LETTERS

The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru

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The modern giant sperm whale *Physeter macrocephalus*, one of the largest known predators, preys upon cephalopods at great depths[1,2]. Lacking a functional upper dentition, it relies on suction for catching its prey[3]; in contrast, several smaller Miocene sperm whales (Physeteroidea) have been interpreted as raptorial (versus suction) feeders[4,5], analogous to the modern killer whale *Orcinus orca*. Whereas very large physeteroid teeth have been discovered in various Miocene localities, associated diagnostic cranial remains have not been found so far[6–8]. Here we report the discovery of a new giant sperm whale from the Middle Miocene of Peru (approximately 12–13 million years ago), *Leviathan melvillei*, described on the basis of a skull with teeth and mandible. With a 3-m-long head, very large upper and lower teeth (maximum diameter and length of 12 cm and greater than 36 cm, respectively), robust jaws and a temporal fossa considerably larger than in *Physeter*, this stem physeteroid represents one of the largest raptorial predators and, to our knowledge, the biggest tetrapod bite ever found. The appearance of gigantic raptorial sperm whales in the fossil record coincides with a phase of diversification and size-range increase of the baleen-bearing mysticetes in the Miocene. We propose that *Leviathan* fed mostly on high-energy content medium-size baleen whales. As a top predator, together with the contemporaneous giant shark *Carcharocles megalodon*, it probably had a profound impact on the structuring of Miocene marine communities. The development of a vast supracranial basin in *Leviathan*, extending on the rostrum as in *Physeter*, might indicate the presence of an enlarged spermaceti organ in the former that is not associated with deep diving or obligatory suction feeding.

With adult males reaching a body length of 18.3 m, the modern sperm whale *Physeter macrocephalus* is one of the largest macropredators ever found. It preys primarily on squid, which it usually hunts at great depths[1,2]. Lacking functional upper dentition, *Physeter* ingests and swallows its prey by suction[3], whereas its lower teeth are mostly used in social interactions[9,10]. However, a raptorial feeding behaviour analogous to that of the modern killer whale *Orcinus orca* has been proposed for several Miocene fossil sperm whales bearing functional upper teeth[4,5,11]. All these taxa are considerably smaller than *Physeter*. For more than a century, isolated large physeteroid teeth with a diameter of 7–9 cm and a maximum length of 27 cm, found in various Neogene localities worldwide, indicated that unusually large sperm whales roamed the oceans in the past[6,7]. But except for fragments of rostrum and mandible from the Miocene of California[8], no known fossil sperm whale could match the size of these teeth, precluding any hypothesis on the diet and feeding strategy of these animals. Here we report the discovery of a giant physeteroid skull from the Miocene of the Pisco basin, Peru, with an associated set of very large teeth and mandible.

Cetacea
Neoceti
Odontoceti
Physeteroidea
Leviathan melvillei gen. et sp. nov.

Etymology. From Hebrew 'Livyatan' ('Leviathan' in Latin); name applied to large marine monsters in popular and mythological stories. Species is dedicated to novelist Herman Melville (1819–1891).
Holotype. Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM) 1676, 75% complete skull, including rostrum with damaged maxillary teeth embedded and the right side of the cranium with dentaries and ten isolated teeth associated (Fig. 1, Supplementary Figs 1–5 and Supplementary Tables 1–6).
Locality. Cerro Colorado, Pisco-Ica desert, 35 km south-southwest of Ica, southern coast of Peru, 14° 20′ 13.4′′ S, 75° 54′ 25.2′′ W.
Horizon. Lowest beds of Pisco Formation, late Middle Miocene, Serravallian stage, about 12–13 million years ago (see Supplementary Information).
Diagnosis. Large stem physeteroid (Fig. 2) defined by two unequivocal autapomorphies: great anterior expansion of the premaxilla on the wide rostrum, reaching the lateral margin of the latter; and maximum tooth diameter greater than 10 cm for most of the dentition. It further differs from all other physeteroids except *Physeter* in the elongated supracranial basin extending along the whole length of the rostrum, and from *Kogia*, *Physeter* and some related fossil forms in the retention of a functional upper dentition and enamel on the teeth.

