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Perucetus colossus: the whale with the heaviest skeleton known among all mammals

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Article

A heavyweight early whale pushes the boundaries of vertebrate morphology

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The fossil record of cetaceans documents how terrestrial animals acquired extreme
adaptations and transitioned to a fully aquatic lifestyle[1,2]. In whales, this is associated
with a substantial increase in maximum body size. Although an elongate body was
acquired early in cetacean evolution[3], the maximum body mass of baleen whales
reflects a recent diversification that culminated in the blue whale[4]. More generally,
hitherto known gigantism among aquatic tetrapods evolved within pelagic, active
swimmers. Here we describe *Perucetus colossus*—a basilosaurid whale from the middle
Eocene epoch of Peru. It displays, to our knowledge, the highest degree of bone mass
increase known to date, an adaptation associated with shallow diving[5]. The estimated
skeletal mass of *P. colossus* exceeds that of any known mammal or aquatic vertebrate.
We show that the bone structure specializations of aquatic mammals are reflected in
the scaling of skeletal fraction (skeletal mass versus whole-body mass) across the
entire disparity of amniotes. We use the skeletal fraction to estimate the body mass
of *P. colossus*, which proves to be a contender for the title of heaviest animal on
record. Cetacean peak body mass had already been reached around 30 million years
before previously assumed, in a coastal context in which primary productivity was
particularly high.

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Reconstruction of *Perucetus colossus* by Alberto Gennari

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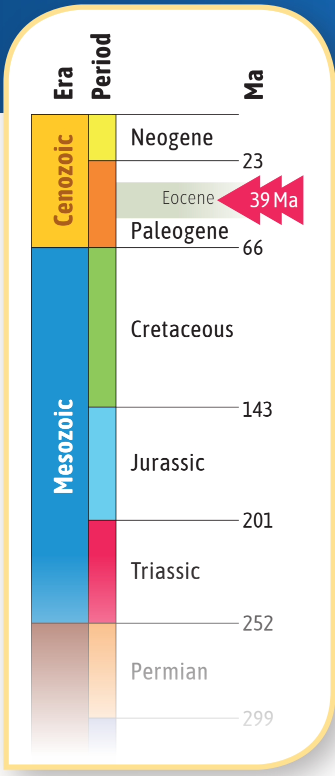
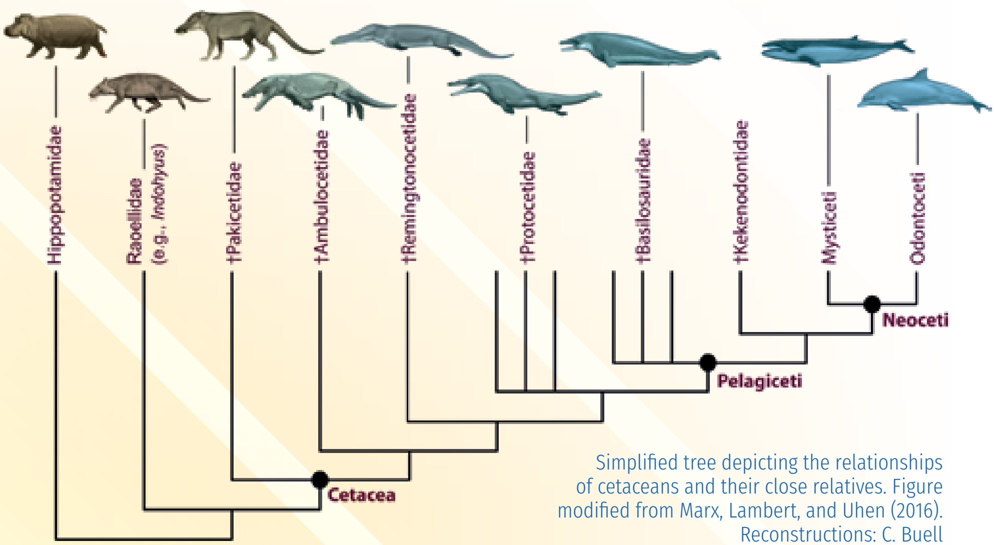
How whales got big

