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## A baenid turtle shell from the Mesaverde Formation (Campanian, Late Cretaceous) of Park County, Wyoming, USA

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### Abstract

The Mesaverde Formation of the Wind River and Bighorn basins of Wyoming preserves a rich yet relatively unstudied terrestrial and marine faunal assemblage dating to the Campanian. To date, turtles within the formation have been represented primarily by isolated fragments diagnostic only to broader clades. A baenid specimen from the lower third of the Mesaverde Formation in the northwestern Bighorn Basin of Park County, Wyoming, includes a partial carapace and plastron and is the most complete turtle specimen yet described from the formation. The entire carapace would have been around 450 mm long and 380 mm wide, indicating a fairly large individual. The preserved portions of the carapace are smooth and unornamented, and the overall oval dorsal profile of the shell is similar to taxa such as *Neurankylus* spp. The anterior plastral lobe in the new specimen is squared off in profile as seen in *Neurankylus* spp., unlike the more rounded or triangular condition in *Boremys* spp., *Eubaena hatcheri*, and *Baena* spp., among others. The likely omega-shaped femoral-anal sulcus differs from the condition in *Neurankylus* spp., better matching the condition seen in many (but not all) Baenodda, although only one half of the fossil preserves the sulcus, and it may lie within expected variation for *Neurankylus*. Based on the overall combination of features in this Mesaverde Formation specimen, we tentatively assign it to *Neurankylus* sp., the first report for this taxon as well as Baenidae in the Mesaverde Formation of the Bighorn Basin.

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## Introduction

Campanian-aged (Late Cretaceous) terrestrial faunal assemblages of western North America have a long history of study, yielding a diverse array of vertebrates ranging from fish to non-avian dinosaurs to mammals. Turtles are perhaps the most common vertebrates encountered in the field, with a high diversity in other Campanian formations (e.g., at least 12 in the Dinosaur Park and Oldman formations of Alberta and at least 14 taxa in the Kaiparowits Formation of Utah; Brinkman, 2003a; Hutchison et al., 2013). Observed diversity of turtles varies by latitude, local paleoenvironment, and geological age, among other factors (Hutchison et al., 2013). Thus, the comparison of turtles across regions has been a fruitful line of research for studies in biogeography, faunal turnover, environmental reconstructions, and more.

The Mesaverde Formation of the Wind River and Bighorn basins in Wyoming is important as a geographically intermediate point between northern (Alberta and Montana) and southern (Utah, New Mexico, Texas, and Coahuila) Campanian assemblages, with potential to test hypotheses around ecological and evolutionary differences across the Western Interior Basin. The best known vertebrate localities in the formation—primarily vertebrate microfossil accumulations—are inferred to preserve estuarine, fluvial, coastal swamp, and lacustrine environments (DeMar & Breithaupt, 2008), although comparatively non-fossiliferous marine facies also occur (Johnson et al., 1998). The Mesaverde Formation is generally considered to be Campanian in age, likely spanning the middle to late Campanian (Lillegraven & McKenna, 1986).

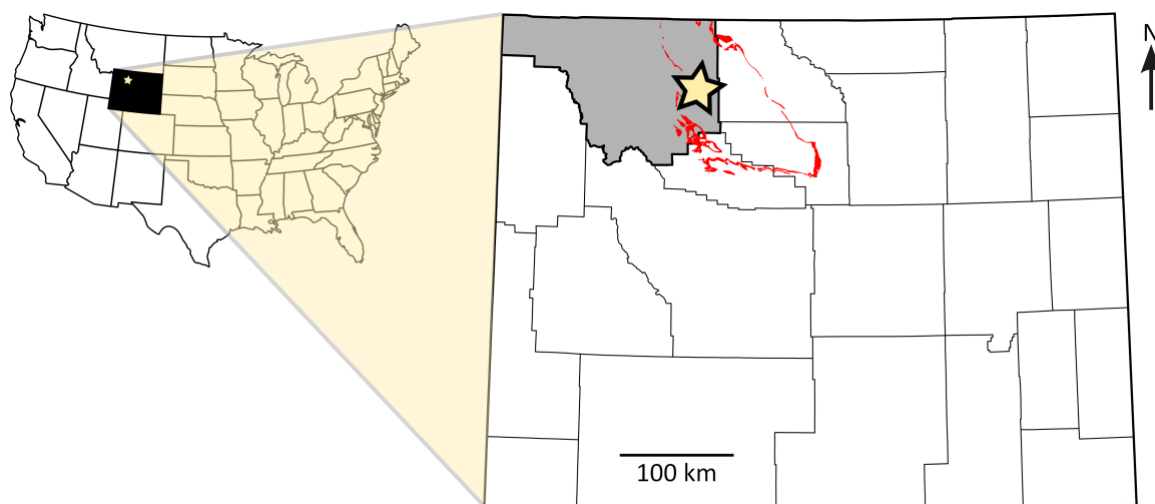
Turtle clades currently identified from the Mesaverde Formation of Wyoming include Chelydridae, Baenidae, Nanhsiungchelyidae, Adocidae, Trionychidae, and Helochelydridae (DeMar & Breithaupt, 2006, 2008; Joyce, 2017). However, because most specimens comprise only shell fragments, more refined taxonomic assignments are often tenuous, and detailed comparison with other turtle assemblages has been limited.