With a skull length of about 3 m and a skull width of 190 cm, *Leviathan melvillei* is the largest known fossil physeteroid. Body length is estimated at 13.5–17.5 m (see Supplementary Information), in the range of adult male *Physeter*[1]. The rostrum is short, slightly longer than the cranium, with a wide base and thick outer margins laterally convex in the anterior portion (Fig. 1). The laterally expanded premaxillae form the floor of the distal part of the elongated supracranial basin. This anterior extension of the basin, only observed as such in *Physeter*, is an indication of the presence of a large spermaceti organ, which, as in *Physeter*, would have reached the anterior tip of the rostrum. The deep neurocranial portion of the supracranial basin is margined laterally by the maxilla, which leaves the posterior wall of the basin uncovered.

Eleven deep alveoli are found in the dentary, and nine in the maxilla. Except for some specimens of the extant dwarf and pygmy sperm whales *Kogia* spp.[12], this is the lowest dentary tooth count in a

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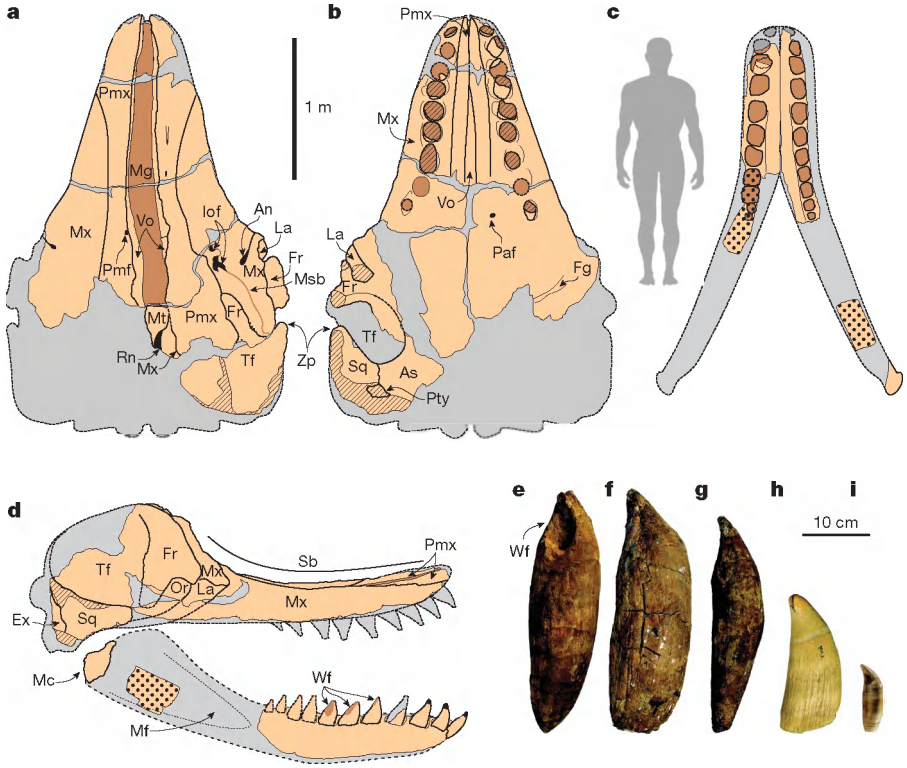


