

# Unique Feeding Morphology in a New Prognathous Extinct Porpoise from the Pliocene of California

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## Summary

Modern porpoises (Odontoceti: Phocoenidae) are some of the smallest cetaceans and usually feed near the seafloor on small fish and cephalopods [1–3]. Within both extinct and extant phocoenids, no evidence for specialized mandibular morphology has been documented [4–7]. Here we describe a new species of extinct porpoise, *Semirostrum ceruttii*, from the marine Pliocene San Diego (4.2–1.6 Ma), and Purisima (5–2.5 Ma) formations of California. The mandibles comprise a long, fused, and nearly edentulous prognathous symphysis, extending farther beyond the rostrum than in any known mammal. Phylogenetic analyses based on morphology reconstruct *Semirostrum ceruttii* as sister to extant (crown) porpoise species with moderate support. We describe the spectacularly preserved holotype specimen based on computed tomography (CT) scans, which allowed visualization of the elongate mental and accessory canals within the symphysis. The elongate canals are similar to those found in *Rynchops* birds [8] and were likely involved in sensory function. Oblique labial wear facets present on numerous small conical mandibular teeth posterior to the symphysis suggest regular contact with benthic substrate. The unique mandibular and dental characteristics, along with robust scapulae, sternum, and unfused cervical vertebrae, support the interpretation that this species employed a form of benthic skim feeding by using its mandible to probe for and obtain prey.

## Results

### Description

Order Cetacea.  
Suborder Odontoceti.  
Family Phocoenidae.  
*Semirostrum ceruttii*.

### Etymology

From “semi,” half, and “rostrum” (Latin), in allusion to the distinctly shortened rostrum relative to the mandible. The

specific epithet *ceruttii* honors Richard A. Cerutti, who collected the holotype and the majority of the San Diego Formation referred specimens.

### Holotype

San Diego Natural History Museum (SDSNH) 65276, collected by Richard A. Cerutti, September 20, 1990 (Figure 1; see also Figures S1–S3, Movie S1, and Supplemental Experimental Procedures I online; for referred specimens from the San Diego and Purisima formations, see Supplemental Experimental Procedures II).

### Horizon

Member 4 of the San Diego Formation, about 3.1–2.6 Ma (Ma); Piacenzian.

### Diagnosis

Stem phocoenid (Figure S4; Supplemental Experimental Procedures I and II) defined by three autapomorphies: prognathous, fused, mostly edentulous mandibular symphysis (greater than or equal to 40% of the length of complete mandible); lingually positioned cylindrical teeth with apex of crown dorsolabially directed; and deltoid shape of posterior process of the periotic (Figure 1E).

The fused, mostly edentulous mandibular symphysis is ~40% the length of the mandible, extending ~18 cm beyond the end of the rostrum in the holotype and SDSNH 23194 (Supplemental Experimental Procedures I). In lateral profile, the mandibular ramus slims dorsoventrally before widening rostrally into the mandibular symphysis (Figures 1B, 2A, 2B, 2D, and S1K); in dorsal view, the mandibular symphysis is transversely compressed (Figures 1B, 2C, 2E, and S1L), similar to that observed in *Rynchops* birds [8]. Dorsal and ventral mental canals appear elongate on the external surface of the mandibles (Figures 1B, 3A, and 3E). Accessory canals, extensions of the mental canal, and possible alveolar canals are present along the symphysis, unlike in extant porpoises, which have two main branches of the mental canal (Figures 3B–3E).

Two alveoli, the right retaining a small, extremely procumbent tooth with a conical crown, are present at the anterior tip of the mandible (Figures S1I and S1J). This is unlike the crowns of mesial teeth in living phocoenids, which are all labiolingually flattened in the apical half of the crown height and vertically oriented. In the holotype mandible (SDSNH 65276) and referred partial mandible SDSNH 24710, the larger, cylindrical teeth posterior to the symphysis have well-developed apical wear facets, making crown morphology difficult to distinguish (Figures 3F and S1D; Supplemental Experimental Procedures II and III). The posterior mandibular teeth are dorsolabially oriented, with their roots supported by the thick lingual bony ridge of the mandible, as seen in the other mandibles of this taxon that lack teeth (e.g., SDSNH 24710). Four left maxillary teeth are preserved posteriorly in the holotype, with short, conical, and well-worn crowns (Figure S1M; Movie S1). The robust mandibular condyle and correspondingly deep glenoid fossa of the squamosal (Figures 1B and S1A) indicate deeper articulation of the mandible with the skull in the fossil specimens compared with other phocoenids. Deeper dorsal condyloid fossae, related to movement of the atlas, than found in extant porpoises or dolphins are present (Figure 1D). The atlas and axis are unfused, and the atlas is rostrocaudally thick

