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Journal

PaleoBios, 30(1)

ISSN

0031-0298

Author

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Publication Date

2011-02-18

DOI

10.5070/P9301021792

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Herpetocetine (Cetacea: Mysticeti) dentaries from the Upper Miocene Santa Margarita Sandstone of Central California

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Two fossil baleen whale (Mysticeti) dentaries from the Upper Miocene (10–12 Ma) Santa Margarita Sandstone of Central California preserve several distinct features similar to the enigmatic herpetocetine whale *Herpetocetus*. These features include an elongate coronoid process, a mandibular condyle with a planar articular surface, and a posteriorly extended angular process. The dentary is unknown for several Herpetocetinae (and the more inclusive clade Cetotheriidae), including the coeval *Nannocetus eremus*. This occurrence would extend the known record of *Herpetocetus* by 6 Ma. Given the currently poor knowledge of Pacific Cetotheriidae during the Miocene, these specimens are identified to the subfamily Herpetocetinae, despite the similarity of these specimens to *Herpetocetus*. As the morphology of the supposedly distinctive lectotype dentary of *Herpetocetus scaldiensis* (the type species of *Herpetocetus*) may not be unique to *Herpetocetus*, this study suggests that the mandibular morphology of fossil mysticetes may be more homoplastic (or conservative) than previously assumed. Mysticete taxonomy should employ autapomorphic characters beyond the morphology of the dentary alone.

INTRODUCTION

Early diverging mysticetes, traditionally referred to as “cetotheres” (Cetotheriidae *sensu lato*), are a group of cetaceans lacking the apomorphies of extant families. Some members of this paraphyletic group exhibit a distinctive suite of rostral, basicranial, and mandibular characteristics and constitute a more exclusive monophyletic group, the Cetotheriidae *sensu stricto* (Bouetel and Muizon 2006) referred to herein as the Cetotheriidae. Bouetel and Muizon (2006) included several genera within this clade, including *Cetotherium*, *Herpetocetus*, *Metopocetus*, *Mixocetus*, *Nannocetus*, and *Piscobalaena*. The phylogenetic hypothesis of Steeman (2007) supported monophyly of this group, although *Mixocetus* grouped outside this clade, while *Cephalotropis* was included. Whitmore and Barnes (2008) presented a classification of the Cetotheriidae, which also included *Amphicetus*, *Heterocetus*, *Mesocetus*, and *Plesiocetopsis*, but not *Piscobalaena*. Many “cetotheres” were also included within “Cetotheriidae *incertae sedis*” by Whitmore and Barnes (2008), which in various cladistic analyses occur as a paraphyletic stem group basal to extant mysticetes (Bouetel and Muizon 2006) or Balaenopteroidea (Steeman 2007, Deméré et al. 2005, Kimura and Ozawa 2002).

The Cetotheriidae has appeared in phylogenies as basal to all extant families (Bouetel and Muizon 2006, Deméré et al. 2005), just crown-ward of a basally positioned Balaenidae (Steeman 2007) and as the sister taxon to Balaenopteridae (Bisconti 2008). The phylogenies of Steeman (2007) and Bisconti (2008) revealed a close relationship between the Eschrichtiidae and Cetotheriidae. Recent reviews of the phylogeny and taxonomic history of “cetotheres” and the Cetotheriidae are found in Bouetel and Muizon (2006), Deméré et al. (2005), Whitmore and Barnes (2008), Steeman (2007), and Kimura and Ozawa (2002).

Members of the Cetotheriidae are typically character-

ized by a V-shaped interdigitation of the rostral elements into the cranium, demarcated by an anteriorly V-shaped frontal-maxillary suture. In later diverging members of this group, such as *Herpetocetus* and *Piscobalaena*, the ascending processes of the maxillae contact medially and exclude the premaxillae and nasals from the vertex, not observed in most other Mysticeti (Whitmore and Barnes 2008, Steeman 2007, Bouetel and Muizon 2006). *Herpetocetus*, *Piscobalaena*, and *Nannocetus* also display a suite of unique characters in the temporal region, including a plug-shaped posterior process of the petiotic (=petrosal) that is exposed laterally on the cranium, a vertically oriented glenoid fossa, and an antero-laterally twisted postglenoid process (Whitmore and Barnes 2008, Bouetel and Muizon 2006).

Several cetotheriids were found to form the Herpetocetinae, a more exclusive clade based on the derived petiotic morphology described above, named by Steeman (2007). This clade includes *Cephalotropis*, *Herpetocetus*, *Metopocetus*, and *Nannocetus*. Whitmore and Barnes (2008) also introduced their concept of the Herpetocetinae, which was restricted to *Herpetocetus* and *Nannocetus*; *Cephalotropis* and *Metopocetus* were included within the “Cetotheriinae,” which may be paraphyletic. The classification of Whitmore and Barnes (2008) was not tested cladistically. Although neither study included *Piscobalaena* within the Herpetocetinae, this taxon shares the derived, plug-shaped morphology of the petiotic and many other features with *Herpetocetus*. Given the similarity of the temporal region and the vertex, and the sister group relationship with *Herpetocetus* (Bouetel and Muizon 2006), *Piscobalaena* should be considered a member of the Herpetocetinae.

Herpetocetine mysticetes also bear a distinctive postglenoid process of the squamosal and a distinctive angular process of the dentary. The postglenoid processes of *Her-*

petocetus, *Nannocetus*, and *Piscobalaena* are oriented nearly vertical and rotated so that the glenoid fossa faces anteromedially. This results in a more vertically oriented cranio-mandibular articulation (Fig. 1) than observed in other fossil and extant mysticetes, with an angular process that projects posteroventrally below the postglenoid process. This morphology is known in *Herpetocetus* and *Piscobalaena*, but not confirmed in *Nannocetus* because the dentary is unknown. Van Beneden (1872) discussed the distinctive mandibular morphology of these mysticetes epitomized by *Herpetocetus* in his description of *Herpetocetus scaldiensis*. In *Herpetocetus*, the angular process extends far posterior to the mandibular condyle. Additionally, the mandibular condyle is antero-posteriorly elongate and bears a flat articular surface. The coronoid process is antero-posteriorly elongated into a vertical crest that is broadly triangular in lateral view, and projects laterally as in extant balaenopterids. The etymology of the generic name *Herpetocetus* was meant to illustrate the similarity between the posteriorly elongate angular process and the retroarticular process in the lower jaws of *H. scaldiensis* and squamate reptiles (O. Lambert *personal communication*, Whitmore and Barnes 2008).

