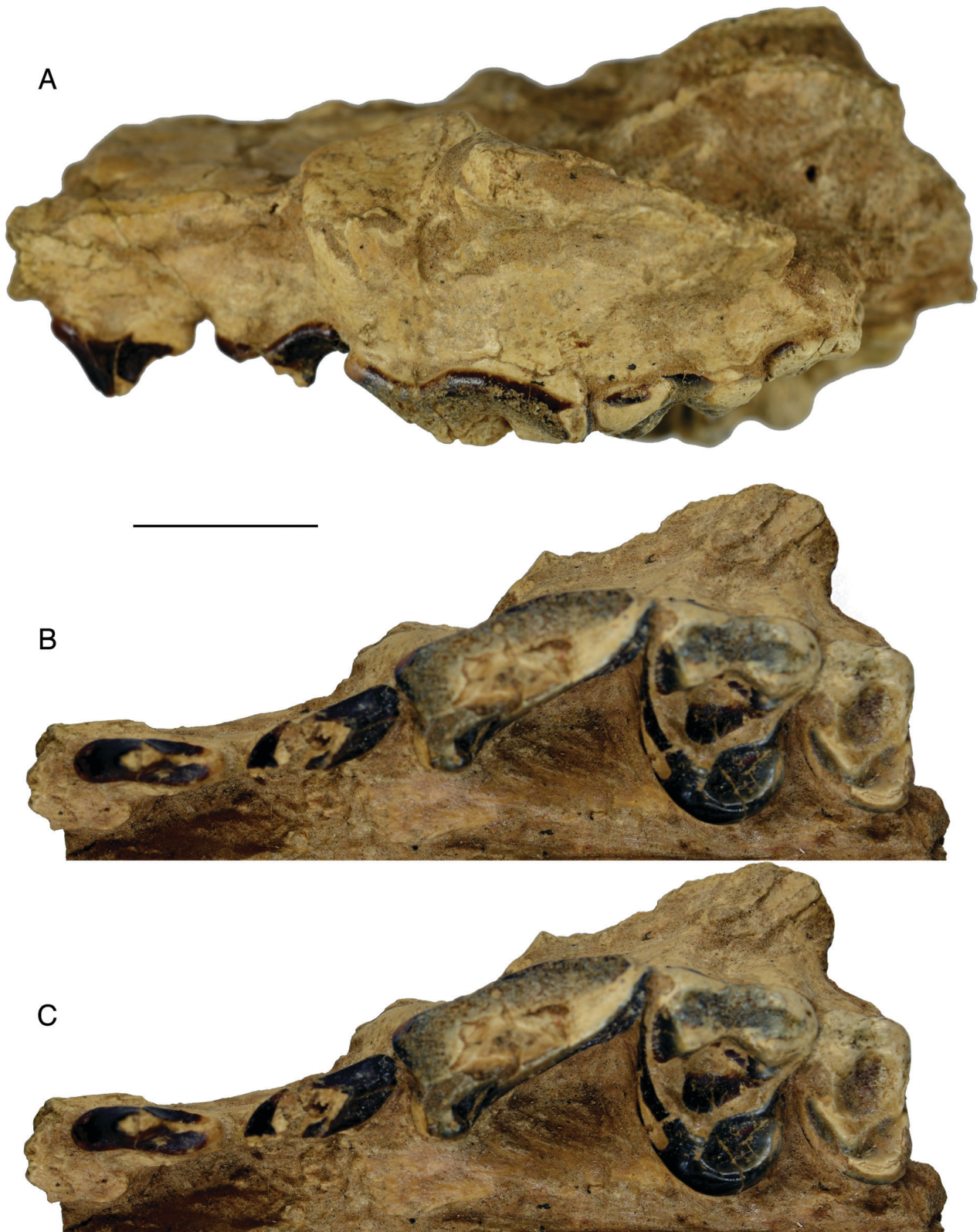


FIGURE 6. UCMP 52423, maxillary fragment of *Eucyon davisi*. **A**, lateral view of left maxillary fragment; **B**, **C**, stereoscopic pair of occlusal view of left maxillary fragment. Scale bar equals 10 mm.

with a more prominent posterior accessory cusp. The p4 is slightly imbricated with m1. The m1 paraconid is about as wide as the protoconid, but the latter is significantly taller. The m1 metaconid is prominent. Both paraconid and protoconid exhibit moderate wear at the tips but preserve a shearing facet. The talonid basin consists of equally sized hypoconid and entoconid that both have been worn down into ridges so that the talonid has become flat. No posterolingual cingulum is present on the m1. The m2 preserves a distinct trigonid that is taller than the talonid, although the cusps of the trigonid have been worn down into a plateau, and the worn cusps of the talonid are indistinguishable. The m3 is missing but represented by an alveolus. The anterior portion of the masseteric fossa is deep and distinct, beginning just rostrally to the m3 alveolus. The ascending ramus is broken dorsocaudally, in the middle of the masseteric fossa.

Compared to *Eucyon davisi*, *Vulpes stenognathus* is smaller and more gracile, especially in the p4 (Fig. 4B). Specimen UCMP 235504, a maxillary fragment bearing M1 and M2, is too worn to preserve cusps that can be adequately described but is assigned to *V. stenognathus* and not *E. davisi* because of the specimen's smaller size and because the M2 is smaller relative to the M1 than in *E. davisi*

(Fig. 11S). Relative to other vulpines, *V. stenognathus* is 26% larger than *V. kernensis* and 20% larger than *Metalopex macconnelli*, based on mean m1 length. Though UCMP 235505 lies in the lower size range of *V. stenognathus* and within the size range of *Metalopex merriami*, UCMP 235505 lacks the elongated diastema between p2 and p3 in *M. merriami* and has a relatively short and rounded m2 compared to that in *M. merriami*.

Tribe CANINI Fischer von Waldheim, 1817
Subtribe CANINA Fischer von Waldheim, 1817
Genus *EUCYON* Tedford and Qiu, 1996
EUCYON DAVISI (Merriam, 1911)

(Fig. 6)

Canis(?) sp.: Merriam, 1906:5, fig. 1.

Canis(?) *davisi* Merriam, 1911:242.

Leptocyon shermanensis Hibbard, 1937:460.

Canis condoni Shotwell, 1956:733.

Eucyon davisi: Tedford and Qiu, 1996:36; Tedford et al., 2009:92.

Stratigraphic Range—Currently known from deposits of early to late Hemphillian age. *Eucyon* in the Mehrten is found from only one site, at Turlock Lake. This site is located around the middle of the Modesto Reservoir Member, stratigraphically near sites containing *B. parvus* and *B. secundus*.

Geographic Range—Oregon, Nevada, Kansas, New Mexico, Oklahoma, Texas, Arizona, California, Florida, and northern Mexico.

Referred Material—LACM locality 3915 (UCMP locality V6874): UCMP 52423, partial palate with left P2–M2 and right P4 broken, M1 broken, and M2 broken.

Description and Comparison—*Eucyon davisi* is represented in the Mehrten Formation by a single fragmentary upper palate with the left dentition better preserved than the right. The specimen does not include the dorsal part of the cranium. The P2 is elongate and slender in occlusal view. The main cusp of the P3 is broken, and there is no posterior accessory cusp, only a posterior cusp created by an elevated posterior cingulum. In occlusal view, the posterior edge of P3 curves laterally more so than in P2, and P3 overall is larger than P2. A small diastema lies between P2 and P3, larger than the gap between P3 and P4. There is no imbrication in the premolars. The P4 is robust, with a smaller and less anteriorly located protocone and a more rounded anterolabial border than in some other specimens of *E. davisi*. This variant—common in *Canis lepophagus*, a more derived canine (Tedford et al., 2009)—differs from most other *E. davisi* specimens that have an anterobuccally projected protocone sharply notching the anterior border of the P4, suggesting that the Mehrten *E. davisi* is a later form. Relative to the molars, the P4 is larger and more robust than in *Vulpes* and *Metalopex*. The M1 and M2 have a low-crowned paracone and metacone and a strong labial cingulum, and the labial borders are weakly indented between the paracone and metacone. The M1 has a cingulum that extends lingually from the base of the paracone across the base of the protocone, continuing into the hypocone and ending at the base of the metacone. The M2 retains a distinct metacone that is significantly smaller than the protocone and has a lingual cingulum, extending from the paracone to the metacone, like the lingual cingulum in the M1.