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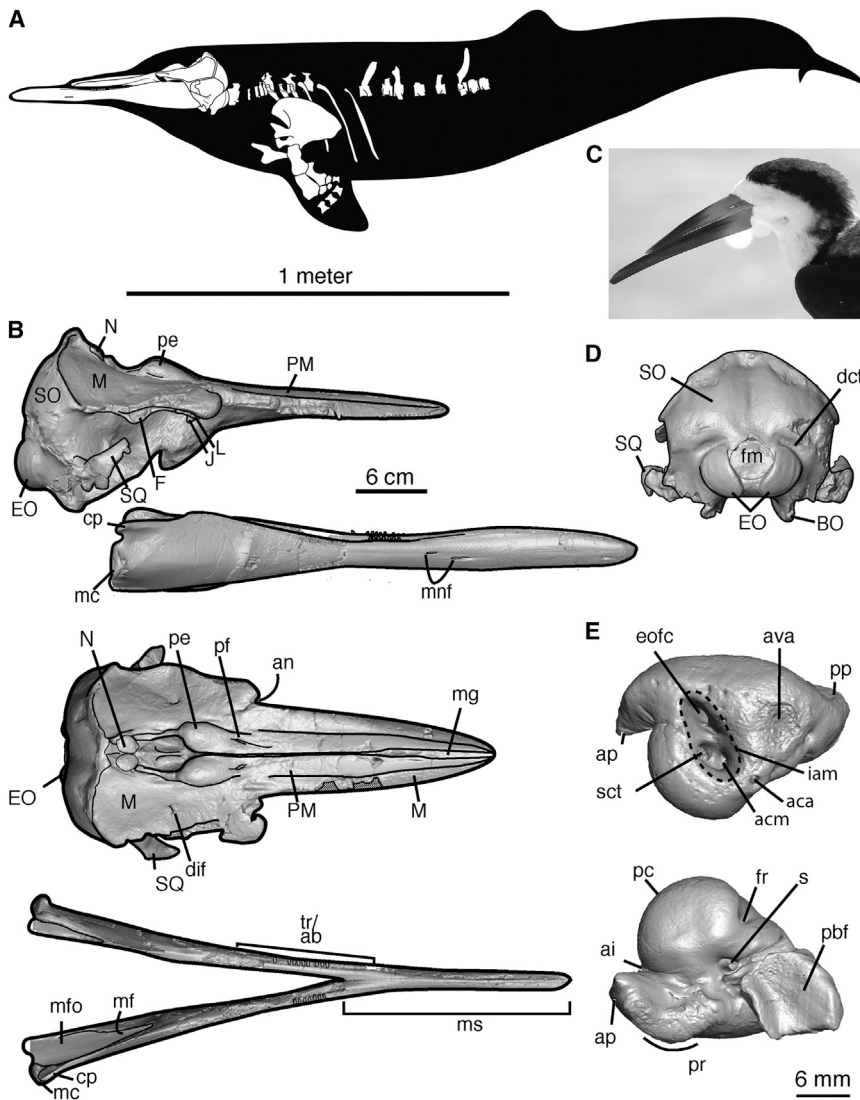


Figure 1. Skull, Mandible, Periotic, and Postcranial Morphology of *Semirostrum ceruttii* Holotype Specimen SDSNH 65276

(A) Schematic reconstruction based on composite postcrania and skull material.

(B) Labeled outlined 3D isosurface reconstructions based on CT scans. From top to bottom: right lateral view of skull, right lateral view of mandible, dorsal view of skull, dorsal view of mandible.

(C) Left lateral view of black skimmer bird *Rynchops niger* with analogous mandibular morphology. (Photo by Don Faulkner, Wikimedia Commons; image cropped and converted to grayscale.)

