

Extreme armour in the world's oldest ankylosaur

Corresponding Author: Professor Susannah Maidment

Any redactions in this file are there to maintain patient confidentiality, the confidentiality of unpublished data, or to remove third-party material.

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Referee #1

(Remarks to the Author)

This is a detailed description of an unusual Jurassic-aged, armoured dinosaur. Of note, based on the associated postcranial skeletal elements and osteoderms, this specimen can clearly be assigned to the dinosaurian group Ankylosauria. As such, it is one of the oldest known members of this clade and is a rare example of an African (Moroccan) ankylosaur species. The morphologies of the associated osteoderms are highly unusual and entirely unique to this species.

A. Summary of the key results

This manuscript describes an associated collection of ankylosaurian dinosaur skeletal materials from the Middle Jurassic of Morocco. The specimen is significant for several reasons: (1) it appears to represent the one of the oldest known ankylosaurs, dating to Middle Jurassic (Bathonian, maybe Callovian?); (2) it is a rare example of an African ankylosaur (to date, it is the only unequivocal example from the entire continent); and (3) the morphology of the osteoderms, including those fused to the dorsal ribs and cervical half-rings, is unprecedented.

This manuscript has important implications for palaeontologists interested in phylogenetics (especially ornithischian dinosaurs), biogeography, and dermal armour.

B. Originality and significance (if not novel, please include reference)

This specimen is significant for all the reasons listed above. The specimen represents one of the earliest known ankylosaurs, an unusual group of dinosaurs characterized by abundant osteoderms, bony organs that are embedded in the skin. Ankylosaurs are rare from Gondwana and very poorly known from Africa. The specimen consists of some remarkably shaped osteoderms, including very elongated spike-like elements.

Phylogenetically, *Spicomellus* appears to represent either a basal member of Ankylosauria (based on a strict reduced consensus tree) or a basal member of Ankylosauridae (based on an extended implied weighting tree). Interestingly, neither analysis recovers a clade of Southern Hemisphere taxa (as had been proposed by previous authors). It is worth noting however, that the interpretation of *Spicomellus* as an ankylosaurid is weakly supported (see below).

C. Data & methodology (validity of approach, quality of data, quality of presentation)

The descriptive approach and phylogenetic investigation are valid, although the different phylogenetic strategies employed offer strikingly different interpretations on the identity of the specimen (as with a basal member of Ankylosauria or basal member of Ankylosauridae). Further, in the Supplementary Materials the authors note that the Ankylosauridae hypothesis is "...weakly supported in this analysis and require further testing with future discoveries". Therefore, the authors should consider revising Figure 3 with both phylogenetic interpretations.

The quality of data presented, and quality of presentation is good, although addition figures of some of the skeletal elements (e.g., possible cranial fragments) are needed. Also, the descriptions in the Supplementary Materials focus on images in the main text and strangely do not refer to the supplementary figures.

More information about the paleoenvironment of the specimen would be helpful.

D. Appropriate use of statistics and treatment of uncertainties

Please see above re: phylogenetics

E. Conclusions: robustness, validity, reliability

The description of the fossil material is very good. A few minor suggestions are provided below (section F).

The interpretation of the elongated spine-like osteoderms as primarily display is certainly plausible, but other hypotheses should also be considered. What is the interpretation of the local (paleo)environment (e.g., Discussion line 256 states that these spike-like osteoderms would be challenging in a densely vegetated setting – is that the case here)? What other species (i.e., possible predators) known from this locality/horizon? Related to this, a recent summary of osteoderm functions was published by Ebel et al., 2024 (<https://doi.org/10.1111/jzo.13224>).

Two strategies were employed to perform the phylogenetic analysis. Although the position of *Spicomellus* varies between them, neither analysis recovers the recently proposed Southern Hemisphere group *Parankylosauria*. Given the material available, the inability to fully resolve the phylogenetic position of this species is expected. That said, why was Extended Implied Weight analysis phylogeny emphasized in the manuscript (figure 3)? In the Supplementary Materials it is acknowledged to be “weakly supported”.