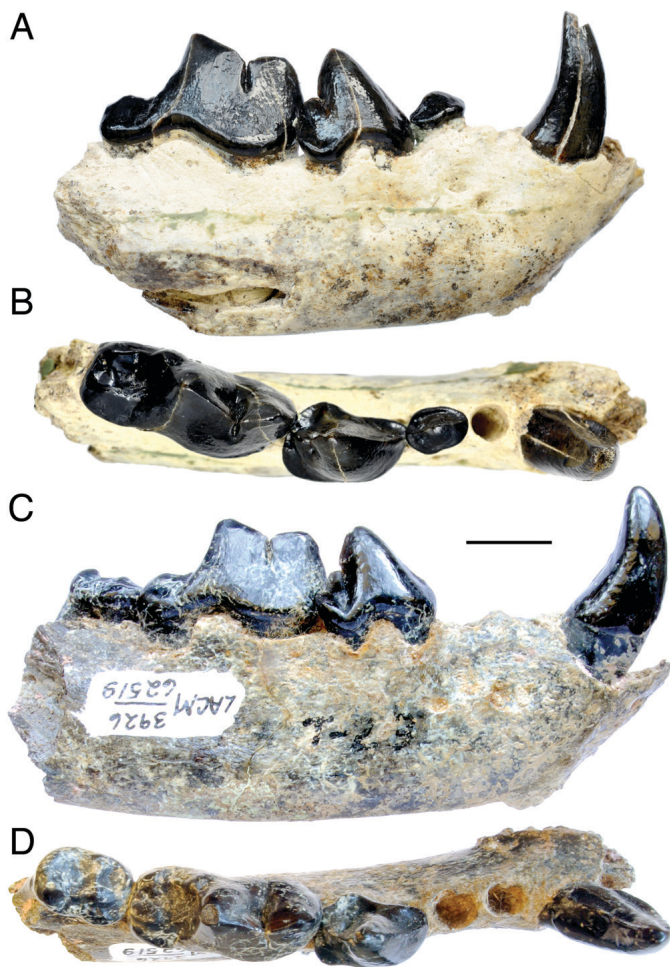


FIGURE 7. Representative lower jaws of robust (A, B) and gracile (C, D) *B. parvus* at the Mehrten. A, UCMP 235508, lateral view. B, UCMP 235508, occlusal view. C, LACM 62519, lateral view. D, LACM 62519, occlusal view. Scale bar equals 10 mm.

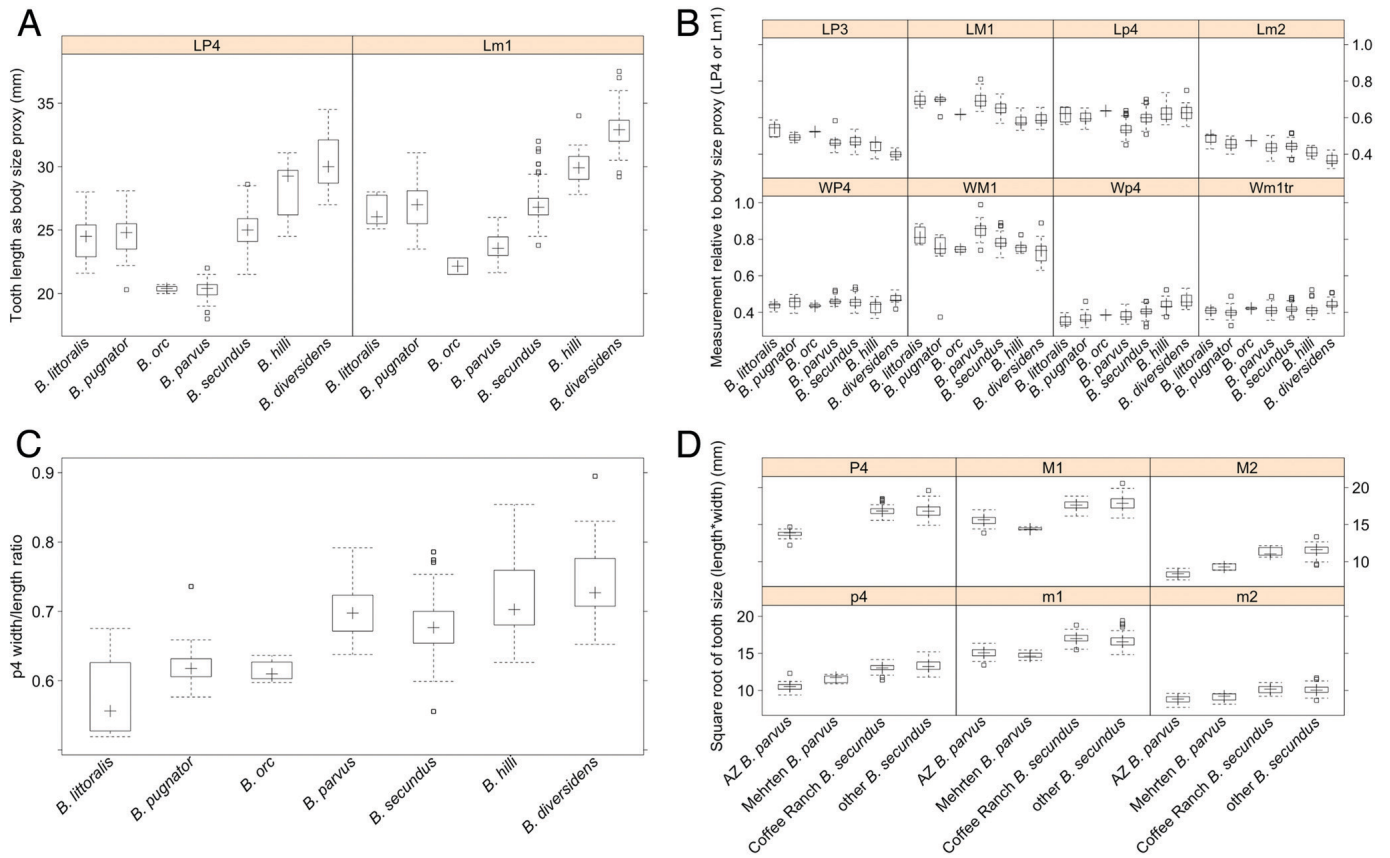


FIGURE 8. Box-whisker plots of *Borophagus* dental measurements. **A**, lengths of P4 and m1 as proxies for body size, showing size increase from less (left) to more (right) derived species. **B**, lengths and widths of teeth relative to body size proxies, showing evolutionary trends toward more hypercarnivorous adaptations in the *Borophagus* lineage. Within each panel, left to right signifies more derived species, with *B. diversidens* the most derived. **C**, ratio of p4 width to length, showing increase in p4 robustness from less to more derived species. **D**, comparisons of tooth sizes of Mehrten *B. parvus* to Arizona *B. parvus* and Coffee Ranch, Texas *B. secundus*. The Mehrten Formation sample of *B. parvus*, though similar in overall body size and most measurements to the Arizona sample, shows a larger p4, smaller M1, and larger M2 than the Arizona sample.

DISCUSSION

Dimorphism in Mehrten Borophagines

Wagner (1981) identified most of the Mehrten borophagines as *Osteoborus cyonoides*, which implicitly assumed a large sexual dimorphism in body size. Wang et al. (1999) reassigned the smaller *O. cyonoides* specimens to *Borophagus parvus* and the larger *O. cyonoides* specimens to *Borophagus secundus*, because *B. parvus* was 13% smaller than *B. secundus* based on basal skull length, a significant size difference that surpasses typical within-species variation in living canids (Gingerich and Winkler, 1979; Van Valkenburgh and Sacco, 2002).

To test Wang et al.'s (1999) hypothesis further, we calculated sexual dimorphism as the ratio of 'male' (*B. secundus*) mean to 'female' (*B. parvus*) mean for a given character. Because the length of m1 is the most commonly available measure among the Mehrten specimens, and because it is also commonly used as a proxy for body size in fossils (Van Valkenburgh, 1990), we discuss the results for m1 length here.

Sexual dimorphism is positively correlated with overall sample variance in extant carnivores. This relationship can be used to predict sexual dimorphism expected in a combined sample of *B. secundus* and *B. parvus* from the Mehrten, if *B. secundus* and *B. parvus* were a single sexually dimorphic species. Using a regression of sexual dimorphism on coefficients of variation (CV; expected dimorphism = $[0.008 * CV] + 1.01$; Van Valkenburgh and Sacco, 2002), we calculated expected sexual dimorphism in

the combined Mehrten *parvus* + *secundus* sample (CV = 4.27) to be 1.044, much less than the observed difference of 1.13. Among extant canids, the maximum level of sexual dimorphism in m1 length is 1.08 (for *Alopex lagopus*, the arctic fox), still much less than the observed difference in *B. secundus* + *B. parvus*. Thus, we reject the hypothesis that *B. secundus* and *B. parvus* are a single, highly dimorphic species. The size difference between these two Mehrten borophagines is too great to warrant their classification as one species.

