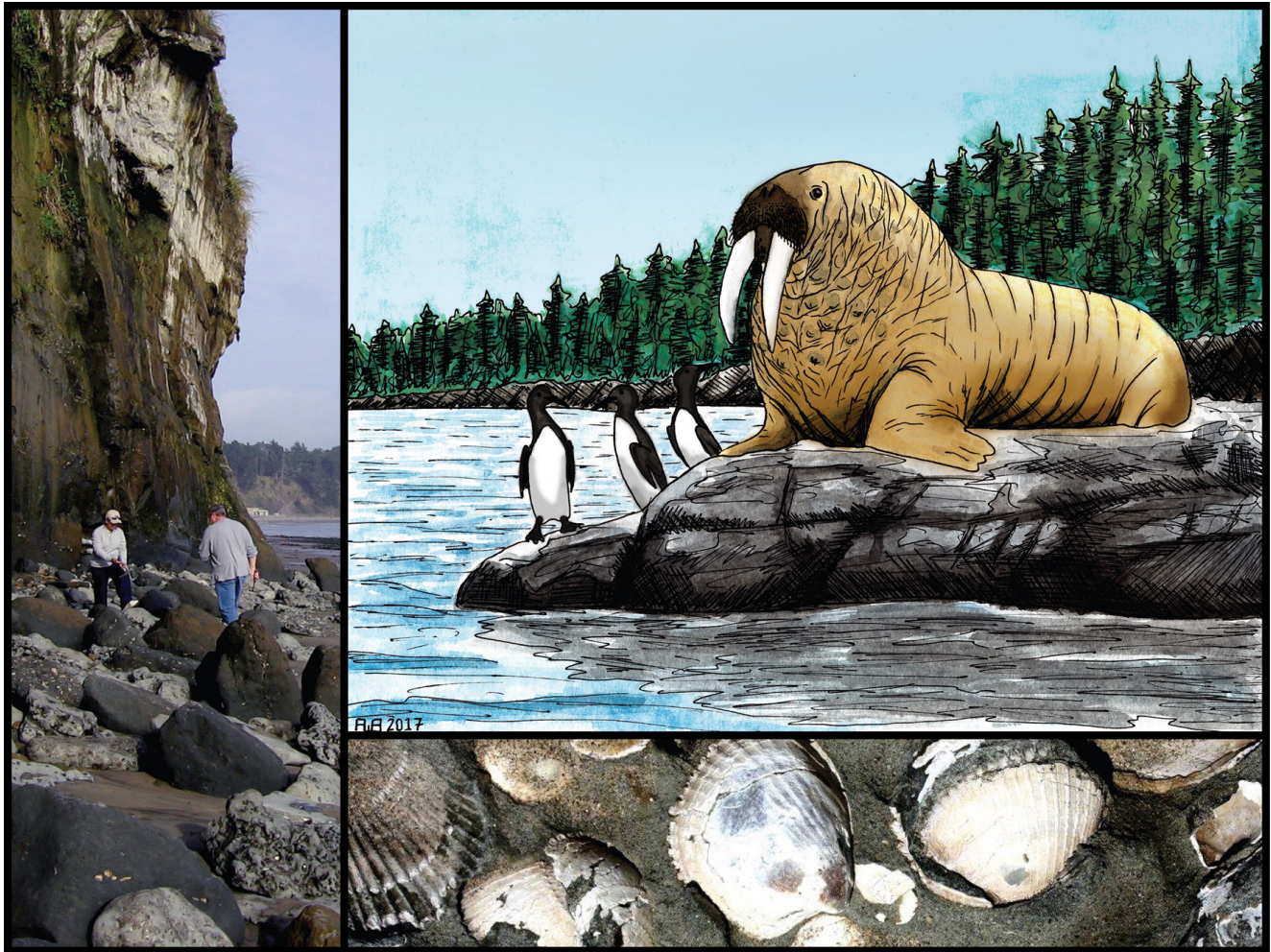


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Cover photo: Life restoration of the extinct Pliocene walrus *Valenictus* and flightless auks (*Mancalla*) hauled out on the rocky shore of the uplifted Coast Ranges of California (top right); cliff exposures of the Purisima Formation near Santa Cruz, from where *Valenictus* was collected by Wayne Thompson (left); bivalves, chiefly *Clinocardium meekianum*, exposed in the Purisima Formation near the locality (bottom).

