

## **A baenid turtle shell from the Mesaverde Formation (Campanian, Late Cretaceous) of Park County, Wyoming, USA – Revision – Response to Reviewers**

We thank the reviewers for their helpful comments. We have incorporated most of them, and provided explanations for areas where we did not incorporate the suggestions. Comments of general nature that did not require a change or rebuttal are not included below, for brevity.

### **Comments from Editor**

- The two reviewers agree that your work is interesting and contributes to the understanding of the baenid fossil record. Both of them provided a detailed review of your manuscript and made a number of pertinent suggestions, notably concerning the identification of the specimen, the shape of the femoral-anal sulcus, and the phylogenetic analysis. I am looking forward to reading a revised version of this paper. Please submit a rebuttal letter referring to the different points raised by the reviewers and a tracked-changes file along with your revision.
  - Thank you. We have addressed all of these points at the appropriate place below.

### **Review by Heather Smith**

- I think the authors are correct not to erect a new taxon based on this specimen. However, I would encourage them to be a bit more definitive regarding taxonomic attributions. Despite lack of resolution in the phylogenetic tree, I downloaded the data matrix and I see that RAM 28750 is identical to *Neurankylus eximius* and *N. torreonensis* for all characters for which it can be coded. Since there are no coded character differences, I think it would be reasonable to tentatively assign RAM 28750 to “*Cf. Neurankylus*” or “*Neurankylus sp.*”. Additionally, adult shell size is also a diagnostic character among baenids with few taxa reaching a carapace length of 450 mm. RAM 28750 is the right size to belong to *Neurankylus*.
  - Based on the overall comments from the reviewer and discussion with other colleagues, we agree that a tentative referral to *Neurankylus* is warranted, and we have adjusted the paper accordingly.
- The only apparently contrasting trait to a diagnosis of *Neurankylus* appears to be the omega-shaped femoral-anal sulcus. I completely agree that this morphology is unexpected for *Neurankylus* and more typical of baenodds; however, given that all other lines of morphological evidence suggest affinities with *Neurankylus*, I’d be inclined to consider the possibility that you could be seeing some individual variation. The sulcus is also incomplete, given that the right side of the plastron is missing, so while it’s reasonable to reconstruct the sulcus shape in RAM 28750 as likely omega-shaped, it’s also not entirely certain.
  - We agree, and have revised our conclusions along these lines.
- The Rollot et al 2022 data matrix used here is generally solid; however, it has also been modified since the original Joyce, Lyson, et al iterations and is now formatted more for assessing relationships among basal baenids and among other paracryptodires (note the large number of non-baenid taxa included). It’s not as well-suited for evaluating the details of relationships among derived baenids. Earlier versions of the matrix, most notably Lyson et al., 2016, include a larger number of baenid taxa, including additional species of *Neurankylus*, *N. baueri* and *N.*

*lithographicus*. I just revisited the Lyson et al. (2016) character list, and I think RAM 28750 for could be coded for more than 7 characters in this dataset, so the resolution may be improved. I'd encourage the authors to code RAM 28750 for the Lyson et al. (2016) characters, re-run the phylogenetic analysis, and see if the topology changes.