(D) Labeled 3D isosurface reconstruction of holotype skull in posterior view.

(E) Labeled 3D isosurface reconstructions of right periotic based on CT scans in dorsal (top) and ventral (bottom) views.

Abbreviations: aca, aperture for cochlear aqueduct; acm, area cribrosa media; ai, anterior incisure; an, antorbital notch; ap, anterior process; ava, aperture for vestibular aqueduct, endolymphatic duct partly obscured; BO, basioccipital; cp, coronoid process; dcf, dorsal condyloid fossa; dif, dorsal infraorbital foramen; EO, exoccipital; eofc, endocranial opening of the facial canal; F, frontal; fm, foramen magnum; fr, fenestra rotunda; iam, internal acoustic meatus; J, jugal; L, lacrimal; M, maxilla; mc, mandibular condyle; mf, mandibular foramen; mfo, mandibular fossa (acoustic window); mnf, mental foramina; mg, mesorostral groove; ms, mandibular symphysis; N, nasal; pbf, posterior bullar facet; pc, pars cochlearis; pe, premaxillary eminence; pf, premaxillary foramen; PM, premaxilla; pp, posterior process; pr, peribullary ridge; S, stapes; sct, spiral cribriform tract; SO, supraoccipital; SQ, squamosal; V, vomer. Scale bars represent 6 cm for images of whole skull and 6 mm for periotics. See also Figures S1 and S2.

(Figure S3F), similar to river dolphins (*Inia*, *Pontoporia*, and *Lipotes*) and monodontids (beluga, *Delphinapterus leucas*, and narwhal, *Monodon monoceros*). The sternum is robust and relatively large (85 mm transverse width; Figure S3C; Supplemental Experimental Procedures I) in comparison with extant porpoises, and the scapula and forelimb material are also relatively large and possess more distinct muscle attachment sites at the acromion and coracoid processes, comparable to those of river dolphins (Figures 1A and S3B; Supplemental Experimental Procedures I and II).

Additional fossil material of *Semirostrum* from the Purisima Formation includes a skull (University of California Museum of Paleontology [UCMP] 219503), partial rostrum (UCMP 219483), isolated periotics (UCMP 137472 and 219484), and mandibles (UCMP 219076) previously identified as an unidentified phocoenid [9]. Of these specimens, the referred mandibles and periotics are of similar geologic age (4.5–2.5 Ma) to the specimens from the San Diego Formation and are morphologically similar. The Purisima Formation skull (UCMP 219503), however, differs from that of the holotype by exhibiting a minor degree of cranial asymmetry, which, in concert with the somewhat older geologic age of this specimen and the partial

rostrum (5.33–3.5 Ma), suggests that these specimens may represent an older, still-unidentified species of

*Semirostrum*. Previously listed specimens [10, 11] referable to *Semirostrum* include two isolated periotics (UCMP 88582 and 88583) from the lower Pliocene portion of the San Diego Formation (Figures S1E and S1F).

### Phylogenetic Results

A phenotype-based phylogenetic analysis was conducted to examine hypotheses for the relationship of *Semirostrum ceruttii* among delphinoids. The strict 50% majority rule consensus of all trees reconstructed *Semirostrum ceruttii* as sister to crown phocoenids with moderate support (52% bootstrap; Figure S4; Supplemental Experimental Procedures II). Crown Phocoenidae (containing only extant taxa) was resolved with strong support (90% bootstrap), while the remaining extinct porpoise species were not reconstructed in resolved positions.

### Discussion

The completeness of the holotype specimen and referred material may explain the moderate support for the position of *Semirostrum ceruttii* as sister to extant porpoises. Low support values for the positions of extinct species represented