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A New Early Pliocene Record of the Toothless Walrus *Valenictus* (Carnivora, Odobenidae) from the Purisima Formation of Northern California

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The walrus (*Odobenus rosmarus*) is a large tusked molluskivore that inhabits the Arctic and is the sole living member of the family Odobenidae. In contrast to the modern walrus, extinct walruses lived in temperate and even subtropical climates as far south as Baja California and Japan in the Pacific, and Florida and Morocco in the Atlantic. Multispecies walrus assemblages are now documented from several localities in the North Pacific, the center of origin for the family. The genus *Valenictus* is a toothless dense-boned walrus reported from several localities in southern California and Baja California. An isolated astragalus from lower Pliocene (5.33–4.89 Ma, Zanclean correlative) sediments of the Purisima Formation of northern California (Santa Cruz County, California) matches the highly derived morphology of *Valenictus chulavistensis*, and is identifiable as *Valenictus* sp. This specimen is the first record of *Valenictus* from the Purisima Formation and the first from northern California.

Keywords: Purisima Formation, Santa Cruz, California, Pliocene, Odobenidae, *Valenictus*

INTRODUCTION

The walrus (*Odobenus rosmarus* Linnaeus, 1758) is arguably the strangest of all modern pinnipeds, bearing a pair of elongated canine tusks, reduced postcanine teeth, and numerous skeletal and soft tissue adaptations for suction feeding on mollusks (Fay 1982). Whereas the modern walrus is monotypic, with an Arctic distribution, extinct walruses inhabited warm temperate and subtropical environments and, in the North Pacific, composed multispecies walrus assemblages (Repenning and Tedford 1977, Deméré 1994a, b, Miyazaki et al. 1995, Boessenecker 2013a). The earliest tusked walruses (Odobenini Deméré, 1994a) appear in lower Pliocene marine sediments of the North Pacific and North Atlantic (Kellogg 1921, Mitchell 1961, Repenning and Tedford 1977, Deméré 1994b, Kohno et al. 1995, 1998, Kohno and Ray 2008). The Odobenini represent a North Pacific diversification of molluskivorous predators, with *Ontocetus* Leidy, 1859 and *Odobenus* Linnaeus, 1758 dispersing from the western North Pacific through the Arctic to the North Atlantic during the Pliocene and Pleistocene (respectively; Kohno et al. 1995, 1998, Kohno and Ray 2008). Records of Odobenini from Pliocene deposits in California and Baja California correspond to a provincial eastern North Pacific marine mammal assemblage (Boessenecker 2013a) and

include the poorly known *Pliopedia pacifica* (Kellogg, 1921), various occurrences of *Valenictus* Mitchell, 1961 (Repenning and Tedford 1977, Deméré 1994a, b), and more fragmentary specimens awaiting formal description. Although formerly based on an isolated humerus (*Valenictus imperialensis* Mitchell, 1961), virtually complete skeletons of *Valenictus* from the Pliocene San Diego Formation of southern California formed the basis of the new species *V. chulavistensis* Deméré, 1994b. *Valenictus* is characterized by pachyosteosclerotic bones (thickened cortex and densification of inner bone) as well as a “toothless” skull lacking non-canine teeth; in these features, *Valenictus* is arguably more derived than extant *Odobenus* (Deméré 1994b). *Valenictus* is an obligate suction feeding molluskivore similar to modern *Odobenus* (Deméré 1994b); pachyosteosclerosis may serve as bone ballast and thus beneficial for mollusk foraging in the many shallow, warm temperate-subtropical embayments *Valenictus* has been reported from (Deméré 1994b, Barnes 2005). It is perhaps not coincidental that some of these occurrences are from hypersaline embayments (e.g., *V. imperialensis*, Proto-Gulf of California; Barnes 2005) – environments where bone ballast would help overcome extreme buoyancy. However, pachyosteosclerosis also characterizes *V. chulavistensis*, found in the open marine San Diego Formation (Deméré, 1994b). This study reports a new record of *Valenictus* from