The fossil record of cetaceans (whales, dolphins, and porpoises) offers a fascinating glimpse into their evolutionary transition from land to sea. Cetaceans stem from a group of land-dwelling mammals (like us). One early close relative, *Indohyus* (found in early Eocene rocks, ~ 50 million years old) from India and Pakistan looked similar to a small deer, but it was incipiently adapted to a semi-aquatic environment. As whales adapted more and more to water during a warm climatic phase, they grew larger, with noticeable elongation of their body.

This is particularly true in the family called Basilosauridae, who were the first fully aquatic cetaceans. Some members of this family could have reached a body length of 20 meters. However, the massive size of modern baleen whales, like the blue whale, only evolved recently (probably less than 10 million years ago). This change is linked to cooler climates in the late Cenozoic era. The blue whale, in particular, has always been considered as the record-holder of the heaviest animal.





Simplified tree depicting the relationships of cetaceans and their close relatives. Figure modified from Marx, Lambert, and Uhen (2016). Reconstructions: C. Buell

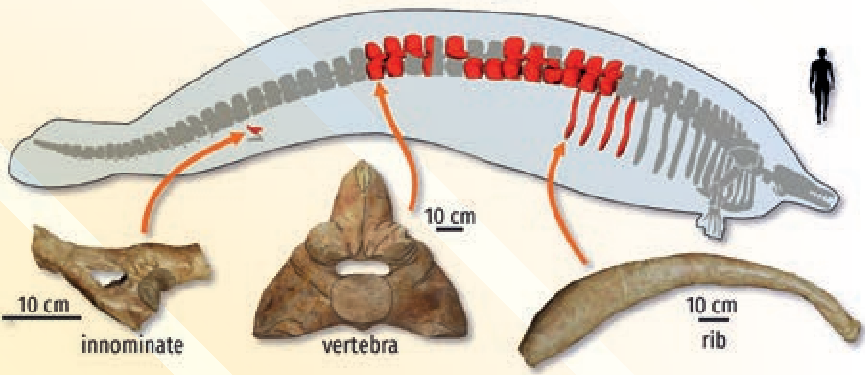
A new early whale, like no other

Fosiil site of *Perucetus colossus* in the Ica desert (southern coast of Peru).

Excavation of some vertebrae in the fossil site.

When Mario Urbina (a co-author of this paleo-guía) first saw the parts of the skeleton of *Perucetus colossus* cropping out of a hill in the Ica desert (southern coast of Peru), it was difficult to believe that it was actually a fossil: the bones were so big, so dense, and weirdly shaped. After a decade-long effort of field work and fossil preparation, the conclusion was clear: this is a new basilosaurid species, which was named *Perucetus colossus*. In total, 13 vertebrae, four ribs, and a partial hip bone have been recovered. This partial skeleton was found in layers dated thanks to the isotopic composition of surrounding minerals and thanks to the associated microfossils to the middle Eocene (~ 39 million years old). Its most notable features are the extreme degree of compactness (bones are usually porous) and the weirdly inflated shape of the bones. Individual vertebrae are actually not longer than those of some of its close relatives (like *Basilosaurus*), but they have tremendously bulbous processes (usually flat laminae attached to the body of the vertebra). The largest recovered vertebra is roughly twice as voluminous as that of a 25-m long blue whale.

Such increase in bone mass is not a disease, this is a typical adaptation that has been acquired in many groups of mammals, reptiles, and amphibians that are shallow divers: It helps them regulate their buoyancy and be stable under water. A very good example of this are sea cows.



Position of the recovered bones of *Perucetus colossus* indicated (in red) on an idealized skeleton of a primitive basilosaurid whale, comparative human scale and examples of original fossils (Giovanni-Bianucci).

