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Expanding the paleontological record of semiaquatic and marine mammals:
Adaptations to freshwater in *Coryphodon* and the history of pinnipeds in the eastern Pacific

By

Ashley William Poust

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

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of the

University of California, Berkeley

Committee in charge:

Professor Charles R. Marshall, Chair
Professor William A. Clemens
Professor Jun Sunseri

Summer 2019

**Expanding the paleontological record of semiaquatic and marine mammals:
Adaptations to freshwater in *Coryphodon* and the history of pinnipeds in the eastern Pacific**

Abstract

Expanding the paleontological record of semiaquatic and marine mammals:
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Major evolutionary innovations in lifestyle can lead to adaptive radiations, change the nature of selective forces, and rearrange ecological interactions. One of the many determinants of lifestyle is body mass, and so change in body mass is often accompanied by change in lifestyle. In the case of mammals, their earliest members from the Late Triassic were small. They remained relatively small throughout the Mesozoic, most likely due to interactions with the diverse large bodied diapsids that dominated Mesozoic large-body ecomorphs, especially dinosaurs in the terrestrial realm. It was not until the early Cenozoic, after the extinction of the non-avian dinosaurs and large bodied marine diapsids, that the body size of mammals expanded, which lead to new mammalian ecomorphs. The initial stages of the Cenozoic mammalian exploration of large-body ecomorphs included at least two novel semiaquatic forms – large amphibious herbivores and large coastal marine carnivores. These ecomorphs were to evolve multiple times throughout the Cenozoic and led to the freshwater Hippopotamidae, the marine Pinnipedia (seals and sea lions), as well as to the fully aquatic marine mammals, the sirenians (manatees and dugongs) and cetaceans (whales and dolphins).

This dissertation employs bone histological methods and the analysis of new fossil specimens to add to our paleontological knowledge of large bodied semiaquatic mammals. The earliest occurrences of these large-bodied semiaquatic forms are poorly understood, and gaps exist in our knowledge of their evolution and distribution. To help address these deficiencies I used bone histological methods to establish the lifestyle of the earliest large-bodied mammal, the Paleocene-Eocene *Coryphodon*. I follow this with the description and analysis of new fossil material that expand our knowledge of the diversity and biogeography of fossil pinnipeds and their earliest stem-relatives, the geologically longest-lived lineage of semiaquatic marine carnivores.

The Late Paleocene to Early Eocene *Coryphodon* was a member of the Pantodonta, the first mammalian group to achieve large body size following the end-Cretaceous mass extinction. Using histological and microanatomical techniques to examine the structure and growth of its bones, I show that *Coryphodon* was semiaquatic and further demonstrate that it had significant adaptations to this way of life rather than merely occupying waterways in a transient manner. A framework for behavioral inference for extinct taxa is presented, which incorporates evidence from multiple timescales. I argue that this approach facilitates the framing of the causal

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relationships between, and interpretation of, the different kinds of evidence that can be brought to bear on our understanding of the origins of major changes in lifestyle. In the case of *Coryphodon*, the concurrent achievement of large body size and semiaquatic lifestyle suggests a reciprocal rather than unidirectional causal relationship between body size and specialization at the beginning of the Cenozoic.

Turning to the origins and biogeography of the pinnipeds, the Pleistocene sea lion *Proterozetes ulysses* belongs to a monophyletic group of North Pacific otariids that includes the living genera *Eumetopias* (Stellar's sea lion) and *Zalophus* (California sea lion). Fossil mandibles of *Proterozetes* from the Port Orford Formation of Oregon are described and found to be intermediate in morphology and size to the other North Pacific otariids, most resembling *Eumetopias*. The presence of this distinct but morphologically intermediate taxon in the eastern North Pacific during the Pleistocene establishes the Pleistocene as a time of increased otariid diversity, in contrast to diversity decline seen in other marine mammal clades. The timing of sea lion diversification along the west coast of North America appears to follow diversification in Japan, reinforcing the possibility of an eastward dispersal trend in the North Pacific after the end-Pliocene. Pleistocene sea lions in the Eastern North Pacific similarly show multitaxon assemblages with overlapping body size and feeding styles, indicating the high diversity possible once the coastal carnivore ecomorph was achieved.

Finally, paleontological investigation of the early history of pinnipeds similarly reveals assemblages of increased diversity and overlapping body size. The pinnipedimorph *Enaliarctos* was a marine-adapted carnivore with dental and locomotor features intermediate between terrestrial arctoid carnivores and living pinnipeds. Newly discovered fossils, described herein, fill a major biogeographic gap in the record of the genus, previously unknown between southern California and central Oregon, and show that stem pinnipeds existed for longer and survived later than previously thought. The new specimens of *Enaliarctos* are at least as old as the previously oldest known specimens from the latest Rupelian (28.1 mya) and extend their youngest age by 3.5 million years to the late Burdigalian (16.6 mya). This discovery of an increased biogeographic and temporal range of *Enaliarctos* indicates that the genus may have interacted with a much wider range of other taxa than previously thought, including plotopterid birds, odontocete whales, and crown pinnipeds such as early odobenids, early otariids, and desmatophocids. The expansion of the known ranges of *Enaliarctos* species and the description of previously undescribed morphological attributes, particularly of the mandible and lower dentition, provides insight into the origins of pinniped diversity and their possible interactions with other early Neogene coastal marine organisms. Though early pinniped relatives were smaller than living members, increasing body size does not appear to have been necessarily superior once the coastal marine ecospace was colonized.

For everyone, especially my parents,
who supported me when I looked like a bad gamble,
who nursed me when I fell,
who celebrated when I crossed finish lines,
and
who kept me on the track,
lap after lap

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Chin is professional and hilarious in equal measure, as I strive to be. Claire Englander was an inspiration of hard work and volunteerism. Chris Mejia was always kind and helpful. Diane Erwin, in addition to her many other roles, kept the labs I needed running and running safely: I couldn't have done this research without her efforts. Similarly, the IB staff deserve thanks for their integral efforts, especially Jill Marchant, Tami Mau, Monica Albe, and Adam Doban.

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Chapter 1
Bone histology and microanatomy of the Early Paleogene *Coryphodon* (Eutheria: Pantodonta) show semiaquatic adaptations in an early large-bodied mammal

Formatted for publication in *Palaeontology*

Abstract: The Late Paleocene to Early Eocene *Coryphodon* was a member of the Pantodonta, one of the first mammalian groups to achieve large body size following the K/Pg extinction. Femora, radii, and ribs of *Coryphodon* from the Early Eocene of Wyoming and Colorado were sectioned for histology and microstructural analysis. The femora belong to three size classes based on length: small (25cm), medium (45cm), and large (50cm), representing a possible subadult and adults of varying sizes. *Coryphodon* histology differs from both modern and contemporaneous mammals. Lines of arrested growth indicating extended periods of slow growth show that body size and mass continued to accumulate through much of life. Remodeling operated across the diameter of the bones, instead of being concentrated in the inner portions of the cortex. Secondary osteons are irregular, with oblique and radial orientations appearing as frequently as longitudinal, which, in contrast, dominate long bones in most living quadrupeds. Extensive remodeling and deposition of compact coarse cancellous bone within a cancellous or closed medullary cavity combine with extensive periosteal deposition of lamellar bone to create very dense, osteosclerotic bone. Histological and microanatomical data concurs with previous studies suggesting an amphibious habit for *Coryphodon* and demonstrate that the taxon had density adaptations to this way of life rather than merely occupying waterways in a transient manner. A framework for behavioral inference is presented, which includes evidence from multiple timescales. Such frameworks help to better frame causal relationships in the evolution of major changes. In the case of *Coryphodon*, the contemporary achievement of large body size and semiaquatic herbivory suggests a reciprocal, rather than unidirectional, causal relationship between body size and specialization early in the Cenozoic.

Introduction
Following the extinction of the non-avian dinosaurs, mammals radiated into an expanding array of niches, adapting to new habitats and increasing their size range by several orders of magnitude (Smith et al. 2010, Grossnickle et al. 2019). Although body size was a primary factor in structuring mammalian communities during both the Mesozoic and the Cenozoic (Chen et al. 2019), little is known about the growth or ontogeny of Paleogene mammals after the K/Pg extinction. Some recent work has begun investigation of the growth of large squamates following this extinction (e.g., Werning et al., 2014), but general knowledge of mammalian growth has lagged behind that of non-mammalian groups (Kolb et al. 2015).

Mesozoic mammals evolved many of the same forms and behaviors present in extant small mammal communities (Luo, 2007; Grossnickle et al. 2019), but they did not evolve large body sizes. Understanding the ecological roles of the first large-bodied mammals is important given that increased body size affected many major mammalian innovations after the K/Pg, including encephalization, folivory, and possibly herding, each of which had major consequences for global terrestrial ecosystems. The entrance of mammals into the sea with the iterative evolution of marine mammals is also tightly linked to body size and life history evolution. While the extreme modern sizes of cetaceans seem to be a relatively recent phenomenon (Slater et al., 2017: but see Fordyce and Marx, 2018), life in marine environments may impose a strong constraint or selective force on mammalian body size (Gearty et al., 2018). In contrast, freshwater semiaquatic mammals have evolved many times and do not seem to be size limited. The term "semiaquatic" is generally applied to animals that have physical adaptations to spending some of their time in water, but this can be expressed in a number of ways. Small-bodied, surface swimming, carnivorous and omnivorous mammals with varying levels of adaptation to life in water are relatively common today and possible fossil members of this ecomorph are known, including several Mesozoic taxa and the Paleocene-Eocene Pantolestidae (Luo 2007). Nonetheless, other adaptations such as herbivory, nocturnal bank feeding, reduced fur, bounding locomotion, sexual dimorphism, large tusks, dorsally-located sensory organs, and denser bone tissue are absent in freshwater semiaquatic mammals until the Cenozoic. Only a very few extant semiaquatic animals (*Hippopotamus*, and to some degree *Hydrochoerus* and *Tapirus)* show this suite of characteristics, designated here as "hippo-like", but possible fossil examples of this ecomorph occur throughout the Cenozoic, including the early proboscidean *Moeritherium*, some members of the family Anthractotheriidae related to hippos, and *Coryphodon*, examined here. Potentially water-adapted mammals had evolved by at least the late Jurassic (Ji et al., 2006), but the evolution of hippo-like forms and the conquest of the oceans may have had to await the evolution of larger body sizes.

Here I investigate histological and microanatomical growth patterns in *Coryphodon,* Owen 1846, a late Paleocene to early Eocene member of Pantodonta, and one of the first large-bodied mammalian genera (>100kg; Fig. 1). Pantodonta is an extinct group of early Paleogene herbivorous mammals with early members known from Asia and South America (Muizon and Marshall, 1992), which later spread to North America and the Holarctic (Muizon, 2015), though the rarity of specimens and reduced interchange between North and South America at this time indicates that these conclusions might be premature (Clemens, 2017). Six families are generally recognized, including perhaps 15 genera, as well as a number of taxa of uncertain placement (Muizon and Marshall, 1992; Lucas, 1998; Muizon et al., 2016; Clemens, 2017). Pantodonta was traditionally placed within Perissodactyla, or the older polyphyletic group "Ungulata". The phylogenetic relationships of pantodonts remain unresolved (Fig. 1D and E). Halliday et al. (2015) place a group of pantodonts plus periptychids sister to carnivorans, with Artiodactyla and Perissodactyla more distantly related, while De Muizon et al. (2016) place them with Tillodontia in a large clade sister to Artiodactyla. Several important genera, such as the long-lived pantodont *Barylambda*, have yet to be included at the genus level in published analyses, leaving internal relationships uncertain as well.

Species-level taxonomy of *Coryphodon* has been complicated, encompassing over 35 named species. Lucas (1984, 1998) reviewed the genus and synonymized all but eight taxa: the type species, *C. eocaenus*, and seven others; *C. simus*, *C. molestus*, *C. anthracoideus*, *C. oweni*, *C. subquadratus*, *C. proterus*, and *C. lobatus*. Uhen and Gingerich (1995) further reduced the

total to six species from North America, removing *C. subquadratus*, *C. simus*, and *C. oweni*, while acknowledging that the last remains a valid taxon for some European specimens. They also recognized an additional species: *C. armatus* Cope, 1872. A wide size range has been long known for coryphodontid pantodonts (Marsh, 1877), of which *Coryphodon* is the largest genus. *C. proterus*, and *C. lobatus* are the largest of the above species, *C. armatus* and *C. eocaenus* the smallest, with the rest falling in between. Several additional factors contribute to this range, including varying size among species (Marsh, 1877; Lucas, 1984; Uhen and Gingerich, 1995), significant within species size variation (Uhen and Gingerich, 1995), and the influence of sampling individuals at different ontogenetic stages, which has not yet been rigorously evaluated.

Coryphodon has long been suggested to have freshwater-dwelling habits (Simons, 1960) but testing this assumption has proved difficult. There are two primary sources of information from which assessments can be made about an extinct organism's adaptations: their depositional context and the fossil remains themselves (Kristoffersen, 2001). Because the original descriptions of the taxon were based on a canine and a molar (Owen, 1845; 1846), little was initially inferred about its ecology or habits. More extensive remains of *Coryphodon* were discovered by Cope and Marsh in fluvial channel deposits of the American west (but see Simons, 1960). Marsh (1893) and Osborn (1892) followed this sedimentological observation with comments on the general form of *Coryphodon* and indeed Marsh's skeletal reconstruction (Fig. 1B) is very hippo-like in posture. However, Osborn (1898) created a new mount for the American Museum of Natural History on the basis of new material, which he used to argue that several of these postural aspects, especially of the legs and feet were incorrect. Thus, the evidence for a semiaquatic *Coryphodon* remained equivocal. Nonetheless, the idea persisted. Halstead (1978) in his popular book "The Evolution of Mammals" said that the spine of *Coryphodon* was too weak to support its weight permanently on land – "another sign that it must have spent much of its time in the water." I have been unable to track down the original source of this assertion, and indeed it is unlikely to be true, but it demonstrates that the conception of *Coryphodon* as a semiaquatic animal was well-established by the later-half of the 20th century. This idea seems to have transferred onto other early large bodied mammals as well, with varying degrees of support, primarily based on overall body form (Meehan and Martin, 2003).

Delta^{18}O values from teeth showed low variability in at least some localities, consistent with semiaquatic feeding (Secord et al., 2008). Clementz et al. (2008) further established that *Coryphodon* spent significant time in freshwater environments. Living *Hippopotamus* spend extensive time in the water leading to low delta^{18}O variation within populations, due to the lake or river providing a homogeneous oxygen source. They also have low delta^{18}O values compared to the rest of their faunas, partly due to the hippos' reduced evaporative cooling. Applying these delta^{18}O parameters to presumed semiaquatic taxa in the fossil record, including large and small specimens of *Coryphodon*, Clementz et al. (2008), found several large quadrupeds did not match the expected isotopic picture for hippo-like semi-aquatic animals. They sampled *Coryphodon* across an interval of warming climate when individuals were generally smaller than those before and after. The generally larger individuals of *Coryphodon* were supported as being semiaquatic, while the smaller *Coryphodon* from the warmer stratigraphic middle of the Big Horn Basin lacked the lowered delta^{18}O values associated with being hippo-like. They were unable to provide an explanation for this discrepency. Clementz et al. showed that some *Coryphodon* spent time in the water, but the possibility of unexpected common cause effects for the differential enrichment and any possible unexpected animal behaviors means additional confirmatory

evidence for semiaquatic habits is of value, especially considering the lack of support for semiaquatic habits in some of the smaller individuals sampled.

An alternative source of data that bear on a semiaquatic habitat comes from bone microanatomy via studies of the distribution of bone tissue. Microanatomy allows the detection of adaptation to particular lifestyles and has predictive power in inferring habitat (e.g., Laurin et al., 2011). It has been used to infer semiaquatic habits in animals from early cetaceans (Houssaye et al., 2015) to dinosaurs (Ibrahim et al., 2014). In addition to further testing behavioral patterns, examination of microanatomy serves as a test for adaptation to those ecological roles, because unlike isotopic composition which is subject to the behavior of the individual organism during brief episodes in its lifetime (i.e., during the deposition of enamel), bone tissue characteristics evolve to fit the animals' circumstances over longer time scales, i.e., on the order of thousands of generations.

To my knowledge only one example of pantodont histology has been published previously, in the voluminous Enlow and Brown (1958). This was a partial section of a rib, showing the presence of Sharpey's fibers and secondary osteons. I include it in my description of rib histology below, but the small section and poor image quality mean it is not informative with respect to the habitat of *Coryphodon*.

Materials and Methods

To evaluate the adaptation of *Coryphodon* bone microanatomy and histology to aquatic conditions I sampled a range of bones for which there existed comparative samples of extant mammalian microanatomical data, including femora, radii and ribs (Fig. 1B; Table 1). To avoid the possibility of a pathological or otherwise uninformative sample, two of each element were selected. Samples were selected on the basis of preservation, identifiability, and sampling permission.

In addition to the above bones, I expanded the sample of femora to include the smallest and largest specimens available to me, totaling four femora. The expanded sample was chosen to increase the likelihood of capturing well-preserved bone, to make sure that observations of tissue were generalizable, and, with the range of different sized bones, to attempt to capture a wider portion of the animal's ontogeny. Femora were chosen because they are widely examined in paleohistology and because in most taxa their growth best reflects whole body signals (e.g., Horner et al. 1999). One femur is small (25cm), two are of more average length (45cm), and one is large (50cm). The largest specimen exceeds the two medium specimens by 10 cm and is more robust. Few postcranial measurements for *Coryphodon* have published, so it is not possible to say with certainty how these femora compare with the full range present in the taxon, but the large specimen is among the largest specimens of the largest North American species, *C. lobatus*, while the medium (40-45 cm) specimens are more typical. The small specimen is half the size of the large, a size difference like that seen in young juvenile long bones (Lucas and Schoch, 1990) Thus, if adult it would likely represent a smaller sex or species.

The four femora and one radius are from the Eocene Willwood Formation of Wyoming, and two ribs and one radius are from the Wasatch Formation of Colorando (Fig. 1, A). These specimens are summarized in Table 1. UCMP Willwood material (V65175) was collected by Reverend Floyd A. Jenkins, an amateur collector. UCMP Wasatch material (V74092) were collected in Colorado during field work conducted by Dr. Malcolm C. McKenna. CM 81669 (femur) part of a partially articulated skeleton collected by J Leroy Kay and party in 1953 in the Early Eocene (Wasatchian/Graybullian) Upper Greybull bed in the Willwood formation of

Wyoming. CM 47208 (radius), part of an associated skeleton, was found at a different locality but in the same depositional context as CM 81669. These specimens are incomplete and not identifiable below genus on the basis of diagnostic characters. The Carnegie specimens (CM 81669 and 47208) are from high in the section and likely represent the larger of the two taxa found in the Upper Greybull, *C. lobatus*. The stratigraphic positions of the UCMP Willwood material is known with less precision, meaning that other taxa are candidates, especially *C. radians*, which is present in the lower part of the Graybullian. The large size of UCMP 238308 strongly suggests that it belongs to *C. lobatus*, the only very large species present. The stratigraphic context for the positions of *Coryphodon* species has not yet been established for Colorado as it has in Wyoming, but the UCMP Colorado specimens are also large and may belong to *C. lobatus*,

Histology

Thin-sections were prepared using standard paleohistological methods (e.g, Chinsamy and Raath, 1992; Lamm, 2013). In most bones, samples were taken from the mid-diaphysis. In the femora, a sampling location slightly distal to the midshaft was selected (Fig. 1C). The large third trochanter of *Coryphodon* is present at the mid-diaphyseal region, leading to the selection of a slightly more distal sampling location, 55-60% of the way from the proximal end, to avoid conflation with the trochanter. To confirm the appropriateness of this sampling location, I inspected natural post-fossilization fracture surfaces of the bones both proximally and near the midshaft. Use of a 20X hand lens with a low-angled light source permitted additional observation of the medullary cavity, zones of diagenetic alteration, endosteal lamellar bone, and distribution of vascular canals in fractures both distal and proximal to the sampling locations.

Being large, the specimens were first stabilized and then bisected using a rock saw with a lapidary wet-cutting diamond blade. The resulting samples were embedded in Silmar-41 clear polyester resin (U.S. Composites, Inc.). Slices were removed from the embedded block using a thin diamond blade Isomet low-speed Saw (Buehler). Penetrant stabilizer (PaleoBond PB002) was added before pre-mount grinding. Specimens were mounted using 2-ton epoxy (Devcon) and allowed to cure for 24 hours. Mounted slides were ground to optical clarity using increasingly fine paper from 120- to 1200-grit on the grinder/polisher.

Slides were examined and imaged using a D300 DSLR camera (Nikon, Inc.) tethered to an Optophot2-Pol light transmission microscope. Digitization using flatbed scanners allowed the capture of the entire plane of section. Filters permitted visualization of histologic structures through enhanced birefringence. These included regular transmitted light (single polarizer), crossed-polarized light, and elliptically polarized light. I adjusted images (leveling, adding labels) in Illustrator (Adobe). Images presented here are also available at high resolution on the MorphoBank repository under project P3487.

Histological terminology follows that of Francillon-Viellot et al. (1990) and major terms are defined here. Bone tissue can be described as falling somewhere on an organizational spectrum from disorganized woven bone to highly organized lamellar bone. Woven bone is composed of disorganized collagen fibers and therefore isotropic under cross polarized light in all orientations. Primary osteons may disrupt this pattern without changing the overall character of the matrix. Osteocyte lacunae vary between taxa, but generally have a random orientation and a rounded shape in woven bone. In lamellar bone, by contrast, collagen fibers are highly ordered into a sub-parallel orientation and is usually compared to plywood because the fiber orientation alternates by 90 degrees between segments. This alternation can be picked up in cross polarized

light as a localized switching in and out of extinction as the slide is turned. Parallel bone generally exists between woven and lamellar bone on the spectrum, with fibers essentially aligned along a single axis. In both lamellar and parallel fibered bone osteocytes are relatively few and appear elongated in the direction of the fiber orientation.

Compacted coarse cancellous bone (CCCB) denotes a tissue composed of lamellar secondary bone deposited upon existing structures of cancellous bone, filling in the spaces between the struts and resulting in a denser structure. Birefringence is variable, owing to the dual origin of the tissues, though overall it often appears high.

Lines of arrested growth (LAGs) are cementing lines representing periods when growth slowed to the point of cessation. These lines can usually be traced around entire structures, but in places they may expand into narrow bands of slower, not fully arrested, growth, referred to as "annuli". LAGs are useful for skeletochronology as yearly indicators. An External Fundamental System (EFS) is a periosteal zone of avascular, lamellar to parallel fibered bone usually enclosing densely packed circumferential growth marks such as LAGs or annuli. The EFS represents the product of a slowing period of growth, and as such is often interpreted as a sign that the animal, or at least the sampled element, is reaching its ultimate or adult size. Resorption lines can have various causes, but in general are assumed to represent former surfaces where osteoclastic activity outpaced bone growth. They can be diagnosed as distinct from other linear structures by their cross-cutting relationships with existing structures and generally wavy appearance, uncommon for LAGs. Below, I use the phrase "open medullary cavity" to specify a central section of a long bone that is free from cancellous bone in the plane of the section. An open medullary cavity will often, but not necessarily, have a well-defined border of endosteal bone.