Herpetocetus is represented by several named and several undescribed specimens. The type species, *Herpetocetus scaldiensis*, is known by the lectotype dentary (Van Beneden 1872) and referred cranial material and earbones from lower Pliocene strata of Belgium (Whitmore and Barnes 2008). *Herpetocetus transatlanticus* is represented by a partial cranium and several referred periotics from the lower Pliocene Yorktown Formation of North Carolina (Whitmore and Barnes 2008). “*Mitzuhoptera*” *sendaicus* (Hatai et al. 1963) was recombined as *Herpetocetus sendaicus* by Oishi and Hasegawa (1995) based on a partial skeleton. Alternatively, this may represent a new species as the *H. sendaicus* holotype is a tympanic bulla, insufficient material to justify a new species. *H. sendaicus* should probably be considered a *nomen dubium*. *Herpetocetus bramblei* is based on a partial cranium

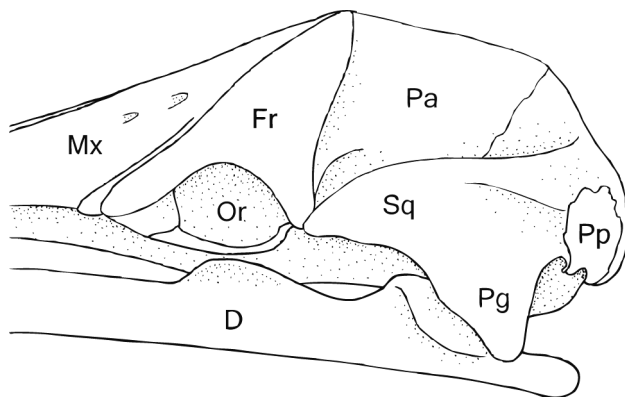


Figure 1. Craniomandibular articulation of *Herpetocetus*, based on crania of *Herpetocetus transatlanticus*, *Herpetocetus* “*sendaicus*,” *Herpetocetus bramblei*, and *Herpetocetus* sp. from the San Diego Formation.

and dentary (Whitmore and Barnes 2008). This taxon is now known by a nearly complete cranium and multiple periotics, tympanics, and dentaries from the Mio-Pliocene Purisima Formation of central California (Boessenecker and Geisler 2008). An additional undescribed species of *Herpetocetus* from the Pliocene San Diego Formation of southern California and Baja California (Deméré and Cerutti 1982) is represented by a partial skeleton (UCMP 124950) with cranium and dentary, and multiple referable crania, tympanoperiotics, and dentaries.

Herpetocetine dentary morphology is distinctive and has historically been used to identify isolated dentaries from California as *Herpetocetus* (Deméré and Cerutti 1982) and *Nannocetus* (Barnes et al. 1981). Whitmore and Barnes (2008) concluded that no known fossil dentaries could be confidently referred to *Nannocetus* because they were not associated with diagnostic cranial material. In fact, Whitmore and Barnes (2008) identified only two specimens as *Nannocetus eremus*: the holotype skull (UCMP 26502) and a referred cranium from the Santa Margarita Sandstone (UCMP 108558). Prior to Whitmore and Barnes (2008), more complete fossils, such as UCMP 124950, and similar herpetocetine fossils were identified as *Nannocetus*. All herpetocetine dentaries from the latest Miocene and Pliocene likely represent *Herpetocetus*, although many specimens in museums still show outdated identifications. Regardless, Whitmore and Barnes (2008) predicted that the dentary of *Nannocetus* would look similar to that of *Herpetocetus*, given the shared morphology of the postglenoid process. Additionally, the dentary and postglenoid process of *Piscobalaena* closely resembles *Herpetocetus* (Bouetel and Muizon 2006). Given the uncertainty surrounding some of the aforementioned identifications, and the fact that the lectotype for the type species of *Herpetocetus* is an isolated dentary, it is the purpose of this paper to describe *Herpetocetus*-like mysticete dentaries from the Upper Miocene (Tortonian correlative) Santa Margarita Sandstone of central California (Fig. 2) and to examine the consequences of taxonomy and identification based on isolated dentaries of early diverging mysticetes.

Abbreviations

Figure abbreviations used are: **ap**, angular process; **cp**, coronoid process; **D**, dentary; **Fr**, frontal; **gf**, gingival foramina; **mc**, mandibular condyle; **mdf**, mandibular foramen; **mdfo**, mandibular fossa; **Mx**, maxilla; **Or**, orbit; **Pa**, parietal; **Pg**, postglenoid process of the squamosal; **Pp**, posterior process of the periotic; **sg**, symphyseal groove; **Sq**, squamosal.

Institutional abbreviations used are: **IRSNB**, Institute Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **SDNHM**, San Diego Natural History Museum, San Diego, California, USA; **UCMP**, University of California Museum of Paleontology, Berkeley, California, USA; **UNC**, University of North Carolina Department of Geology, Chapel Hill, North Carolina, USA; **VMW**, Vertebrate collection, Sierra College Natural History Museum, Rocklin, California, USA.

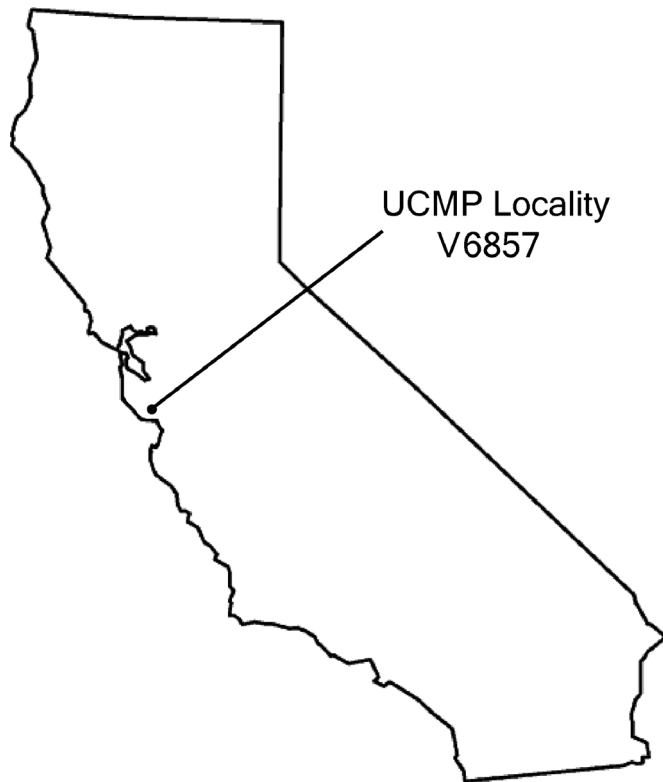


Figure 2. Map of California showing locality UCMP V-6857.

