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Pleistocene survival of an archaic dwarf baleen whale (Mysticeti: Cetotheriidae)

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Abstract Pliocene baleen whale assemblages are characterized by a mix of early records

of extant mysticetes, extinct genera within modern families, and late surviving members

of the extinct family Cetotheriidae. Although Pleistocene baleen whales are poorly

known, thus far they include only fossils of extant genera, indicating late Pliocene

extinctions of numerous mysticetes alongside other marine mammals. Here, a new fossil

of the late Neogene cetotheriid mysticete *Herpetocetus* is reported from the Lower to

Middle Pleistocene Falor Formation of Northern California. This find demonstrates that

at least one archaic mysticete survived well into the Quaternary Period, indicating a

recent loss of a unique niche and a more complex pattern of Plio-Pleistocene faunal

overturn for marine mammals than has been previously acknowledged. This discovery

also lends indirect support to the hypothesis that the pygmy right whale (*Caperea

marginata*) is an extant cetotheriid, as it documents another cetotheriid nearly surviving

to modern times.

Introduction

The four modern baleen whale (Cetacea: Mysticeti) families include fifteen gigantic filter-feeding species. Although Pleistocene marine mammal assemblages are poorly known (Whitmore 1994; Boessenecker 2011b), all previously reported Pleistocene fossil mysticetes represent modern genera. In contrast, Miocene and Pliocene mysticete assemblages included generally smaller body sizes than at present, the latter epoch typically including a mix of modern and extinct mysticete genera, including late surviving archaic cetotheriids (Barnes, 1977 Whitmore 1994; Whitmore and Kaltenbach 2008; Lambert et al. 2010). The Cetotheriidae are a supposedly extinct clade of mysticetes with narrow rostra, V-shaped interdigitation of the rostral and braincase elements, peculiar features of the basicranium, and generally small body sizes, and originated during the middle Miocene (Bouetel and Muizon, 2006; Marx, 2011). Although formerly treated as a 'wastebasket' group of archaic mysticetes lacking the diagnostic features of modern families, Bouetel and Muizon (2006) found a monophyletic group of mysticetes including *Cetotherium rathkii* which they termed the Cetotheriidae *sensu stricto* (=Cetotheriidae herein). Late-surviving members of this clade include *Piscobalaena nana* from the late Miocene of Peru and *Herpetocetus* spp. from the late Miocene to Middle Pliocene of numerous North Pacific and North Atlantic localities (Bouetel and Muizon, 2006; Whitmore and Barnes, 2008; Boessenecker, 2011a). *Herpetocetus* is a small-bodied (3-4 m) baleen whale with a unique mandibular

articulation (Whitmore and Barnes, 2008) which would have restricted its ability to abduct its mandible (Whitmore, 1994) and therefore drastically reduced maximum oral volume. This suggests it was not a lunge feeder (El Adli and Boessenecker, 2011), and in concert with its tiny size, indicates the existence of an additional niche during the Pliocene that is not currently occupied by baleen whales. Within Pliocene marine mammal assemblages, *Herpetocetus* co-occurs with early representatives of modern mysticete genera, in addition to archaic balaenids, balaenopterids, and eschrichtiids (Barnes, 1977 Whitmore, 1994; Oishi and Hasegawa, 1995b; Whitmore and Kaltenbach, 2008).

The period in which the modern mysticete fauna first originated is poorly constrained. Early and Middle Pliocene marine mammal assemblages include a mix of extinct and extant genera, although most Pleistocene marine mammal assemblages only include modern genera (Oishi and Hasegawa, 1995a; Deméré et al., 2003; Boessenecker, 2011b), which suggests a period of faunal turnover near the Pliocene-Pleistocene boundary (Boessenecker, 2011b). In the eastern North Pacific, inferred events include 1) extinction of *Dusignathus* and *Valenictus* (walruses), *Herpetocetus*, dwarf balaenids (right whales), archaic balaenopterids (rorquals), archaic phocoenids (porpoises), and archaic delphinapterines (belugas), 2) invasion of the region by "otariine" sea lions, harbor seals, elephant seals, sea otters, and 3) diversification of modern species of balaenopterids, delphinids, and ziphiids (Boessenecker, 2011b). Here, I report a surprisingly late occurring fossil cranium of *Herpetocetus* from the Pleistocene Falor Formation of Northern California (Fig. 1), indicating that archaic cetotheriid mysticetes

survived until much later than previously recognized, and suggesting a more complex

pattern of faunal turnover in the eastern North Pacific.

Materials and Methods

Fossil mysticete specimen

VMW-65 is a partial mysticete braincase collected by R. J. Bushell from near

Boulder Creek in the vicinity of Blue Lake, Humboldt County, California. The skull

includes the parietals, alisphenoids, occipital, left petrosal, and parts of the frontals,

maxillae, premaxillae, pterygoids, squamosals, and vomer. VMW-65 lacks the rostrum,

palatines, tympanics, zygomatic processes of the squamosals, and supraorbital processes

of the frontals.