Microanatomy

Cross-sections obtained from histology were digitized and transformed into binary images using Adobe Photoshop CC 2018. Microstructural analysis was performed using Bone Profiler (Girondot and Laurin, 2003). Measures derived from Bone Profiler allow precise evaluation of bone compactness calculated from the center of the bone towards the periphery and provide both graphable measures (Fig. 3) and parameterized values (Table 2). Previous studies (Canoville and Laurin, 2010; Quemeneur et al., 2013, Germaine and Laurin, 2005) have built lifestyle models on bone compactness profile parameters extracted from this program. Kriloff et al. (2008) found a significant relationship between long bone compactness and habitat. In addition to modelled and observed general compactness, Bone Profiler also calculates common metrics of other authors for evaluating bone density, including R/t and CDI values (Currey and Alexander, 1985; Castanet et al., 2000; see Table 2).

Results

Taphonomic alteration of fossil bone tissue in specimens from the Early Eocene of Wyoming is often extensive. Several of the smaller specimens, the ribs and smallest femur in particular, are significantly altered diagenetically, with crystal growth or microbial action affecting the preservation of tissues, but all samples preserve the microstructural arrangement of the bone and some original tissue. The more highly vascularized, disorganized inner tissues appear to have been more strongly affected by this alteration; in several samples the lamellar outer cortex is preserved while inner tissues have been severely altered (UCMP 178303, CM 81669; Fig. 3A,

C). Unfortunately, the smallest femur preserves almost no unaltered bone, except on the outermost periosteal surface, rendering histological inference difficult.

Histology

Femur – The smallest femur, UCMP 238309, is nearly circular in transverse cross-section. Its medullary cavity is almost completely in-filled with cancellous bone, except for a small and irregular open medullary cavity. Taphonomically altered, it has a thin cortex of fibrolamellar bone with low vascularity where preserved. No lines of arrested growth (LAGs) can be seen.

The medium femora (UCMP 178303 and CM 81669) are ovoid in cross section with the narrowed end facing laterally. The gradation from the compacta to the spongiosa is gradual and no distinct medullary cavity is present, except in one more proximal thin-section of CM 81669 (Fig. 3C) which has a small, irregular open medullary cavity similar to that of UCMP 238309. Close to the center the cancellous struts are thin and covered externally by usually only a single layer of lamellar bone. In both specimens there is wide section of the cortex where alteration has made most features indiscernible. Some secondary osteons are visible through the dark, altered material, as are open spaces, which may be erosion rooms, or space between segments of cancellous bone. Just external to this wide altered band, two tissue types are visible. Near the border of the altered zone are patches of remodeled bone with several generations of secondary osteons. The osteons are large and longitudinal to oblique in orientation. At least one and possibly two LAGs are visible as remnants between these secondary osteons. Outside of these areas the predominant preserved tissue type is poorly vascularized lamellar bone. This tissue is characterized by flattened osteocytes and subparallel fiber direction (Fig. 3B). The near total lack of vasculature may have contributed to the resistance of these regions to diagenetic or fungal alteration. This region of lamellar bone is large, comprising up to 25% the thickness of the cortex and 10% of the diameter of the medium sized femora. The outer section of this periosteal zone is interrupted in both specimens by numerous, closely spaced LAGs comprising an external fundamental system (EFS). These LAGs are traceable around the circumference of the sections and are mildly birefringent under elliptically polarized light. In the less altered CM 81669 femur, the EFS contains at least ten of these LAGs at the very exterior (Fig. 5B), which, when added to the one or two LAGs in the remodeled section and the two in the inner portion of the lamellar region yields a minimum age of 13-14 years.

The gross shape of the largest specimen is somewhat crushed, but is the best preserved histologically (Fig. 4). There is no evidence of an open medullary cavity, though due to crushing this is not conclusive. Gross examination of other segments of the femur at the proximal end of the diaphysis, the midshaft, and distal to the sampling location failed to reveal any evidence of an open medullary cavity. It shows secondary remodeling in both the cortical and cancellous bone (Fig 4A). The cortex is thick and heavily remodeled by several generations of secondary osteons with some relict fibrolamellar bone. In places this remodeling extends to the periosteal surface (Fig. 4A, D). Across the inner cortex, the struts of the cancellous bone are covered with layers of secondary lamellar tissue, in places filling in space between the struts entirely (Fig. 4B). Though the presence of the original cancellous bone is difficult to confirm across much of the cortex where secondary remodeling has overprinted it, I interpret this tissue to be compacted coarse cancellous bone (CCCB). Little calcified cartilage and few Howship's lacunae are discernable. In places the secondary lamellar deposition appears to have infilled large erosion rooms in addition to coating thin cancellous struts (Fig. 4A, B). The interior portions of the cortex are made up primarily of this infilled secondary tissue. In the outer portions, the secondary osteons sit in a

matrix of fibrolamellar bone, but the remodeling is so dense little of this is visible. No primary osteons are visible, but the remaining matrix has a less organized arrangement of osteocytes and more variable fiber orientation, so I interpret it here as relict primary fibrolamellar bone. The outermost 1-2 mm of the cortex is lamellar bone, which is nearly avascular except where pierced by secondary osteons. These outer portions are interrupted by numerous LAGs, some of which are double or triple LAGs (Fig. 4A, C, D; Table 3). In the inner portions of preserved cortex, the LAGs can be traced through the remaining fibrolamellar bone matrix between remodeled areas. In the outer portions where the secondary osteons are less common, the LAGs are very close together and form an external fundamental system (EFS) with no primary vasculature. In total, at least 15 LAGs are traceable, but it is likely that at least several more have been obscured by remodeling and cortical expansion.

Radius – Both radii have been heavily altered and preserve little visible bone tissue. The cortex is very thick, and the medullary cavity filled with cancellous bone. Overgrinding of UCMP 238310 revealed a preserved portion of the outer cortex (Fig. 3A). The bone is remineralized with some visible crystal growth and the tissues are invaded by what look like fungal hyphae. But though thin and poorly birefringent, the remaining tissues show poorly vascularized lamellar bone, occasional secondary osteons as far out as the periosteal surface, and at least 5 LAGs, the last three of which are closely packed to the outer surface in an EFS.

Ribs – Preservation of microscopic tissues was poor in both ribs sampled. Little can be discerned about the tissues themselves, though the distribution of bone is preserved. The ribs are somewhat inflated and rounded (pachyostotic), with no clear impression for the costal groove. They have no medullary cavity and very little internal open space, in great contrast to other mammals of similar size (see Fig. 5 for comparisons with ribs of Pleistocene *Equus*, a more typical large bodied mammal). Enlow and Brown (1958) sampled a better preserved *Coryphodon* rib, which showed some secondary remodeling and was mostly composed of circumferential lamellae. In the context of the femoral histology described above, it seems likely that this lamellar bone records the same extended growth seen in the appendicular skeleton.

Microstructural analysis

  The overall gross morphology revealed by the binary images highlights the morphology resulting from the histological trends revealed in thin-section: the cortices of all specimens are thick and solid, and the medullary cavities are mostly or completely filled with cancellous bone (Fig. 2, C-F). Analysis with Bone Profiler yields high global compactness values for all elements, with particularly high values in the ribs (Table 2). Compactness profiles (Fig. 3, A-B) show that the transitions from the spongiosa to the denser compacta occur relatively gradually in the long bones, a consequence of the in-filled medullary cavities. Uniquely, CM 81669 has a raised compactness value surrounding the medullary cavity. This may be a consequence of the internal remodeling front working to fill in the medullary cavity further, or alternately may be a taphonomic feature due to secondary crystalline growth in this region. In the ribs, conversely, the cavities are so filled as to be essentially absent, leaving the transition mostly flat.

Discussion
Histology

The presence of an extended, multiyear period of slow growth later in ontogeny can be inferred from the wide periosteal lamellar zone and external fundamental system with many LAGs. Since this accounts for as much as 10 percent of the diameter of the femur it represents significant growth in mass continuing to accrue throughout life. Determining whether this could account for some of the size variation seen in the genus will require additional data, but since body sizes in previous work have generally been calculated using molar dimensions (e.g., Uhen and Gingerich, 1995), our general picture of *Coryphodon* species taxonomy should remain the same if eruption times do not vary significantly between taxa. Continued growth throughout life may mean that whole body size or mass may have more overlap between species than indicated by molar dimensions, given that *Coryphodon's* brachydont teeth cease growing at eruption. The presence of this late growth raises the possibility that smaller bodied *Coryphodon* from intervening warm periods achieved smaller body size at least in part by earlier truncation of growth (progenesis), or even by shortened life expectancy. Testing this hypothesis would require sampling a number of individuals across these warmer intervals.

Coryphodon is distinct from both extant and contemporaneous members of Laurasiatheria in that extensive remodeling reaches the outer cortex of the femur and radius. While a variety of amniotes do this across the cortex, most large-bodied mammals heavily remodel only the inner third (e.g., *Equus*, *Cervus*) or in a confined band between more lamellar cortical and endosteal bone (e.g., Carnivora, *Phenacodus*). None of the sampled *Coryphodon* specimens have the plexiform fibrolamellar bone seen in many large mammals (Kolb et al., 2015b). Additionally, the secondary osteons in the long bones of most mammals are longitudinal, whereas in *Coryphodon* oblique and radial orientations are common, resulting in a high volume of bone replacement. Unlike most mammals *Coryphodon* did not increase its open medullary cavity with circumferential growth, but rather maintained or increased the extent of trabecular bone. These features suggest rapid initial growth and osteoclast inhibition later in ontogeny. A functional need for this period of bone densifying growth may partly account for the unusually long period of continued slow growth indicated by the wide, LAG-rich EFS.

Little histological work has been done on animals which might be ecological equivalents of *Coryphodon*. The dinosaur *Spinosaurus*, inferred to be semiaquatic from several lines of evidence including high bone compactness, maintains the reticularly vascularized fibrolamellar bone common to related theropods (Ibrahim et al. 2014; Supp. Info.). In *Spinosaurus* the dense inner cortex and closed medullary cavities are filled with haversian bone. Among mammals, Kolb et al. (2015) sampled an island dwarf *Hippopotamus*, *H. minor* from the Mediterranean island of Cyprus. The ecological role of the Cypriot hippos has not been evaluated, but they are presumed to have been similar to their mainland relatives. The bone is plexiform fibrolamellar bone with strong remodeling by dense Haversian bone (secondary osteons). There are some similarities here with *Coryphodon*, including the more parallel-fibered periosteal bone and the secondary remodeling across the cortex, but overall the *H. minor* histology resembles typical artiodactyl bone much more closely, lacking the lamellar bone, dense LAGs, broad EFS, oblique secondary osteons, and compacted coarse cancellous bone that make *Coryphodon* distinctive. Determining whether these differences are phylogenetic or related to adaptations particular to the drier climates of Mediterranean islands will require broader sampling within Hippopotamoidea.

Coryphodon has similarities to Xenarthra, where oblong secondary osteons and irregular vascularization are present. The presence of CCCB may also be a similarity since it is found

extensively in *Dasypus novemcinctus* (Heck et al., 2019). In *Coryphodon*, however, the tissue is concentrated more internally and punctuated with more secondary osteons. Similar bone distribution and trabecular osteosclerosis lacking calcified cartilage may also be found in South American aquatic giant sloths (Amson et al., 2014). The tissues of *Coryphodon* are unlike those found in later large mammals and yet show similarity with the bone histology and organization of some secondarily aquatic tetrapods, supporting a previously suggested semiaquatic lifestyle.

      I use the term "EFS" here to designate the compact external packet of LAGs and avascular lamellar bone that surrounds the larger bones, it is not at all clear that this structure means the same thing for an animal where it represents 5-10% of the diameter of the femur, compared with negligible increase it represents in other taxa. The small distance between LAGs is minimal compared to the distance between other cortical LAGs and so it most certainly represents a significant slowing of growth, but more work is required before the presence of an EFS in early large mammals should be taken to represent completion of growth or adulthood.

Microanatomy

The overall distribution of bone is similar to that of aquatic or semiaquatic mammals. Aquatic mammals tend of have thicker cortices than terrestrial relatives (Laurin et al. 2011). *Coryphodon* shows both extreme osteosclerosis across the body and incipient pachyostosis in the ribs.

      The global compactness of terrestrial animal ribs varies from 0.347 to 0.817 (Buffrénil et al. 2010). *Coryphodon* exceeds this and so can be considered to have a derived osteosclerotic condition of the ribs. Its 0.937 global compactness values approach the high values of 0.9 and above seen in sirenians and aquatic sloths (Buffrénil et al. 2010; Amson et al. 2014). The femur and radius of *Coryphodon* have a similarly osteosclerotic structure. Pachyostosis is more difficult to diagnose from these partial rib samples because previously proposed methods for evaluating it require measurements from the whole rib (Buffrénil et al., 2010). The ribs do show a swollen external aspect derived from extra deposition of cortical bone (Fig. 3, E) corresponding to the presence of pachyostosis *sensu lato* (Houssaye, 2009), but this may be of limited extent.

      The histological expression of this bone density increase shares some similarities to that of *Claudiosaurus,* a nothosaur relative whose histology was described by Buffrenil and Mazin (1989). While there is nowhere near the degree of external cortical thickening present in *Claudiosaurus*, which was marine and much smaller (~2 ft) than *Coryphodon*, it nonetheless underwent some similar processes internally, including multiple generations of intensive haversian remodeling and relatively high osteoblastic activity in the medullary region. In fact, *Coryphodon* lacks the open medullary cavity present in *Claudiosaurus* – in *Coryphodon* the medullary cavity is has more or even complete in-filling of haversian systems and erosion bays, with the addition of lamellae to the bony struts of cancellous bone. This may indicate two different approaches to generating more dense bones: external expansion in *Claudiosaurus* and internal remodeling in *Coryphodon*. Archaeocetes, sea otters, hippos, tapirs, pinnipeds, and all modern cetaceans have infilled medullary cavities, that rather than being open are crossed by varying densities of trabecular struts (Madar, 1998).

      The high density seen across the ribs, femora, and radii is a consistent feature of an animal with a history of selection for an increased whole-body density to allow a deeper neutral depth (Wall 1983). Sirenians by comparison, have increased bone density in the thoracic cavity and the forelimbs, while allowing the vertebral column to remain more spongiose, and ultimately losing their hindlimbs (Domning, 2000). This pattern is consistent with a pattern of gaining hydrodynamic advantage through managing horizontality (Buffrenil et al., 1990; Domning and

Buffrenil, 1991; Madar, 1998). The more uniform density found in *Coryphodon* suggests the maintenance of terrestrial capacity and adaptation to a form of aquatic locomotion where pitch is less important, such as hippo-like underwater bounding or surface swimming.

The higher compactness values of the ribs may be functional since the ribs' position allows them to counteract the buoyancy of the lungs, or it may be developmental. Enlow and Brown (1958) point out that if secondary haversian canals are present anywhere they are present in the ribs, so the higher density found in the ribs might be a consequence of higher remodeling in these bones.

The radius density in *Coryphodon* is not much higher than that seen in terrestrial animals (Germain and Laurin, 2005). Several possibilities may account for this, including the already high mean compactness value for terrestrial radii recovered by Germain and Laurin, or selection for relatively uniform bone compactness across the body as discussed above. In general, several studies have shown that bone microanatomy and particularly compactness of some elements such as the radius and tibia may have low predictive power for distinguishing between terrestrial and semiaquatic taxa (Germain and Laurin, 1995; Kriloff et al., 2008). However, the taxa used in these studies for semiaquatic mammals are of small body size and primarily locomote using surface swimming. This suggests that: (A) the current models for the evaluation of semiaquatic mammal bone compactness are attuned to a particular version of habitat utilization and, (B) extant analogues for behavior in *Coryphodon* may be sparse.

Madar (1998) record both *Hippopotamus* and *Hexaprotodon* as falling in the compactness range of terrestrial ungulates even though the bone density is "undoubtedly greater" owing to the dense randomly oriented trabeculae that fill the medullary cavities of these genera. Tapirs also have trabeculae-filled bones and are habitual swimmers (Madar 1998, Nowak, 1991). In hippos and tapir this extends into the metapodials. Global compactness in *Coryphodon* is much higher than in these taxa; its rib compactness value of 0.937 easily exceeds that found in *Hippopotamus* (0.730) and *Rhinoceros sondaicus* (0.857) which are the highest values among non-marine mammals, except, oddly, *Rattus norvegicus* (0.913; Buffrénil et al., 2010). The value even exceeds that of the marine desmostylian *Paleoparadoxia* (0.850), leaving Sirenia and later species of aquatic giant sloth, *Thalassocnus littoralis and T. carolomartini,* as the only known taxa with more compact ribs, valuing 0.755-0.999 and 0.939-0.955 respectively (de Buffrénil et al., 2010; Amson et al., 2014).

Ontogeny
The specimens analyzed above were chosen to represent a broad range of sizes in *Coryphodon*, but there are several reasons why the sample might not represent a true growth series. First, the aforementioned taxonomic issues leave us with uncertainty over the number of co-occurring species of North American *Coryphodon*. While I attribute these specimens to *Coryphodon lobatus*, there remains the possibility that the smaller *Coryphodon armatus* may have co-occurred, complicating the attribution of the smaller femur. Similarly, sexual size differences have yet to be evaluated for *Coryphodon*, despite the recognition of sexual dimorphism in canine size (Uhen and Gingerich, 1995). Sexual size dimorphism is present in both extant hippos and fossil anthracotheres inferred to be semiaquatic (Lihoreau and Ducrocq, 2007) and may be common in hippo-like semiaquatic mammals.

In-filling of the medullary cavity with cancellous bone occurs as the long bones of *Coryphodon* grow. This process is followed or accompanied by the creation of CCCB. Osteosclerosis appears primarily as a consequence of secondary in-filling of the spaces in the

cancellous bone by lamellar accretion along the existing spicules and surfaces. At some point in growth, the tissues prioritize putting energy into making the bone dense at the expense of faster whole bone growth. Overprinting by secondary bone tissue is severe enough that it remains unclear whether the transition from fibrolamellar bone to lamellar bone is abrupt or gradual, or exactly how early in ontogeny this occurs.

To date, ontogenetic trends in bone compactness of mammals have not been extensively investigated. Laurin et al. (2011) suggested that lower than expected compactness in a radius of *Amblonyx* might be due to its status as a juvenile. The smaller *Coryphodon* femur (UCMP 238309) differs from the larger femora by possessing a small, open medullary cavity, a more gradual transition from spongiosa to compacta, and a thinner cortical zone. But a small central opening is also present in one slide of the clearly adult CM 81669 and the global compactness scores are all very similar (Table 3).

Traditional markers of osteological maturity, including sutural fusion, tooth eruption, and tooth wear have been applied to *Coryphodon* (e.g., Lucas and Schoch, 1990; Uhen and Gingerich, 1995). While these might be valid relative indicators, it should be noted that unless their appearance were significantly delayed, growth would have continued long after these markers appeared, and so they should be applied with caution to questions linking maturity with cessation of growth, or maximal size. For example, conclusions of absolute age based on direct comparison with *Hippopotamus* (Lucas and Schoch, 1990) should be questioned in light of the extended growth window in *Coryphodon*. Additionally, suggestions that tooth growth and eruption may be decoupled from overall growth rates in Paleogene mammals (e.g. Bastl and Nagel, 2014; Poust, 2015) are supported by these results. Previous work, using relative markers to suggest quick growth and early eruption (Lucas and Schoch, 1990) conflicts with presence of extensive lamellar bone and numerous LAGs. If the traditional assumption of fusion representing cessation of growth holds, the fused distal epiphyses of the smaller femur suggest that it may not be a young juvenile. Lucas and Schoch (1990) found that the distal epiphyses of the femur fused early, before the eruption of all adult teeth, leaving an uncertain time window for the smaller femur. Given the uncertain implications of this fusion, the need for species level taxonomic revisions within *Coryphodon*, and the lack of consideration given thus far to sexual size differences, the incomplete preservation of the small femur unfortunately does not allow further ontogenetic inferences.

Gross morphology
In light of evidence from isotopes (Clementz et al., 2008), histology, and microanatomical data presented here, the macroscopic anatomical characteristics of *Coryphodon* deserve new consideration. While an exhaustive treatment of these characters in the context of whole-body anatomy is warranted, it is beyond the scope of the current study. Nonetheless, a few comments are in order. First, isotopic data have largely rejected the hypothesis that there is a direct relationship between the graviportal body type of the "hippo ecomorph" of Meehan and Martin (2003) and actual semiaquatic behavior (Clementz et al., 2008). It is possible that this shape is a preadaptation to a semiaquatic habit or that it can evolve in graviportal animals under unrelated selective regimes. However, in the semiaquatic *Coryphodon* the body form may be adaptive to a hippo-like style of life. The splay of the feet, the dorsal position of the nares and eyes, and the height of neural spines in lumbar and caudal vertebrae are all characters that have been suggested as semiaquatic adaptations (Buffrénil and Mazin, 2001), but have not received quantitative evaluation in *Coryphodon*. Second, close comparison with related forms is warranted; for

example, the posterior neural spines in *Coryphodon* are not particularly high, but they are high in the large tail of the closely related pantodont *Barylambda,* which may indicate some adaptation to a different locomotor mode. Pantodont locomotion has not received much attention since the days of Marsh, and in light of new evidence for semiaquatic habits, deserves to be revisited.

Coryphodon as an isotopic proxy

Previous authors have used *Coryphodon* fossils in a number of isotopic studies (e.g., Koch et al., 1995; Secord et al., 2008). Fricke and Wing (2004) used *Coryphodon* enamel to generate surface water O^{18} values, which could in turn help calculate local atmospheric temperature. The use of *Coryphodon* teeth assumed that body mass or a water-dwelling lifestyle led to high enough intake of surface water to properly represent O^{18}. The assessment of the taxon as adapted to life in water and leading a hippo-like existence using independent, non-isotopic data serves as a positive test to this method. It confirms behavioral suppositions and carbon and oxygen isotope records suggesting that *Coryphodon* is a better proxy for some climate parameters than other, more terrestrial Paleocene/Eocene mammals.

