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Miocene whale-fall from California demonstrates that cetacean size did not determine the evolution of modern whale-fall communities

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Whale-fall communities support a deep-sea invertebrate assemblage that subsists entirely on the decaying carcasses of large cetaceans. The oldest whale-falls are Late Eocene in age, but these early whale-falls differ in faunal content and host cetacean size from Neogene and Recent whale-falls. Vesicomyid bivalves, for example, are major components of the sulphophilic stage in Miocene and Recent whale-fall communities, but they are absent from Palaeogene fossil whale-falls. The differences between Palaeogene and Neogene communities led to the hypothesis that the origin of modern whale-fall communities was linked with the evolution of extremely large mysticetes, which provided sufficient biomass and oil to sustain the modern complement of whale-fall invertebrates. Here, we describe a fossil whale-fall community from the Miocene of California, showing vesicomyid bivalves in direct association with a host mysticete smaller than the adult individuals of any living mysticete species. This association, which is the youngest yet reported from the Neogene of North America, demonstrates that body size is not a necessary factor for the formation of modern whale-fall communities. Instead, we suggest that high skeletal oil content may have been a more important factor, which, based on the age of the fossil whale-fall, evolved at least by the Late Miocene.

Keywords: whale-fall; deep-sea communities; Cetacea; Vesicomyidae; fossil record; body size

1. INTRODUCTION

Sunken whale carcasses, or whale-falls, provide an enormous resource in the otherwise nutrient-poor deep-sea (Smith 2006). This large input of biomass to the benthos sustains a diverse community of benthic organisms, and it has been estimated that whale-fall communities can persist on a large decaying cetacean carcass for decades (Smith 2006). Whale-fall communities undergo successional development, culminating in a sulphophilic stage characterized by chemosynthetic bivalves (e.g. vesicomyid and bathymodiolid bivalves) that rely on the decomposition of cetacean bone lipids coupled with sulphate reduction in seawater (Smith & Baco 2003). Some chemosynthetic invertebrates are endemic to whale-falls, while others occur in different chemosynthetic environments, such as cold seeps and hydrothermal vents (Smith & Baco 2003). The presence of cognate invertebrate taxa among whale-fall, seep and vent communities may reflect shared evolutionary origins, but the significant discrepancies between molecular divergence dates and known stratigraphic ranges of these taxa have led to different hypotheses about the timing and mode of the evolution of deep-sea chemosynthetic communities (Smith & Baco 2003; Kiel & Little 2006).

The fossil record of whale-fall communities extends into the Palaeogene, with examples described from the Late Eocene and Oligocene of Washington State (Squires *et al.* 1991; Goedert *et al.* 1995; Nesbitt 2005) and the Miocene of Japan (Amano & Little 2005; Amano *et al.* 2007). The Palaeogene occurrences, however, exhibit a markedly different faunal composition from Neogene or Recent communities. Vesicomyid bivalves are unknown from Palaeogene whale-fall communities, but they are abundant members of Miocene and Recent communities (Goedert *et al.* 1995; Amano *et al.* 2007). Notably, Palaeogene host cetaceans (including both archaic baleen and toothed whales) are smaller in size than any living mysticete known to support modern whale-fall communities (Goedert *et al.* 1995), which led to the hypothesis that modern whale-fall communities formed only with the evolution of large mysticetes with lipid-rich bones (Kiel & Goedert 2006). Here, we report a fossil whale-fall community from the Middle Miocene of California, represented by a small, cetotheriid mysticete skeleton (figure 1*a*), associated with fossil molluscs that are directly attached to the skull and vertebrae (figure 1*a*–*d*). Because the host mysticete is smaller than any species of living baleen whale, this new fossil whale-fall occurrence demonstrates that host body size is not a necessary factor for the formation of modern whale-fall communities.

2. MATERIAL AND METHODS

(a) *Locality and geological age*

The fossil whale-fall locality (University of California Museum of Paleontology (UCMP) V99594) is at the base of the Pleistocene terrace deposit on Año Neuvo Island, California (37°06′27′ N, 122°20′6′ W). Because the mysticete skeleton (UCMP 150000) was recovered as a Monterey Formation clast in the terrace, it is impossible to determine a precise age for the skeleton. The high degree of silicification and induration of the skeletal elements, as well as the presence of abundant Monterey Formation clasts within the terrace, indicate that the specimen originates from the upper Monterey Formation (11–15 Myr old). Diatoms have been recovered from the Monterey Formation on Point Año Neuvo, located on the mainland approximately 1 km from the island, and they are assignable to subzone b of the *Denticulopsis lauta* Zone of the Pacific Coast of North America (Middle Miocene, 13.5–15.5 Myr old; Barron 1986; L. D. White 1989, Unpublished PhD dissertation). Benthic foraminifers recovered from the same location (Barron 1986) indicate a Luisian age, consistent with the diatom data, and the basal cherty layers of Monterey Formation at Point Año Nuevo are estimated to be 14.7–15 Myr old (L. D. White 1989, Unpublished PhD dissertation). Independent biostratigraphic evidence thus provides a lower age constraint of 15 Myr old for the fossils from the locality.