Institutional abbreviations

UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.

VMW, Sierra College Natural History Museum, Rocklin, California, U.S.A.

Locality and geological age

VMW-65 was found as a loose boulder of gray, calcareous, fine-grained sandstone in a

river bank near Blue Lake, California (Fig. 1). Fossils of invertebrates and occasional

marine vertebrates are abundantly present within cobbles of identical lithology in the

riverbed, matching the lithology of adjacent Falor Formation exposures. VMW-65 could

not have been reworked from older marine rocks, because the Falor Formation was

deposited directly upon Mesozoic basement rocks of the Franciscan Complex (Manning

and Ogle, 1950), and no other Cenozoic sedimentary rocks are exposed in the vicinity

(Fig. 1c). Furthermore, the nearest marine rocks of Miocene and Pliocene age (Pullen and

Rio Dell Formations, Wildcat Group) crop out 35 km to the south within a separate

drainage basin. An ash bed that is chemically correlated with the 2.1 Ma Huckleberry

Ridge Tuff occurs at the base of the Falor Formation (Kelsey and Carver 1988), and the

lack of syndepositional deformation indicates deposition ceased prior to initiation of

tectonism along the Mad River fault zone at about 0.7 Ma (Kelsey and Carver 1988);

thus, the age of the Falor Formation can be summarized as 2.1-0.7 Ma, or Lower-Middle

Pleistocene. The Falor Formation was deposited in a narrow embayment, and is

considered to be a lateral equivalent of the Moonstone Beach Formation and Wildcat

Group within the Eel River Basin (Nilsen and Clark 1989). Additional evidence for the

age of the Falor Formation includes 1.0-0.35 Ma Th/U ratios from fossil corals, late

Pleistocene correlative mollusks, Irvingtonian to Rancholabrean NALMA land mammals,

and 0.71 ± 0.01 Ma Amino Acid Racemization dates from the Moonstone Beach

Formation (Kilmer 1972; Wehmiller et al., 1978; Roth 1979; Kelsey and Carver 1988).

This study follows Boessenecker (2011b) and Boessenecker and Smith (2011) in using

the traditionally defined Pliocene-Pleistocene boundary defined at the 1.88 Ma Gelasian-

Calabrian Boundary, as advocated by Hilgen et al. (2012).

Results

VMW-65 preserves several cetotheriid characteristics identified by Bouetel and Muizon

2006) as synapomorphies of the family, including posterolaterally concave frontal-

maxillary sutures, premaxillae that terminate anteriorly to the ascending processes of the

maxillae, ascending processes of the maxillae which contact each other medially, and anterior processes of the petrosals that are anteroposteriorly directed with straight apices (Figures 1-2; Bouetel and Muizon 2006). Herpetocetine features (Whitmore and Barnes 2008) include plug-like posterior processes of the petrotympanics, transversely compressed anterior processes of the petrosals, and the presence of postparietal foramina between the squamosals, alisphenoids, and parietals. Characteristics that identify VMW-65 as *Herpetocetus* (Whitmore and Barnes 2008) include hypertrophied alisphenoids externally exposed on the braincase, blade-like anterior processes of the petrosals closely appressed to the squamosals, triangular lateral tuberosities of the petrosals that are ventrolaterally bent and appressed to underlap the squamosals, and a dorsoventrally deep, pyramidal braincase (Figs. 1-2). The skull is further characterized by its sharply triangular and steeply sloping supraoccipital shield, vertically directed nuchal crests (Fig. 1), and small size (21.4 cm exoccipital width), with an estimated body length of 3.95 m (Supplementary Material). Given the long medial contact of the maxillae, the nasals of VMW-65 must have terminated well anterior to the vertex, as in *Herpetocetus bramblei* (UCMP 219111). The ascending processes of the maxillae exhibit an anteroposteriorly elongate medial contact, bear several dorsal infraorbital foramina with posteriorly ascending sulci, and exclude contact of the premaxillae with the frontals (Fig. 1). Although damaged, the right ascending processes of the maxilla becomes transversely narrow and splint-like near the vertex, similar to *Herpetocetus* "*sendaicus*" from the early Pliocene of Japan. VMW-65 is identified as *Herpetocetus* sp., owing to its incompleteness.