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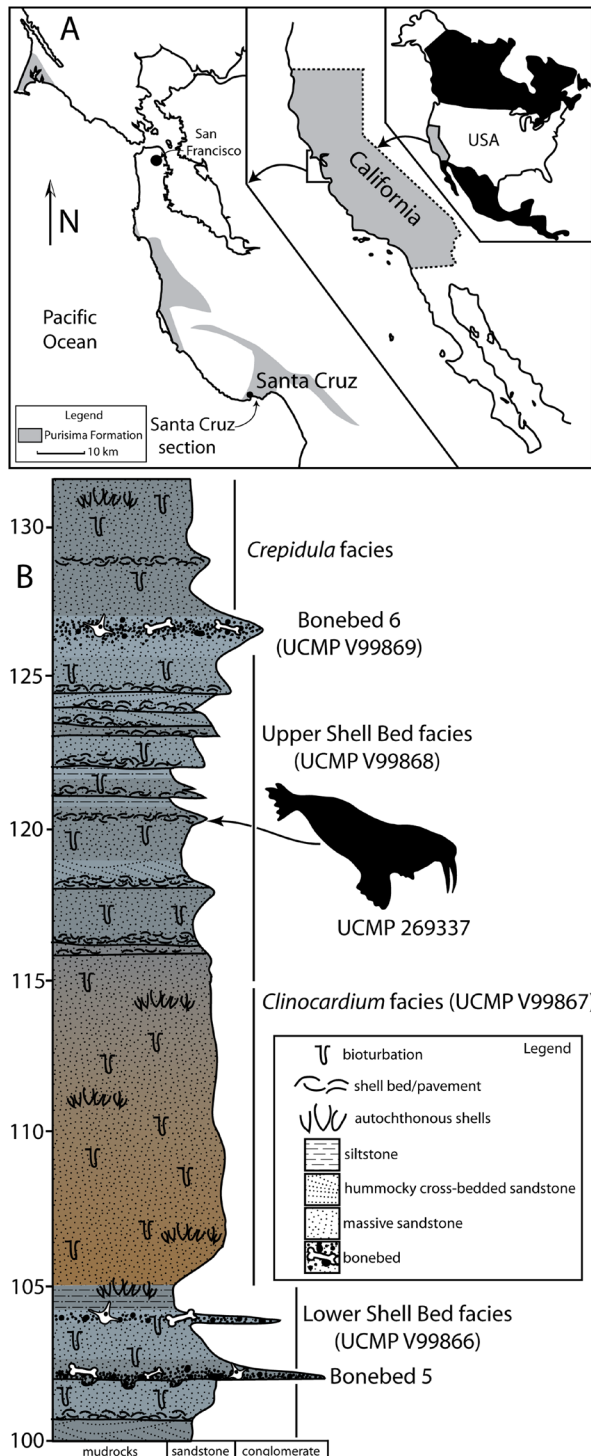


Figure 1. The Purisima Formation and geologic context of *Valenictus* sp. A. Map of Purisima Formation exposures in northern California (modified from Boessenecker, 2013a). B. Stratigraphic column of the middle part of the Purisima Formation (modified from Boessenecker et al., 2014).

the Purisima Formation of northern California (Figs. 1, 2), representing the northernmost occurrence for the genus.

METHODS

Initial preparation of UCMP 269337 was done by Mr. A.W. Thompson and was followed up by the author at the Mace Brown Museum of Natural History; concretionary matrix was removed using a pneumatic air scribe and finished by immersion in 5% acetic acid. UCMP 269337 was photographed with a Canon EOS Rebel XS and 85 mm zoom lens. Anatomical terminology follows Deméré (1994b). The definition of the Pliocene-Pleistocene boundary at 2.5 Ma, with inclusion of the Gelasian stage within the early Pleistocene is followed here (Gradstein et al. 2012), but note that earlier studies of Purisima vertebrates used the old definition with the Gelasian stage included within the Pliocene and the Plio-Pleistocene boundary set at 1.81 Ma (e.g., Boessenecker 2013a).