- The Lyson et al. 2016 matrix has been superseded by other matrices (e.g., Lyson et al. 2021 on *Palatabaena knellerorum*) that have revised characters and broader taxon sampling within Baenidae. Prior to the initial submission of the manuscript, we coded RAM 28750 into some of these, although the resolution was not improved. For the purposes of this paper – simply to test the general position of RAM 28750 – we believe that the Rollot et al. matrix works well, because it 1) establishes the identity of RAM 28750 as baenid; and 2) shows the generally fragmentary nature of the specimen prohibits a more detailed assignment. We also attempted adding some characters used in previous analyses, but similarly didn't gain any resolution.
- If/when you run a new phylogenetic analysis, you might also try adjusting a few settings. For example, 100,000 replications is a lot! It's not surprising that you ended up with 75k trees and a strict consensus with minimal resolution. According to my reading, both Rollot et al. (2022) and Lyson et al. (2016) used 1000 replications. That's probably plenty. You might also consider assessing the majority-rule consensus tree rather than the strict consensus to see if there are any patterns that are being overlooked in the more conservative strict version. Rollot et al. also ran the analysis again using implied weighting of K=12, which you could try. (In TNT, it's under Settings-> Implied Weighting-> Basic Settings-> Click "Using Implied Weights" and change the "weight with default function" to K = 12).
  - Thank you for the comments. Running with fewer replications achieved an identical strict consensus tree. A 50% majority rule consensus tree showed RAM 28750 within Baenodda, but we caution that it is equally parsimonious to place outside Baenodda (as implied by the strict consensus tree). Thus, we feel the majority rule consensus tree would not help in resolving the affinities of RAM 28750.
  - We reran the analysis with implied weighting of K = 12 as suggested, but achieved identical results for the position of RAM 28750 to the analysis presented here.
- I'd love to see a phylogenetic tree included as a figure in the Results, even if the resolution is suboptimal.
  - Given the poor resolution, we have elected to not incorporate a figure, but note that it is accessible via the supplemental information for those who are interested.
- Lines 161-164: The anterior plastral lobe is also trapezoidal in *Neurankylus torreonensis*. This morphology is characteristic of *Neurankylus*.
  - Complete
- Lines 168-169: The posterior plastral lobe is reportedly larger than the anterior plastral lobe in *N. eximius* and *N. lithographicus*, but not *N. baueri*.

- A deeper dive into the literatures shows that this feature is variable within species, so we have added some text along those lines.
- Lines 180-181: The phrase “narrowing just anterior to the midpoint” here is a bit unclear. Do you mean the anteroposterior midpoint of the carapace? Please clarify.
  - Complete
- Lines 191-194: *N. torrejonensis* has posterior scalloping, but some other *Neurankylus* species do not. Given the other morphological affinities to *Neurankylus*, I think this would be worth mentioning.
  - The condition in *N. torrejonensis* is somewhat ambiguous, only deemed as “likely scalloped” by Lyson et al., due to the incomplete preservation along the posterior margin. We have added some text about scalloping in this relevant part of the description.
- Can you tell how well developed the axillary and inguinal buttresses are? Do they contact the costals broadly? This is the case in many baenids and seems likely here, so it would be worth mentioning if you can tell.
  - We have added some text to this effect.
- Many baenid taxa are shell-only. Thus, the absence of a skull typically does not dictate the decision as to whether to name a new taxon. For example, I don’t believe a skull is known for *Neurankylus baueri*. Thus, I’d suggest deleting the phrase “in addition to the lack of a skull” from line 209.
  - Complete
- Figure 2 caption: Anterior and posterior “pleural” lobes, should be “plastral” lobes. Pleural scutes are on the carapace.
  - Complete
- Line 21: Suggest deleting the phrase “of the Cretaceous”. Readers of the paper will generally know that the Campanian falls within the Cretaceous.
  - Complete
- Line 30: Suggest changing “anal-femoral” to “femoral-anal”
  - Complete
- Line 57: Are dates known? If so, I’d suggest listing them here.
  - Frustratingly, no radiometric dates are known for the areas under study here.
- Line 65: Suggest changing “collecting” to “collection”.
  - Complete
- Line 79: Add a comma after “basin”.

- Complete
- Line 83: Should “near shore” by “nearshore”? I’ve more often seen it written as one word, although perhaps it’s a matter of personal preference.
  - Complete
- Line 109: Since other measurements are listed in Arabic numerals, I’d suggest changing “one to three cm” to “1-3 cm” for consistency.
  - Complete
- Lines 104-122: The prep section is substantially longer and more detailed than most fossil turtle papers I’ve read. While I appreciate the forthcoming nature of the information, I’d encourage the authors to consider condensing it a bit as the level of detail detracts slightly from the more significant parts of the paper, the morphological descriptions and implications.
  - We have elected to keep the preparation methods in their current form, in line with evolving best practice suggestions for professional fossil preparators. Although we agree that the morphology is certainly the primary interest point for our manuscript, the preparation impacts how morphology is viewed, and so is quite relevant. Furthermore, we view this as an important and readily accessible record for future researchers studying the specimen, if they wish to know how the morphology of the fossil may have been altered (or not altered) between discovery and publication.
- Line 120: Suggest changing “place” to “location” or “position”.
  - Complete
- Line 126: Suggest changing “run” to “conducted” or “performed”.
  - Complete
- Line 128: While I understand what you mean, the consecutive numbers and commas in the phrase “random seed of 1, 100,000 replications...” could look confusing to the reader. Perhaps swap the order to “100,000 replications, random seed of 1...” or write out the word “one” for clarity.
  - Complete
- Line 163: “*lithographica*” should be “*lithographicus*”
  - Complete
- Line 187: “*Denizenemys*” should be “*Denazinemys*”.
  - Complete
- Line 200: “*Lakotaemys*” should be “*Lakotemys*”
  - Complete