PREVIOUS WORK

Geology

UCMP locality V6857 occurs within the uppermost portion of the highly fossiliferous Santa Margarita Sandstone in the southern Santa Cruz Mountains, Santa Cruz County, California (Fig. 2). The formation thins from over 140 m thick to the north to about 25 m thick at V6875 in the south limb of the Scotts Valley anticline, and continues to thin to the south (Clark 1981, Repenning and Tedford 1977). Locally, the 20 m thick Santa Margarita Sandstone is a white-yellow, thickly cross-bedded, friable arkosic sandstone with a thick cross-bedded pebble-conglomerate above the basal unconformity with the older Monterey Formation (Phillips 1983, Clark 1981). To the north, the Santa Margarita Sandstone thickens to over 120 m and is composed of giant-scale cross-bedded conglomerate and conglomeratic sandstone (Phillips 1983). Isopach maps and sedimentologic data indicate the Santa Margarita Sandstone in the vicinity of Scotts Valley (north of UCMP V6857) was deposited in a large northeast-southwest trending channel connecting the Pacific Ocean to the west with the marine San Joaquin basin to the east (Phillips 1983). The Santa Margarita Sandstone correlates with the provincial "Margaritan" molluscan stage (Addicott 1972), the Mohnian and Delmontian foramaniferal stages (Clark 1981), and the Clarendonian North American Land Mammal Age (NALMA) (Repenning and Tedford 1977). In terms of international marine biochronology, the Santa Margarita Sandstone was

deposited during the early Tortonian stage. The age of the Santa Margarita Sandstone is approximately 10–12 Ma (Clark 1981, Repenning and Tedford 1977).

Vertebrate Paleontology

Vertebrate taxa reported from the Santa Margarita Sandstone in the southern Santa Cruz Mountains are listed in Table 1. Fossil sharks (Perry 1993, Clark 1981), fish, birds (Domning 1978), marine mammals (Table 1, Repenning and Tedford 1977, Barnes 1976, Mitchell and Repenning 1963), and terrestrial mammals (Table 1, Clark 1981, Perry 1977, Repenning and Tedford 1977) occur throughout the formation in this area. Highly abraded isolated elements including bones, calcified elasmobranch cartilage, and vertebrate teeth occur within the lower gravels (Phillips 1983). Associated and articulated skeletons, isolated bones, and teeth occur sporadically throughout the finer-grained sandstones of the upper portion of the Santa Margarita Sandstone (Phillips 1983). A bonebed occurring near the top of the unit contains a mixture of terrigenous clasts with bones and teeth of mammals, sharks, and birds. This bonebed grades laterally into a thicker, more sparsely fossiliferous horizon containing V6857. This time-averaged fossil-rich zone may represent a condensed section before grading laterally into the single hiatal bonebed surface.

SYSTEMATIC PALEONTOLOGY

ORDER: CETACEA Brisson 1762

SUBORDER: MYSTICETI Flower 1864

FAMILY: CETOTHERIIDAE Brandt 1872

SUBFAMILY: HERPETOCETINAE Steeman 2007

SUBFAMILY: HERPETOCETINAE genus et species indeterminate

Referred Specimens—UCMP 85431, partial skeleton including complete right dentary and associated forelimb elements and vertebrae, collected August 8, 1968, by R. Bowman and L.G. Barnes, and UCMP 85429, nearly complete right dentary missing only the mandibular condyle and angular process, collected 1969 by C.A. Repenning. UCMP 85429 is slightly smaller than UCMP 85431. These dentaries are morphologically identical and share a characteristic anteroposteriorly elongate, laterally projecting coronoid process and an anterior extension of the mandibular foramen opening (see below). A third dentary from the same locality (UCMP 85430) is missing the diagnostic posterior-most portion. The horizontal ramus is morphologically identical, though smaller in absolute size compared to UCMP 85429, and may also be referable to this unidentified herpetocetine taxon.

Locality—UCMP V6857, Taylor Quarry, uppermost Santa Margarita Sandstone, Santa Cruz County, California. Detailed locality information available on request to qualified researchers.

Description—This description of UCMP 85431 and 85429 is restricted to mandibular morphology because vertebrae and ribs are generally not diagnostic in cetaceans

(Deméré et al. 2005, Barnes 1976) and beyond the scope of this study. The description of the posterior portion of the dentary is based on UCMP 85431 (Figs. 3–5), while that of the anterior portion of the dentary is based on both

Table 1. Aggregate mammal assemblage from the Santa Margarita Sandstone in Santa Cruz County, with references listed for fossil occurrences.

Carnivora	
Desmatophocidae	<i>Alloidesmus</i> sp. (Repenning and Tedford 1977)
Odobenidae	<i>Imagotaria downsi</i> (Repenning and Tedford 1977, Barnes 1971) “Desmatophocine” sp. A (Barnes 1972)
Otariidae	<i>Pithanotaria starri</i> (Repenning and Tedford 1977)
Cetacea	
Odontoceti	
Delphinidae	Delphinidae indet. (Domning 1978) “Kentriodontidae” <i>Liolithax</i> sp. (Barnes 1978)
Monodontidae	Delphinapterinae indet. (Barnes 1976)
Allodelphinidae	<i>Zarhinocetus errabundus</i> (Domning 1978)
Physeteridae	Physeteridae indet. (Domning 1978)
Mysticeti	
Cetotheriidae	<i>Nannocetus eremus</i> (Whitmore and Barnes 2008) Herpetocetinae genus and species indet. (this study)
Balaenopteridae	Balaenopteridae indet. (Domning 1978) “ <i>Megaptera</i> ” <i>miocaena</i> (Boessenecker <i>unpublished data</i>)
Desmostylia	
Desmostylidae	<i>Desmostylus</i> sp. (Barnes 1978)
Paleoparadoxiidae	<i>Paleoparadoxia</i> sp. (Mitchell and Repenning 1963)
Sirenia	
Dugongidae	<i>Dusisiren jordani</i> (Domning 1978)
Proboscidea	
Gomphotheriidae	<i>Gomphotherium</i> sp. (Clark 1981)
Perissodactyla	
Equidae	<i>Archaeohippus</i> cf. <i>mourningi</i> (Clark 1981) <i>Hipparion</i> cf. <i>forcei</i> (Clark 1981) <i>Cormohipparion occidentale</i> (Clark 1981) <i>Pliohippus</i> sp. (Clark 1981)
Artiodactyla	
Camelidae	Camelidae indet. (Clark 1981)