Institutional Abbreviations—LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; SCMNH, Santa Cruz Museum of Natural History, Santa Cruz, California, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

SYSTEMATIC PALEONTOLOGY

MAMMALIA LINNAEUS, 1758
 CARNIVORA BOWDITCH, 1821
 ODOBENIDAE ALLEN, 1880
 ODOBENINAE MITCHELL, 1968
 VALENICTUS MITCHELL, 1961
Valenictus sp.
 (Fig. 2A–D)

Referred Specimen—UCMP 269337, isolated right astragalus, collected from the “Upper Shell Bed Facies” of Perry (1988) by A. W. Thompson on December 31, 2014.

Locality and Geological Setting—The upper Miocene to upper Pliocene Purisima Formation (Messinian-Piacenzian correlative) crops out in northern California (Fig. 1A) west of the San Andreas Fault in the vicinity of Half Moon Bay (San Mateo County), Point Reyes (Marin County), and Santa Cruz (Santa Cruz County). The unit consists of richly fossiliferous, pervasively bioturbated mudrocks, diatomites, sandstones, and occasional phosphatic pebble lags and shell beds reflecting upper shoreface to offshore deposition (Norris 1986, Powell et al. 2007, Boessenecker et al. 2014). A large vertebrate assemblage including 70+ vertebrate taxa (including bony fish, sharks, sea birds, fur seals, walrus, dolphins, porpoises, sperm whales, baleen whales, a sea cow, and terrestrial mammals) has been preliminarily reported from the Purisima Formation near Santa Cruz (Boessenecker et al. 2014: table 1, and references therein), though many

