Meloro, C

Evolution: The shape of cetacean skulls through deep time

Meloro, C ORCID logoORCID: https://orcid.org/0000-0003-0175-1706 (2022) Evolution: The shape of cetacean skulls through deep time. Current Biology, 32 (10). R457-R481. ISSN 0960-9822

DISPATCH

Evolution: the shape of cetacean skulls through deep time

Carlo Meloro

Research Centre in Evolutionary Anthropology and Palaeoecology, School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK. E-mail: C.Meloro@ljmu.ac.uk

Cetaceans (comprising whales, dolphins and porpoises) adapted towards a fully aquatic lifestyle. These adaptations are especially evident in their skull. Based on a rich sample of fossil and extant cetacean skulls, a new study identifies links between shape changes and ecological specialisation through deep time.

Whales, dolphins and porpoises are the main representatives of a unique group of mammals: the cetaceans. Cetaceans are characterized by a fusiform body shape, flippers, flukes and blowholes, and provide a classic example of evolutionary adaptations towards fully aquatic lifestyle[1]. Nonetheless, the cetacean diversity we are able to observe nowadays is only the tip of a much broader variety of species that started their evolutionary journey during the early Eocene[2], a period when the Earth was much warmer than today (Figure 1). Fossils of the earliest cetaceans date to 53.5 million years ago and include semi-aquatic species that had not evolved flippers yet[3]. These early representatives are classified within the Archaeoceti, a subgroup that subsequently colonised and dominated the oceans for more than 30 million years. It is not until the end of the Eocene, about 35 million years ago, that we find evidence of the earliest Neoceti, a larger clade that includes baleen (Mysticeti) and toothed whales (Odontoceti), of which about 10 and 70 species, respectively, are alive today. In mysticetes the typical vertebrate teeth were reduced and eventually lost quite early during their evolution in favour of a highly efficient filter-feeding system involving baleen, a laminar structure made up of keratin. This unique feeding strategy interplayed with the onset of oceanographic upwelling cycles ~3.6 million years ago to favour the evolution of gigantic species[4,5], with the blue whale holding the record within the animal kingdom reaching up to 190 tonnes of body mass. In contrast, odontocetes evolved homodonty and polydonty (a higher number of homogeneous teeth compared to the ancestral mammalian condition) and include a much more diverse range of species from the relatively small vaquita (~50 kg) to the giant sperm whale (~66 tonnes). The evolutionary steps towards living cetaceans have been clearly depicted by embryological studies, supplied by the detailed description of key fossil species that provide evidence for the extreme skeletal modifications associated with the acquisition of fully aquatic lifestyle[6]. However, the tempo and mode of evolution of such an incredible transition from a small, terrestrial hoofed mammal ancestor to fully aquatic whales, dolphins and porpoises remain to be clarified. In a new study, in this issue of *Current Biology*, Ellen Coombs and colleagues[7] assemble one of the largest datasets of 3D models for extant and extinct cetacean skulls and provide a complex picture of their evolutionary transitions through deep time.

During cetacean evolution, the skull underwent an incredibly complex re-organisation with some bones (mainly the maxilla and premaxilla) extending backwards to form a 'telescope'-like shape in living whales and dolphins[8] (Figure 1). Quantifying such a spatial shift in the skull of several hundreds of species is quite challenging. By using 3D spatial coordinates of highly dense anatomical landmarks, Coombs and colleagues[7] describe the diversity of skull shapes in the living and extinct cetaceans in remarkable detail. This dataset was supported by a time-calibrated phylogeny that allows quantification of evolutionary rates, which tell us how fast or slow shape changes occur since the Eocene. As evidenced for many other mammalian and, more generally, vertebrate clades[9], Coombs and colleagues[7] found that skull shape markedly differs between major cetacean subgroups, each showing unique adaptive features and distinctive patterns in tempo and mode of evolution.

Even though Archaeoceti are underrepresented in the studied sample due to the scarcity of complete fossils, Coombs and colleagues[7] found that their skulls rapidly changed shape during evolution, possibly due to the lack of competition and novel opportunities provided by their initial colonisation of the aquatic environment (Figure 1). For the odontocetes, the authors found intermediate rates of skull shape change, although their morphological diversity is much higher than that of all the other groups. The mysticete skulls showed the slowest evolutionary pace. These different patterns in evolutionary rates are accompanied by a complex interplay between skull shape and ecological adaptations, which for cetaceans include echolocation, feeding modes and habitats. A sonar system evolved exclusively in odontocetes and is associated with higher rates of shape change for bones in the skull, specifically the frontal and the premaxilla. The latter accommodates the melon, a mass of adipose tissue that focuses and modulates high-frequency vocalizations, and is among the most asymmetric parts of the odontocete skull[10]. One feeding mode, piscivory (dietary specialisation for eating fish) equally favoured a broad diversification in skull shape of toothed whales, while filter feeding maintained relatively low levels of diversification for the baleen whales. Still, a peak in evolutionary rates of skull shape is detectable for mysticetes in the late Oligocene when some species may have possessed both teeth and proto-baleen. Habitat adaptation also plays a role in explaining morphological evolution of cetacean skulls. For instance, deep-diving sperm whales showed high rates of evolution during the Miocene when several specialised forms of suction feeding evolved (Figure 1). On the other hand, riverine dolphins, such as the Amazon river dolphin, exhibit low diversification in skull shape. The suite of adaptations adopted by freshwater dolphins in separate continents is quite specific and relates to their piscivorous diet, such that similar skull designs evolved and were maintained through time[11].