Despite the size disparity, the two Mehrten borophagines are similar in their morphology and bear features peculiar to this formation. Mehrten specimens of *B. parvus* display characteristics rarely seen in the large sample of specimens from the type locality of Old Cabin Quarry in Arizona—such as a broadened posterior edge of p4 and a lost p1—that often occur in *B. secundus* or more advanced species of *Borophagus*. Though the loss of p1 in other mammal taxa may be sufficient to erect a new species, this tooth has been lost in only about a quarter of the Arizona population of *B. parvus*; in the remainder of the Arizona population that still retains it, p1 is quite reduced. The presence of p1 is an ancestral trait in the *Borophagus* lineage and has been shown to be labile within other *Borophagus* species, like *B. pugnator* and *B. orc* (Wang et al., 1999). Therefore, we retain the diagnosis of the smaller Mehrten borophagine as *B. parvus*, with geographic variation in p1.

Within Mehrten *B. parvus*, there are two morphs—a more robust form and a more gracile form—that exhibit co-varying

gradients in jaw robustness, dental wear, and bone loss that may represent age variation, with more robust and worn individuals being older (Fig. 7). Alternatively, these gradients may represent sexual differences in diet and/or hunting behavior. We examined potential sexual dimorphism in m1 length of *B. parvus* between the more robust ($n = 8$; e.g., UCMP 235508 and LACM 61692) and more gracile ($n = 7$; e.g., LACM 62519 and UCMP 235510) forms. If *B. parvus* is sexually dimorphic, given the observed CV of *B. parvus* m1 length = 4.42, we predicted sexual dimorphism level to be $[(0.008 * 4.42) + 1.01] = 1.05$. We calculated observed dimorphism in m1 length of Mehrten *B. parvus* to be 1.08, slightly above the predicted level but within the range of sexual dimorphism in m1 length of extant canids (from 1.0 in *Canis latrans*, the coyote, to 1.08 in *Alopex lagopus*; Van Valkenburgh and Sacco, 2002). Therefore, though the sample size is too small to be conclusive, it is possible that the two morphs of *B. parvus* include male and female sexes.

Dental Evolution in *Borophagus*

Mammalian hypercarnivores—animals that feed on diets consisting of over 70% vertebrate meat—tend to simplify the tooth row, emphasizing the slicing function of the dentition (e.g., carnassials) and reducing or losing the grinding aspects of the teeth (e.g., post-carnassial molars; Van Valkenburgh, 1991). Bone cracking, a further specialization of hypercarnivory, is marked by modification of certain teeth to process bone. Bone-cracking teeth tend to be enlarged, both compared to other teeth in the same row and compared to the same tooth in non-bone-cracking relatives, with a broad base and a pyramidal shape to withstand the increased mechanical demands of processing bone (Werdelin, 1989). Carnivores of different phylogenetic affinities have modified different teeth for bone processing. Extant hyaenids, for example, crack bones with the upper and lower third premolars (P3/p3), freeing their carnassials (P4/m1) for meat slicing. Borophagine canids, on the other hand, used the upper and lower fourth premolars (P4/p4), also involving the trigonid blade of the adjacent lower carnassial (m1; Werdelin, 1989).

Borophagus displays changes in dental morphology consistent with an evolution toward bone-cracking hypercarnivory. Figure 8A shows an increase in the lengths of P4 and m1, commonly used proxies for body size, from *B. parvus* to *B. diversidens*. Figure 8B presents linear dental measurements relative to these body size proxies. From *B. orc* to *B. diversidens*, the upper third premolar (P3) and lower second molar (m2) tend to decrease in anteroposterior length relative to body size. Relative length and width of the upper first molar (M1) both also decrease from *B. parvus* to *B. diversidens* (Fig. 8B). The progressively smaller size of the post-carnassial molars M1 and m2 signifies a reduction in grinding ability, whereas the concomitant shortening of the tooth row brings the P4, p4, and m1 trigonid blade—the bone-cracking dental complex—closer to the fulcrum of the jaw joint, increasing mechanical advantage of the bite at these teeth. Both the upper carnassial (P4) and lower first molar trigonid (m1tr) enlarge over time but maintain the same ratio of buccolingual width relative to their length (Fig. 8B), suggesting that, for *Borophagus*, an optimal relative width of these teeth is maintained and perhaps constrained by the demands of bone cracking at different body sizes. Length and width of the lower fourth premolar (p4) both increase relative to body size (Fig. 8B), although p4 width increases more quickly than p4 length from less to more derived species (Fig. 8C), gradually making the tooth more robust and resistant to breakage. The reduction of anterior premolars and posterior molars, isometric increase in relative P4 and m1 trigonid width, and enlargement of the p4 progressively optimize *Borophagus* for bone-cracking hypercarnivory.

Wang et al. (1999) suggested that certain features in the Mehrten sample of *Borophagus parvus* were transitional between the Arizona *B. parvus* sample and *B. secundus*. Like *B. secundus*, Mehrten *B. parvus* has lost the lower first premolar yet it is like the Arizona *B. parvus* sample in retaining a lower fourth premolar that is not extremely tall-crowned and prominently reclined as in *B. secundus*. Compared to *B. parvus* from Arizona, Mehrten *B. parvus* has a smaller M1, larger M2, and larger p4 (Fig. 8D). The Mehrten *B. parvus* and the Arizona *B. parvus* sample are indistinguishable in the length of the lower first molars. However, the Mehrten sample has upper second molars and lower fourth premolars that are intermediate in size between Arizona *B. parvus* and the Coffee Ranch (Texas) sample of *B. secundus*, supporting previous suggestions that the Mehrten *B. parvus* sample represents a transition between *B. secundus* and *B. parvus*.

Morgan and White (2005) briefly summarized published materials from the Redington Local Fauna (including Old Cabin Quarry, type locality of *B. parvus*) from the lower member of the Quiburis Formation in Pima County, south-eastern Arizona. A late Hemphillian age (Hh3) was assigned to the Redington Local Fauna based on paleomagnetic studies by Lindsay et al. (1984), in which the main fossil quarries fall within a normally magnetized zone that is correlated to chron C3An.2n with an ATNTS2012 calibration of 6.436–6.733 Ma (Hilgen et al., 2012). So far, the Modesto Reservoir Local Fauna of Wagner (1981), which includes the Mehrten *B. parvus* sample, has no radiometric or paleomagnetic dates. Wagner (1976, 1981) noted a strong faunal similarity to the Pinole Tuff Local Fauna of Contra Costa County, California, which was radiometrically dated to 5.2 Ma (Evernden et al., 1964). If the Mehrten assemblage is indeed similar in age to the Pinole Tuff Local Fauna, *B. parvus* from the Turlock Lake area may be more than one million years younger than those from Redington, Arizona. The above morphological differences can then be accounted for in terms of chronological variation, in addition to geographical variation. Although samples from the older Coyote Hill Local Fauna are too poor to evaluate the potential for in situ evolution in the Mehrten area, the partial loss of p1 in the stratigraphically older Arizona population and the full loss of p1 in the stratigraphically younger California population support the derived state of California *B. parvus* relative to Arizona *B. parvus*.

Wang et al.'s (1999) phylogeny postulated the *B. parvus* + *B. secundus* clade as sister to *B. orc*. They noted similarities between *B. parvus* and *B. orc* but classified the two species separately in part because of differences in temporal and geographic distribution: *Borophagus parvus* occupied the late Hemphillian of the southwestern United States, whereas *B. orc* is restricted to the early late Hemphillian of Florida. In turn, *B. orc* possibly represents an independent lineage that, along with the *B. parvus* + *B. secundus* clade, is sister to *B. pugnator* (Wang et al., 1999: fig. 141).

Wang et al. (1999) observed that *B. parvus* is morphologically intermediate between *B. pugnator* and *B. secundus*; potentially, then, *B. pugnator* gave rise to *B. parvus* + *B. secundus*. Yet, whereas *B. pugnator* is widely distributed across the Great Plains and Gulf Coast, it is not found in the early Hemphillian of California, which may present a difficulty in framing it as an ancestor to the *B. parvus* + *B. secundus* clade in the Southwest. In this present study, however, we note that a p4 from the early Hemphillian Coyote Hill fauna in the Mehrten Formation (UCMP 97982; Wagner's [1981] *Osteoborus* near *O. cyonoides*) may represent a transition between *B. pugnator* and *B. secundus*. Though its dimensions fall within the range of other *B. secundus*, it is narrower: its width-to-length ratio (0.60) is closer to *B. pugnator* mean p4 width-to-length ratio (0.61) than to the mean for all *B.*

secundus (0.68). Therefore, the Coyote Hill p4 may represent a phylogenetically plausible transition between *B. pugnator* and *B. secundus* (Wang et al., 1999:fig. 141). However, in the absence of more specimens definitively linking the Coyote Hill p4 to *B. pugnator*, we assign it to *B. secundus*. *Borophagus pugnator* is postulated to have arisen from *B. littoralis*, the most ancestral species of *Borophagus*, which is found in the Clarendonian to early Hemphillian of California. The *B. parvus* + *B. secundus* clade, therefore, may have arisen from *B. littoralis* either directly or by way of *B. pugnator*.

