

# A NEW SPECIES OF LATE EARLY MIOCENE *CETORHINUS* (LAMNIFORMES: CETORHINIDAE) FROM THE ASTORIA FORMATION OF OREGON, AND COEVAL *CETORHINUS* FROM WASHINGTON AND CALIFORNIA<sup>1</sup>

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**ABSTRACT.** Microphagous lamniforms of the family Cetorhinidae have a significant Cenozoic history in the North Pacific Ocean. The Late Eocene *Keasius taylori* occurs in the Keasey Formation of Oregon, and *K. parvus* may occur in the Oligocene Lincoln Creek Formation of southwestern Washington. The genus *Cetorhinus* has one extant species, *C. maximus*, and a fossil record, including the Middle Miocene *C. huddlestoni* from the middle Round Mountain Silt, Sharktooth Hill Bonebed, California, and *C. maximus* from the Late Miocene through Pleistocene of Oregon and California.

An intermediate-sized cetorhinid, *Cetorhinus piersoni*, new species, is named on teeth from the late Early Miocene Astoria Formation from Lincoln County, Oregon, and coeval deposits of the lower Round Mountain Silt from the southeast part of California's San Joaquin Valley. Teeth of *C. piersoni* from California, but not Oregon, occur in association with very small teeth of an as yet undescribed species of *Keasius*. The type series of *C. piersoni* is morphologically diverse, although, many of the adult teeth have low, broadly triangular crowns, large roots, and well-developed root lobes reminiscent of the genus *Alopias*. *Cetorhinus piersoni* may have had a wider range in diet than *C. maximus*, feeding on small fishes as well as plankton.

Calcified vertebrae of a small basking shark from a late Early Miocene section of the Astoria Formation in southwestern Washington are described and referred to the genus *Cetorhinus*. These vertebrae differ from those of *Keasius* in being anteroposteriorly elongated, and in having intermedialia with well-developed perforated concentric lamellae and no calcified radii extending outward from the primary double cone or peripheral to the outermost concentric lamellae. The vertebrae come from marine deposits coeval with the Oregon Astoria Formation type locality of *C. piersoni*, but without associated teeth, a specific taxonomic assignment is not possible.

The depositional environments represented by the Astoria Formation in Washington and Oregon, and the Round Mountain Silt in California, indicate that *Cetorhinus piersoni*, and *C. huddlestoni* were warm-water nektonic feeders over both deep and shallow waters of the continental shelf.

## INTRODUCTION

Cetorhinid sharks are a small group of microphagous lamniformes that are first known from Middle Eocene rocks of Antarctica (Cione and Reguero, 1998) and also occur in Oligocene through Pleistocene strata of Europe, Asia, and the Americas (Cappetta, 2012; Welton, 2013a, 2013b, 2014). The family includes one extant genus, *Cetorhinus* Blainville, 1816, and a single living species, the basking shark, *Cetorhinus maximus* (Gunnerus, 1765) (Springer and Gilbert, 1976; Compagno, 1984, 2001). Basking sharks are among the largest living neoselachians, exceeded in size only by the whale shark *Rhincodon typus* (Smith, 1828), attaining a maximum total length of 12.2–15.2 m, although generally not exceeding 9.8 m (Compagno, 2001). The living basking shark is coastal pelagic to oceanic with a circumglobal distribution in boreal to warm temperate waters of the continental and insular shelves. It occurs both offshore and in shallow coastal waters and enters enclosed bays (Compagno, 2001).

During most of the Cenozoic, the Cetorhinidae had a significant history in the North Pacific Ocean (Long, 1994; Welton, 2013a, 2013b, 2014). Until recently, all fossil cetorhinids were assigned to the genus *Cetorhinus*, but new morphologic information on the dentition, gill rakers, and vertebrae of a Late Eocene basking shark from Oregon provided a basis for recognition of an extinct cetorhinid genus and species, *Keasius taylori* Welton, 2013a. The well known Oligocene species, *C. parvus* Leriche, 1908, was also placed in the genus *Keasius* by

Welton (2013a), based on the morphology of a remarkable articulated skeleton described by Hovestadt and Hovestadt-Euler (2011) from the Oligocene (Rupelian), Grube Unterfeld (Frauenweiler) clay pit, Germany. This species may also be present in the Oligocene Lincoln Creek Formation of southwestern Washington (J.L. Goedert in Kiel, 2010:248), and at least one, and perhaps two, as yet undescribed species of *Keasius* occur in the earliest Miocene (Mitchell and Tedford, 1973; Olson and Welton, 1986) and late Early Miocene (Welton, 2014) of the southeastern San Joaquin Valley, near Bakersfield, California.

The fossil record of *Cetorhinus* along the west coast of the United States includes numerous occurrences of *C. maximus* in latest Miocene to Pleistocene marine deposits in California (Kanakoff, 1956; Fitch, 1970; Langenwaller, 1975; Long, 1994; Boessenecker, 2011), and Oregon (Welton, 2013b), and *C. huddlestoni* Welton, 2014, from the Middle Miocene Round Mountain Silt, Sharktooth Hill Bonebed, in the southeastern San Joaquin Valley near Bakersfield, California.

A new species of *Cetorhinus* is described here from the late Early Miocene Astoria Formation in Oregon and coeval deposits of the lower Round Mountain Silt, in the southeastern San Joaquin Valley, California. Also described are vertebrae of a small basking shark from the Astoria Formation in southwestern Washington and their possible relationship to the new *Cetorhinus* species.

## LOCATION, STRATIGRAPHY, AGE, AND CORRELATION OF THE ASTORIA FORMATION IN THE NEWPORT EMBAYMENT, CENTRAL OREGON COAST

Teeth belonging to a new species of *Cetorhinus* were collected between 1981 and 1986, by G.H. Pierson, J.L. Goedert, and G.H. Goedert, from sea cliff exposures of the marine Astoria Formation north of Newport, Lincoln County, Oregon (Fig. 1). Here, the

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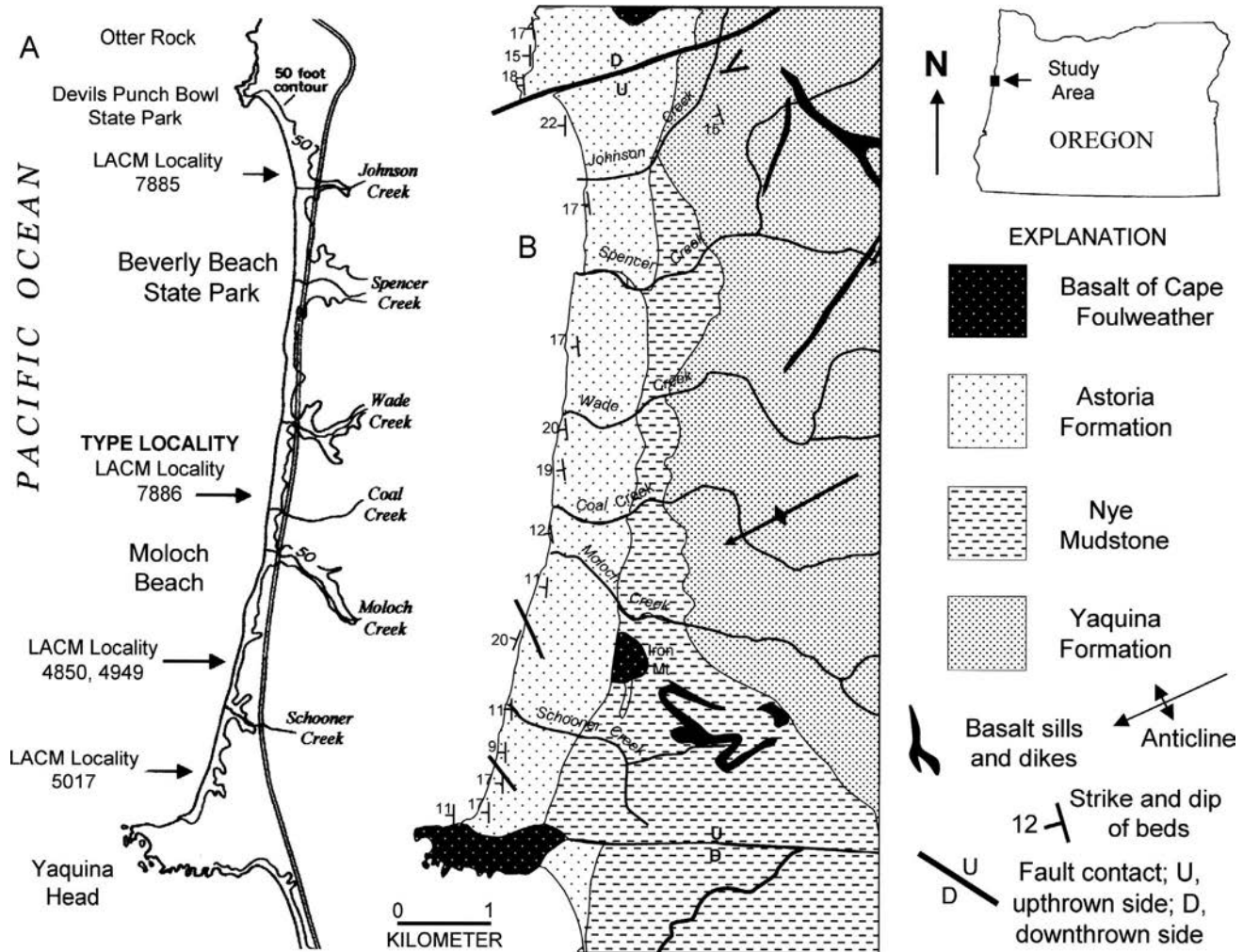


Figure 1 A. Index map of the Oregon coast, from Yaquina Head to Otter Rock, showing the location of LACM locality 7886, type locality for *Cetorhinus piersoni*, new species, and other localities for paratype and referred specimens. B. Generalized geologic map of coastal Oregon between Yaquina Head and Otter Rock (modified from Snavely and MacLeod, 1971).

Astoria Formation disconformably overlies the lower Miocene Nye Mudstone, and is unconformably overlain by Pleistocene terrace deposits. The lower part of the Astoria Formation is exposed from the mouth of Little Creek to the south flank of Yaquina Head, on Agate Beach (section D of Moore, 1963:pl. 33; Prothero et al., 2001a), and is approximately 130 m thick. The thickest and most complete section of the Astoria Formation (192 m) crops out on the north side of Yaquina Head (Snavely et al., 1964; Prothero et al., 2001a) and extends intermittently north along the coast for approximately 8 km to Otter Rock (Fig. 1A, B). Within this section, beds of the Astoria Formation have a westerly dip of 9 to 28 degrees, and strike generally north, paralleling the coastline (Snavely and MacLeod, 1971:pl. 1; Snavely et al., 1976). The section is complicated by north-trending en echelon faults (Snavely et al., 1964). The most common lithologies include olive-gray, fine- to medium-grained, micaceous, arkosic, sandstone and dark-gray carbonaceous siltstone. Sandstone beds in the Astoria Formation are thin to thickly bedded, moderately to well indurated, with stratigraphically continuous concretionary beds or discrete concretions up to 0.5 m in diameter. Many of the sands

are extensively bioturbated, although small-scale planar and ripple laminae, cross-bedding, and slump structures are common in some intervals. Interbedded volcanoclastics include granule to coarse-grained basaltic sandstone beds (up to 4.4 m) and tuffs (up to 5.5 m) (Snavely et al., 1964).

Teeth belonging to a new species of *Cetorhinus* are presently known from five localities in the Astoria Formation section north of Yaquina Head (Fig. 1A). The teeth are small, usually less than 5 mm in total height (TH, Appendix 1), and *in situ* preservation ranges from rounded and abraded to well preserved. LACM locality 5017 (Fig. 1A) is a cliff exposure approximately midway between Yaquina Head and Schooner Creek, and LACM localities 4850 and 4949 are both cliff and slump-block outcrops just north of Schooner Creek in an area known as the "Iron Mountain Beds." This stratigraphic interval has produced numerous pinnipeds, a desmostylian, cetaceans, and terrestrial mammals (Condon, 1906; Packard and Kellogg, 1934; Mitchell and Repenning, 1963; Coombs, 1979; Munthe and Coombs, 1979; Barnes, 1987, 1989, 1990, 1992; Berta, 1994a, 1994b; Barnes and Hirota, 1995; Kohno et al., 1995; Demere and Berta,

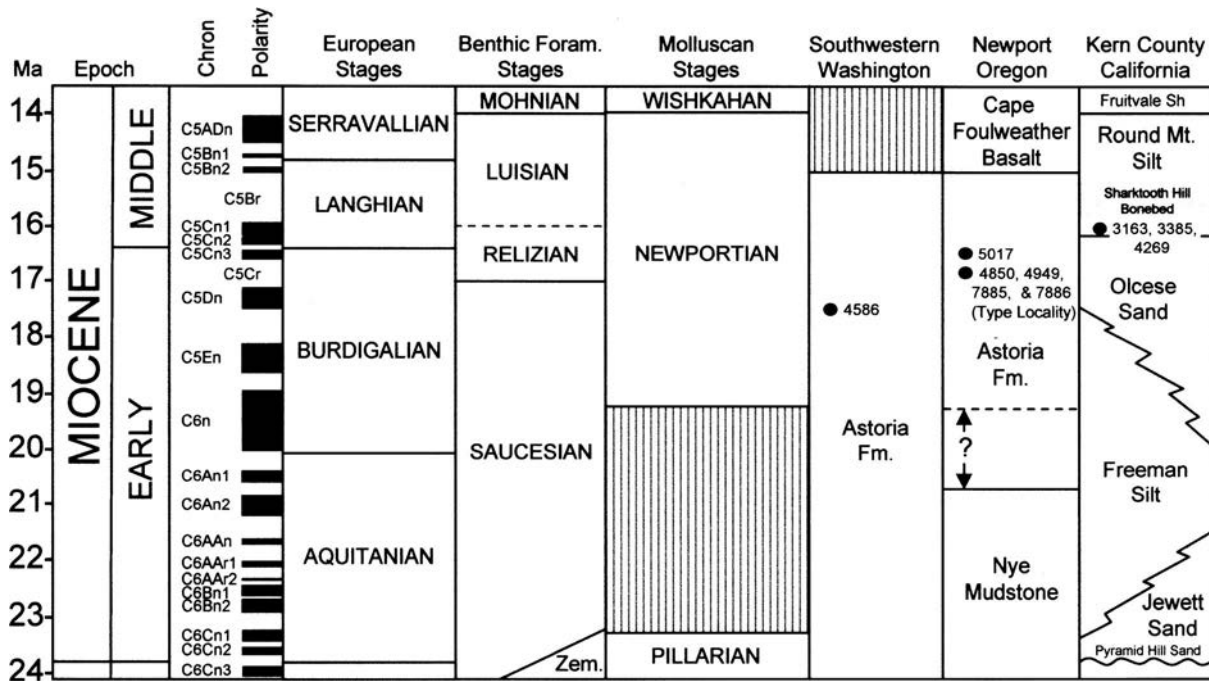


Figure 2 Correlation chart for Miocene chronostratigraphic–biostratigraphic zones and lithologic units from southwestern Washington, the Newport Embayment on the central Oregon coast near Newport, and the southeastern San Joaquin Valley, Kern County, California. Time scale after Prothero (2001:388, fig. 4). Chronostratigraphy and biostratigraphy of the Astoria Formation in southwestern Washington after Moore and Addicott (1987), Prothero (2001), Prothero and Burns (2001), and Prothero et al. (2008a). The age of the Astoria and Nye formations at Newport, Oregon, is based on Prothero (2001) and Prothero et al. (2001a, 2001b). Olson (1988, 1990), Prothero et al. (2008b), and Pyenson et al. (2009) are followed for the lithostratigraphy, biostratigraphy, and chronostratigraphy of the Early to Middle Miocene section in Kern County, California. Numbers associated with dots indicate the chronostratigraphic position of LACM localities for the holotype, paratypes, and referred specimens of *Cetorhinus piersoni*, new species. The horizontal grey box within the Round Mountain Silt section highlights the chronologic range of the Sharktooth Hill Bonebed condensed section (after Pyenson et al., 2009). Abbreviations: Zem., Zemorrian; Ma, millions of years ago (mega-annum).