Mapping cetacean morphological evolution against the climate record[12] allows us to appreciate how these deep time evolutionary trends connect with episodes of climatic shifts followed by changes in oceanic water circulation (Figure 1). Still, a more precise assessment is required accounting for the inevitable gaps in the fossil record. Extensive datasets recording mammalian skull shape changes through deep time remain rare. However, surface scanning and 3D modelling continuously improve access to fossil specimens[13], and time is ripe to fully understand complex evolutionary transitions. Can we predict the future of cetaceans based on current models of morphological evolution? The palaeontologist Stephen Jay Gould[14] noted that 're-playing the tape of life' might not yield the same creatures we observe today, and the simulation of long-term evolutionary changes can be very difficult to accomplish. Morphological data coupled with phylogenetic information provide vital additional toolkits to better understand — and preserve — species diversity. Cetaceans, in particular, demonstrate how fragile our aquatic environments can be, and as deep time evolutionary patterns in their skull shape have been elucidated, more questions remain to be answered: what is the link between cetacean morphological diversity and major changes in the Earth system? Did this group colonise the aquatic environment to escape competition on land from other clades? And more importantly: can we minimise the impact of our own species on the aquatic ecosystems to ensure more opportunities for evolutionary changes in such a fascinating group of mammals?

Declaration of interests

The author declares no competing interests.