Adding time to conceptual frameworks

The choice of conceptual framework affects the conclusions drawn from biological or fossil data. A number of authors have proposed frameworks for the assessment of ecology or behavior of extinct animals. Some of these address the evolution of specific suites of characters and tend to imply directional acquisition of characteristics (e.g., Hocking et al., 2017). Others are more generalized and are meant to better collate certain types of data (e.g., Cooper et al. 2016). For the latter type, an additional component is useful for behavioral assessment: the amount of evolutionary time captured by the evidence under consideration (Fig. 6). Different data yield the possibility of inference at varying temporal scales, from the nearly instantaneous evidence of behavior captured by trace fossils, to the possibly millions of years needed to accumulate whole suites of gross ecophysiological adaptations. While the lack of data determining the time needed for the evolution of many gross anatomical characters requires that they be time averaged, still the implied duration of different data allows inferences about *Coryphodon* to be made across several temporal orders of magnitude (Table 3). Isotopic data demonstrates that some individuals lived a semiaquatic existence, at least while they grew their adult teeth (Clementz et al., 2008). The isotopic record under examination was created during a portion of the individuals' lifespan and therefore shows us evidence of animal behavior on that scale. This limitation combined with the fact that not all sampled *Coryphodon* showed a significant signal of semiaquatic behavior calls into question the long-term evolutionary impact of the recorded behavior. Using a temporally calibrated conceptual framework allows us to select the data that would fill this gap. Microanatomy and histology evolve quickly, but still require the longer, multigenerational time spans associated with evolution, and so this type of evidence reflects selective processes operating on much longer timescales. The combination of evidence from several scales acts as a force multiplier; by using data sources from the short and long ends of the scale we can show that not only did individuals behave in a particular way, but that such actions were sustained and important enough to the species to generate evolutionary change. Conversely, the isotopic data records specific behaviors of individuals and can act as a check to the possibility of common cause issues that might arise for morphological data. We can more confidently infer that the distinctive histological adaptations in *Coryphodon* evolved in the context of semiaquatic behavior, because by comparing data from different temporal scales we know that individual

Coryphodon actually behaved semiaquatically. By integrating a stricter phylogenetic context than is currently possible for *Coryphodon,* this process can be applied even more powerfully in the future.

Evolution and biogeography

Behavioral and life-history information is important for understanding the specific place *Coryphodon* held in early Cenozoic ecosystems, and helps contextualize the early evolution of large size in mammals. Further, the demonstration that its large size co-occurred with adaptations for a semiaquatic lifestyle is relevant to its utility in modelling the evolution of Cenozoic mammals. *Coryphodon* is one of the earliest megafaunal mammals included in most datasets (e.g. Alroy, 1999; Smith et al. 2010) and as such influences the shape of trends across the early Cenozoic. Though its large size is not in dispute, comparisons with fully terrestrial animals and evaluations of the evolution of large size should take into account that it may have been under very different selective pressures, both mechanical and ecological, such as escape from predators (see below).

Similarly, inference about the evolution of body size in response to extrinsic pressures, such as temperature (Uhen and Gingerich, 1995; Brown et al., 1994) should include the recognition that the life history and habitats of *Coryphodon* may guide its reactions differently than smaller, faster growing, or more terrestrial taxa. As a water dwelling animal, it may have been insulated against change in some variables, even as it was made more dependent on others, such as precipitation or sea level.

Coryphodon is known from a very wide geographic range (Simons, 1960; Dawson 2012), encompassing Asia, Europe, North America and intervening parts of the arctic circle. The warm temperate conditions of the Paleocene/Eocene clearly allowed for broad mesic zones with appropriate plant life and available water. Commitment to a semiaquatic lifestyle may have influenced its ability to disperse across the connected Holarctic landmass, and conversely means that appropriate aquatic conditions were present across much of the northern landmasses.

Morphological fitness landscapes mark the fitness peaks across a morphospace defined by hypothetical ranges of animal phenotypes (Marshall, 2014). From a fitness landscape perspective, the major morphogenetic rules present in Cenozoic mammals were almost certainly inherited from lineages that survived the K/Pg extinction, nonetheless, the landscapes continued to change by altering the position of peaks (type 4 innovation of Marshall, 2014) and by altering the size of the landscape (type 3 innovation). The development of more grinding surfaces on teeth in response to the continued rise of angiosperms (Chen et al, 2019) is an example of type 4 innovation, where an ecological change led to the raised fitness peaks of certain tooth morphologies. The new body sizes occupied by mammals following the K/Pg better fits the concept of type 3 innovation, where the permissible range of an existing dimension (body size) expands leading to newly accessible morphospace. The peak occupied by *Coryphodon* seems to be only accessible in the new section of this resultant expanded landscape; despite the wide morphological disparity of Mesozoic mammals, semiaquatic folivory appears to have been inaccessible prior to this expansion of morphospace.

Lovegrove and Mowoe (2013) propose that plantigrade mammals are body size limited during most of the Cenozoic by competition and top-down control by increasingly efficient carnivores. Although the locomotor mode of *Coryphodon* deserves reassessment, as discussed above, if accepted as plantigrade its status as a semi-aquatic mammal moves it from a "plantigrade constrained" mammal to a "plantigrade unconstrained" mammal, not limited to

smaller mass by overwhelming pressure by fleeter carnivores. Far from changing the general form of their conclusions, this reassignment removes one of the few possible outliers to the pattern Lovegrove and Mowoe (2013) describe. Hypothetical placement on a fitness landscape where rising "sea-level" represents the evolutionary escalation of efficiency in carnivores (Marshall, 2014; Fig. 8) finds *Coryphodon* in a region of the fitness landscape where the fitness 'sea-level' is not rising, because the increased locomotor ability of possible carnivores does not transfer to the aquatic environment. In effect, *Coryphodon* may have "opted-out" of this particular arms race. While it is uncertain that this is generalizable to members of other guilds, it suggests that large mammals may have been seeking ecological escape from predator-imposed limitations as early as the late Paleocene.

Future work
The results of this study provide important insights into the conditions under which large body size evolved in early Cenozoic mammals and suggest many future avenues. Beyond the implications for the ecological and behavioral conditions under which mammals evolved, the distinctive growth style and the large number of LAGs are rarities among placental mammals. Establishing the presence or absence of these characters in other closely related or contemporaneous mammals will help to contextualize the histological patterns of *Coryphodon* within the Paleogene.

Whether *Coryphodon* is a behavioral outlier among Paleogene large-bodied mammals will remain unknown until histologic or isotopic methods (ideally both) can be applied more broadly. Sampling other taxa within Pantodonta is outside the scope of this study, and complicated in many cases by a lack of diagnostic postcrania but remains an important future goal. Especially important will be testing other pantodonts for aquatic adaptations, especially earlier pantodonts, such as the large *Titanoides*, and *Barylambda*, which possesses an enlarged tail of uncertain function. Neither of these has yet been included in a phylogenetic analysis or sampled histologically, and knowledge of these presumed terrestrial pantodonts will better establish the plesiomorphic state of bone growth within the group and allow assessment of the input from body size and gait separate from semiaquatic habits. When possible, broader sampling in a phylogenetic context will be the next step in evaluating when and how these microanatomical adaptations were acquired, and what that means for the evolution of early mammalian herbivores.

Conclusions
Microantomical and histological analyses of *Coryphodon* bones support a number of conclusions:

1. *Coryphodon*, one of the first large bodied placental mammals, grew for more than 15 years, with a long (10+ years) duration of slow growth. Extensive remodeling and deposition of compacted coarse cancellous bone within a closed medullary cavity combine with extensive periosteal deposition of lamellar bone to create very dense, osteosclerotic bone.

2. Extended periods of slow growth show that body size and mass continued to accumulate through much of life. Non-histological indicators of maturity in *Coryphodon*, including tooth wear, while possibly still informative about relative ontogenetic stage, may be present significantly before cessation of growth and lead to underestimates of maximum size. Caution

should be used when analyzing body size through time or using size to address taxonomic questions.

3. Histological and microanatomical data concurs with previous studies suggesting an amphibious habit for *Coryphodon*, and further demonstrates that the taxon had significant adaptations to this way of life rather than merely occupying waterways in a transient manner.

4. Microanatomical evidence of amphibious habit provides independent, non-isotopic confirmation of *Coryphodon* enamel as an appropriate proxy for surface water O^{18} values, validating its use in calculating climate parameters, such as terrestrial mean annual temperature.

5. Frameworks for behavioral inference benefit from an appreciation of the evolutionary timescale of the evidence involved, helping to avoid discrepancies between timescales of question and evidence in hypothesis testing, and to better frame causal relationships in the evolution of major changes. In this case, one of the first large mammals was both a herbivore and spent significant time in the water, evolving multi-scalar adaptations to that way of life. The contemporary achievement of large body size and semiaquatic herbivory suggests a reciprocal, rather than unidirectional, causal relationship between body size and specialization at the beginning of the Cenozoic.

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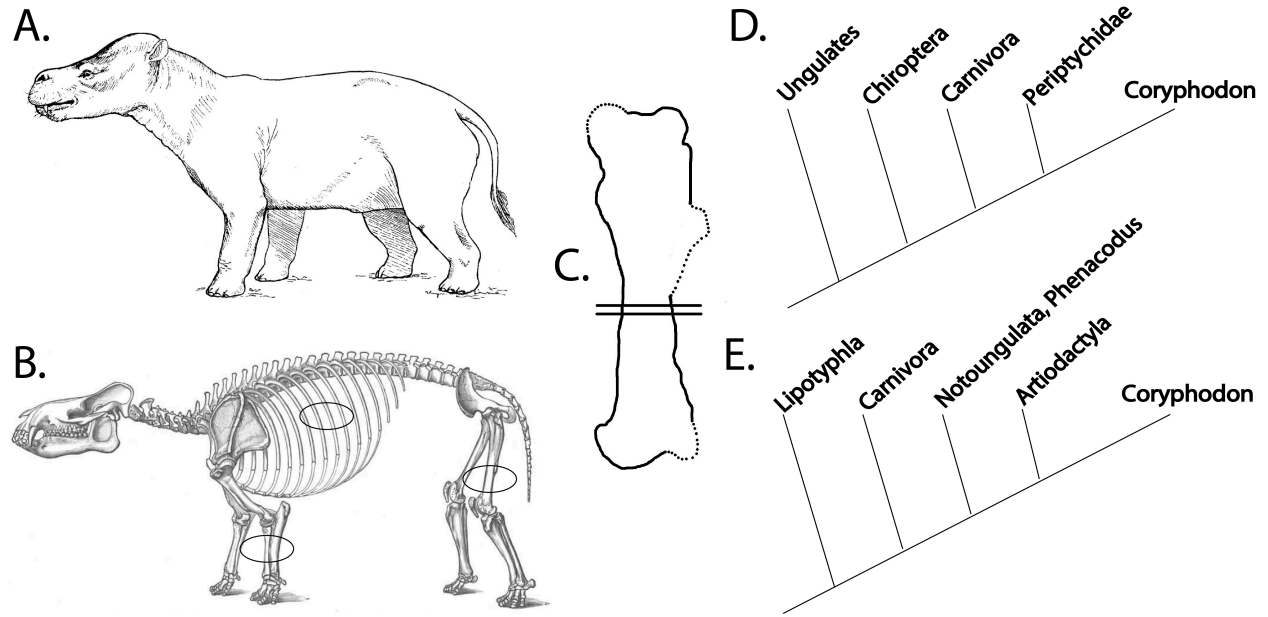
FIGURES

FIGURE 1. *Coryphodon*; A, Life reconstruction Simons, 1960 B, Skeletal reconstruction, after Marsh, 1893. Ovals show locations of histological samples. C, Schematic outline of *Coryphodon* femur UCMP 238309, showing sampling location for femora. D, hypothesized phylogenetic position after Halliday et al., 2015. E, hypothesized phylogenetic position after De Muizon et al., 2016, Fig. 122.
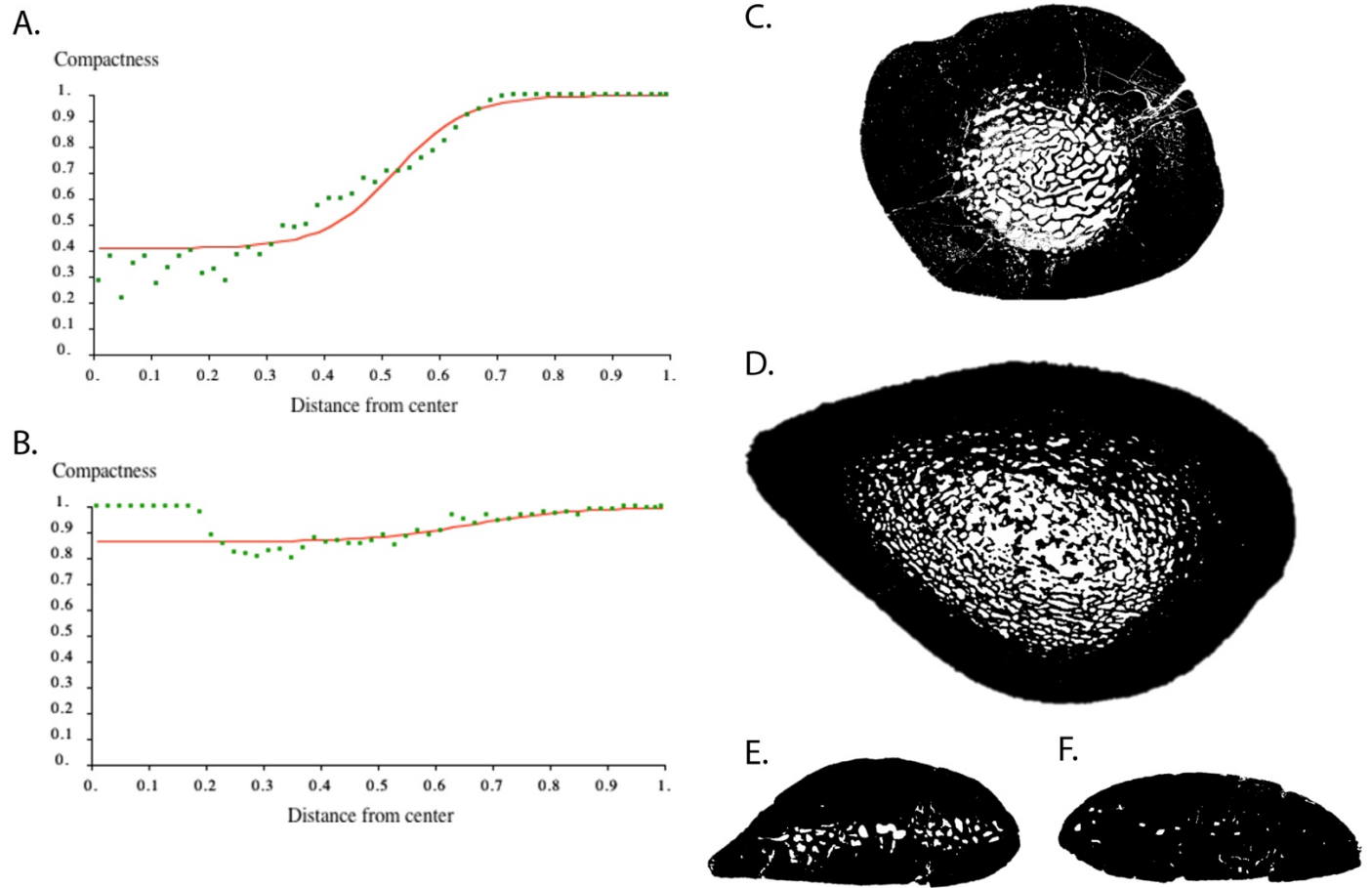
FIGURE 2. Microanatomy of *Coryphodon*. A and B, profiles of bone microanatomy from femur (UCMP 178303, see D.) and rib (UCMP 238311, see E) respectively. Profiles represent radial estimations of concentric surfaces. C, binary drawing of radius, UCMP 238310. D, binary drawing of femur UCMP 178303. E, binary drawing of rib 1 UCMP 238311. F, binary drawing of UCMP 238312.
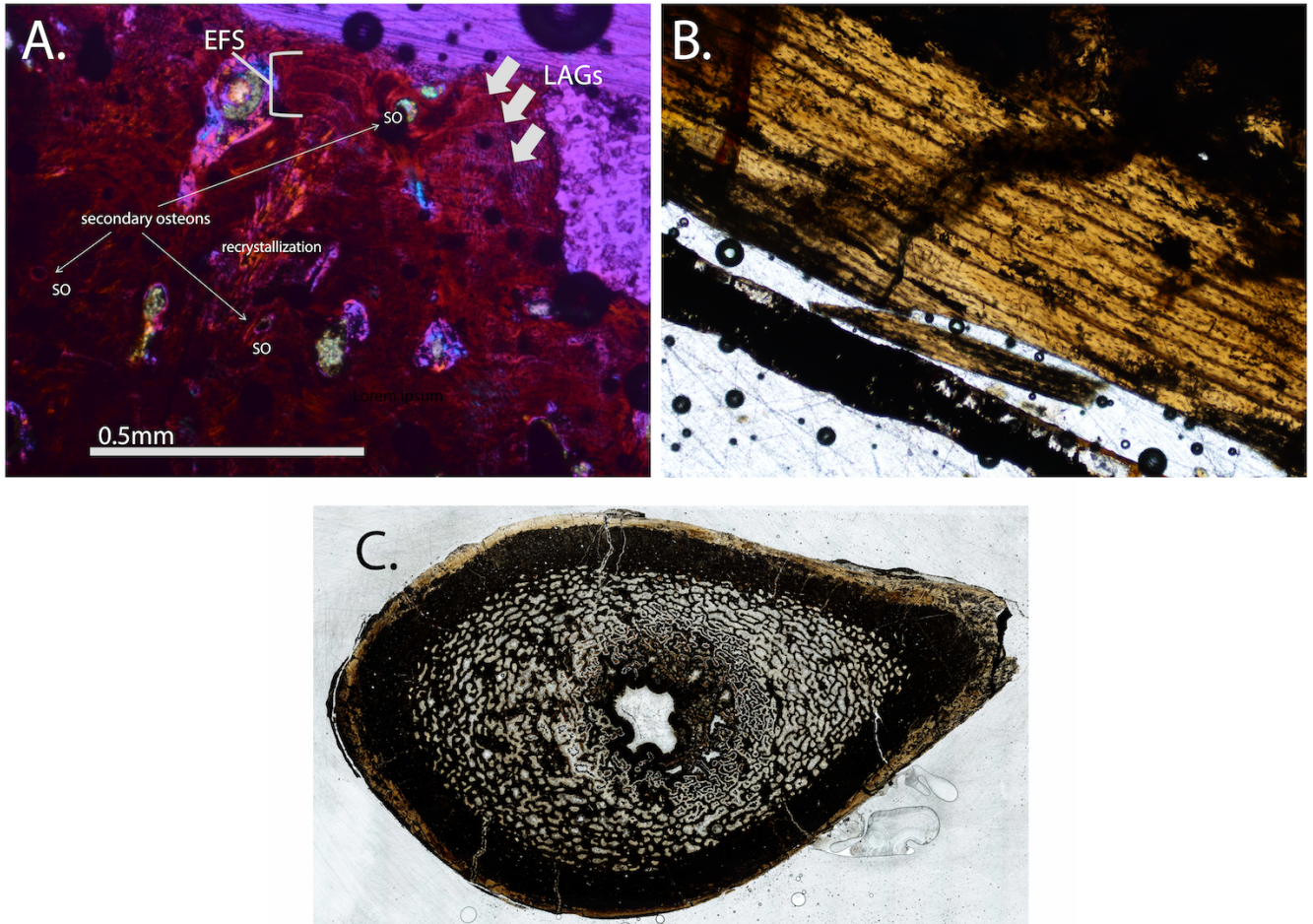
FIGURE 3. Additional histology of *Coryphodon*. A, detail of radius UCMP 238310, showing EFS, LAGs and secondary osteons (note slide is slightly over-ground to visualize diagenetically altered structures). B, detail of femur CM 81669 periosteum, showing densely packed LAGs. C, photomosaic of CM 81669, showing open medullary cavity of proximal-most thin section.
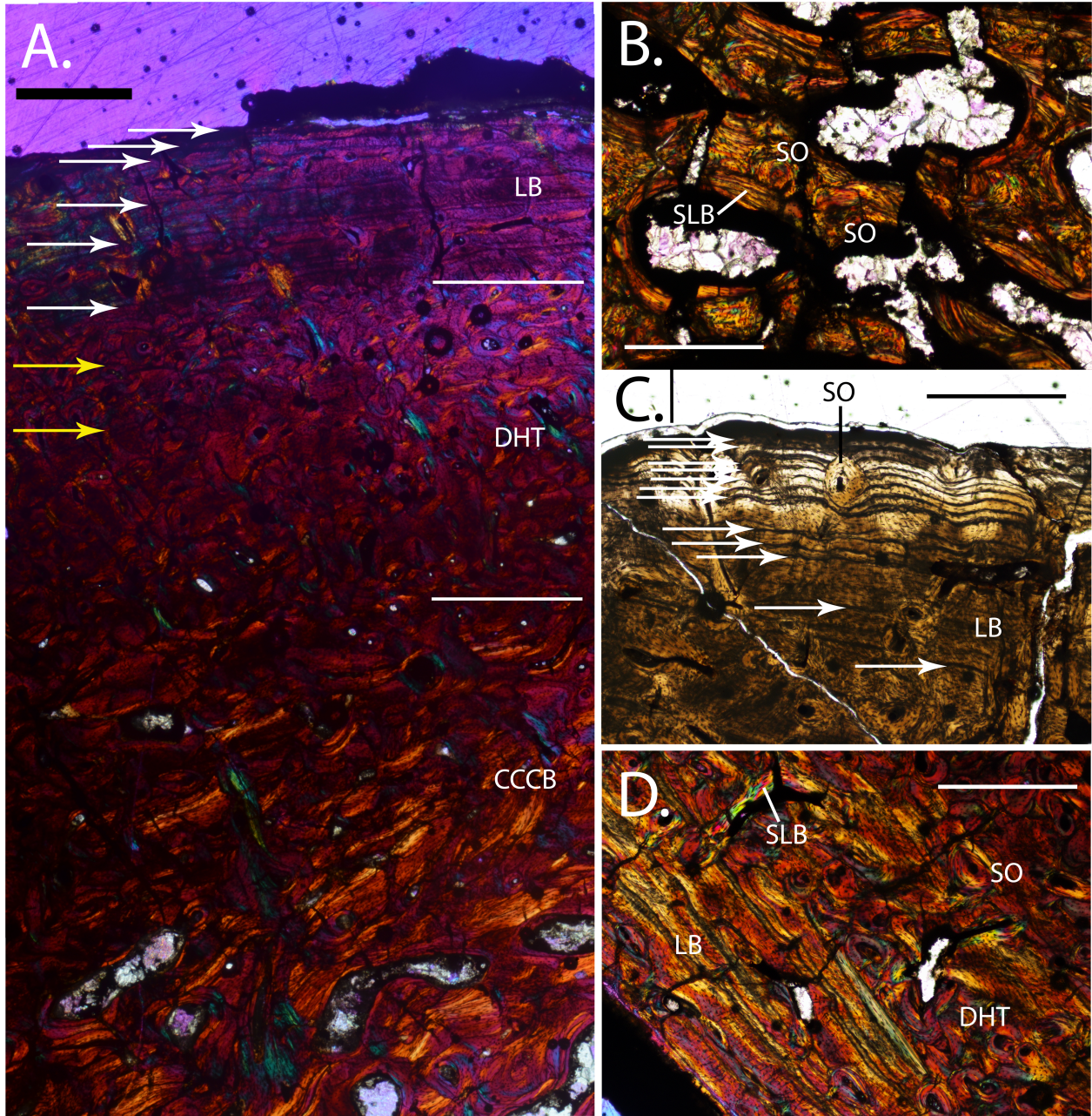
FIGURE 4. Histology of large *Coryphodon* femur, UCMP 238308. A, transect of bone histology with periosteal surface at top, under elliptically polarized light with a lambda tint plate. Major zones of bone separated by white lines. Arrows indicate LAGs, with two inner LAGs visible elsewhere around the circumference. B, detail of cancellous bone under plane polarized light, showing deposition of secondary lamellar bone. C, detail of outer cortex under elliptically polarized light, showing intact EFS with 12 LAGs visible (arrows). D, detail of outer cortex under elliptically polarized light showing mixture of bone types. CCCB, coarse cancellous bone; DHT, dense Haversian tissue; LB, lamellar bone; SLB, secondary lamellar bone; SO, secondary osteon
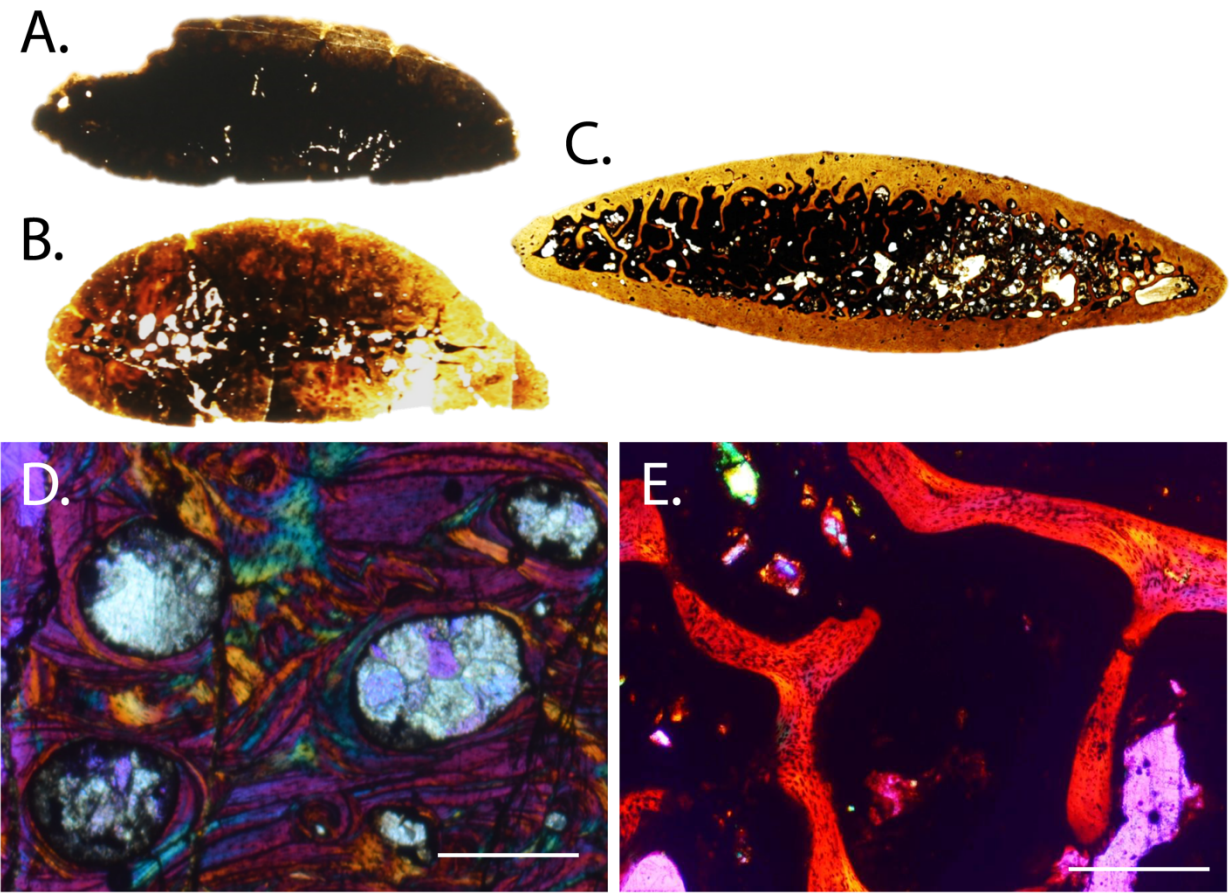
FIGURE 5. *Coryphodon* rib anatomy and cancellous histology in comparison with *Equus*. A, cross section of *Coryphodon* rib (UCMP 238312). B, cross section of *Coryphodon* rib (UCMP 238311). C, cross section of Pleistocene horse rib. Note expansive medullary cavity, here filled with black tar. D, close up of *Coryphodon* cancellous bone showing complex fiber orientation and secondary lamellar bone. E, close up of *Equus* cancellous bone, showing basic spicules.
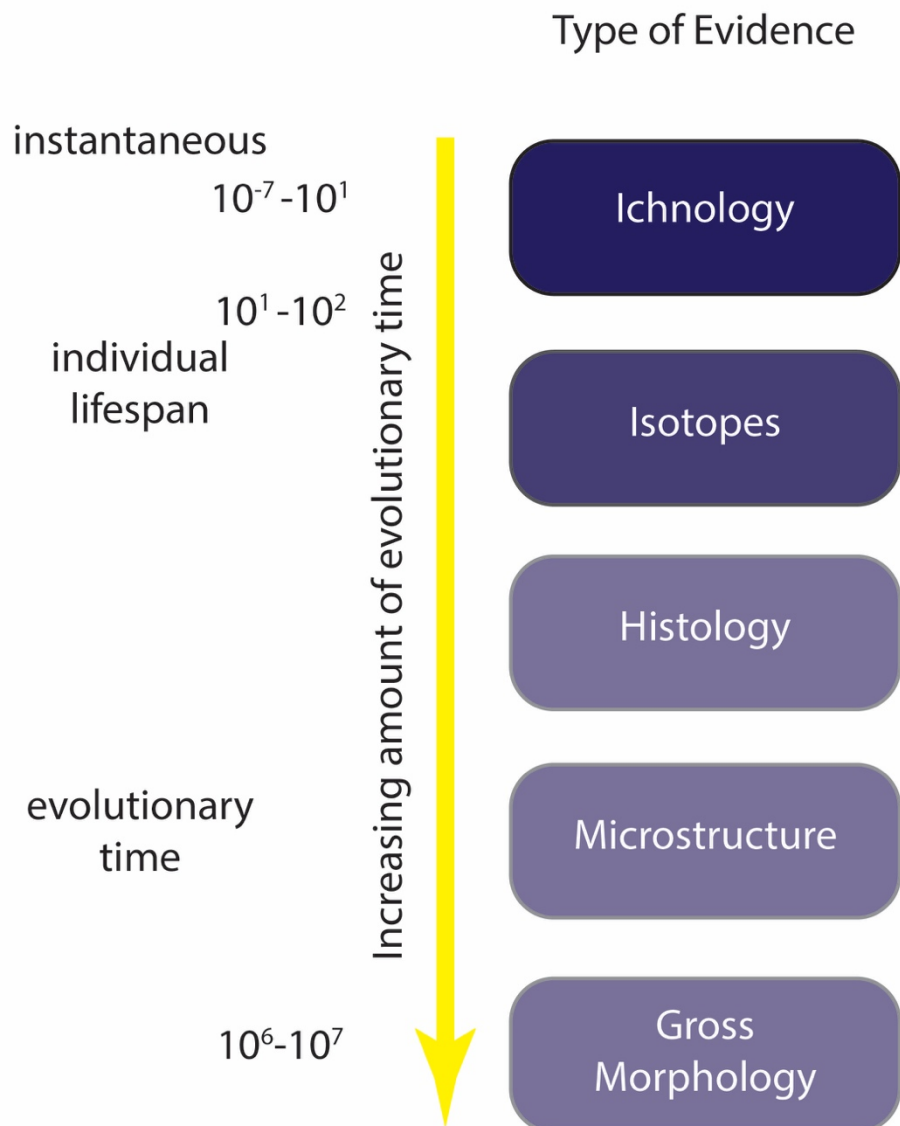
FIGURE 6. Exemplar representation of timescale dependent evidence for behavioral adaptation.