2001). The holotype tooth of the new *Cetorhinus* species was collected by J.L. Goedert and G.H. Goedert from LACM 7886, approximately 300 m north of the mouth of Coal Creek (Fig. 1A), in a sandstone adjacent to beds composed almost entirely of the bivalve *Anadara devincta* (Conrad, 1849). The most northern locality in the Astoria Formation for *Cetorhinus*, is LACM 7885, just north of the mouth of Johnson Creek, and north of Beverly Beach State Park (Fig. 1A).

The Astoria Formation in the Newport Embayment (*sensu* Snively et al., 1964) is the type area for the Newportian Molluscan Stage of Addicott (1976a) and is late Early to Middle Miocene in age (Addicott, 1977; Moore and Addicott, 1987; Prothero et al., 2001a). The base of the Astoria Formation, at its contact with the Nye Mudstone, correlates with Chron C5Bn2 (19.2 millions of years ago [Ma]) or C5Cn1 (20.7 Ma) (Prothero, 2001; Prothero et al., 2001a) (Fig. 2), and the Cape Foulweather basalts that cap the Astoria Formation at Yaquina Head, have been dated at 15.1–15.7 Ma (Wells et al., 1989).

A chalicotherium cranium referred to *Tylocephalonyx* sp. and the rhinoceros *Aphelops* (Coombs, 1979; Munthe and Coombs, 1979) from the Iron Mountain Beds, in sea cliffs north of Schooner Creek and just south of Moloch Beach (or Moolack Beach as locally used) (Fig. 1A), are correlative with Chron C5Cr (16.6 and 17.3 Ma) (Prothero et al., 2001a:279) and a Hemingfordian Land Mammal Age (Barnes, 1987).

Prothero et al. (2001a) investigated the magnetic stratigraphy of the Astoria Formation along sea cliffs north and south of Yaquina Head at Newport, Oregon. Thirty-seven stratigraphic

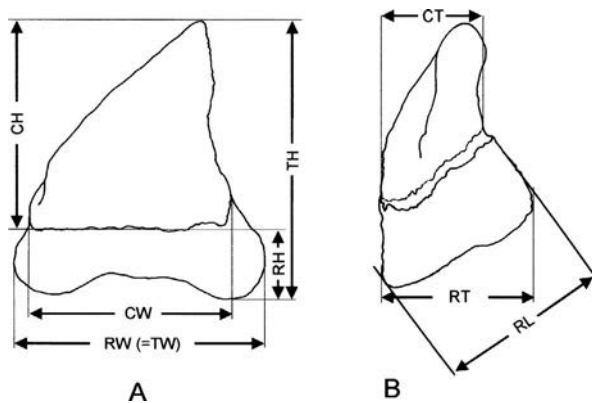
samples were collected from just north of Schooner Creek, south to Yaquina Head (Prothero et al., 2001a:278, fig. 6). LACM locality 5017 corresponds approximately to samples 16 and 17, and LACM localities 4850 and 4949 are close to samples 1 and 2. The remaining two *Cetorhinus* localities occur north along the coastal outcrop, near Coal Creek (LACM locality 7886), and just north of Beverly Beach State Park and Johnson Creek (LACM locality 7885) (Fig. 1A). These latter two localities lie nearly on strike with samples 1–8 (Snively et al., 1976; Prothero et al., 2001a), and I assume they are stratigraphically close to one another (Fig. 1A, B). According to the magnetic stratigraphy of the Moloch Beach and Schooner Creek section north of Yaquina Head (Prothero et al., 2001a:figs. 6, 7), LACM localities 4850, 4949, 7886, and 7885 correlate with Chron C5Cr (16.6–17.3 Ma), and LACM locality 5017 correlates with Chron C5Cn3 (16.5–16.6 Ma) (Fig. 2).

METHODS AND MATERIALS

Comparisons are based on the descriptions and illustrations of the dentition of the living species, *Cetorhinus maximus* (Gunnerus, 1765), provided by Herman et al. (1993) and Welton (2013a), and of *C. buddlestoni* Welton, 2014.

*Cetorhinus* tooth measurements are illustrated in Figure 3 and generally follow Shimada et al. (2014). Tooth row group and anatomical terminology follows Compagno (1970, 2001) and Welton (2013a, 2014), and anatomical terms for vertebral centra and their internal calcifications are derived from Ridewood (1921), Wintner and Cliff (1999), Wintner (2000), and Welton (2013a, 2013b). Patterns of heterodonty are defined





**Figure 3** Dental measurements for teeth of *Cetorhinus* using the holotype of *C. piersoni*, new species, as an example. **A.** Labial view; **B.** distal view. Abbreviations: CH, crown height; CT, crown thickness; CW, crown width; RH, root height; RL, root length; RT, root thickness; RW, root width; TH, total tooth height; TW, total tooth width (in *Cetorhinus*, TW, almost always = RW, the exception generally being teeth near the distal ends of the dental series).

by Compagno (1970), and this study follows Welton (2013a, 2014) in their application to *Cetorhinus*. All line illustrations of teeth were done by the author using a Wild M5 stereomicroscope and camera lucida attachment. Photographs were taken with a Cannon Rebel T3i digital camera and 100-mm macro lens.

The dentitions of Recent *Cetorhinus maximus* described are in the Department of Ichthyology of the Natural History Museum of Los Angeles County, California (LACM): LACM 35876-1, adult male, 600–670 cm total length, wet-preserved upper and lower jaws with dentition, collected off Morro Bay, San Luis Obispo, California, 30 June 1976; LACM 44280-1, immature female, 540.6 cm total length, wet-preserved upper and lower jaws, collected on Oceano Beach, San Luis Obispo County, California, 2 November 1978; LACM 39461-1, female, 635 cm total length, dried jaws with dentition, collected November 1956 from near San Pedro, California.

All of the fossil *Cetorhinus* specimens are in the Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, California. Reference is made to invertebrate fossils from the Astoria Formation near Altoona, Washington, in collections of the University of Washington Burke Museum (UWBM). Detailed locality descriptions are available from the Department of Vertebrate Paleontology (LACM).

### SYSTEMATICS

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Cohort Euselachii Hay, 1902

Subcohort Neoselachii Compagno, 1977

Order Lamniformes Berg, 1958

Family Cetorhinidae Gill, 1862

Genus *Cetorhinus* Blainville, 1816

**EMENDED DIAGNOSIS OF GENUS (DENTITION AND VERTEBRAE).** A genus of Cetorhinidae differing from *Keasius* Welton, 2013a, by having a nearly homodont dentition; weak gradient monognathic heterodonty in both jaws; weak dignathic heterodonty with largest teeth in the lower jaw; strong ontogenetic heterodonty with erect to nearly horizontal cusps in juvenile individuals, and more erect, narrow to broad cusps in adults of both sexes; sexual dimorphism unknown; dental series on either side of symphysis in upper and lower jaws with 100 or

more rows; tooth size largest about the center of the dental band in both jaws, decreasing in size mesially and distally; crown with a single narrow to wide cusp, with straight to weakly concave or convex mesial and distal margins that are continuous with the crown base; cusp apex moderately sharp in juvenile individuals, rounded or acute in adults; cusplets generally absent, but when present are most commonly found in juvenile teeth, less frequently in adult teeth, and usually restricted to one cusplet at the mesial crown foot, or developed on a low blade just above the mesial crown foot; lingual crown face weakly convex and smooth, or finely ornamented with irregular fine to coarse ridges and enameloid folds; labial face moderately to strongly convex, smooth or ornamented with numerous, fine, subparallel longitudinal ridges that may develop anywhere on the crown face; lingual crown foot with or without a slight basal ledge; teeth of juvenile individuals have erect to hook-shaped, nearly horizontal cusps relative to the base; cusps almost erect in adults of both sexes; mesial and distal cutting edges in juvenile individuals continuous to near crown foot; cutting edges in adult individuals generally do not reach the crown foot; labial crown foot smooth or with numerous deep, short enameloid folds that are covered with irregular pits and short enameloid ridges in some juvenile teeth; enameloid folds at labial crown foot reduced or absent in adults; root usually weakly convex to strongly rounded lingually in mesial or distal view, with horizontal to strongly convex basal attachment surface; root lobes widely separated and well developed, reduced, or absent; lingual protuberance weakly convex to strongly convex, and reduced in size toward mesial and distal ends of the dental series; apex of cusp extends beyond lingual face of root in mesial or distal view; vertebrae anteroposteriorly long; radial calcifications of intermedialia external to concentric lamellae in precaudal vertebrae, and replace concentric lamellae in some caudal centra, or absent entirely in some vertebrae; radial calcifications reach dorsal, ventral, and lateral margins of centra; concentric lamella walls perforated by numerous radiating calcified tubes; diagonal lamellae absent.

**INCLUDED SPECIES. Recent:** *Cetorhinus maximus* (Günnerus, 1765). **Fossil:** *Cetorhinus huddlestoni* Welton 2014, Middle Miocene, Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California; *Cetorhinus piersoni*, new species, late Early Miocene, Astoria Formation, Oregon; late Early Miocene, lower Round Mountain Silt, southeastern San Joaquin Valley, Kern County, California.

#### *Cetorhinus piersoni*, new species

Figures 4–7

*Cetorhinus* sp.: Long, 1994:82, states *Cetorhinus* “extends back into the Hemingfordian of the Round Mountain Silt.”

*Cetorhinus* sp.: Welton, 2013b:74, 86.

*Cetorhinus* sp.: Welton, 2014:1.

**DIAGNOSIS OF SPECIES.** A species of *Cetorhinus*, apparently smaller as adults than the Recent *C. maximus* and extinct *C. huddlestoni*; differing from *C. maximus* and *C. huddlestoni* by having many adult teeth with robust, broad-based triangular crowns, although there is a wide range of variation in crown shape; crown height in labial view greater than 2.5 times root height; cutting edges smooth, but anomalous “pseudoserrations” develop on the lower half of the crown on some large adult teeth; short longitudinal enameloid ridges developed on lingual crown face near cusp apex in approximately 50% of teeth; enameloid folds at the labial crown foot occasionally present on largest teeth, but generally absent; differing further from *C. maximus* by having weak lingual cusp inclination, with cusp apex rarely

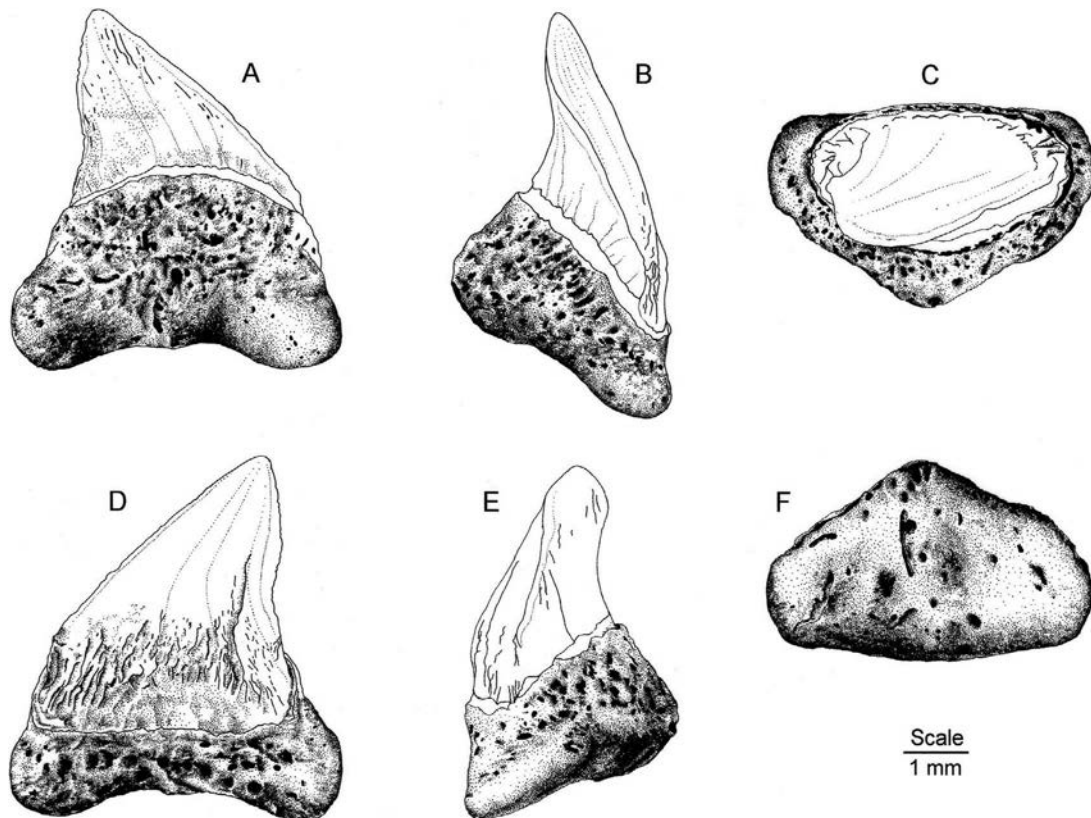


Figure 4 *Cetorhinus piersoni*, new species, holotype tooth, LACM 155792, from LACM locality 7886, Astoria Formation, Lincoln County, Oregon. A. lingual view; B. mesial view; C. apical view; D. labial view; E. distal view; F. basal view. Scale bar = 1 mm.

extending beyond protuberance; pronounced axial twist in the distal half to third of cusp such that the labial crown face on the distal end of the cusp may lie in a plain almost normal to the lingual crown face; crown margins not strongly constricted in most teeth at level of crown–root junction; cutting edges extend from cusp apex basally for a distance of one-half to two-thirds or more of the crown height, reaching the crown foot in some large adult teeth; cusplets usually absent or sometimes developed above the mesial crown foot, as a short, labiolingually compressed bladelike structure; root lobes well developed, widely diverging, short, tabular near distal ends, or rounded and robust; lingual protuberance ranges from strongly convex and developed over the entire lingual root face, to small and robust, positioned high on the root near the crown foot, or low on the root, just above the basal attachment surface; basal margin of root, between the mesial and distal root lobes, is apically convex, broadly rounded to subangular; differing further from *C. huddlestoni* by having a rounded cusp apex in many teeth.

**HOLOTYPE.** LACM 155792, complete adult tooth (Fig. 4A–F).

**TYPE LOCALITY.** LACM locality 7886, in sea cliff exposures north of Yaquina Head, approximately 1000 m north of Coal Creek, Lincoln County, Oregon (Fig. 1A).

**PARATYPES.** LACM 155772, 155773 (Fig. 7.3A–C), 155774, 155777–155778, five teeth from LACM locality 4850; LACM 155798 (Fig. 6.1A–C), 155799 (Fig. 6.3A–C), 155803 (Fig. 6.4A–C), 155804 (Fig. 7.4A–C), 155805, 155806 (Fig. 6.2A–C), 155807, 155808 (Fig. 6.6A–C), 155809, 155811 (Fig. 6.5A–C), 155812 (Fig. 7.1A–C), 155814, 155815 (Fig. 7.5A–C), 155816 (Fig. 7.2A–C), 14 teeth from LACM locality 4949; LACM

155779, 155781, 155783–155791, five teeth from LACM locality 5017; LACM 155785 (Fig. 5.4A–C), 155786 (Fig. 5.5A–C), 155787–155790, six teeth from LACM locality 7885; LACM 155793 (Fig. 5.2A), 155794 (Fig. 5.3A), 155795 (Fig. 5.6A–C), 155796 (Fig. 5.1A–C), 156958 (Fig. 5.7A–C), five teeth from LACM locality 7886.

**REFERRED SPECIMENS FROM THE ASTORIA FORMATION, OREGON.** LACM 155776, one tooth from LACM locality 4850; LACM 155797, 155800–155802, 155810, five teeth from LACM locality 4949; LACM 155780, 155782, two teeth from LACM locality 5017.