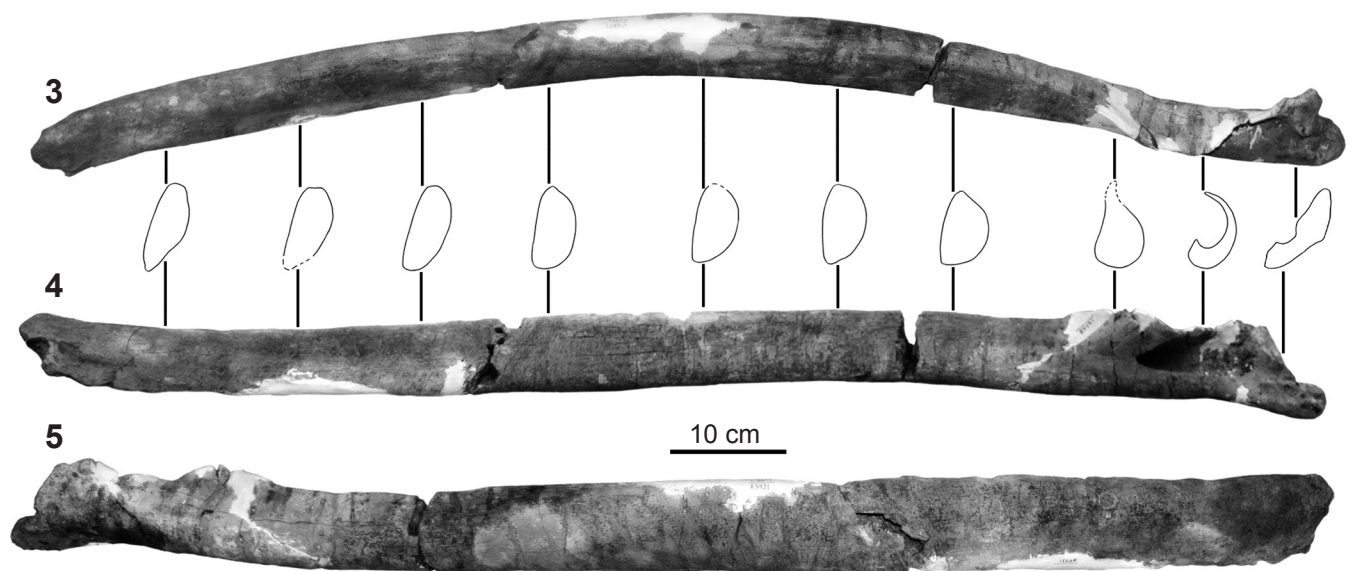
specimens (Figs. 3–8). In dorsal aspect the dentary is slightly bowed laterally, and less laterally bowed than most extant balaenopterids. The medial surface is slightly convex, while the lateral surface is strongly convex, in contrast to extant *Balaenoptera* (Deméré 1986). Anteriorly, the cross sectional shape of the dentary progressively increases in dorsoventral diameter and narrows transversely. In addition, the anterior third of the dentary is also longitudinally rotated so that the medial surface of the dentary faces dorso-medially rather than medially like the posterior two thirds; among extant mysticetes, this feature is unique to balaenopterids (Deméré 1986). The dentary of UCMP 85431 is slightly larger in overall size than UCMP 85429 (Table 2).

On the medial surface of the anteriormost portion of the horizontal ramus, a faint ridge defines the symphyseal groove, which extends for the anterior 1/6 of the dentary. Fourteen anteriorly oriented gingival foramina are arrayed along the dorsolateral surface of the dentary, laterally adjacent to a blunt crest that runs longitudinally along the entire dorsal surface. These foramina are anteroposteriorly short posteriorly, and increase in length toward the anterior extremity of the dentary. The anteriormost gingival foramen in UCMP 85429 (and UCMP 85430) occurs nearly at the anterior apex of the horizontal ramus, but lies ventral to the other foramina, and is instead manifested on the lateral surface as a large and anteroposteriorly short foramen; this feature is present but damaged in UCMP 85431.

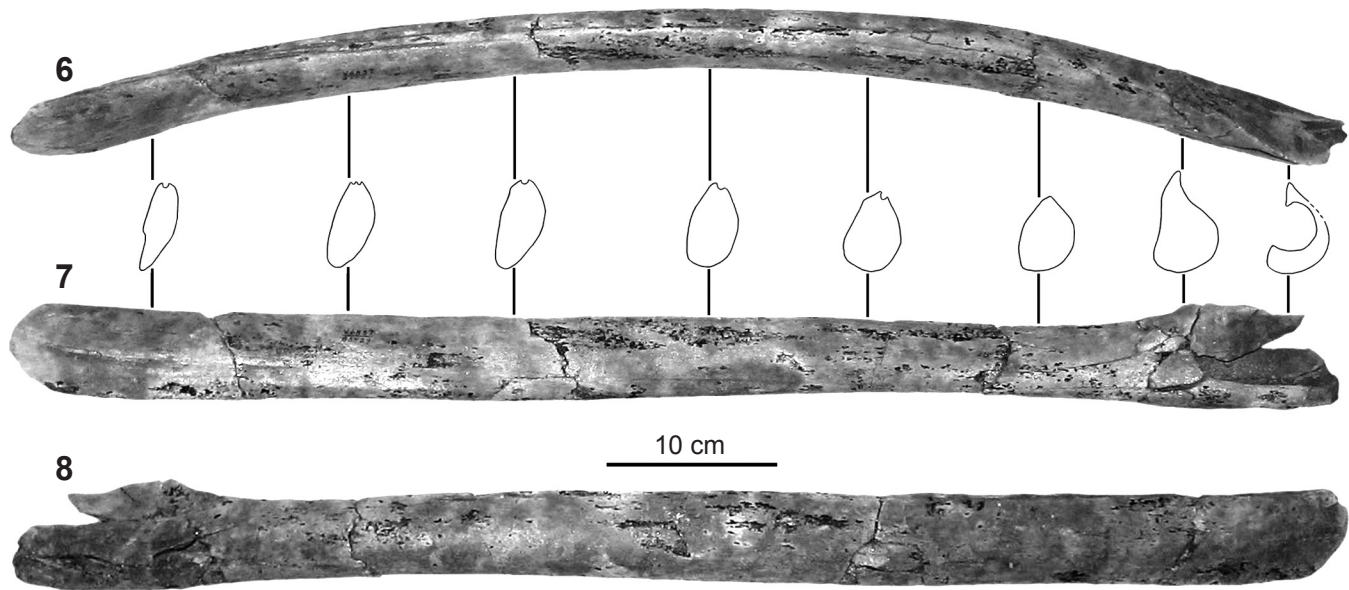
In UCMP 85429, a series of six anteriorly oriented foramina occur on the dorsal surface, medially adjacent to the dorsal crest, anterior to the coronoid process, and posterior to the posterior-most gingival foramen. This dorsal crest merges posteriorly with the coronoid process, which is damaged in UCMP 85431, but intact in UCMP 85429. In the latter,

the coronoid process is an elongate, broadly triangular crest that projects laterally at the apex. The medial surface of the horizontal ramus at the position of the coronoid process is planar, vertically oriented, and merges dorsally with the medially positioned coronoid process. Lateral and adjacent to the coronoid process, a shallow fossa occurs on the dorsal surface of the ramus. The posterior coronoid crest is a small ridge that descends from the coronoid process to form the medial edge of a thin, flat shelf that overhangs the mandibular foramen dorsally. The anterior portion of this ridge projects medially. This feature was termed the inward elevation by Kimura (2002) and was postulated to serve as the attachment for the frontomandibular stay in balaenopterids (Lambertsen et al. 1995). A small ridge extends posterolaterally from the coronoid crest to merge with the anterodorsal margin of the mandibular condyle. The anteriorly V-shaped anterior margin of the mandibular foramen is located below the coronoid process in both UCMP 85431 and 85429 (Figs. 4, 7). The mandibular foramen opens posteriorly into a well-defined cylindrical mandibular fossa, demarcated laterally by the mandibular condyle and a slight ridge medially that forms the bony margin of the mandibular foramen anteriorly. In cross section, the widened portion of the mandibular foramen extends further anteriorly in the horizontal ramus than the coronoid process.

