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New records of the fur seal *Callorhinus* (Carnivora: Otariidae) from the Plio-Pleistocene Rio Dell Formation of Northern California and comments on otariid dental evolution.

ROBERT W. BOESSENECKER; Department of Earth Sciences, Montana State University, Bozeman, Montana 59715 U.S.A., robert.boessenecker@msu.montana.edu

RH: BOESSENECKER—PLIO-PLEISTOCENE FUR SEALS

ABSTRACT— New fossils representing two species of the fur seal *Callorhinus* are reported from the uppermost Pliocene to lower Pleistocene Rio Dell Formation of Northern California. The finds include latest Pliocene-earliest Pleistocene dentaries and postcrania of *Callorhinus gilmorei*, and a partial dentary of Early Pleistocene age identified as *Callorhinus* sp. The aforementioned material is ascribed to *C. gilmorei* due to the incipient single rooted condition of the p1-2, retention of double rooted p3-m1 and overall small size. The dentary identified as *Callorhinus* sp. exhibits a more derived pattern of tooth morphology including single-rooted p1-p4 (and double rooted m1), larger size than *C. gilmorei* and in the size range of extant *Callorhinus ursinus* (which typically exhibit fused roots on all postcanine teeth). Fusion of postcanine roots began with the p2 and continued posteriorly, and is likely an adaptation to accommodate crowded teeth anteriorly in the jaws. *Callorhinus gilmorei* has previously been reported from the Upper Pliocene of southern California and Japan, and this new record extends the range of this taxon further north in the Northeast Pacific. *Callorhinus* sp. is the most complete pinniped fossil to be described from the Early Pleistocene of the Northeast Pacific. The

wide biogeographic range of *Callorhinus* during the Pliocene and Pleistocene documents the persistence of this taxon, potentially as a Pliocene-Holocene anagenetic lineage. This highlights the antiquity of the *Callorhinus* lineage, which has persisted in the Northeast Pacific since the Pliocene, establishing it as the oldest and earliest diverging crown otariid.

INTRODUCTION

The Pleistocene marine mammal record of the Northeast Pacific region is represented by a small number of assemblages, all of which are Middle and Late Pleistocene (none of Early Pleistocene age), few of which are substantiated by detailed descriptions (exceptions being Leffler, 1964; Mitchell, 1966; Kilmer, 1972; Barnes and Mitchell, 1975; Barnes et al., 2006). Most Middle and Upper Pleistocene assemblages only include extant marine mammal genera, suggesting whatever turnover responsible for the faunal juxtaposition occurred earlier in the Pleistocene. Middle Pleistocene marine mammal assemblages include those from the Port Orford Formation (Roth, 1979) of southern Oregon (erroneously stated as Late Pliocene by Barnes et al., 2006), the Moonstone Beach Formation of Humboldt County, California (Kilmer, 1972), and the San Pedro Formation in Los Angeles County, California (Jefferson, 1991). The Palos Verdes Sand yielded the only diverse Late Pleistocene marine mammal assemblage from the Northeast Pacific (Miller, 1971; Jefferson, 1991). Although the Pleistocene marine mammal record is fraught with the diversity of problems outlined above, it can be improved by publication of descriptions from established collections, use of up-to-date

age determinations for Pleistocene strata, and discovery and description of new Pleistocene marine mammal assemblages.

Recent collecting in the Plio-Pleistocene Rio Dell Formation in the Eel River Basin of Humboldt County, California (Figs. 1, 2), by amateur collector Ron J. Bushell (formerly of Eureka, California) has established a small yet important collection. This collection documents two distinct species of the fur seal *Callorhinus*, including the late Pliocene *C. gilmorei* (Fig. 3), and a possible unrecognized taxon (Fig. 4) that is temporally (and potentially morphologically) intermediate between *C. gilmorei* and the extant *C. ursinus*, preliminarily reported by Boessenecker (2007). This latter taxon is incomplete, and formal taxonomic recognition awaits discovery of more complete and diagnostic remains. Nevertheless, this is the first described pinniped fossil from the Early Pleistocene of the Northeast Pacific. *Callorhinus* is the earliest known extant pinniped taxon represented from the fossil record of the Northeast Pacific, and extant *C. ursinus* consistently exhibits the basal most phylogenetic position among extant Otariidae in molecular (Wynen et al., 2001; Yonezawa et al. 2009) and morphological phylogenetic hypotheses (Berta and Deméré, 1986; Berta and Wyss, 1994; Deméré and Berta, 2005; Kohno and Yanagisawa, 1997; but see Brunner, 2004). Whereas (de Muizon, 1978) placed the Mio-Pliocene fur seal *Thalassoleon* and *Callorhinus* within the subfamily “Callorhininae”, cladistic analyses have placed *Thalassoleon* as an early diverging otariid (Berta and Deméré, 1986). Whereas the morphological analysis by Berta and Deméré (1986) supported monophyly of the “Arctocephalinae” (*Arctocephalus* + *Callorhinus*), numerous molecular and morphologic phylogenetic hypotheses indicate that the “Arctocephalinae” (and even the genus *Arctocephalus*) are probably paraphyletic (Wynen

et al., 2001; Brunner, 2004; Yonezawa et al., 2009). Other issues surrounding otariid phylogeny concern the “Otariinae” (fossil and extant sea lions; *Eumetopias*, *Neophoca*, *Otaria*, *Phocarcos*, *Proterozetes*, and *Zalophus*), which are also probably paraphyletic (Wynen et al., 2001; Brunner, 2004; Yonezawa et al., 2009). Out of convenience, sea lions are referred to herein as the “otariines”, recognizing the possibility that this is a paraphyletic grade. Future phylogenetic studies incorporating fossil and extant taxa and the eventual discovery of additional otariid fossils will be paramount to exacting further resolution of the evolution of fur seals and sea lions.

Institutional Abbreviations—**CAS**, California Academy of Sciences, San Francisco, California, U.S.A.; **SDNHM**, San Diego Natural History Museum, San Diego, California, U.S.A.; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **USNM**, United States National Museum, Smithsonian Institution, Washington D.C., U.S.A.; **VMS** and **VM**, Sierra College Natural History Museum vertebrate collection, Rocklin, California, U.S.A.