**REFERRED SPECIMENS FROM THE LOWER ROUND MOUNTAIN SILT, SOUTHEASTERN SAN JOAQUIN VALLEY, KERN COUNTY, CALIFORNIA.** Marine rocks of correlative age to the Astoria Formation in the Pacific Northwest occur in outcrops along the southeastern margin of the San Joaquin Valley, near Bakersfield, in Kern County, California (Moore, 1963; Addicott, 1970; Prothero, 2001; Prothero et al., 2008b). Overlying inner shelf and fluvial deposits of the Olcese Sand are late Early Miocene to Middle Miocene transgressive marine sediments of the Round Mountain Silt, including the well-known Sharktooth Hill Bonebed (Olson, 1988; Pyenson et al., 2009). Teeth of *Cetorhinus huddlestoni* are abundant in the Middle Miocene bonebed, and teeth of *C. piersoni* and *Keasius*, occur in late Early Miocene shell lags near the base of the formation, at LACM localities 3385, 4269, and 3163.

**REFERRED specimens from the lower Round Mountain Silt, Crab Canyon locality.** LACM 156959 (Fig. 8.3A–C), LACM 156960 (Fig. 8.7A–C), LACM 156961 (Fig. 8.5A–C), LACM 156962

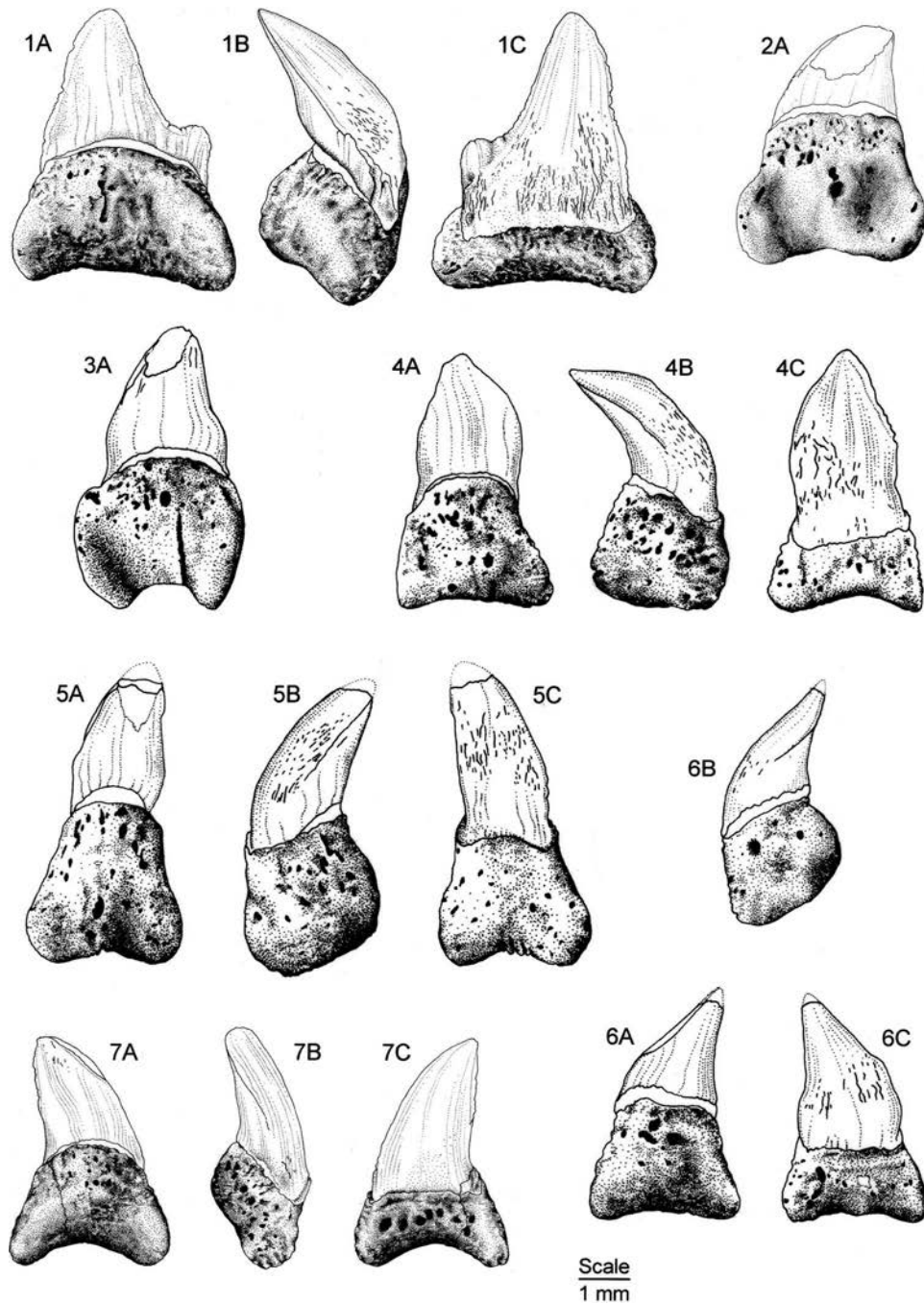


Figure 5 Paratype teeth of *Cetorhinus piersoni*, new species, Astoria Formation, Lincoln County, Oregon. A. lingual view; B. mesial view; C. labial view. Teeth from LACM locality 7886: 1, LACM 155796; 2, LACM 155793; 3, LACM 155794; 6, LACM 155795. Teeth from LACM locality 7885: 4, LACM 155785; 5, LACM 155786; 7, LACM 156958. Scale bar = 1 mm.

(Fig. 8.2A–C), LACM 156963 (Fig. 8.6A–C), LACM 156964 (Fig. 8.4A–C), LACM 156965 (Fig. 8.1A–C), seven teeth collected by B.J. Welton in 1982.

**Locality.** LACM locality 3385, Crab Canyon, several kilometers northwest of Barkers Ranch, Kern County, California; collected from a 6-cm-thick, concentrated shell lag, with medium- to fine-grained quartz sand, scattered granule to small

black pebbles, mammalian bone fragments, numerous teleost otoliths, including abundant sciaenids and bothids, and teeth of sharks and rays.

**Formation and age.** Lower Round Mountain Silt (Diepenbrock, 1933; Keen, 1943; Addicott, 1970; Bartow, 1984) transgressive lag deposit at the base of the formation. This locality has approximately the same stratigraphic position in the



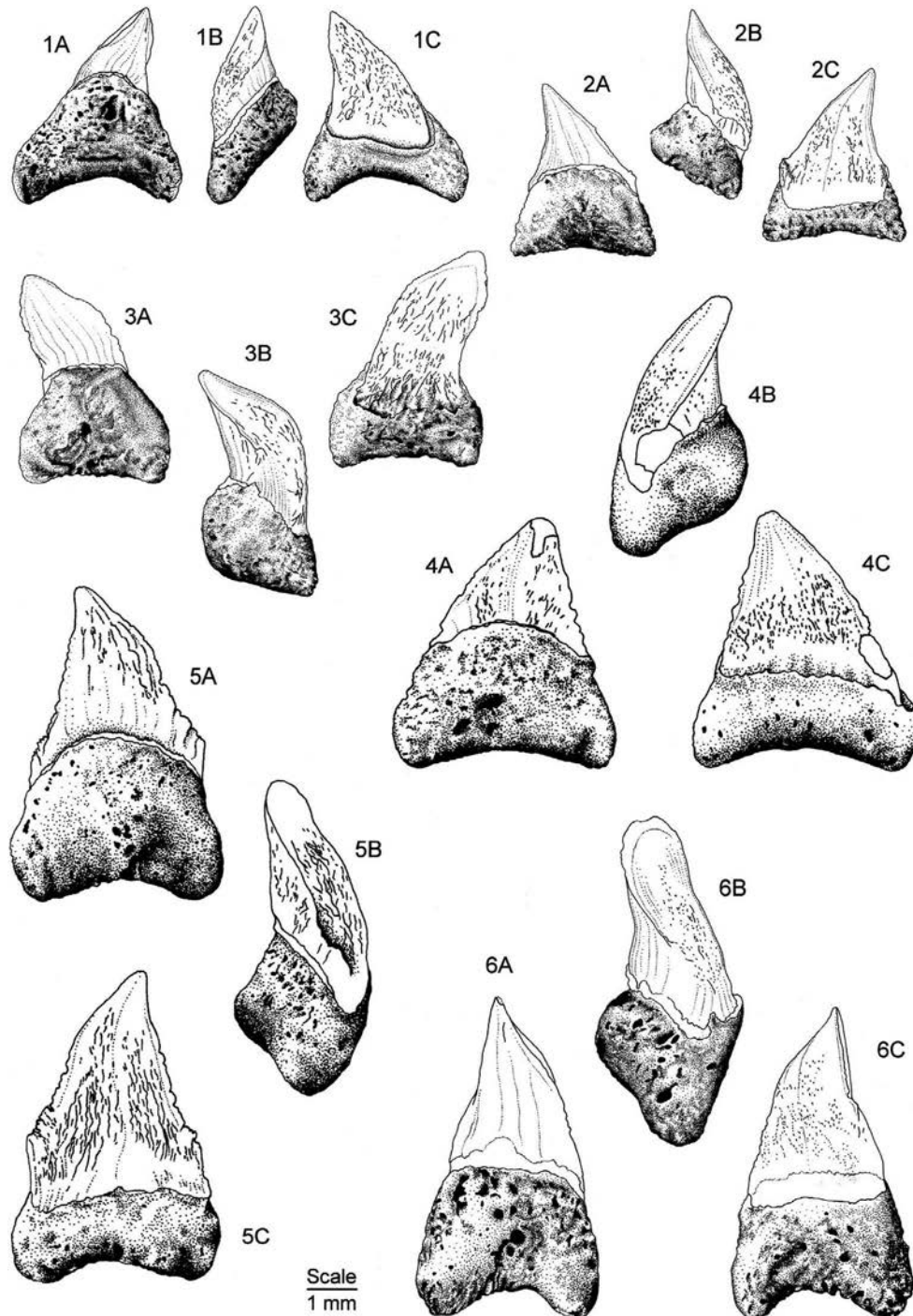


Figure 6 Paratype teeth of *Cetorhinus piersoni*, new species, Astoria Formation, Lincoln County, Oregon. A. lingual view; B. mesial view; C. labial view. LACM locality 4949: 1, LACM 155798; 2, LACM 155806; 3, LACM 155799; 4, LACM 155803; 5, LACM 155811; 6, LACM 155808. Scale bar = 1 mm.

lower Round Mountain Silt as LACM 4269 and is assumed to be correlative with the base of Chron C5Br (16.0 Ma) (Prothero et al., 2008b) (Fig. 2).

Referred specimens from the lower Round Mountain Silt, Poso Creek locality. LACM 156973 (Fig. 9.1A–C), LACM 156974 (Fig. 9.3A–C), LACM 156975 (Fig. 9.4A–C), LACM 156976

(Fig. 9.5A–C), LACM 156977–156979, LACM 156980 (Fig. 9.2A–C), eight teeth collected by B.J. Welton between 1980 and March 2013.

Locality. LACM locality 4269, Poso Creek, Kern County, California; collected from a 13–20-cm-thick clastic shell lag, exposed in a roadcut along Poso Creek, on Round Mountain Road, north of Bakersfield. Where exposed to weathering, this

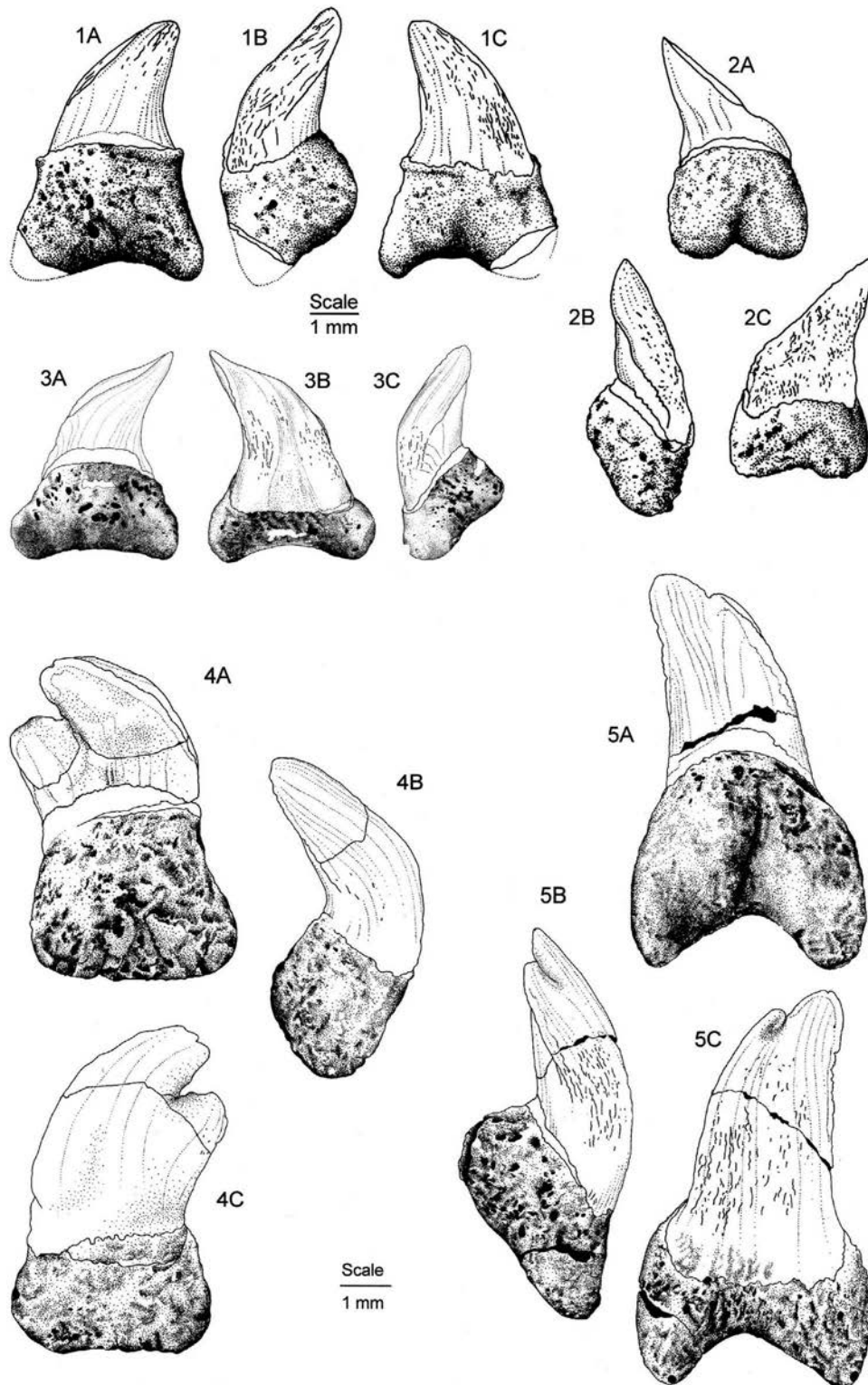


Figure 7 Paratype teeth of *Cetorhinus piersoni*, new species, Astoria Formation, Lincoln County, Oregon. A. lingual view; B. mesial view; C. labial view. Teeth from LACM locality 4949: 1, LACM 155812; 2, LACM 155816. Scale bars = 1 mm. Tooth from LACM locality 4850: 3, LACM 155773. Abnormal paratype teeth from LACM locality 4949: 4, LACM 155804; 5, LACM 155815. Upper left scale bar applies to Figs. 7.1–7.3, and scale bar near bottom center applies to Figs. 7.4–7.5.