The mandibular condyle is antero-posteriorly elongate, with a flattened articular surface that is D-shaped in posterior view. The condyle is slightly disc-shaped, with a planar medial margin, and a convex lateral margin. The condyle is offset laterally from the ramus. The articular surface of the condyle is oriented approximately 45° from the horizontal plane when viewed in lateral or medial aspect (Figs. 4, 5, 10, 12). A shallow notch occurs at the medial base of the



Figures 3–5. Dentary of *Herpetocetinae* genus and species indet., UCMP 85431, with cross sections drawn to scale. **3.** Dentary in dorsal view. **4.** Dentary in medial view. **5.** Dentary in lateral view.



Figures 6–8. Dentary of Herpetocetinae genus and species indet., UCMP 85429, with cross sections drawn to scale. 6. Dentary in dorsal view. 7. Dentary in medial view. 8. Dentary in lateral view.

coronoid process at the site of the internal pterygoid muscle insertion (Bouetel and Muizon 2006, Kellogg 1968). The angular process is small, and posteroventrally projects to form a flat shelf posterior to the mandibular condyle. The posterior end of the angular process is round in dorsal and lateral aspect. Figures 9–11 show a reconstruction of the complete dentary, based on UCMP 85431 and 85429.

DISCUSSION

Comparisons

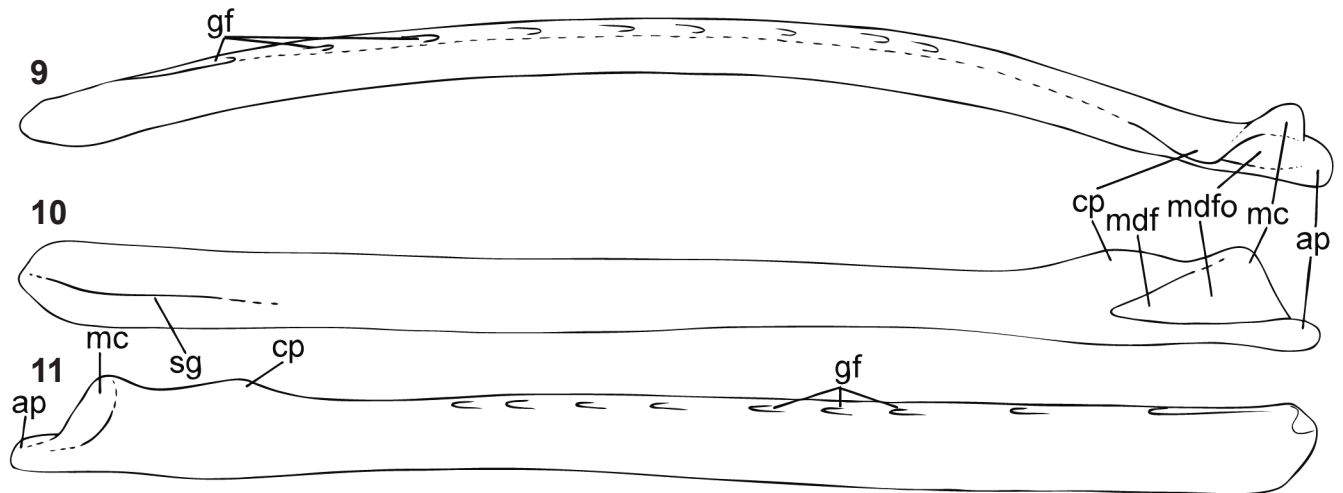
The dentaries of UCMP 85431 and UCMP 85429 share many features with the dentary IRSNB 14 (Fig. 16) originally described by Van Beneden (1872) as *Herpetocetus scaldiensis*. Van Beneden did not designate a holotype, but this specimen was later designated as the lectotype for *H. scaldiensis* by Abel (1938). Dentaries that are confidently associated with crania of *Herpetocetus sendaicus* (Fig. 14) and *Herpetocetus* sp. (Fig. 15) from the San Diego Formation (Deméré and Cerutti 1982) are nearly identical to UCMP 85431 and 85429. However, UCMP 85431 and 85429 dif-

fer from the dentaries of *Herpetocetus* (Figs. 14–16) in the following details. The most striking difference is the anterior extension of the mandibular foramen, which in both UCMP 85431 and 85429 extends anteriorly to a position below the coronoid process. In *H. sendaicus* (Fig. 14) and *H. sp.* (Fig. 15), the mandibular foramen opens posterior to the coronoid process, typically between the posterior coronoid crest and the mandibular condyle. Additionally, the angular process of UCMP 85431 is relatively shorter and the coronoid process is not as strongly developed compared to *H. scaldiensis*, *H. sendaicus*, and *H. sp.* from the San Diego Formation.

The dentary of UCMP 85431 shares fewer similarities with *Piscobalaena nana* than *Herpetocetus*. The dentary of *Piscobalaena* (Fig. 17) has a less pronounced and less anteroposteriorly elongated coronoid process, a more vertically oriented mandibular condyle, and the dentary is dorsoventrally shorter between these two features than in UCMP 85431. While the angular process of *Piscobalaena* is nearly as elongated posteriorly as UCMP 85431, it is much more massive and dorsoventrally thicker. The mandibular foramen

Table 2. Table of measurements of fossil herpetocetine dentaries.

Specimen	UCMP 85431	UCMP 85429
Length (linear)	100.3 cm	78.3 cm (incomplete)
Length (curvilinear)	101.0 cm	80.8 cm (incomplete)
Depth of ramus at mandibular condyle	5.5 cm	—
Transverse width of mandibular condyle	3.2 cm	—
Anterior margin of mandibular foramen to anterior edge of condyle	10.5 cm	—
Depth of ramus at coronoid process	6.4 cm (incomplete)	6.5 cm



Figures 9–11. Reconstruction of dentary of Herpetocetinae genus and species indet., based on UCMP 85431 and 85429. 9. Dentary in dorsal view. 10. Dentary in medial view. 11. Dentary in lateral view.