GEOLOGIC SETTING

Fossils of *Callorhinus gilmorei* were recovered from the type section of the Wildcat Group at Scotia Bluffs, from the Lower Member of the Rio Dell Formation (Figs. 1, 2), which is correlative with the 'Venturian' and 'Wheelerian' provincial foraminiferal stages, or Middle to Late Pliocene in age (Roth, 1979; Haller, 1980). Roth (1979) assigned the Lower and Middle Members of the Rio Dell Formation to the Pliocene-correlative ‘Moclipsian’ provincial megainvertebrate stage of Addicott (1976).

The dentary of *Callorhinus* sp. was collected from near the top of the Upper Member of the Rio Dell Formation (Fig. 2), which is correlative with the Calabrian Stage and Early Pleistocene in age (Haller, 1980). The Upper Member of the Rio Dell Formation has yielded a foraminiferal assemblage assignable to the provincial Pleistocene ‘Hallian’ stage (Haller, 1980). The mollusks and echinoids from the Upper Member of the Rio Dell Formation are diagnostic for the ‘Arcatan’ provincial megainvertebrate stage, which Roth (1979) defined to encompass Early Pleistocene megainvertebrate assemblages from the Upper Member of the Rio Dell Formation and Moonstone Beach Formation. Although the type section is slightly older than strata at Centerville Beach, extrapolation of paleomagnetic and ash correlation results from the Centerville Beach section allows further (albeit tentative) resolution. At Centerville Beach, the Lower Member of the Rio Dell formation is bracketed above by a 2.0 Ma ash unit (that occurs within the Middle Member of the Rio Dell Formation) and below by a 3.0 Ma ash bed exposed in the Eel River Formation at Scotia Bluffs (Sarna-Wojcicki et al., 1982). The *Callorhinus* sp. record is bracketed by the 1.2–1.3 Ma Rio Dell Ash (exposed in the Upper Rio Dell Formation at Centerville Beach and in the Carlotta Formation in the type section at Scotia Bluffs) and by a stratigraphically lower, 2.0 Ma ash unit as well as by the beginning (1.87 Ma) of the Olduvai Normal Polarity Subchronozone (Sarna-Wojcicki et al., 1982). In summary, fossils reported herein of *Callorhinus gilmorei* are 3.0–2.0 Ma (latest Middle to Late Pliocene) and *Callorhinus* sp. is 2.0–1.2 Ma (Latest Pliocene to Early Pleistocene). Although the Pliocene-Pleistocene boundary was recently revised from 1.806 Ma to 2.588 Ma by inclusion of the Late Pliocene Gelasian stage within the Early Pleistocene and modification of the Quaternary concept (Gibbard et al., 2009), this

change is based on chronostratigraphy and does not reflect the biostratigraphic integrity of the traditionally defined Pleistocene epoch (Aubry et al., 2009). Thus, for the purposes of this paper, the traditional definition of the Pliocene-Pleistocene boundary at the 1.806 Ma Gelasian-Calabrian stage boundary is retained along with a threefold division of the Pliocene epoch (Lower, Middle, and Upper being equivalent with the Zanclean, Piacenzian, and Gelasian stages, respectively). Other vertebrate fossils from this locality will be the subject of future study.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

CARNIVORA Bowditch, 1821

OTARIIDAE Gill, 1866

CALLORHINUS Gray, 1859

Type Species—*Callorhinus ursinus* (Linnaeus 1758).

Diagnosis—A genus that differs from all other otariids in possessing forelimb fur that terminates at the wrist, nasal processes that are anterodorsally flared, facial angle less than 125°, reduced premaxilla (premaxilla width under 40% of nasal length), short lower postcanine tooth row, dorsally directed anterior margin of mandibular foramen, cranial border of scapula rotated toward vertebral border, and innominate shorter relative to

length of tibia/fibula (modified from Berta and Deméré, 1986, and Kohno and Yanagisawa, 1997).

CALLORHINUS GILMOREI Berta and Deméré 1986

(Fig. 3)

Emended Diagnosis—*Callorhinus gilmorei* differs from other species of *Callorhinus* in the combined possession of a small upper third incisor with oval cross-section, double-rooted P2-P4 and M1-2, M1-2 closely spaced, variably developed lower postcanine roots (but typically single-rooted p1-2 and double-rooted p3-m1), long, shallow pterygoid process not forming a medial shelf, and dorsally directed anterior margin of mandibular foramen (possible apomorphy).

Referred Specimens—UCMP 219999 , associated pair of dentaries including complete right dentary with c1, and partial left dentary missing the middle portion of the ramus, with broken c1 and p2 (Fig. 3A-G); VMS 13, left metacarpal I; VMS 7, complete left radius; VM 174, distal right radial epiphysis; all collected by R. J. Bushell from the upper Pliocene Rio Dell Formation. Detailed locality data is available per request to qualified researchers.

Formation and Age—UCMP 219999 was found in a large, one-meter wide calcareous siltstone nodule (Fig. 3A) as ‘float’ (ex situ) in a gravel bar of the Eel River (UCMP locality V99861) during a period of low flow by R. J. Bushell in Summer 2004 (Fig. 1B). The fossil was discovered upstream from the Upper and Middle Members of the Rio Dell Formation, and likely originated from the Lower Member of the Rio Dell

Formation (Fig. 2). Slumping frequently introduces large volumes of sediment laden with fossiliferous concretions into the river, and exposures of the Lower Member of the Rio Dell Formation occur adjacent to where UCMP 219999 was discovered. Other referred specimens were all collected (in situ) from the Lower and Middle Members. Age data (Roth, 1979; Haller, 1980; Sarna-Wojcicki et al., 1982; see Geologic Setting) indicate a late Pliocene age for these fossils, or 3.0–2.0 Ma (Sarna-Wojcicki et al., 1982), and are correlative with the Piacenzian (3.6–2.588 Ma) and Gelasian (2.588–1.806 Ma) stages of international usage (Figs. 1c, 2).

Distribution—Middle to Late Pliocene (4–2 Ma) of the Northwest Pacific and Northeast Pacific, from 32.5°N to 40.5°N latitude (Fig. 5).

