**Peer Review File**

**Manuscript Title:** A heavyweight early whale pushes the boundaries of vertebrate morphology

## Reviewer Comments & Author Rebuttals

### Reviewer Reports on the Initial Version:

Referees' comments:

Referee #1 (Remarks to the Author):

A. The current manuscript describes a new cetacean from the Eocene of Peru, undoubtedly a new genus and species of basilosaurid, extremely unique in its morphology. The authors make functional inferences from the morphology, mostly vertebral morphology. Many of these inferences are sound, some are not. B and H. This specimen is certainly novel and the description is appropriate in its clarity and context.
C. This whale is different from all others: study of bones and their microstructure is taken to suggest, correctly in my view, that this is a slow moving species with heavy bones. E. Comparisons made are mostly to blue whales, which are not slow swimming. More appropriate comparisons to Greenland Right Whales would be more appropriate.
C. This specimen is unique and the vertebrae/ribs well studied and illustrated. The study of vertebral microstructure is appropriate and well-executed. I am less impressed with the study of vertebral mobility (Extended data Fig 8), as such mobility is determined to a large extent by the thickness of the intervertebral discs, which do not fossilize. E. Given the low number of vertebrae/ribs preserved and the absence of nearly all of the rest of the skeleton, I also believe it goes too far to suggest that this may be the heaviest vertebrate ever. That comment also addresses the quality of available data (C).
E. In summary, I believe that this is a very interesting specimen and possibly the strangest late Eocene whale known. However, the actual number of elements discovered for this whale gives me pause in making far reaching inferences.

Referee #2 (Remarks to the Author):

This new species from the Eocene of Peru is quite unusual and interesting indeed. It is clearly distinctly different from any other known whale, and thus deserving of being named a new genus and species.

I am curious about its taxonomic placement. It clearly has numerous features in common with Pachycetus and Antaecetus, which have been placed in the Pachycetinae. Even if you did not support the subfamilies within Basilosauridae, I think it's affinities with these taxa should be fleshed out more. Given those affinities, I think more close comparison with those taxa are in order. Pachycetus wardii, according to Uhen 2001 (then Eocetus wardii) has only 12 thoracic vertebrae. Antaecetus, according to Gingerich et al 2022 has 13 thoracic vertebrae, and 10 or more lumbar vertebrae.

Given these numbers, I'm not sure comparison and scaling to Cynthiacetus is warranted.Having 13 thoracic vertebrae is a symplesiomorphy of pachycetines with protocetids. It is possible that pachycetines also had a smaller number of lumbars than non-pachycetine basilosaurids (somewhere between 10 and 20), and thus were not as long as Cynthiacetus. A recalculations of the skeletal and body masses with these more conservative numbers of vertebrae would be helpful. If these masses are still larger than that of blue whale, it would further support the claim

of the heaviest animal ever. If not, it suggests caution in making such claims.

I think there is quite enough that is strange and interesting about this animal without making the claims regarding its mass. Both the odd osteology and the inclusion of the innominate are interesting enough in and of themselves.

**Author Rebuttals to Initial Comments:**

Reviewer 1.

- **Comparisons made are mostly to blue whales, which are not slow swimming. More appropriate comparisons to Greenland Right Whales would be more appropriate.**

The first part of the manuscript deals with maximum skeletal and body masses in vertebrates. For that reason, we have compared our estimates to the hitherto largest known animal, the blue whale. We fully agree, however, that this species is probably not a good model for the swimming style of the new species (see comparison with manatees). Despite their body that is more massive than in balaenopterids, the right whales have a swimming style similar to that of other extant cetaceans (and probably different from that of the new species). Furthermore, the right whales' head is proportionally much larger compared to basilosaurids (and also compared to balaenopterids, but to a lesser extent). In the final functional interpretation section, we initially refrained from referring to extant cetaceans altogether, as they swim using the carangiform with lunate-tail style (Fish 1998; new citation now added in the revised manuscript). We have added a reference to this in the revised manuscript (lines 230-233). Furthermore, we added a mention to both balaenopterids and balaenids (displaying similarly thin vertebral processes) in the section 'The heaviest mammalian skeleton' (lines 152-154).