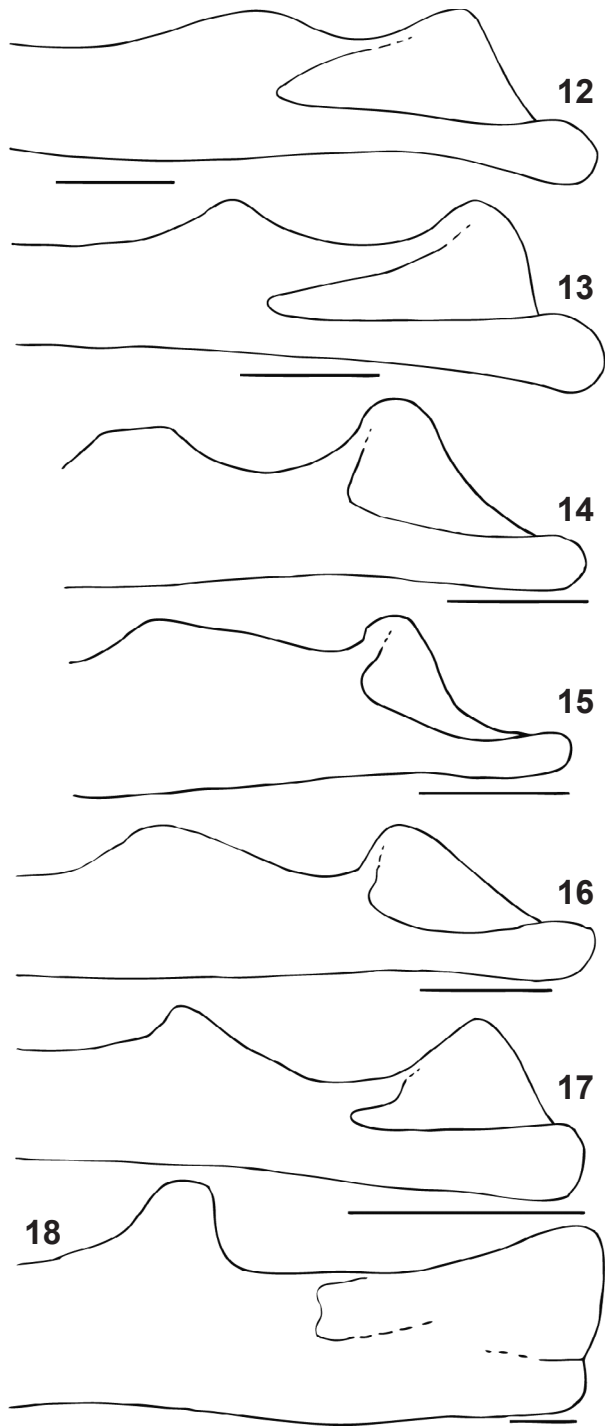
of *Piscobalaena* is approximately 50% smaller in diameter than UCMP 85431. Lastly, the mandibular foramen of *Piscobalaena*, like *Herpetocetus*, is positioned posterior to the posterior coronoid crest, unlike UCMP 85431.

The diameter of the mandibular foramen in UCMP 85431, UCMP 85429, *Piscobalaena*, and *Herpetocetus* is slightly greater than in extant Mysticeti. Roth (1978) considered a large mandibular foramen to be a plesiomorphic feature among mysticetes, a hypothesis supported by the early diverging position of members of Cetotheriidae in the phylogenies of Bouetel and Muizon (2006) and Deméré et al. (2005), the morphology of the dentary of the stem edentulous mysticete *Eomysticetus whitmorei* (Sanders and Barnes 2002), and the aetiocetid *Aetiocetus weltoni* (Deméré and Berta 2008). Most toothed and archaic edentulous mysticetes (Fitzgerald 2010) and some “cetotheres” (Steeiman 2009; Kimura 2002) also exhibit enlarged mandibular foramina. Although Steeman (2009) considered the mandibular foramen and cavity to be reduced in *Herpetocetus*, the mandibular foramen of *Herpetocetus* and UCMP 85431 and 85429 (as well as *Piscobalaena*) is enlarged relative to extant mysticetes, albeit slightly reduced relative to earlier diverging mysticetes. Enlarged mandibular foramina are related to the development of the mandibular fat pad, a feature that first appeared in ambulocetid and remingtonocetid archaeocetes (and retained in extant odontocetes) and adapted for underwater hearing (Nummela et al. 2007). The reduction of the mandibular foramen in extant and many fossil mysticetes was postulated by Steeman (2009) to be related to the adaptation for hearing low frequency sounds, which does not require a mandibular fat pad. The slightly reduced condition of the mandibular foramen in the herpetocetines is intermediate between that of earlier diverging mysticetes and extant mysticetes.

A dentary (SDNHM 59008; Fig. 13) similar to UCMP 85429 and 85431 was collected from the late Late Miocene San Luis Rey River Local Fauna of the San Mateo Forma-

tion (Domning and Deméré 1984). This specimen bears the distinctive anterior extension of the mandibular foramen to a position below the coronoid process and the typical *Herpetocetus*-like configuration of the mandibular condyle and angular process. The San Luis Rey River Local Fauna of the San Mateo Formation is correlative with the early Hemphillian and possibly latest Clarendonian North American Land Mammal Age (Domning and Deméré 1984), and late Tortonian (Europe/Asia), approximately 7–9 Ma. The similarity in morphology and geologic age of SDNHM 59008 suggests these belong to the same taxon as UCMP 85429 and 85431 from the Santa Margarita Sandstone.

An isolated dentary, UNC 4298, identified as “*Siphonocetus*” sp. by Baum and Wheeler (1977) from the Miocene “St. Mary’s Formation” of Virginia, is of similar geologic age and shares mandibular morphological features with the above herpetocetines. “*Siphonocetus*” (Cope 1895) is based on undiagnostic material and considered an invalid taxon (Kellogg 1968). UNC 4298 exhibits an anterior extension of the mandibular foramen. While the posterior end bears minor damage, the dentary preserves many of the same characteristics typical of *Herpetocetus* such as an elongate, flattened, laterally offset mandibular condyle, and a shelf-like angular process (albeit much more subtle than in *Herpetocetus*). The coronoid process of UNC 4298 is not anteroposteriorly elongate as in *Herpetocetus*, *Piscobalaena*, and the herpetocetine dentaries described herein, and instead is a small subtriangular hook-like crest, similar to that of balaenopterids (Fig. 18) and some “cetotheres.” Nevertheless, this dentary (UNC 4298) shares several features unique to herpetocetine mysticetes, and may represent an intermediate morphology between conservative mysticete dentaries and the derived morphology of *Herpetocetus*. Although Baum and Wheeler (1977) reported this specimen was from the St. Mary’s Formation, this unit does extend as far southeast as Cobham Wharf, where UNC 4298 was collected (Ward 2008). Local stratigraphy of the Cobham



Figures 12–18. Generalized drawings of posterior portion of mysticete dentaries in medial view, scale bars=5 cm. **12.** Herpetocetinae genus and species indet., based on UCMP 85431 and 85429. **13.** Herpetocetinae genus and species indet., SDNHM 59008, reversed. **14.** *Herpetocetus "sendaicus,"* redrawn from Bouetel and Muizon (2006). **15.** *Herpetocetus* sp., SDNHM 23057, San Diego Formation, reversed. **16.** *Herpetocetus scaldien-sis*, IRSNB 14, redrawn from Van Beneden (1882), reversed. **17.** *Piscobalaena nana*, redrawn from Bouetel and Muizon (2006), reversed. **18.** *Balaenoptera acutorostrata*, redrawn from Déméré (1986).