TABLE 1. Specimens used in this study

Specimen #	element	size	length	locality	location	formation
UCMP 238309	femur	small	>26 cm	V65175	Bighorn Basin, WY	Willwood
UCMP 178303	femur	medium	>40 cm	V65175	Bighorn Basin, WY	Willwood
UCMP 238308	femur	large	>45 cm	V65175	Bighorn Basin, WY	Willwood
CM 81669	femur	medium	>40 (est.)	3 miles west of basin	Bighorn Basin, WY	Willwood,Upper Graybull
UCMP 238310	radius	medium	?	V74092	Moffat Co., CO	Wasatch
CM 47208	radius	medium	?	Bighorn Basin	Bighorn Basin, WY	Willwood,Upper Graybull
UCMP 238311	rib	medium	na	V74092	Moffat Co., CO	Wasatch
UCMP 238312	rib	medium	na	V74092	Moffat Co., CO	Wasatch

TABLE 2. Bone histology characteristics

Specimen #	element	open medullary cavity	EFS	# of LAGs	secondary osteons
UCMP 238309	femur	Y	Y	?	N
UCMP 178303	femur	N	Y	>3	Y
UCMP 238308	femur	N (?)	N	>15	Y
CM 81669	femur	Y/N (variable by section)	Y	>12	Y
UCMP 238310	radius	N	Y	>5	Y
CM 47208	radius	N	Y	?	Y
UCMP 238311	rib	N	?	?	not visible
UCMP 238312	rib	N	?	?	not visible

TABLE 3. Results of microstructural analysis using Bone Profiler
Mean terrestrial values from Amson et al. 2014, sourced from the following papers: femur, Quemeneur et al., 2013; radius, Germain and Laurin, 2005; rib, Buffrénil et al., 2010.

Specimen #	Global compactness	Min	Max	S	P	R/t	CDI	mean terrestrial compactness
UCMP 238309	0.8	0.595	1	0.078	0.689	3.216	0.311	0.594 (femur)
UCMP 178303	0.83	0.412	1	0.062	0.522	2.092	0.478	
UCMP 238308	0.841	0.764	1	0.043	0.816	5.434	0.184	
CM 81669	0.805	0.624	0.994	0.032	0.707	3.418	0.293	
UCMP 238310	0.807	0.306	0.982	0.055	0.494	1.980	0.5051	0.815 (radius)
CM 47208	0.816	0.352	0.994	0.057	0.513	2.017	0.497	
UCMP 238311	0.937	0.865	0.998	0.085	0.66	2.940	0.340	0.566 (rib)
UCMP 238312	0.985	0.913	1	0.091	0.71	2.99	0.320	

TABLE 4. Evidence for semi-aquatic behavior in *Coryphodon*

type of evidence	relative time scale	year range (approx.)	evidence	Citation
Ichnology	instantaneous	10^{-7}-10^1	none	-
Sedimentology	instantaneous to lifespan	10^{-7}-10^1	presence in channel deposits	equivocal
Isotopes	individual lifespan	10^1-10^2	low mean delta^{18}O values; low delta^{13}C$_E$ values	Clementz et al., 2008; Secord et al., 2008
Histology	generations to evolutionary	10^3-10^6	extensive remodeling, CCCB leading to osteosclerosis	This study
Microstructure	generations to evolutionary	10^3-10^6	high bone compactness, in-filled medullary cavity, incipient pachyostosis	This study
Gross Morphology	evolutionary time	10^6-10^7	body shape, broad feet, dorsal eye position, etc.	Simons, 1960; Meehan and Martin, 2003

Chapter 2
Mandibles of the sea lion *Proterozetes ulysses* from the Middle Pleistocene Port Orford Formation of Oregon

ABSTRACT

      The Pleistocene sea lion *Proterozetes ulysses* belongs to a monophyletic group of North Pacific otariids that includes the living genera *Eumetopias* and *Zalophus*. Mandibles of *Proterozetes* from the Port Orford Formation of Oregon are described and found to be intermediate in morphology and size to the other North Pacific otariids, sharing the most features with *Eumetopias*. Among other features, the presence of an oblong prominence on the anterior lingual surface links the taxon to *Eumetopias* where it is commonly observed. Uniquely among North Pacific otariids, *Proterozetes* possesses a p1 alveolus distinctively smaller than that of the p2. The presence of a distinct but morphologically intermediate taxon in the eastern North Pacific during the Pleistocene establishes it as a time of increased otariid diversity in contrast to a suggested decline in other marine mammal clades. The timing of sea lion diversification along the west coast of North America appears to follow that in Japan, reinforcing the possibility of an eastward dispersal trend in the North Pacific after the end-Pliocene.

INTRODUCTION

      The fossil record of fur seals and sea lions (Otariidae) extends to the early middle Miocene (Boessenecker and Churchill, 2015) and is largely restricted to the North Pacific. In contrast to the extant otariid fauna from the eastern North Pacific (ENP) which includes two fur seals (*Arctocephalus townsendi*, *Callorhinus ursinus*) and two sea lions (*Eumetopias jubatus*, *Zalophus californianus*), Miocene and Pliocene marine mammal assemblages typically contain only one fur seal species (*Eotaria crypta*, early middle Miocene "Topanga" Formation; *Pithanotaria starri*, early late Miocene Monterey and Santa Margarita formations; *Thalassoleon mexicanus*, latest Miocene Almejas and Capistrano formations; *Thalassleon macnallyae*, Purisima Formation; *Callorhinus gilmorei*, San Diego and Rio Dell Formations; Kellogg, 1925; Repenning and Tedford, 1977; Berta and Deméré, 1986; Deméré and Berta, 2005; Boessenecker, 2011, 2013a; Boessenecker and Churchill, 2015). More diverse otariid assemblages are known from the Plio-Pleistocene of Japan and Pleistocene of California and Oregon (Miyazaki et al., 1995, and references therein), which differs markedly from the suggested decrease in cetacean diversity during those epochs (Uhen and Pyenson, 2007; Quental and Marshall, 2010). Critical toward understanding the evolutionary history of living marine mammals is documenting rare

Pleistocene fossils that bridge the gap between comparably richer Pliocene assemblages and the living fauna (Boessenecker, 2011, 2013a, 2013b; Tsai and Boessenecker, 2015).

One such locality is the Port Orford Formation in southwestern Oregon, which yielded the first named true sea lion from the fossil record of the eastern North pacific, *Proterozetes ulysses* (Barnes et al., 2006). *Proterozetes ulysses* is known from the nearly complete holotype skull (USNM 187108), a referred mandible (USNM 18709, figured but not described) and an assortment of referred material (Packard, 1947a; Barnes et al., 2006; Boessenecker, 2013c). The Port Orford Formation is middle Pleistocene in age (Boessenecker, 2013c) though initially considered late Pliocene by Barnes et al. (2006). Their phylogenetic analysis supported a sister group relationship between *Proterozetes* and extant Steller's sea lion (*Eumetopias jubatus*). Churchill et al. (2014) also recovered *P. ulysses* as sister to *Eumetopias* and included both within a northern sea lion clade with *Zalophus*. Curiously, prior to publication earlier workers considered *Proterozetes ulysses* to be a new extinct species within the extant genus *Eumetopias* (Repenning and Tedford, 1977). It is possible that *Proterozetes* is a junior synonym of *Eumetopias*, a hypothesis that may be testable using similar methods towards reevaluation of the New Zealand Pleistocene otariid *Neophoca palatina* (Churchill and Boessenecker, 2016). *Proterozetes ulysses* possesses one of the most well-preserved crania of any fossil otariid, though the mandibular morphology of *Proterozetes ulysses* remains unreported (except for one illustration: Barnes et al., 2006: Fig. 4). This study reports a new mandible of *Proterozetes ulysses* from the Port Orford Formation of Oregon, and provides a supplementary description of the referred mandible originally illustrated by Barnes et al. (2006).

METHODS

UCMP 2190377 was prepared in dilute (5%) acetic acid and resistant fragments of calcium carbonate-cemented siltstone were physically prepared by air chisel and air-abrasive unit. Measurements were recorded to the nearest tenth of a millimeter with digital calipers (Mitutoyo). Specimens were photographed with a Canon Rebel XS and 80mm zoom lens. For the purposes of chronostratigraphy, we place the Plio-Pleistocene transition at the Gelasian-Calabrian boundary; at ~1.8 Ma as recommended by Hilgen et al. (2012).

Institutional Abbreviations

UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; **USNM**, Smithsonian, Washington D.C., USA; **MVZ**, Museum of Vertebrate Zoology, Berkeley, CA.

GEOLOGIC SETTING

Fossils of *Proterozetes ulysses* occur within the Port Orford Formation in Curry County, Oregon (Barnes et al., 2006; Boessenecker, 2013c). The Port Orford Formation comprises four members described by Roth (1979), which, from oldest to youngest, are the lower conglomerate member (LCM), lower brown sandstone member (LBSM), blue argillaceous siltstone member (BASM), and the upper brown sandstone member (UBSM) (Fig. 1). Sedimentology of the Port Orford Formation indicates 1) an initial period of fluvial incision and deposition of the lower conglomeratic member; 2) subsequent deepening and shallow marine deposition of the lower brown sandstone member within a north-south trending embayment with estuarine influence; 3) maximum deepening of the embayment reflected by deposition of the blue argillaceous sandstone member; and 4) shallowing of the embayment and deposition of the upper brown member above fair weather wave base (Roth, 1979; Boessenecker, 2013c). The ichthyofauna

includes many extant demersal species consistent with a muddy or sandy bottom; the presence of rockfish (*Sebastes* spp.) suggests nearby rocky shore habitat (Welton, 2015) corroborated by rocky shore macroinvertebrates such as *Mytilus californicus* and certain gastropods (Roth, 1979) and sea urchins (cf. *Strongylocentrotus*; R.W. Boessenecker, pers. obs.). The Port Orford Formation unconformably overlies the late Miocene "Empire" Formation (=Cape Blanco Formation of Roth, 1979), and is in turn overlain by Upper Pleistocene terrace deposits (Addicott, 1964; Roth, 1979). The Port Orford Formation is Middle Pleistocene in age, and based on molluscan and echinoderm biostratigraphy, and amino acid racemization, the Port Orford Formation can be summarized as 0.7-0.5 Ma (Wehmiller et al., 1978; Roth, 1979). This unit was erroneously reported as late Pliocene by Barnes et al. (2006). The Port Orford Formation is richly fossiliferous and includes foraminifera, a rich macroinvertebrate fauna including 112 species of mollusks and echinoderms (Roth 1979) and a vertebrate assemblage (Merriam, 1913; Packard, 1947a; 1947b; Leffler, 1964; Welton, 1979; Barnes et al., 2006; Boessenecker 2013c; Welton, 2015) including 21 species of teleost fish, elasmobranchs (*Cetorhinus* sp., *Raja binoculata*, *Squalus suckleyi*), birds (*Chendytes* sp., *Larus* sp.), a sea otter (*Enhydra* sp.), a harbor seal (*Phoca* sp., cf. *P. vitulina*), three otariids (*Callorhinus* sp., ?*Zalophus* sp., and *Proterozetes ulysses*), baleen whales (*Balaena* sp., *Balaenoptera acutorostrata*), an indeterminate proboscidean, and a tapir (*Tapirus* sp.).

UCMP 2190377 (Fig. 2) was collected as an isolated concretion adjacent to exposures of the blue argillaceous siltstone member of the Port Orford Formation. The lithology of the associated concretion closely matches that of other concretions in the vicinity in addition to *in situ* concretions of the BASM. USNM 187109 (Fig. 3) was similarly described as having been found "in a concretion in place in blue-grey argillaceous sand" (Barnes et al. 2006). Specimens of *Proterozetes* originate principally from the lower brown sandstone and blue argillaceous siltstone members, although a single juvenile radius was collected from the basal conglomerate (equals LCM) (Barnes et al. 2006).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
CARNIVORA Bowditch, 1821
OTARIIDAE Gill, 1866
PROTEROZETES Barnes, Ray, and Koretsky, 2006

Type species—*Proterozetes ulysses* (Barnes, Ray, and Koretsky 2006)
Amended Diagnosis—Otariid pinniped intermediate in size between *Zalophus* and *Eumetopias*, and differing from all other Otariidae in combined possession of single rooted postcanine dentition, long P4-M1 diastema present, M2 present, p1 with much smaller alveolus than p2, prenarial process reduced, dorsally arched dorsal profile of interorbital region of skull, narrowest intertemporal constriction midway between supraorbital process and braincase, anteroposteriorly elongate and dorsally convex sagittal crest, anterolateral profile of braincase smooth and lacking corner, mandible deepest below p1-2, mandible lacking crest-like digastric insertion, and coronoid process of mandible that is not posteriorly overhanging.

PROTEROZETES ULYSSES Barnes, Ray, and Koretsky 2006
(Figs. 2–3)

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Referred specimens—UCMP 219377, a right mandible comprising the complete horizontal ramus, the ventral portion of the ascending ramus, and partial canine, collected by A.W. Poust, L.E. Hall, and R.W. Boessenecker, March 14, 2009.

USNM 187109, a complete left mandible including p1 and m1, collected by Douglas R. Emlong in the early 1970's and referred to *Proterozetes ulysses* by Barnes et al. (2006).

Locality and Age—Port Orford Formation, blue argillaceous siltstone member, Middle Pleistocene (0.7-0.5 Ma), Curry County, Oregon. Detailed locality information is available on request from UCMP or the authors.

Description

Mandible—The horizontal ramus of the mandible is roughly rectangular with parallel dorsal and ventral margins. It is dorsoventrally deepest anteriorly accommodating the canine and there is no drop in mandibular ramus height posterior to m1. A cluster of three large mental foramina occur below the p1 and p2; a fourth foramen is present below p3. Multiple smaller foramina occur on the anterior half of the mandible. The small genial tuberosity is positioned below the p1 alveolus and forms the dorsoventrally deepest part of the mandible. An oblong, posteroventrally oriented prominence is present lingually, posterior to the symphysis. The mandibular foramen is large and positioned anterior to the pterygoid process. It is oriented slightly anteroventrally, more horizontally than in other taxa such as *Callorhinus*. The masseteric fossa is anteroposteriorly broad. The anterior edge of the muscle scar is more vertical than specimens of *Callorhinus gilmorei* where the leading edge of the scar runs at a 45 degree angle (Boessenecker 2011). The coronoid process is anteroposteriorly broad, making up approximately one third of the length of the mandible. In USNM 187109 it begins almost immediately posterior to the m1 alveolus and rises to a height approximately equal to the depth of the ramus. The anterior angle is steeper than in other sea lions, resulting in a process that rises nearly perpendicularly to the ramus and is much more symmetrical in outline than the swept back processes of *Callorhinus* or *Zalophus*. The crest of the process is rounded and broad, rather than pointed. The posterior edge of the coronoid process is straight rather than concave and indented in outline where it meets the mandibular condyle. The mandibular condyle is broad, with a well-developed articular surface. The posterior portion of the ramus does not appear to have a distinct digastric insertion.