Description

Dentary—Both dentaries of UCMP 219999 are preserved in relief in a large calcareous siltstone concretion, with the medial portion of the left dentary and the lateral portion of the right dentary exposed (Fig. 3A). Descriptions of medial features are based on the left dentary, whereas descriptions of lateral features are based on the right dentary. Measurements of both dentaries of UCMP 219999 are given in Table 1. The dentaries possess a relatively short coronoid process and a long horizontal ramus, the dorsal and ventral margins of which are parallel (Fig. 3F–G). The articular surface of the mandibular symphysis is rugose, pitted, and teardrop-shaped with a posteroventrally oriented apex. The medial surface of the horizontal ramus is smooth. Small convex projections occur on the dorsal margin of the ramus along the rims of the p4 and m1 alveoli. The anterior extremity of the ramus is thinned into a keel-like crest. A cluster of five mental foramina

occurs on the lateral surface below the p1, p3, and p4. A subtle genial tuberosity occurs along the ventral margin, below the p2. The coronoid process is broad based (measuring approximately one-third of the length of the dentary). Its anterior margin intersects the horizontal ramus at approximately 133° in the left dentary and 129° in the right dentary (Table 1); this angle in extant *Callorhinus ursinus* ranges from 122-131°. The apex of the coronoid process is broad and rounded. The posterior margin of the coronoid process is vertical, and its medial surface is concave dorsally. The deep massateric fossa on the lateral side of the coronoid process extends ventrally to the level of the pterygoid process. The ventral margin of the massateric fossa is a horizontal ridge that is posteriorly continuous with the lateral margin of the mandibular condyle (Fig. 3F). The digastric prominence is a weakly-developed ridge, ventral to the anterior margin of the massateric fossa. The pterygoid process is located at a position below the apex of the coronoid process, extending posteriorly below the mandibular condyle, and is not expanded into a medially-directed shelf. The posterior apex of the pterygoid process is cubic in shape, and has a squared-off posterior margin when viewed in lateral aspect. The mandibular foramen is positioned just above the pterygoid process, at a position below the apex of the coronoid process. The mandibular foramen is oriented anteriorly. The mandibular condyle is located at the level of the tooth row.

The dentaries of UCMP 219999 differ from *Proterozetes ulysses* and all extant otariids by lacking a medially directed shelf on the pterygoid process, and are smaller than *Thalassoleon* spp., *Hydrarctos lomasiensis*, *P. ulysses*, and all extant otariids (except *Arctocephalus galapagoensis*). These dentaries of UCMP 219999 lack the well developed digastric process of fossil and extant "otariines" and *Arctocephalus*, and they

also lack the sinuous ventral margin of the horizontal ramus as seen in *Otaria* and *Phocarctos*. The coronoid processes are higher than those in *A. galapagoensis*, *A. gazella*, *A. phillippii*, and *A. townsendi*. UCMP 219999 differs from *A. australis*, *A. forsteri*, *H. lomasiensis*, *Zalophus* spp., *Otaria*, *Eumetopias*, *Phocarctos*, and *P. ulysses*, by not possessing a mandibular condyle elevated above the toothrow. They also have a deeper masseteric fossa than *Thalassoleon mexicanus*, *H. lomasiensis*, and *Arctocephalus* and have a dorsoventrally shallower horizontal ramus than *A. australis*, *A. pusillus*, *A. tropicalis*, *H. lomasiensis*, *P. ulysses*, and extant "otariines". UCMP 219999 has dentaries that are approximately the same size and morphology as those of *C. gilmorei* previously reported from California and Japan (Berta and Deméré, 1986; Kohno and Yanagisawa, 1997).

Lower Dentition—Both left and right c1s and the left p2 are the only teeth present (Fig. 3F-G). Two incisor alveoli are present. The i2 alveolus is small, and located posteromedial to the larger i3 alveolus. The i2 alveolus is approximately one-half the diameter of the i3 alveolus. The i3 alveolus is positioned anteromedial to c1. The canines have longitudinally striated enamel, and they are robust and erect with large roots. The conical crowns of the c1s are slightly posteriorly recurved, with well developed, smooth posterior, longitudinal cristae. The anterior surfaces of the c1s are convex and smooth, lacking cristae. No wear facets are visible on the exposed surfaces of the canines. Part of the medial surface of the left c1 is missing, and it is unclear if a medial cingulum was present. Whereas the i2, i3, and c1 are all closely appressed, there is a slight diastema (4 mm) between c1 and p1 in both dentaries (Fig. 3C). The p1 alveolus indicates that the p1 was single rooted, as in all other Carnivora.

The crown of the left p2 is preserved, and it bears a small, pointed, triangular, principal cusp (protoconid; Barnes, 1989) with smooth enamel (Fig. 3B, D, G). The labial surface is not exposed. The smooth lingual cingulum is sinuous and W-shaped, so that it is dorsally arched in the middle, posterior, and anterior portions of the crown. A well defined anterior accessory cusp is located anteriorly at the base of the crown and merges with the lingual cingulum. There are well-developed, smooth, longitudinal cristae on the anterior and posterior edges of the crown, as well as a slight crista bisecting the lingual surface of the tooth. The posterior crista continues to the base of the crown; there is no posterior accessory cusp. The lingual surface of the p2 is slightly convex, and a slight posterodorsally oriented wear facet is located at the apex of the cusp. The root of the p2 is not bifurcated and lacks a longitudinal sulcus. Instead it appears to have a cylindrical, single root (Fig. 3B, D) because the right p2 alveolus lacks an interalveolar septum (Fig. 3C). Each p3 alveolus bears a slight interalveolar septum (Fig. 3C), indicating a bilobate or double-rooted condition. Both the right p4 and m1 alveoli have well-developed intra-alveolar septa preserved (Fig. 3C), indicating strongly double-rooted teeth. These alveoli are incompletely preserved on the left dentary. Unlike the small c1-p1 diastema, there are no diastemata between p1-m1, indicating that these teeth were closely appressed.

The c1 of UCMP 219999 is smaller (relative to the size of the dentary) than in fossil and extant “otariines” but compares well with those of *Thalassoleon* spp., fossil and extant *Callorhinus*, and *Arctocephalus*. The p2 of UCMP 219999 is most similar to the premolars of *C. ursinus* and *C. gilmorei*, which also exhibit small crowns with a pointed principal cusp and distinct anterior accessory cusps (Fig. 7). The lower postcanine dentition of UCMP 219999 differs from *Pithanotaria starri* and *Thalassoleon*

spp. by possessing single rooted p1-2 (those taxa have double rooted p2-m1), and it differs from *H. lomasiensis*, *P. ulysses*, and all extant otariids in retaining double rooted p3-m1 (which all have single rooted lower p1-m1; Figs. 6, 8). The presence of a distinct anterior accessory cusp on the p2 of UCMP 219999 differs from the postcanine condition in *P. starri*, *Thalassoleon* spp., *A. gazella*, *A. phillippii*, *A. townsendi*, which all possess unicuspid lower postcanine teeth that lack anterior and posterior accessory cusps (Repenning et al., 1971; Deméré and Berta, 2005; Fig. 7). The lack of a labial cingulum distinguishes UCMP 219999, *P. starri*, *Thalassoleon* spp., *H. lomasiensis*, *Callorhinus*, and *Arctocephalus* from fossil and extant "otariines" (Deméré and Berta, 2005). The presence of a lingual cingulum in UCMP 219999 differs from *P. starri*, *A. phillippii*, and *A. townsendi*, which lack lingual cingula (Repenning et al., 1971). The p2 of UCMP 219999 and the postcanines of *C. gilmorei* and *C. ursinus* are proportionally smaller than those of fossil and extant "otariines" and *Arctocephalus* (Figs. 6, 8).