- Lines 207-208: “anterior plastral lobe of the plastron” is a bit redundant. Suggest just “anterior plastral lobe.”
  - Complete
- Lyson, T.R. Joyce, W.G., Lucas, S.G., and Sullivan, R.M. 2016. A new baenid turtle from the early Paleocene (Torrejonian) of New Mexico and a species-level phylogenetic analysis of Baenidae. *Journal of Paleontology* 90, 305–316. <https://doi.org/10.1017/jpa.2016.47>
  - We have cited this paper at the appropriate points in our manuscript.

## Review by Brent Adrian

### Review:

- As correctly interpreted by the authors, RAM 28750 preserves almost all of the key diagnostic features of the well known baenid *Neurankylus baueri* Gilmore 1916. A single feature (the shape of the femoral- anal sulcus) differs from the diagnostic condition of the entire genus where the sulcus is unilaterally straight or curved, but is not omega-shaped bilaterally. This is a trait characterizing the derived clade of Baenidae, Baenodda, of which *Neurankylus* is definitively not a member. While the diagnosis of the genus is quite correct in including this uncontroversial feature, damage to the area prevents the precise shape of the sulcus, as documented by Fig. 2 of RAM 28750, from being determined. What is apparent is that the unilaterally preserved sulcus is curved and not straight, and its shape is perhaps not a simple curve. However, given evidence in *N. baueri* of more substantial variation (i.e., the shape of inframarginal scales), the ambiguity in RAM 28750 is perhaps of less import than the authors present.
  - Given this suggestion about the potential variability and uncertain importance (or lack thereof) for the femoral-anal sulcus, we have moderated our weighting of this character in our identification.
- Further, though I appreciate the bilateral presentation in Figure 2D, the reader must keep in mind that any apparent difference with *N. bauri* is represented by not just a single specimen, but a single xiphiplastron. Given the fragmentary nature of the specimen and the unilateral and unclear nature of the suture, I am not convinced that the true shape of the sulcus can be determined. Unless, perhaps an additional detail photograph under oblique lighting could show the sulcus better. Additionally, I believe RAM 28750 could be accurately referred to cf. *N. baueri* based on the other clear similarities in size, general plastral proportions, and arrangement of gular/intergular scales. Additional discoveries could very conceivably confirm this attribution with a well preserved xiphiplastron. Additional discoveries could also produce a clearly omega-shaped femoral-anal sulcus, which would be evidence of a new taxon.
  - We did attempt additional photography under low-angle lighting, but just weren't able to get a satisfactory result due to the fracturing of the fossil. However, we do agree that the situation is somewhat ambiguous for RAM 28750, and have adjusted the text accordingly (as mentioned above).
- As more Late Cretaceous baenid discoveries are demonstrating, the utility of Baenodda as a concept is limited since it is not phylogenetically defined, and excludes taxa that have a unique combination of baenodda traits, but not the full suite (e.g., “*Trinitichelys*” *maini*, *Thescelus* spp.).
  - We generally agree, but have retained usage of the term here because it is already widespread in the literature (even if not well-defined) and does have some useful aspects.