Perucetus colossus, series of dorsal vertebrae.

The heaviest skeleton of all mammals / of all aquatic vertebrates

Surface-scanning of the vertebrae at the Museo de Historia Natural-Universidad Nacional Mayor de San Marcos, Lima, Peru.

Each of the recovered bones was scanned with a surface-scanner to measure their volume (and to illustrate them too) in order to estimate the total volume of the skeleton. But because only a partial skeleton was recovered, the missing bones had to be reconstructed, which was done using closely related species for which complete skeletons are known. Several basilosaurids with different vertebral counts were used, to account for the uncertainty in the skeletal composition of *P. colossus*.

Drillings in several representative areas of the vertebrae and thin-sections were used to measure bone compactness, which is the proportion of bone to porosity in the skeleton. Combining the volume and compactness (and a standard fresh bone tissue density), the total mass of the skeleton of *P. colossus* was estimated to be between 5.3 and 7.6 tonnes. As a comparison, this is two to three times as much as that of a 25-m long blue whale. Only some large sauropods (long-necked dinosaurs) might have had a heavier skeleton.

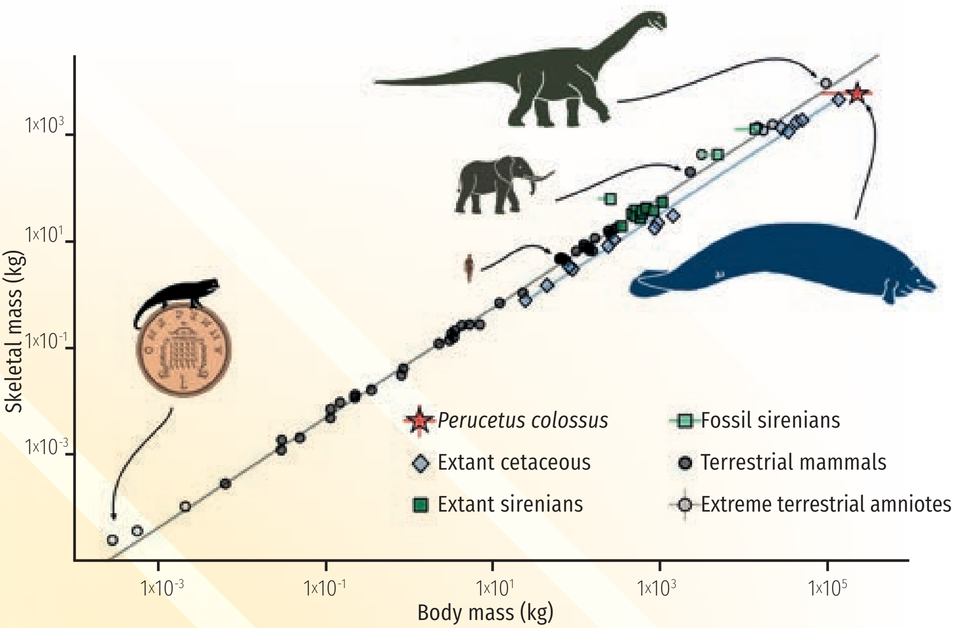
The inner structure of bones has been assessed through core-drills, here in the centre of a vertebra.

Fleshing out a gigantic skeleton

Statistical analyses were used to study the scaling of skeletal fraction, in other words, assess if the ratio of bone mass to soft tissue mass is consistent across animals of all sizes and of different life habits, or if this ratio varies depending on the size or habits of the animals. The skeletal fraction has therefore been gathered for various terrestrial and aquatic species, including cetaceans and sirenians. Compared to terrestrial animals, living cetaceans have relatively little bone. Sirenians, on the other hand, have a higher skeletal fraction: they have the bone mass increase so typical of this type of shallow diving animal.