Additionally, Wang et al. (1999) noted a combination of ancestral and derived features in LACM 62705, a partial maxillary with C1 and P2–M2, here assigned to *B. secundus* (Fig. 3). Like most *B. secundus*, LACM 62705 has a large M2, but its reduced P4 parastyle is more diagnostic of *B. hilli* and *B. diversidens*, both more derived species of *Borophagus*. In the absence of more specimens from the Mehrten Formation, we support Wang et al.'s (1999) provisional identification of LACM 62705 as *B. secundus* but highlight the features that distinguish the Mehrten specimens from *B. secundus* elsewhere. Given the origin of the *Borophagus* clade in *B. littoralis* from the early Clarendonian of California, the Mehrten Formation likely records part of the early evolution of *Borophagus*, preserving intermediate and fleeting forms that we here classify as *B. parvus* and *B. secundus* as the clade was expanding in the early Hemphillian to the Great Plains.

CONCLUSIONS

Four species of canids are described from materials collected in the early Pliocene Mehrten Formation in central California: two borophagines, *Borophagus parvus* and *Borophagus secundus*, and two canines, *Eucyon davisi* and *Vulpes stenognathus*. At least ten individuals of *B. parvus*, three *B. secundus*, one *E. davisi*, and several specimens of *V. stenognathus* are preserved in the sequence. All individuals of *B. parvus* are in the Modesto Reservoir Member of the Mehrten Formation. The *B. secundus* specimen at Coyote Hill extends the stratigraphic range of the species in California: previously recognized to span only the late Hemphillian, *Borophagus secundus* is now also represented in the early Hemphillian. Specimens of *B. parvus* co-occur with *B. secundus* only in the lower part of the Modesto Reservoir Member; higher in the sequence, in the upper part of the Modesto Reservoir Member, *B. parvus* co-occurs only with canines (Fig. 1C). The presence of the geographically widespread *B. secundus* in the Mehrten, though sparse, is the only evidence of co-occurrence of two species of *Borophagus* in the late Hemphillian of North America (Wang et al., 1999). Despite the shift in its co-inhabitants, *B. parvus* exhibits no size change over the sequence, belying the possibility of character displacement.


Although previously considered a single species with significant sexual dimorphism, *B. parvus* and *B. secundus* are here assigned to different species mainly based on size differences surpassing levels of size sexual dimorphism in extant canids. Mehrten Formation *B. parvus* can be divided into two morphotypes—one gracile and the other robust—possibly, although not definitively, attributable to sexual differences. A p4 previously diagnosed as *Osteoborus* near *O. cyonoides* from the older Coyote Hill deposit is here assigned to *B. secundus* based on its resemblance to other *B. secundus* from California and from Coffee Ranch, Texas, although given more material this specimen may prove to be a transitional form affiliated with the more ancestral *B. pugnator*. Though radiometric or magnetic dates are not available for the Modesto Reservoir Member of the Mehrten, faunal similarity to the Pinole Local Tuff Fauna supports an approximate date of 5 Ma. Given this timing, morphological characteristics in both Mehrten *B. parvus* and *B. secundus* that are intermediate between other populations of these species (e.g., Arizona *B. parvus*; Coffee Ranch, Texas *B. secundus*) and more derived species of *Borophagus* (e.g., *B. hilli*,


B. diversidens) indicate chronological and geographic variation. Though sample sizes at the Mehrten are too low to define the local populations of *B. parvus* and *B. secundus* as species separate from their continental counterparts, the presence of these mosaic morphs at the Mehrten suggests that central California may have hosted a period of rapid morphological change as the *Borophagus* lineage expanded in the early Hemphillian to the Great Plains.

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Fossil canids from the Mehrten Formation, Late Cenozoic of Northern California

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TABLE 1S. Locality numbers and corresponding names for Mehrten Formation localities bearing specimens examined in this study.

Locality Number	Locality Name	Canid Species
LACM 3908 (UCMP V81248)	Rock Point	<i>B. parvus</i>
LACM 3909 (UCMP V5405)	Sand Point	<i>B. parvus</i>
LACM 3914	Turlock Lake 3	<i>B. secundus</i>
LACM 3915 (UCMP V6874)	Turlock Lake 4	<i>E. davisii</i>
LACM 3917 (UCMP V6878)	Cement Goose Pit Island	<i>B. parvus, V. stenognathus</i>
LACM 3922 (UCMP V5836)	Badger Point	<i>V. stenognathus</i>
LACM 3924 (UCMP V71137)	Turtle Cliff	<i>B. parvus</i>
LACM 3925 (UCMP V68135)	Turlock Lake 7	<i>B. parvus</i>
LACM 3926	Turlock Lake 2	<i>B. parvus</i>
LACM 3942	Rhino Island	<i>B. parvus, B. secundus</i>
LACM 3950	Turlock Lake General	<i>B. parvus</i>
LACM 4670	Picnic Bench	<i>B. parvus</i>
UCMP V65711	Turlock Lake General	<i>B. secundus</i>
UCMP V68134 (LACM 3937)	Turlock Lake 14	<i>B. parvus</i>
UCMP V72005	Coyote Hill	<i>B. secundus</i>
UCMP V80040	Fosters Max	<i>B. parvus</i>

TABLE 2S. Dental measurements (in mm) of specimens of *Borophagus parvus* from the Mehrten Formation. See Wang *et al.* (1999, appendix III) for summary statistics for the species.

Specimen	P2l or P3l	M1l	M1w	M2l	M2w
LACM 62701		12.91	15.82		
LACM 121534		12.87	16.79		
UCMP 124658		12.47	16.7	7.1	11.07
UCMP 235515	9.17				

Specimen	c1l	c1w	p2l	p3l	p4l	p4w	m1l	m1trw	m1tlw	m2l	m2w
LACM 61650					14.78	9.77	24.01	10.16	8.95	9.46	6.75
LACM 61690							24.3	10.12	9.24	11.36	7.95
LACM 61691							24.19	10.22	8.75	10.04	7.47
LACM 61692				8.09	14.91	9.94	24.76	10.39	9.87	10.36	8.04
LACM 61693				6.8	13.76	8.67	22.8	9.39	8.39		
LACM 62519	9.93	7.3			13.52	8.79	21.64	9.73	9.43	10.87	8.02
LACM 62696					14.28	9.99	22.96	9.82	9.44	11.42	7.97
LACM 62697							23.15	9.44	9.25		
LACM 62698					14.26	9.47					
LACM 62346	9.45	8.51	5.62								
UCMP 44670					14.2	9.51	22.65	10.35	9.27	10.01	7.72
UCMP 65196	10.14	7.33			13.43	8.9	22.03	9.87	9.39	10.7	8
UCMP 233508	9.88	7.69		7.45	14.4	9.47	24.99	9.91	9.57		
UCMP 233510					12.94	9.42	22.2	9.8	9.46	10.33	8.14
UCMP 233512				8.17	14.14	10.15	24.46	11.08	9.67	8.86	
UCMP 235513						9.79	23.77	10.14	8.84		
UCMP 235514			5.62		14.54	9.45	23.56	10.25	8.74	9.37	7.23

TABLE 3S. Dental measurements (in mm) of *Borophagus secundus* from the Mehrten Formation. See Wang *et al.* (1999, appendix III) for summary statistics for the species.

Specimen	P1l	P2l	P3l	P4l	P4w	M1l	M1w
LACM 62705	9.45		11.79	26.17	12.23	18.93	21.22

Specimen	p4l	p4w
UCMP 97982	17.43	10.44

TABLE 4S. Dental measurements (in mm) of *Vulpes stenognathus* from the Mehrten Formation. See Tedford *et al.* (2009) for summary statistics for the species.

Specimen	P2l	P3l	M1l	M1w	M2l	M2w
LACM 62332	7.23	8.38				
UCMP 235504			9.68	11.5	5.76	8.21

Specimen	c1l	c1w	p2l	p3l	p4l	p4w	m1l	m1trw	m1tlw	m2l	m2w
LACM 62335				6.87							
UCMP 235505	6.42	4.19	7.03	7.99	8.67	3.7	13.88	4.94	5.16	6.74	5.02

TABLE 5S. Dental measurements (in mm) of *Eucyon davisi* from the Mehrten Formation. See Tedford *et al.* (2009) for summary statistics for the species.