Figure 1 | Skull, mandible and tooth morphology of the holotype of *L. melvillei* MUSM 1676. a–d, Schematic drawings of skull and mandible. Skull in dorsal (**a**) and ventral (**b**) view, mandible in dorsal view (**c**), skull and mandible in right lateral view (**d**). **e–g**, Right lower teeth in labial view. **h, i**, Teeth of modern sperm whale *Physeter* (**h**) and killer whale *Orcinus* (**i**) for comparison. An, antorbital notch; As, alisphenoid; Ex, exoccipital; Fg, frontal groove; Fr, frontal; Iof, infraorbital foramen; La, lacrimal; Mc, mandibular condyle; Mf, mandibular foramen; Mg, mesorostral groove; Msb, margin supracranial basin; Mt, mesethmoid; Mx, maxilla; Or, orbit; Paf, palatine foramen; Pmf, premaxillary foramen; Pmx, premaxilla; Pty, posterior process tympanic; Rn, right bony naris; Sb, supracranial basin; Sq, squamosal; Tf, temporal fossa; Vo, vomer; Wf, wear facet; Zp, zygomatic process squamosal.

physeteroid. Together with the premaxilla and the vomer, the maxilla reaches the apex of the rostrum; no premaxillary alveoli are present. The maxillary alveolar groove is offset internally from the lateral margin of the rostrum, a condition differing from other fossil physeteroids. Only partial roots of maxillary teeth were preserved *in situ*, but several lower teeth are complete. With a maximum diameter ranging from 8.1 to 12.1 cm and a total length of more than 36.2 cm, these teeth are much larger than the largest recorded teeth of *Physeter* (25 cm[1]; Fig. 1h). Combined with the length of the jaws, this represents one of the largest bites for vertebrates and certainly the biggest bite for tetrapods. The enamelled crown is low with a small diameter. The robust root is covered with a thick layer of cement, typical of continuously growing sperm whale teeth[13]. Apical lower teeth are more recurved than the nearly cylindrical and massive other teeth. Deep vertical wear facets on either the distolabial or mesiolabial surface of the dentary teeth indicate that the upper and lower teeth occluded for a long distance, suggesting an important shearing component during the bite. To accommodate the large roots, the alveolar-bearing part of the mandible is deep and wide. The anterior part of the rostrum is upturned, and the anterior upper and lower teeth project forwards at an angle of approximately 45°.

The enormous temporal fossa is much longer anteroposteriorly than the orbit area of the skull, which differs from the small fossa of *Physeter* (Fig. 3). The wide space between the zygomatic process of squamosal and the medial surface of the temporal fossa indicates that the fossa could accommodate a large volume of musculus temporalis.

There is a short and wide rostrum allowing a more powerful bite by the anterior teeth and better resistance to lateral movements of the struggling prey[14], procumbent anterior teeth for grasping voluminous prey with moderately convex body surfaces, very robust upper and lower teeth deeply embedded in the jaw bones, a deep and wide tooth-bearing portion of the dentary and a vast temporal fossa. This is indicative of feeding by means of raptorial predation for *Leviathan*, as in several other, much smaller, Miocene physeteroids, but strongly contrasts with the suction feeding adaptations of *Physeter*.

This sperm whale could firmly hold large prey with its interlocking teeth, inflict deep wounds and tear large pieces from the body of the victim, as performed on a smaller scale by the delphinid *Orcinus*, the main modern meat-eating cetacean[15,16]. With a maximum body size under 9 m and a skull length of about 1 m, *Orcinus* has been reported occasionally to cooperatively attack and kill most of the large baleen whale species and sperm whales[17,18], as well as smaller odontocetes, pinnipeds, fish, seabirds and cephalopods[1].

Besides small-to-medium size odontocetes, the most common marine mammals in Cerro Colorado are mysticetes (more than 20 skeletons of a new cetotheriid with a body length approaching 10 m have been found). A similarly large number of 5–13-m-long mysticetes has been described in other Miocene localities of the Pisco Formation, related to high local productivity[19]. More generally, Serravallian to Tortonian stages correspond to a peak of diversity for cetaceans[20,21], and particularly for mysticetes[22] (Fig. 4a and Supplementary Information).