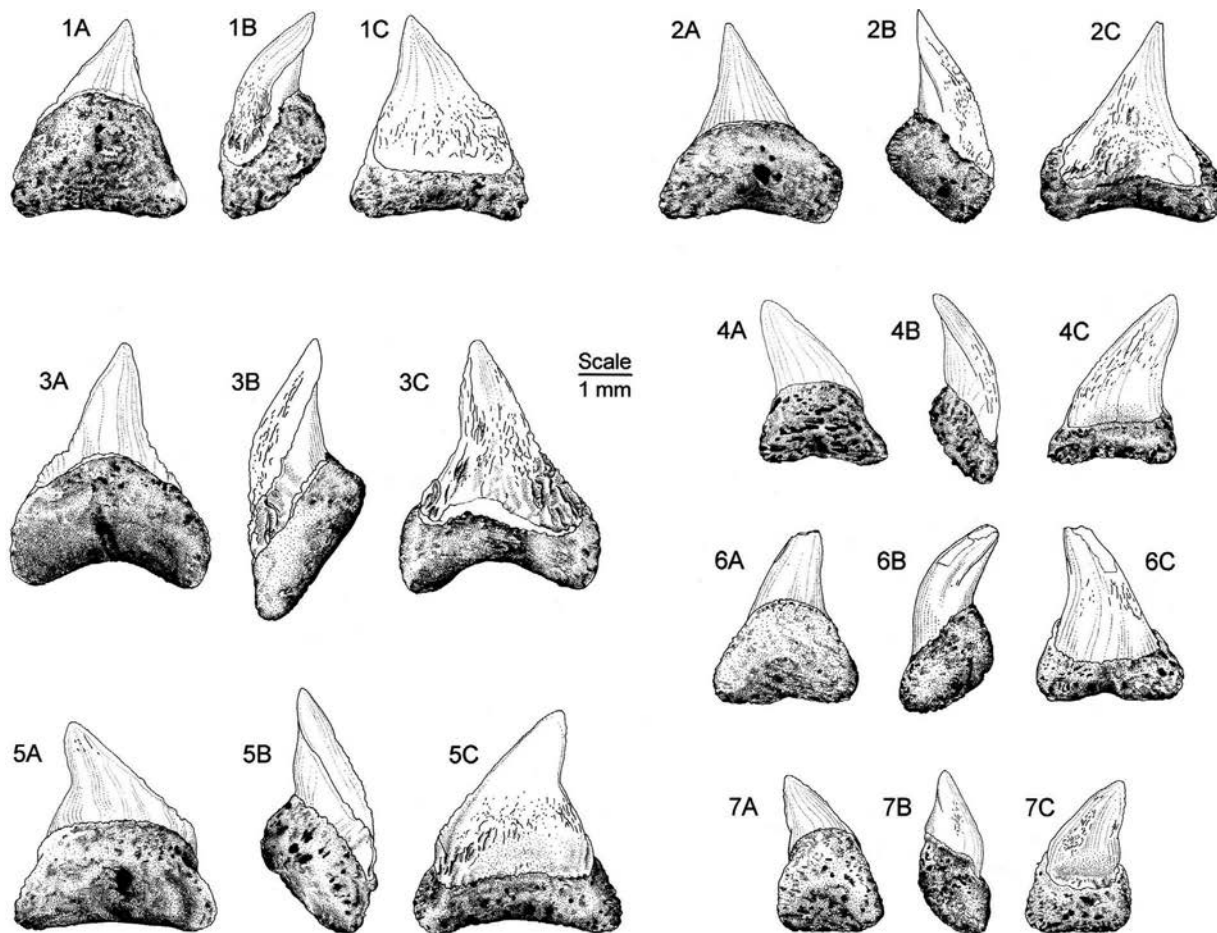


Figure 8 Teeth referred to *Cetorhinus piersoni*, new species, from LACM locality 3385, Crab Canyon, lower Round Mountain Silt, southeastern San Joaquin Valley, Kern County, California. A. lingual view; B. mesial view; C. labial view. 1, LACM 156965; 2, LACM 156962; 3, LACM 156959; 4, LACM 156964; 5, LACM 156961; 6, LACM 156963; 7, LACM 156960. Scale bar = 1 mm.

shell bed is often unconsolidated but is otherwise cemented with calcium carbonate. The matrix is a white siltstone with subordinate very fine grained sand and clay. Larger clasts include abundant fragmentary cetorhinid gill rakers, crab claws, and carapace fragments, rounded pebbles, and abundant shark and ray teeth. This shell bed is lenticular, between 1 and 9 m in horizontal extent, with variable thickness. Horizontally discontinuous beds of this same character occur in adjacent gullies and road cuts, at approximately the same stratigraphic level, to the east of this locality.

**Formation and age.** Lower Round Mountain Silt (Diepenbrock, 1933; Keen, 1943; Addicott, 1970; Prothero et al., 2008b), 4.3 m stratigraphically above its unconformable contact with the Olcese Sand. The Round Mountain Silt contains a Luisian benthic foraminiferal fauna, ranging between 14 and 15.5 Ma (Olson, 1990; Barron and Isaacs, 2001; Prothero, 2001). A thick (51 m) diatomite, occurring stratigraphically beneath the Sharktooth Hill Bonebed, and above LACM locality 4269, contains diatoms characteristic of the *Denticulopsis lauta* A zone (Barron, in Bartow and McDougall, 1984; Olson, 1990; Prothero et al., 2008b), indicating an age between 15 and 16 Ma (Barron, 1981; Olson, 1990; Prothero et al., 2008b). Magnetic samples taken at LACM 4269 by Prothero et al. (2008b:363, figs. 6, 7) correlate with the base of Chron C5Br (16.0 Ma) (Fig. 2).

**Referred specimens from the lower Round Mountain Silt, Kern Bluff locality.** LACM 156966 (Fig. 10.1A–C), 156967 (Fig. 10.3A, C), 156968 (Fig. 10.7A–C), 156969 (Fig. 10.2A–C), 156970 (Fig. 10.4A–C), 156971 (Fig. 10.5A–C), 156972 (Fig. 10.6A–C), seven teeth collected by B.J. Welton in 1983.

**Locality.** LACM locality 3163, Kern Bluff, Kern County, California; collected from a clastic shell bed, exposed on the south side of Kern River, southeast of Hart Park.

**Formation and age.** Lower Round Mountain Silt (Bartow, 1984), approximately 40 m above the base of the Round Mountain Silt and 90–110 m stratigraphically below the Sharktooth Hill Bonebed. The Kern Bluff locality probably correlates with early Chron C5Br based on its stratigraphic position in the lower Round Mountain Silt (Fig. 2).

The teeth of *Cetorhinus piersoni* from LACM localities 3385, 4269, and 3163 are about 0.5 Ma younger than the youngest Oregon Astoria Formation occurrences of the species (LACM locality 5017) and predate *C. huddlestoni* from the Sharktooth Hill Bonebed by about 0.5 Ma.

**ETYMOLOGY.** The species name, *piersoni*, is in honor of Mr. Guy E. Pierson, who collected many of the Astoria Formation teeth of *Cetorhinus piersoni* between 1981 and 1986.

**DESCRIPTION OF THE HOLOTYPE.** The holotype, LACM 155792 (Fig. 4A–F), is a complete, well-preserved, lower left or

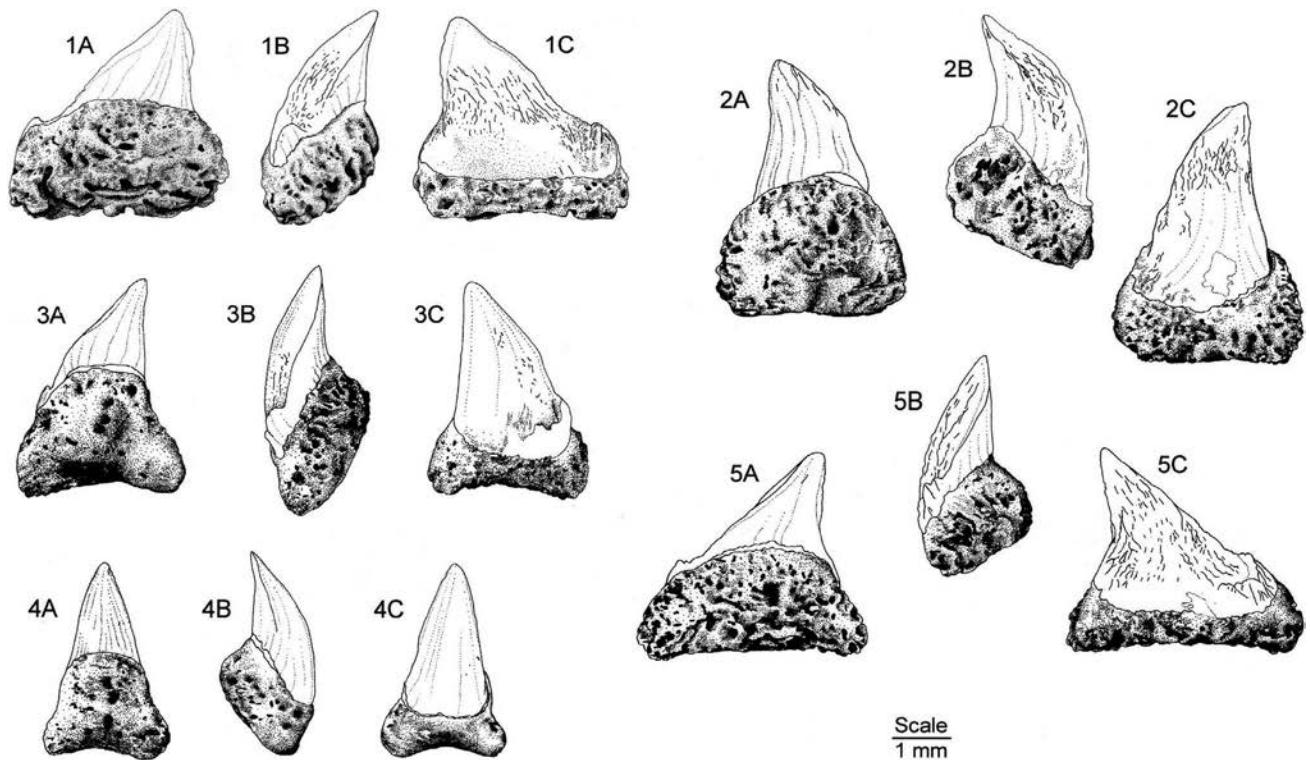


Figure 9 Teeth referred to *Cetorhinus piersoni*, new species, from LACM locality 4269, Poso Creek, lower Round Mountain Silt, southeastern San Joaquin Valley, Kern County, California. A. lingual view; B. mesial view; C. labial view. 1, LACM 156973; 2, LACM 156980; 3, LACM 156974; 4, LACM 156975; 5, LACM 156976. Scale bar = 1 mm.

upper right adult tooth, possibly from a row distal to the central row in the dental series. The tooth measures 5.7 mm in tooth height and 5.2 mm in root width (Fig. 3 and Appendix 1). The crown height is slightly less than the root height lingually and greater than 2.5 times the root height labially. In labial view, the mesial and distal tooth profile across the crown foot–root junction is nearly straight, not concave. A narrow trough is developed at the crown–root junction and completely encircles the tooth. The crown is broadly triangular and short, and narrows to a moderately sharp apex, with a strong axial twist (*sensu* Welton, 2014). The mesial crown margin is weakly convex, and the distal margin is convex in the upper half and concave in the lower half. The lingual crown face is strongly convex just above the crown foot, above which it flattens to the apex. Coarse, rounded enameloid folds occur just above the crown foot along the entire lingual face, and very coarse, short, longitudinal enameloid ridges occur on the distal half of the crown face and extend almost to the apex. The labial crown face is strongly convex and bordered basally by a wide neck, and robust crown foot, with a strong basal ledge. Numerous, very fine, short enameloid ridges are concentrated over the lower half of the crown, and longer, coarse, widely spaced enameloid ridges, bounded by shallow and wide depressions, border the entire labial crown foot. A narrow, continuous lingual neck underlies the crown foot. The cusp apex is only very slightly recurved labially, and in lingual view, the entire crown is moderately inclined distally. The cusp apex does not extend distally beyond the crown foot. In mesial view, the cutting edge is smooth and continuous across the cusp apex and almost reaches the crown foot, above which it expands slightly into a low blade. In distal view, the cutting edge extends from the apex basally for a distance of about four-fifths of the crown height and does not

reach the crown foot. Cusplets are not developed. The root is massive and strongly bilobate, and the mesial and distal margins of the root lobes extend well beyond the crown foot. In lingual view, the protuberance is very prominent, narrow, is situated high on the root, and projects lingually well beyond the root lobes. A small central foramen is situated at the apex of the protuberance, and there is no evidence of a nutrient groove. A slight ridge extends basally along the underside of the protuberance and is bordered mesially and distally by shallow troughs, from which are developed the mesial and distal root lobes. The basal attachment surface of the root is strongly convex and flattened, giving the root lobes a tabular appearance. Small foramina cover the lingual face of the root and are only slightly enlarged just below the crown foot. The root is very short labially, and a series of large foramina are developed below and parallel to the crown foot, extending mesially and distally on to the root lobes.

#### DESCRIPTION OF PARATYPES AND REFERRED TEETH.

The paratype series includes 35 unassociated teeth from five localities in the lower half of the Astoria Formation (LACM localities 4850, 4949, 5017, 7885, and 7886; Fig. 1A). Eighteen of the paratypes are illustrated in Figures 5–7, and tooth measurements and other dental attributes are summarized in Appendix 1. The statistical averages, ranges, and ratios given below are based on paratype teeth, plus selective measurements taken from eight incomplete teeth referred to *Cetorhinus piersoni* from the same five localities in the Newport Embayment (Appendix 1).

Based on the morphologic variability observed in *Cetorhinus piersoni*, one can reasonably assume that it is due to a combination of ontogenetic heterodonty, with teeth representing juvenile (e.g., Figs. 6.1A–C, 6.2A–C) to large adults (e.g., Figs. 6.5A–C, 6.6A–C), and intermediate growth stages, in



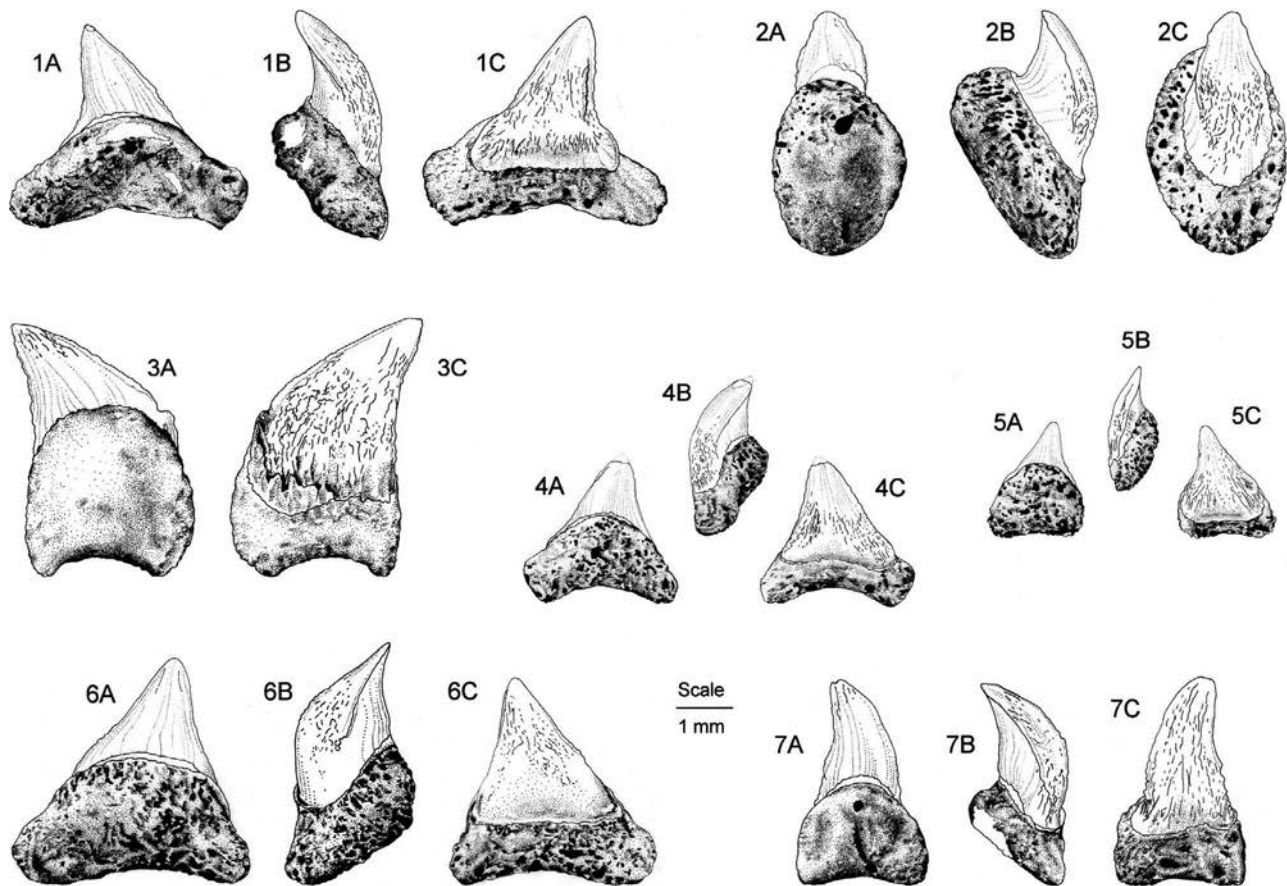


Figure 10 Teeth referred to *Cetorhinus piersoni*, new species, from the LACM locality 3163, Kern Bluff, lower Round Mountain Silt, southeastern San Joaquin Valley, Kern County, California. A. lingual view; B. mesial view; C. labial view. 1, LACM 156966; 2, LACM 156969; 3, LACM 156967; 4, LACM 156970; 5, LACM 156971; 6, LACM 156972; 7, LACM 156968. Scale bar = 1 mm.