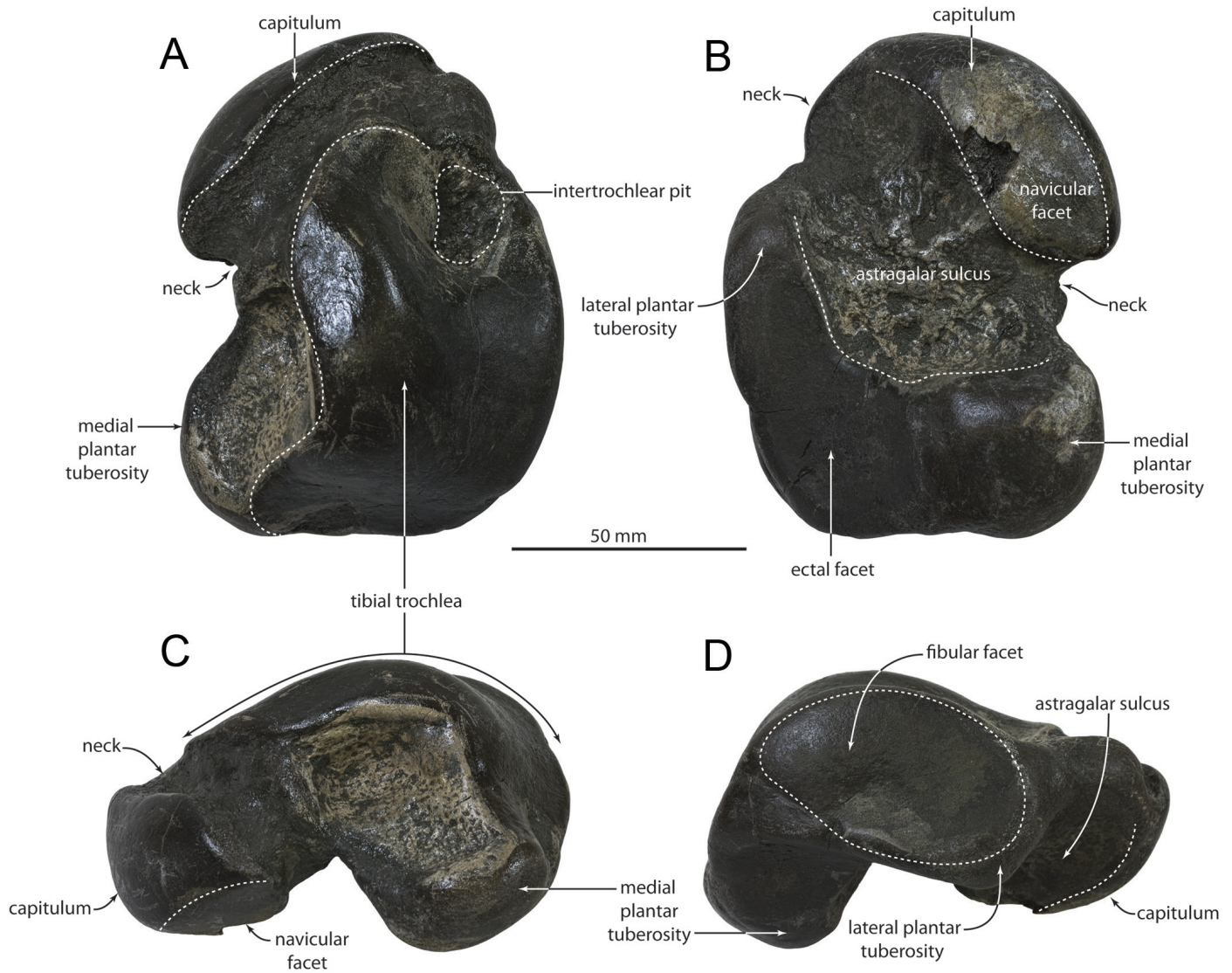


Figure 2. Astragalus of *Valenictus* sp., UCMP 269337. **A.** Tibial view. **B.** Plantar view. **C.** Medial view. **D.** Lateral view.

occurrences await formal description.

UCMP 269337 was collected from the “Upper Shell Bed Facies” of Perry (1988), corresponding to a horizon approximately 15–20 meters above the base of Section 3 of Boessenecker et al. (2014), approximately 120 meters above the base of the Santa Cruz section of the Purisima Formation (Fig. 1B). This section consists of bioturbated silty sandstone with intermittent hummocky cross-stratified sandstone with basal shell lags, reflecting intermittent storm-driven concentration of mollusk skeletal material followed by combined flow deposition and quiescent fair weather deposition between storm weather wave base and fair weather wave base in the lower shoreface (Boessenecker et al. 2014, and references therein). UCMP 269337 was preserved in a shell bed containing abundant mollusks such as the bivalves

Anadara trilineata Conrad, 1856, *Protothaca staleyi* Gabb, 1866, *Spisula coosensis* Howe, 1922, and the gastropods *Mitrella gausapata* Gould, 1850 and *Nassarius grammatus* Dall, 1917 (identified from Perry 1988, figs. 9–12). This horizon corresponds to an interval overlying the Miocene-Pliocene boundary (Madrid et al. 1986, Dumont et al. 1986, Powell et al. 2007) and lies below Bonebed 6 (Fig. 1B) of Boessenecker et al. (2014; = pebbly marker horizon of Madrid et al. 1986). Paleomagnetic zonation indicates that Bonebed 6 reflects a depositional hiatus corresponding to most of the Gilbert chron (specifically Chrons C2Ar through C3n.3n; Madrid et al. 1986). Updated paleomagnetic dates indicate that this hiatus is thus 4.89–3.59 Ma (Zanclean, early Pliocene; Gradstein et al. 2012). In summary, UCMP 269337 is earliest Pliocene (Zanclean) in age, and dates to 5.33–4.89

Ma. Detailed locality information is available on request from UCMP.

Description and Comparisons—UCMP 269337 is a relatively large astragalus (103.1 mm anteroposterior length; 83.5 mm transverse width) composed of extremely dense, osteosclerotic bone where exposed in fractures (Fig. 2A–D). UCMP 269337 lacks a distinct neck and a distinct lateral tuberosity. The tibial trochlea exhibits an anteroposteriorly longer medial trochlear ridge that nearly contacts the navicular facet anteriorly and the medial plantar tuberosity posteromedially. Anteriorly the medial ridge transitions to a flattened shelf that is separated from the lateral ridge by a deep intertrochlear pit (Fig. 2A). A deep pit is present on the medial surface between the medial trochlear ridge, the neck, and the medial tuberosity; a teardrop-shaped flattened fibular facet is developed laterally. The enlarged capitulum (Fig. 2C, D) is transversely wide relative to the proximal end (69.5 mm maximum diameter, 83.2% of transverse width); the neck is poorly developed and nearly as wide as the capitulum (59.1 mm minimum transverse diameter; 85% of capitulum width). Dorsally, the navicular facet of the capitulum is separated from the trochlea by a deep, posteromedially oriented sulcus; ventrally, the capitulum is separated by a broad, shallow astragalar sulcus. Ventrally, the navicular facet and sustentacular facet are poorly differentiated and separated only by a subtle, low ridge; the sustentacular facet is transversely wider than anteroposteriorly long. The ectal facet is “J-shaped” (e.g., Deméré 1994b) with a narrow lateral portion (Fig. 2B); the facet is transversely concave and laterally contiguous with the enlarged, hemispherical medial plantar tuberosity. The medial plantar tuberosity extends far ventral to the poorly developed lateral plantar tuberosity (Fig. 2D).