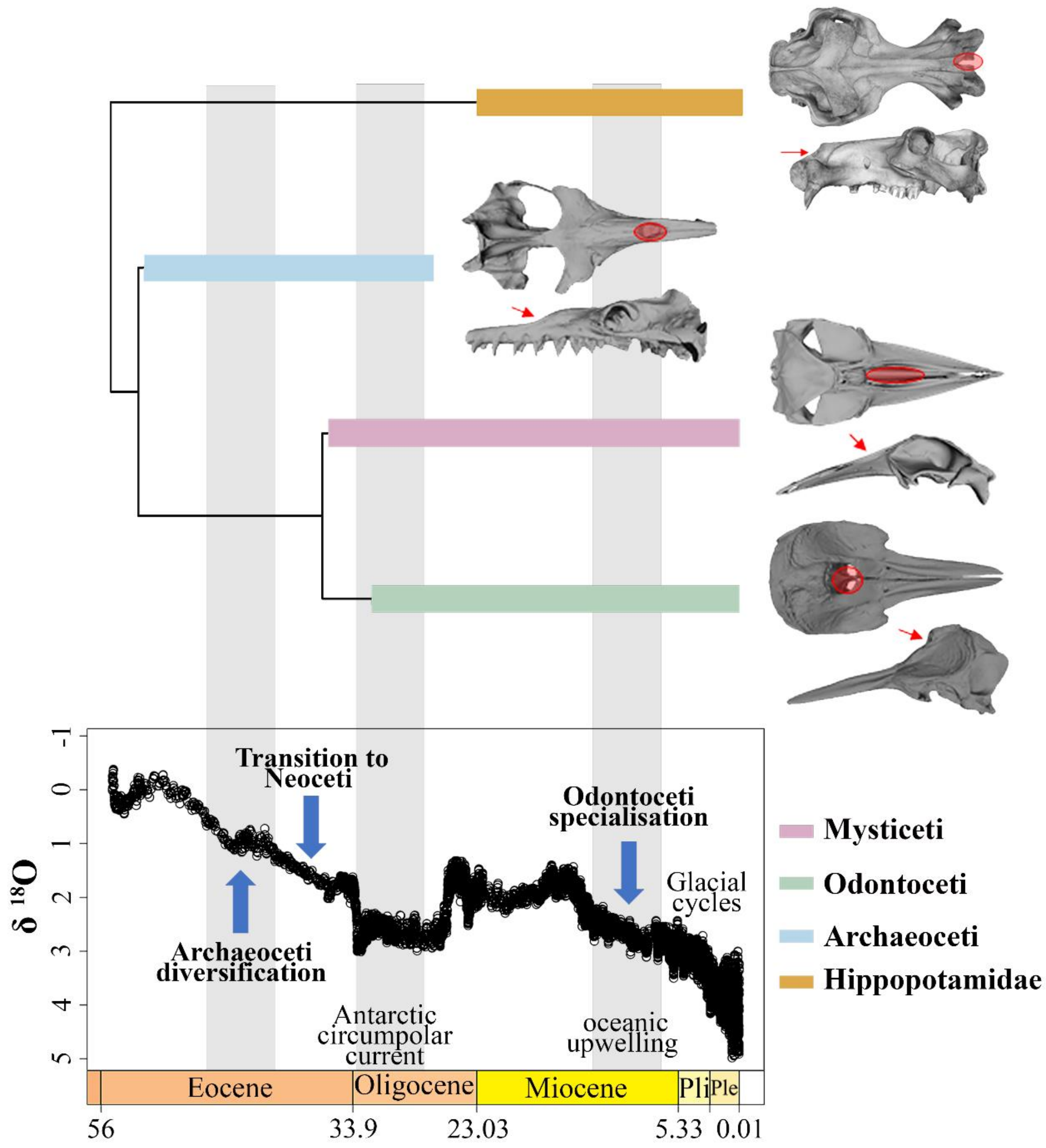

Figure 1. Simplified phylogeny showing the evolutionary history of major cetacean clades.

Below the phylogenetic tree, an oxygen isotopic curve displays climate changes with higher δ18O values corresponding to cooler temperatures[12]. Blue arrows indicate periods of rapid evolutionary changes in skull shape. Grey-shaded areas represent periods of major changes in climate and oceanic current system significant to Cetacea as in Slater *et al*.[4] (the 3D skull models that accompany the phylogenetic tree belong to (from top to the bottom): the modern hippo (*Hippopotamus amphibius*, University of Dundee Museum Collection, DNUC 1990), the archaeocete whale *Zygorhiza kochii* (Smithsonian Institution, National Museum of Natural History, Department of Paleobiology, USNM V 11962), the minke whale (*Balaenoptera acutorostrata*, Reidenberg Collection) and the bottle-nosed dolphin (*Tursiops* *truncatus*, Charleston Museum CM256). Red arrows indicate the position of the bony nares that underwent dramatic migration during cetacean evolution. Models are not to scale, and they are all freely accessible via phenome10k.org[13] and sketchfab.com).

References

1. Huggenberger, S., and Cozzi, B. (2017). Cetacean Morphology. In Encyclopedia of Animal Cognition and Behavior, J. Vonk, and T. Shackelford eds. Springer, Cham. https://doi.org/10.1007/978-3-319-47829-6_988-1
2. Fordyce, R. E., and Barnes, L. G. (1994). The evolutionary history of whales and dolphins. Ann. Rev. Earth Planet. Sci. *22*, 419-455.
3. Fordyce, R.E. (2009). Cetacean fossil record. In Encyclopedia of marine mammals (second edition), W.F. Perrin, B. Würsig, and J.G.M. Thewissen eds. (Academic Press) pp. 207-215.
4. Slater, G.J., Goldbogen, J.A., and Pyenson, N.D. (2017). Independent evolution of baleen whale gigantism linked to Plio-Pleistocene ocean dynamics. Proc. Roy. Soc. B: Biol. Sci. *284*, 20170546.
5. Bianucci, G., Marx, F.G., Collareta, A., Di Stefano, A., Landini, W., Morigi, C., and Varola, A. (2019). Rise of the titans: baleen whales became giants earlier than thought. Biol. Lett. *15*, 20190175.
6. Thewissen, J.G.M., Cooper, L.N., George, J.C., and Bajpai, S. (2009). From land to water: the origin of whales, dolphins, and porpoises. Evo. Edu. Outreach *2*, 272-288.
7. Coombs, E.J., Felice, R.N., Clavel, J., Park, T., Bennion, R., Churchill, M., Geisler, J., Beatty, B., and Goswami, A. (2022). Making waves, the rising and falling tempo of cetacean cranial evolution. Curr. Biol.
8. Roston, R. A., Roth, V.L. (2019). Cetacean skull telescoping brings evolution of cranial sutures into focus. Anat. Rec. *302*, 1055–1073
9. Pough, F.H., Janis, C.M., and Heiser, J.B. (1999). Vertebrate life (Vol. 733). Upper Saddle River, NJ: Prentice Hall.
10. Coombs, E.J., Clavel, J., Park, T., Churchill, M., and Goswami, A. (2020). Wonky whales: the evolution of cranial asymmetry in cetaceans. BMC biology *18*, 1-24.
11. Page, C.E., and Cooper, N. (2017). Morphological convergence in ‘river dolphin’ skulls. PeerJ *10535*, e4090.
12. Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. Science *292*, 686-693.

13. Goswami, A. (2015). Phenome10K: a free online repository for 3-D scans of biological and palaeontological specimens. www.phenome10k.org.
14. Gould, S.J. (1990). Wonderful life: the burgess shale and the nature of history. New York, NY: W.W. Norton & Co.