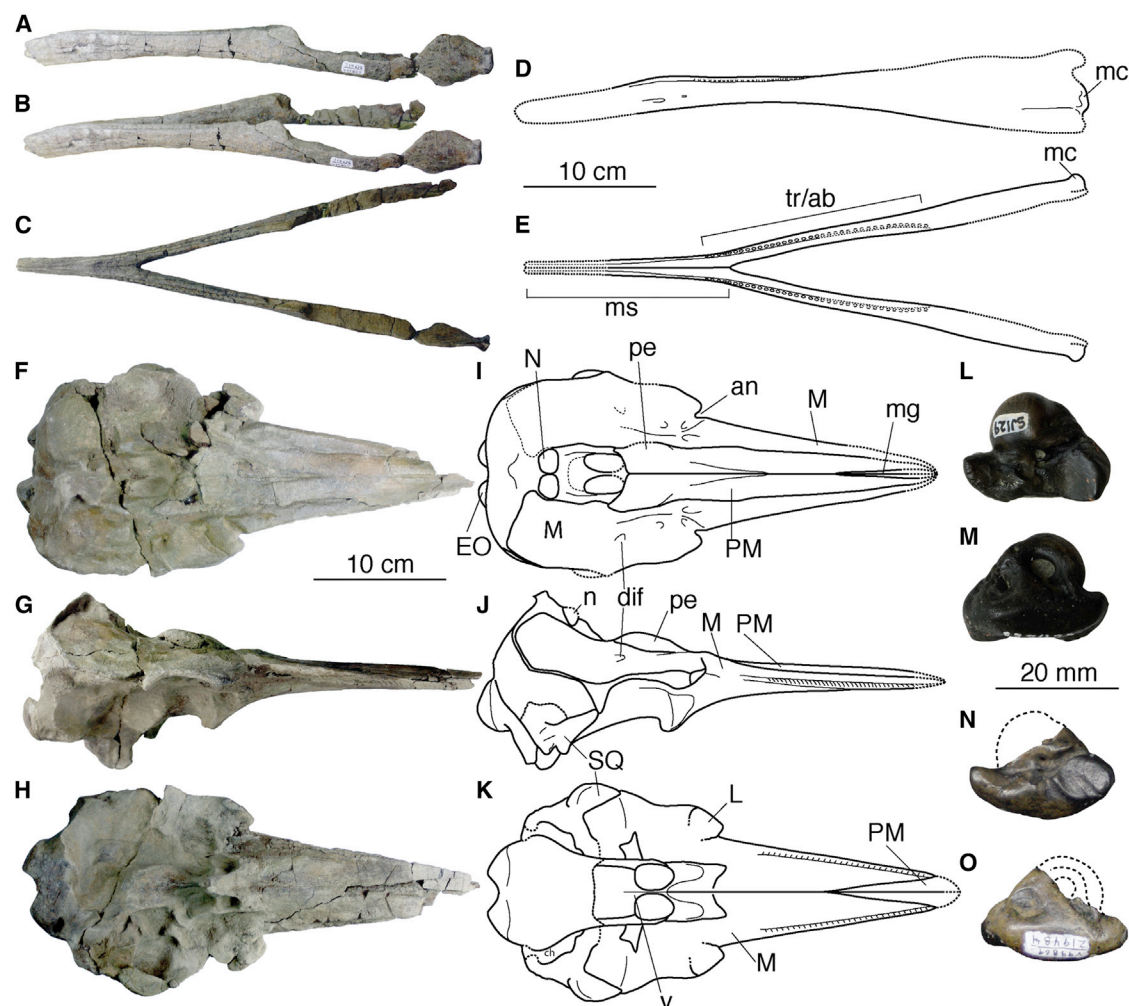


Figure 2. *Semirostrum ceruttii* and *Semirostrum* sp. from the Purisima Formation  
(A–C) *Semirostrum ceruttii* mandibles (UCMP 219076) in lateral (A), dorsolateral (B), and dorsal (C) aspect.  
(D and E) Reconstruction of UCMP 219076 in lateral (D) and dorsal (E) aspect.  
(F–H) Cranium of *Semirostrum* sp. (UCMP 219503) in dorsal (F), lateral (G), and ventral (H) aspect.  
(I–K) Reconstruction of UCMP 219503 in dorsal (I), lateral (J), and ventral (K) aspect.  
(L–O) Periotics of *Semirostrum ceruttii*, UCMP 137472 (L and M), and UCMP 219484 (N and O) in ventral (L and N) and dorsal (M and O) aspect.

among the remainder of Phocoenidae draw attention to the need for additional analyses (such as partitioned Bayesian analyses or alternative weighting and ordering schemes for parsimony analyses) and examination or modification of phenotypic characters in the future to better understand phocoenid and other odontocete relationships. Nonetheless, despite its unusual morphology, the extinct *Semirostrum ceruttii* is clearly nested within the Phocoenidae in the phylogenetic hypothesis presented here.