Specimen	P2l	P3l	P4l	P4w	M1l	M1w	M2l	M2w
UCMP 52423	8.39	9.28	14.7	7.24	9.51	12.3	6.23	9.1

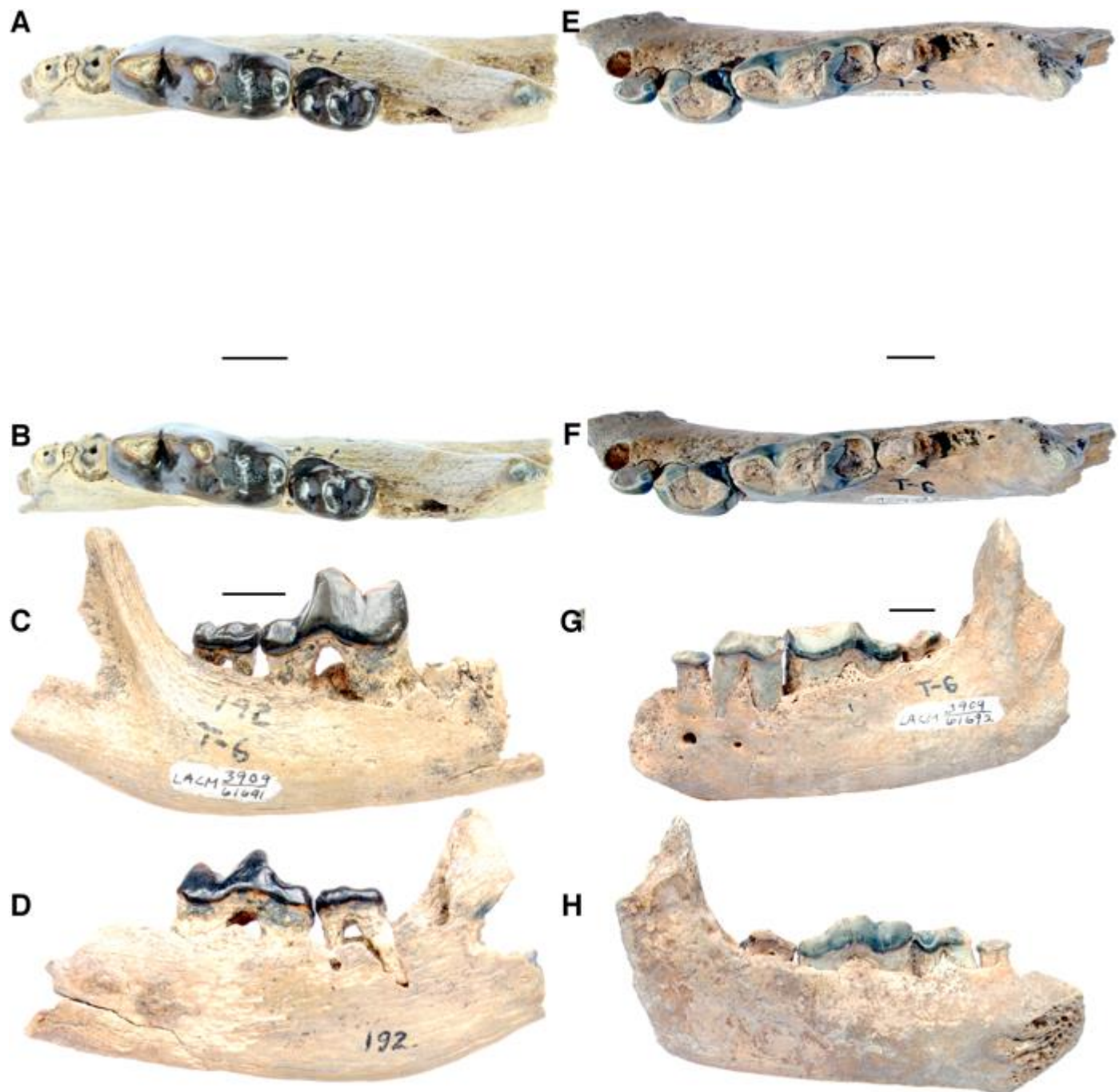


FIGURE 1S. LACM 61691 and 61692, right and left dentaries of *Borophagus parvus*. **A, B**, stereoscopic pair of occlusal view of right dentary; **C**, lateral view of right dentary; **D**, medial view of right dentary; **E, F**, stereoscopic pair of occlusal view of left dentary; **G**, lateral view of left dentary; **H**, medial view of left dentary. Upper scale bars are for stereoscopic pairs, lower scale bars for lateral and medial views; all equal 10 mm. [planned for page width]

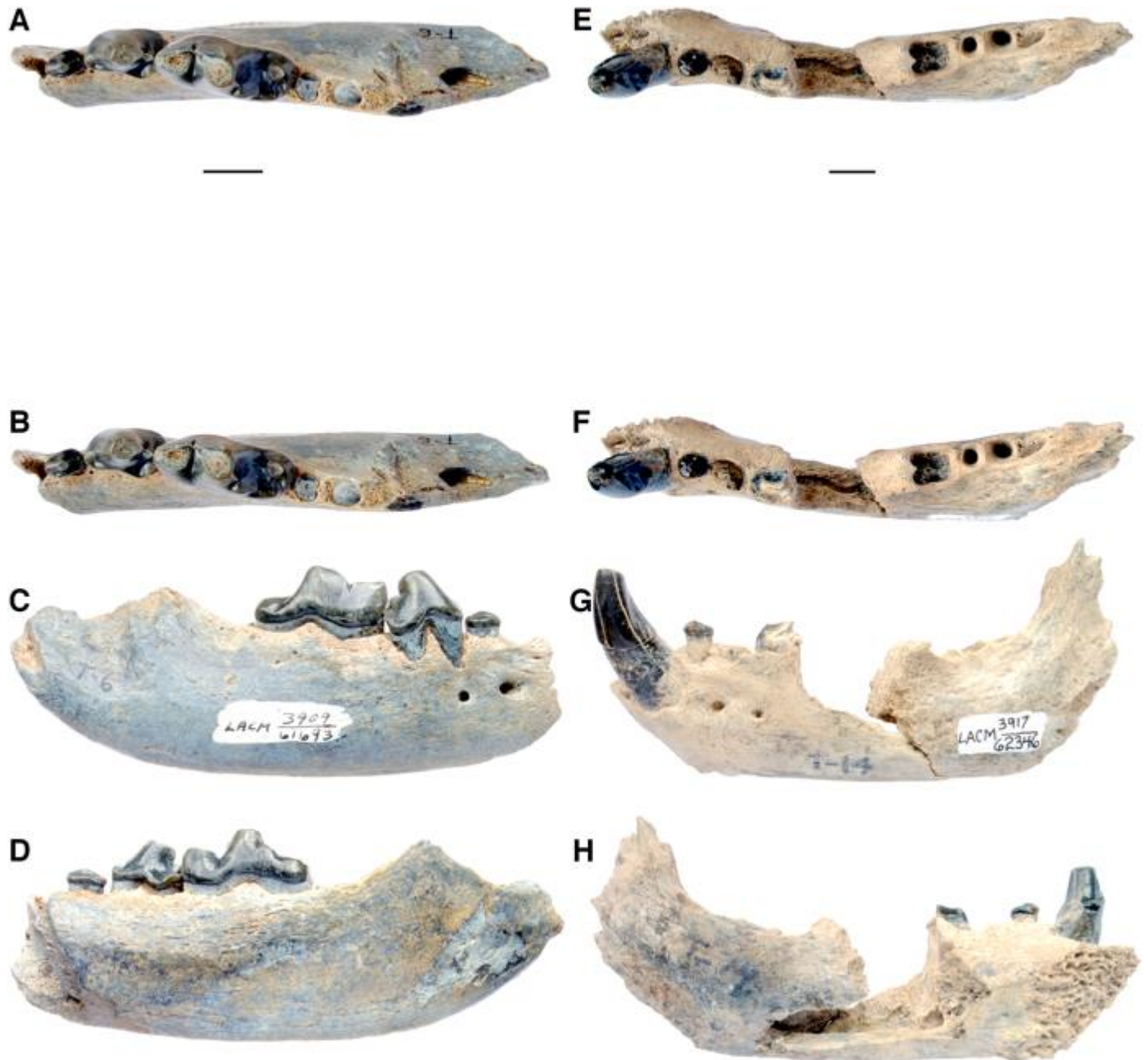


FIGURE 2S. LACM 61693 and 62346, right and left dentaries of *Borophagus parvus*. **A, B**, stereoscopic pair of occlusal view of right dentary; **C**, lateral view of right dentary; **D**, medial view of right dentary; **E, F**, stereoscopic pair of occlusal view of left dentary; **G**, lateral view of left dentary; **H**, medial view of left dentary. Scale bars equal 10 mm. [planned for page width]