Discussion

Prior reports have established that archaic toothless mysticetes (Eomysticetidae, Cetotheriidae, stem balaenopteroids) – with a few exceptions – were primarily Oligocene and Miocene in age (Barnes 1977; Fordyce and Muizon 2001). Pliocene fossils of *Herpetocetus* represent the geochronologically latest surviving examples of cetotheriids (Fig. 3; Barnes 1977; Boessenecker 2011a). Prior to this discovery, the youngest records of cetotheriids were *Herpetocetus* sp. from the Middle Pliocene San Diego Formation of southern California (Deméré and Cerutti 1982), and a single mandibular fragment of a possible cetotheriid from the latest Pliocene Sarumaru Formation of Nagano, Japan (Kimura and Hasegawa 2009). This newly reported fossil of *Herpetocetus* is Early-Middle Pleistocene in age, firmly establishing it as the youngest known fossil of a cetotheriid, and extending the range of this extinct baleen whale well into the Pleistocene (Fig. 3). Furthermore, this is the youngest known record of any extinct mysticete genus, and one of few records of an extinct cetacean from the Pleistocene.

Little research has focused on Plio-Pleistocene patterns of faunal overturn in marine mammals, and because of the low number of Pleistocene marine-mammal localities (in comparison to older strata), most aspects of faunal change need to be inferred based on differences between the modern fauna and that of the Pliocene (Fordyce, 2009; Boessenecker 2011b; Valenzuela-Toro et al., 2013). Pliocene marine mammal assemblages in particular have been previously identified as comprising an eclectic mix of species with seemingly bizarre adaptations, relatives of modern species with unexpected geographic distributions, and early representatives of extant genera (Whitmore, 1994; Oishi and Hasegawa, 1995b; Fordyce et al., 2002; Fitzgerald, 2005).

Herpetocetus was formerly considered to become extinct along with many of the other members of this strange assemblage at the close of the Pliocene, as the majority of Pleistocene marine mammal records represent extant genera (Deméré et al., 2003; Boessenecker, 2011b; Valenzuela-Toro et al., 2013). Major faunal changes in marine mammals appear to occur in the late Pliocene-early Pleistocene interval and thus predate the widespread megafaunal extinctions (45-9 Ka) at the close of the Pleistocene and early Holocene (Barnosky et al., 2004). Interestingly, the only marine mammals in the eastern North Pacific that appear to have remained stable through the Plio-Pleistocene interval were the fur seal *Callorhinus* and the sea cow *Hydrodamalis* (Boessenecker, 2011b). Previously reported mysticetes identified past the family level from the Pleistocene only include extant genera (*Balaenoptera*, *Eschrichtius*, *Eubalaena*, and *Megaptera*; Barnes and McLeod 1984; Morgan 1994; Nagasawa et al. 2004; Oishi and Hasegawa 1995a). This new discovery indicates that some members of the 'Pliocene' marine mammal fauna such as *Herpetocetus* survived well into the Pleistocene (Fig. 3), and that the modern character of the baleen whale fauna was not realized until very recently, perhaps only within the last 1 Ma. In parallel, a surprisingly late occurrence of an archaic sperm whale has been reported from the Middle Pleistocene of the equatorial Pacific (Fitzgerald 2011). The presence of a typical 'Pliocene' mysticete in the Early-Middle Pleistocene contrasts strongly with the pinniped record, which is dominated by extant genera in eastern North Pacific deposits (Deméré et al., 2003; Barnes et al., 2006; Boessenecker, 2011b), suggesting that the modern marine mammal fauna arose in a stepwise fashion.

Examples of Pleistocene marine mammals such as VMW-65 provide rare glimpses into this poorly sampled interval, and indicate that the actual pattern of faunal

turnover is more complex than previously noted. The Pleistocene is already known (by inference) to be a period of declining cetacean diversity (Barnes 1976; Marx and Uhen 2010) with cetotheriids having experienced a decline in diversity since the Late Miocene (Marx 2011). Pleistocene persistence of dwarf cetotheriids (3-4 m body length) is additionally surprising in the context of extreme body size increases among other mysticetes during the Plio-Pleistocene interval (Lambert et al 2010: fig. 4). Although only a 1 Ma extension in range, this new discovery is profound as it documents that *Herpetocetus* nearly survived to the modern era and survived climatic and ecologic perturbations resulting in the extinction of other marine mammals at the close of the Pliocene, additionally indicating the recent loss of a unique niche that is no longer inhabited by baleen whales. The Pliocene was characterized by warmer than present oceans, relaxed upwelling, lower productivity, and permanent "El Nino" conditions in the Pacific (Filippelli and Flores, 2009; Wara et al., 2005), followed by increased cooling related to northern hemisphere glaciation toward the end of the Pliocene (Ravelo et al., 2004). Late Pliocene closure of the Central American Seaway altered oceanic circulation (Coates et al., 1992), preluding intensified upwelling and productivity during the Pleistocene, and rapid, high-amplitude changes in eustatic sea level beginning in the middle Pleistocene (Miller et al., 2005). Shallow marine environments along the eastern North Pacific coast changed during the Pleistocene with the development of extensive rocky shore habitats (Jacobs et al., 2004). Changes in circulation, upwelling, and climate at the close of the Pliocene may have caused extirpations and extinctions in some cetaceans, while fostering dispersal and cosmopolitan feeding habits of others, leading to the widespread distributions of modern mysticetes.