Extant porpoises exhibit pedomorphism [7, 12], a type of heterochrony involving retention of juvenile characteristics at sexual maturity, which may constrain levels of morphospace exploitation including feeding specializations or sexually selected adornments. In baleen whales, rostral growth is constrained in species exhibiting pedomorphism and appears to be unconstrained in peramorphic species [13]. *Semirostrum ceruttii* thus may exhibit peramorphosis (a type of heterochrony involving addition of new adult characteristics to the end of an ancestral developmental sequence) in its distinctive mandibular morphology. Further investigation of the potential

developmental mechanisms involved in specializations of the mandible and other aspects of the skull is warranted.

The closest analogous mandibular morphology to *Semirostrum ceruttii* is found in birds known as skimmers (*Rynchops*) (Figure 1C) or in half-beak fish (*Hemiramphus*). *Rynchops* uses a form of skim feeding that involves flying at the surface of shallow bodies of water, angling the body and head down, and extending the tip of the streamlined mandible into the water to probe for and take small fish and crustaceans. When *Rynchops* strikes a submerged object, the upper jaw closes and the head moves posteriorly, grasping prey [8]. *Rynchops* has extensive mental and trigeminal nerve rami that innervate the surface of the mandibles, likely allowing the bird to sense prey and other subsurface obstacles [8]. *Hemiramphus* feeds on nocturnal plankton, possibly using the rostrally extended lateral line system for prey detection [14]. Observations of both *Rynchops* and *Hemiramphus* indicate that these species are mainly nocturnal or crepuscular, emphasizing the importance of their sensitive mandibular apparatuses for feeding in low-light conditions [8, 14].