With their large size and robust jaws, *Leviathan* adults were surely free from predation. However, besides being an antipredator strategy (large sharks are abundant in Cerro Colorado) and/or having thermal advantages, when associated with an efficient raptorial feeding apparatus gigantism allows preying upon larger animals[23,24]. A correlation between the emergence of the giant shark *Carcharocles megalodon* and the Miocene diversification of the mysticetes has already been proposed[22,25]. Considering the distinct increase in the range of sizes for mysticetes since the Langhian stage, progressively reaching greater maximum sizes (Fig. 4b and Supplementary Information), the record

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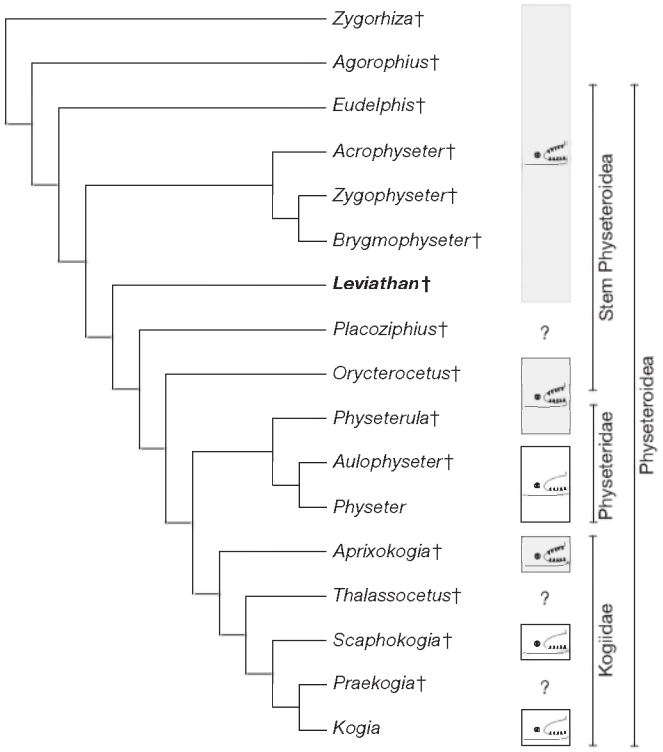


Figure 2 | Phylogeny of physeteroids illustrating the relationships of *Leviathan* with other stem physeteroids, physeterids and kogiids. A maximum parsimony cladogram obtained with a PAUP (phylogenetic analysis using parsimony) branch-and-bound search, using a data set modified from previous works. The consistency (CI) and retention (RI) indices of the single shortest tree are 0.61 and 0.65, respectively. Schematic skulls illustrate the presence or absence of functional upper dentition in each taxon. Question marks indicate unknown condition. The daggers indicate extinct species. See Supplementary Information for further details.

of two giant marine predators, *C. megalodon* and *L. melvillei*, in the same mysticete-rich Serravallian locality might be relevant. Functionally able to feed on other groups of marine animals, including large fish, pinnipeds and odontocetes, *Leviathan* may have predominantly preyed on higher-energy content medium-size mysticetes, which would have provided the large amount of fat required to fulfil

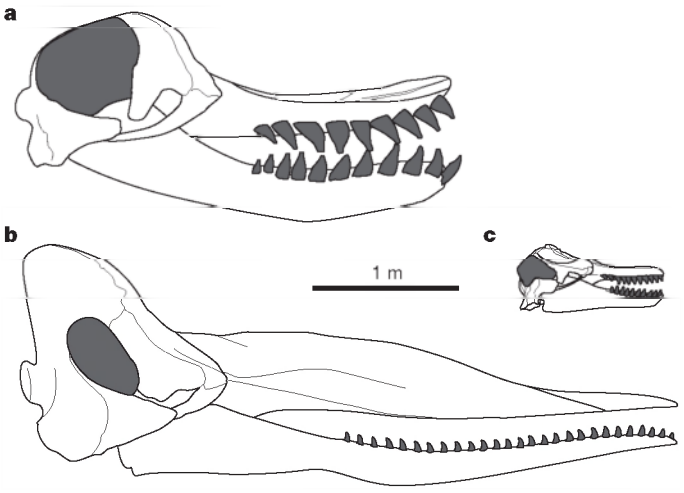


Figure 3 | Comparison of the outline of the skull and mandible of *Leviathan* with modern giant sperm whale *Physeter* and killer whale *Orcinus*. **a**–**c**, Skull and mandible of *Leviathan* (**a**), *Physeter* (**b**) and *Orcinus* (**c**), in right lateral view. Note the large size and proportionally large temporal fossa and teeth of *Leviathan*. All outlines are to the same scale.