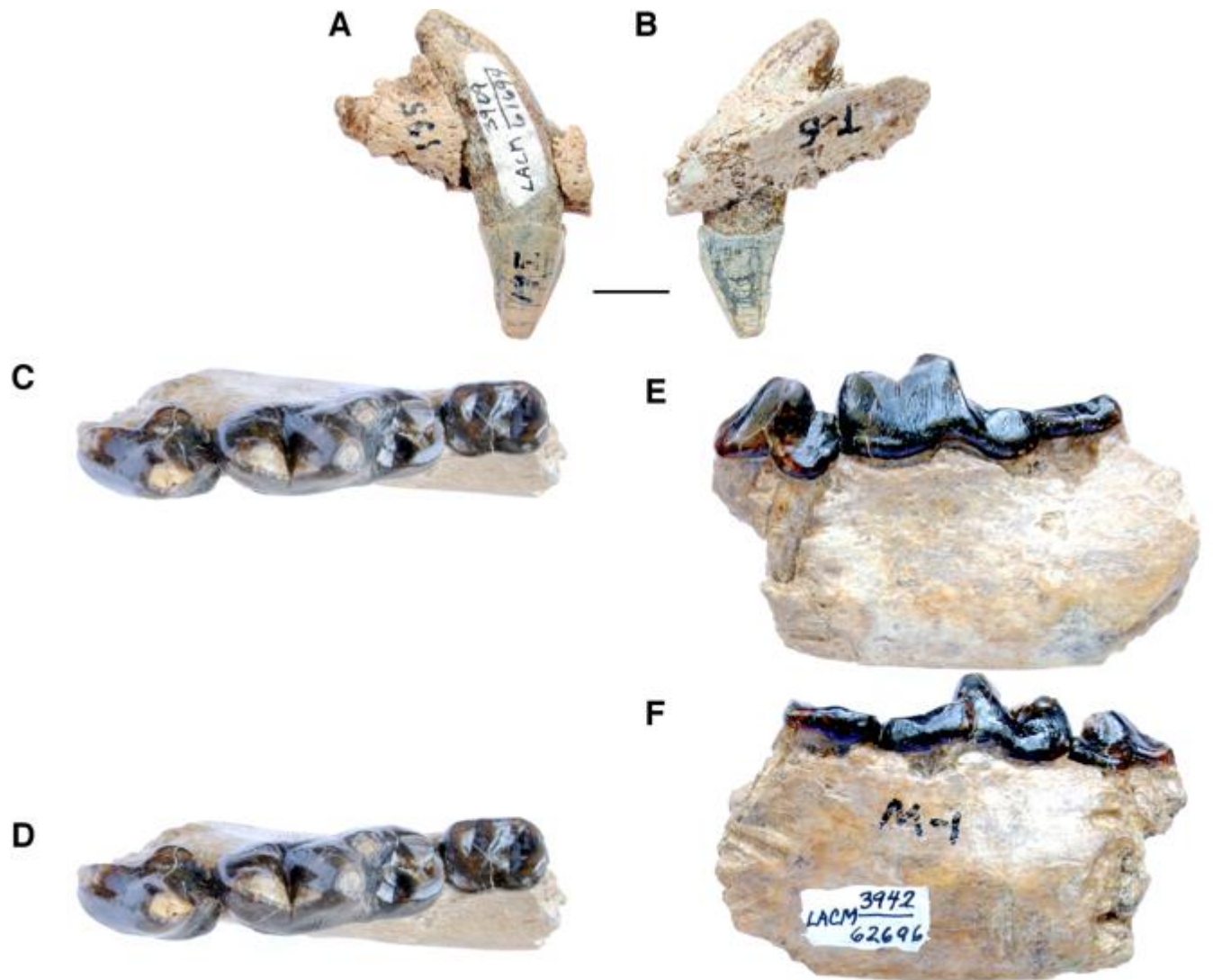


FIGURE 3S. LACM 61694 and 62696, right maxillary fragment and left dentary of *Borophagus parvus*. **A**, lateral view of maxillary fragment; **B**, medial view of maxillary fragment; **C**, **D**, stereoscopic pair of occlusal view of left dentary; **E**, lateral view of left dentary; **F**, medial view of left dentary. Scale bar equals 10 mm. [planned for page width]

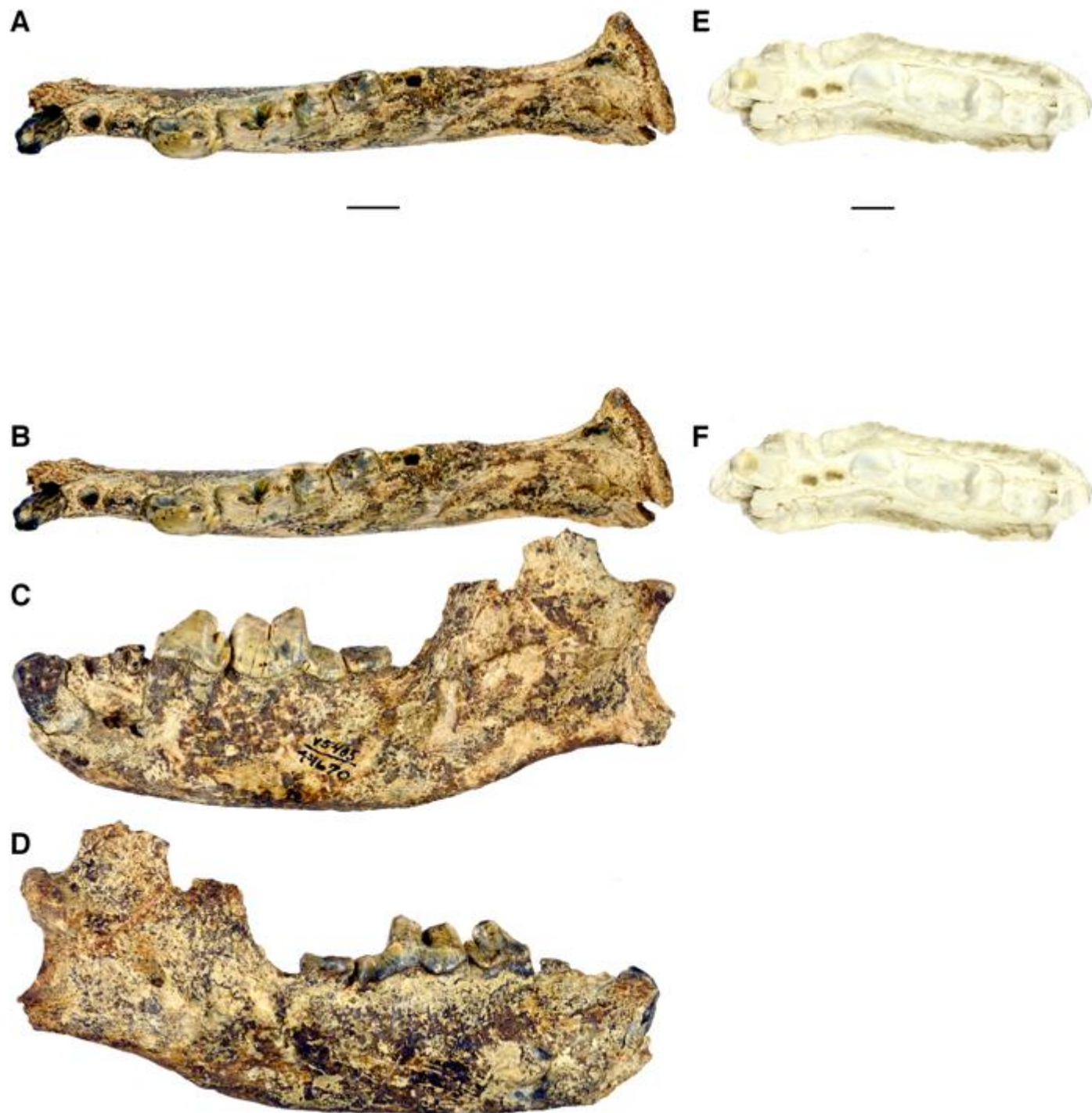


FIGURE 4S. UCMF 44670 and 65196 (cast), left and right dentaries of *Borophagus parvus*. **A**, **B**, stereoscopic pair of occlusal view of left dentary; **C**, lateral view of left dentary; **D**, medial view of left dentary; **E**, **F**, stereoscopic pair of occlusal view of right dentary. Scale bars equal 10 mm.