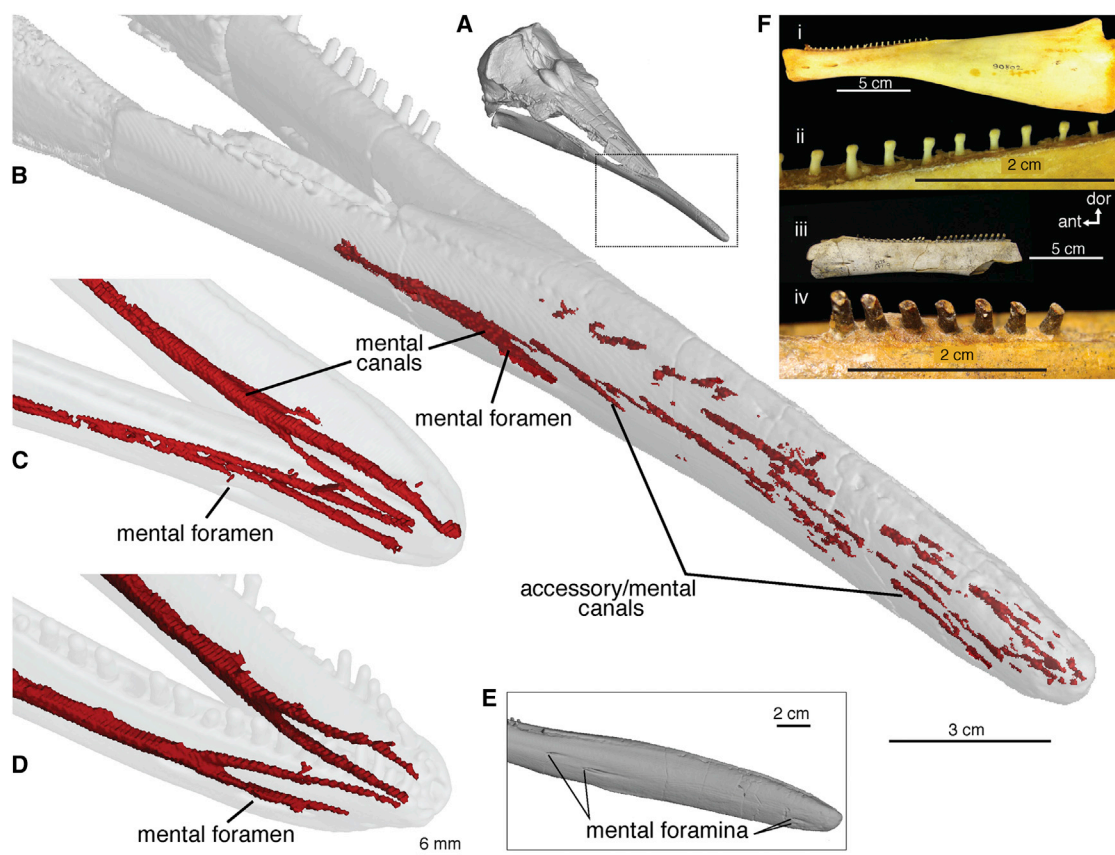


Figure 3. Mental and Accessory Mandibular Canals and Tooth Wear Evidence in *Semirostrum ceruttii* Compared with Extant Species

(A) Digital rendering of skull and mandible showing rough location of mandible imagery in (B)–(E).

(B) Right dorsolateral view of *Semirostrum ceruttii* rendered at 50% transparency, with mental and accessory canals on right side digitally isolated and rendered in red.

(C and D) Right dorsolateral view of *Phocoenoides dalli* (C) and *Phocoena phocoena* (D), each rendered at 50% transparency, with mental canals digitally isolated and rendered in red.

(E) Digital rendering based on CT data of right lateral view of *Semirostrum ceruttii* showing elongate mental foramina.

(F) Comparison of tooth wear in *Phocoena phocoena* and *Semirostrum ceruttii*.

(Fii and Fiv) Labial view of left mandible of *Phocoena phocoena* (AMNH 90802) (Fii), with a close-up view of the blunt, cusp-flattening wear typical of species (Fii).

(Fiii and Fiv) Labial view of left referred mandible of *Semirostrum ceruttii* (SDSNH 24710) (Fiii) and close-up of labial view of dentition of right holotype mandible (SDSNH 65276) (Fiv), exhibiting similar dental wear.

The extensive and elongate mental canals and accessory rami in *Semirostrum ceruttii* (Figure 3B) certainly involved arterial nourishment and innervation of the soft tissues in the mandible, likely allowing a tactile sensory function. Benthic probing may have evolved in low light or conditions unsuitable to extensive biosonar use for prey capture or communication (e.g., to avoid predators). The transversely thin, blade-like shape of the mandible does not seem conducive to scooping or specialized biting, as proposed in the extinct elephant-like gomphotheres [15], but prey may have rolled up the rostrum during a kind of skimming followed by clamping of the upper jaw after encountering prey. The streamlined mandible may have eased forward aquatic movement, with the head angled downward to monitor (via echolocation) and probe (via the mandible) for prey at the seafloor. A probing and feeding function is further supported by regional specialization of the rostral portion of the mandible for feeding in extant odontocetes [16].

The distinctive skull and postcranial characters of *Semirostrum ceruttii* imply some degree of ecological similarity with

river dolphins, which are characterized by slower but more maneuverable swimming [17]. In *Semirostrum ceruttii*, the deep dorsal condyloid fossae allowed more extensive movement and rotation of the skull at the atlanto-occipital joint and may have provided deep neck muscle attachment for stabilizing and maneuvering the head and elongate mandibles. This functional complex likely allowed for more precise and controlled movement of the head of *Semirostrum ceruttii* as it foraged. The presence of robust and unfused cervical vertebrae further supports this hypothesis. These features may have ameliorated the increased moment arm of drag induced on the rostrum during probing and benthic feeding events, analogous to the enormous supraoccipital region in balaenopterid mysticetes modified to cope with the stresses that rorquals experience during engulfment feeding [18, 19].