Remarks—The combination of the postcanine root condition in the dentaries, a premolar with moderately-developed accessory cusps, small size, and lack of a pterygoid 'shelf' supports referral of UCMP 219999 to *C. gilmorei* (Fig. 6). The relatively large and erect canines suggest that UCMP 219999 is a male; these dentaries are more robust than most specimens of *C. gilmorei* from the San Diego Formation (e.g. SDNHM 25176, 25554, 26239), and are roughly the size of the largest known specimens. Like *C. gilmorei* from the San Diego Formation, the dentaries of UCMP 219999 are smaller and less robust than those of *Thalassoleon* spp. and extant *C. ursinus*. Despite their small size, the deep masseteric fossa, fully erupted canines and p2, and fully developed coronoid process all indicate this individual was mature (Brunner et al., 2004). Additionally, the horizontal

rami are roughly rectangular in lateral aspect. To accommodate the large, growing canine, the horizontal ramus of juvenile otariid dentaries is dorsoventrally deeper near the symphysis (Boessenecker, pers. obs.). The tabular shape of the horizontal rami in UCMP 219999 also indicative of maturity.

Fossil dentaries of *C. gilmorei* are similar in size to those of *A. galapagoensis* and *A. townsendi*, the smallest extant otariids. The referred radius (VMS 7) exhibits many features similar to radii of *T. mexicanus*, such as a pronator teres process that is positioned more distally than in *C. ursinus* (and all other extant otariids), suggesting a longer moment arm for the pronator teres (Deméré and Berta, 2005). Additionally, the distal half of VMS 7 is very robust and expanded much more anteriorly than in *T. mexicanus*, *C. ursinus*, and other extant and fossil otariids. This new record extends the geographic range of *C. gilmorei* approximately 750 miles north (adjusted for strike-slip displacement) along the eastern margin of the Pacific Ocean (Fig. 5). This range extension, in addition to the Late Pliocene record of *C. gilmorei* from Japan (Kohno and Yanagisawa, 1997), indicates that this taxon was widely distributed not only in a circum-North Pacific pattern, but latitudinally as well, from 32.5° N to 40.5° N (paleolatitude for the San Diego Formation and the Rio Dell Formation, respectively; Hall, 2002; Fig. 5). Extant *C. ursinus* inhabits a very similar, circum-North Pacific range (Gentry, 1981) to that now known for *C. gilmorei* (Fig. 5). Some isolated postcranial elements from the Rio Dell Formation will be featured in a wider study of new fossils of *Callorhinus gilmorei* in the future.

CALLORHINUS sp.

(Fig. 4)

Referred Specimen—VMS 15, partial right dentary lacking posterior portion of ramus, with partial c1 and m1 (Fig. 4A-C), collected R. J. Bushell, 1994.

Formation and Age—VMS 15 was collected from an exposure of the uppermost Upper Member of the Rio Dell Formation; ash dates, molluscan biostratigraphy and foraminiferal biostratigraphy indicate a latest Pliocene to Early Pleistocene age for this stratigraphic horizon (see Geologic Setting), correlative with the latest Gelasian (2.588-1.806 Ma) and Calabrian (1.806-0.781 Ma) stages of international usage.

Distribution—latest Pliocene to Early Pleistocene (2.1–1.2 Ma) of the Northeast Pacific Ocean.

Description

Dentary—The posterior portion of VMS 15 was eroded away prior to discovery, and the canine was damaged during collection. Measurements of VMS 15 are given in Table 1. The horizontal ramus of VMS 15 is deep dorsoventrally, with parallel dorsal and ventral margins (Fig. 4A, B). The portion of the ramus anterior to c1 is transversely narrow, forming a sharp keel on the anterior margin of the dentary, near c1, the dentary is transversely thickest and rugose, and posteriorly, the horizontal ramus becomes transversely thinner (Fig. 4C). The articular surface of the mandibular symphysis is rugose and nearly circular in shape, the posterior margin of which is oriented vertically. The i2 alveolus opens onto the anterodorsal portion of this articular surface (Fig. 4B, C). The small genial tuberosity is positioned just posterior to the mandibular symphysis. Four

large mental foramina are positioned below p1-3. The medial surface of the horizontal ramus is broad and flat. The masseteric fossa is shallow, the anterior portion of which is preserved below the ascending ramus (Fig. 4A). The anterior margin of the coronoid process and the horizontal ramus intersect at approximately 105° , in contrast to the larger angle in the dentaries of *Callorhinus gilmorei* described above (Table 1). The break through the posterior portion of the mandible shows the mandibular foramen in cross-section, and it is positioned just ventral to the level of the toothrow. The area of insertion for the digastric is not clearly marked (Fig. 4A, B).

Lower Dentition—Two distinct lower incisor alveoli are present slightly ventral to the level of the postcanine alveoli (Fig. 4C). The i2 alveolus is small relative to that of i3, and it is positioned almost completely posterior to the i3 alveolus and medial to c1. The i3 alveolus is situated anteromedial to the c1. The c1 is massive and very broad transversely and anteroposteriorly. Much of its crown is broken, revealing an oval cross-section. X-ray imaging shows that the c1 root is massive and extends posteroventrally in the dentary ventral to the p2 alveolus. There is no diastema between the c1 and p1, and the p1-4 and m1 are separated only by very thin, incomplete bony septa. The p1-4 alveoli are all cylindrical, indicating that all premolars possessed completely fused, single roots, rather than being double-rooted (Fig. 4C). The p1-2 are slightly anteriorly oriented, whereas the p3-m1 are dorsally oriented. Based on x-ray imaging, the m1 has widely divergent roots, in contrast to the single-rooted p1-4 alveoli. The m1 crown bears a triangular principal cusp (protoconid), and has a slight wear facet on the posterior portion of its apex. The crown is dorsally arched at its base, and it possesses well developed anterior and posterior accessory cusps and longitudinal cristae on the anterior and

posterior edges of the crown (Fig. 4A, B). The labial surface is convex and lacks a cingulum. Both accessory cusps merge medially with a well-developed lingual cingulum with finely developed crenations.