combination with some degree of gradient monognathic and dignathic heterodonty, similar to that interpreted for *C. huddlestoni* (Welton, 2014) and observed in *C. maximus* (Herman et al., 1993; Shimada, 2002; Welton, 2013a). Consideration was given to reconstructing the upper and lower dental series as a means of further evaluating the heterodonty in this species; however, this concept was rejected for a number of reasons. First, the sample size is too small to provide a reasonable understanding of the range of heterodonty in the species. Based on an interpretation of the upper and lower dental series in *C. huddlestoni* (Welton, 2014), a minimum unbiased sample of at least 350–400 juvenile and adult teeth is required to make a partial reconstruction of the dentition (e.g., ~10 representative teeth each from the upper and lower dental series, assuming approximately 100 rows in each jaw). Second, the Astoria teeth were collected by surface prospecting, and the sample is probably biased in favor of larger (adult) teeth. Third, attempts to assign individual teeth of *C. piersoni* to the upper or lower jaw were not successful. The dental criteria cited by Welton (2013a) for distinguishing upper and lower teeth in *C. maximus* did not yield convincing results when applied to *C. piersoni*, and the problem was again compounded by the small sample size.

The teeth of *Cetorhinus piersoni* display a wide range of crown and root morphologies, not all of which are found in the holotype. Adult teeth are small relative to *C. maximus*, with an average TH of 4.7 mm (range: 3.3–6.5 mm;  $n = 26$ ), and an average TW of 3.3 mm (range: 1.8–5.2 mm;  $n = 30$ ). The TH/RW ratio ranges

from 1.0 to 1.8 ( $n = 21$ ) and averages 1.4 (Appendix 1). Only one tooth in the type series has a root width that equals the tooth height. The crowns are tall, averaging 3.3 mm in CH (range: 1.6–4.8 mm;  $n = 35$ ), and CW averages 1.5 mm (range: 0.8–2.3 mm;  $n = 41$ ). Relative to *C. huddlestoni*, the root is thick, averaging 2.4 mm (range: 1.3–3.2 mm;  $n = 36$ ), and CH exceeds CW in all of the paratypes (average CH/CW ratio 2.3; range: 1.6–3.2) (Appendix 1). Unlike the holotype tooth, some adult teeth (Figs. 5.3–5.5) have tall, narrow crowns that are constricted at the crown foot, then expand mesially and distally at about half the crown height. The cusp apex in many teeth is broadly rounded, with a weak to strong apical twist. Other teeth have crowns similar to the holotype (Fig. 5.1; Figs. 6.4–6.6) in being very broad based, triangular, and of varying heights, with straight to weakly convex mesial and distal crown margins. Mesial cusplets and blades are rarely developed, but present on two adult teeth (Figs. 5.1, 6.5C). The cutting edges of almost all teeth are smooth and continuous across the cusp apex and extend basally, on mesial and distal crown margins, for a distance of about two-thirds the crown height. The cutting edges on one large adult tooth (Fig. 6.5) have very irregular pseudoserrations. The lingual face is moderately convex in all teeth, and about 50% of the teeth have coarse, short enameloid ridges near the cusp apex (Figs. 6.4–6.6, 7.1A). The labial crown face is weakly to heavily ornamented, with enameloid folds and short longitudinal ridges, without any consistent placement on the crown face. A narrow lingual neck is present on all teeth and is less well defined labially. The base of



the neck, at its intersection with the root, may be developed into a narrow but distinct trough that may encircle the crown foot. Roots on all teeth are robust, with short to long, rounded to labiolingually tabular, lobes. The basal profile of the root is subangular to convex, and the lingual protuberance is large and strongly convex in most teeth. Some teeth have a central lingual foramen (Figs. 5.2A, 5.3A, 6.6A) and a nutritive groove is usually absent, or short and weakly developed if present (Fig. 5.1A).

The juvenile teeth of *Cetorhinus piersoni* appear to be very similar to those of *C. huddlestoni* (see Welton, 2014:fig. 9b). They possess narrow, distally inclined cusps that taper sharply with a pronounced axial twist (Figs. 6.1, 6.2, 7.2, 7.3). Root lobes are generally well developed and widely separated. Cusps are never horizontal or hook-shaped in mesial or distal view. The cutting edges do not reach the crown foot in most teeth. Mesial and distal blades are not developed, and a small mesial cusplet may be present on some teeth (Fig. 6.2A–C). Crown ornamentation is highly variable labially, and small enameloid ridges near the cusp apex may or may not be present on the lingual face (Figs. 6.1, 6.2). The roots are generally not massive and have well defined root lobes, and the lingual protuberance is moderate to weakly developed. As in the adult teeth, a central lingual foramen is present or absent, and an associated nutritive groove is not developed.

**ABNORMAL TEETH.** Shimada (2002:fig. 3), and Welton (2013a:17, fig. 9) describe abnormal teeth in *Cetorhinus maximus*, including multicusped teeth attributed to tooth splitting, mesodistally compressed teeth occurring as isolated teeth between normal tooth rows, and row reversal. Two anomalous teeth occur in the paratype series of *C. piersoni* (LACM 155804 and 155815, both from LACM locality 4949; Figs. 7.4A–C, 7.5A–C). Both teeth are large and assumed to be from adult individuals. The crown ornamentation and root morphology of LACM 155815 (Fig. 7.5A–C) are well within the range of morphologic variation found in other teeth of *C. piersoni*, while the second tooth (Fig. 7.4A–C) is more problematic, having a massive root without lobes and almost no ornamentation on the labial crown face.

The occurrence of anomalous teeth in a relatively small sample of *Cetorhinus piersoni* ( $n = 44$ ) suggests that this dental attribute was probably well established in *Cetorhinus* by the late Early Miocene and persists to the Recent in *C. maximus*. Interestingly, no multicusped crowns were found in a much larger sample of 369 teeth from the Middle Miocene *C. huddlestoni* (Welton, 2014). Small, laterally compressed teeth, similar to the isolated teeth found between normal tooth rows in *C. maximus* (Welton, 2013a:17, fig. 9) were the only anomalous teeth found in *C. huddlestoni* (Welton, 2014).

## DISCUSSION

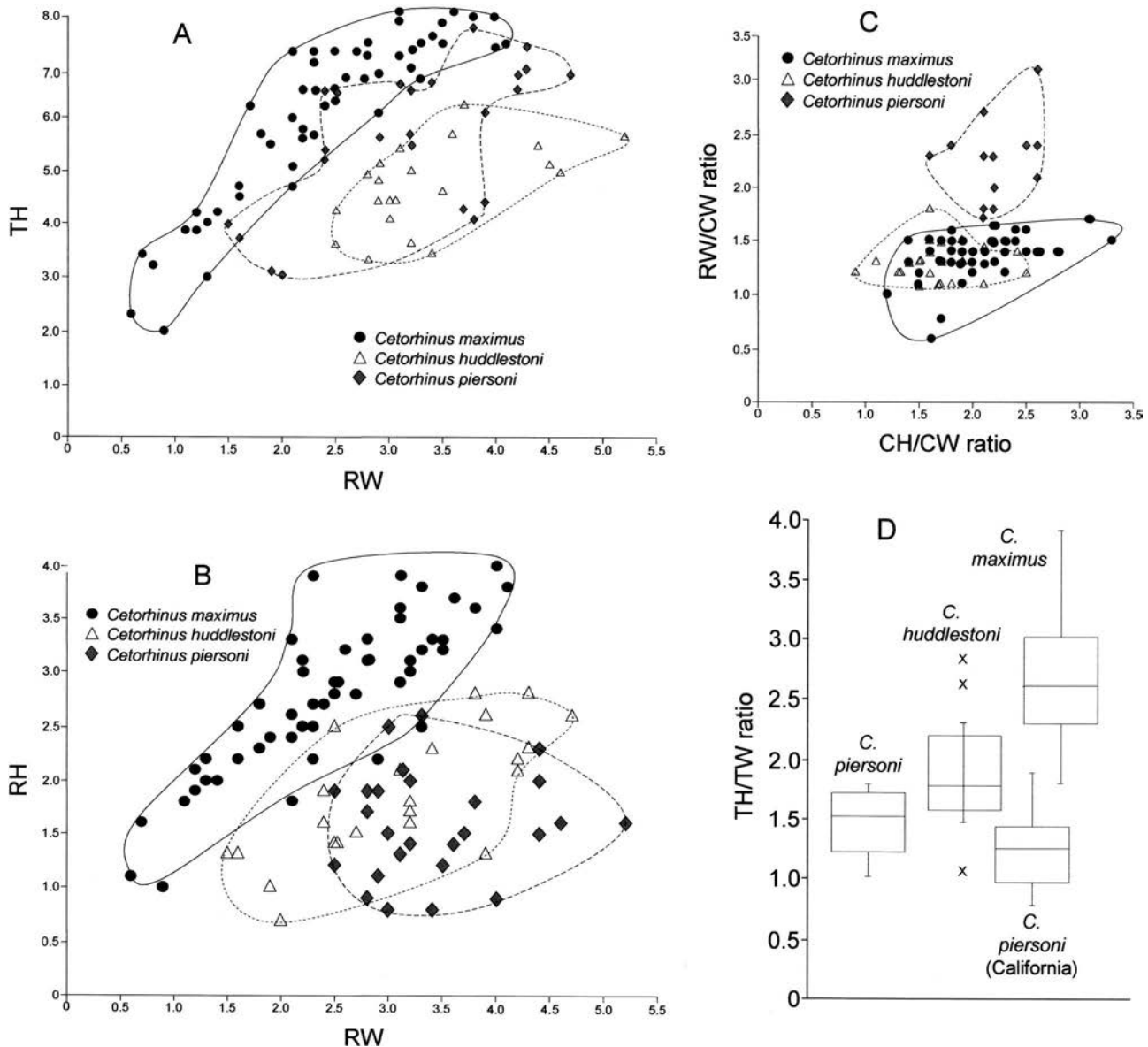
The genus *Cetorhinus* is previously known from two species: the Late Miocene–Recent *C. maximus* and the Middle Miocene *C. huddlestoni* (Welton, 2013a, 2013b, 2014). Based on data presented in Welton (2013a, 2013b, 2014) and new dental measurements for Recent *C. maximus* (Appendix 3) and *C. huddlestoni* (Appendix 2), a series of bivariate scatter plots and box plots (Fig. 11) are used in combination with morphologic attributes of individual teeth to differentiate the two species from *C. piersoni*.

### COMPARISON OF *CETORHINUS PIERSONI* AND *C. MAXIMUS*

The teeth of adult *Cetorhinus piersoni* are smaller than those of adult *C. maximus*. The average TH of *C. piersoni* is 4.7 mm

(range: 3.3–6.5 mm;  $n = 26$ ), and for a 6.0–6.5-m adult (total length) male *C. maximus*, the average TH is 6.3 mm (range: 2.0–8.2 mm;  $n = 52$ ). Cappetta (1987) notes that some teeth approach 1 cm in TH. Figure 11A, B shows cross-plots of tooth height (TH) to root width (RW) and root height (RH) to root width (RW) ratios for *C. maximus* and *C. piersoni* and the substantial difference between the two species. The teeth of *C. piersoni* have lower crowns and wider roots (TH/RW ratio averages 1.4; range: 1.0–1.8;  $n = 21$ ) relative to *C. maximus* (TH/RW ratio averages 2.6; range: 1.8–3.6;  $n = 52$ ), and the roots of *C. piersoni* are shorter and much wider (average RH/RW ratio of 0.5; range: 0.2–0.8;  $n = 26$ ; Appendix 1) than those of *C. maximus* (average RH/RW ratio 1.2; range: 0.8–2.3;  $n = 52$ ). The ratios of RW/RT and RH/RT, show very little overlap between *C. piersoni* and *C. maximus* and generally strong separation due to the much wider roots relative to labiolingual root thickness at the lingual protuberance in *C. piersoni*. The RW/RT ratios for *C. maximus* are strongly clustered, with an average RW/RT ratio of 0.8 (range: 0.4–1.3;  $n = 52$ ), indicative of its globose root morphology, whereas the average RW/RT ratio for *C. piersoni* is 1.4 (range: 0.9–1.8;  $n = 30$ ). The lingual protuberance is large relative to the root height in *C. piersoni* (average RH/RT ratio 0.6; range: 0.3–1.0;  $n = 28$ ), and the RH/RT ratio for *C. maximus* is approximately equal (average RH/RT ratio 0.9; range: 0.9–1.9;  $n = 52$ ), again reflecting the globose nature of the root. The crown base in *C. piersoni* is highly variable but generally does not narrow at the crown foot as in *C. maximus* and is more like *C. huddlestoni*. Exceptions to this can be seen in Figs. 5.3–5.5, where these teeth resemble those of *C. maximus* in this attribute. In other characters, the teeth of *C. piersoni* differ from those of *C. maximus* in having short, weak to strong enameloid ridges on the lingual crown face, especially near the cusp apex, weaker lingual cusp inclination, and less lingual projection of the cusp apex beyond the crown foot. Figure 11C shows a scatter plot of RW/CW ratio and CH/CW ratio, with a substantial difference between *C. maximus* and *C. piersoni*. These data show that roots in *C. piersoni* are significantly wider than the crown when compared with *C. maximus*, but the difference in CH/CW ratios for the two species is similar (average CH/CW ratio for *C. piersoni* is 2.3 (range: 1.7–3.2;  $n = 31$ ); average CH/CW ratio for *C. maximus* is 2.0 (range: 1.2–3.3;  $n = 52$ ). Root lobes are well developed, short, and tabular to rounded and robust in most *C. piersoni* and generally absent or, if present, only weakly developed in *C. maximus* (Welton, 2013a:fig. 7). The basal attachment surface of the root (area between the root lobes in labial or lingual view) is gently to strongly convex (apically) to subangular, whereas, in *C. maximus*, roots are globose, with weak to strongly convex basal attachment surfaces (Welton, 2013a:fig. 2).