- **I am less impressed with the study of vertebral mobility (Extended data Fig 8), as such mobility is determined to a large extent by the thickness of the intervertebral discs, which do not fossilize.**

We have added information regarding the estimation of intervertebral discs (it is based on the data of Long et al. (1997; new citation now added in the revised manuscript) for *Delphinus delphis* (Methods, lines 665-666, and legend of Extended Data Fig. 8), which was lacking from the manuscript. We believe that this analysis does bring interesting elements of discussion to better understand the paleobiology of the new species. That being said, this analysis is not strictly necessary to reach the major conclusions of the manuscript, and can be removed if that is the wish of the editor (also if the manuscript requires to be shortened).

- **Given the low number of vertebrae/ribs preserved and the absence of nearly all of the rest of the skeleton, I also believe it goes too far to suggest that this may be the heaviest vertebrate ever.**

All the preserved parts of the new species' skeleton are tremendously pachyosteosclerotic. It is therefore extremely likely that all vertebrae and ribs were similarly pachyosteosclerotic, as seen in the few other marine tetrapods showing systemic pachyosteosclerosis. However, throughout the analyses and their interpretations, we have used a conservative approach: 1) cranial and limb elements were not ascribed additional volume associated with the pachyostosis (even though the innominate is pachyostotic); 2) the vertebral centra compactness (used to ascribe a bone mass the corresponding skeletal elements) is most likely an underestimate (see Supplementary Discussion: Bone microanatomy); 3) the new species was referred to as a contender to the title of heaviest animal (not a definitive overtaking). We have now added an extra conservative estimate of the skeletal and body masses (see below), which let us draw the same conclusion.

Reviewer 2.

- **I am curious about its taxonomic placement. It clearly has numerous features in common with *Pachycetus* and *Antaecetus*, which have been placed in the Pachycetinae. Even if you did not support the subfamilies within Basilosauridae, I think it's affinities with these taxa should be fleshed out more.**

We modified a sentence in the section 'Systematic palaeontology' to insist on the similar centrum proportions observed in the new species and the two pachycetine genera (lines 116-117). But given that another subfamily, the Basilosaurinae, acquired an even more derived elongation of the centra, the intermediate condition seen in the new species and pachycetines could very well be plesiomorphic for a potential clade grouping these two subfamilies (and in that case this character should not be seen as an apomorphy shared by the new species and pachycetines). We prefer not to refer to the bone mass increase as a feature that the new species shares with pachycetines, because 1) bone mass increase is documented (with various degrees) in all basilosaurid subfamilies as well as in other early Pelagiceti such as the toothed mysticete *Mystacodon*; and 2) bone mass increase can vary dramatically within specific clades (see for instance each clade of marine mammal part of the Badenian fauna of Paratethys and their respective sister species; Dewaele et al., 2022: phocid seals, cetotheriid baleen whales and platanistid dolphins). Finally, the innominate of *Pachycetus wardii* (USNM 310633), even if fragmentary, seems to differ quite substantially from that of the new species (this is now stated, line 113). We hence consider that there are no strong arguments to consider the new species as more closely related to pachycetines than other basilosaurids. Assessing more precisely the affinities for the new species will require finding more material, here and for other fragmentarily known taxa.

- **Given those affinities, I think more close comparison with those taxa are in order. [...] I'm not sure comparison and scaling to Cynthiacetus is warranted. [...] A recalculations of the skeletal and body masses with these more conservative numbers of vertebrae would be helpful.**

Given the unknown skeleton composition of the new species, we used in the initial version of the analyses the well-known basilosaurid skeletons (not only *Cynthiacetus*, but also *Basilosaurus* and *Dorudon*). We had considered having a skeletal estimate based on a pachycetine skeleton composition, but initially refrained from doing so because no complete (or nearly complete) series are known for this subfamily. The most complete column is probably that of *Antaecetus* FSAC Bouj-200, for which the total number of thoracics is not known (Gingerich et al., 2022: p26); the skeleton is furthermore not preserved posterior to L10. We acknowledge, though, that a more conservative estimate can be obtained using the fragmentary data available for pachycetines: we made an additional estimation with the absolute minimum of 12 thoracics (*Pachycetus wardii*, Uhen 2001) and 15 lumbars, which is the minimum count documented in the Basilosauridae (Martínez-Cáceres et al., 2017; the most complete but still fragmentary lumbar series in Pachycetinae comprises at least 10 vertebrae, see above). Running the analyses with this extra conservative hypothesis, the skeletal mass of the new species is still twice that of a 25-m long *B. musculus*, and the body mass estimate still falls in or exceeds the distribution of that species. A corresponding skeletal length estimate was also added. We have revised the main text (including Methods section lines 120, 181, 210, 212, 635-636) as well as the Supplementary Information accordingly (Supplementary Methods, and Supplementary Tables 18, 22).