Comparisons and Remarks—This specimen differs from *Thalassoleon* and *Pithanotaria* by having single-rooted p2-p4 (Fig. 6) with well-developed accessory cusps, and a larger, more robust ramus than *Pithanotaria*. VMS 15 differs from *Hydrarctos lomasiensis* by having an anteroposteriorly broader postcanine crown with well-developed accessory cusps and postcanine teeth and alveoli that are oriented vertically rather than posterodorsally. VMS 15 lacks a small diastema between the c1 and p1, like *Callorhinus ursinus*, in contrast to *C. gilmorei* and *Thalassoleon* spp. VMS 15 differs from fossil and extant "otariines" in the smaller size of the dentary and the absence of a labial cingulum. The presence of well developed anterior and posterior accessory cusps distinguish this specimen from *Arctocephalus townsendi* and *A. phillipii*, which also have a horizontal ramus that is much less robust than VMS 15. The lack of a well-developed digastric process distinguishes VMS 15, *C. gilmorei*, *C. ursinus*, and *Thalassoleon* spp. from *Arctocephalus*, *H. lomasiensis*, and all fossil and extant "otariines". The large size of the canine and the robust horizontal ramus suggest that this specimen is also a male. The fully erupted canine and m1, robust and tabular horizontal ramus, and deep masseteric fossa are all indicative of maturity (Brunner et al., 2004).

In order to evaluate the significance of the root fusion in fossil *Callorhinus*, dentaries of extant *C. ursinus* from the CAS collections (n = 54) were examined. All variation in the fusion of lower postcanines occurred with the m1; 65.2% of specimens (n = 35) exhibited single rooted m1 with a cylindrical or oval root, 33% of specimens (n =

18) exhibited a bilobate m1 (single rooted with strong longitudinal sulci on the lingual and labial root surfaces), and only 1.8% ($n = 1$) exhibited a double-rooted m1. Although rare cases of *C. ursinus* with double-rooted m1 do exist, these data indicate that VMS 15 likely does not fall within the range of normal variation for extant *C. ursinus*, and that this morphology is potentially ancestral to *C. ursinus* (Fig. 6). Dentaries of *C. gilmorei* exhibit a far less advanced stage of root fusion (single rooted p1-2 and double rooted p3-m1) than this specimen (Fig. 6), they are smaller than VMS 15. Within a morphological series, VMS 15 is more derived than *C. gilmorei* and less derived than *C. ursinus* (Fig. 6). This pattern is consistent with the intermediate geologic age of fossil and extant *Callorhinus*.

DISCUSSION

Previous to this study, the only published vertebrate fossils from the Rio Dell Formation were teeth of the vole *Pitymys mcnowni* from Centerville Beach (Repenning, 1983), somewhat surprising for marine sediments. This study presents the first detailed description of vertebrate fossils from the Rio Dell Formation, and indeed the first record of otariids from the Early Pleistocene of the Northeast Pacific. Further field investigation of Pleistocene marine units would likely result in additional fossil discoveries that would vastly improve the currently poor Pleistocene marine mammal record, and further refine the timing of biogeographic and extinction events. Extinction events in the Plio-Pleistocene of the Northeast Pacific include (by inference) the extinction of dusignathine

and odobenine (e.g. *Valenictus*) walruses, herpetocetine mysticetes, dwarf balaenid mysticetes, archaic balaenopterid mysticetes, archaic phocoenid porpoises, and archaic delphinapterine odontocetes (none of which occur in Late Pleistocene assemblages or the modern fauna of the Northeast Pacific). Additionally, during this time, the temperate Northeast Pacific was possibly invaded by "otarine" sea lions (*Zalophus*, '*Proterozetes*', and *Eumetopias*), harbor seals (*Phoca vitulina*), elephant seals (*Mirounga angustirostris*), and the sea otter (*Enhydra*), all of which are known from Middle and Late Pleistocene assemblages in this region but not from Pliocene fossil assemblages. By the Late Pleistocene, *Odobenus* had reinvaded the Northeast Pacific (Deméré et al., 2003); again, *Odobenus* is known from the Pliocene of Japan, but not from the Northeast Pacific until the late Pleistocene (Deméré et al., 2003). It is certainly possible that future field investigation will ultimately discover fossils of these taxa in Pliocene marine strata in California. It is also equally possible that these taxa invaded from the Northwest Pacific, Arctic (as postulated for *Phoca* and *Odobenus*; Deméré et al., 2003), or southern Pacific (as hypothesized for *Mirounga*; Deméré et al. 2003) at the close of the Pliocene, or that some inhabited higher latitudes during the Pliocene (and thus are not preserved within lower latitude Pliocene assemblages of California).

Anagenesis in *Callorhinus*

In addition to the extant Northern Fur Seal *Callorhinus ursinus*, which currently has a circum-North Pacific distribution (Fig. 5), representatives of the fur seal *Callorhinus* are now recorded from the Upper Pliocene of the Northwest and Northeast Pacific (*C. gilmorei*, Berta and Deméré, 1986; Kohno and Yanagisawa, 1997; this study;

Fig. 5), the Lower Pleistocene of the Northeast (this study) and Northwest Pacific (Miyazaki et al., 1995), the middle Pleistocene (Barnes et al., 2006) of the Northeast Pacific, and the Upper Pleistocene of the Northwest and Northeast Pacific (Kurtén and Anderson, 1980; Miyazaki et al., 1995). This suggests that *Callorhinus* has maintained a circum-North Pacific population since at least the Pliocene. The near continuous fossil record of *Callorhinus*, which is restricted to the North Pacific realm, strongly indicates a circum-North Pacific, Pliocene-Holocene lineage endemic to this region, including *C. gilmorei* and *Callorhinus* sp., and culminating in the extant Northern Fur Seal, *C. ursinus*, which currently occupies a circum-North Pacific distribution (Gentry, 1981; Fig. 5).