(b) *Mysticete host and molluscan assemblage*

The host mysticete skeleton (UCMP 150000) represents an undescribed species of cetotheriid mysticete (Bouetel & de Muizon 2006). The skeleton represents a subadult individual close to adult

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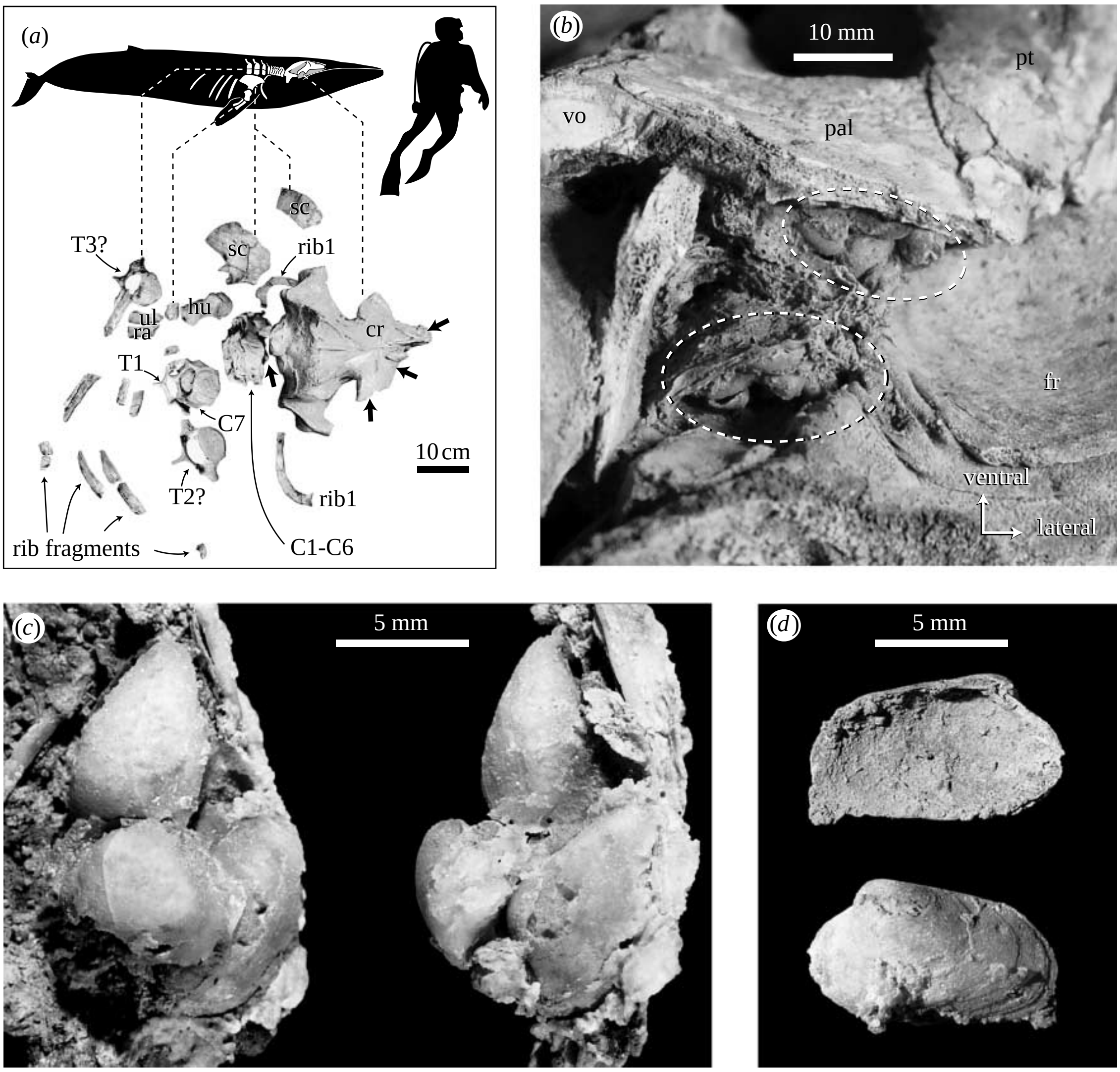