**Reviewer Reports on the First Revision:**

Referees' comments:

Referee #1 (Remarks to the Author):

Summary: It accurately reflects the interest of the species: a very large Eocene cetacean, with extraordinary bones.
Significance: This is clearly a new species, and a very unusual one at that, the direction of its specialization is more extreme than other pachyostotic cetaceans.
Methods:The bone histology and gross morphology is appropriate and excellent. I remain worried about functional interpretations based on such an incomplete skeleton. The weight interpretation is not firm, but its assumptions are spelled out, and this is certainly a very unusual species.
Statistics: not relevant here
Conclusions: appropriate and nuanced.
References: appropriate
Clarity: quite good, not perfect. Acceptable

Referee #2 (Remarks to the Author):

I still have basically the same concerns that I had in my initial review. This animal seems to have several characteristics of the Pachycetinae, so I'm still not sure why the authors hesitate to include it in that subfamily. True, the distribution of these characters might not be synapomorphic, but then a phylogenetic analysis would be in order to determine that. Lacking such an analysis, I still think it is most like the taxa in Pachycetinae. Baring that, perhaps the authors could list "subfamily indeterminate" in the systematic paleontology section to be crystal clear on their views.

As for the body mass calculation, I still think they could be even more conservative. IF the maximum number of lumbars known from any of these pachycetines is 11, then perhaps use 10 lumbars in the calculation. Using the most conservative numbers and still having the most massive whale would strengthen the argument.

**Author Rebuttals to First Revision:**

Referee 1.

- **I remain worried about functional interpretations based on such an incomplete skeleton.**

We have marginally edited the functional interpretation that deals with swimming style with an introductory sentence to slightly temper our conclusions (revised MS, lines 348-350). The conclusions related to the new species' lifestyle are mostly based on the specimen's bone microanatomy and histology: generalised pachyosteosclerosis has been clearly demonstrated, so the corollary functional interpretations should be viewed as well supported.

Referee 2.

- **This animal seems to have several characteristics of the Pachycetinae […] a phylogenetic analysis would be in order […] Baring that, perhaps the authors could list "subfamily indeterminate" in the systematic paleontology section to be crystal clear on their views.**

We thank the Referee for their useful suggestions about the systematic placement of this new basilosaurid. We are happy to add 'Subfamily indet.' (line 99). However, we refrained from performing a phylogenetic analysis because of the fragmentary nature of the holotype, as well as the fact that most of the traits characterising the new species are automorphic. Without cranial material, we strongly expect that such an analysis will be inconclusive, and we tend to think that bone microstructure-related character will prove highly homoplastic, as previously demonstrated in crown cetaceans and pinnipeds (Dewaele et al., 2022).

- **[…] IF the maximum number of lumbars known from any of these pachycetines is 11, then perhaps use 10 lumbars in the calculation. Using the most conservative numbers and still having the most massive whale would strengthen the argument.**

We refrained from using the maximum number of lumbars known in pachycetines, 10 (Gingerich et al. 2022), because the specimen in question (*Antaecetus aithai*, FSAC Bouj-200) is known to be incomplete: the specimen's most caudal preserved element is L10, so it could (and most likely had) more lumbar vertebrae. We therefore see no justification to use such a lumbar count for an estimation (one has also to bear in mind that the new species' holotype also counts at least 11 lumbar vertebrae). Out of curiosity, we nevertheless re-ran the analysis, substracting additional vertebrae (L6-L12 of *Cynthiacetus peruvianus*' holotype, used as a basis) to reach a 10-vertebra lumbar count: the skeletal mass drops to 4.68 tonnes, and the minimum body mass to 74.9 tonnes. Our conclusions still hold, even using the suggested incomplete skeleton.