F. Suggested improvements (experiments, data for possible revision)

Minor

- There is a bit of discrepancy in the age information between the holotype (Upper Bathonian/Callovian; Maidment et al. 2021) and the present material (Bathonian). Both appear to be from the same horizon and similar locations, but perhaps more detailed could be provided.
- Description, lines 70-73: to avoid confusion, the terms ‘spike’ and ‘plate’ should be used as morphological descriptors of osteoderms (i.e., spike-like osteoderms, plate-like osteoderms). Also, the term ‘compound osteoderm’ is already used to describe the multi-partite osteoderms of some scincids (e.g., <https://www.nature.com/articles/s41598-024-66451-w>). Thus, an alternative descriptor for the elements of *Spicomellus* should be employed.
- Description, lines 77-83: the presence of ‘handle’ vertebrae (fused caudal vertebrae) is significant towards the interpretation of having a tail club. Additional images of this feature in the Supplemental Materials would be helpful.
- Description, line 99 (see also Supplementary p. 16: the use of ‘scapulocoracoids (Fig. S7) are indistinguishably fused’ is confusing. Perhaps the scapula and coracoid are fused creating a single element?
- Description, line 123: identify the location of the brevis fossa on Fig. S8
- Description, lines 131-132: the imperforate acetabulum is described as ‘...closed medially by fusion of the ischium’. Fusion of the ischium to what? Are the sutures between the individual pelvic elements visible? I could not see this on Fig. S8.
- As the location of most of the osteoderms depicted in Figure 2 are speculative and as some are already shown in Figure 1, this image should be placed into Supplementary information. Even though the title includes the disclaimer “hypothetical positions” the figure presents a false sense of certainty.
- Discussion, lines 254-261: with respect to the interpretation of function(s), it is noted that these elongate cervical osteoderms may have “...hindered locomotion in densely vegetated environments” – what is known about the paleoenvironment/paleoecology of the El Mers III Formation?
- Related to the above, osteoderms have been associated with a number of functional roles (see Ebel et al., 2024, <https://doi.org/10.1111/jzo.13224>), but defensive/protective seems to be the most intuitive (and is even implied by the title of this manuscript with the term ‘armour’). It is thus confusing to suggest (lines 257-259) that the spike-like cervical osteoderms of *Spicomellus* are “...structures with limited obvious functionality...”. What other taxa (especially carnivorous forms) are known from the same horizon as *Spicomellus*? While sexual selection cannot be ruled out, it seems a bit premature to raise the profile of this hypothesis over that of (for example) protection against predation or even intraspecific combat.
- Discussion, lines 262-274: the interpretation of Cretaceous ankylosaurs evolving a more simplified osteoderm morphology is interesting, but perhaps overstated and alternatives should be considered. It is unclear if the shape change relates to an entirely different function (visual display vs physical protection) or something more nuanced. For example, such morphological differences may reflect a more active defensive weapon role in *Spicomellus* vs. some Cretaceous forms. It may also relate to a difference in potential predators and predatory strategies.
- Possible cranial fragments USMBA 38 and 66 are not figured in the Supplementary information. Why is USMBA 38 suggested to be cranial?

- The pathology on USMBA 51 (Fig. S3) should be labeled.
- Is there an image of the sacral ribs and their association with the acetabulum?

G. References (appropriate credit to previous work)

H. Clarity and context (lucidity of abstract/summary, appropriateness of abstract intro and conclusions)

Overall, this is a remarkable specimen, with a distinctive morphology and important biogeographical implications.

The abstract and conclusions provide a good summary of the manuscript, although the interpretation of the dermal armour as being purely display rather speculative/is not well-supported in the Discussion. Alternative explanations are not considered.

Referee #2

(Remarks to the Author)

The manuscript reported new material of the oldest ankylosaur *Spicomellus* after. Previous studies reported only an incomplete rib and osteoderms. Due to significant morphological differences from previously known ankylosaurs, reviewers questioned whether *Spicomellus* belonged to Ankylosauria during the initial manuscript review. The new material not only exhibits many characteristics unique to ankylosaurs but also shows that *Spicomellus* differs greatly from traditional ankylosaurs, possessing numerous morphological features entirely distinct from other ankylosaurs. This not only enhances our current morphological understanding of *Spicomellus*, also expands our knowledge of ankylosaur morphology.

This paper is of great importance for a better understanding of the morphological diversity and evolution of ankylosaurs.

However, I have the following suggestions for the authors to consider.

(1) In abstract, the authors claimed the tail club was previously thought to have evolved only in the Late Cretaceous. The tail club knob might evolved in late Early Cretaceous: *Jinyunpelta* (Zheng et al., 2018). And the tail club handle evolved earlier, such as *Liaoningosaurus* and *Zhongyuansaurus* from Early Cretaceous (Xu et al., 2001; Zhang et al., 2025).

(2) In the early evolution of ankylosaur, I think it should include the "*Tianchisaurus*". It might be a nomen nudum, but there is no doubt that "*Tianchisaurus*" is an ankylosaur.