Wharf area suggests these fossils may have been collected from the Eastover Formation, the oldest stratigraphic unit exposed locally (Ward 2008). The Eastover Formation in Virginia is approximately 7–10.5 Ma (Tortonian equivalent). It overlies the Upper Miocene St. Mary's Formation further north and is itself overlain by the lower Pliocene Yorktown Formation (Ward and Blackwelder 1980). The Eastover Formation has previously yielded bones of a "kentriodontid" dolphin and a balaenopterid mysticete (Gottfried et al. 1994). Although unknown in the Eastover Formation (aside from UNC 4298), cetotheriids such as *Cephalotropis coronatus* and *Cetotherium megalophysum* occur in the stratigraphically lower St. Mary's Formation (Gottfried et al. 1994) and UNC 4298 may belong to one of these taxa. Cetotheriidae for which no confidently referred or well-preserved dentaries exist (and hence are not comparable) include *Cetotherium rathkei*, *Mixocetus elysius*, *Metopocetus durinasus*, and *Nannocetus eremus*.

UCMP 85429 and 85431 differ from the dentaries of all extant mysticetes in that they both possess a combination of characters including an elongate posterior projecting angular process, an elongate coronoid process, a cavernous mandibular foramen and fossa, and an antero-posteriorly elongate mandibular condyle. These specimens further differ from Balaenidae and Eschrichtiidae by having a well-developed coronoid process, and a dentary that is slightly bowed laterally. This bowing is not as extreme laterally as in some Balaenopteridae, although the anterior third of the dentary is rotated so the medial surface faces dorsomedially as in extant Balaenopteridae. UCMP 85429 and 85431 measure 85 cm (estimated) and 100.3 cm in length, respectively (Table 2), and are smaller than all extant mysticete species with the exception of *Caperea marginata*. *C. marginata* is readily distinguished from herpetocetine dentaries by the lack of a strongly defined coronoid process and extreme transverse compression of dorsoventrally high and straight horizontal ramus. Another similarity between UCMP 85431 and 86429 and extant balaenopterids is the lateral projection of the apex of the coronoid process, a feature also shared by *Herpetocetus* and *Piscobalaena*.

Taxonomic Implications

At 10–12 Ma, UCMP 85431 and 85429 are twice as old as most credible records of *Herpetocetus* and *Piscobalaena* and are contemporaneous with *Nannocetus* (Whitmore and Barnes 2008, Bouetel and Muizon 2006, Barnes 1976). The oldest confirmed record of *Herpetocetus* from the Northeast Pacific region is a partial cranium (VMW-64) of *Herpetocetus* aff. *bramblei* (Boessenecker, *personal observation*.) from the Upper Miocene (6.0–6.8 Ma) Santa Cruz Mudstone near Bolinas, California, close to the type locality of *Parabalaenoptera baulinensis* (Zeigler et al. 1997). It is not clear when *Nannocetus* became extinct and when *Herpetocetus* first evolved, or whether the two overlapped temporally or share an ancestor-descendant relationship.

This uncertainty may be eliminated by further study of

a collection of undescribed herpetocetine material from the San Luis Rey River Local Fauna in the San Mateo Formation, briefly summarized by Barnes et al. (1981). This local fauna is intermediate in age (approximately 6–8 Ma) between the older (10–12 Ma) Santa Margarita Sandstone assemblage that includes UCMP 85431 and 85429 and younger deposits containing confirmable *Herpetocetus* (2–6 Ma). Specimens from the San Mateo Formation (UCMP 88667, 94648, 119999, 125323, 194060, and many referable SDNHM specimens) consist of a partial skull, isolated periotics, tympanics, and dentaries (Barnes et al. 1981), and bear similarities to both *Herpetocetus* and *Nannocetus*. This material was originally identified as *Nannocetus* by Barnes et al. (1981), but remains undescribed. If this assemblage (which includes SDNHM 59008) represents one taxon, the similarity of the dentaries suggests that the San Mateo Formation material is at least congeneric with the fossils described herein from the Santa Margarita Sandstone, as outlined above. Description and further collection of material from this locality and similarly aged deposits will help resolve this issue.

The age of the Santa Margarita Sandstone has serious implications for the identification of UCMP 85431 and 85429. If UCMP 85431 and 85429 belong to *Herpetocetus*, then it would nearly double the known stratigraphic range of the taxon. While they most closely resemble dentaries of *Herpetocetus*, *Piscobalaena* or *Nannocetus* remain an alternative taxonomic assignment.

The holotype (UCMP 26502) and referred cranium (UCMP 108588) of *Nannocetus* are much smaller (24.8 cm bizygomatic width) than adult *Herpetocetus* (*Herpetocetus transatlanticus*: 45.3 cm bizygomatic width, Whitmore and Barnes 2008; *Herpetocetus "sendaicus"*: 38 cm bizygomatic width, Bouetel and Muizon 2006) and *Piscobalaena* (40.5–43.3 cm bizygomatic width, Bouetel and Muizon 2006). UCMP 85429 is 85 cm (est.) long and UCMP 85431 is 100.3 cm long, while the *Nannocetus* holotype is estimated to be 63.5 cm in condylobasal skull length (extrapolated from bizygomatic width and condylobasal skull length measurements of *Piscobalaena*, from Bouetel and Muizon 2006). The Santa Margarita Sandstone specimens are nearly as large as the largest known dentaries of *Herpetocetus*. This implies a mysticete of comparable size (approximately 1 m condylobasal skull length) to *Herpetocetus bramblei* and *Piscobalaena*, slightly larger than *Herpetocetus sendaicus*, and slightly smaller than *Herpetocetus transatlanticus*. If the known crania of *Nannocetus* are adults, then size alone may exclude UCMP 85431 and 85429 from this taxon. Whitmore and Barnes (2008), however, argue that the known crania of *Nannocetus* represent juveniles. In this case, then *Nannocetus* and *Herpetocetus* adults may have been of similar size. This study agrees with Whitmore and Barnes' (2008) observation that dentaries cannot be unequivocally referred to *Nannocetus*.