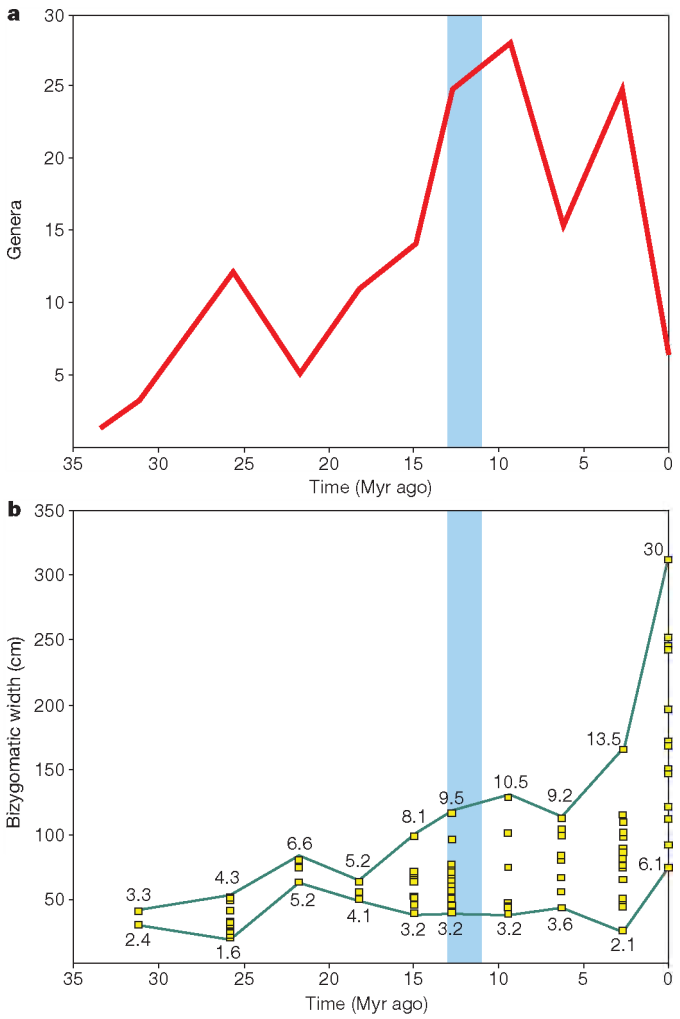


Figure 4 | Evolution of the diversity and size of mysticetes from Oligocene to present. **a**, Plot of the number of mysticete genera for each stage against time. **b**, Plot of the bizygomatic width (in centimetres) of the skull of mysticete specimens for each stage against time. The numbers on the graph indicate total body length estimates (in metres) for maximum and minimum bizygomatic width for each stage (see Supplementary Information for data and equation). The thick vertical line corresponds to the age of the sediments in which *Leviathan* was discovered. Pliocene is considered as a single time interval. Myr, millions of years.

the high caloric demands of this huge endothermic aquatic predator (for comments on energetic value of the prey species of *Orcinus*, see ref. 26).

Furthermore, large physeteroid teeth found in other Miocene localities worldwide[6,7] indicate that giant raptorial sperm whales occupied a top predator position in various marine regions during the Miocene, a role now mostly taken by *Orcinus*. As such, the appearance of these sperm whales probably had a profound impact on the structuring of Middle to Late Miocene marine communities and food chains, similar to the impact of *Orcinus*[15,22,27].