(3) As the caudal 'handle' vertebrae have important characteristics, they need to be present in multiple views in the figure.

(4) The most significant issue with this paper lies in the phylogenetic cladistic analysis. Firstly, regarding matrix selection, Soto-Acuña et al. (2021) chose five different matrices and added new characters, all of which resulted in the clade of Parankylosauria. However, the matrix used in this paper does not incorporate the additional characters proposed by Soto-Acuña et al. (2021). I recommend either adding additional characters proposed by Soto-Acuña et al. (2021) or using the matrices employed by Soto-Acuña et al. (2021) to re-evaluate the phylogenetic results. Secondly, the analytical methods. During the safe taxonomic reduction analysis, no taxonomic equivalents were identified. In the first analysis, Iterative PCR identified 19 unstable taxa. In the second analysis, these 19 taxa were a priori deactivated, which is methodologically problematic. Even if taxa are unstable, they still contain systematically useful information and should not be arbitrarily removed from the analysis. A notable inconsistency in the results is that *Borealopelta* is placed within Ankylosauridae, which conflicts with other studies and even the authors' first analysis. Relying on such an analytical result is scientifically unsound.

(5) "Ankylosauridae" is misspelled in Figure 3.

References

- Soto-Acuña, S., Vargas, A. O., Kaluza, J., Leppe, M. A., Botelho, J. F., Palma-Liberona, J., Simon-Gutstein, C., Fernández, R. A., Ortiz, H., Milla, V., Aravena, B., Manríquez, L. M. E., Alarcón-Muñoz, J., Pino, J. P., Trevisan, C., Mansilla, H., Hinojosa, L. F., Muñoz-Walther, V., & Rubilar-Rogers, D. (2021). Bizarre tail weaponry in a transitional ankylosaur from subantarctic Chile. *Nature*. <https://doi.org/10.1038/s41586-021-04147-1>
- Xu, X., Wang, X.-L., & You, H.-L. (2001). A juvenile ankylosaur from China. *Naturwissenschaften*, 88(7), 297–300. <https://doi.org/10.1007/s001140100233>
- Zhang, J., Jia, L., Xu, L., You, H., Gao, D., Liu, D., Li, Y., & Wang, Y. (2025). New ankylosaurid material from the Lower Cretaceous of the Ruyang Basin, Henan Province. *Acta Palaeontologica Sinica*, 64(1), 60-73. <https://doi.org/10.19800/j.cnki.aps.2023037>
- Zheng, W., Jin, X., Azuma, Y., Wang, Q., Miyata, K., & Xu, X. (2018). The most basal ankylosaurine dinosaur from the Albian–Cenomanian of China, with implications for the evolution of the tail club. *Scientific Reports*, 8(1), 3711. <https://doi.org/10.1038/s41598-018-21924-7>

Version 1:

Reviewer comments:

Referee #1

(Remarks to the Author)

The authors have provided useful responses to most of my comments, and I appreciate the limitations of what can be determined re: the paleoenvironment at this time.

Comments:

1. Some of the main conclusions of this work center on the presence of 'handle' (fused caudal) vertebrae providing evidence of tail weaponry. Unfortunately, the 'handle' element of *Spicomellus* is only visible in one view (ventral). As this specimen also includes a dorsal vertebra with a pathology (Fig. S4, USMBA 51), it raises the possibility that the 'handle' is also pathological and thus does not provide evidence of tail weaponry. Related to this, I would note that *Spicomellus* is only distantly related to other ankylosaurs known to have well-preserved 'handle' vertebrae and tail weaponry, and so the presence of this anatomical feature in this species is entirely unexpected. Therefore, while it remains possible that the element in question is a 'handle', the alternative (that the vertebrae are pathological and do not relate to the presence of tail weaponry) must also be considered. Accordingly, the emphasis placed on tail club evolution (in the Abstract/Summary, first paragraph of the Discussion, and Conclusion) should be revised, and the alternative hypothesis included.

2. While I agree that Cretaceous ankylosaurs had less elaborate cervical osteoderms, it seems premature to refer to these as being simplified (suggesting they evolved to become less ostentatious). Alternatively, *Spicomellus* alone may have developed the unusual elaborate phenotype. Thus, instead of asking why the cervical osteoderms of Cretaceous forms become less extravagant, it may be questioned why did *Spicomellus* (alone) evolve the lengthy, spike-like elements.