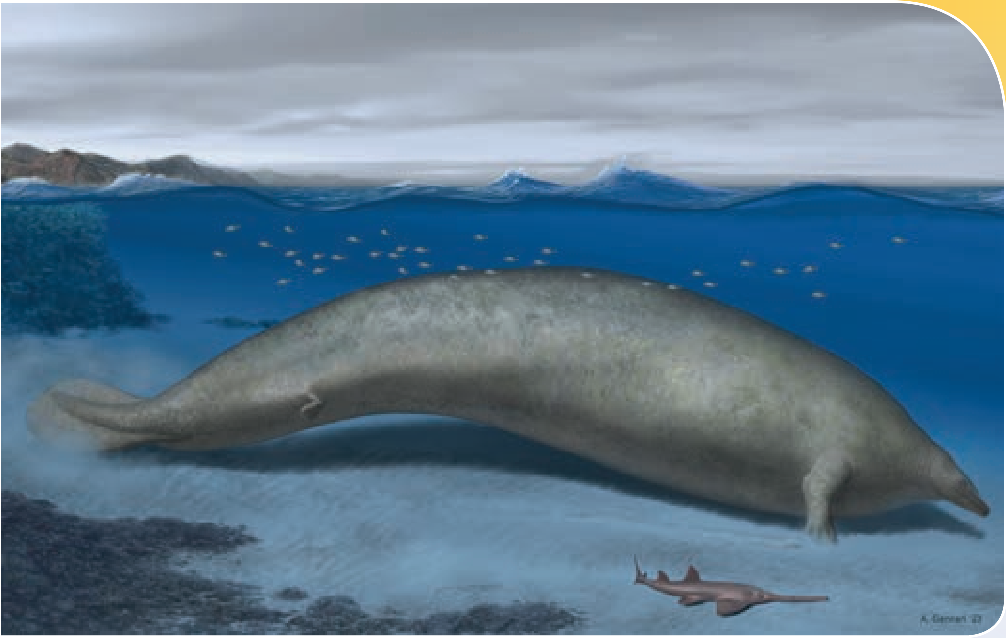
It is not really possible to know the skeletal fraction of *P. colossus*, so the range of values known in living aquatic mammals was used to make a final estimation, that of its body mass. Given its skeletal mass (and the uncertainty associated with it), it could have weighed between 85 and 340 tonnes.

Assessing the volume of *P. colossus* has not been attempted in the study: this would require to know the proportion of fat, a lower density tissue, in the body: some whales, like the right whales, have a layer of fatty blubber that is almost half a meter thick!



Scaling of skeletal mass to body mass across the range of sizes of reptiles and mammals.

The lifestyle of *Perucetus colossus* and what it means for cetacean evolution



Artistic reconstruction of *Perucetus colossus* and its habitat by Alberto Gennari.

Its extremely dense and voluminous bones suggest that *Perucetus colossus* lived in shallow waters, like modern sirenians. It probably inhabited coastal areas, and its massive size might have allowed it to handle strong waves. Its exact swimming style is unclear, though, due to the incompleteness of the fossil. The anatomy of the vertebrae indicates it swam with up-and-down undulations, not side-to-side like in its close relative *Basilosaurus*. This motion, along with its size, might have evolved to balance the high energy needed for this swimming style, as seen in early ichthyosaurs (marine reptiles from the time of dinosaurs).

No skull or teeth have been found up to now for *P. colossus*, so its diet is uncertain.

It might have fed on seagrass, though being herbivorous is unlikely for a cetacean. It is more plausible it ate bottom-dwelling animals like crustaceans or used a suction or filter-feeding method similar to the living grey whale. It might also have fed on carcasses.

In any case, finding such a giant and heavy early cetacean changed our understanding of their evolution: they reached tremendous weights roughly 30 million years before the baleen whales started to become so big. *P. colossus* along other members of the basilosaurid family, were likely hyper-specialised, which might have caused their demise, as a drastic climate change happened at the end of the Eocene (~ 34 millions years ago).

Photograph of part of the field and research teams excavating the bones of *Perucetus colossus* in the Ica desert (southern coast of Peru).

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