UCMP 269337 compares very well with *Valenictus chulavistensis* in sharing (to the exclusion of all other Odobenidae) 1) an enlarged capitulum with a broad neck, 2) navicular and sustentacular facets that are not differentiated by a groove, 3) poorly developed lateral tuberosity and 4) a trochlea with anteroposteriorly longer medial trochlear ridge. UCMP 269337 notably differs from *V. chulavistensis* in having a deeper intertrochlear pit and a medial plantar tuberosity that is less distinctly separated from the ectal facet. UCMP 269337 differs from other Odobenini (*Otocetus*, *Odobenus*) in exhibiting a reduced sustentacular facet, a broad, poorly formed neck, and a reduced lateral tuberosity. It further differs from “imagotariines” *Proneotherium repenningi* Kohno et al., 1995, *Neotherium mirum* Kellogg, 1931, and *Imagotaria downsi* Mitchell, 1968 in lacking a triangular posterior spur and an astragalar canal. Owing to the incompleteness of UCMP 269337, several observed differences between it and specimens of *V. chulavistensis*, and the lack of an astragalus

for *V. imperialensis*, UCMP 269337 is identified as *Valenictus* sp.

DISCUSSION AND CONCLUSIONS

UCMP 269337 represents the first record of *Valenictus* from the Purisima Formation of northern California. The basal Purisima Formation in Santa Cruz County (6.9–5.3 Ma, Messinian correlative) has yielded a diverse pinniped assemblage including an otariid fur seal (*Thalassoleon macnallyae* Repenning and Tedford, 1977), an imagotariine walrus (cf. *Imagotaria* Mitchell, 1968), two dusignathine walruses (*Dusignathus santacruzensis* Kellogg, 1927, *Gomphotaria* sp. Barnes and Raschke, 1991), and an indeterminate odobenine (Kellogg 1927, Mitchell 1962, Repenning and Tedford 1977, Barnes and Raschke 1991, Boessenecker 2013a, Boessenecker et al. 2014); most of these specimens await formal description or reinterpretation. The aggregate Pliocene pinniped assemblage from the San Gregorio and Santa Cruz sections of the Purisima Formation includes a fur seal (*Callorhinus* sp., cf. *C. gilmorei* Berta and Deméré, 1986) and two walruses (*Dusignathus* sp., cf. *D. seftoni* Deméré, 1994b, *Valenictus* sp.) and is practically identical to that of the slightly younger San Diego Formation (3–2 Ma; Deméré, 1994b) of southern California (*C. gilmorei*, *D. seftoni*, *V. chulavistensis*, *Odobenini* indet.). Other possible specimens of *Valenictus* awaiting preparation and study are recorded from the Purisima Formation (cranium, UCMP 219091; femur, SCMNH 21366); a skull of a toothless odobenine from Bonebed 6 of Boessenecker et al. (2014) initially reported by Barnes and Perry (1989) may also represent *Valenictus*, but awaits formal description.