Minor:

- The descriptive term 'extremely' is unnecessary in the context of the descriptions of cervical half ring spikes and caudal vertebrae (simply, they are elongate), and the postacetabular ridge (simply, it is robust)
- Related to the use of the term 'compound osteoderm', it has been argued that osteoderms represent a deep homology common across tetrapods. While readers are unlikely to confuse the compound osteoderms of scincids with those of *Spicomellus*, it seems unnecessary to give two distinctive phenotypes the same name.

Referee #2

(Remarks to the Author)

This discovery is of great significance for understanding the morphology and evolution of ankylosaurs. The points I raised in the previous round of review have been satisfactorily addressed, except that in the abstract, the author simply deleted the "Late" about the evolution of the tail club. I recommend using the "Early" instead.

permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

In cases where reviewers are anonymous, credit should be given to 'Anonymous Referee' and the source.

The images or other third party material in this Peer Review File are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder.

To view a copy of this license, visit <https://creativecommons.org/licenses/by/4.0/>

Responses to reviewer comments

Referee #1 (Remarks to the Author):

The descriptive approach and phylogenetic investigation are valid, although the different phylogenetic strategies employed offer strikingly different interpretations on the identity of the specimen (as with a basal member of Ankylosauria or basal member of Ankylosauridae). Further, in the Supplementary Materials the authors note that the Ankylosauridae hypothesis is “...weakly supported in this analysis and require further testing with future discoveries”. Therefore, the authors should consider revising Figure 3 with both phylogenetic interpretations.

We don't favour one analysis over the other in the discussion, and present both in the supplementary material, but we have now replaced Fig. 3 with the PCR tree given the comments of reviewer 2. Unfortunately, weak support is a feature of ornithischian dinosaur phylogenies, especially where we have a lot of taxa that are partial and fragmentary. We have added 'putative phylogenetic position' to the figure caption to indicate uncertainty.

The quality of data presented, and quality of presentation is good, although addition figures of some of the skeletal elements (e.g., possible cranial fragments) are needed.

A figure of the possible cranial fragments has been added to the supplementary data and figure numbers updated throughout.

Also, the descriptions in the Supplementary Materials focus on images in the main text and strangely do not refer to the supplementary figures.

Corrected. Supplementary figures are now cross-referenced in the text.

More information about the paleoenvironment of the specimen would be helpful.

A sentence has been added to the methods to detail that the El Mers III Formation was deposited on a floodplain. More detailed sedimentology and stratigraphy can be found in Maidment et al. (2020). A detailed examination of the sedimentology and biostratigraphy of the formation at Boulahfa Plain is forthcoming from our team.

The interpretation of the elongated spine-like osteoderms as primarily display is certainly plausible, but other hypotheses should also be considered. What is the interpretation of the local (paleo)environment (e.g., Discussion line 256 states that these spike-like osteoderms would be challenging in a densely vegetated setting – is that the case here)? What other species (i.e., possible predators) known from this locality/horizon? Related to this, a recent summary of osteoderm functions was published by Ebel et al., 2024 (<https://doi.org/10.1111/jzo.13224>).

A detailed account of the palaeoenvironment is forthcoming from our team, but this has not previously been documented. That said, we do not find large amounts of fossilized wood in the formation, and thus we have removed the reference to dense vegetation being problematic for *Spicomellus*.

Prior to the start of work by our team in 2018, there had never been any systematic exploration of the El Mers Group for vertebrate fossils and thus the only dinosaurs so far known from the Formation are those we have reported. Theropods are currently unknown from the Formation, except from a few isolated teeth, and these are undescribed.

As shown by the useful review the reviewer has provided, osteoderms are unlikely to have had a single function. We have nuanced the discussion to suggest that the osteoderms may have had a role in display as well as defence.

Two strategies were employed to perform the phylogenetic analysis. Although the position of *Spicomellus* varies between them, neither analysis recovers the recently proposed Southern Hemisphere group Parankylosauria. Given the material available, the inability to fully resolve the phylogenetic position of this species is expected. That said, why was Extended Implied Weight analysis phylogeny emphasized in the manuscript (figure 3)? In the Supplementary Materials it is acknowledged to be “weakly supported”.

We don't favour one analysis over the other in the discussion, and present both in the supplementary material, but we have now replaced Fig. 3 with the PCR tree given the comments of reviewer 2.

There is a bit of discrepancy in the age information between the holotype (Upper Bathonian/Callovia; Maidment et al. 2021) and the present material (Bathonian). Both appear to be from the same horizon and similar locations, but perhaps more detailed could be provided.

A sentence has been added to the supplementary data that further biostratigraphic work by our team has indicated a Bathonian age for the entire El Mers Group. Our work on this is forthcoming.