Although extinctions among invertebrates and some vertebrates in the eastern

North Pacific were minimal in the Plio-Pleistocene interval (Valentine and Jablonski,

1991; Jacobs et al., 2004; Harnik et al., 2012), marine birds and marine mammals fared

differently. Bony toothed birds (Pelagornithidae) disappeared at the end of the Pliocene

in the eastern North Pacific (Boessenecker and Smith, 2011) and sulids (boobies and

gannets) and the flightless auk *Mancalla* became extinct in the region during the Late

Pleistocene (Warheit, 1992), possibly owing to competition for shoreline haul out and

breeding space with newly arriving otariids and elephant seals (Warheit and Lindberg,

1988). The Plio-Pleistocene marine mammal fossil record in the eastern North Pacific

indicates numerous groups became extinct near the Plio-Pleistocene boundary, their

niches filled by primarily modern genera by the Middle Pleistocene. It is unclear at

present what fostered the persistence of *Herpetocetus* along with members of the modern

marine mammal fauna, and better understanding of its feeding ecology is necessary as

changes in continental shelf area caused by high-amplitude changes in sea level may have

influenced the ecology and abundance of resources for mysticetes and other marine

mammals during the past two million years (Pyenson and Lindberg, 2011). Further

discoveries of Pleistocene marine mammals are necessary to improve our understanding

of marine mammal extinctions ultimately leading to the current faunal configuration

(Boessenecker, 2011b; Valenzuela-Toro et al., 2013), as well as to establish a 'deep time'

context for interpreting broad ecological changes which currently affect modern marine

mammals (Harnik et al., 2012).

Although traditionally viewed as a balaenoid mysticete, a recent phylogenetic

hypothesis posits that the extant pygmy right whale *Caperea marginata* is closely related

to herpetocetine mysticetes (Fordyce and Marx, 2013), representing a highly derived extant lineage of Cetotheriidae. A recent evolutionary link with *Herpetocetus* in particular is not likely, given the derived *Caperea*-like morphology of the late Miocene pygmy right whale *Miocaperea*, instead suggesting divergence between the neobalaenines and herpetocetines earlier than the Pliocene. However, the discovery of a Pleistocene *Herpetocetus* does offer additional support to this hypothesis as it documents a possible close relative of *Caperea* surviving nearly to the present. The late survival alongside larger, anatomically modern mysticetes illustrates *Herpetocetus* as a northern hemisphere analogue of the pygmy right whale, evolving in parallel with *Caperea* as a peculiar small-bodied whale which nearly became a member of the modern fauna.