In the Pliocene of the Northern Pacific, *Herpetocetus* appears (on the basis of crania and periotics) to be the sole surviving herpetocetine genus. Thus, in the case of Pliocene

rock units of this region, the referral of isolated dentaries to this genus may be valid. It is possible, however, that this dentary morphotype may have evolved earlier than *Herpetocetus*, especially considering the similarity with *Piscobalaena*. In the case of the Middle Miocene and the early Late Miocene where the herpetocetine record is incomplete, crania or periotics associated with dentaries are required to confidently assign isolated herpetocetine dentaries to specific taxa.

Until more herpetocetine specimens from the Middle and Late Miocene are discovered and described, the referral of isolated dentaries to *Herpetocetus* is discouraged (aside from the Pliocene of the Northern Pacific), given the paucity of knowledge concerning other herpetocetine mysticetes in the Northern Pacific. While isolated dentaries of fossil mysticetes can be of significant systematic importance as demonstrated for fossil balaenopterids by Deméré (1986), fossil cetotheriids (and specifically, herpetocetines) are less well known in the fossil record and many taxa (e.g., *Mixocetus*, *Nannocetus*, *Metopocetus*) lack fossil dentaries. The dentaries described above may belong to *Nannocetus*, but this can only be confirmed when crania or periotics of *Nannocetus* are discovered with associated dentaries. These specimens may also represent some as-yet unknown herpetocetine. In summary, the lack of reliably identified *Nannocetus* dentaries, the uncertain ontogenetic age of known *Nannocetus* crania, general similarities with *Piscobalaena* and *Herpetocetus*, and the significantly older age than *Herpetocetus*, prevent identification of these dentaries past the subfamilial level.

How valid are fossil cetacean taxa based solely on isolated dentaries? In a discussion of the “nomenclatural nightmare” associated with Belgian fossil mysticetes, Deméré et al. (2005) highlighted the problematic taxonomic history of *Herpetocetus scaldiensis*. Van Beneden (1872) did not designate a holotype for *H. scaldiensis*. In addition to the dentary (IRSNB 14), there were other fragments (cranial, axial, appendicular) probably representing other taxa (Deméré et al. 2005, pp. 104–106). While the dentary (Fig. 16) is the most distinctive element among the syntypes (Deméré et al. 2005), it is also similar to UCMP 85431 and 85429 (which may represent *Herpetocetus*, *Nannocetus*, or neither) and *Piscobalaena* (Fig. 17). Deméré et al. (2005) suggested either selecting lectotypes from among Van Beneden's described material (syntypes), or designate these problematic taxa as *nomina dubia*. Whitmore and Barnes (2008) noted that Abel (1938:22) selected the dentary IRSNB 14 as the lectotype for *H. scaldiensis*.

The dentaries described herein are nearly identical to IRSNB 14; whether this results from synonymy at the generic level or homoplasy cannot be ascertained without additional study of cranial material associated with the Santa Margarita Sandstone taxon and a comparison with *Herpetocetus*. The much older geologic age of UCMP 85431 and 85429 than the oldest demonstrable *Herpetocetus* material indicates the possibility that the archetypal *Herpetocetus* jaw morphology may not be unique to *Herpetocetus*. Because the lectotype of

the type species (*H. scaldiensis*) of *Herpetocetus* is a dentary, the taxonomic stability of *Herpetocetus* may be in question. Fortunately, Van Beneden (1882:85) referred a squamosal (IRSNB 405) to *H. scaldiensis*, which Whitmore and Barnes (2008) concluded was probably associated with the lectotype dentary. Additionally, the Santa Margarita Sandstone specimens described herein can be distinguished from *H. scaldiensis* (and other *Herpetocetus*) by the anteriorly elongate mandibular foramen. While these two features tentatively suggest that *Herpetocetus* is a valid taxon, this case illustrates problems associated with cetacean taxa based solely on dentaries. This study endorses the guidelines proposed by Barnes (1976) to include cranial material for fossil cetacean holotypes and discourage the designation of dentaries as holotypes of fossil mysticete taxa. It is likely that the mysticete dentary is more homoplastic, at least within the Cetotheriidae, and aspects of mandibular morphology are far less diagnostic than generally assumed. It should be immediately obvious from this discussion of mysticete taxonomy that the practice of relying on isolated mysticete dentaries has contributed to an unnecessary degree of taxonomic confusion, and in some cases “taxonomic paralysis,” *sensu* Deméré et al. (2005).

CONCLUSIONS

UCMP 85431 and 85429, two dentaries from the Upper Miocene (Tortonian equivalent, 10–12 Ma) Santa Margarita Sandstone of central California, possess numerous similarities with dentaries of the younger taxon *Herpetocetus*. However, these specimens are only reliably identifiable to the subfamily Herpetocetinae because dentaries are unreported for several members of this clade, including *Nannocetus eremus*. Additionally, since the oldest demonstrable record of *Herpetocetus* is 6.0–6.8 Ma, it is possible that this dentary morphology evolved before *Herpetocetus*, and may be diagnostic of a more inclusive clade. Caution is warranted in the referral of isolated dentaries beyond the family level for the Cetotheriidae, particularly for Miocene specimens. As the distinctive dentary morphology described herein may not be unique to *Herpetocetus*, the designation of a dentary as the lectotype for the type species has direct implications for the taxonomic stability of *Herpetocetus* and other genera based on dentaries. The example presented in this study illustrates the inherent difficulties of higher-level taxonomy based on isolated cetacean dentaries, a practice which has contributed to taxonomic confusion, and is strongly discouraged.

ACKNOWLEDGEMENTS

Constructive reviews by T.A. Deméré and A. Dooley greatly improved the quality of this study, and thanks also go to the editors M. Goodwin and A. Stegner for facilitating this process. Special thanks go to J. El Adli, for extensive discussions of herpetocetine morphology, systematics, and function, as well as graciously providing photos of undescribed herpetocetines. This study benefited from discussions with

T.A. Deméré, A. Dooley, J. El Adli, E.M.G. Fitzgerald, J.H. Geisler, O. Lambert, F.A. Perry, and N.D. Pyenson. T.A. Deméré and O. Lambert kindly supplied photographs of Belgian, Japanese, and Peruvian fossil cetaceans; O. Lambert also graciously provided translations of Van Beneden (1872) regarding the etymology of *Herpetocetus*. Comments from M.C. Churchill, D.W. Fowler, L. Hall, F.A. Perry, and J.B. Scannella greatly improved earlier versions of this manuscript. I appreciate M.H. Gardner for inspiring this project. I would like to thank the following, who allowed me to examine museum specimens under their care: G.E. Bromm and R.P. Hilton (SCNHM), F.A. Perry (SCMNH), K.A. Randall and T.A. Deméré (SDNHM), and P.A. Holroyd (UCMP).

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