Description, lines 70-73: to avoid confusion, the terms ‘spike’ and ‘plate’ should be used as morphological descriptors of osteoderms (i.e., spike-like osteoderms, plate-like osteoderms). Also, the term ‘compound osteoderm’ is already used to describe the multi-partite osteoderms of some scincids (e.g., <https://www.nature.com/articles/s41598-024-66451-w>). Thus, an alternative descriptor for the elements of *Spicomellus* should be employed.

Spike and plate are very common terms used to describe thyrophan osteoderms and are used descriptively. Likewise, ‘compound osteoderm’ is a descriptive term.

We think it unlikely that anyone will consider we are suggesting that the compound osteoderms of scincids are homologous to those of *Spicomellus*, so we prefer to stick with our more succinct terminology.

Description, lines 77-83: the presence of ‘handle’ vertebrae (fused caudal vertebrae) is significant towards the interpretation of having a tail club. Additional images of this feature in the Supplemental Materials would be helpful.

Unfortunately the handle vertebrae are preserved squashed into the space between the preacetabular process and the pubic peduncle of the ilium, and cannot be freed without breaking the ilium with the prep facilities we have available to us in Morocco. They are only visible in ventral view and the photos we have provided are the best we can do.

Description, line 99 (see also Supplementary p. 16: the use of ‘scapulocoracoids (Fig. S7) are indistinguishably fused’ is confusing. Perhaps the scapula and coracoid are fused creating a single element?

Corrected to ‘scapula and coracoids’

Description, line 123: identify the location of the brevis fossa on Fig. S8

Done – this has been added to the figure (now S9).

Description, lines 131-132: the imperforate acetabulum is described as ‘...closed medially by fusion of the ischium’. Fusion of the ischium to what? Are the sutures between the individual pelvic elements visible? I could not see this on Fig. S8.

Corrected to state ‘closed medially by fusion of the ischium to the ilium’. We state in the ilium description of the main ms: “Sutures between these elements are not visible” already.

As the location of most of the osteoderms depicted in Figure 2 are speculative and as some are already shown in Figure 1, this image should be placed into Supplementary information. Even though the title includes the disclaimer “hypothetical positions” the figure presents a false sense of certainty.

We’d like to keep this figure because it gives us the opportunity to figure many more pieces of dermal armour than we do in Fig. 1, and showcase the variety of osteoderms. However, we’re happy to be guided by the Editor on this.

Discussion, lines 254-261: with respect to the interpretation of function(s), it is noted that these elongate cervical osteoderms may have “...hindered locomotion in

densely vegetated environments” – what is known about the paleoenvironment/paleoecology of the El Mers III Formation?

A detailed account of the palaeoenvironment is forthcoming from our team, but this has not previously been documented at Boulahfa other than by Maidment et al. (2020). It is a floodplain environment but detailed palynology is needed to determine what was living there. We are in the very early stages of exploration of these rocks. We have now removed this sentence from the paper.

Related to the above, osteoderms have been associated with a number of functional roles (see Ebel et al., 2024, <https://doi.org/10.1111/jzo.13224>), but defensive/protective seems to be the most intuitive (and is even implied by the title of this manuscript with the term ‘armour’). It is thus confusing to suggest (lines 257-259) that the spike-like cervical osteoderms of *Spicomellus* are “...structures with limited obvious functionality...”. What other taxa (especially carnivorous forms) are known from the same horizon as *Spicomellus*? While sexual selection cannot be ruled out, it seems a bit premature to raise the profile of this hypothesis over that of (for example) protection against predation or even intraspecific combat.

We have now nuanced the discussion (and abstract) to suggest that display might have been a function of the dermal armour alongside defence.

Prior to the start of work by our team in 2018, there had never been any systematic exploration of the El Mers Group for vertebrate fossils and thus the only dinosaurs so far known from the Formation are those we have reported. Theropods are currently unknown from the Formation, except from a few isolated teeth.

Discussion, lines 262-274: the interpretation of Cretaceous ankylosaurs evolving a more simplified osteoderm morphology is interesting, but perhaps overstated and alternatives should be considered. It is unclear if the shape change relates to an entirely different function (visual display vs physical protection) or something more nuanced. For example, such morphological differences may reflect a more active defensive weapon role in *Spicomellus* vs. some Cretaceous forms. It may also relate to a difference in potential predators and predatory strategies.

It's quite difficult to see how the neck armour could have been used as an active defensive weapon in *Spicomellus*, given where it occurs on the body. Tail clubs might well have been active defensive weapons, but were best developed in the Late Cretaceous and there has been some research that suggests their use in intraspecific combat. We have now nuanced our discussion of dermal armour to suggest a display as well as a defensive function.