Dentition—The i2 and i3 alveoli preserved between the c1 and the symphysis are small and exposed below the level of the rest of the tooth row; the dorsal margin of i3 is abraded in UCMP 219377, as is the anterior-most part of the mandible including the i2 alveolus. The alveoli of p2-p4 are similar in size to one another. The canine of UCMP 219377 is broken just above the rim of its alveolus. The c1 is robust with a large root and longitudinally striated enamel. The pulp cavity is large, and the width of the enamel and dentine layers of the tooth varies between 3.1 and 4.4 mm at the anterolateral and posteromedial borders respectively. The p1 crown of USNM 187109 is simple, sub-conical, and lacks obvious paraconid and hypoconid cusps. A smooth lingual cingulum is present, and a labial cingulum absent. The p1 alveolus is approximately 50% the anteroposterior and transverse diameter of p2. The m1 of USNM 187109 appears single rooted (corroborated by the alveolus in UCMP 219377), and possesses a simple crown also lacking a labial cingulum but possessing a smoothed, dorsally arched lingual cingulum; a

hypoconid cusp is not evident. The anterior part of the m1 crown is obliterated by a large wear facet. Alveoli of p2-p4 similarly indicate the presence of bilobate single roots; interalveolar septa (indicating double-rooted condition) are not evident. The toothrow is oriented obliquely with respect to the mandible, with the p1 positioned labially and the m1 lingually. No diastemata are present.

Comparisons—Among the living Otariidae, *Proterozetes* shares the most features with extant northern hemisphere sea lions, *Eumetopias* and *Zalophus*. In these taxa, the lack of a post-m1 decrease in ramus height differs from the dorsoventral constriction of the jaw seen in the Oligo-Miocene *Eotaria*, *Enaliarctos,* and *Pteronarctos*, and many extant phocids. The rounded coronoid process of *Proterozetes* is distinctive. The symmetry provided by the steep anterior angle differs from most taxa where the anterior margin is at a higher angle to the ramus. The straighter posterior edge also distinguishes the coronoid of *Proterozetes*; it lacks a concavity near the mandibular condyle present in many taxa. Uncommonly, the posterior margin will be straight to convex in *Eumetopias*. Of all otariines, a coronoid with a similar outline is present only in *Thalassoleon*, which may be distinguished by a more gracile ramus. The ratio of the postcanine tooth row to mandible length is similar in all ENP otariids at about one third, but it is longest relative to the jaw in *Proterozetes* (0.35:1). The absence of the insertion of the digastric distinguishes these specimens from taxa where that feature is present, such as *Callorhinus gilmorei* where it is transversely convex without a sharp edge and other sea lions where it is posteroventrally expanded, though it is possible that the absence is taphonomic.

Though closely resembling the jaws of extant sea lions, UCMP 219377 and USNM 187109 share several unique features. The anterolingual convexity present in UCMP 219377 is present in many adult *Eumetopias*, including members of both sexes and those significantly advanced in age. We could locate this convexity in only one member of *Zalophus*, an immature specimen: UCMP 123110. It may be the result of accommodation for the erupting canine, but the edges are more distinct than in other taxa making it recognizable in *Eumetopias* and *Proterozetes*. Most distinctively, the alveolus of the first premolar is markedly smaller than those of the remaining postcanine teeth. In *Callorhinus*, the dimensions of the p1 alveolus are similar to those of other postcanine teeth. The p1 is marginally smaller than p2-m1 in *Eumetopias* and *Zalophus* specimens from the Museum of Vertebrate Zoology (MVZ) and UCMP, but not to the degree present in *Proterozetes*. In order to test that this character was distinctive in *Proterozetes*, we measured the alveoli of the two fossils and 80 mandibles of extant ENP otariids from the collections of the UCMP and the MVZ. Of these, 9 mandibles were either damaged or too young to have an erupted p1, allowing us to compare the anteroposterior alveolar length of the first and second premolars from 73 specimens (Fig. 4). The *Proterozetes* specimens are the only lower outliers based on interquartile range, and the 95 percent confidence intervals of *Zalophus* and *Eumetopias* overlap significantly. The extant sea lions share similar average p1/p2 ratios of 0.84 and 0.87 respectively. *Callorhinus* individuals have the most similar p1/p2 alveolar size (average equals 0.93). Though the sample size for *Proterozetes* remains small, their lack of overlap with other taxa suggests a relatively small p1 alveolus (average ratio equals 0.58) may be an autopomorphy rather than a feature shared with *Eumetopias* as suggested by Churchill et al. (2014).

DISCUSSION

The mandibular morphology of *Proterozetes* is similar to extant *Eumetopias jubatus* and *Zalophus californianus*. Though we can detect no synapomorphies that *Proterozetes* uniquely shares with *Zalophus*, several mandibular features appear to unite *Proterozetes* and *Eumetopias*: 1) The genial tuberosity is anteriorly positioned so that the deepest part of the mandibular ramus is under the p1, or between p1-p2. In all sea lions this feature occurs in a relatively anterior position, but this resembles the position in *Eumetopias* more than that below p2-p3 in *Zalophus* as well as in *Arctocephalus* and *Callorhinus*. 2) The oblique curvature of the tooth row is also distinctively more similar to *Eumetopias* than to the straighter orientation of *Zalophus*. 3) The anterior ventral portion of the lingual side has a convexity present in all *Eumetopias* but only in some few very immature *Zalophus*. In addition to these characters, the new specimen of *Proterozetes* (UCMP 219377) is intermediate in size between *Zalophus* and *Eumetopias*. Though no known specimen approaches the size of an adult *Eumetopias jubatus*, USNM 187109 is notably larger than UCMP 219377 (see Table 1). On the basis of the incomplete eruption of the proportionally large canine and large pulp cavity, USNM 219377 is best interpreted as a subadult male of the same species.

These observations parallel the morphology of the holotype cranium of *Proterozetes ulysses* (Barnes et al., 2006; Churchill et al., 2015), which includes several *Zalophus*-like features (large dorsally convex sagittal crest that approaches the supraorbital processes; nuchal crests) and *Eumetopias*-like features (reduction of prenarial process; "domed" frontal profile of the interorbital region of the braincase; large size). Yonezawa et al. (2009) considered *Proterozetes* to be closest to *Eumetopias*, and cladistic analyses carried out by Churchill et al. (2014) consistently recovered a sister taxon relationship between *Proterozetes* and *Eumetopias*. Whether or not seemingly minor differences between *Eumetopias* and *Proterozetes* reported by Barnes et al. (2006) predicates recognition of a separate genus awaits testing by discovery of new material or reevaluation of cranial morphology using principal components analysis (e.g. Churchill and Boessenecker, 2016).

The fossil record of Otariidae in the Eastern North Pacific is predominantly monogeneric and the presence of multiple otariid taxa appears to be relatively recent. Not until the Pleistocene do sea lions appear alongside *Callorhinus* in the North Pacific heralding a time of marked regional diversity in otariids. Japanese records of *Zalophus* and *Eumetopias* from Pliocene rocks predate known records from North America. The re-interpretation of the Port Orford Formation as Pleistocene indicates sea lions were absent in the eastern North Pacific during the Pliocene (Boessenecker, 2013a), suggesting that sea lions evolved in the WNP during the Pliocene and dispersed to the ENP after an end-Pliocene period of marine mammal extinctions or faunal turnover, similar to that inferred for the gray whale *Eschrichtius robustus* (Tsai and Boessenecker 2015). As part of this turn over, the extinction of dusignathine walruses at the end of the Pliocene (Demere et al., 2003; Boessenecker, 2013a) may have provided ecological opportunities for ecologically similar otariids to thrive in the ENP.

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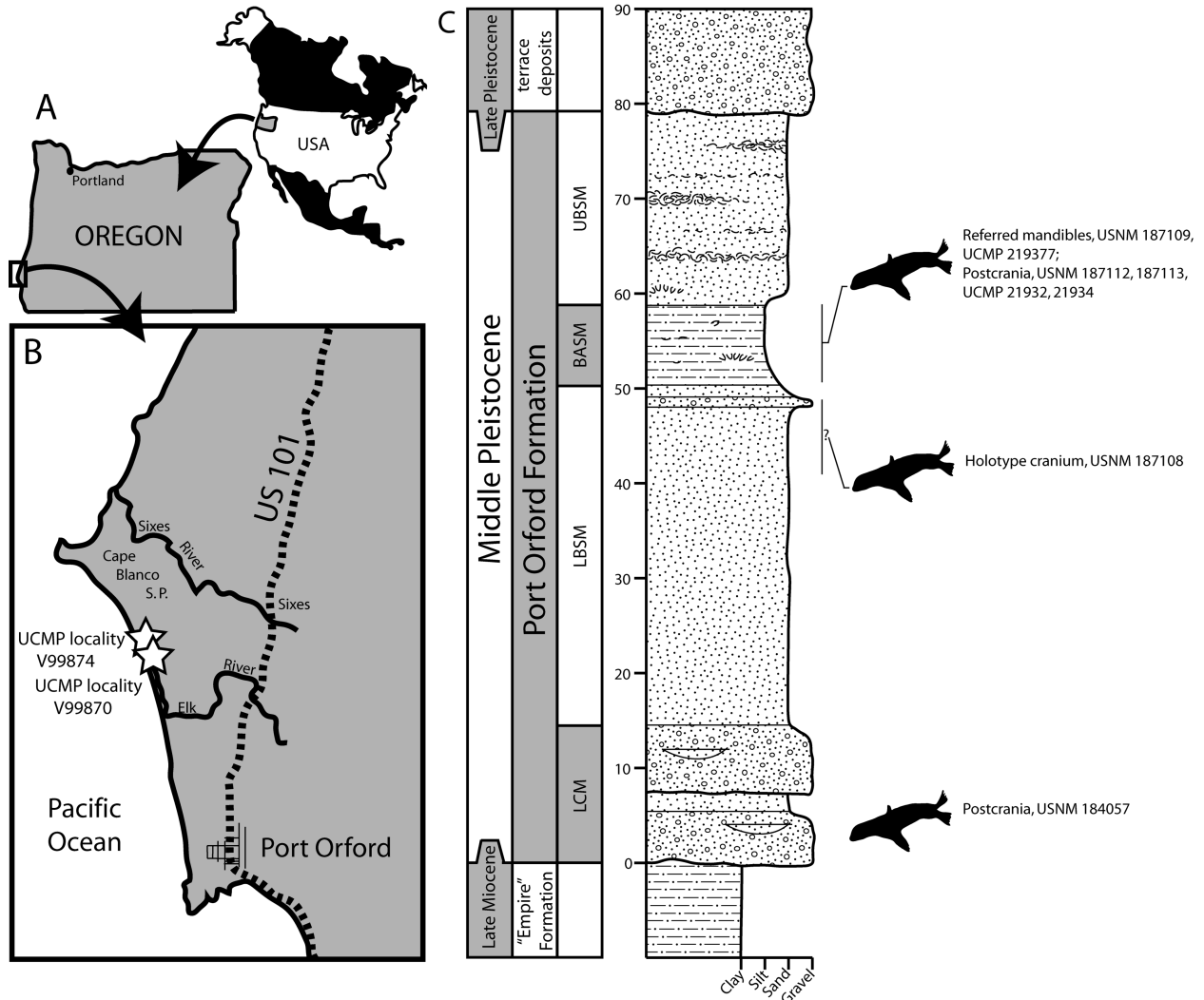
FIGURE 1. Geographic and geologic context of *Proterozetes ulysses*. **A–B**, map of the Cape Blanco region, Oregon, modified from Boessenecker (2013c). **C**, stratigraphic column of the Port Orford Formation with stratigraphic origin of *Proterozetes* remains (modified from Roth, 1979).
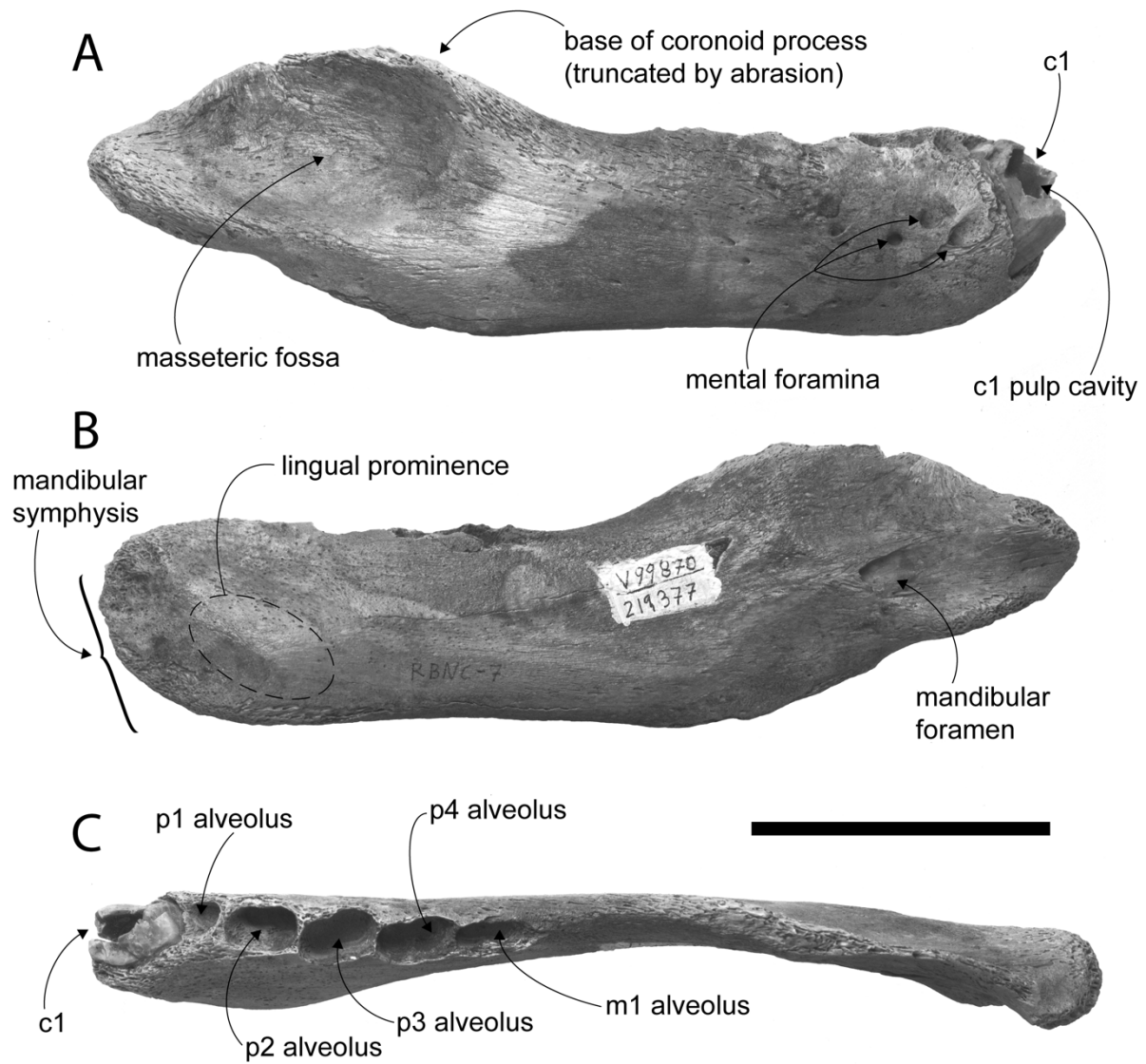
FIGURE 2. Right mandible of *Proterozetes ulysses*, UCMP 219377. **A**, lateral view; **B**, medial view; **C**, dorsal view. Scale bar equals 5 cm.
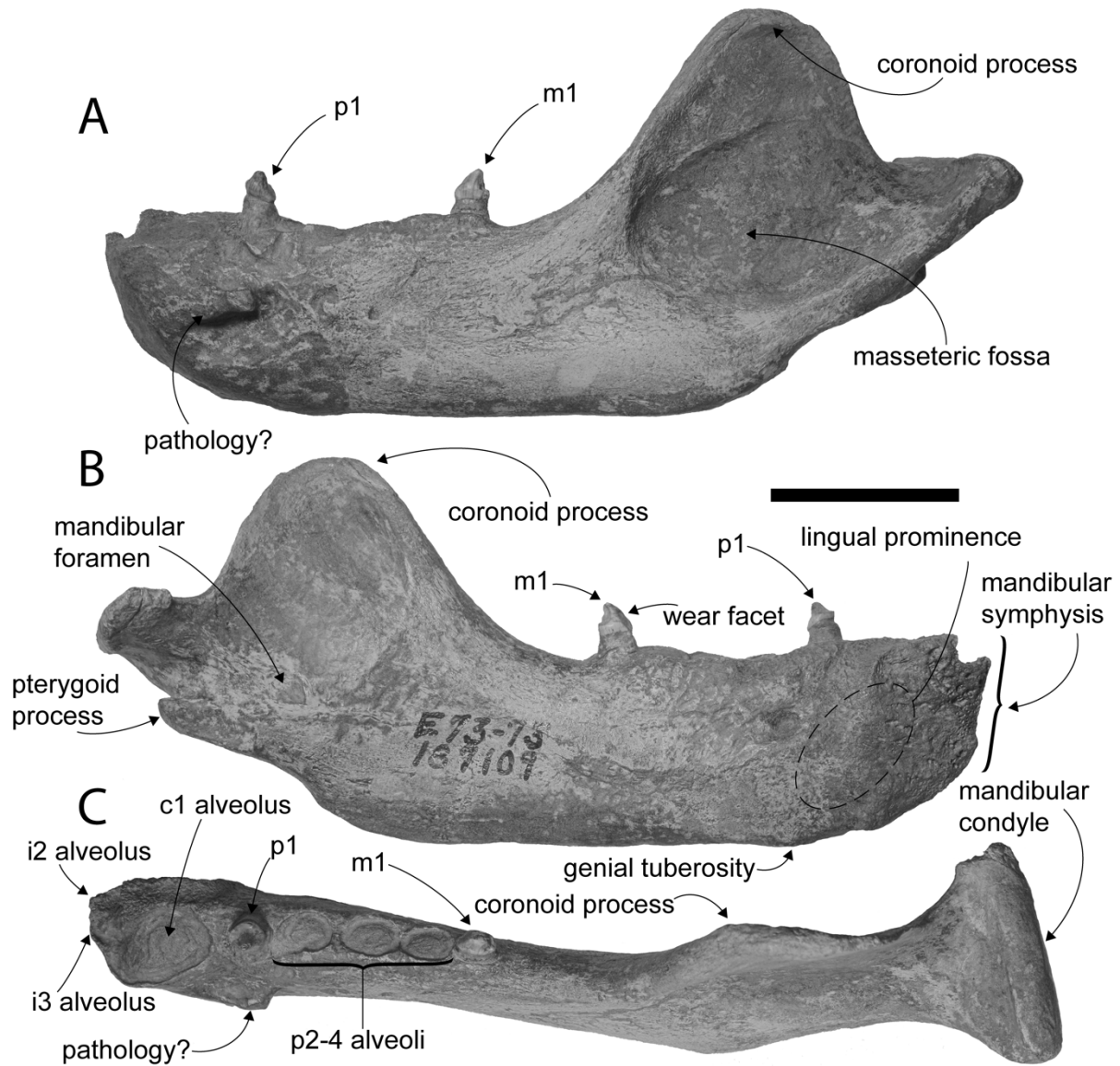
FIGURE 3. Left mandible of *Proterozetes ulysses,* USNM 187109. **A**, lateral view; **B**, medial view; **C**, dorsal view. Scale bar equals 5 cm.
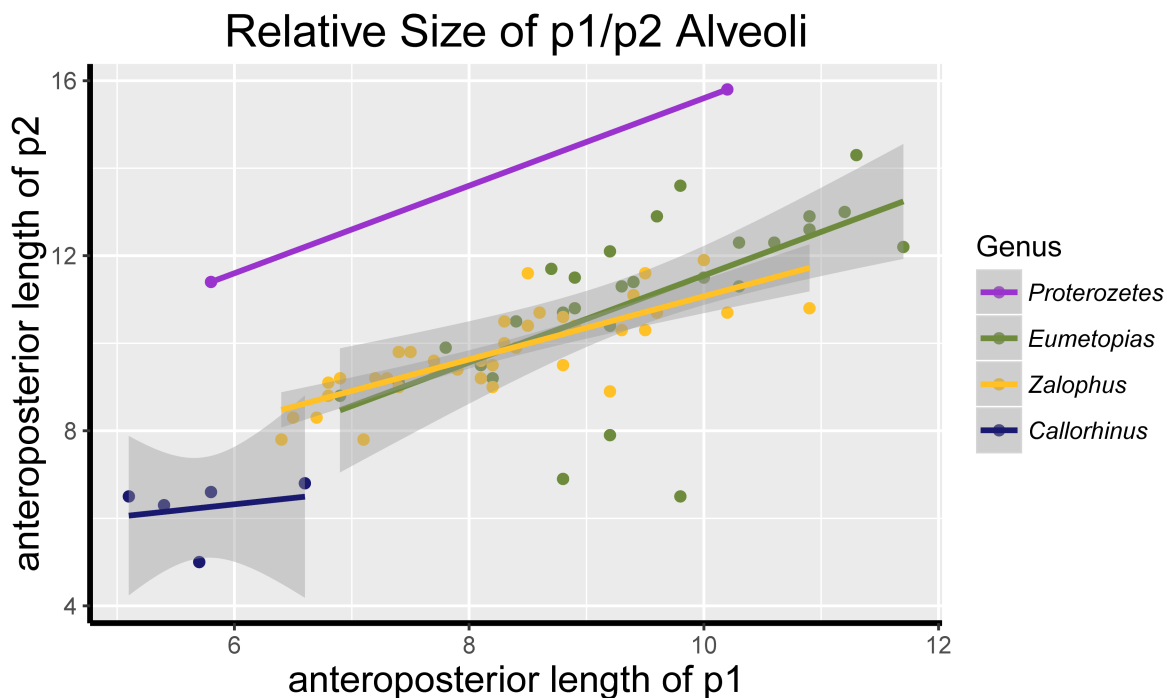
FIGURE 4. Plot comparing anteroposterior length of p1 and p2 alveoli in specimens of extant ENP otariids and *Proterozetes*. Gray polygons show 95% confidence interval of regression line.

TABLE 1. Linear measurements for *Proterozetes* mandibles (USNM 187109 and UCMP 219377).

	Measurements taken in mm	USNM 187109	UCMP 219377
1.	Total length	235	164.9
2.	Maximum height	97.2	47.75
3.	Minimum depth of horizontal ramus posterior to last tooth	48.6	32.75
4.	Breadth of articular condyle	51.9	?
5.	Greatest length of symphysis	(56)	36
6.	Minimum breadth of symphysis	38.8	11.8
7.	Anteroposterior diameter of canine alveolus	26.8	20.4
8.	Transverse diameter of canine alveolus	17.2	13.7
9.	Distance from anterior edge of canine alveolus to posterior edge of m1 alveolus	96.2	72.4
10.	Length of postcanine tooth row on tooth crowns	62.6	?
11.	Length of postcanine tooth row on alveolar borders	64.8	57.6
12.	Anteroposterior diameter of crown of p1	8.8	?
13.	Transverse diameter of crown of p1	6.5	?
14.	Anteroposterior diameter of crown of m1	8.1	?
15.	Transverse diameter of crown of m1	5.8	?