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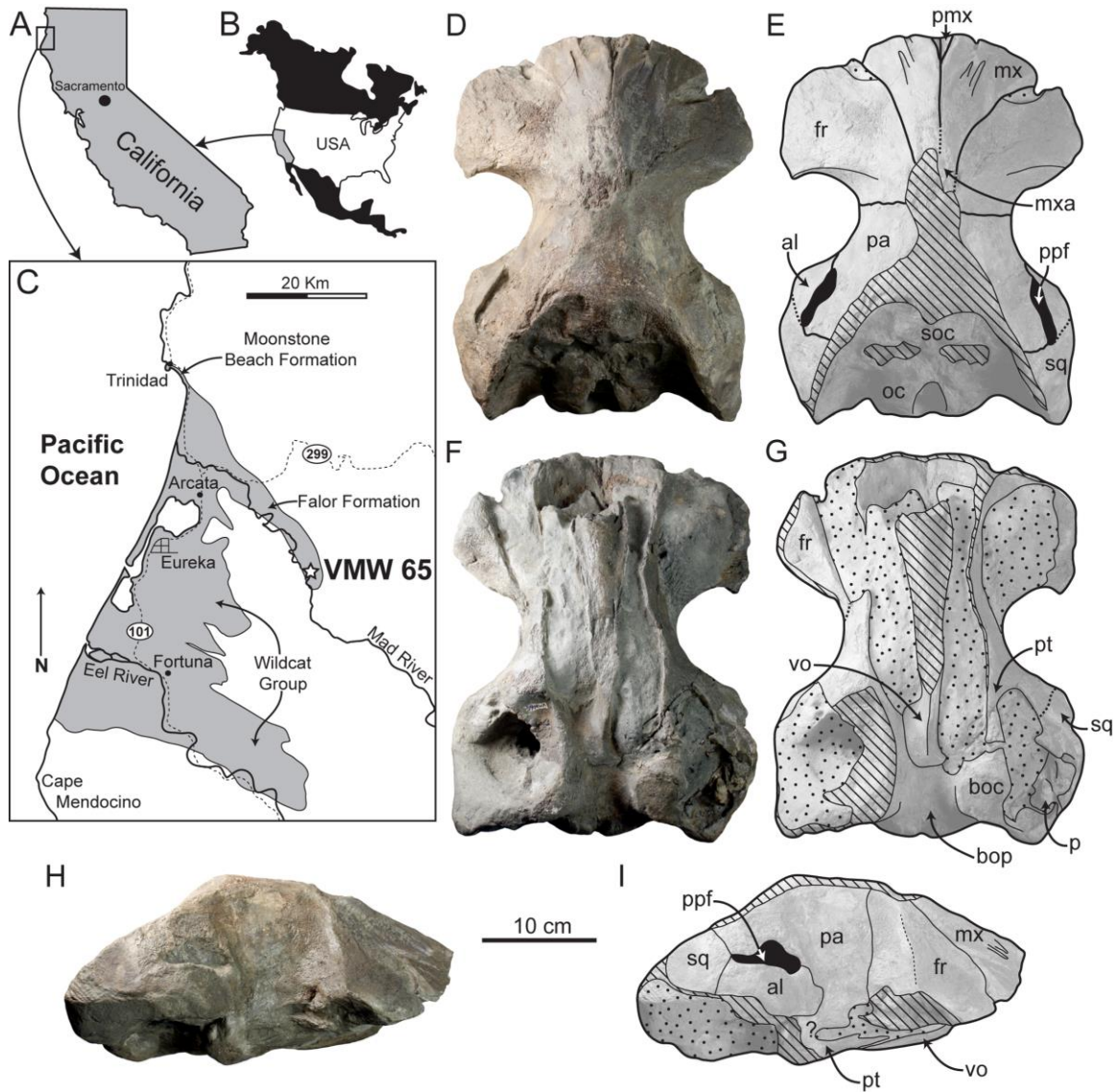
Fig. 1 Locality and partial cranium of *Herpetocetus* sp. Map of California **A**, North America **B**, and **C** Eel River region showing late Neogene sediments of Eel River Basin, Falor Formation, and VMW 65 locality. **D** VMW-65 in dorsal aspect; **E** dorsal interpretive line drawing. F VMW-65 in ventral aspect; **G** ventral interpretive line drawing. **H** VMW-65 in right lateral aspect; **I** lateral interpretive line drawing. Geologic map based on Manning and Ogle (1950) and Kelsey and Carver (1988). Abbreviations: al, alisphenoid; boc, basioccipital crest; bop, basioccipital; fr, frontal; mx, maxilla; mxa, ascending process of maxilla; oc, occipital; p, petrosal; pmx, premaxilla; ppf, postparietal foramen; pt, pterygoid; soc, supraoccipital; sq, squamosal; vo, vomer
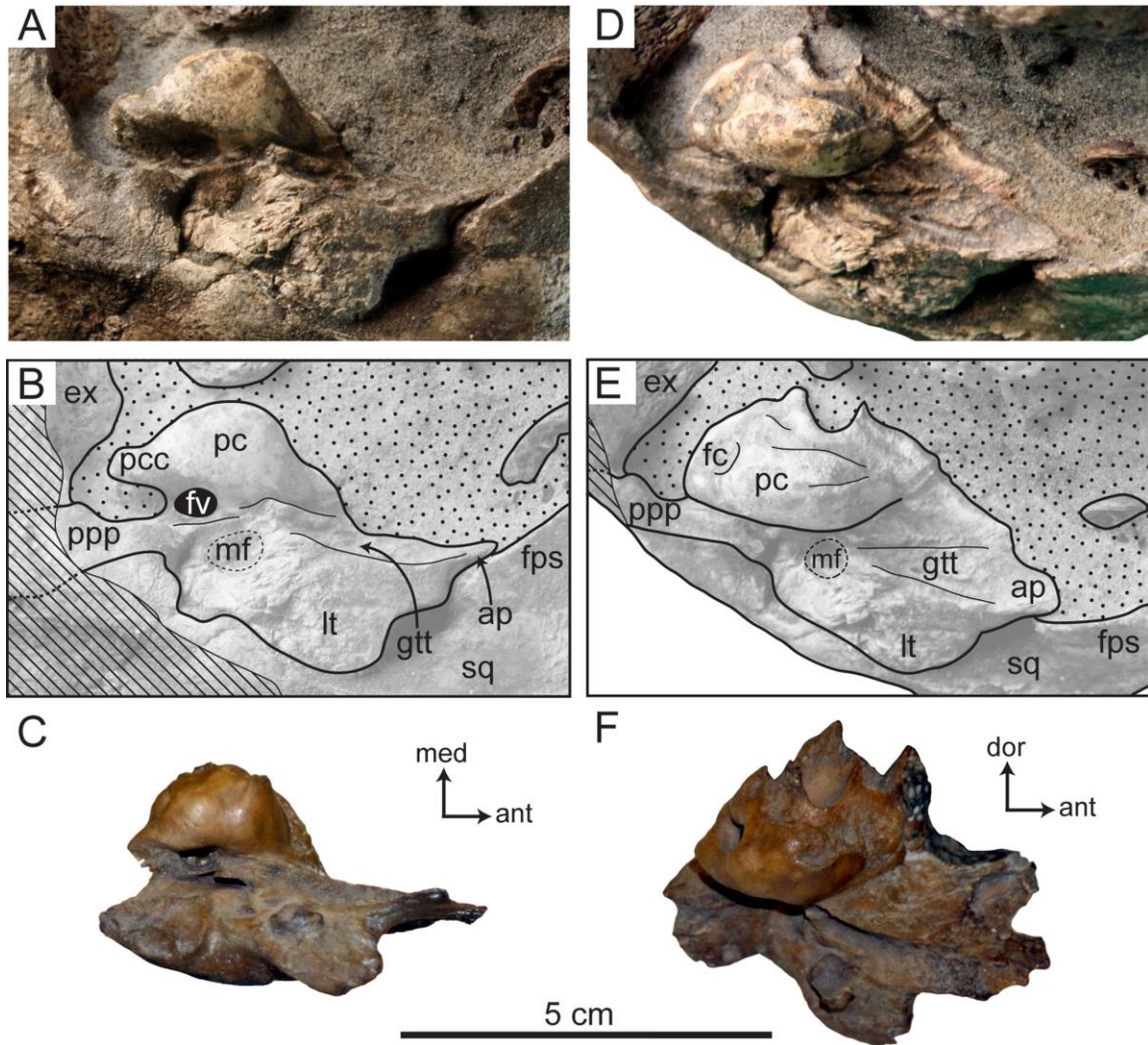