We already discuss the change in predators and predation pressures in the paragraph at the end of the discussion: “It has been argued that predation pressures increased in the Late Cretaceous due to the radiation of numerous medium- and large-

bodied theropod clades and the evolution of larger mammals, crocodilians and snakes, and were much greater than in extant ecosystems...". Also, throughout the discussion, we use phrases like "could" and "might suggest" to indicate that we are suggesting a hypothesis, rather than making definitive statements.

Possible cranial fragments USMBA 38 and 66 are not figured in the Supplementary information. Why is USMBA 38 suggested to be cranial?

A figure of these has now been added to the supplementary information. We don't really know what these bits are, but they don't correspond morphologically to anything in the postcranium that we can think of, and the relatively thin laminae and outline shape could be reminiscent of skull bones.

The pathology on USMBA 51 (Fig. S3) should be labeled.

Done – now labelled in the figure (now S4).

Is there an image of the sacral ribs and their association with the acetabulum?

No, the ilia and sacra are preserved in several blocks that do not fit closely together, having been excavated with a pick-axe by the farmer prior to our (more careful) excavation of the site.

Referee #2 (Remarks to the Author):

(1) In abstract, the authors claimed the tail club was previously thought to have evolved only in the Late Cretaceous. The tail club knob might evolved in late Early Cretaceous: *Jinyunpelta* (Zheng et al., 2018). And the tail club handle evolved earlier, such as *Liaoningosaurus* and *Zhongyuansaurus* from Early Cretaceous (Xu et al., 2001; Zhang et al., 2025).

'Late' has been deleted

(2) In the early evolution of ankylosaur, I think it should include the "*Tianchisaurus*". It might be a nomen nudum, but there is no doubt that "*Tianchisaurus*" is an ankylosaur.

Tianchisaurus is from the Toutunhe Formation of the Junggar Basin. When it was first described, it was thought that the Toutunhe was Middle Jurassic, but our understanding is that the most recent dating suggests it is Late Jurassic (Oxfordian or Kimmeridgian). There are a number of other Late Jurassic ankylosaurs and this section in the introduction deals with the Early to Middle Jurassic fossil record, so it

is not appropriate to mention here. Age ref is Huang (2019):
<https://link.springer.com/article/10.1007/s11430-017-9268-7>

(3) As the caudal 'handle' vertebrae have important characteristics, they need to be present in multiple views in the figure.

Unfortunately the handle vertebrae are preserved squashed into the space between the preacetabular process and the pubic peduncle of the ilium, and cannot be freed without breaking the ilium with the prep facilities we have available to us in Morocco. They are only visible in ventral view and the photos we have provided are the best we can do. We do mention this in the supplementary material.

(4) The most significant issue with this paper lies in the phylogenetic cladistic analysis. Firstly, regarding matrix selection, Soto-Acuña et al. (2021) chose five different matrices and added new characters, all of which resulted in the clade of Parankylosauria. However, the matrix used in this paper does not incorporate the additional characters proposed by Soto-Acuña et al. (2021). I recommend either adding additional characters proposed by Soto-Acuña et al. (2021) or using the matrices employed by Soto-Acuña et al. (2021) to re-evaluate the phylogenetic results.

The phylogenetic analysis we have used here is that of Raven et al. (2023) modified by the addition of all thyreophoran dinosaurs that have been published since that work. This represents the most comprehensive analysis of thyreophoran dinosaurs ever undertaken, includes all valid thyreophoran taxa, synthesized all previous work, including characters from all of the analyses the reviewer mentions above, and is therefore clearly the best dataset available to test the phylogenetic position of *Spicomellus*. Raven et al. (2023) used numerous analytical techniques, including Bayesian and parsimony algorithms, and presented several different phylogenetic hypotheses as a consequence, but none of these recovered 'Parankylosauria'. Raven et al. (2023) was published after the publication of Soto-Acuña et al. (2021), which is why it wasn't available for those authors to use. Herein, we have added *Stegouros*, the taxon described by Soto-Acuña et al. to the matrix of Raven et al. (2023) and have not recovered Parankylosauria either.

Soto-Acuña et al. (2021) used five phylogenetic matrices to examine the phylogenetic position of *Stegouros*. These include Han et al. (2018), an ornithischian matrix designed to examine the phylogenetic position of a basal ceratopsian, with a focus on Neornithischia. This matrix originally only included three ankylosaurs, to which Soto-Acuña added three southern hemisphere taxa. It therefore does not have the power to resolve the phylogenetic position of *Stegouros*, *Spicomellus*, or indeed any other ankylosaur, and cannot be used to test the 'Parankylosauria' hypothesis.