A



B



C



D



FIGURE 5S (on previous page). UCMP 235508, right dentary of *Borophagus parvus*. **A**, lateral view of right dentary; **B**, medial view of right dentary; **C, D**, stereoscopic pair of occlusal view of right dentary. Upper scale bar is for **lateral and medial views**, lower scale bar for **stereoscopic pair**; both equal 10 mm. [planned for page width]

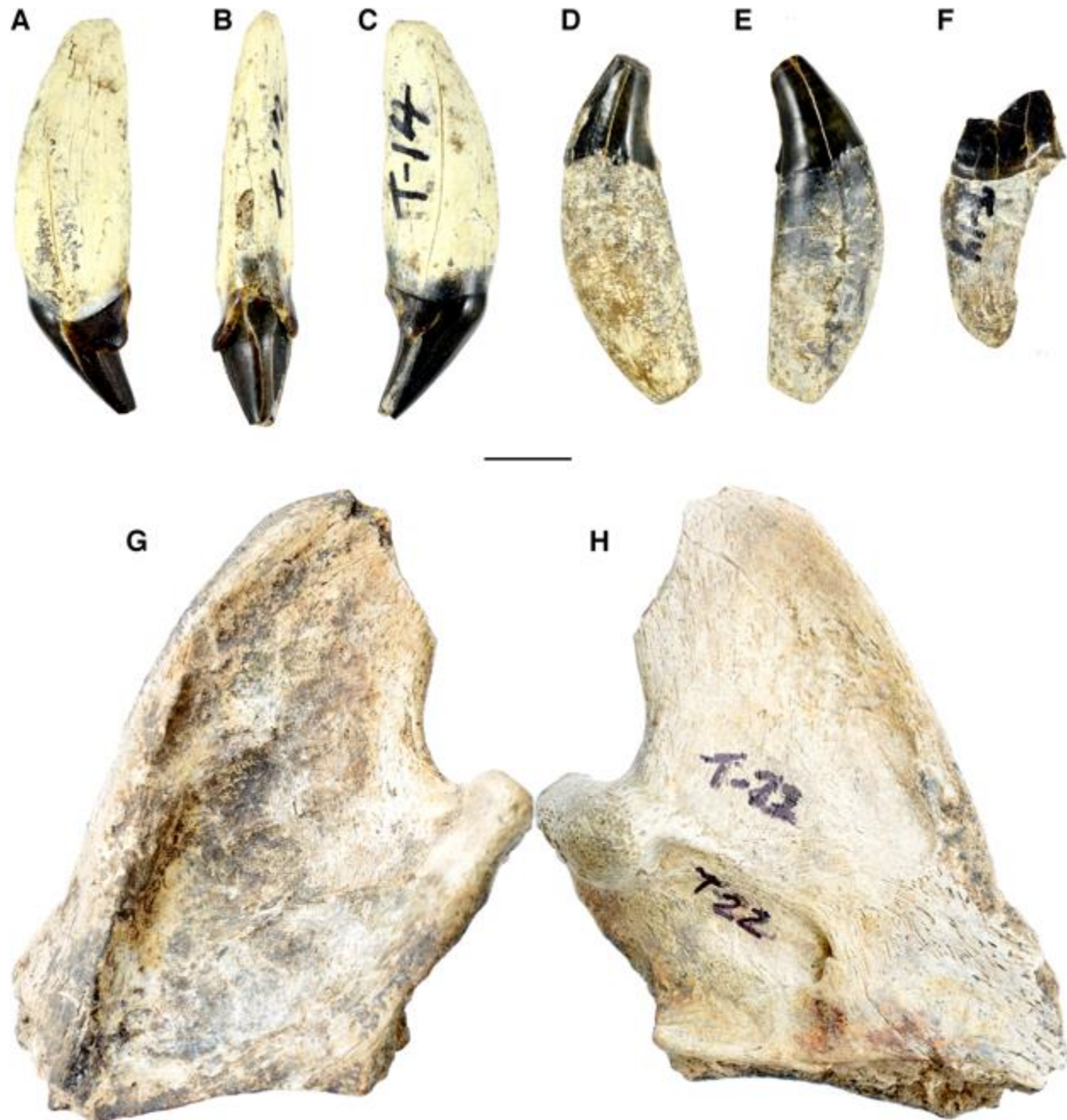


FIGURE 6S. UCMP 235509 and 235511, isolated teeth and left posterior dentary of *Borophagus parvus*. **A**, medial view of right I3; **B**, lingual view of right I3; **C**, lateral view of right I3; **D**, medial view of right c; **E**, lateral view of right c; **F**, lateral view of partial left m1; **G**, lateral view of left posterior dentary; **H**, medial view of left posterior dentary. Scale bar equals 10 mm. [planned for page width]

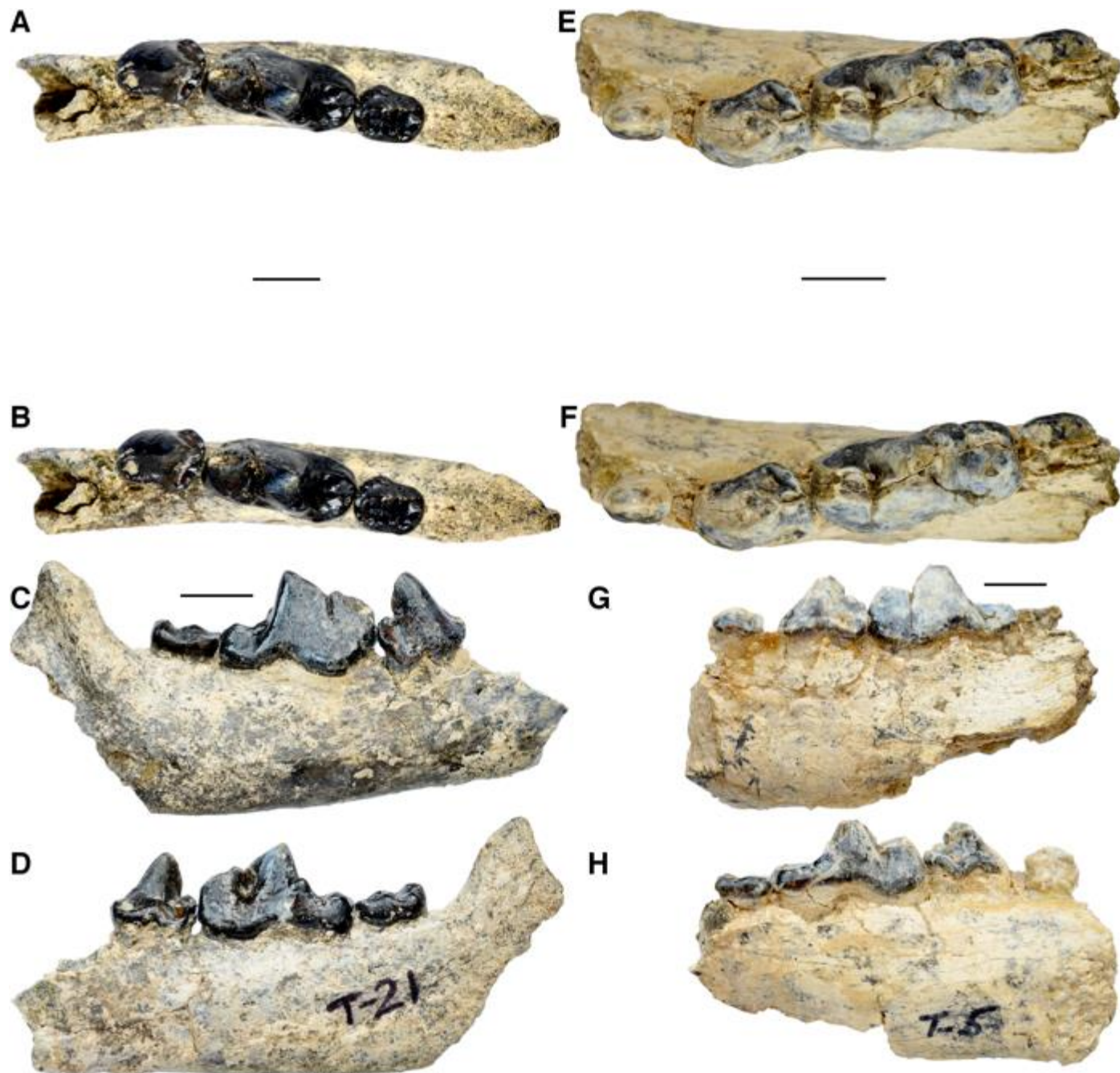


FIGURE 7S. UCMP 235510 and 235512, right and left dentaries of *Borophagus parvus*. **A, B**, stereoscopic pair of occlusal view of right dentary; **C**, lateral view of right dentary; **D**, medial view of right dentary; **E, F**, stereoscopic pair of occlusal view of left dentary; **G**, lateral view of left dentary; **H**, medial view of left dentary. Upper scale bars are for stereoscopic pairs, lower scale bars for lateral and medial views; both equal 10 mm. [planned for page width]