Fig. 2 Petrosals of *Herpetocetus*. **A** petrosal of VMW-65 in ventrolateral aspect; **B** ventrolateral interpretive line drawing. **C** Holotype petrosal of *Herpetocetus bramblei* (UCMP 82465) for comparison in ventrolateral aspect. **D** petrosal of VMW-65 in ventromedial aspect; **E** ventromedial interpretive line drawing. **F** Holotype petrosal of *Herpetocetus bramblei* in ventromedial aspect.. Abbreviations: ant, anterior; ap, anterior process of petrosal; dor, dorsal; ex, exoccipital; fc, fenestra cochleae; fps, falciform process of squamosal; fv, fenestra vestibuli; gtt, groove for tensor tympani muscle; lt, lateral tuberosity; med, medial; mf, mallear fossa; pc, pars cochlearis; pcc, posterior cochlear crest; ppp, posterior process of petrotympanic; sq, squamosal
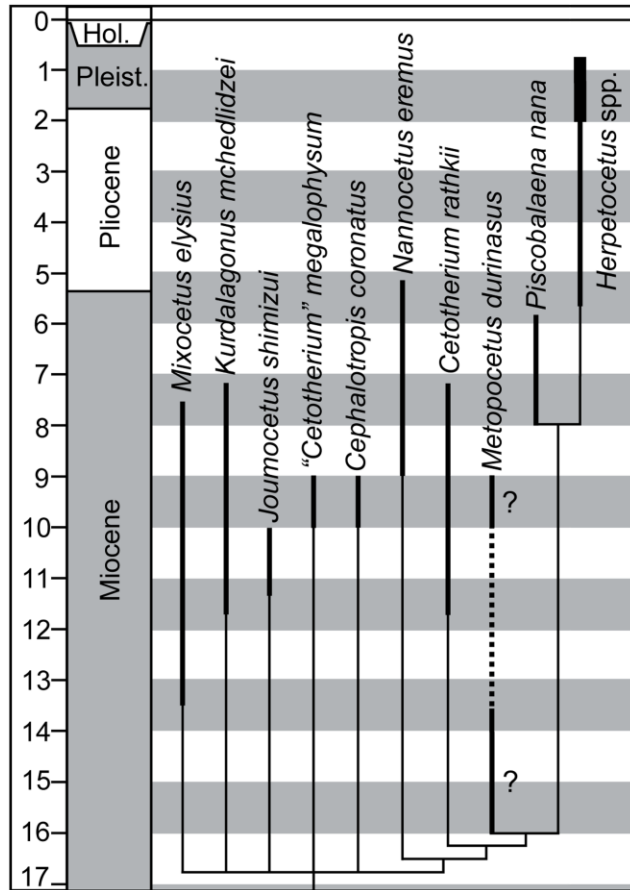
Fig. 3 Time calibrated phylogeny of the Cetotheriidae. Millions of years and geologic epochs on left. Bold line indicates Pleistocene age extension of *Herpetocetus* reported herein. Phylogeny based on Bouetel and Muizon (2006), and other cetotheriids shown unresolved. See supplementary material for stratigraphic ranges of Cetotheriidae.