Although they bear a notably similar long supracranial basin, the modern physeterid *Physeter* and the stem physeteroid *Leviathan* are not closely related and the latter seems to have occupied a completely different ecological niche. This information should be taken into account during future discussion of the potential function(s) (buoyancy regulation, echolocation, acoustic stunning of prey, acoustic display, battering ram for intraspecific aggressions) and evolutionary history of the spermaceti organ, which fills the supracranial basin in *Physeter*[28,29]. We propose that the enlarged basin was not associated with deep diving, obligate suction feeding or teuthophagy in *Leviathan*.

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The specialized ecology emerging in the lineage of *Physeter* allowed members of this lineage to survive the late Neogene physical and faunal changes (cooling following the mid-Miocene climatic optimum[30], a drop in diversity and increased size for some mysticetes (Fig. 4), Pliocene diversification of delphinids[23] etc.), co-occurring with the extinction of all raptorial sperm whales. Further data on the timing of this extinction and the appearance of large raptorial delphinids during the Pliocene will be crucial to investigate further this marked ecological replacement and its relationships with other late Neogene events.

METHODS SUMMARY

The holotype of *Leviathan melvillei* was discovered by K.P. during our fieldtrip in the Pisco basin in November 2008. It was mechanically prepared and mounted at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, where it will be curated.

See Supplementary Information for measurements and further photos of the skull, mandible and teeth.

The body length of *L. melvillei* was estimated based on measurements of two physeteroids: the modern *Physeter macrocephalus* and the Miocene *Zygophyseter varolai*. See Supplementary Information for data sets, references, calculations and a life reconstruction of *L. melvillei*.

The phylogenetic analysis was undertaken based on a modified existing matrix of morphological characters. See Supplementary Information for a list of characters, the matrix and the details of the analysis including bootstrap values.

The evolution of diversity and size for mysticetes since the Oligocene was investigated mostly based on the Paleobiology Database Online Systematics Archive 9, Cetacea, compiled by M. D. Uhen, and bibliographical data. We measured some extra specimens, mostly from the Neogene of Peru. See Supplementary Information for data lists, equations and related references.