- As a further consideration, *Neurankylus eximius* is typically associated with higher latitudes, and though this would be a relatively northern occurrence of *N. baueri*, its presence at Mesaverde is certainly possible. Further, I am not the only one to follow this reasoning. Though the authors mention that baenid material is known from the Mesaverde, they do not mention that cf. *Neurankylus* sp. is included in the faunal lists of DeMar & Breithaupt 2006, 2008. However, material attributed to cf. *Neurankylus* sp. is not figured or described, which is odd because the remaining turtle referrals in those studies are sound and well-supported. So, in summary, I recommend that the authors show more confidence in the affinity of this specimen with *N. baueri*. The significant contribution remains that the authors can confirm the inclusion of cf. *Neurankylus* on the faunal list of DeMar and Breithaupt 2006, 2008, and provides a well supported description and figure focusing the attribution to cf. *Neurankylus baueri* specifically. The results of the phylogenetic analysis conducted by the authors is not surprisingly unhelpful given the quantity of missing data in RAM 28750. I think a table summarizing the differential traits between *Neurankylus* species or even individual specimens would provide a more robust framework of support for the attribution I advise, to be included in the results or discussion. Further, the discussion could be expanded by a re-evaluation of the specimen in light of what is known about variation within the genus, and potential ecological or depositional insights into the Mesaverde faunal assemblage. Also, the authors should check to see whether the occurrence of *N. baueri* at Mesaverde constitutes any sort of geographical range extension for the species.

  - These are all important comments, covering many different areas. To address the major areas:
    - Although we think an assignment to *Neurankylus* sp. can be supported, a species-level assignment is difficult to justify in our opinion, particularly because many of the relevant features are incomplete in RAM 28750. For instance, we can't tell if the extragulars were separated entirely by the gulars, an important feature for species such as *N. baueri* (Sullivan et al., 2013; note that they refer to the gulars as "intergulars" and the extragulars as "gulars."). We spent considerable time with the specimen under various angles of low-angle light, and just can't pull out the sulci for this region with any more confidence.
    - We have added more text around the DeMar & Breithaupt listings of *Neurankylus* for the Mesaverde Basin. We note that their reports were for the Wind River Basin, and also note along with the reviewer that the report did not include description or specimen numbers.
    - We have added some text about variation in the genus and how it impacts identification, in the description and discussion.
    - We have also added some text in the discussion about what this specimen implies about the depositional environment for the locality.
- **Lines 29, 161, 165, 207, 213:** In several places, "trapezoidal" is used to describe the shape of the margin of the plastral lobes. This is an atypical term used in plastral descriptions, mainly because many of the (anterior lobes especially) shapes are various proportions of trapezoids. A more helpful way to describe those regions and the shape of the margins is the degree of roundedness. Figure 21.1 in Larson et al. (2013) has a nice comparison of *Neurankylus* specimens. The phrase "squared off" vs. rounded vs. subtriangular is another descriptive option that I have seen.

- We have clarified this, adding that the anterior margin of the anterior plastral lobe is squared off.
- Speaking of plastral lobes and comparisons, I'll call the authors' attention to an interesting finding from a paper that I have currently in review (otherwise I would include it). I came across a nice little dataset in Archibald (1977), his dissertation, in which he has a table of measurements (Table 57, Page 557). In this, for each taxon he samples (many of which are baenids), he has an index of "Ant. Lobe length/Post. Lobe length". In the process of using this data in an analysis, I found that *Neurankylus eximius*, *N. baeuri*, and *N. lithographicus* had a quite constrained ratio range of 0.8-0.9. A great fact about RAM 28750 is that the lengths of the articulated carapace and plastron are preserved and don't need to be estimated. If the ratio of lobe lengths in the specimen is between 0.8 and 0.9, it would add to the already ample evidence that this is *Neurankylus*. Comparative taxa might need to be added to establish this, but it is an under-reported morphological metric that seems to have some phylogenetic correlation (at least in baenids). In any case, a small comparative assessment of this trait would be interesting for the discussion.
  - This is indeed very interesting! Hutchison et al. (2013) also talked about this for distinguishing two purported *Neurankylus* species in the Kaiparowits Formation of Utah using proportions of anterior and posterior lobes of the plastron, although Joyce and Lyson (2013) later downplayed the significance of the ratio. Given this mixed signal and pending further investigation (and because the reviewer's conclusions are not yet published), we have not included this.
- Below it is the Archibald reference. If the authors have a hard time finding it or need other references mentioned herein, please contact me directly and I am happy to share PDFs.
  - Archibald, D.J. 1977. Fossil Mammalia and Testudines of the Hell Creek Formation, and the Geology of the Tullock and Hell Creek Formations, Garfield County. Ph.D. Thesis, University of California, Berkeley.
    - Thank you!
- Line 45: Campanian sites are named in parentheses, so "other Campanian" should replace "many" added before "formations".
  - Complete
- Line 56: Replace "unit" with "Mesaverde Formation".
  - Complete
- **Line 58-61:** This paragraph would benefit from more detail. When possible, please identify sympatric genera rather than family. For instance, it is notable that *Boremys* is recognized in the Mesaverde, and even more so because DeMar and Breithaupt attribute cervical vertebrae to *Boremys pulchra* rather than its substantially larger congeneric, *B. grandis*. Not reporting genus level sympatrics loses this detail. It is intriguing that the two baenids represented are apparently a very small derived species and a quite large, more primitive generalist species. Though I don't recall seeing this in a study, it's my impression that sympatric baenids, especially as pairs, seem to have body size and locomotor/dietary differences suggestive of niche separation. The presence of two baenid taxa is similar to many pre-Campanian assemblages, and does not