Due to the similarities in morphology and circum-North Pacific range of *C. ursinus* and *C. gilmorei* (Fig. 5), Kohno and Yanagisawa (1997) hypothesized that these two species were end members of an anagenetic lineage. As stated above, the morphology of this new Pleistocene specimen is more derived than *C. gilmorei* and potentially ancestral to *C. ursinus*. The morphology and intermediate age of *Callorhinus* sp. supports the anagenetic hypothesis of Kohno and Yanagisawa (1997). Taken in concert with the continuous (albeit poor) Pliocene-Holocene fossil record of *Callorhinus*, this suggests that the extant Northern fur seal *Callorhinus* has existed as an endemic circum-North Pacific taxon since the Pliocene. Coincidentally, *Callorhinus* persistently holds the most basal position among extant otariids in morphological (Berta and Deméré, 1986; Deméré and Berta, 2005) and molecular (Wynen et al., 2001; Yonezawa et al., 2009) phylogenetic hypotheses. Fossils referred to *C. gilmorei* and *Callorhinus* sp. from the Pliocene and Pleistocene of the Northern Pacific represent a morphological continuum, with the extant *C. ursinus* as an end member. There are no morphological

features in either fossil taxon that would preclude the evolution of the subsequent taxon from the former, and in the absence of any evidence indicating cladogenesis within *Callorhinus* since the Pliocene, anagenesis is preferred as the simpler (or null) hypothesis.

These three taxa (*Callorhinus gilmorei*, *Callorhinus* sp., and *Callorhinus ursinus*) exhibit increasingly derived morphology toward the recent, and they can be considered 'cross sections' or samples of the *Callorhinus* lineage through time. This is best exemplified with the state of postcanine root fusion in each taxon (Fig. 6). *C. gilmorei* displays incipient postcanine root fusion, most often with a single rooted p2, although some specimens have p1-3 single rooted whereas others have double rooted p2-m1 (Berta and Deméré, 1986). *Callorhinus* sp. exhibits a more derived stage of root fusion than *C. gilmorei*, the m1 being the only remaining double rooted tooth. Finally, in extant *C. ursinus*, the majority of specimens have a single rooted m1, although some occasionally (perhaps atavistically) exhibit a bilobate or even more rarely a double rooted m1; this variation mirrors that seen in *C. gilmorei*. This degree of dental variation has likely always existed within the *Callorhinus* lineage, with the locus of root fusion migrating posteriorly through the postcanine teeth with time. The longevity of this lineage (~4 Ma) in the North Pacific indicates that *Callorhinus* has survived extinctions, extirpations, and invasions of other marine mammals since the Pliocene. *C. ursinus*, if viewed as a modern 'cross-section' of a 4 Ma lineage, is the longest surviving pinniped taxon in the Northeast Pacific, attesting to the antiquity of these distinctive marine mammals. Further study of Plio–Pleistocene otariid fossils, and more complete material of *Callorhinus* sp. and other

Pleistocene Otariidae will be paramount to further testing of the anagenesis hypothesis of Kohno and Yanagisawa (1997).

Dental Evolution

Several changes have been observed in the dentition of the Pinnipedia relative to their terrestrial forebears. Modern pinnipeds are characterized by generally homodont postcanine teeth (achieved by reduction in crown size, complexity, and root coalescence; Fig. 7) and loss of dental integration of the shearing postcanine teeth. Early diverging pinnipedimorphs, namely *Enaliarctos*, retain a functional shearing dentition similar to terrestrial arctoids (Mitchell and Tedford, 1973). Although technically homodont, most phocid seals (e.g. *Phoca*) retain double rooted, multicusped postcanine teeth (i.e. well developed protoconid, paraconids, talonids, and occasionally metaconids), which in some cases are little changed from the primitive “enaliarctine” condition (Fig. 7). Some phocids, such as *Mirounga* and *Halichoerus*, have developed single rooted postcanines with simpler cusps (Boessenecker, pers. obs.). The extinct desmatophocid *Allodesmus* retained only a bulbous principal cusp (Barnes, 1972). A similar pattern of simple, unicuspid bulbous postcanines also evolved in the dusignathine and odobenine walruses (Deméré, 1994; Fig. 7). The homodont postcanine teeth of fossil and extant otariids ranges from relatively simple unicuspid crowns lacking anterior and posterior accessory cusps and cingula (*Pithanotaria*, *Arctocephalus townsendi*, *Arctocephalus phillippii*) to more complex crowns with strongly developed anterior and posterior accessory cusps, labial and lingual cingula with crenations, and rough enamel in the “otariines” (Brunner, 2004; Deméré and Berta, 2005; Fig. 7).

Kellogg (1922) originally proposed that the rather simple homodont dentition of most pinnipeds was simplified from the more complex crowns of their terrestrial ancestors and that cusp elaboration as seen in the "Otariinae" (Brunner, 2004; Deméré and Berta, 2005) represents a reversal. Chiasson (1957) strongly criticized this idea because he could not envisage an adaptive scenario where dental simplification could occur. This would suggest that the mammalian ancestors of pinnipeds possessed a homodont dentition, arguing against a carnivoran or 'creodont' ancestry. The dentition of archaic pinnipeds such as *Enaliarctos* and the putative stem-pinniped *Puijila* exhibit complex postcanine crown morphology (Fig. 7), that with other features 'root' the pinnipeds with arctoid ancestry (Mitchell and Tedford, 1973; Barnes, 1989; Rybczynski et al. 2009). In the case of basal pinnipeds, postcanine crown simplification is an adaptation for pierce feeding (Adam and Berta, 2002), where prey items are caught and swallowed whole, rather than masticated and processed. Interestingly, basal otariids such as *Pithanotaria* and *Thalassoleon* exhibit extremely simplified postcanine teeth (Fig. 7), and extant otariids exhibit a variety of postcanine crown complexity, with the most complex morphologies (among the Otariidae) occurring in extant "otariines" (Repenning and Tedford, 1977; Deméré and Berta, 2005; Fig. 7). Although circuitous, the initial crown simplification (e.g. *Pithanotaria* and *Thalassoleon*) and subsequent evolution of accessory cusps (anterior and posterior accessory cusps representing reversals to regaining the paraconid and talonid cusps, respectively) and labial cingula as originally hypothesized by Kellogg (1922) is now borne out by the otariid fossil record, *contra* Chiasson (1957; Fig. 7).