Chapter 3
Expanding the geographic and geochronologic range of early pinnipeds: new specimens of *Enaliarctos* from Northern California and Oregon

ABSTRACT

The early pinnipedimorph *Enaliarctos* was a marine-adapted carnivore with dental and locomotor features intermediate between terrestrial arctoids and living pinnipeds. New specimens of *Enaliarctos* are described from Oligocene and Miocene deposits on the Pacific coast of North America, and include the oldest enaliarctine mandible (Yaquina Formation, 30.6-27.4 Ma), the first enaliarctine from Northern California (Skooner Gulch Formation, 23.8-22 Ma), and the stratigraphically youngest fossil of the genus (Astoria Formation, 17.3-16.6 Ma). The wide biogeographic and temporal range of *Enaliarctos* provided the potential for interaction with members of multiple ecologically significant clades. The expansion of the known ranges *Enaliarctos* species and the description of additional morphology, particularly of the mandible and lower dentition, provides insight into the origins of pinniped diversity and their possible interactions with other early Neogene coastal marine organisms.

INTRODUCTION

PINNIPEDS are one of three diverse, extant clades of marine mammals and differ principally from the obligately aquatic cetaceans and sirenians in retaining the capability for terrestrial locomotion and returning to land to rest and breed. All pinnipeds evolved from a terrestrial common ancestor sometime in the Oligocene shortly after the Eocene diversification of Arctoidea (Berta et al., 1989). Enaliarctines are the geochronologically earliest pinnipedimorphs, and species of the Oligo-Miocene *Enaliarctos* already possessed a suite of locomotor adaptations for swimming including shortened humeri and femora and flipper-like manus and pes (Berta et al. 1989; Berta and Ray 1990) yet retained shearing carnassials typical of terrestrial arctoids (Mitchell and Tedford 1973; Adam and Berta 2002; Churchill and Clementz 2016). Enaliarctines have been reported from the late Oligocene and early Miocene of the eastern North Pacific, and include *Enaliarctos* spp. (Chattian-Aquitanian, California and Oregon; Mitchell and Tedford 1973; Barnes 1979; Berta 1991), *Pteronarctos goedertae* (Barnes 1989; 1990; Berta 1994b), *Pteronarctos piersoni* and *Pacificotaria hadromma* (Barnes 1990, 1992; possible synonyms of *P. goedertae* according to Berta 1994b), and *Pinnarctidion* spp. (considered a basal phocoid according to Berta 1994a). Other aquatic arctoids, including the ursid-like molluskivore *Kolponomos* (Tedford et al. 1994) and the otter-like *Puijila darwini* (Rybczynski et al. 2009) have been linked to Pinnipedimorpha.

This study reports several new specimens of *Enaliarctos* from California and Oregon, USA, including the oldest described mandible and lower dentition of *Enaliarctos* (Yaquina Formation, Oregon), the northernmost record of *Enaliarctos mealsi* (Skooner Gulch Formation, California), and the geochronologically youngest specimen of *Enaliarctos* (Burdigalian Astoria Formation, Oregon).

Institutional Abbreviations. **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A; **USNM**, Smithsonian, Washington D.C., USA; **UWBM**, Burke Museum of Natural History and Culture, Seattle, Washington, USA.

GEOLOGICAL BACKGROUND

Skooner Gulch Formation. The Skooner Gulch Formation crops out at a single locality along 500 meters of coastal cliffs near Gallaway, Mendocino County, California (Fig. 1, "C"). The Skooner Gulch Formation consists of 15-90 meters of massively bedded sandstones that become increasingly glauconitic towards the top of the unit. The Skooner Gulch Formation nonconformably overlies the upper Oligocene Iversen Basalt and is conformably overlain by the lower Miocene Gallaway Formation (Phillips et al. 1976). The base of the Skooner Gulch Formation has yielded a molluscan faunule indicating correlation with the "Vaqueros" provincial megainvertebrate age and deposition in shallow (neritic) marine settings (Addicott 1967; Phillips et al. 1976). Abundant "turbidites" capped by intensely bioturbated glauconitic sandstones with phosphatic nodules indicate long periods of nondeposition between turbidity flows (Phillips et al. 1976), suggestive of submarine fan deposition (Loomis and Ingle 1995). Foraminifera from the Skooner Gulch Formation indicate a much deeper, middle bathyal setting (Phillips et al. 1976) and are indicative of Zemorrian-Saucesian benthic foraminiferal ages; Phillips et al. (1976) tentatively identified the Zemorrian-Saucesian boundary within the lower part of the overlying Gallaway Formation. According to Prothero (2001) the Zemorrian benthic foraminiferal stage is as young as 22 Ma in places (Aquitanian, early Miocene). A maximum age of 23.8 Ma is provided by a K/Ar date from the underlying Iversen Basalt (Turner 1970; Loomis and Ingle 1995). Miller (1981) notes that diagnostic Oligocene microfossils are absent in the Skooner Gulch Formation; owing to this, Barboza et al. (2017) indicate an entirely Miocene age. Therefore, the age of the Skooner Gulch Formation can be summarized as 23.03-22 Ma (earliest Miocene, Aquitanian correlative). Fossil vertebrates previously reported from the Skooner Gulch Formation include elasmobranchs (*Carcharocles auriculatus*, *Chlamydoselachus* sp., cf. *C. tobleri*, *Centrophorus* sp., *Echinorhinus* sp., cf. *E. caspius*, *Galeocerdo* sp., cf. *G. acutus*, *Heterodontus* sp., *Hexanchus* sp., cf. *H. gigas*, *Isurus* sp. A, *Isurus* sp. B, *Megachasma applegatei*, *Mitsukurina* sp., cf. *M. maslinensis*, *Odontaspis* sp., cf. *O. ferox, Pristiophorus* sp., ?*Scymnodon* sp.), desmostylians (*Desmostylus* sp., *Archaeoparadoxia weltoni*), cetaceans (cf. *Argyrocetus*; cf. Waipatiidae indet.), and the *Enaliarctos* mandible and metacarpal described herein (Addicott 1967; Phillips et al. 1976; Barnes 1979; Clark 1991; Shimada et al. 2014). The newly reported specimens were collected from UCMP locality V-73135, a glauconitic horizon in the upper part of the Skooner Gulch Formation, for which an age control of 23.8-22 Ma can be assigned (see above).

Yaquina Formation. The Yaquina Formation crops out along the eastern shore of Yaquina Bay near Newport, Oregon, and along the coast between Seal Rock and Beaver Creek approximately 20 km south of Newport, Oregon. The Yaquina Formation consists of up to 700 m of fine-coarse cross-bedded sandstone with abundant carbonized wood and lenses of pebbly sandstone,

tuffaceous siltstone, and coal (Parke et al. 1976; Prothero et al. 2001b). The Yaquina Formation conformably overlies the lower Oligocene Alsea Formation and is in turn conformably overlain by the lower Miocene Nye Mudstone. Sedimentology and benthic foraminiferal assemblages indicate shallow marine shelf deposition, possibly deltaic in origin (Prothero et al, 2001b). Benthic foraminifera reported by Rau (1981) indicate a Zemorrian age (33-22 Ma; Prothero et al., 2001) whereas mollusk assemblages indicate correlation with the Juanian provincial megainvertebrate stage (28.5-24 Ma; Prothero et al. 2001b) of the Pacific Northwest and the Vaqueros stage (30-19 Ma; Prothero et al. 2001b) of California (Addicott 1976). Fossil vertebrates reported from the Yaquina Formation include a megamouth shark (*Megachasma applegatei*), the enaliarctine pinniped *Enaliarctos tedfordi*, toothed mysticetes (*Aetiocetus cotylalveus*, *Aetiocetus weltoni*), and several desmostylians (*Behemotops proteus*, *Cornwallius sookensis*, *Seuku emlongi*; Emlong 1966; Domning et al. 1986; Berta 1991; Barnes et al. 1995; Deméré and Berta 2008; Shimada et al. 2014). The newly reported specimen (UCMP 253400) was collected as float within a boulder of sandstone matching the lithology of the Yaquina Formation. Though assignment to a specific stratigraphic interval within the Yaquina Formation is not possible, a recent paleomagnetic study by Prothero et al. (2001b) indicates that the type section of the Yaquina Formation to the Northeast at Yaquina Bay is older than considered by Armentrout (1981) and Deméré and Berta (2008), and ranging in age from 30.6-27.4 Ma (late Rupelian to early Chattian; chrons C12n-C9r; dates from Ogg 2012). An age older than Chattian is unlikely given that only the uppermost few meters of the Yaquina Formation is exposed at these localities (Deméré and Berta 2008), but we retain the full range reported by Prothero et al. (2001b) given the lack of stratigraphic control and occurrence of UCMP 253400 within a loose block.

Astoria Formation. The Astoria Formation crops out along the banks of the Columbia River near Astoria, Oregon, and along coastal exposures in Lincoln County near Newport, Oregon (Fig. 1, "B"). Within the Newport embayment in coastal Oregon, the Astoria Formation consists of 150 m of massively bedded sandstone and mudrocks disconformably overlying the lower Miocene Nye Mudstone and is unconformably overlain by Pleistocene terrace deposits (Parke et al. 1976). Mollusk assemblages suggest shelf deposition below storm weather wave base and as deep as 100 m (Moore 1963; Colbath 1975). A diverse marine vertebrate assemblage has been documented from the Astoria Formation near Newport including sharks (*Hexanchus*, *Squalus*, *Pristiophorus*, *Squatina*, *Odontaspis*, *Carcharodon hastalis*, *Isurus planus*, *Cetorhinus piersoni*, *Carcharocles megalodon*, *Myliobatis*; Welton 1972, 2015), birds (*Pelagornis* sp., Olson 1985), pinnipeds (*Pteronarctos goedertae*, *Pteronarctos* "*piersoni*", *Pacificotaria hadromma*, *Proneotherium repenningi*, *Desmatophoca oregonensis*, "Allodesminae" indet.; Condon 1906; Barnes 1989, 1990, 1992; Kohno et al. 1995; Deméré and Berta 2001), cetaceans (Squalodontidae indet., *Cophocetus oregonensis*; Dooley 1994; Packard and Kellogg 1936), desmostylians (*Desmostylus hesperus*; Hannibal, 1922), and even land mammals (*Aphelops* sp., *Tylocephalonyx* sp.; Mitchell and Repenning 1963; Munthe and Coombs 1979).

UWBM 89114 was collected from as an isolated concretion from Moloch Beach and derived from the Iron Mountain Bed, a concretionary horizon within the upper part of the Astoria Formation which yielded the holotype and paratype specimens of the pinnipedimorphs *Pteronarctos* "*piersoni*", *Pacificotaria hadromma*, and *Proneotherium repenningi* (Barnes, 1990, 2992; Deméré and Berta, 2001; Prothero et al., 2001a). Based on a combination of foraminiferal, molluscan, and land mammal biostratigraphy, Barnes (1990) estimated the Iron Mountain Bed to be approximately 16 Ma in age. Deméré and Berta (2001) adopted a more skeptical approach and

considered the Astoria Formation (and the Iron Mountain Bed) to be 20-15 Ma. Paleomagnetic studies by Prothero et al. (2001a) vindicated both age assessments, providing a range of 20.7-15.1 Ma for the Astoria formation within the Newport embayment and a finer range of 17.3-16.6 Ma (Burdigalian, late early Miocene) for the Iron Mountain Bed.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
CARNIVORA Bowditch, 1821
PINNIPEDIMORPHA Berta, Ray, and Wyss 1989
ENALIARCTOS Mitchell and Tedford, 1973

Diagnosis. A small pinnipedimorph different from all others in possessing the following combination of plesiomorphic characters: deep embrasure pit present between P4 and M1; P4-M2 with multiple roots; P4 with protocone shelf; C1 with a posterolingual bulge; M1 with well-developed hypoconid & trigonid cusps around talonid; six lumbar vertebrae; ulna lacking posteriorly extended olecranon process; radius lacking a strongly flattened and expanded distal end; fifth intermediate manual phalanx unreduced; teres femoris ligament pit present on femur; metapodials with cylindrical diaphysis, keeled heads, and strongly trochleated phalangeal articulations (modified from Berta, 1991).

ENALIARCTOS MEALSI Mitchell and Tedford, 1973

Referred Specimens. UCMP 114474, isolated left mandible, collected by B. J. Welton, October 6, 1975; UCMP 276804, partial metacarpal, collected by R.W. Boessenecker and R. Hilton July 21, 2015.

Locality and Horizon. Skooner Gulch I, Mendocino County, California (UCMP locality V75135); Skooner Gulch Formation, Early Miocene (23.8-22 Ma).

DESCRIPTION

UCMP 114474 includes the anterior left mandible, missing the posterior end behind the M_2 alveolus (Fig. 2). The preserved portion of the horizontal ramus is rectangular, deepening only at the root of the canine located ventral of the P_2. The anteroventral margin is broken and the genial tuberosity is missing. Two large (4.0mm and 2.0mm) mental foramina are positioned on the middle of the mandible below P_2 and P_3, respectively. The dorsal margin is flat except where the alveolar rims rise above this surface.

Dentition. The anterior portion of UCMP 114474 is missing, including the incisors. The canine is in place despite lacking much of the bone surrounding the root. It is relatively small and dorsoventrally short with mild posterior curvature. A shallow buccal wear facet is seen on the posterior bulge of the crown as in some other carnivores. The canine bears two cristae just lingual of its posterior edge. These converge slightly towards the tip, but do not meet.

All preserved postcanine teeth are double-rooted, except the alveoli of P_1 and M_2. The P_2 has a high but anteroposteriorly narrow crown with a large, distinct, nearly recurved, conical paraconid, no clear metaconid, and a low, crest-like hypoconid encircling a shallow posteromedially placed talonid basin. The P_3 crown bears a larger, robust and conical paraconid, a high protoconid, a small metaconid, and a small hypoconid positioned posteriorly on a crest

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defining a somewhat larger talonid basin. The P_4 continues the trend of enlarging the paraconid, possesses a high, pointed protoconid, and a large metaconid; the hypoconid resembles that of P_3 but encircles a more deeply excavated talonid basin which is separated into posterior and posteromedial portions by the base of the metaconid, which drops precipitously into the basin. In dorsal view the protoconid of P_4 and M_1 have two distinct wear surfaces separated by a narrow ridge. The metaconids of P_3-M_1 are high and positioned apically near the protoconid. All premolars exhibit poorly developed labial cingulum and distinct but smooth (i.e. not cuspate) lingual cingula.

The M_1 has a dorsoventrally lower crown with a lower, sharper protoconid than in the premolars. The metaconid is conical but apically rounded and offset lingually from the protoconid. The hypoconid is large, labiolingually broad and more apically prominent than in the premolars. No diastemata are present in the postcanines.

Metacarpal. UCMP 276804 is a partial distal metacarpal of uncertain position (Fig. 3). Proximally the cross-section is nearly circular. The distal end is somewhat hemispherical and bears a slight keel; it is rounded in dorsal view, differing from the flattened joint in extant pinnipeds. The keel protrudes strongly on the palmar side, suggesting a wider range of motion in the foreflipper of *Enaliarctos*, perhaps relating to prey acquisition and processing (e.g. Hocking et al., 2016).

Comparisons. UCMP 114474 is identifiable as *Enaliarctos* in exhibiting a lingual bulge on the base of the canine crown, postcanine teeth with apically positioned, strongly developed metaconid cusps and trenchant paraconid cusps. Advanced wear of the cusps suggests this specimen represents an adult, and a relatively narrow canine in comparison with other enaliarctines suggests that UCMP 114474 is female. UCMP 114474 differs from *Enaliarctos emlongi* in exhibiting well-developed labial cingulum and cuspate posterolingual cingulum, and shares these features with *E. mealsi* and *E. barnesi*. UCMP 114474 differs from *E. barnesi* in exhibiting a deeper notch between the paraconid and protoconid on the M_1, a lower M_1 protoconid, and more apically prominent metaconids on P_3-P_4. These differences are not noted in comparison with isolated lower teeth referred to *E. mealsi* (Mitchell and Tedford 1973; Barnes 1979), the presumed P_3-P_4 and M_1 of which are indistinguishable from UCMP 114474. Owing to these shared features (prominent metaconids, extensive labial and lingual cingulum, trenchant paraconids, low protoconid on m1 with deeper notch anteriorly) we refer UCMP 114474 to *Enaliarctos mealsi*. We note that *E. barnesi* and *E. mealsi* may be synonymous (see below) and another possibility may be that these dental features are attributable to sexual dimorphism, as the *E. barnesi* holotype is a presumed male and UCMP 114474 is a presumed female. UCMP 276804 is tentatively referred as *Enaliarctos* sp., cf. *E. mealsi* owing to its cylindrical diaphysis and strongly keeled distal trochlea (Berta, 1991); metapodials are unknown for other enaliarctines (*Pacificotaria*, *Pinnarctidion*, *Pteronarctos*) or the enliarctine-like basal odobenid *Proneotherium*, rendering this referral provisional.

<center>*ENALIARCTOS* sp., cf *E. TEDFORDI*</center>

Referred Specimen. UCMP 253400, associated right mandible, thoracic vertebra and two ribs, collected by J. T. Gregory, October 6, 1963. The block containing UCMP 253400 remained unprepared and undescribed for over fifty years (Fig. 4, "A"). The bones are preserved out of articulation but in contact with one another along a single plane in the block. The matrix is a

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well-sorted, moderately fine-grained sandstone. Immediately surrounding the bones the sandstone is iron-stained and more friable than the remainder of the matrix. In addition to the mammalian bones, the sandstone block includes fish vertebrae, scales, and bone fragments and some lignitized plant material. In places, the sandstone is composed of masses of small pelites with a radius of about a millimetre.

Locality and Horizon. Ona Beach, Lincoln County, Oregon (UCMP locality V79036); collected from a loose concretion of the Yaquina Formation, late Oligocene (30.6-27.4 Ma, late Rupelian-early Chattian equivalent; Prothero et al. 2001b). Detailed locality information available on request to qualified researchers from UCMP or the authors.

DESCRIPTION

Mandible. UCMP 253400 includes the anterior right mandible, missing the posterior end behind the P_4 (Fig. 4). The preserved portion of the horizontal ramus is subrectangular and relatively dorsoventrally shallow. A strongly expressed genial tuberosity occurs below P_1/P_2 and marks the deepest point on the mandible. Two large mental foramina are positioned below P_2 (3.8mm) and P_3 (3.1mm), similar to those of the other enaliarctine mandibles described. The symphyseal surface is poorly preserved but appears to have been broadly lanceolate.

The alveolar margin is linear, though the P_2, P_3, and P_4 are consistently higher with more root exposed; it is unclear if these teeth were slightly displaced out of their alveoli during decomposition and prior to burial. Posterior to this the mandible is not preserved, but the impression of the M_1 shows that this trend was not continued in the molars, suggesting postmortem displacement of the anterior teeth.

Dentition. No incisors are preserved in UCMP 253400. The canine is relatively small and dorsoventrally short and curves posteriorly. The canine exhibits a posterior bulge on the base of the crown, the buccal side of which has a deep, oval wear facet from the upper canine that has penetrated the enamel. Above this bulge on the lingual side is an upward-tapering wear facet, formed from occlusion with I^3. The C_1 bears a double posterior crista. Towards the root, the ancillary ridge deflects medially, dividing the postero-medial half of the tooth crown into three triangular faces.

The alveolus of the P_1 indicates that the tooth was single-rooted. The remaining premolars are double-rooted. The P_2 has a large crown with a small conical paraconid, a very small metaconid on the mid-crown, and a low but well-defined hypoconid. The P_3 crown bears a larger, more rounded paraconid, a high protoconid, and a metaconid elevated to mid-crown height; the hypoconid is a low cusp situated at the posterior terminus of the lingual cingulum which encircles a shallow talonid basin. The P_4 has a larger conical paraconid, a high, sharp protoconid, and a well-developed metaconid, more distinct from the principal cusp than in P_3; the hypoconid is broken, but the impression shows it was a very low, conical cusp. All premolars are labially smooth and lack labial cingulum, but possess well developed smooth lingual cingulum.

The M_1 is lost, but an impression of the lingual surface remains in the sandstone block (Fig. 4, "E"). The mold shows an anteroposteriorly elongate crown with a low protoconid cusp and a high trenchant paraconid. The protoconid is similar height to P_4, with a distinct, rounded metaconid; an impression of the hypoconid is not preserved. The diastema between P_3 and P_4 is particularly large at 5.5 mm, whereas no diastema between the teeth of the other specimens here described exceeds 2 mm.

Posterior cervical vertebra. The convex, oval anterior articular surface of the centrum sits below a large dorsoventrally flattened neural canal. The laminae are flat, broad, and inclined slightly anteriorly. Gracile transverse processes extend from the anterior surface of the pedicles, tilting anterolaterally at approximately a 45˚ from the dorsal plane. The blades of the transverse processes bifurcate into a "T"-shape with a flat lateral edge. Prezygapophyses are not preserved; the postzygapophyses are broad, arranged at a greater 45˚ from the sagittal plane, and have facets facing ventrolateral, more or less in line with the wings of the transverse processes. The neural spine is broken, but appears to have been low and posteriorly inclined. The posterior articular surface of the centrum is raised slightly dorsally relative to the anterior face to allow increased axial flexion.

Ribs. The two partial ribs of UCMP 253400 are short segments of the distal and mid-shafts respectively; positions are unclear. Rib A was preserved beneath the mandible (see fig. 4 "A") and extends from a somewhat flattened mid-shaft to a distal end more circular in cross-section with rough, porous cortical bone where the element met costal cartilage. Rib B is very incomplete, and is represented in part by a natural mold of the internal surface of the mid-shaft showing a very distinct, anterior costal groove.

Comparisons. UCMP 114474 shares with *Enaliarctos emlongi* smooth labial crown surfaces further lacking labial cingula, relatively small paraconid cusps, and low metaconid cusps. UCMP 114474 is from the Oligocene Yaquina Formation (28.1-27.4 Ma) and therefore much older than *Enaliarctos emlongi* from uppermost Nye Mudstone or lowermost Astoria Formation (20.2-19.1 Ma); owing to this age difference, UCMP 114474 is probably not referable to *E. emlongi*. However, *E. tedfordi*, which is not known from a mandible or lower dentition, shares loss of the labial cingulum and reduction of the lingual cingulum of the upper dentition with *E. emlongi*. *Enaliarctos tedfordi* originates from the Yaquina Formation, and assuming that the lower dentition parallels the upper dentition as in *E. emlongi*, UCMP 114474 is tentatively referable to *E. tedfordi*.

<p style="text-align:center">*ENALIARCTOS* sp.</p>

Referred Specimen. UWBM 89114, a partial skeleton exposed in relief in a small concretion including left and right mandibles with I_2-I_3, C_1, P_1-P_4 and M_1, atlas, axis, C6, C7, T1, several other thoracic vertebrae, one rib, and parts of three sternebrae. Collected by Jason Love in March 2004, from UWBM locality C1024.

Locality and Horizon. Moloch Beach, Lincoln County, Oregon, USA, Iron Mountain Bed, Astoria Formation, late early Miocene (17.3-16.6 Ma; Burdigalian equivalent). Detailed locality information available on request to qualified researchers from UWBM or the authors.

DESCRIPTION
Mandible. UWBM 89114 includes both mandibles, with the right mandible missing the posterior end and worn down below the alveolar margin posterior to the P_2 (Figs. 5 and 6). Minimal wear of the teeth argues against advanced age, but the postcanine teeth are not crowded as in juveniles, suggesting subadult or possibly adult status; the canine is relatively large and similar in proportion to the presumed male *E. emlongi* holotype, suggesting that UWBM 89114 is a male.