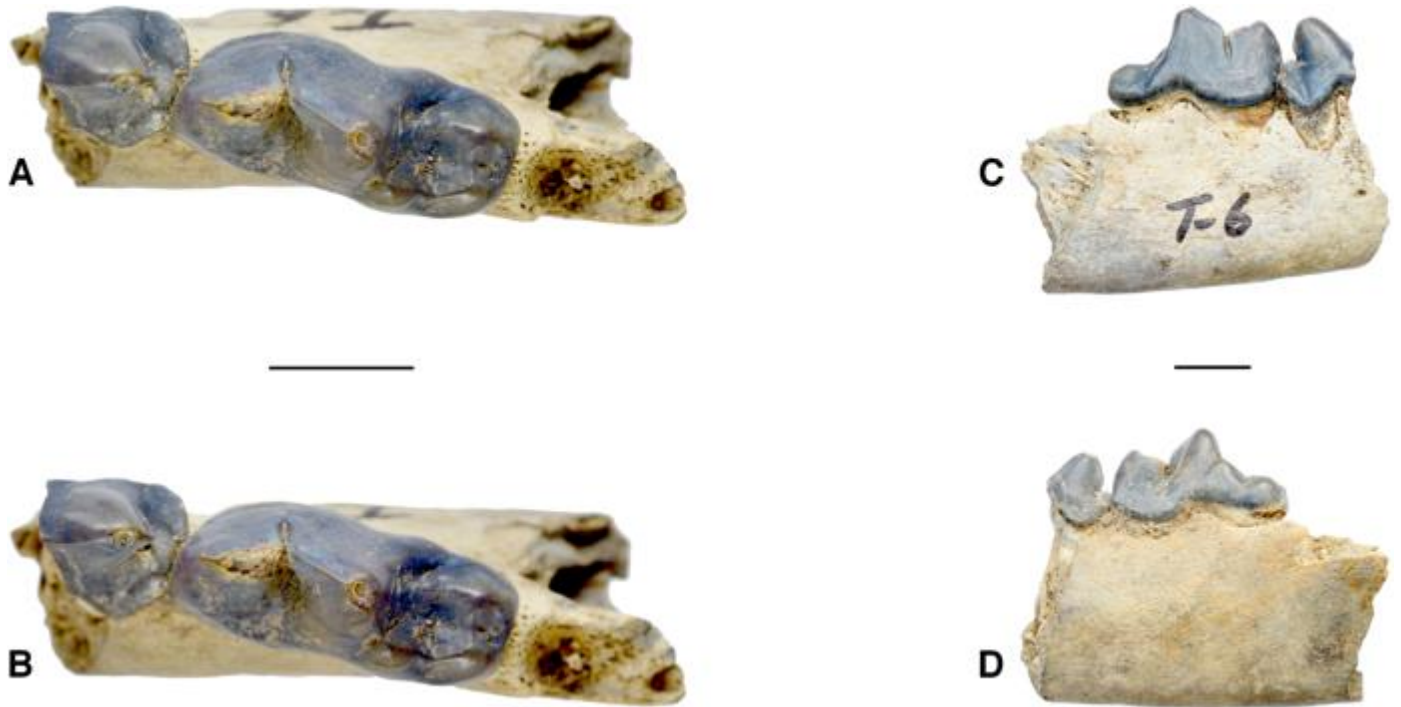


FIGURE 8S. UCMP 235513, right dentary of *Borophagus parvus*. **A**, **B**, stereoscopic pair of occlusal view of right dentary; **C**, lateral view of right dentary; **D**, medial view of right dentary. **Left** scale bar is for stereoscopic pair, **right** scale bar for lateral and medial views; both equal 10 mm. [planned for **page** width]

A



B



C



FIGURE 9S (on previous page). UCMP 235514, left dentary of *Borophagus parvus*. **A**, lateral view of left dentary; **B, C**, stereoscopic pair of occlusal view of left dentary. Upper scale bar is for **lateral view**, lower scale bar for **stereoscopic pair**; both equal 10 mm. [planned for page width]

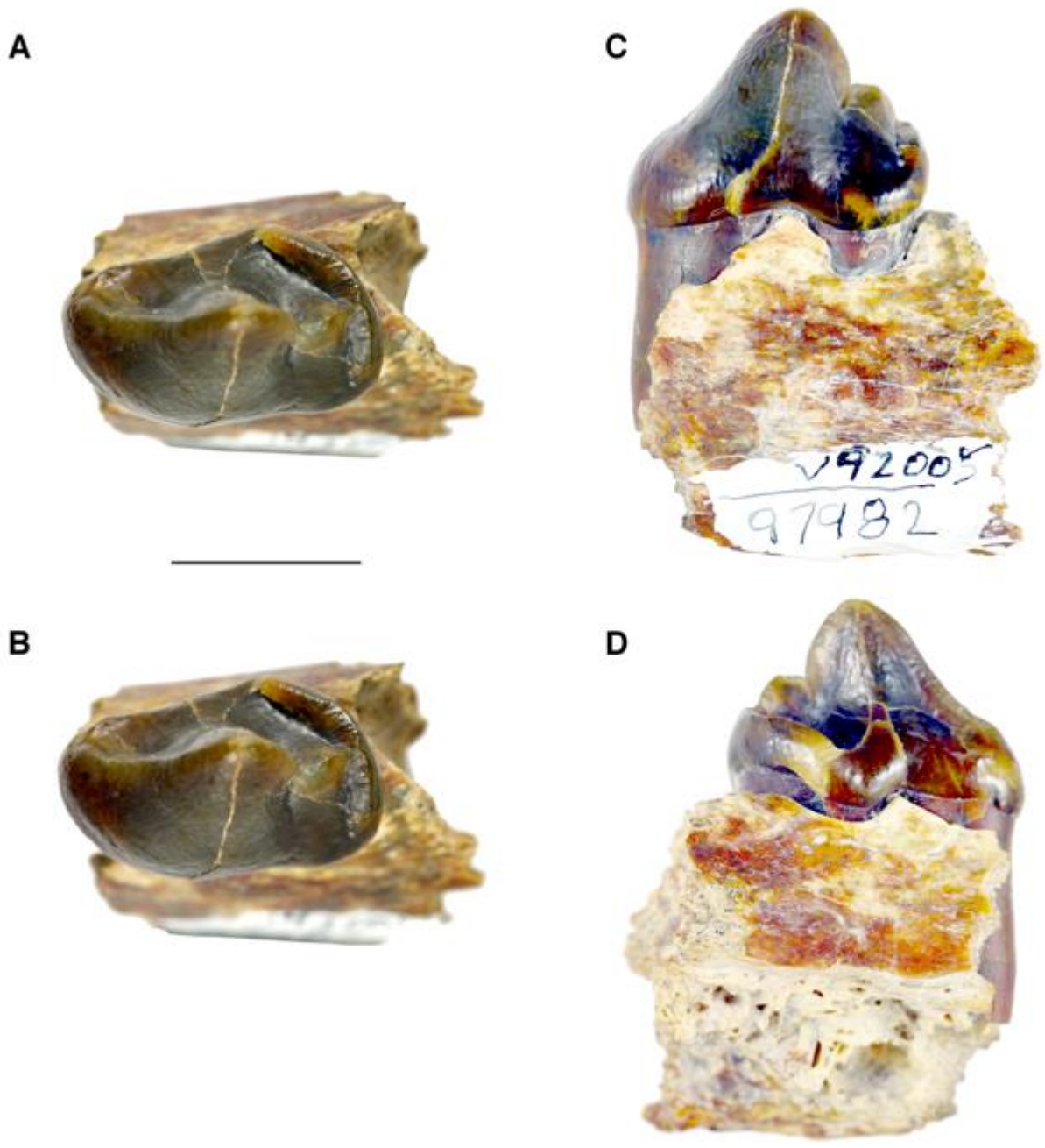


FIGURE 10S. UCMP 97982, left p4 in dentary fragment of *Borophagus secundus*. **A, B**, stereoscopic pair of occlusal view of left p4; **C**, lateral view of left p4; **D**, medial view of left p4. Scale bar equals 10 mm. [planned for page width]

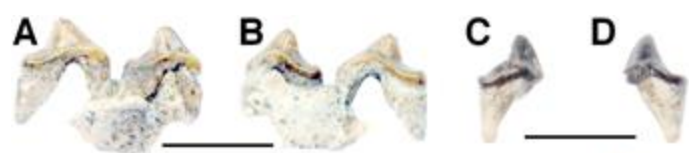


FIGURE 11S (on previous page). LACM 62332, 62335, 62338, and 235504, premolars, edentulous left dentary, and left maxillary fragment with M1–2 of *Vulpes stenognathus*. **A**, lateral view of right p2–p3; **B**, medial view of right p2 – p3; **C**, medial view of left p3; **D**, lateral view of left p3; **E**, lateral view of left dentary; **F**, medial view of left dentary; **G**, occlusal view of left dentary; **H, I**, stereoscopic pair of occlusal view of left maxillary fragment with M1–2. Scale bars equal 10 mm. [planned for column width]