Figure 1. Fossil whale-fall community from Año Nuevo Island. (*a*) UCMP 150000, cetotheriid mysticete arranged according to quarry maps, dorsal surface up. Mysticete silhouette indicates location of elements via dashed lines to quarry arrangement. Thick arrows indicate location of associated molluscs. (*b*) Clusters of vesicomyid bivalves encrusted on the right orbit of the skull, in oblique ventral view, highlighted by circles. (*c*) Close-up of UCMP 55526, a cluster of three vesicomyid bivalves removed from the skull, in perpendicular views. (*d*) UCMP 55522, an isolated vesicomyid found on the skeleton, in internal (top) and external (bottom) views. C, cervical vertebra; cr, cranium; fr, frontal; hu, humerus; pal, palatine; pt, pterygoid; ra, radius; T, thoracic vertebra; sc, scapula; ul, ulna; vo, vomer.

size, based on cranial suture fusion, measurements from living mysticetes (Lockyer 1976) and other members of this mysticete group (Bouetel & de Muizon 2006). Regardless of skeletal maturity, the estimated total length of the host mysticete (3.3 m) is almost half that of the smallest living mysticete species, the pygmy right whale (*Caperea marginata,* 5.5–6.5 m; Nowak 1999). We reconstructed total length based on a proxy measurement of the skull (width across the exoccipital processes), using regressions from a database of skull and skeletal measurements of all living mysticete species (Pyenson & Sponberg 2007). Fossil molluscs recovered from the mysticete skeleton include 21 individual bivalves (UCMP 55522–55532) and 1 gastropod (UCMP 55521).

3. RESULTS AND DISCUSSION

The partially articulated skeleton was collected from a Pleistocene marine terrace that unconformably overlies the upper Monterey Formation of Año Nuevo Island, California, and all the available evidence indicates that it was exhumed and reburied prior to the Recent. During preparation, 22 silicified molluscs (including 21 bivalves and 1 gastropod) were recovered from the skull and cervical vertebrae. The bivalves are small (less than 1 cm in length), occur in clumps and are predominately preserved as casts and moulds in fissures and crevices on the skull (figure 1*b–d*), with very few found elsewhere on the skeleton. The best preserved bivalve specimen (figure 1*d*) exhibits heterodont dentition with a large and well-developed ligament pit on the hinge plate. Externally, the shell is elongated posterior to the well-developed umbo and exhibits an anteriorly directed beak. This combination of features is most consistent with Vesicomyidae (Coan *et al.* 2000). The shell morphology of other bivalve specimens recovered from UCMP 150000 is poorly preserved, but given their similar size, they are provisionally referred to Vesicomyidae. Many of the vesicomyids are directly cemented to multiple elements of the skeleton, and therefore, their association with the skeleton does not appear to be the result of transport and deposition by currents. We interpret this fossil association as a whale-fall community based on several criteria (Smith & Baco 2003): the preservation of the mysticete skeleton in articulation, like host skeletons in modern communities; its origin from a bathyal facies of the Monterey

Formation indicating a palaeodepth consistent with modern whale-fall communities; and the presence of invertebrate taxa (vesicomyids) whose modern representatives harbour chemosymbionts and also occur in whale-fall communities.

The Año Nuevo whale-fall is the first fossil whale-fall community from California, and the first yet documented from the Neogene of the eastern North Pacific Ocean. Most examples of fossil whale-fall communities are based on cetacean–mollusc associations with isolated and non-diagnostic host skeletal elements that are contained in calcareous concretions (Goedert *et al.* 1995). In contrast, the Año Nuevo whale-fall community preserves a partial skull and skeleton in articulation and includes molluscs in direct association with the skeletal elements. More importantly, it exhibits a modern complement of chemosynthetic bivalves, characterized by vesicomyids, indicating a sulphophilic-stage community. The host mysticete is smaller than any modern whale-fall mysticete host (reconstructed length, 3.3 m; Pyenson & Sponberg 2007), suggesting that host body size did not constrain the origin of modern whale-fall communities (Kiel & Goedert 2006). Lipid content remains a possible factor, and the age of the Año Nuevo whale-fall indicates that high lipid content in mysticete bone (Robineau & de Buffrénil 1993) originated at least by the Late Miocene (approx. 11 Ma), providing a minimum time origin for modern whale-fall communities.

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