In contrast with the wider variety of feeding styles exhibited by delphinids, extant phocoenids are largely limited to feeding in shallower waters near the seafloor [2, 3, 20]. The macroscopic dental wear seen in the posterior mandibular dentition of *Semirostrum ceruttii* is most similar to that seen in



Figure 4. Life Reconstruction of *Semirostrum ceruttii* Probing Near the Sediment

*Phocoena phocoena* (Figures 3Fi–3Fiv; Supplemental Experimental Procedures III). The teeth in the Pliocene species are heavily worn and rounded, indicating polishing by fine-grained abrasives, not breakage. Assuming similar gingival thickness for *Semirostrum* to other taxa within its extant phylogenetic bracket (e.g., *Delphinus* and *Phocoena*; Figures 3Fi and 3Fii), the teeth of *Semirostrum ceruttii* were likely worn down to the gingiva. This condition is most similar to that of *Phocoena* and the populations of *Orcinus* that prey on sharks [21] and superficially resembles the wear seen on the teeth of the Oligocene toothed mysticete *Mammalodon* and the earliest diverging beaked whale, *Ninziphius platyrostris*, which are hypothesized to have been benthic feeders [22, 23]. The similarities between the dentition of *Phocoena*, *Orcinus*, and *Mammalodon* relate to their exposure to abrasives and exemplify how dental wear must be considered in the context of the mechanical events taking place, not as a simple dietary association. The teeth are not notably different from those of other delphinoids, and it is expected that the material properties of their teeth are similar to those of phocoenids because few differences are present between the material properties of the bracketing phocoenid and delphinid dental tissues [24]. Because this type of wear in extant phocoenids is the result of their tendency to feed in close proximity to the seafloor, it is most parsimonious in the case of *Semirostrum ceruttii* to interpret this wear as indicative that it fed on benthic or demersal prey (Figure 4).

Benthic feeding in phocoenids could be a specialization of the more generalized feeding in a delphinid-like ancestor, perhaps in conjunction with increases in seafloor productivity near coastal regions that characterized the Miocene [5] and accelerated during the Pliocene [25]. In support of this hypothesis, several other extinct marine mammals from the San Diego and Purisima formations have been interpreted as having benthic feeding lifestyles, including the extinct cetotheriid baleen whale *Herpetocetus* [26] and *Valenictus*, an extinct, nearly edentulous odobenine walrus that was likely a benthic molluscivore [27]. Extensive shallow marine embayments existed along the coastal margin of California during the Miocene and Pliocene [28, 29]; the greater area of shelf habitat perhaps explains the unparalleled diversity of large benthic foraging mammals at this time. Occurrences of

*Semirostrum ceruttii* within both the San Diego and Purisima formations indicates that this bizarre porpoise was widely distributed across at least 450 km of the California shelf during the Pliocene [28]. The increased diversity of phocoenids in the Pliocene that included *Semirostrum ceruttii* may have been driven by this increase in benthic productivity.

## Conclusions

*Semirostrum ceruttii* exhibits unusual mandibular morphology not previously described in mammals, likely reflecting a unique feeding strategy. Tooth wear and computed tomography (CT)-based reconstructions of elongate mental and accessory canals support interpretation of this morphology as specialization for a form of benthic probing and feeding. The probing function is analogous to that employed by *Rynchops* (skimmer) birds and *Hemiramphus* (half-beak) fish, which are hypothesized to use similarly elongate mandibles to sense prey. *Semirostrum ceruttii* was found to be sister to crown porpoises, within a moderately supported monophyletic Delphinoidea. Analyses of the functional and developmental trajectories that led to the prognathous mandibular symphysis in this species deserve further investigation as they relate to the morphospace explored by odontocetes.

## Experimental Procedures

### CT Scanning and Imagery

All CT scan parameters and other information are listed in Table S1. Segmentation of the mental canals and subsequent imagery were performed in VGStudio MAX v2.2; additional imagery and scan measurements were obtained in Avizo v6. Scan data are available directly from the authors or via <http://digimorph.org/>.

### Phylogenetic Analyses

A standard parsimony stepwise random addition tree bisection-reconnection bootstrap analysis (1,000 replicates) was conducted in PAUP\* v4.0b10 using a modified phenotype-only matrix (including character codings for the new taxon *Semirostrum ceruttii* and additional data) based on previous work [5, 6]. All characters were considered unweighted and unordered. All 246 phenotypic characters were parsimony informative.

### Accession Numbers

The phylogenetic analysis data matrix in nexus format is available at <http://morphobank.org/> under project number 933.

### Supplemental Information

Supplemental Information includes four figures, Supplemental Experimental Procedures, and one movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.02.031>.

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