As outlined above, *Callorhinus* sp. is intermediate in morphology and age between Pliocene *C. gilmorei* and extant *C. ursinus*, as evidenced primarily by the intermediate stage of root fusion (Fig. 6b-e). Some variation of root morphology is present in *C. gilmorei* (Berta and Deméré 1986), although the p4 and m1 are rarely single rooted, in contrast to *Callorhinus* sp. (which has a single rooted p1-4 and double rooted m1) and *C. ursinus* (both p4 and m1 are single rooted). Among extant otariids, occurrences of double-rooted (or bilobate) postcanine roots are more common in fur seals than in "otariine" sea lions and *Arctocephalus pusillus* (Repenning et al., 1971). Interestingly, data on root fusion in *C. ursinus* that was gathered as part of the present study indicates a different pattern of root variation for the upper dentition as compared to that of the lower dentition reported above. As compared to 65% of specimens exhibiting a single rooted m1, the M1 is single rooted in only 13% of specimens ($n = 7$), whereas 56% were bilobate ($n = 30$), and 31% ($n = 17$) were double rooted. The only other variable teeth were the P4 and M2, of which 5.5% ($n = 3$) and 9.2% ($n = 5$) were bilobate (respectively). It is noteworthy that these teeth in terrestrial carnivorans possess three roots, and these are the first teeth to begin root fusion within early diverging pinnipedimorphs (Barnes, 1989; Berta, 1991; Berta, 1994). This pattern of root variation within *C. ursinus* is potentially explained by the double rooted cheek teeth (i.e. P2-3, p2-m1) achieving single-rootedness earlier than triple rooted cheek teeth. Interestingly, in the extinct desmatophocid *Allodesmus kernenesis*, the M1 is the only tooth that exhibits any tendency towards double rooting (Barnes, 1972).

Other patterns of informative pinniped dental variation include the atavistic reappearance of the m2 in extant otariids (Drehmer et al., 2004) and dental agenesis

(Loch et al., 2010). The high incidence of dental variation in otariids (relative to terrestrial carnivorans) indicates that dental anomalies probably do not adversely affect feeding ability (Drehmer et al., 2004; Loch et al., 2010). Indeed, phocid seals have been shown to exhibit greater dental variation relative to terrestrial carnivores, probably related to the non-occluding nature of pinniped dentitions relative to the integrated dentition of terrestrial carnivorans (Miller et al., 2007), a functional constraint from which pinnipeds have been released. Posterior upper postcanines (i.e. M1-2) of otariids have recently been observed to lie medial to the lower toothrow, and hence do not occlude at all (Adam and Berta, 2002). Additionally, the “hanging” posterior cheek teeth (M2 in most fur seals, M1 in *Eumetopias* and other “otariines”) in the upper jaw of many otariids lie completely posterior to the lower toothrow (due to a long diastema in *Eumetopias*), lack a lower antagonist, and thus have been interpreted as being vestigial (Chiasson, 1957; Kubota and Togawa, 1964; Drehmer et al., 2004). However, it is important to note that pierce feeders do not masticate, and the lack of a lower antagonist does not necessarily indicate these teeth lack any function because the dentition merely serves to seize and hold prey items which are swallowed whole,. Furthermore, it is interesting to note that the posteriormost upper postcanines (M1 only in *Eumetopias*, sometimes both M1-2) are consistently oriented in a posteroventral direction among most extant otariids (Boessenecker, pers. obs.). These teeth can function as an oral ‘trap’ that secures large and struggling prey from escaping the oral cavity during capture and inertial swallowing, as has been suggested for the pterygoid teeth of mosasaurs (Lee et al., 1999). The loss of the m2 was identified as a potential synapomorphy of the Pinnipedia by Berta and Wyss (1994); however, m2 is present in the desmatophocid *Allodesmus* (Barnes, 1972), the

designathine walrus *Pontolis magnus* (Deméré, 1994), and occasionally present in *Imagotaria downsi* (Repenning and Tedford, 1977). Given the tendency for other dental features to evolve in parallel within the Pinnipedia (see below), it is possible the m2 was convergently lost in several pinniped clades.

Fusion of postcanine roots was initiated by coalescence of the two posterior (protocone and metacone) roots of the P4 (Barnes, 1989), and then coalescence of the double-rooted P2-M2 and p2-m1, from anterior to posterior (Barnes et al., 2006). Given the new fossils described herein, this pattern of root fusion is now best exemplified by the fossil record and evolution of *Callorhinus* (See Anagenesis in *Callorhinus*). Additionally, as evidenced by the intermediate root conditions in *Imagotaria downsi* (Repenning and Tedford, 1977) and *Pontolis magnus* (Deméré, 1994), fusion of postcanine roots was simultaneously initiated in the upper and lower dentitions (also anterior to posterior). Fusion of postcanine roots evolved independently in multiple pinniped groups, potentially seven times, including *Callorhinus* (this study), stem-odobenids (Repenning and Tedford, 1977; Deméré, 1994), desmatophocids (Deméré and Berta, 2002), the "Otariinae" + *Arctocephalus* clade (King, 1983; Barnes et al., 2006), basal phocinae (*Cystophora cristata*; Gray, 1848; *Halichoerus grypus*, Bininda-Emonds and Russell, 1996) and elephant seals, *Mirounga* spp. (Briggs and Morejohn, 1976). Fewer parallelisms on this condition may be possible if some reversals to the double rooted condition occurred. Future investigation of pinniped dental evolution should involve phylogenetic tracing of these characters on well supported phylogenies.

The parallel evolution of single-rooted cheek teeth in so many different pinniped clades suggests strong selection for this feature, which in this case is most likely related

to feeding. The lack of mastication in extant (and most fossil) pinnipeds (Adam and Berta, 2002), and the reduced necessity of multicusped, multirooted, integrated cheek teeth is another parallel phenomenon within the pinnipeds. Perhaps single rooting simply results from the smaller size of simpler, homodont teeth. However, as evidenced by the homodont dentitions of *Pithanotaria* and *Thalassoleon*, homodonty (within the otariids) preceded the development of single rooted teeth (Figs. 6a, 7), indicating that root fusion is related to some other factor. Anterior migration of the toothrow is potentially an adaptation to increase gape in pierce-feeding pinnipeds (Adam and Berta, 2002), which, unlike terrestrial carnivores, do not masticate and thus are not substantially constrained by bite force (Adam and Berta, 2002). Because single-rooted teeth are anteroposteriorly narrower than double-rooted teeth (Figs. 6, 8), fusion of double-rooted postcanine teeth may accommodate crowding of these teeth anteriorly as a means to further increase gape. This offers a possible explanation for the convergent fusion of double-rooted postcanine teeth in multiple pinniped groups. The extreme degree of parallel evolution of various dental features (root fusion, homodonty, tooth loss) within pinnipeds perhaps results in the relatively poor correlation between functional anatomy and feeding ecology of extant pinnipeds (Adam and Berta, 2002). Furthermore, future analysis of the highly contested phylogenetic relationships within the Pinnipedimorpha and their position within the Carnivora must carefully take into account the known patterns of dental parallelisms when selecting dental characteristics.