Inferred juvenile teeth of *Cetorhinus piersoni* (Figs. 6.1, 6.2) differ strongly from those of *C. maximus* (Welton, 2013a:figs. 4, 5) in having short, broadly triangular and erect crowns and wide, bilobate roots. The crowns are not hook-shaped and are strongly horizontal as in *C. maximus*. The lingual crown face in *C. piersoni* may have enameloid ridges (Fig. 6.1A), and the labial crown foot lacks strongly folded enameloid, a common character in juvenile *C. maximus*. Mesial and distal cutting edges in juvenile *C. maximus* almost always terminate into blades that wrap around the crown, especially mesially, terminating on the labial crown face. In *C. piersoni*, the cutting edges may end well above the crown foot as in adult teeth, or they may merge into blades or cuspletlike prominences near the crown foot (Fig. 6.2A–C). The basal attachment surface in *C. maximus* is wide and flat, whereas in *C. piersoni*, it is narrow and extends mesially and distally on divergent root lobes.



**Figure 11** Comparisons between teeth of extant *Cetorhinus maximus* and teeth of the Middle Miocene *C. huddlestoni* Welton 2014, and *C. piersoni*, new species. Measurement data for all three species in Appendices 1–4. See Figure 3 for dental measurements and abbreviations. **A.** Scatter plot between tooth height (TH) and root width (RW), comparing *C. maximus* (n = 52), *C. huddlestoni* (n = 23), and *C. piersoni*, new species (n = 21). **B.** Scatter plot between root height (RH) and root width (RW), comparing *C. maximus* (n = 52), *C. huddlestoni* (n = 23), and *C. piersoni*, new species (n = 23). **C.** Scatter plot between RW/CW ratio and CH/CW ratio comparing *C. maximus* (n = 52), *C. huddlestoni* (n = 23), and *C. piersoni*, new species, (n = 13). **D.** Box-and-whisker plots of TH/RW ratios for *C. maximus* (n = 52), *C. huddlestoni* (n = 23), *C. piersoni*, new species (n = 23), and teeth referred to *C. piersoni* (California) (n = 22).

#### COMPARISON OF *CETORHINUS PIERSONI* AND *C. HUDDLESTONI*

The teeth of adult *Cetorhinus piersoni* are smaller than those of adult *C. huddlestoni*. The average TH of *C. piersoni* is 4.7 mm (range: 3.3–6.5 mm; n = 26), and the average for *C. huddlestoni* is 5.6 mm (range: 2.9–7.9 mm; n = 23), and Welton (2014) reports one tooth having a TH of 8.4 mm. TH/RW and RH/RW ratios for *C. huddlestoni* and *C. piersoni*, are compared in Fig. 11A, B, and in both plots, the differences between these attributes in *C. piersoni* and *C. huddlestoni* are not as strong as those between *C. piersoni* and *C. maximus*. The teeth of *C. piersoni* have lower crowns and

wider roots (TH/RW ratio averages 1.4; range: 1.1–2.8; n = 23) relative to *C. huddlestoni* (TH/RW ratio averages 1.9; range: 1.8–3.6; n = 52), while the roots of *C. piersoni* have about the same RH/RW ratio (average RH/RW ratio of 0.5; range: 0.2–0.8; n = 26) as those of *C. huddlestoni* (average RH/RW ratio 0.6; range: 0.3–1.03; n = 23). The roots of *C. piersoni* are wider than those of *C. huddlestoni*, and the lingual protuberance in *C. piersoni* is more pronounced than in most teeth of *C. huddlestoni*. The RW/RT ratios for *C. huddlestoni* fall between *C. maximus* and *C. piersoni*, with an average of 1.2 (range: 0.9–2.3; n = 23) whereas the slightly higher average RW/RT ratio for *C. piersoni* is 1.4 (range: 0.9–1.8; n = 30). The lingual protuberance is large relative to the root

height in *C. piersoni* (average RH/RT ratio 0.6; range: 0.3–1.0; n = 28), and the RH/RT ratio for *C. huddlestoni* is almost the same as *C. piersoni* (average 0.7; range: 0.5–1.2; n = 23). The crown base in *C. piersoni* is highly variable but generally does not narrow at the crown foot as in *C. maximus* and is very similar to *C. huddlestoni* in this respect. Exceptions to this can be seen in Figs. 5.3–5.5, where these teeth resemble those of *C. maximus* in this attribute. In other characters, the teeth of *C. piersoni* differ from those of *C. huddlestoni* in having many adult teeth with much broader, triangular crowns (Figs. 4, 5.1, 6.4–6.6), ridges on the lingual crown face (Figs. 5.7A, 6.1A, 6.4A, 6.5A, 6.6A, 7.1A), and a cusp apex which is more broadly rounded, as in *C. maximus*. Lingual crown ridges similar to those in *C. piersoni* are extremely rare in *C. huddlestoni*, but the feature does occur on at least one tooth (see Welton, 2014:fig. 5D). A scatter plot of RW/CW ratio and CH/CW ratio (Fig. 11C) shows a substantial difference between *C. huddlestoni* and *C. piersoni*. The average RW/CW ratio for *C. piersoni* is 2.2 (range: 1.5–3.2; n = 23), and the average is 1.3 (range: 1.1–1.8; n = 23) for *C. huddlestoni*. These data show that roots in *C. piersoni* are significantly wider than the crown when compared with *C. huddlestoni* or *C. maximus*, and crowns in *C. huddlestoni* are a little more robust than in *C. piersoni*, as shown by the CH/CW ratios. The average CH/CW ratio for *C. piersoni* is 2.3 (range: 1.7–3.2; n = 31) and for *C. huddlestoni* it is 1.7 (range: 0.9–2.5; n = 23). Root lobes are well developed, ranging from short and tabular to rounded and robust in most *C. piersoni* and appear to be slightly less developed, or reduced significantly, in some adult teeth of *C. huddlestoni* (Welton, 2013b:fig. 9).

Differences in TH/RW ratios between the three species are clearly shown using box plots (Fig. 11D), in which the interquartile ranges for *Cetorhinus piersoni* and *C. huddlestoni* partly overlap, and there is separation between the two fossil species and *C. maximus*. There is also overlap in the vertical whiskers between all three species, possibly attributed to ontogenetic heterodonty, as well as considerable morphologic variability found in the polyodont dentition of Recent and fossil *Cetorhinus*.

Juvenile teeth of *Cetorhinus piersoni* are rare in the Astoria Formation sample, and their paucity is probably the result of collecting bias. Based on their size and comparison with the reconstructed juvenile dentition of *C. huddlestoni* (Welton, 2014: fig. 9), the teeth illustrated in Figures 6.1A–C, 6.2A–C, 6.3A–C, and 7.3A–C most likely belong to juvenile *C. piersoni*. The labial crown faces of *C. piersoni* generally have many small, moderately strong enameloid ridges, and at least one tooth (Fig. 6.1A) has a few lingual enameloid ridges near the cusp apex, an attribute also found in many adult teeth. The juvenile teeth of *C. huddlestoni* usually have smooth crown faces, or if enameloid ridges are present, they are weak, sparsely distributed, and restricted to the labial crown face.

#### COMPARISON OF *CETORHINUS PIERSONI* WITH REFERRED TEETH FROM THE SOUTHEASTERN SAN JOAQUIN VALLEY, CALIFORNIA

In addition to the types of *Cetorhinus piersoni* from the late Early Miocene Astoria Formation, 22 additional teeth from the lower Round Mountain Silt, California, are available for comparison (Figs. 8–10). Dental measurements for teeth from LACM localities 3385, 4269, and 3163 are listed in Appendix 4. A box plot based on TH/RW ratios for the referred specimens is illustrated in Fig. 11D. The upper interquartile range for the referred teeth from California overlaps with the lower quartile range of the Astoria teeth. Although the whiskers of the California teeth encompass the total range given for the Astoria teeth, the overall lower interquartile range and mean reflect the lower tooth height and greater root width in the California teeth. The ratios of

RH/RW, RW/RT, and RH/RT are close in the Oregon and California teeth. Many of the dental characters cited above for the holotype and paratypes of *C. piersoni* are found in the California teeth, with the following exceptions: the average TH for the referred specimens is 3.7 mm (range: 2.8–4.9 mm; n = 22), smaller than the average 4.7 mm TH for Astoria Formation teeth (range: 3.3–6.5 mm; n = 26); CH/CW ratios average 2.3 (range: 1.7–3.2; n = 31), and 1.3 (range: 0.8–2.2; n = 22) for the type and referred samples, indicating that many of the California specimens have shorter and broader crowns than those of the type series; root width of the type series averages over twice the crown width (RW/CW average 2.2; range: 1.5–3.2; n = 23) relative to the referred teeth (average 1.4; range: 1.1–1.7; n = 20); 30% of the referred teeth have lingual crown ridges, usually near the cusp apex, whereas 50% of the type series have lingual crown ridges (n = 30); a higher percentage of the referred teeth have a mesial cusplet (22%: n = 18) versus 9% (n = 43) in the Astoria Formation sample. Welton (2014) noted that presence of a mesial cusplet in *C. huddlestoni* appears to be an ontogenetic attribute, being more common in teeth from the distal tooth rows in juveniles. The lower frequency of cusplets in the Astoria sample may be a reflection of the bias toward adult teeth, if the observations for *C. huddlestoni* are applicable to *C. piersoni*. Mesial cusplets are less common in adult teeth. The type series includes 34 adult teeth, four juvenile teeth, and five teeth of uncertain ontogenetic stage (e.g., they may represent small teeth from the mesial or distal end of the dental series). The referred teeth from California include 10 adults and eight juveniles, or 44% juveniles versus 21% (with uncertain teeth, or 9% with higher confidence juvenile estimate) for the Astoria type series.

#### COMPARISON OF *CETORHINUS PIERSONI* WITH UNNAMED PUBLISHED AND FIGURED TEETH OF MIOCENE *CETORHINUS*

Purdy et al. (2001:109, fig. 22b–d) identified a tooth from the Early Miocene (Aquitainian) Pungo River Formation, Lee Creek Mine, North Carolina, as *Cetorhinus* sp. As noted by Purdy et al. (2001:109), the recumbent crown of this tooth is very similar to that found in Recent juvenile teeth of *C. maximus*; however, according to the description provided, it also possesses a shallow transverse groove with a central foramen and transverse notch. These morphologies are sometimes present in *Cetorhinus* teeth (Welton, 2013a) but not usually well developed. Unfortunately, the tooth is poorly figured, and the specimen needs to be reevaluated to clearly establish its identity.

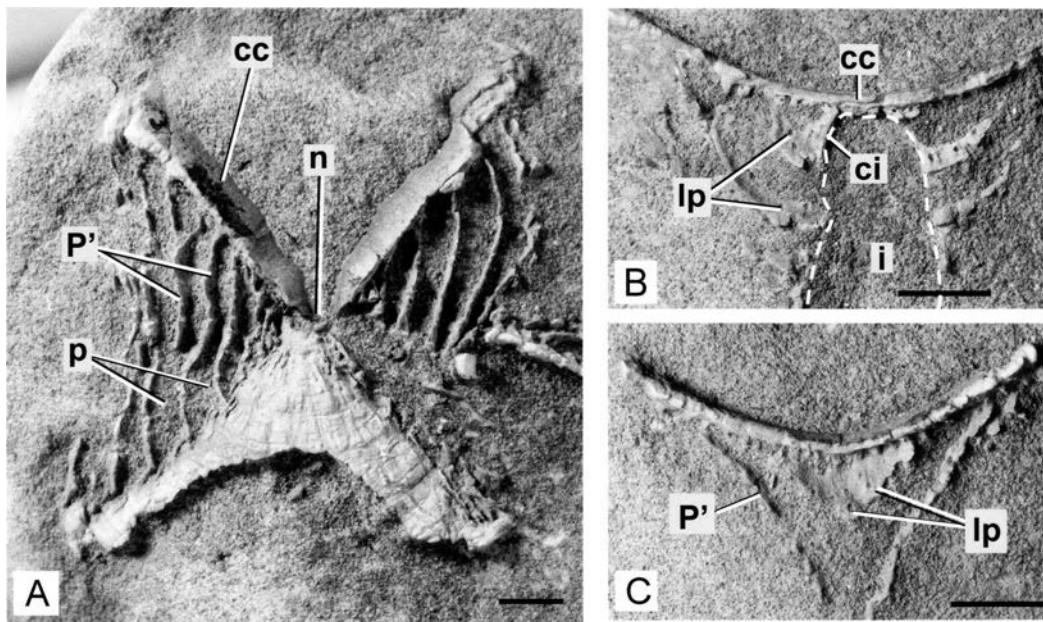
Van Den Bosch (1984:217, fig. 30a, b) illustrates a Middle Miocene tooth of *Cetorhinus* from the Dingdener Schichten at Dingden near Bocholt, Germany. The crown appears to be well preserved with numerous short, longitudinal ridges covering the lower half of the labial face, and the lingual face appears to be smooth (as illustrated in mesial view). The root is incomplete, and details of the root lobes are not preserved. The crown morphology of this tooth resembles *C. huddlestoni* more than *C. piersoni*, in being tall and narrow and in lacking ridges on the lingual crown face. However, these attributes are present on some teeth in both species, and a much larger sample size is needed to characterize the morphology and relationships of the Dingden *Cetorhinus*.

*Cetorhinus* sp.

Figure 12

REFERRED SPECIMEN. LACM 121001, three incomplete, associated vertebrae collected in 1979 by J.L. Goedert and G.H. Goedert.





**Figure 12** Calcified vertebrae of *Cetorhinus* sp. (LACM 121001) from the Astoria Formation (LACM locality 4586, near Altoona, Wahkiakum County, Washington), exposed in weathered relief on the surface of a calcareous sandstone concretion. **A.** Longitudinal section of vertebra exposing well-preserved concentric calcifications surrounding the primary double cone. **B.** Vertebral fragment with a section of the corpus calcareum and an insertion (dashed white line) for one of the arch cartilages. **C.** Vertebral fragment with a section of the corpus calcareum and several calcified lamellae with exposed perforations. Abbreviations: cc, corpus calcareum; ci, calcified wedge face of intermedialia; i, insertion for neural or hemal arch cartilage; lp, lamellar perforation; n, passage of notochord; p, uncalcified cartilaginous part of intermedialia; p', calcified concentric lamellae. Scale bars = 5 mm.

**LOCALITY.** LACM locality 4586, Pigeon Bluff, Altoona, Wahkiakum County, Washington. Specimen collected among cobbles at low tide, at the base of Pigeon Bluff, on the north shore of the Columbia River (J.L. Goedert, personal communication, 2014). This site is close to the type locality of the crabs *Lophomastix altoonaensis* Nyborg and Vega, 2008, and *Anisospinus wahkiakumensis* (Berglund and Goedert, 1992). LACM locality 4586 is approximately equal to UWBM locality B5497 (see Berglund and Goedert, 1992:fig. 1) and fossil sites 1, 43, and 58, as shown on the geologic map of Wolfe and McKee (1972; fig. 4) (J.L. Goedert, personal communication, 2014).

**FORMATION AND AGE.** In southwestern Washington, the Astoria Formation unconformably overlies the Lincoln Creek Formation and is unconformably overlain by the upper Miocene Montesano Formation (Prothero et al., 2001a). As defined by Wolfe and McKee (1972:45–47, fig. 4), Unit II consists of siltstone to fine-grained sandstone composed of quartz, feldspar, and abundant volcanic detritus in a silt and clay matrix. The lithology of the float concretion containing *Cetorhinus* vertebrae (LACM 121001) is a very fine to fine-grained, moderately well sorted sand composed mostly of quartz, with other abundant dark lithic fragments in a sparse silt to clay matrix, with carbonate cement. The lithology of this concretion is consistent with that described for Unit II by Wolfe and McKee (1972), and the specimen was most likely derived from nearby outcrops of the Astoria Formation. Other vertebrate fossils from LACM locality 4586 are undescribed teleost and cetacean bones, including an incomplete odontocete skull (collections of LACM and J.L. Goedert, personal communication, 2014).