Electronic Supplementary Material for:

Pleistocene survival of an archaic dwarf baleen whale (Mysticeti: Cetotheriidae)

Robert W. Boessenecker

ESM Contents:
1. Measurements of VMW-65
2. Estimation of body length of VMW-65
3. Discussion of stratigraphic ranges of selected Cetotheriidae (Cetacea: Mysticeti)

1. Measurements of VMW-65

Measurements in mm

Total length as preserved	339
Least intertemporal width	134.62
Exoccipital width	214.26
Transverse width of lateral edges of basioccipital crests	127.88
Transverse width of medial edges of basioccipital crests	43.09
Transverse width of occipital condyles	107.85
Transverse width of foramen magnum	31.91
Dorsoventral depth of foramen magnum	41.85
Anteroposterior length of body of petrosal	58.76
Anteroposterior length of pars cochlearis	32.54

2. Estimation of body length of VMW-65

Two recent studies have presented methods to estimate the body length of extinct mysticetes: Lambert et al. (2011) and Pyenson and Sponberg (2011). Both of these studies advocated the use of bizygomatic width as a predictor of body length; unfortunately, this measurement is not possible due to the incompleteness of VMW-65. However, VMW-65 is nearly identical in size to a nearly complete skull of *Herpetocetus bramblei* (UCMP 219111) from the latest Miocene section of the Purisima Formation near Santa Cruz; for example, their occipital condyle breadth is 107.85 mm (VMW-65) and 108mm (UCMP 219111). If the bizygomatic width of UCMP 219111 is 40 cm; if this is applied to VMW-65, this results in a body length estimate of 3.95 meters (based on Lambert et al., 2010) and 6.16 meters (based on Pyenson and Sponberg, 2011). When examining the regression presented in Lambert et al. (2010: supplementary figure 9), it is apparent that 6.16 meters is an overestimate for a mysticete with 40 cm bizygomatic width, and that at this end of the regression, the scatter about the regression line is of less magnitude than this overestimate. This suggests that the estimate of 3.95 meters is more accurate – which is independently corroborated by the well preserved skeleton of the closely related *Cetotherium riabinini* from the Miocene of Ukraine, which has an approximately 3 m long skeleton and a bizygomatic width of 36.2 cm (Gol'Din et al.,

accepted), approximating the regression line in Lambert et al. (2010: supplementary figure 9).

3. Discussion of stratigraphic ranges of selected Cetotheriidae (Cetacea: Mysticeti)

"*Cetotherium*" *megalophysum* Cope 1895 and *Cephalotropis coronatus* Cope 1895

The holotype specimens of both of these taxa were collected from the Chesapeake Bay region but without detailed stratigraphic data (Cope 1895). Additional referred crania of these taxa have been collected from the St. Mary's Formation in Maryland (e.g. Gottfried et al 1994), suggesting these taxa are Tortonian in age. The age of these taxa can be summarized as 10-9 Ma (Gottfried et al 1994).

Cetotherium rathkii Brandt 1843

The type specimen of *Cetotherium rathkii* was reported from unnamed middle-upper Sarmatian strata of southern Ukraine (Brandt 1873). In deposits of the eastern Paratethys, the middle and upper Sarmatian are roughly equivalent to the Tortonian stage (Radionova et al 2012). Although the original strata which *Cetotherium* was originally collected from remain unknown, the age of *Cetotherium rathkii* is summarized herein as 11.6-7.2 Ma (Tortonian stage).

Herpetocetus spp. Van Beneden 1872

The genus *Herpetocetus* is now represented by several species with a circum-northern hemisphere distribution, including *Herpetocetus* "*sendaicus*" (Japan), *Herpetocetus transatlanticus* (North Carolina, U.S.A.), *Herpetocetus scaldiensis* (Belgium), and *Herpetocetus bramblei* (California, U.S.A.; Whitmore and Barnes 2008). Most of these are early Pliocene in age (Whitmore and Barnes 2008), although *Herpetocetus bramblei* is latest Miocene in age (Whitmore and Barnes 2008; Boessenecker 2011). Fossils of *Herpetocetus bramblei* are present within the Purisima Formation above a 5.6 Ma ash bed and occur up to strata dated to 4.5 Ma via paleomagnetism (Powell et al 2007). Prior to discovery of the new Pleistocene *Herpetocetus* cranium from the Falor Formation, the youngest known record of *Herpetocetus* was from the late Pliocene San Diego Formation (Deméré and Cerutti 1982). The new fossil, in concert with *Herpetocetus bramblei*, indicate a geochronologic range of 5.6-0.7 Ma for the genus.