approach the richness seen in the most speciose units of the latest Cretaceous (e.g., Hell Creek, which boasts at least 11 baenids).

- For the introduction, the purpose is to introduce the overall turtle clades, and so we have left this section at the family level. We did, however, revise the manuscript to expand upon the Baenidae referrals by DeMar and Breithaupt in the discussion. We note that the *Boremys* referrals are tentative (and indeed, the carapace material has not been figured, so we have not yet been able to verify the identification). The identification of cervical vertebrae was considered tentative by DeMar and Breithaupt.
- In locating this information myself in the DeMar and Breithaupt publications, I noticed that the faunal lists include a “cf. *Neurankylus* sp.”, but not much else is mentioned of this taxon. This material should be addressed and differentiated from or related to RAM 28750, if even possible (the material is not figured). Also, if possible, an idea of the sample size of the represented Mesverde collection would be helpful in the paragraph beginning on line 62. Speaking of the author, it appears that “DeMar” is the correct spelling, so this should be corrected throughout.
  - We have expanded our reference to the DeMar and Breithaupt listing of *Neurankylus*, and also ensured consistency of spelling for “DeMar”.
- Line 83: If “an uncommon record of” is replaced with “few”, it makes the next sentence read more smoothly.
  - Complete
- Line 85: Please replace “easterly” with “eastward”.
  - Complete
- **Regarding Line 99:** It is significant that the host matrix of RAM 28750 is siltstone, as most relatively complete baenids are recovered from sandstones and thus had a fluvial deposition. *Neurankylus* has been an exception to this nearly ubiquitous trend, and its presence in non-fluvial or potentially lacustrine deposits suggests a difference in habitat from most baenids. This is summarized in Adrian et al. (2019) on page 7 with more references therein: “Specifically, fine- to coarse-grained channel sandstone accounts for nearly all deposits from which relatively complete (≥50% of the shell) baenid shells have been recovered (Hutchison, 1980; Hutchison, 1984; Hutchison and Archibald, 1986).”
  - This is a great point! The coal seam in the same deposit is another point of evidence for a non-fluvial depositional environment for RAM 28750. We have added some text along this line, including a citation to Hutchison & Archibald (1986) as well as Sullivan et al. (1988).
- This should be mentioned in the discussion because though *Neurankylus* is a well known genus both phylogenetically and morphologically, the number of relatively complete described specimens other than types is low, and variation is poorly understood. Larson et al. (2013) discusses variation in the genus and provides some additional insights into its paleoecology. This is particularly relevant to RAM 28750, as the shape of the femoral-anal sulcus is the only preserved trait differing from *N. baueri*. Compared to the apparent variability of inframarginal shape noted in *N. baueri*, the slight variation seen in the present femoral-anal sulcus seems to be within a similarly modest range of variability. Another helpful reference for paleoecology and a good review of the taxonomic history of the genus is provided in: Lichtig, A.J., and Lucas, S.G.



2018. *Neurankylus*, a Cretaceous-Paleocene baenid turtle from North America. New Mexico Museum of Natural History and Science Bulletin, 79:323-361.