The second matrix used by Soto-Acuna et al (2021) was that of Raven & Maidment (2018), a matrix designed to test the ingroup relationships of stegosaurian dinosaurs. The original analysis also only included three ankylosaurs, to which Soto-Acuna et al. (2021) added three southern hemisphere taxa. Once again, this analysis was not designed to examine ankylosaurian relationships and does not have the power to do so, so no conclusions about the validity of Parankylosauria can be drawn from it.

Soto-Acuna et al. (2021) also used the matrix of Norman (2021), which was a very small analysis with an extremely limited taxon sample designed to examine the relationships of basal thyreophorans. The thing that has the single biggest effect on the phylogenetic position of a taxon is taxon sampling. Norman (2021) only included seven ankylosaurs, to which Soto-Acuna et al (2021) added three southern-hemisphere taxa. Once again, this analysis does not have an appropriate taxon sample to test ankylosaur ingroup relationships and was not designed to do so.

The analysis of Weisma and Irmis (2018) was also used by Soto-Acuna et al. (2021). This analysis is focused on ankylosaurid dinosaurs, and only samples four nodosaurid taxa. It therefore does not have the power to resolve the phylogenetic position of taxa that do not fall within Ankylosauridae, a clade *within* ankylosaurs. The Parankylosauria hypothesis cannot, therefore, be tested with this analysis, because the southern-hemisphere taxa may represent nodosaurids but this cannot be resolved because most nodosaurids are not included.

Arbour et al. (2016) was the most comprehensive ankylosaur phylogeny prior to the publication of Raven et al. (2023). It is an expanded version of Arbour & Currie (2016). The latter was a phylogenetic analysis of ankylosaurid dinosaurs and therefore had a limited taxon sample nodosaurids (12 were included). Arbour et al. (2016) expanded this analysis to add some additional nodosaurids (30 were included) for a total of 54 ankylosaurs. By way of contrast, Raven et al. (2023) included 69 ankylosaurs, including several that were undescribed at the time of publication of Arbour et al. (2016) and Weisma & Irmis (2018). To Raven et al. (2023), we have added or modified the scores of three additional ankylosaurs which have been published subsequently, including *Stegouros*, new data published on *Antarctopelta* (also by Soto-Acuna and colleagues) and *Patagopelta*, which was originally in the matrix but as an OTU called the 'Argentinian ankylosaur'. We also added two new putative basal thyreophorans which have been described since Raven et al. (2023) and whose character states will likely have an effect on the 'basal condition' of Ankylosauria (*Jakapil* and *Yuxisaurus*). It's worth noting that these taxa are not in any of the analyses presented by Soto-Acuna et al. (2021).

It should be clear from the above account of the analyses carried out by Soto-Acuna et al. (2021) that the only one that actually had the power to examine the validity of the Parankylosauria hypothesis is Arbour et al. (2016). It is worth saying that Arbour et al. (2016) already included *Antarctopelta*, *Kunbarrasaurus* and *Patagopelta* but did not recover Parankylosauria. This analysis is also now nine years old, and a large

number of additional ankylosaurs and basal thyreophorans have been described since then. All of the characters included in Arbour et al. (2016) were assessed and included in Raven et al. (2023). The reviewer has noted that an additional 12 ‘new’ characters were added to Arbour et al. (2016) by Soto-Acuna et al. (2021). In fact, most of these characters are not new, but have appeared in thyreophoran phylogenetic analyses before (several are clearly derived from Raven & Maidment 2018 because the wording is identical). Of the 12 ‘new’ characters, eight are already present in Raven et al. (2023), leaving just four novel characters. These pertain to the maxilla, mid to posterior caudals (only scorable for taxa without handle vertebrae in this part of the tail), manual and pedal phalanges. The final of these is likely invalid as it is strongly correlated with another character on pedal phalanges and is therefore not independent. None of these characters can be scored for *Spicomellus*.

It's not clear, therefore, what additional benefit would be gained from adding *Spicomellus* to the Arbour et al. (2016) matrix. The taxa and characters used are already incorporated into Raven et al. (2023), but the latter has a larger and more up to date taxon sampling. The results of our analyses are actually in keeping with Arbour et al. (2016), in finding *Kunbarrasaurus* and *Antarctopelta* as nodosaurids, with the former as the most basal member of that clade.