Although Boessenecker (2011) noted a slightly older fossil he identified as *Herpetocetus* aff. *bramblei* from the 6-6.8 Ma Santa Cruz Mudstone, it exhibits inflated postglenoid processes and thus may represent a young record of *Nannocetus*, and *Herpetocetus bramblei* is here considered to be the oldest record. Further study of Californian herpetocetines is clearly warranted.

Joumocetus shimizui Kimura and Hasegawa 2010

The type specimen of *Joumocetus* was collected from the Haraichi Formation of Gunma Prefecture, Japan, and stratigraphically above the 11.26-11.29 Ma Kamiokoizawa tuff, and stratigraphically below the undated Baba tuff, which has been estimated to be 10 Ma in age (Kimura and Hasegawa 2010). Thus, the geochronologic range of *Joumocetus* is summarized as 11.3-10 Ma.

Kurdalagonus mchedlidzei Tarasenko and Lopatin 2012

The type and only known specimen of *Kurdalogonus* was reported by Tarasenko and Lopatin (2012) as originating from the Blinovo Formation of Adygea in the northwestern Caucasus. According to Tarasenko and Lopatin (2012), the Blinovo Formation is "uppermost middle Miocene, middle Sarmatian". The middle Sarmatian is roughly correlative with the early Tortonian stage in the Eastern Paratethys (Radionova et al 2012), and is summarized herein as 11.6-7.2 Ma (Tortonian stage).

Metopocetus durinasus Cope 1896

The type specimen of *Metopocetus* was originally described by Cope (1896) from the mouth of the Potomac River in Maryland, U.S.A., from an unidentified unit. Subsequent researchers interpreted the type locality as the middle Miocene Calvert Formation (Langhian Stage; Kellogg 1968) or the Saint Mary's Formation (Tortonian; Case 1904). The age of *Metopocetus* is thus summarized as 16-13.6 Ma (Langhian stage) or 10-9 Ma (age of the St. Mary's Formation; Gottfried et al 1994).

Mixocetus elysius Kellogg 1934

The type and only known specimen of *Mixocetus elysius* was collected from the Modelo Formation near Los Angeles, California, U.S.A. (Kellogg 1934). Fritsche (1993) considered the Modelo Formation to be correlative with the Mohnian diatom stage (13.5-7.5 Ma).

Nannocetus eremus Kellogg 1929

Although the type specimen of *Nannocetus eremus* was originally reported from the Pico Formation in the San Gabriel Mountains (Kellogg 1929), later work by Whitmore and Barnes (2008) indicate that the type specimen originated from the Towsley Formation which they considered to be correlative with the "Margaritan" provincial megainvertebrate stage. Whitmore and Barnes (2008) noted that other marine mammals including *Dusisiren jordani* and *Imagotaria downsi* had been previously reported from the same unit, which typify early Late Miocene Tortonian-equivalent marine mammal assemblages (e.g. Monterey Formation, Santa Margarita Sandstone; Repenning and Tedford 1977; Domning 1978; Barnes et al 1985). Whitmore and Barnes (2008) described a partial braincase of *Nannocetus eremus* from the uppermost Santa Margarita Sandstone in Santa Cruz County, California, which has been estimated by Repenning and Tedford (1977) to be approximately 9 Ma in age; they estimated the entire unit to be 12-9 Ma in age. More recent work by Beyer et al (2009) indicates the Towsley Formation has

yielded Delmontian microfossils, and is thus 7.7-5.2 Ma in age. Altogether, this indicates a geochronologic age of 9-5.2 Ma for *Nannocetus eremus*. Additional supporting evidence for such a young age (in comparison to that suggested by Whitmore and Barnes 2008) includes latest Miocene specimens of *Nannocetus* reported by Barnes et al (1981) from the San Mateo Formation near Oceanside in San Diego County, California.

Piscobalaena nana Pilleri and Siber 1989

Fossils of Piscobalaena are well known from the late Neogene Pisco Formation in Peru, and have been reported from the Sud-Sacaco and Aguada de Lomas levels of the Pisco Formation (Bouetel and Muizon 2006). The Aguada de Lomas and Sud-Sacaco levels of the Pisco Formation are roughly 8-7 and 5-4 Ma (Messinian and Piacenzian, respectively; Muizon and deVries 1985). More recently, Ehret et al (2012) have reported a series of strontium isotope dates for the Pisco Formation, which in particular has resulted in a reevaluation of the age of Sud-Sacaco, which has yielded a ^{87}Sr-^{86}Sr date of 5.89 Ma. The geochronologic range of *Piscobalaena* can be summarized as 8-5.89 Ma (Muizon and deVries 1985; Bouetel and Muizon 2006; Ehret et al., 2012).

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