- These are very good points! We have added some text about variation in sulci for *Neurankylus*, and also referenced the Lichtig and Lucas paper where appropriate in several areas of our revised manuscript.
- Line 107: Please move “also” to after “were”.
  - Complete
- Line 109: This is partially out of self interest, but are the authors able to provide any more insight about the iron concretions around and on the bone? I have encountered iron-rich deposits on baenids before. Similar concretions were prevalent on the type specimen of the recently described baenid *Edowa zuniensis* from the Turonian of the San Juan Basin in New Mexico. Similarly, a complete shell of “*Trinitichelys maini*” was totally infilled with sand/ironstone from the Cenomanian Lewisville Formation in Texas (paper is now in review). I don’t know much about the underlying geochemistry, but I have wondered if the iron content in these concretions could be related to anoxic conditions or the presence of brackish water. Do the authors have any further observations? Are these concretions present widely in the Mesaverde or certain deposits, and do they affect any other fossils? There actually doesn’t need to be any change made, but any additional insight into this phenomenon might be of interest to some readers. One additional question- I presume the concretions were removed mechanically?
  - This is an interesting question, and one that we’re only just beginning to understand as we collect in the Mesaverde Formation more broadly. Concretions were removed mechanically, yes, and this has been clarified. Anecdotally, we have observed similar concretions on specimens of other taxa.
- **Paragraph beginning at line 123 (Phylogenetic analysis):** I understand the rationale for choosing the character matrix of Rollot et al. (2022). Unfortunately, the baenid phylogenetic matrix has become somewhat of a Frankenstein cobbled together from several iterations of analyses by different authors. Due to missing data, the phylogenetic analysis was unable to provide any clarification beyond Baenidae, which could be gleaned by the fusion of the plastron and the lack of ornamental texture. A more informative approach that might summarize the traits better is a table comparing the characters (plastral lobe shape/proportions, sulcus shape, etc.) of Campanian baenids mentioned in the differential comparisons. An example of what I mean is Table 21.1 in Larson et al. (2013).
  - See comments above relative to the phylogeny. We have not included a table, because we feel that the text is sufficient for the limited material at hand.
- **Line 152-153:** In the caption for Figure 3, anterior and posterior “pleural” lobes should be changed to anterior and posterior “plastral” lobes. Pleurals are carapacial scales.
  - Complete
- **Line 206:** There are several observations stating that RAM 28750 is relatively large, but it should be specified that this is compared to other baenids, as only a certain subset are above about 40 cm.
  - Complete

- **Line 209-210:** I agree that due to incompleteness and preservation (to some extent), this would not make a clearly diagnosable type specimen for a new taxon. However, I don't think that a skull is necessary (though it would be ideal) to define a new species, but that doesn't apply here.
  - We have removed the reference to crania.
  
- **Lines 211-221:** I appreciate the description of the margin of taxonomic uncertainty regarding RAM 28750. However, I think somewhat more certainty is warranted in this case. RAM 28750 is indeed almost identical to *Neurankylus* (cf. *N. baueri*). The omega-like shape of the femoral-anal sulcus is the only differentiating character. However, there is some variation between straight and curved femoral- anal sulci known in *Neurankylus*, though sexual dimorphism isn't known for the genus (to my knowledge). In any case, this sort of variation has been noted for other baenids (as noted in the manuscript), and there is evidence of dimorphism in other baenids. A close look at the high resolution version of Figure 2B doesn't clearly show the sulcus, though it seems to be curved. In any case, there is a lot of damage in this area, so the precise shape is not clearly defined. There is also a possibility that the sulcus could be something intermediate between curved and omega-shaped, as depicted in Fig. 21.3b in Larson et al. (2013).
  - We have clarified the associated text. Based on the feedback from the reviewers, we agree that the femoral-anal sulcus shape may not be as outside the norm in our specimen as we initially thought, and the overall evidence seems to align with *Neurankylus* as an identification.
  
- **Line 224-225:** Please add "the" before "strong", and replace "taxa" with "discoveries". The authors don't make a case for a new taxon, and evidence hasn't been presented that RAM 28750 is the first recognition of *Neurankylus* in the unit (see faunal lists of DeMar & Breithaupt 2006, 2008)
  - We have edited the paragraph slightly, along these lines. We do note that the DeMar and Breithaupt occurrence of *Neurankylus* sp. was only for the Wind River Basin, was quite tentative, and did not include a voucher specimen reference or description/illustration of the relevant material.
  
- **Line 307:** Larson et al. (2013) is out of alphabetical order at the end of the "L" refs.
  - Complete