CONCLUSIONS

New pinniped fossils from different stratigraphic levels in the Plio-Pleistocene Rio Dell Formation in Northern California represent a Late Pliocene fur seal, *Callorhinus gilmorei*, and a more derived Early Pleistocene taxon, *Callorhinus* sp. The dental morphology of *C. gilmorei* is less derived than the extant Northern Fur Seal, *C. ursinus*, primarily by the retention of double-rooted p3-m1 and less complex postcanine crown morphology. The dental morphology of *Callorhinus* sp. is closer to *C. ursinus*, in possessing single rooted p3-4 and only retaining a double-rooted m1 (which is typically single rooted in the extant species). Fusion of tooth roots in fossil *Callorhinus* was initiated by fusion of the p2 roots, and progressed posteriorly to the m1, a pattern which parallels other pinniped groups that achieved single-rooted postcanines. Fusion of postcanine roots is likely an adaptation to crowd teeth anteriorly in the jaw to increase effective gape, and is a convergent feature among pinnipeds that has possibly evolved in parallel seven times. The different instances of parallel evolution within pinniped dentitions have implications for the selection of dental characters for phylogenetic analysis. The paleobiogeographic distribution of *C. gilmorei*, coupled with multiple occurrences of *Callorhinus* in lower, middle, and upper Pleistocene deposits of the Northwest and Northeast Pacific indicates that *Callorhinus* has remained endemic to the North Pacific, even after the extirpation of walruses at the end of the Pliocene and invasion of this region by five other species of otariids and phocids. This suggests that extant *C. ursinus* represents the living end-member of a Pliocene-Holocene anagenetic lineage, which has enjoyed a circum-North Pacific distribution for approximately 4 million years, greatly attesting to the antiquity of this peculiar extant pinniped.

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FIGURE 1. Generalized geologic map and stratigraphy of the Wildcat Group in Humboldt County, California. **A**, map of northern California, with box showing map in **B**; **B**, geologic map of the Rio Dell Formation in Humboldt County, with "X" marking UCMP locality V99861 and Sierra College localities; **C**, generalized stratigraphy of the Wildcat Group in Humboldt County (modified from Sarna-Wojcicki et al., 1982, and Leithold and Bourgeois, 1989). [planned for page width]

FIGURE 2. Simplified stratigraphic column of the type section of the Rio Dell Formation at Scotia Bluffs, California (modified from Haller, 1980), showing stratigraphic positions of *Callorhinus gilmorei* and *Callorhinus* sp. Rows (from left) are epoch, stage, stratigraphic unit, and thickness (in meters). [planned for column width]

FIGURE 3. Dentaries and lower dentition of *Callorhinus gilmorei* (UCMP 219999). **A**, dentaries exposed in relief in concretion; **B**, lingual aspect of left c1 and p2; **C**, right dentary in occlusal aspect; **D**, dorsolingual aspect of left p2; **E**, labial aspect of right c1; **F**, right dentary in lateral aspect; **G**, left dentary in medial aspect (note reconstructed middle portion of horizontal ramus). [planned for page width]

FIGURE 4. Dentary of *Callorhinus* sp. (VMS 15). **A**, dentary in lateral aspect; **B**, dentary in medial aspect; **C**, dentary in dorsal aspect. [planned for page width]

FIGURE 5. Map of the modern North Pacific showing the fossil distribution of *Callorhinus gilmorei* (stars) and the current range of the extant Northern Fur Seal, *Callorhinus ursinus* (shaded in gray). [planned for page width]

FIGURE 6. Schematic diagrams (drawn in lateral aspect) of dentaries and postcanine root morphology in the anagenetic *Callorhinus* lineage, and *Thalassoleon mexicanus* for comparison. **A**, *Thalassoleon mexicanus*, reversed (redrawn from Deméré and Berta, 2005); **B**, *Callorhinus gilmorei* from the Rio Dell Formation (UCMP 219999); **C**, *Callorhinus gilmorei*, holotype specimen from the San Diego Formation, reversed (redrawn from Berta and Deméré, 1986); **D**, *Callorhinus* sp. (VMS 15); **E**, *Callorhinus ursinus* (redrawn from Brunner, 2004). The depicted root morphology is based on alveolar morphology, whereas *Callorhinus* sp. is directly drawn from an X-ray. Missing parts of fossils have been reconstructed. Scale bars equal 20 mm. [planned for column width]

FIGURE 7. Postcanine tooth variation within the Pinnipedimorpha. Posterior left lower postcanines are depicted in lingual aspect, usually the p4 (the p3 of *Dusingathus santacruzensis*, *Pithanotaria starri*, *Callorhinus gilmorei*, and m1 of *Callorhinus sp.* were depicted because other postcanines were missing), on a simplified version of the composite phylogenetic hypothesis presented by Deméré et al. (2003:fig. 3.3) showing inferred phylogenetic position of *Callorhinus gilmorei* (after Deméré and Berta, 2005) and *Callorhinus sp.* (this study). Anterior is to the right. Drawings are not to scale. [planned for page width]

FIGURE 8. Schematic drawings (drawn in lateral aspect) of dentaries and postcanine root morphology of the basal pinnipedimorph *Enaliarctos emlongi* and other otariids. **A**, *Enaliarctos emlongi*, holotype right dentary (redrawn from Berta, 1991); **B**, *Hydrarctos lomasiensis*, holotype right dentary (redrawn from Muizon, 1978); **C**, *Arctocephalus pusillus* (redrawn from Brunner, 2004); **D**, *Zalophus californianus* (redrawn from Brunner, 2004); **E**, *Eumetopias jubatus* (redrawn from Brunner, 2004). The depicted root morphology is based on alveolar morphology, and missing parts of fossils have been reconstructed. Scale bars equal 20 mm. [planned for column width]