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1. Rice, D. W. in *Handbook of Marine Mammals* Vol. 56 (eds Ridgway, S. H. & Harrison, R.) 177–233 (Academic, 1989).
2. Watwood, S. L., Miller, P. J. O., Johnson, M., Madsen, P. T. & Tyack, P. L. Deep-diving behaviour of sperm whales (*Physeter macrocephalus*). *J. Anim. Ecol.* **75,** 814–825 (2006).
3. Werth, A. J. Functional anatomy of the sperm whale tongue, with reference to suction feeding. *Aquat. Mamm.* **30,** 405–418 (2004).
4. Bianucci, G. & Landini, W. Killer sperm whale: a new basal physeteroid (Mammalia, Cetacea) from the Late Miocene of Italy. *Zool. J. Linn. Soc.* **148,** 103–131 (2006).
5. Lambert, O., Bianucci, G. & de Muizon, C. A new stem-sperm whale (Cetacea, Odontoceti, Physeteroidea) from the latest Miocene of Peru. *C. R. Palevol.* **7,** 361–369 (2008).
6. Leidy, J. Description of vertebrate remains, chiefly from the phosphate beds of South Carolina. *J. Acad. Nat. Sci. Phila.* **8,** 209–261 (1877).
7. Abel, O. Les Odontocètes du Boldérien (Miocène supérieur) des environs d'Anvers. *Mém. Mus. R. Hist. Nat. Belg.* **3,** 1–155 (1905).
8. Kellogg, R. Two fossil physeteroid whales from California. *Contr. Paleontol. Carnegie Inst. Wash.* **348,** 1–34 (1925).
9. Kato, H. Observation of tooth scars on the head of male sperm whale, as an indication of intra-sexual fighting. *Sci. Rep. Whales Res. Inst.* **35,** 39–46 (1984).
10. Whitehead, H. *Sperm Whales: Social Evolution in the Ocean* (Univ. Chicago Press, 2003).
11. Hirota, K. & Barnes, L. G. A new species of Middle Miocene sperm whale of the genus *Scaldicetus* (Cetacea; Physeteridae) from Shiga-Mura, Japan. *Isl. Arc* **3,** 453–472 (1996).
12. Caldwell, D. K. & Caldwell, M. C. in *Handbook of Marine Mammals* Vol. 4 (eds Ridgway, S. H. & Harrison, R.) 235–260 (Academic, 1989).
13. Hohn, A. A. in *Encyclopedia of Marine Mammals* 2nd edn (eds Perrin, W. F., Würsig, B. & Thewissen, J. G. M.) 11–18 (Academic, 2009).
14. Taylor, M. A. Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England. *Philos. Trans. R. Soc. Lond. B* **335,** 247–280 (1992).
15. Dalheim, M. E. & Heyning, J. E. in *Handbook of Marine Mammals* Vol. 6 (eds Ridgway, S. H. & Harrison, R.) 281–322 (Academic, 1999).
16. Werth, A. J. in *Feeding: Form, Function, and Evolution in Tetrapod Vertebrates* (ed. Schwenk, K.) 487–526 (Academic, 2000).
17. Jefferson, T. A., Stacey, P. J. & Baird, R. W. A review of killer whale interactions with other marine mammals: predation to co-existence. *Mammal Rev.* **21,** 151–180 (1991).
18. Reeves, R. R., Berger, J. & Clapham, P. J. in *Whales, Whaling, and Ocean Ecosystems* (eds Estes J. A. *et al.*) 174–187 (Univ. California Press, 2006).
19. Brand, L. R., Esperante, R., Chadwick, A. V., Pomas, O. & Alomía, M. Fossil whale preservation implies high diatom accumulation rate in the Miocene–Pliocene Pisco Formation of Peru. *Geology* **32,** 165–168 (2004).
20. Uhen, M. D. & Pyenson, N. D. Diversity estimates, biases, and historiographic effects: resolving cetacean diversity in the Tertiary. *Palaeontol. Electronica* **10,** 11–22 (2007).
21. Marx, F. G. Marine mammals through time: when less is more in studying palaeodiversity. *Proc. R. Soc. Lond. B* **276,** 887–892 (2009).
22. Lindberg, D. R. & Pyenson, N. D. in *Whales, Whaling, and Ocean Ecosystems* (eds Estes J. A. *et al.*) 67–81 (Univ. California Press, 2006).
23. Fordyce, R. E. & de Muizon, C. in *Secondary Adaptation of Tetrapods to Life in Water* (eds Mazin, J.-M. & de Buffrénil, V.) 169–233 (Dr. Friedrich Pfeil, 2001).
24. Hone, D. W. E. & Benton, M. J. The evolution of large size: how does Cope's Rule work? *Trends Ecol. Evol.* **20,** 4–6 (2005).
25. Purdy, R. 1996. in *Great White Sharks: the Biology of* Carcharodon carcharias (eds Klimley, A. P. & Ainley D. G.) 67–78 (Academic, 1996).
26. Williams, T. M., Estes, J. A., Doak, D. F. & Springer, A. M. Killer appetites: assessing the role of predators in ecological communities. *Ecology* **85,** 3373–3384 (2004).
27. Springer, A. M. *et al.* Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling. *Proc. Natl Acad. Sci. USA* **100,** 12223–12228 (2003).
28. Cranford, T. W. The sperm whale's nose: sexual selection on a grand scale? *Mar. Mamm. Sci.* **15,** 1133–1157 (1999).
29. Carrier, D. R., Deban, S. M. & Otterstrom, J. The face that sank the Essex: potential function of the spermaceti organ in aggression. *J. Exp. Biol.* **205,** 1755–1763 (2002).
30. Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292,** 686–693 (2001).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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