The left mandible is nearly complete and is missing only the coronoid process, mandibular condyle, and angular process. The medial surface of the right mandible and lateral surface of the left mandible are exposed. The horizontal ramus of the mandible is subrectangular, relatively shallow dorsoventrally, and is deepest posteriorly at the level of the P_3. Three mental foramina are positioned on the middle of the mandible below P_{2-3}. The symphyseal surface is rugose and is lenticular in shape; no genial tuberosity is developed, but a delicate ventral crest is present posteroventral to the symphysis.

The alveolar margin is undulatory and descends ventrally at the level of the P3, giving the toothrow a somewhat dorsally concave profile in lateral view. The alveolar margin rises toward the M_1 and descends again to give the margin anterior to the coronoid process a dorsally concave profile. The masseteric fossa is shallow and does not extend ventral to the toothrow.

Dentition. Both I_2 and I_3 are preserved and exhibit transversely narrow roots with slightly wider crowns bearing apical transverse grooves (Fig. 6, "B" and "D"). The canine is relatively small, transversely wide but dorsoventrally short and posteriorly curving. The canine exhibits a posterior bulge on the base of the crown, and bears a posterior crista, mesial crista, and lingual cingulum. A small wear facet from the upper canine is present labially on the base of the crown as in *Enaliarctos* sp., cf. *E. tedfordi* (UCMP 253400, see above).

The P_1 is single-rooted and bears a small crown with an indistinct paraconid (=anterior accessory cusp), a low protoconid (=principal cusp), and a low hypoconid (=posterior accessory cusp); the metaconid is absent. As in other enaliarctines the P_2-P_4 are double-rooted. The P_2 bears a somewhat larger crown with an indistinct paraconid, a small metaconid, and a small hypoconid. The P_3 crown is lower than the P_2 owing to the "dip" in the alveolar margin of the mandible and bears a small conical paraconid, a high protoconid, and a metaconid elevated to mid-crown height; the hypoconid is obscured by matrix. The P_4 has a larger conical paraconid, a high but apically worn protoconid, and a well-developed metaconid like P_3; the hypoconid is low and conical. All premolar crowns are labially smooth and lack a labial cingulum.

The M_1 is double-rooted and bears a low, anteroposteriorly elongate crown with a low, trenchant paraconid, a low protoconid, an indistinct metaconid, and a conical and low hypoconid. The M_2 is absent but a small partially prepared alveolus indicates a single circular root. All lower postcanines are tightly spaced and no diastemata are apparent.

Atlas. The anterior condylar facets are concave, transversely narrow ventrally and broad and widely separated dorsally (Fig. 5). A low neural spine is present. The transverse process is subrectangular and posteroventrally oriented in lateral view, approximately 15-20° from vertical. The transverse process is pierced by a lateral vertebral canal positioned medially within a fossa on the anterior surface.

Axis. The Axis bears a well developed conical odontoid process with a convex and transversely narrow atlantal facet. The centrum bears a longitudinal ridge dorsally within the neural foramen and a deep ridge ventrally, flanked by deep ventrolateral fossae. A secondary fossa is present on the posterolateral surface below the pedicle of the neural arch, separated by the ventrolateral fossa by a thin ridge. The neural spine is large, falcate, and extends anteriorly to the level of the odontoid apex in lateral view; the neural spine rises posteriorly towards its dorsal apex. A small tongue-shaped postzygapophysis is present. A small, posterolaterally projecting transverse process is developed.

Third? or fourth? cervical vertebra. One incompletely preserved vertebra exhibits a circular lateral vertebral canal larger than C6; it bears a low subrectangular neural spine with an apical

tubercle and a small fan-shaped transverse process that is less elongate than C6. Owing to the short transverse process this vertebra represents an anterior cervical.

Sixth cervical vertebra. A small, rectangular anterior articular surface of the centrum flanked by small oval lateral vertebral canals (Fig. 7). The transverse process is elongate, ventrolaterally projecting and bears a sharp anterior crest. Small triangular prongs are present anteriorly at the level of the ventral margin of the centrum; the ventrolateral apex of the transverse process is bifurcated. A low neural spine is present; spoon-like prezygapophyses are present and have dorsomedially facing articular surfaces approximately 45° from the sagittal plane, whereas the postzygapophyses have subhorizontal facets with small medial tubercles.

Seventh cervical vertebra. The C7 differs from the C6 in having a taller neural spine and a short, transversely oriented transverse process with a laterally deepening, fan-like shape. The posterior articular surface of the centrum is oval-shaped. The neural spine bears an apical tubercle for the nuchal ligament.

Thoracic vertebrae. The T1 is similar to the C7 but has a further dorsally positioned transverse process with a concave facet for the first rib and a dorsal spur, and a slightly taller neural spine. Two other thoracic vertebrae of uncertain position are preserved (one consists only of an arch and neural spine) and exhibit a more cylindrical centrum, posteriorly inclined neural spine lacking an apical tubercle, and horizontal postzygapophyses on the posterior part of the neural arch.

Ribs. The proximal end of one rib is preserved and includes a bulbous, spherical capitulum, a short neck, and a flattened tubercle. A low lateral ridge is present anteriorly.

Sternebrae. Parts of three sternebrae are present (Figs. 5 and 7). One is complete and subcylindrical in overall form and exhibits a rugose and quadrate articular surface; it is transversely and dorsoventrally narrow or "pinched" in the middle.

Comparisons. UWBM 89114 differs from all other enaliarctines for which a mandible is known (*Enaliarctos barnesi*, *Enaliarctos emlongi*, *Enaliarctos mealsi*, *Pteronarctos goedertae*) in its smaller absolute size and mandible with sinuous alveolar margin and a masseteric fossa not extending ventral to the toothrow, and further differs from *E. barnesi* and *E. mealsi* in lacking labial cingulum (which it shares with *E. emlongi*). UWBM 89114 is identifiable as *Enaliarctos* based on the presence of a lingual bulge on the base of the canine crown (shared with *Potamotherium*, *Puijila*, and other arctoid 'fissipeds'), differing from all Pinnipediformes; it shares this feature with all *Enaliarctos* spp. for which a lower canine is known. UWBM 89114 further differs from *E. emlongi* in possessing somewhat more inflated protoconid cusps on P_2-P_4, more basally positioned metaconids on P_2-M_1, and a lower protoconid on M_1. UWBM 89114 shares similar small size with *E. mitchelli*, and has a postcanine toothrow length of 45 mm, which is somewhat smaller than the upper postcanine toothrow length of *E. mitchelli* (53-62 mm); in *E. emlongi*, the toothrow is approximately 70 mm, and in *E. barnesi* the toothrow measures 56 mm. Within *Enaliarctos*, loss of upper postcanine labial cingulum is shared by *E. emlongi*, *E. mitchelli*, and *E. tedfordi*, with *E. emlongi* showing loss of the labial cingulum in both the upper and lower dentition (Berta 1991). With the exception of *Enaliarctos mealsi* (Berta and Ray, 1990), postcrania are sporadically reported amongst enaliarctine pinnipeds. The transverse process of the atlas is subrectangular, unlike the rounded margin in *Pteronarctos* (Berta, 1994). The axis shares an anteroposteriorly elongate, fan-shaped neural spine with *E. mealsi*. Thoracic vertebrae, ribs, and sternebrae do not differ from *E. mealsi* except in size. Though UWBM 89114 is much younger chronologically than all reported species of *Enaliarctos*, its small size may suggest affinities with *E. mitchelli*, the youngest named species of *Enaliarctos*,

recorded from the approximate level of the Nye Mudstone-Astoria Formation contact (Berta 1994b), and dated to 24-19.1 Ma (Prothero et al. 2001a). Owing to the stratigraphic separation between UWBM 89114 and the referred cranium of *E. mitchelli* from the Nye-Astoria contact, we conservatively identify this specimen as *Enaliarctos* sp.

DISCUSSION AND CONCLUSIONS

Geographic and Stratigraphic distribution of *Enaliarctos*: Fossils of enaliarctines (*Enaliarctos*, *Pacificotaria*, *Pinnarctidion*, *Pteronarctos*) are reported only from the late Oligocene and early Miocene of California and Oregon, though the published record is already quite densely sampled (Mitchell and Tedford 1973; Barnes 1979, 1989, 1990, 1992; Berta 1991, 1994a, 1994b; Berta et al., 1989; Cullen et al. 2014; this study); unnamed enaliarctines are also known from the Pysht Formation of Washington (Hunt and Barnes 1994). *Enaliarctos* in particular is now reported from the Jewett Sand at Pyramid Hill, California, the Skooner Gulch Formation in Mendocino County, California, and the Yaquina Formation, Nye Mudstone, and Astoria Formation of the Newport Embayment in Lincoln County, Oregon (Table 3). This study critically reports *Enaliarctos* sp. from the "Iron Mountain Bed" of the Astoria Formation (17.4-16.6 Ma; Prothero et al. 2001a), extending the range of the genus into the late Burdigalian stage (Fig. 8). This new record clearly indicates that *Enaliarctos* geochronologically overlapped with not only other more derived enaliarctines (*Pteronarctos goedertae*, *Pacificotaria hadromma*, *Pinnarctidion rayi*; Barnes 1989, 1990, 1992; Berta 1994a, 1994b) but also the earliest odobenids (*Proneotherium repenningi*, *Pelagiarctos*; Kohno et al. 1995; Deméré and Berta 2001; Boessenecker and Churchill 2013) and the earliest otariids (*Eotaria*; Boessenecker and Churchill 2015). Early otariids and small imagotariines were enaliarctine-like in craniodental morphology (Kohno et al. 1995; Boessenecker and Churchill 2015; Velez-Juarbe 2017) and no obvious differences in feeding ecology are apparent, suggesting unexplained diversity during the late early Miocene. The increased temporal overlap of these clades suggests that further analysis, such as functional diversity modelling (e.g. Novack-Gottshall 2007; Dineen 2014) or various specimen-based approaches (e.g. Kloess and Parham 2017), may inform our understanding of their respective diversifications.

The geochronologically youngest enaliarctines are all reported from the "Iron Mountain Bed" of the upper Astoria Formation, which preserves a diverse pinniped fauna including three enaliarctines (*Enaliarctos* sp., *Pacificotaria hadromma*, *Pteronarctos goedertae*), the desmatophocid seal *Desmatophoca oregonensis* and a larger undescribed *Allodesmus*-like desmatophocid, and the early odobenid *Proneotherium repenningi* (Barnes 1987, 1989, 1990, 1992; Berta 1994b; Deméré and Berta 2001, 2002; this study). Geochronologically earlier (Chattian-Aquitanian) assemblages are lower in diversity and consist entirely of enaliarctines (e.g. Yaquina Formation, Nye Mudstone, Jewett Sand; Table 3). Later assemblages lack enaliarctines, but possess small-bodied early diverging odobenids and otariids as well as larger-bodied odobenids and species of *Allodesmus* (Miyazaki et al. 1995). Reasons for enaliarctine extinction are unclear, yet it seems likely that small imagotariines and early otariids may reflect surviving ecological analogs in the middle and late Miocene. Further studies of early Miocene enaliarctines, feeding morphology, and isotopic analyses may highlight possible modes of competition and extinction.

Taxonomy and Diversity of *Enaliarctos*: The taxonomy of *Enaliarctos* has not been evaluated since publication of Berta (1991), who reported three new species (*Enaliarctos barnesi*, *E. emlongi*, and *E. tedfordi*) from the Yaquina Formation, Nye Mudstone, and/or Astoria Formation of Oregon. With five species reported, it may be that the genus *Enaliarctos* is oversplit. For example, *Enaliarctos barnesi* and *Enaliarctos mealsi* both share, to the exclusion of all other species, widely flaring nasals with a concave lateral margin and strongly developed labial and lingual cingulum (Berta 1991); they differ only in the presence of a posterolingual shelf on P_3 and a more spur-like palatine process of the maxilla in *E. barnesi* (Berta 1991). It is possible that these are either sister taxa or the same species, possibilities further supported by their similar geochronologic age (Table 3; Berta 1991; Prothero et al. 2001b; Barboza et al. 2017) – although Berta (1991: fig. 21) did not recover a sister taxon relationship between these species (Fig. 8). Possible synonymies within the remaining species are more difficult to assess owing to their stratigraphic separation. *Enaliarctos mitchelli* is distinctive in small adult size (Barnes 1979; Berta 1991) but *Enaliarctos emlongi* differs from *Enaliarctos tedfordi* only in exhibiting larger metacone crests on P_{2-3} and P_3 with a larger posterolingual shelf. Craniodental similarities and limited differences between these two species, in concert with stratigraphic separation, suggest they may represent chronospecies within a single lineage. Dental similarities (e.g. loss of cingula), and the cladogram of Berta (1991: fig. 21) further suggest that *E. mitchelli* could be a terminal species in this lineage (though *E. emlongi* and E. mitchelli may temporally overlap; Fig. 8). Description of many additional undescribed enaliarctine specimens within LACM and USNM collections will permit re-evaluation of enaliarctine variation, taxonomy, and phylogeny, and test hypotheses presented herein.

Early Pinnipedimorphs, Cetaceans, and Flightless Seabirds: Several studies have investigated possible evolutionary interactions between early pinnipedimorphs, cetaceans, and sea birds (Olson 1985; Olson and Hasegawa 1979; Ando and Fordyce 2014; Marx et al. 2015). Oligocene toothed baleen whales were quite small (e.g. 2-4 m body length, *Fucaia buelli*; Marx et al., 2015) and some at least were raptorial piscivores (Barnes et al. 1995) like early pinnipedimorphs (Churchill and Clementz 2015, 2016), raising the possibility that they competed for prey. Furthermore, the diversification of toothed mysticetes during the Oligocene coincides with the appearance of the earliest pinnipedimorphs (Marx and Fordyce 2015). We note that large-bodied (e.g. 2+ meter body length) pinnipeds do not appear until the Burdigalian (*Desmatophoca*, *Pelagiarctos*; Churchill et al. 2015), well after the presumed Chattian-Aquitanian extinction of toothed mysticetes (but see Staley and Barnes 2008). Pinnipedimorph diversification has been implicated in the extinction of the giant flightless wing-propelled penguin-like plotopterids and giant Oligo-Miocene penguins (Olson 1985; Olson and Hasegawa 1979). However, analyses of diversity trends find little long term evidence for competitive displacement of penguins and plotopterids by pinnipeds, instead highlighting echolocating toothed whales (Odontoceti) as competitors (Ando and Fordyce 2014). Given various differences in feeding morphology between early pinnipedimorphs and toothed mysticetes (Churchill and Clementz 20145, 2016; Marx and Fordyce 2015; Marx et al. 2016), perhaps odontocetes occupy a more competitive role that could explain the extinction of toothed mysticetes. Lastly, we note that the diminutive enaliarctine *Enaliarctos* sp. now overlaps in age with the tiny enaliarctine-like otariid *Eotaria* from California (Figure 8; Boessenecker and Churchill. 2015; Velez-Juarbe, 2017). The small body size of each taxon suggests the possibility of niche partitioning and

further highlights the geochronologic antiquity of diverse pinniped communities in the North Pacific (e.g. Velez-Juarbe 2017).

Enaliarctines, *Puijila*, *Kolponomos*, and the Origin of Pinnipedia: Enaliarctines are regarded as the earliest diverging and geochronologically earliest pinnipedimorphs (Mitchell and Tedford 1973; Berta et al. 1989). Recently, a semiaquatic otter-like arctoid, *Puijila darwini*, was reported from lower Miocene nonmarine deposits of the Canadian arctic (Rybczynski et al. 2009). Despite lacking flipper-like manus and pes, shortened tail, and postdating the earliest *Enaliarctos* by nearly 10 my, this taxon exhibits several craniodental features unique to pinnipedimorphs including a posteriorly expanded hard palate, an enlarged infraorbital foramen, a shelf-like p4 protocone, and a reduced and lingually positioned M_2; cladistic analysis supported *Puijila* and the anatomically similar *Potamotherium valletoni* (Oligo-Miocene, France and Germany) as sister to *Enaliarctos* (Rynczynski et al. 2009). If these relationships are borne out by future cladistic study, it is important to note that most of these features are also present in the enigmatic amphicynodontid *Kolponomos* (except shelf-like P_4 protocone; Tedford et al. 1994), a bear-like molluskivore with enlarged sea otter-like cheek teeth, binocular vision, and adaptations for high bite force convergent with sabretooth cats (Tedford et al. 1994; Tseng et al. 2016). Like the nonmarine otter-like *Potamotherium* and *Puijila*, initial cladistic analysis identified *Kolponomos* as the possible sister taxon to Pinnipedimorpha (Tedford et al. 1994). Since these taxa are rare, continued description of fossils from the long record of enaliarctines such as we present here holds the promise of more confidently resolving these relationships through a better understanding of species-level taxonomy and an expanded matrix including more non-cranial characters. Further cladistic analysis is needed, but if indeed these taxa are all early pinniped relatives, the clade comprising them may represent a wider radiation of arctoid carnivores into various aquatic niches, including littoral molluskivores (*Kolponomos*), small otter-like freshwater taxa (*Potamotherium*, *Puijila*), and the highly successful marine pinnipedimorphs.

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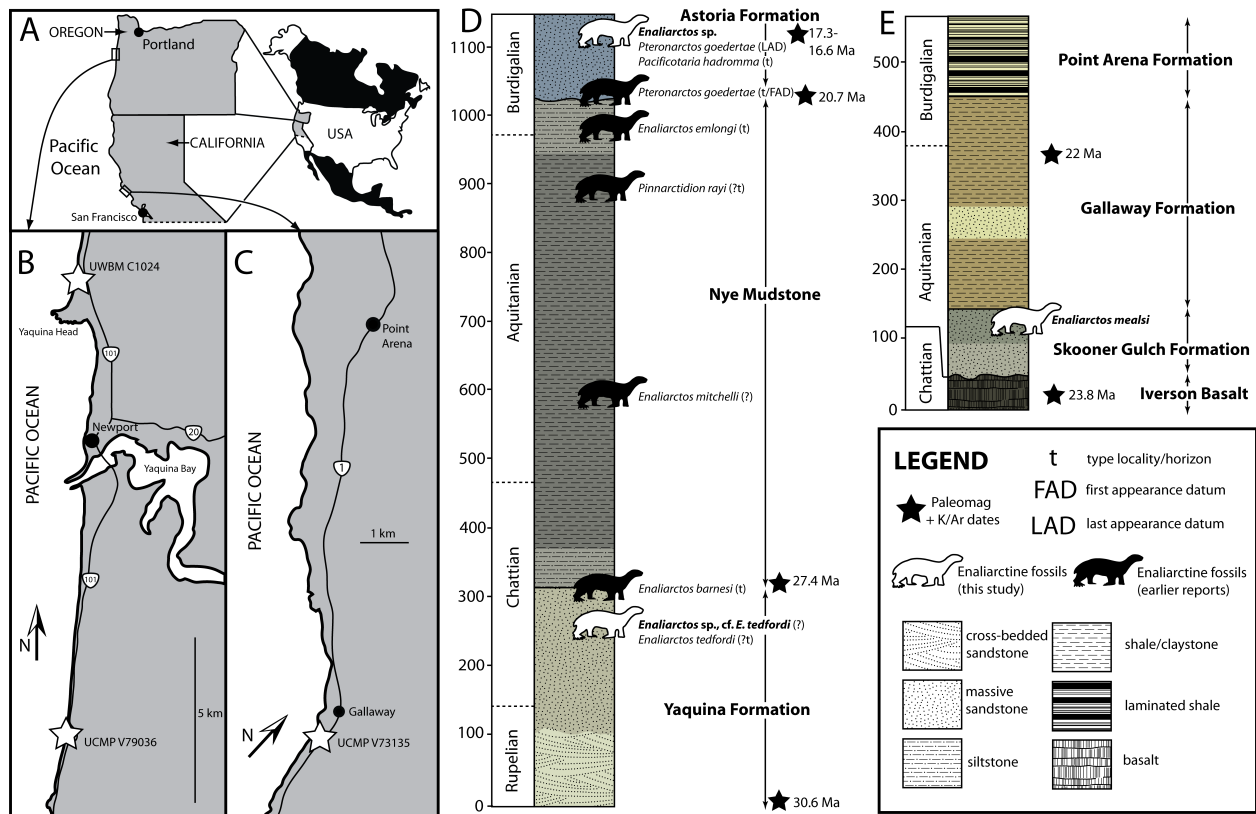
Fig. 1. Locality map for fossils of enaliarctines. Map of Oregon and California (**A**), the coastline near Newport, Oregon (**B**), the coastline near Point Arena, California (**C**). Stratigraphic columns of Oregon (**D**) and California (**E**) localities. Columns based on Snavely et al. (1964) and Phillips et al. (1976); paleomagnetic and K/Ar dates from Prothero et al. (2001a, b) and Phillips et al. (1976). In the interest of clarity non-enaliarctine marine carnivores are omitted. Modified from Moore (1963) and Phillips et al. (1976). Abbreviations: FAD, first appearance datum; LAD, last appearance datum; t, type locality/horizon.
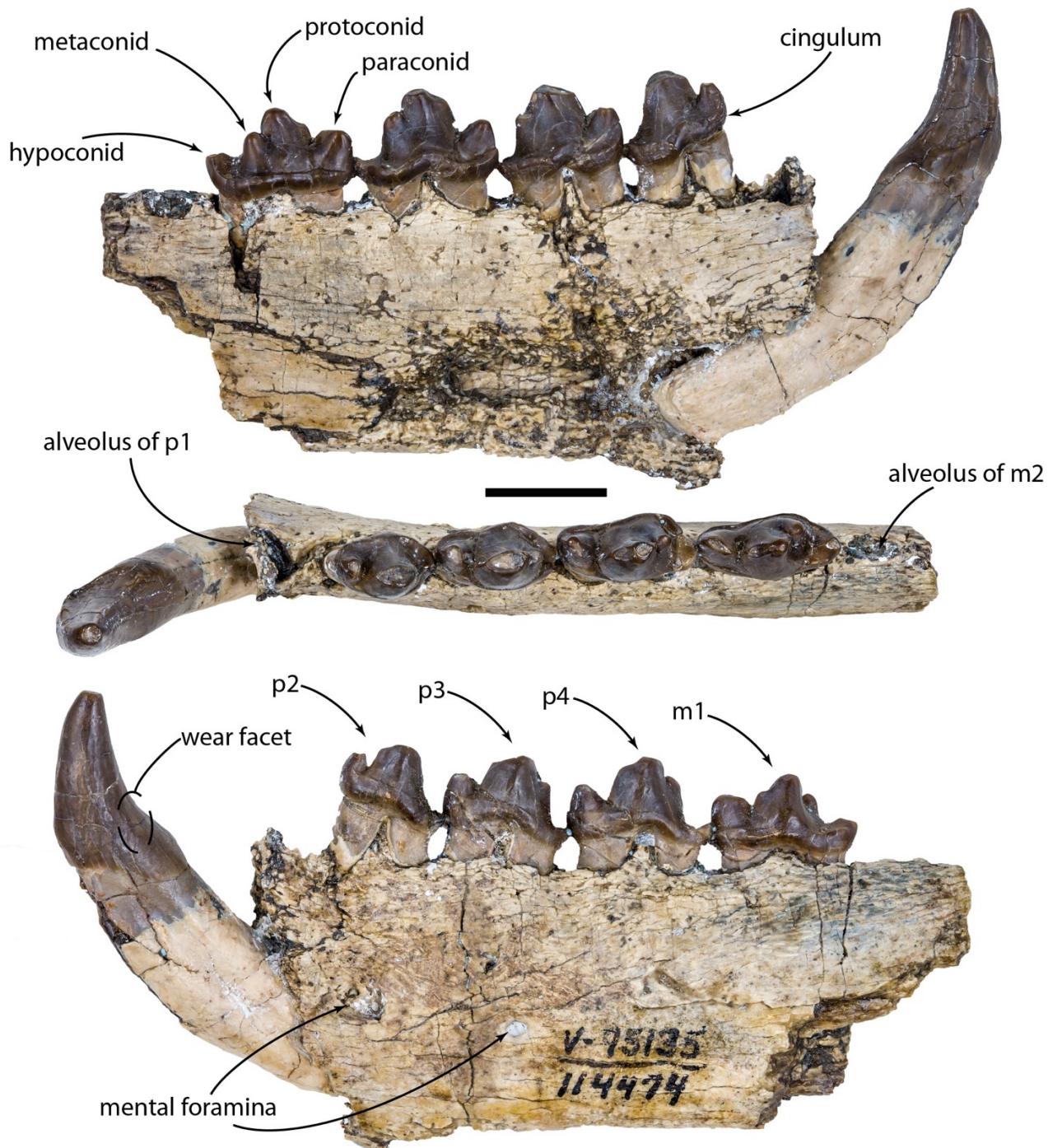
Fig. 2. Mandible of pinniped mammal *Enaliarctos mealsi* (UCMP 114474) from Schooner Gulch, Mendocino County, California, earliest Miocene; in lingual (**A**), occlusal (**B**), and labial (**C**) views.

