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Evolution: Back to heavy bones in salty seas

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In amniote vertebrates that transitioned from land to sea, bone mass typically increases and later decreases as active swimming evolves. A new study now has found that heavy bones re-evolved in some fossil marine mammals, suggesting that this trajectory can be reversed.

Amniotes — the vertebrate clade comprising reptiles (including birds) and mammals — evolved on land but various groups became aquatic from the Early Permian (about 300 million years ago) onward and especially after the EndPermian mass extinction (about 250 million years ago). These numerous land-to-sea transitions occurred independently in various mammal and reptile lineages, such as cetaceans, sirenians, ichthyosaurs or plesiosaurs. Such a change of milieu, and thus of environmental constraints, is naturally associated with various morphological, locomotor, physiological and reproductive modifications[1], including nearly always changes in the internal structure of bones[2]. Two main specializations stand out: first, an increase in bone mass, generally in less active swimmers hovering at shallow depths. Such heavy bones serve as ballast for hydrostatic control of buoyancy when diving and for maintaining a horizontal orientation of the body while swimming. Second, in active swimmers with great maneuvering and acceleration capabilities, which rely on hydrodynamic control of buoyancy and body trim, bones become spongy, showing a cancellous organization[3,4]. Increased bone mass characterizes especially the early stages of a lineage's transition to an open ocean lifestyle. The affected animals inhabit shallow waters, show a more 'terrestriallike' morphology and rely on drag-based propulsion with paddling appendages. Conversely, later evolutionary stages are characterized by a cancellous organization in more active swimmers with streamlined bodies, paddles and reliance on an oscillating hydrofoil, as in whales and mosasaurs (a clade of Mesozoic marine reptiles)[5,6]. This apparently stepwise trajectory has led to the suggestion that a compact structure was a necessary transitional step towards a cancellous organization[7]. This evolutionary shift in bone microanatomy was thus considered unidirectional.

However, in a new study in this issue of Current Biology, Leonard Dewaele, Vivian de Buffrenil and colleagues [8] highlight the first known reversal of this evolutionary trajectory, with the re-emergence of increased bone mass in pinnipeds and cetaceans from the Paratethys sea during the Miocene (23–5 million years ago).

Increased bone mass consists of an increase in bone compactness through unbalanced remodeling (a process in which old bone is resorbed and new bone is deposited, and which maintains or adapts bone structure and repairs the skeleton) with inhibited resorption or excessive secondary bone deposition. It can also be caused by additional peripheral deposits[4]. In the fossil record, localized bone mass increase is observed in many early whales from the Eocene (56–34 million years ago), with varying degrees of intensity and distribution, but vanishes later in their evolutionary history[9,10]. The fossil record thus appears to be consistent with the unidirectional trajectory of bone mass evolution.

In their new study, however, Dewaele and colleagues[8], based on an analysis of the inner structure of ribs and long bones, show that bone mass increased in pinnipeds and cetaceans from the Miocene of the Paratethys sea. The occurrence of this specialization in both clades of whale — odontocetes and mysticetes — clearly indicates a reversal from a cancellous to a compact condition in the cetaceans analyzed (Figure 1). For pinnipeds (seals, sea lions, walruses), data are scarcer: modern pinnipeds and the few fossil phocids for which data are available[8] show a cancellous organization. However, Dewaele and colleagues[8] observed a very high bone mass in the Miocene Paratethys

phocids. In addition, a Miocene phocine from Belgium (Nanophoca vitulinoides) shows a surprising case of generalized bone mass increase in its postcranial skeleton[11]. Unfortunately, the phylogenetic relationships between all of these phocid species remain unknown (especially due to the lack of cranial material) and conditions in other early pinnipeds are not documented so the shift from a cancellous to a compact structure, although highly likely to have occurred several times, cannot be ascertained in this lineage.

The independent, yet concomitant reappearance of this specialization in these three distinct lineages — phocids, baleen whales and toothed whales — with different functional requirements, such as swimming, diving and acceleration, clearly highlights its convergent nature and seems to reflect strong selective pressure. All the specimens studied by Dewaele and colleagues[8] come from the Miocene Paratethys, suggesting local, convergent evolution. The Paratethys was a shallow sea that extended from the European Alps through Central Europe to the Aral Sea in Central Asia. Tectonics and sea-level variation resulted in various degrees of extension of the Paratethys — it reached its largest size during the late Miocene — and connections with other seas. Today, the remnants of the Paratethys are the Black Sea, the Caspian Sea and the almost vanished Aral Sea, as well as a few lakes[12]. During the middle Miocene, between 13.8 and 13.4 million years ago, connection between the Mediterranean and the Paratethys was lost leading to the latter becoming hypersaline, a period known as the Badenian Salinity Crisis[13]. However, increased bone mass is known not to be directly influenced by local environmental conditions, as taxa with varied bone structures are observed together in similar outcrops or present-day habitats[2]. Instead, different bone structures reflect species-specific adaptations. Dewaele and colleagues[8] do not call this statement into question. Rather, the authors conclude that while local environmental conditions appear to be the cause of this increase in bone mass, it is likely through the response of the skeleton to a change in functional constraints. Indeed, hypersalinity increases the buoyancy that aquatic mammals have to overcome when they dive. Greater bone mass would have been favored, resulting in this evolutionary shift.

The shift in bone mass observed by Dewaele and colleagues[8] concerns marine mammals that lived approximately one to six million years after the Badenian Salinity Crisis, suggesting it was a relatively long-term adaptive process. Moreover, it is also found in forms that lived further East, where waters were brackish and not hypersaline. Although the increase in bone mass evolved during the crisis, this feature remained characteristic of the Miocene aquatic mammal fauna endemic to the Paratethys, particularly through the dispersal of the lineages involved. The reason for a potentially similar independent change in the Phocid Nanophoca from the Miocene of Belgium[11], and thus not from the Paratethys, should be investigated to better understand the selective pressures driving this cancellous-compact shift and how it took place.

The increase in bone mass evolved comparatively fast, over less than a million years, which is perhaps not surprising. The internal structure of bone is known to be plastic and appears to evolve more rapidly than bone shape, as evidenced by significant changes in bone inner structure in taxa with otherwise limited adaptations to an aquatic life-style[2,14]. Dewaele and colleagues[8] highlight that heavy bones persisted after the crisis was over and salinity returned to normal. The reasons for this persistence remain unclear; perhaps they were an exaptation to benthic foraging, as mentioned by the authors[8], or a more general lack of strong selective pressure against high bone mass.

The study by Dewaele and colleagues[8] on the bone structure of fossil seals, dolphins and whales from the Miocene Paratethys add a twist to our understanding of adaptation to the aquatic realm in these mammal lineages. But more generally, this first documented

Humeri
Ribs
Pakicetidae
Protocetidae
Pachyacanthus
Platanista
Delphinus
Phocoena
Delphinida indet.
Cethotheriidae indet.
Cethotheriidae indet.
Basilosauridae
* *

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Figure 1. Shifts in bone microanatomy during whale evolution.

Black and white representation of humerus and rib sections from various cetaceans for which data are available plotted on a simplified phylogeny (modified from Gatesy et al.[15]) showing the independent shifts from a cancellous to a compact structure (/). *Specimens from the Miocene Paratethys.

shift from a cancellous to a compact bone structure extends our understanding of the development of these specializations in amniotes that adapted to an aquatic lifestyle.

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