Wolfe and McKee (1972) reported Saucian Stage benthic foraminifers from Unit II of the Astoria Formation, and Moore and Addicott (1987) assigned Units II and III in the Grays River Quadrangle, Wahkiakum County (Wolfe and McKee, 1972), to

the Newportian Molluscan Stage of Addicott (1976a). This assignment was based on the presence of the zonal bivalve fossil *Patinopecten propatulus* and other associated mollusks and benthic foraminifers. The Astoria Formation in Washington was interpreted by Prothero et al. (2008a:fig. 4) as being bounded by temporal hiatuses, and largely correlative with the Newportian Molluscan Zone, and ranges from Chrons C6r to C5Cr (20.5–17 Ma), or older than the Newportian in the Newport Embayment (C6n to C5Bn2: 19.2–15.2 Ma). Subsequent analysis of the magnetic stratigraphy of the Lincoln Creek and Astoria formations, east of Knappton, in southwestern Washington (Prothero et al., 2008a), placed the age of the lower Astoria Formation in one of the reversed intervals in Chron C6C: C6C1r, C6C2r, or later reversed intervals (Prothero et al., 2008a:71). This age correlates with the type Pillarian Stage (Addicott, 1976b) in the Clallam Formation, Washington (Prothero and Burns, 2001), and is temporally equivalent to the lower part of the original stratotype for the Astoria Formation at Astoria, Oregon (Addicott, 1976a; Moore and Addicott, 1987; Prothero et al., 2008a) (Fig. 2).

In the absence of additional biostratigraphic data or refined magnetic stratigraphy of the Altoona section of Unit II of the Astoria Formation, the *Cetorhinus* vertebrae from this locality are probably Newportian, and the Altoona section appears coeval with the Astoria Formation of the Newport Embayment (Chrons C6n–C5Bn2: 19.2–15.1 Ma, or C6An2–C5Cn1: 20.7–16.0 Ma; Prothero et al., 2001a).

**DESCRIPTION OF VERTEBRAE.** Three incomplete, associated, disarticulated vertebral centra of a small *Cetorhinus* sp. (LACM 121001) are preserved in a calcareous sandstone concretion (Fig. 12A–C). The vertebrae are exposed in partial relief on the weathered fracture face of the concretion. The counterpart of the concretion, presumably containing the rest of

the centra, was not found by the collectors. There are no associated teeth, gill rakers, placoid scales, or other nonvertebral calcified cartilages preserved in the concretion. Based on similarity in size and calcified vertebral structures, the three vertebrae are assumed to belong to one individual. The largest centrum (Fig. 12A) is about 50% complete and exposed in longitudinal section, cutting the primary double cone at a slight tangent. The other two centra are fragmentary, each with a portion of one primary double cone and fragments of concentric calcified lamellae (Fig. 12B, C). The anteroposterior length of the largest centrum (Fig. 12A) is 49.6 mm, as measured between the anterior and posterior rims of the primary double cone, and the transverse width across the primary double cone is 33.4 mm. The vertebral length/width ratio is 1.5. The two fragmentary centra have incomplete primary double cone widths of 24.9 and 26.1 mm. It is not possible to determine the shape of the centra (e.g., oval or circular) in axial view because of their preservation. The external (axial) face of the corpus calcareum is partly exposed on all three centra, but there is no evidence of growth banding. The most complete, and largest centrum has very deep primary double cones, with a depth of almost 18 mm, and a cone angle of 54 degrees. The arch cartilage insertions are not exposed, and there is no evidence of calcified radiating lamellae within the intermedialia or external to the last calcified lamellae near the margin of the centrum. The smallest fragmentary vertebra has a partially preserved insertion (Fig. 12B), and the wedge faces are calcified. The outer zone cartilage of the intermedialia has between seven and eight complete and fragmentary concentric calcified lamellae in the most complete vertebra (Fig. 12A), and two to three concentric lamellae preserved with each of the small fragmentary vertebrae (Fig. 12B, C). The lamellae are widely spaced, and their walls have numerous, small, sieve-like perforations (Fig. 12B, C), but there is no evidence of radiating calcified tubes passing through or connecting adjacent lamellae.

**DISCUSSION.** Individual precaudal vertebrae of *Cetorhinus* are distinguished from those of all other lamniform sharks by their greater anteroposterior length, presence of numerous concentric calcified lamellae in all intermedialia, absence of radial lamellae extending from the margin of the centrum inward to the primary double cone, and presence of perforated concentric lamella walls (Welton, 2013a). The Astoria Formation vertebrae possess all of the attributes listed above for the Genus *Cetorhinus* and differ from *Keasius* in having longer centra, presence of concentric lamellae in the intermedialia, and absence of radial lamellae extending from the primary double cone outward to the margin of the centrum.

The vertebrae of *Cetorhinus* from southwestern Washington are much smaller than those of the living basking shark, and they have approximately one-half to two-thirds the number of concentric calcifications found in an adult *C. maximus* (see Natanson et al., 2008:fig. 1). In the absence of a much larger fossil sample, it is not possible to determine if these vertebrae are small because they are from a juvenile individual, or if they are from a much smaller species of *Cetorhinus*. The teeth of *C. piersoni* from the Astoria Formation near Newport average about half the size of an adult modern basking shark, although some teeth are >8 mm in TH. Assuming that tooth size correlates with body length, *C. piersoni* may have been close to *C. maximus* in adult length. The Astoria Formation *Cetorhinus* locality in Washington is probably coeval with the type locality of *C. piersoni* from the Newport Embayment (Fig. 2); however, in the absence of associated teeth and the absence of vertebrae referable to *C. piersoni* from the Astoria Formation in Oregon and California, it is not possible to determine if these vertebrae belong to *C. piersoni*. Until more fossils of this late Early Miocene

*Cetorhinus* are discovered, little additional information can be inferred from these vertebrae other than they represent the earliest record of the *Cetorhinus* vertebrae in the eastern North Pacific.

Purdy et al. (2001:109, fig. 22b–d) identified a vertebra from the Early Miocene (Aquitani) Pungo River Formation, Lee Creek Mine, North Carolina, as *Cetorhinus* sp. As previously noted by Welton (2014), the vertebra appears to have a morphology typical of most lamnoids, but not *Cetorhinus*. The vertebrae of Recent *C. maximus* are about as long as they are wide or tall, and the most complete late Early Miocene vertebra from the Astoria Formation (Fig. 12A) has a dorsoventral height/anteroposterior length ratio of 1.5. The vertebra figured by Purdy et al. (2001) has a height/length ratio of 0.4. *Cetorhinus* may have radial calcifications, similar to that figured by Purdy et al. (2001), external to the most distal concentric lamellae; however, in the absence of details of the internal calcifications of this vertebra, its assignment to *Cetorhinus* is tentative.

### TAXONOMY OF CENOZOIC CETORHINIDS

A variety of Cenozoic fossil cetorhinids from the eastern North Pacific are documented in the paleontologic literature (see summaries in Long, 1994; Welton, 2013a, 2013b, 2014, this study), and more as yet undescribed fossil species are now represented in museum collections by articulated or associated skeletons or isolated skeletal elements from the Oligocene and Early Miocene of Washington and California. Description of these fossils should provide new information on the taxonomy, morphology, and phylogenetic relationships of *Keasius* and *Cetorhinus*.

Although several nominal fossil cetorhinids have been described from isolated gill rakers (Van Beneden, 1871; Leriche, 1908), recent studies (Hovestadt and Hovestadt-Euler, 2011; Welton, 2013a) suggest these structures may be of questionable taxonomic value based on significant morphologic and ontogenetic variation along the gill arch and the absence of knowledge on their intraspecific variation in morphology. Isolated vertebrae were used as a basis for describing several nominal fossil species of *Cetorhinus* (Hasse, 1882; Noetling, 1885), the validity of which was questioned by Cappetta (2006). As documented by Welton (2013a), vertebral morphology is very useful in differentiating *Keasius* from *Cetorhinus* (Welton, 2013a, this study) and probably has significant phylogenetic importance as well. However, interspecific differences in vertebral calcification patterns in *Cetorhinus* are insufficiently known at this time, due entirely to the fact that the only two fossil species, *C. piersoni* and *C. buddlestoni*, have no associated vertebrae with which to compare with *C. maximus*. Welton (2013a, 2014, this study) has used associated and isolated teeth for holotypes, providing a basis for directly comparable hard parts between *C. maximus*, *C. buddlestoni*, and *C. piersoni*. Based on these studies, teeth have significantly greater taxonomic value relative to gill rakers or vertebrae, and I recommend that new cetorhinid species be based, at least, on teeth.

The taxonomic diversity of Cenozoic Cetorhinidae is significantly greater than that reflected in the literature, primarily due to the historical practice of referring almost all fossils to either *Cetorhinus parvus* (Leriche, 1908) (Eocene–Early Miocene), *C. maximus* (Miocene–Recent) (Cappetta, 1987), or *Cetorhinus* sp. The taxonomy of Oligocene and younger cetorhinids needs to be reexamined in light of the generic distinction now being made between *Keasius* and *Cetorhinus* (Welton, 2013a). *Cetorhinus* first appears in the late Early Miocene (*C. piersoni*), or possibly the earliest Miocene (Purdy et al., 2001), and is represented in the



Middle Miocene by *C. huddlestoni* (Welton, 2014); *C. maximus* ranges from the Late Miocene to Recent (Long, 1994; Welton, 2013b). *Keasius taylori* Welton, 2013a, which first appears in the Middle Eocene (Cione and Reguero, 1998), is replaced in the Oligocene by *K. parvus* (Leriche, 1908), and the genus is last known from the late Early Miocene of California and possibly the Middle Miocene of Europe (Van Den Bosch, 1984).

#### PALEOECOLOGY OF EARLY AND MIDDLE MIOCENE *CETORHINUS* IN THE EASTERN NORTH PACIFIC

Although cetorhinid gill rakers have not been found in the Astoria Formation of Oregon or Washington, there is no reason to believe that *Cetorhinus piersoni*, like *C. huddlestoni* and all younger *Cetorhinus*, were planktivorous filter feeders. The reconstructed dentition of *C. huddlestoni* has weak gradient monognathic heterodonty, moderate dignathic heterodonty, no disjunct monognathic heterodonty in either jaw, and strong ontogenetic heterodonty (Welton, 2014). Although the small number of teeth available for *C. piersoni* made it unreasonable to reconstruct its dentition, the similarities between it and *C. huddlestoni* would suggest similar heterodonty. Many, but not all, of the teeth of *C. piersoni* differ from *C. huddlestoni* and *C. maximus* in having broad-based, low, triangular crowns and well-developed mesial and distal root lobes. Root lobes are absent in many adult teeth of *C. maximus* and some *C. huddlestoni* (Welton, 2013a, 2014). In some respects, the teeth of *C. piersoni* resemble those of *Alopias Rafinesque*, 1810, and perhaps *C. piersoni* had a wider range in diet than *C. maximus*, feeding on small fishes as well as plankton.

Based on foraminiferal and molluscan data, the water depth of the Astoria Formation near Altoona may have been between 30 and 150 m (Wolfe and McKee 1972); water temperatures were warm (Moore and Addicott, 1987), and associated terrestrial plants suggest a subtropical climate (Berglund and Goedert, 1992). These sediments were deposited within a small Early Miocene embayment (Wolfe and McKee, 1972). The Astoria Formation section north of Yaquina Head, in Lincoln County, Oregon, was deposited in warm, temperate waters on an open coastline at shallow to moderate depths of 10–100 m (Moore, 1963; Colbath, 1985). Teeth of *Cetorhinus piersoni* from California, occurring in warm water, inner to outer shelf siltstones of the lower Round Mountain Silt (Olson, 1990), and the overlying Sharktooth Hill Bonebed with *C. huddlestoni*, was deposited in warm waters during a marine transgression, at possibly outer shelf depths (Pyenson et al., 2009). *Cetorhinus*, but not *Keasius*, is absent from the highly fossiliferous inner shelf sediments of the upper Olcese Sand (Addicott, 1970; Olson, 1988), immediately underlying and interfingering with the base of the Round Mountain Silt. Based on the above data, these Early to Middle Miocene *Cetorhinus* appear to have been warm-water nektopelagic feeders over shallow to deep waters of the continental shelf. One can speculate that the evolution of cetorhinids is associated with exploitation of zones of high marine productivity in areas of coastal and offshore upwelling.

#### CONCLUSIONS

1. *Cetorhinus piersoni* is a new cetorhinid shark known by isolated teeth from late Early Miocene (16.0–17.3 Ma) marine deposits of the Astoria Formation near Newport, Oregon. Teeth referred to *C. piersoni* also occur in coeval marine sediments of the lower Round Mountain Silt, in California's southeastern San Joaquin Valley, Kern County, California. Sufficient numbers of teeth are available to

- confidently differentiate *C. piersoni* from the extant *C. maximus* and the Middle Miocene *C. huddlestoni*.
2. The fossil record of *Cetorhinus* is relatively well documented for the eastern North Pacific, where teeth of *C. piersoni* occur in the late Early Miocene of Oregon and California; vertebrae of *Cetorhinus* sp. are found in equivalent age rocks of southwestern Washington, and teeth of *C. huddlestoni* are abundant in the Middle Miocene, Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California. *Cetorhinus maximus* is reported from the Late Miocene through Pleistocene of Oregon and California.
3. Prior to 2013, all fossil basking sharks were referred to the genus *Cetorhinus*, usually based on isolated gill rakers and, less commonly, teeth or vertebrae. With the recent description of a second, and extinct, cetorhinid, *Keasius*, most Oligocene *Cetorhinus* are now referable to *Keasius* (*K. parvus*), and other Oligocene and Miocene reports of *Cetorhinus* (e.g., *C. parvus*, *C. maximus*, and *Cetorhinus* sp.) have uncertain taxonomic status pending reevaluation based, at least, on their dentition. This study documents the contemporaneous occurrence of *Cetorhinus* and *Keasius* in the late Early Miocene of California, and these genera probably coexist in the Miocene of Europe. The genus *Cetorhinus* ranges from the late Early Miocene, and possibly the earliest Miocene (Purdy et al., 2001) to Recent.
4. The depositional environments represented by the Astoria Formation in Washington and Oregon and the Round Mountain Silt in California indicate these Miocene *Cetorhinus* were warm-water nektopelagic feeders over both deep and shallow waters of the continental shelf. *Cetorhinus piersoni* may have had a wider range in diet than *C. maximus*, feeding on small fishes as well as plankton.

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## APPENDIXES

**Appendix 1** Tooth measurements (mm) and other dental characteristics of the holotype (\*) and paratype specimens of *Cetorhinus piersoni*, new species (“+” indicates measurement incomplete due to broken or worn tooth). Abbreviations: nMC, number of mesial cusplets; nDC, number of distal cusplets (see Fig. 3 for an explanation of other dental variables).