Pliocene occurrences of *Valenictus* are now reported from coastal deposits of northern (this study) and southern California (Deméré 1994b) and Baja California (Barnes 1998, 2005), the San Joaquin embayment (Repenning and Tedford 1977), and the Proto-Gulf of California (Mitchell 1961, Barnes 1998, 2005, Atterholt et al. 2007). Though many records are preliminary and await formal description (Barnes 1998, 2005, Atterholt et al. 2007), these records nonetheless demonstrate an extensive geographic record of *Valenictus* throughout subtropical to temperate latitudes in multiple embayments and shorelines in the eastern North Pacific. The Purisima Formation was deposited near the mouth of the San Joaquin embayment (Powell et al. 2007), where *Valenictus* sp. has also been reported from the San Joaquin Formation, deposited within the San Joaquin embayment (Repenning and Tedford 1977, Deméré 1994a).

Other tusked walruses (*Odobenini*) are in evidence from the Pliocene of California. These include the fragmentary *Pliopedia pacifica*, reported from the Mio-Pliocene Paso Robles Formation (6–5 Ma) and Etchegoin Formation (> 5

Ma) on the basis of associated postcrania and a partial braincase (Kellogg 1921, Repenning and Tedford 1977; ages from Boessenecker 2013a, appendix). A possible third record of Odobenini is represented by a set of associated postcanine teeth and short tusks with globular dentine (a synapomorphy for Odobenini) from the San Diego Formation (LACM 28432), historically misinterpreted as a Pliocene elephant seal (Boessenecker 2013a, p. 904, Boessenecker and Churchill 2016). It is possible that this taxon may be conspecific with *P. pacifica*, but confirmation awaits discovery of specimens with overlapping skeletal elements. Available evidence indicates that during the Pliocene an aggregate assemblage including at least four to five walrus species (*Dusignathus seftoni*, *P. pacifica*, *Valenictus chulavistensis*, *V. imperialensis*, Odobenini indeterminate) inhabited the temperate-subtropical shorelines and embayments of the eastern North Pacific (Deméré 1994b). This pattern strongly contrasts with the monotypic extant walrus restricted to polar seas (Fay 1982, Deméré 1994b).

Loss of walrus biodiversity coincides with marine vertebrate faunal turnover at the Pliocene-Pleistocene transition in the North Pacific, involving 1) loss of a phocoenid-dominated odontocete fauna and replacement by delphinids (Boessenecker 2013a); 2) replacement of archaic members of extant families of baleen whales by 'neospecies' (Boessenecker 2013a, Tsai and Boessenecker 2015, 2017); 3) loss of a number of small-bodied mysticete whales (Boessenecker 2013a, b); 4) Pleistocene invasion of sea lions from the western North Pacific (Poust and Boessenecker 2017), phocid seals from the Atlantic and southern hemisphere (Barnes and Mitchell 1975, Boessenecker and Churchill 2016), and sea otters from the Arctic or North Atlantic (Boessenecker 2016); and 5) loss of flightless mancalline auks and giant bony toothed pelagornithid birds (Warheit 1992, Boessenecker and Smith 2011). These faunal changes came about in conjunction with uplift of the California Coast Ranges, loss of widespread shallow marine embayments, proliferation of rocky shore habitats, and rapid glacioeustatic changes in sea level (Jacobs et al. 2004, Boessenecker 2013a).

Ecological factors supporting unique aspects of the Pliocene marine mammal fauna in the eastern North Pacific—including multispecies walrus assemblages—remain poorly understood. However, the link between molluskivorous walruses and shallow marine foraging habitat suggests that the emergence and drainage of shallow marine embayments on the California margin as a possible driver for Pliocene walrus extinction in the eastern North Pacific. These nutrient-enriched embayments hosted mollusk assemblages characterized by unusually large body sizes (Vermeij 2012). It is perhaps not coincidental that other inferred benthic

feeding marine mammals including bizarre porpoises and cetotheriid mysticetes (Boessenecker 2013b, Racicot et al. 2014) became extinct as the shoreline transitioned from a series of shallow embayments to a rugged, rocky coast.

Future study of tusked walrus evolution in the eastern North Pacific will benefit from formal description and study of new material of *Valenictus* from the Deguyos, Purisima, Salada, and San Diego formations of California and Baja California, paleohistologic or CT investigation of pachyosteosclerosis in *Valenictus*, and field research at poorly explored localities in the California Coast Ranges that may yield additional odobenid specimens and shed light on Pliocene walrus biogeography (Paso Robles Formation, San Joaquin Formation, Pismo Formation).

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