Fig. 3 Metacarpal of pinniped mammal *Enaliarctos mealsi* Mitchell and Tedford, 1973 (UCMP 276804) from Schooner Gulch, Mendocino County, California, earliest Miocene; in dorsal (**A**), lateral (**B**), and ventral/palmar (**C**) views.
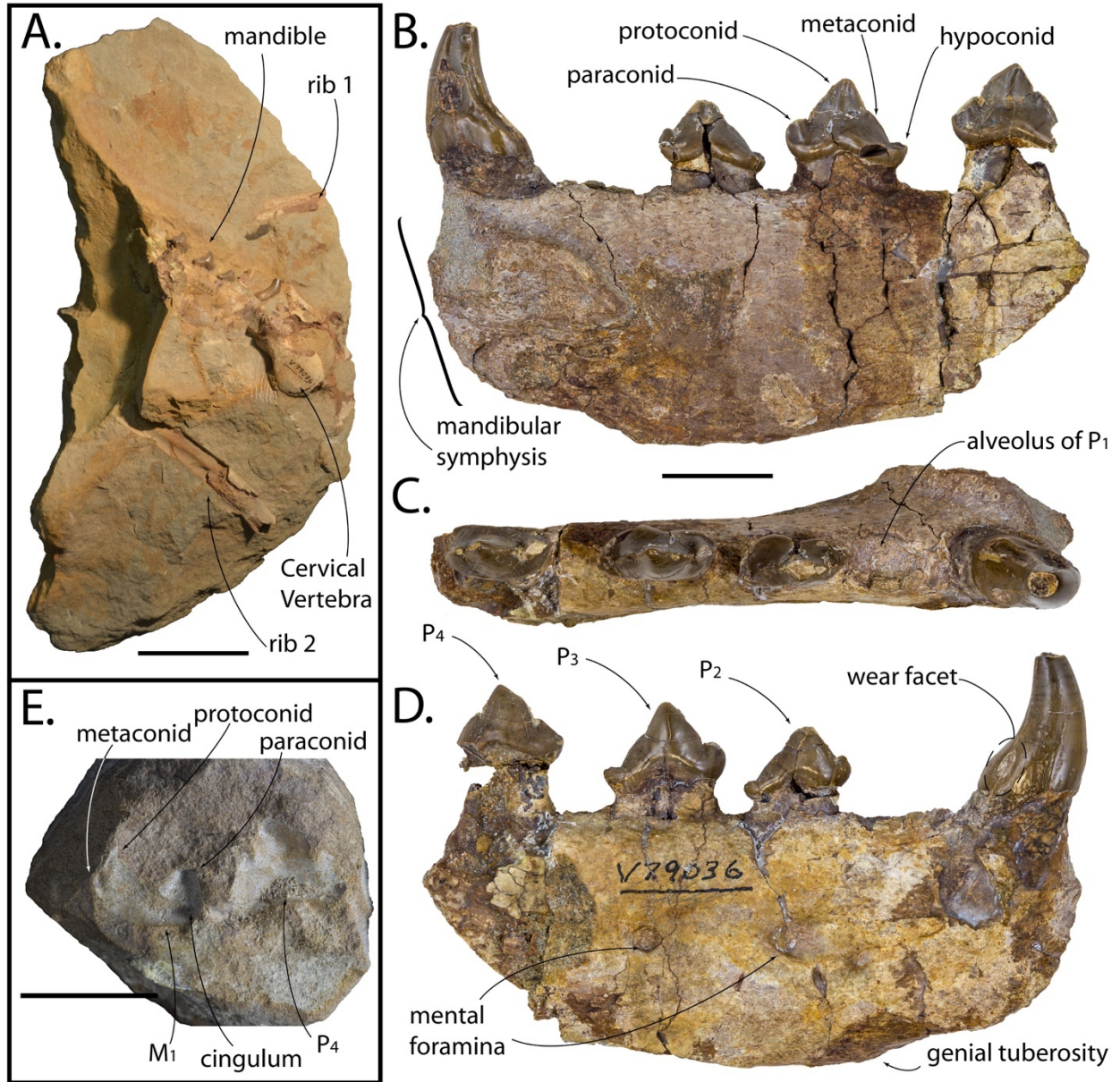
Fig. 4. Elements of pinniped mammal *Enaliarctos* sp., cf. *E. tedfordi* Berta, 1991 (UCMP 253400) from Ona Beach, Lincoln County, Oregon, Yaquina Formation, early late Oligocene; overview of original block (**A**), lingual (**B**), occlusal (**C**), and labial (**D**) views; matrix preserving impression of lingual side of p4 and m1 (**E**).
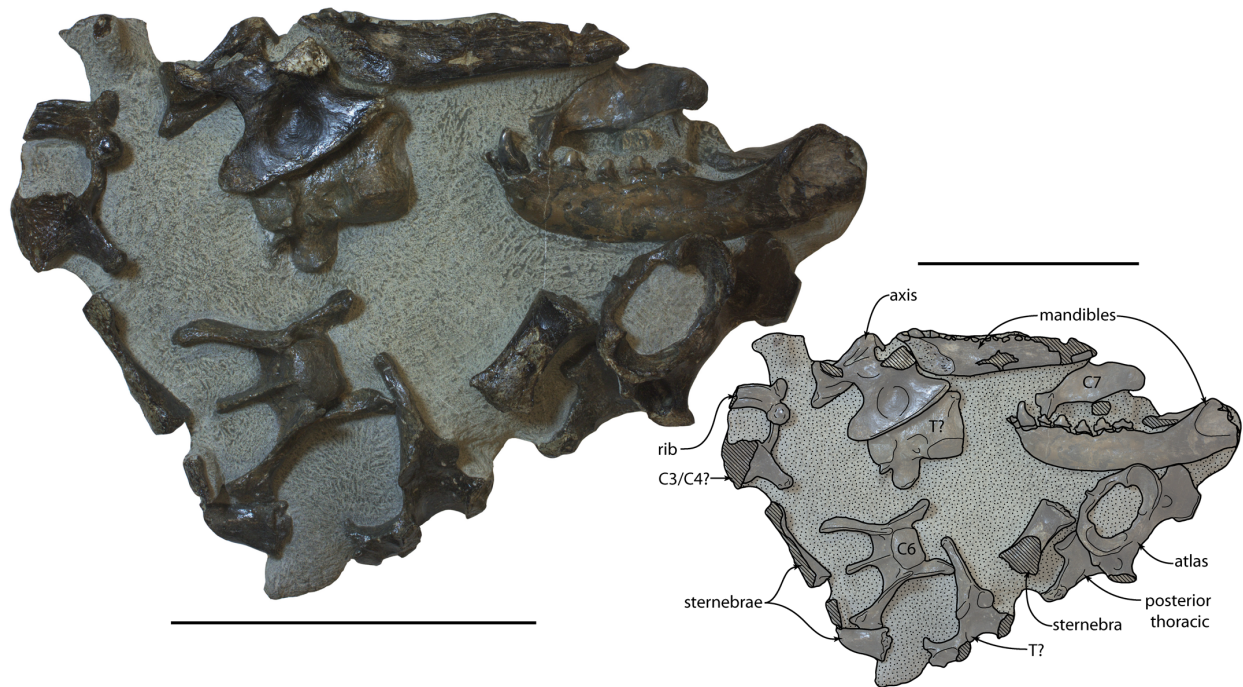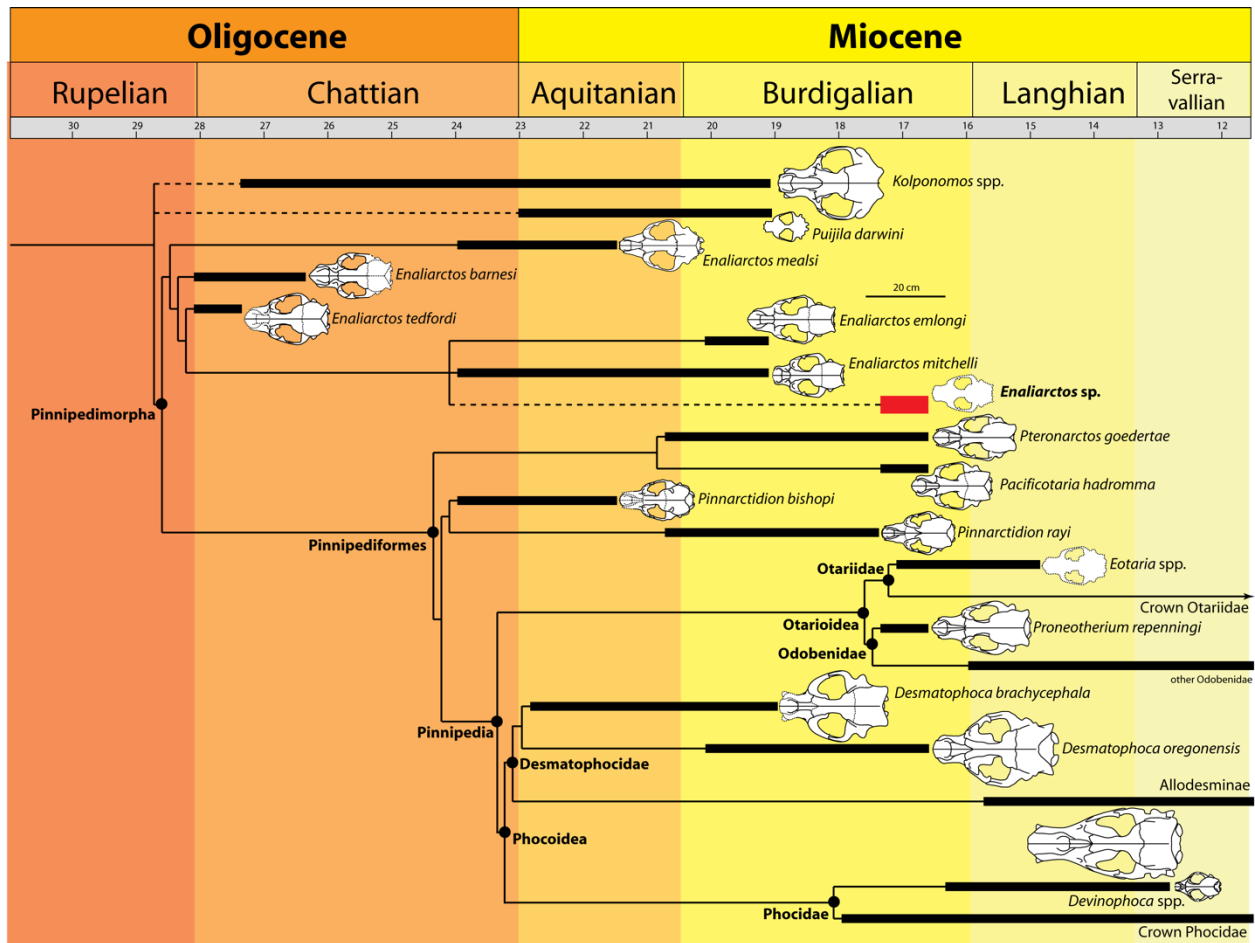
FIG.5. Referred mandibles and vertebrae of Enaliarctos sp. (UWBM 89114).
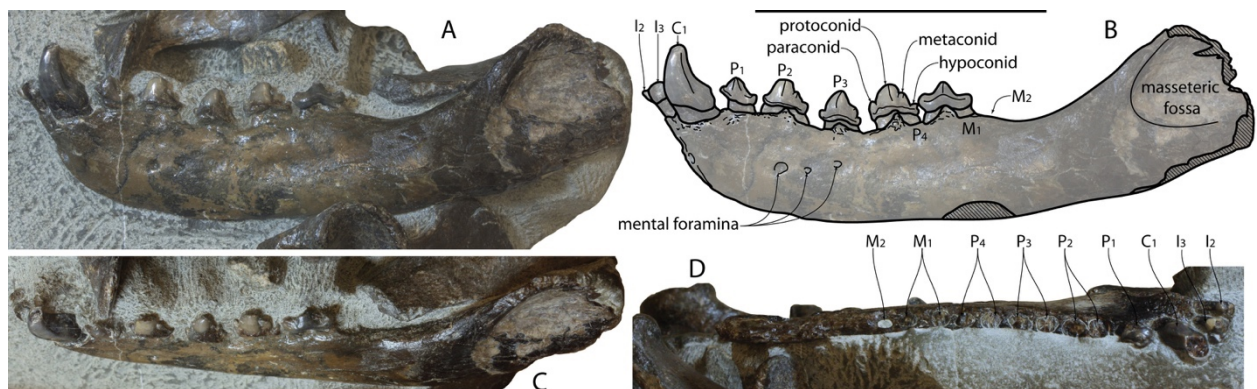
FIG. 6. Referred mandibles and vertebrae of Enaliarctos sp. (UWBM 89114). A-B, left mandible in labial view; C, left mandible in occlusal view; D, right mandible in occlusal view.
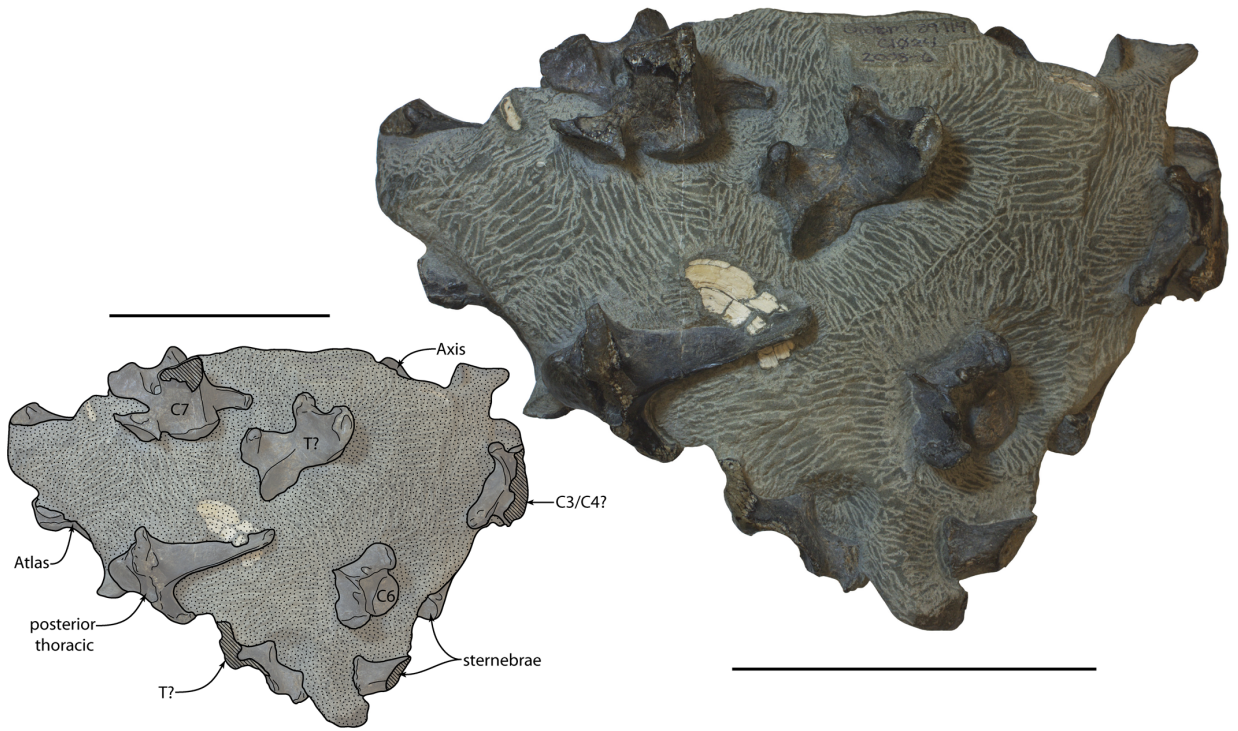
FIG. 7. Referred mandibles and vertebrae of Enaliarctos sp. (UWBM 89114). Opposite view of block pictured in Fig. 5.

Fig. 8. Time calibrated composite phylogenetic hypothesis of early pinnipedimorphs and putative allies, with an emphasis on Oligo-Miocene pinnipedimorphs from the eastern North Pacific. Topology based on Boessenecker and Churchill (2015); Enaliarctos topology from Berta (1991); Phocoidea topology after Boessenecker and Churchill (in press); and placement of Pacificotaria from Demere and Berta (2001). Puijila and Kolponomos shown as sister to Pinnipedimorpha after Tedford et al. (1994) and Rybczynski et al. (2009); placement of Enaliarctos sp. (UWBM 89114) based on shared dental synapomorphies with E. emlongi and E. mitchelli. Geochronologic ranges from Table 3 (this study), Boessenecker and Churchill (2015: supplementary information; In Press, supplementary information), and Rybczynskiet al. (2009).

Table 1. Measurements of *Enaliarctos* sp. mandibles.

Measurement	Left, UWBM 89114	Right, UWBM 89114	Right, UCMP 253400	Left, UCMP 114474
Total length as preserved	100.7	85.98	58.44	72.15
Length postcanine tooth row	46.84	46.87	>45.19	>56.70
Anterior tip to base of coronoid	58	-	-	-
Greatest length of symphysis	-	25.13	23.29	-
Mandibular depth at C1	14.14	14.06	20.41	23.97
"" P1	14.64	17.38	22.20	24.06
"" P2	17.74	18.76	23.54	22.35
"" P3	16.06	-	22.25	20.36
"" P4	16.44	-	-	21.32
"" M1	16.95	-	-	22.03
"" M2	16.71	-	-	-
Length of toothrow C1 to M1	50.53	53.4	57.22	51.70
Length M1 to base of coronoid	14	-	-	-
AP length/dorsoventral depth I2	-/-	3.81/2.54	-	-
"" I3	-/3.51	4.26/2.61	-	-
"" C1	7.29/11.55	-/-	9.28/13.10	10.57/14.99
"" P1	6.54/4.91	5.71/-	-	-
"" P2	7.9/4.39	-/-	9.53/5.88	9.23/5.68
"" P3	7.91/6.36	-/-	10.93/8.75	10.41/8.23
"" P4	8.14/5.35	-/-	10.83/7.94	11.52/7.44
"" M1	9.16/4.25	-/-	-	

Table 2. Measurements of *Enaliarctos* sp. postcrania

	Atlas UWBM 89114	Axis UWBM 89114	C6 UWBM 89114	C7 UWBM 89114	Posterior thoracic UWBM 89114	UCMP 253400 C6 or C7	UCMP 276804 Metacarpal
Transverse width anterior facets	45.28	-	-	-	-	-	-
Total height	34.74	49.65	-	60.26	59.01	-	-
Height neural foramen	18.75		10.2	9	8.32	13.79	-
Transverse width neural foramen	17.6	18.96	15.4	17.47	15.69	22.74	-
Anteroposterior length neural spine	-	52.27	-	-	-	-	-
Greatest width across transverse processes	72.4	34.86	57.2	62.48	25.94	80.3	-
Height of anterior articular surface	17.46	14.9	16.06	-	17.81	-	-
Transverse width anterior articular surface	-	31.2	18.09	23.5	19.19	-	-
Height of posterior articular surface	-	15	14.27	16	-	17.5	-
Transverse width posterior articular surface	-	18.5	19.86	22.3	-	16.7	-
Centrum length	-	43.13	25	32.33	29.58	36.04	-
Midshaft dorsoventral height	-	-	-	-	-	-	8.04
Midshaft transverse width	-	-	-	-	-	-	10.63
distal (head) dorsoventral height	-	-	-	-	-	-	15.21
distal (head) transverse width	-	-	-	-	-	-	13.90

TABLE 3. Fossil occurrences and geochronologic age control for enaliarctine pinnipedimorphs.

Taxon	Formation	Age	Citation (Age)	Citation (record)
Enaliarctos barnesi	Uppermost Yaquina Fm. or lower Nye Mudstone	28.1-26.4 Ma	Prothero et al. (2001b)	Berta (1991)
Enaliarctos emlongi	Uppermost Nye Mudstone or lowermost Astoria Fm.	20.2-19.1 Ma	Prothero et al. (2001b)	Berta (1991)
Enaliarctos mealsi	Jewett Sand, Skooner Gulch Formation	24-21.5 Ma	Scheirer and Magoon (2007), Barboza et al. (2017)	Mitchell and Tedford (1973), Barnes (1979)
Enaliarctos mitchelli	Nye Mudstone, Jewett Sand	24-19.1 Ma	Prothero et al., (2001b), Scheirer and Magoon (2007), Barboza et al. (2017)	Barnes (1979), Berta (1991)
Enaliarctos tedfordi	Yaquina Fm.	28.1-27.4 Ma	Prothero et al. (2001b)	Berta (1991)
Enaliarctos sp.	Astoria Fm.	17.3-16.6 Ma	Prothero et al. (2001a)	This Study
Pteronarctos goedertae	Astoria Fm.	20.7-16.6 Ma	Prothero et al. (2001a)	Barnes (1989, 1990), Berta (1994b)
Pacificotaria hadromma	Astoria Fm.	17.3-16.6 Ma	Prothero et al. (2001a)	Barnes (1992)
Pinnarctidion bishopi	Jewett Sand	24-21.5 Ma	Scheirer and Magoon (2007), Barboza et al. (2017)	Barnes (1979)
Pinnarctidion rayi	Nye Mudstone	20.7-17.3 Ma	Prothero et al. (2001a, 2001b)	Berta (1994a)