LACM specimen	LACM locality	Figure	TH	TW	RW	CH	CW	RH	RT	RL	CT	nMC	nDC
155772	4850		4.3	2.5	2.5	3.1	1.4	1.2	2.0			0	0
155773	4850	7.3	4.6	3.5	3.5	3.4	1.5	1.2	2.5			0	0
155774	4850		5.7	3.6	3.6	4.3	1.7	1.4	2.2			0	0
155776	4850		3.6			2.4		1.2					0
155777	4850		4.1+	4.0	4.0	3.2	1.2	0.9	2.8			0	0
155778	4850		3.4	3.4	3.4	2.6	1.2	0.8	2.1			1	0
155797	4949		4.8+			3.8	1.7	1.1+				0	0
155798	4949	6.1	3.7	3.2	3.2	2.3	1.4	1.4	1.9	2.7	1.5	0	0
155799	4949	6.3	4.4	2.9	2.9	3.2	1.2	1.1	2.2	2.9	2.0	0	0
155800	4949		3.7+				1.5		2.2			0	0
155801	4949					1.6						0	0
155802	4949					4.5	1.4					0	0
155803	4949	6.4	5.0	4.6	4.6	3.4	1.9	1.6	2.5	3.5	2.3	0	0
155804	4949	7.4	5.0	3.2	3.2	3.8	1.8	2.0	2.0			0	0
155805	4949		3.6	2.5	2.5	2.7	1.2	0.9	1.9			0	0
155806	4949	6.2	3.3	2.8	2.8	2.6	1.2	0.7	1.8	1.9	1.3	1	0
155807	4949		3.7+	3.0+	3.0+	2.8+	1.2	0.9+	1.6+			0	0
155808	4949	6.6	5.7	3.3+	3.3+	4.6	1.8	1.1	2.7			0	0
155809	4949		5.1	2.8	2.8	3.2	1.5	1.9	2.2			0	0
155810	4949		4.8+			4.6	2.0	0.2+	2.8			0	0
155811	4949	6.5	6.5	4.4	4.4	4.6	1.8	2.0	2.8	3.3	2.0	0	0
155812	4949	7.1	5.8+	4.0+	4.0+	3.2		2.3+	2.5			0	0
155814	4949		6.2+	4.4	4.4	3.9+	1.8	2.3	3.0			0	0
155815	4949	7.5	6.2	3.7	3.7	4.7	1.5	1.5	2.9			0	0
155816	4949	7.2	4.4	3.0	3.0	3.1	1.2	1.5	2.2			0	0
155779	5017		3.4	2.4+	2.4+	2.6	1.2	0.9	1.5+			0	0
155780	5017		4.2	*	*	2.7	1.2	1.5	2.0			0	0
155781	5017		2.5+	2.0	2.0	1.8	1.0	0.8+	1.3			0	0
155782	5017					2.3	1.5					1	0
155783	5017		2.3+	1.8	1.8	1.6+	0.8	0.7+	1.6			0	0
155784	5017		3.0+	1.9+	1.9+	2.2	1.2		1.6			0	0
155791	5017		5.2+	3.4	3.4	3.6+	1.8	1.5+	2.2			0	0
155785	7885	5.4	5.4	3.1	3.1	4.8	1.5	1.3	2.5	2.9	2.0	0	0
155786	7885	5.5	5.9+	3.0	3.0	3.4+	1.8	2.5	2.8	3.3	1.9	0	0
155787	7885		4.1	3.0	3.0	3.3	1.2	0.8	2.4			0	0
155788	7885		4.9	2.8	2.8	4.0	1.9	0.9	3.2			0	0
155789	7885		4.7+	3.1	3.1	2.9+	1.8	2.1	2.8			0	0
155790	7885		4.6	2.2+	2.2+	2.9	1.5	1.6				0	0
156958	7886	5.7	4.8	2.9	2.9	3.0	1.2	1.9	2.0	2.5	1.7	0	0
*155792	7886	4	5.7	5.2	5.2	4.1	2.3	1.6	3.2	3.6	2.1	0	0
155793	7886	5.2		3.8	3.8		1.8	1.8	2.6			0	0
155794	7886	5.3		3.3	3.3		2.2	2.6	3.0			0	0
155795	7886	5.6	4.5	3.0	3.0	3.1	1.7		2.3	2.7	1.9	0	0
155796	7886	5.1	5.5	4.4	4.4	4.0	1.7	1.5	3.0	3.1	2.2	1	0



**Appendix 2** Tooth measurements (mm) and other dental characteristics of the holotype (\*) and paratype specimens of *Cetorhinus huddlestoni* Welton, 2014, taken from illustrations in Welton (2014:figs. 3–5). Abbreviations: nMC, number of mesial cusplets; nDC, number of distal cusplets (see Fig. 3 for an explanation of other dental variables).

LACM specimen	Jaw	Figure	TH	TW	RW	CH	CW	RH	RT	RL	CT	nMC	nDC
155727	Upper	4A	3.1	1.9	1.9	2.1	1.3	1.0	1.8	2.3	1.8	0	0
155728	Upper	4B	5.7	2.5	2.5	4.3	1.8	1.4	2.8	3.3	2.2	0	0
155729	Upper	4C	6.5	2.5	2.5	4.0	2.4	2.5	2.8	3.9	2.1	0	0
155730	Upper	4D	6.7	3.1	3.1	4.6	2.4	2.1	2.9	3.8	2.0	0	0
155731	Upper	4E	6.8	3.4	3.4	4.4	2.3	2.3	2.8	3.6	2.0	0	0
155732	Upper	4F	6.6	3.2	3.2	4.9	2.3	1.7	2.9	4.0	2.1	0	0
155733	Upper	4G	6.6	2.4	2.4	5.0	2.0	1.6	2.7	3.3	1.8	0	0
155734	Upper	4H	5.2	2.4	2.4	3.3	1.9	1.9	2.5	3.1	2.0	0	0
155735	Upper	4I	3.0	2.0	2.0	2.3	1.6	0.7	1.4	1.5	1.2	0	0
155736	Lower	5A	4.1	1.5	1.5	2.8	1.3	1.3	1.1	2.2	1.4	0	0
155737	Lower	5B	5.4	2.4	2.4	4.0	2.2	1.4	2.5	3.3	2.1	0	0
155738	Lower	5C	5.5	3.2	3.2	3.6	2.3	1.8	2.8	3.6	2.1	0	0
155739	Lower	5D	7.0	4.7	4.7	4.4	2.7	2.6	3.1	3.7	1.9	0	0
155740	Lower	5E	7.1	4.3	4.3	4.9	2.9	2.3	2.8	4.1	2.1	0	0
155741	Lower	5F	7.0	4.2	4.2	4.8	3.2	2.2	2.5	4.0	2.0	0	0
*155726	Lower	3, 5G	4.3	2.7	2.7	2.8	2.1	1.5	1.9	2.6	1.5	0	0
155742	Lower	5H	6.7	4.2	4.2	4.6	3.5	2.1	3.1	4.0	2.4	1	0
155743	Lower	5I	7.9	3.8	3.8	5.0	3.4	2.8	3.6	5.4	2.6	0	0
155744	Lower	5J	7.5	4.3	4.3	4.7	3.6	2.8	3.4	4.3	2.0	1	0
155745	Lower	5K	6.1	3.9	3.9	3.5	3.1	2.6	2.9	3.8	1.8	1	0
155746	Lower	5L	5.7	3.2	3.2	4.1	2.6	1.6	2.8	3.8	1.8	0	0
155747	Lower	5M	4.4	3.9	3.9	3.1	3.4	1.3	1.7	2.8	1.3	0	0
155748	Lower	5N	3.7	1.6	1.6	2.4	1.4	1.3	1.8	2.4	1.2	0	0

**Appendix 3** Tooth measurements (mm) and other dental characteristics of *Cetorhinus maximus*, taken from the upper right and lower left jaws of LACM 33876-1 (adult male, 6.0–6.7 m total length, collected off Morro Bay, San Luis Obispo, California, 30 June 1976). Abbreviations: nMC, number of mesial cusplets; nDC, number of distal cusplets (see Fig. 3 for an explanation of other dental variables).

Jaw	Row no.	TH	TW	RW	CH	CW	RH	RT	RL	CT	nMC	nDC
Upper right	1	3.4	1.8	0.7	1.8	1.2	1.6	0.9	1.3	1.2	0	0
Upper right	2	2.3	0.6	0.6	1.1	0.7	1.1	1.5	1.8	1.2	0	0
Upper right	3	3.9	1.5	1.1	2.0	0.9	1.8	1.8	2.7	1.7	0	0
Upper right	4	4.0	1.7	1.3	1.9	0.9	2.0	1.8	2.9	1.5	0	0
Upper right	6	4.2	1.6	1.2	2.1	1.1	2.1	2.1	3.2	1.9	0	0
Upper right	8	4.2	1.7	1.4	2.2	1.0	2.0	2.1	2.8	1.8	0	0
Upper right	10	3.9	1.6	1.2	2.1	1.0	1.9	1.8	2.5	1.4	0	0
Upper right	12	4.5	1.6	1.6	2.3	1.1	2.2	2.1	3.1	1.5	0	0
Upper right	14	4.7	2.1	2.1	2.9	1.3	1.8	2.4	3.3	1.4	0	0
Upper right	16	4.8	1.6	1.6	2.3	1.2	2.5	1.9	3.3	1.5	0	0
Upper right	18	5.5	1.9	1.9	3.0	1.3	2.4	2.5	3.7	1.8	0	0
Upper right	20	5.1	2.1	2.1	2.7	1.5	2.4	2.5	3.1	1.7	0	0
Upper right	22	5.8	2.2	2.2	3.3	1.6	2.5	2.5	3.6	1.8	0	0
Upper right	24	5.7	2.3	2.3	3.2	1.5	2.5	2.7	3.4	2.1	0	0
Upper right	26	5.8	2.2	2.2	2.9	1.7	3.0	3.1	4.0	2.1	0	0
Upper right	28	6.3	2.5	2.5	3.5	1.8	2.8	2.9	3.3	2.1	0	0
Upper right	30	6.0	2.1	2.1	3.4	1.6	2.6	2.9	3.4	2.1	0	0
Upper right	32	6.5	2.2	2.2	3.4	1.4	3.1	3.2	3.3	2.2	0	0
Upper right	35	7.2	2.3	2.3	4.5	1.6	2.7	3.1	3.9	1.9	0	0
Upper right	36	7.0	2.9	2.9	4.0	2.7	3.1	3.2	3.6	1.7	0	0
Upper right	40	7.5	3.2	3.2	4.5	2.3	3.0	3.5	4.1	1.9	0	0
Upper right	42	7.4	2.7	2.7	4.7	1.9	2.8	3.5	4.4	2.2	0	0
Upper right	44	7.6	3.3	3.3	4.4	2.3	3.2	3.9	4.0	1.9	0	0
Upper right	46	6.9	2.6	2.6	3.6	1.9	3.3	3.6	3.4	1.9	0	0
Upper right	48	5.7	2.0	1.8	3.0	1.2	2.7	2.9	3.8	2.4	0	0
Upper right	50	7.6	3.5	3.5	4.4	2.4	3.2	3.4	4.2	2.1	0	0
Upper right	52	7.1	3.2	3.2	4.0	3.3	3.1	3.7	3.4	2.2	0	0
Upper right	54	8.1	4.0	4.0	4.2	3.0	4.0	4.1	4.9	2.2	0	0
Upper right	56	7.5	2.8	2.8	4.4	1.8	3.1	3.7	4.2	2.3	0	0
Upper right	58	7.3	3.1	3.1	3.4	2.1	3.9	3.8	4.2	2.1	0	0
Upper right	60	7.7	3.4	3.4	4.4	2.5	3.3	4.0	4.7	2.1	0	0
Upper right	62	8.0	3.5	3.5	4.7	2.5	3.3	3.9	4.0	1.9	0	0
Upper right	67	7.5	4.0	4.0	4.1	2.6	3.4	3.8	4.4	2.2	0	0
Upper right	70	8.2	3.1	3.1	4.7	2.1	3.5	4.1	5.1	2.3	0	0
Upper right	85	7.4	2.5	2.5	4.4	1.4	2.9	3.4	4.5	1.9	0	0
Upper right	87	7.3	2.8	2.8	4.0	2.0	3.3	3.3	4.7	1.9	0	0
Upper right	89	8.2	3.6	3.6	4.4	2.5	3.7	3.8	4.9	2.1	0	0
Upper right	92	7.6	2.8	2.8	4.5	1.9	3.1	3.4	3.7	2.1	0	0
Upper right	102	6.7	2.5	2.5	3.8	1.8	2.9	3.2	3.6	1.7	0	0
Upper right	112	6.2	1.7	1.7	3.8	1.2	2.3	2.6	2.9	1.9	0	0
Upper right	116	6.6	2.3	2.3	4.3	1.6	2.3	2.7	3.5	1.9	0	0
Upper right	117	6.1	2.9	2.9	3.9	1.8	2.2	2.3	2.9	1.2	0	0
Lower left	1	2.0	0.9	0.9	1.0	0.6	1.0	1.1	1.3	1.0	0	0
Lower left	14	6.9	3.3	3.3	4.4	2.3	2.5	3.4	3.5	2.1	0	0
Lower left	28	7.5	3.3	3.3	3.6	2.2	3.8	3.8	4.0	2.2	0	0
Lower left	50	8.1	3.8	3.8	4.5	2.5	3.6	4.4	4.0	1.9	0	0
Lower left	59	7.5	4.1	4.1	3.9	2.8	3.8	3.9	4.3	1.9	0	0
Lower left	79	8.0	3.1	3.1	4.4	2.4	3.6	4.3	4.1	2.3	0	0
Lower left	98	7.4	2.3	2.3	3.5	1.8	3.9	3.7	4.7	1.9	0	0
Lower left	117	7.4	2.2	2.1	4.1	1.5	3.3	3.3	4.8	1.7	0	0
Lower left	125	6.2	2.4	2.4	3.5	1.9	2.7	3.4	3.8	1.7	0	0
Lower left	126	3.9	1.4	1.3	1.6	1.1	2.2	2.6	2.9	2.2	0	0

**Appendix 4** Tooth measurements (mm) and other dental characteristics of referred specimens of *Cetorhinus piersoni*, new species, from the lower Round Mountain Silt, southeastern San Joaquin Valley, Kern County, California (“+” indicates measurement incomplete due to broken or worn tooth). Abbreviations: nMC, number of mesial cusplets; nDC, number of distal cusplets (see Fig. 3 for an explanation of other dental variables).

LACM specimen	LACM locality	Figure	TH	TW	RW	CH	CW	RH	RT	RL	CT	nMC	nDC
156980	4269	9.2	4.7	3.4	3.4	3.7	2.7	1.1	2.4	3.3	2.4	0	0
156974	4269	9.3	3.7	2.8	2.8	2.8	2.1	0.9	1.5	2.2	1.1	1	0
156977	4269		3.7	3.3	3.3	2.7	2.2	0.9	1.9	2.3	1.4	0	0
156975	4269	9.4	3.5	2.2	2.2	2.1	1.4	0.7	1.7	2.1	1.1	0	0
156976	4269	9.5	3.6	3.9	3.9	3.0	3.1	0.5	2.2	2.5	1.2	1	0
156978	4269		3.1	3.8+	3.8+	2.3	2.9	0.8	1.7	2.1	1.8	0	0
156979	4269		3.5	3.2	3.2	2.9	2.7	0.6	0.9	1.9	1.2	0	0
156973	4269	9.1	3.6+	3.6+	3.6+	2.7	3.3	0.9+	1.9+	2.2+	1.2	1	0
156966	3163	10.1	4.7	5.2	5.2	3.5	3.2	1.2	2.4	3.7	1.4	0	0
156967	3163	10.3	4.7	3.1	3.1	3.7	2.7	0.9	2.2	3.3	1.5	1	0
156968	3163	10.7	4.0	2.4	2.4	3.1	1.9	0.9	1.7	2.4	1.2	0	0
156969	3163	10.2	4.7	2.4	2.4	3.1	1.4	1.5	2.6	3.6	1.7	0	0
156970	3163	10.4	3.6+	4.0	4.0	2.7	2.9	0.9	1.9	2.4	1.4	0	0
156971	3163	10.5	2.9	2.4	2.4	2.3	2.1	0.6+	1.2	2.3	0.7	0	0
156972	3163	10.6	4.0	4.0	4.0	2.8	2.6	1.2	1.8	3.1	1.5	0	0
156959	3385	8.3	4.9	3.6	3.6	3.6	3.1	1.2	1.9	3.1	1.4	0	0
156960	3385	8.7	2.8	1.9	1.9	2.0	1.2	0.9	1.2	1.9	0.9	0	0
156961	3385	8.5	4.4	3.8	3.8	3.5	3.1	0.9	2.1	2.4	1.2	1	0
156962	3385	8.2	3.6	3.3	3.3	3.2	2.4	0.5	1.8	2.1	0.9	0	0
156963	3385	8.6	3.7	2.7	2.7	3.0	1.8	0.7	1.4	2.3	1.1	0	0
156964	3385	8.4	3.3	2.4	2.4	2.4	1.8	0.9	1.2	1.8	1.5	0	0
156965	3385	8.1	3.7	3.3	3.3	2.8	2.6	0.9	1.8	1.5	1.1	0	0