Secondly, the analytical methods. During the safe taxonomic reduction analysis, no taxonomic equivalents were identified. In the first analysis, Iterative PCR identified 19 unstable taxa. In the second analysis, these 19 taxa were a priori deactivated, which is methodologically problematic. Even if taxa are unstable, they still contain systematically useful information and should not be arbitrarily removed from the analysis. A notable inconsistency in the results is that *Borealopelta* is placed within Ankylosauridae, which conflicts with other studies and even the authors' first analysis. Relying on such an analytical result is scientifically unsound.

The point of Iterative PCR is to identify wildcard taxa that are causing instability in phylogenetic trees either because of character conflict or (commonly) lack of data, which means taxa could occupy multiple positions in the tree. We agree with the reviewer that it would be ideal to not delete any taxa; however, this results in lack of structure and no insight into the phylogenetic position of *Spicomellus*. At least by using IterPCR to identify wildcard taxa we are producing a rationale for *a priori* taxon deletion and making our analysis repeatable and explorable by others. We have also presented the full results of both analyses in the supplement and discuss both in the paper, not favouring the results of one over the other. However, in recognition that the reviewer is right here, we have changed the phylogeny presented in Fig. 3 to the PCR tree.

(5) “Ankylosauridae” is misspelled in Figure 3.

Oops. Corrected.

Referees' comments:

Referee #1 (Remarks to the Author):

The authors have provided useful responses to most of my comments, and I appreciate the limitations of what can be determined re: the paleoenvironment at this time.

Comments:

1. Some of the main conclusions of this work center on the presence of 'handle' (fused caudal) vertebrae providing evidence of tail weaponry. Unfortunately, the 'handle' element of *Spicomellus* is only visible in one view (ventral). As this specimen also includes a dorsal vertebra with a pathology (Fig. S4, USMBA 51), it raises the possibility that the 'handle' is also pathological and thus does not provide evidence of tail weaponry. Related to this, I would note that *Spicomellus* is only distantly related to other ankylosaurs known to have well-preserved 'handle' vertebrae and tail weaponry, and so the presence of this anatomical feature in this species is entirely unexpected. Therefore, while it remains possible that the element in question is a 'handle', the alternative (that the vertebrae are pathological and do not relate to the presence of tail weaponry) must also be considered. Accordingly, the emphasis placed on tail club evolution (in the Abstract/Summary, first paragraph of the Discussion, and Conclusion) should be revised, and the alternative hypothesis included.

These vertebrae are clearly not pathologic. The 'handle' tendons are symmetrical either side of the midline and composed of normal bone, unlike the asymmetric pathology which is composed of highly vascular bone. Furthermore, the vertebra has

an elongate prezygapophysis, as seen in handle vertebrae of other ankylosaurs. Bone pathologies are quite obvious in dinosaurs and these vertebrae are clearly not pathologic.

2. While I agree that Cretaceous ankylosaurs had less elaborate cervical osteoderms, it seems premature to refer to these as being simplified (suggesting they evolved to become less ostentatious). Alternatively, *Spicomellus* alone may have developed the unusual elaborate phenotype. Thus, instead of asking why the cervical osteoderms of Cretaceous forms become less extravagant, it may be questioned why did *Spicomellus* (alone) evolve the lengthy, spike-like elements. Based on currently available data, neither hypothesis is better or worse than the other. We need to find more early southern hemisphere ankylosaurs to test whether *Spicomellus* was particularly unusual or whether it is characteristic of basal members of the group. The strange, fan-like weapon of *Stegouros* certainly indicates unusual armour in southern hemisphere members of the clade.

Minor:

- The descriptive term 'extremely' is unnecessary in the context of the descriptions of cervical half ring spikes and caudal vertebrae (simply, they are elongate), and the postacetabular ridge (simply, it is robust)

We disagree; they are extremely elongate.

- Related to the use of the term 'compound osteoderm', it has been argued that osteoderms represent a deep homology common across tetrapods. While readers are unlikely to confuse the compound osteoderms of scincids with those of *Spicomellus*, it seems unnecessary to give two distinctive phenotypes the same name.

We disagree; this is a descriptive term that many people will understand and has been used in the past for osteoderms of *Yuxisaurus*, which we cite.

Referee #2 (Remarks to the Author):

This discovery is of great significance for understanding the morphology and evolution of ankylosaurs. The points I raised in the previous round of review have been satisfactorily addressed, except that in the abstract, the author simply deleted the "Late" about the evolution of the tail club. I recommend using the "Early" instead.

Wenjie Zheng

Done