Since 2019, the Raymond M. Alf Museum of Paleontology at The Webb Schools has been exploring outcrops in the Oregon Basin region along the northwestern flank of the Bighorn Basin (Figure 1). Previously, only fragmentary vertebrate bones were known from this area (Hewett, 1926), and this ongoing fieldwork fills a significant geographic gap in fossil collections for the Mesaverde Formation of Wyoming. During fieldwork in 2021, museum volunteer and co-author Frank Varriale along with volunteer Alex Maya-Romero discovered a baenid turtle shell (Figure 2). Preparation showed that it was an unusually complete specimen for this formation, likely the most complete turtle known to date. Here, we describe and interpret the fossil.

### *Local Geological Background*

The Mesaverde Formation in the Oregon Basin crops out as thick, indurated sandstone hogbacks interspersed with thinner, less resistant mud- and claystones. Hewett (1926) records a thickness of 303 to 442 meters for the formation across the basin. The upper part, the Teapot Sandstone Member, is composed of sandstone beds approximately 37–94 m thick that are fine to medium grained and white to gray in color (Hewett, 1926; Johnson et al., 1998). The Teapot contains some of the most consolidated sandstones of the Mesaverde, where it forms the most prominent hogbacks ringing the basin via the differential erosion of the softer overlying Meeteetse Formation. The middle and lower parts of the Mesaverde Formation are composed of channel sandstone beds 1.5–15 m thick that are interspersed with more numerous clay- and siltstone beds (0.3–9 m) than in the overlying Teapot Sandstone Member. (Hewett, 1926; Johnson et al, 1998). In the middle part of the basin, these sands are easily distinguished from the Teapot Sandstone because they are lighter in color and more dissected, appearing as graduated tiers. Coal beds of varying size are found throughout the Mesaverde Formation, with the most prominent

concentration in the lower 91–122 meters (Hewett, 1926). The Mesaverde of the Oregon Basin is interpreted as predominantly coastal plain fluvial deposits, with a few nearshore shallow and marginal marine environments seen in some sandstones and shales. This contrasts with the general increase of these marine and marine-influenced paleoenvironments in the Mesaverde Formation progressing eastward across the Bighorn Basin (Johnson et al., 1998).



**Figure 1** - Locality RAM V2021009 (star), discovery site of RAM 28750, within outcrops of the Mesaverde Formation (red) in the Bighorn Basin of Wyoming, USA. The gray area indicates Park County.

#### *Institutional abbreviations*

AMNH, American Museum of Natural History, New York, New York, USA; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; RAM, Raymond M. Alf Museum of Paleontology at The Webb Schools, Claremont, California, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; USNM, National Museum of Natural History, Washington, D.C., USA.

## Methods

#### *Collection and preparation*

At the time of discovery, RAM 28750 had partially eroded out of the host siltstone, roughly parallel to the midline of the fossil. Loose pieces were collected, and after removing the obscuring silt and sand, more plastron was seen *in situ*. The shell was further exposed in the poorly consolidated siltstone using hand tools and was stabilized with a field consolidant, Butvar B-76 dissolved in acetone. A burlap and plaster field jacket was built after the shell margin was exposed.

In the fossil preparation lab at the Raymond M. Alf Museum of Paleontology, preparation of RAM 28750 was completed primarily with two pneumatic aircsribes—the Stone HW65 and PaleoTools Micro Jack 6—and consolidated and glued with either Butvar B-76 or Paraloid B-72 dissolved in acetone. Although the majority of the matrix around the fossil was poorly consolidated siltstone, iron concretions were also abundant. Closer to the bone, the matrix became highly heterogeneous, consisting of siltstone, iron concretions, clay clasts, and small vertebrate teeth and bone fragments. Several iron-rich concretions of 1–3 cm in diameter had accreted onto the bone surface, requiring careful mechanical removal.

Additionally, significant portions of the shell had a ~1 mm layer of iron precipitated onto the surface; this layer was left intact in areas where the specimen was too unstable for continued use of a pneumatic tool, especially near the shell margin and weathered edge of the plastron. The outer margins of the shell were highly fragmented, so were held in position with Butvar B-76 until a more permanent application of archival putty—a mixture of Paraloid B-72 in acetone and marble powder—could be used as a gap filler and adhesive. Other portions of the shell were stabilized with Paraloid B-72 or Butvar B-76. A portion of matrix was left between the carapace and plastron to provide support, given that a clamshell jacket would be required to allow for dorsal and ventral views. This clamshell was made with several layers of Hydrocal FGR-95 and fiberglass, and coated with Butvar B-76 in acetone. The liner is ¼" ethafoam rather than polyester felt, to prevent the liner catching on rough portions of the shell. Several fragments of RAM 28750 collected as float were adhered at the appropriate position on the specimen shell with Paraloid B-72, but the majority of fragments were too weathered or too small to find confident fits.

#### *Phylogenetic analysis*

In order to assess the phylogenetic position of RAM 28750, the fossil was coded into the phylogenetic matrix of Rollot et al. (2022), which is derived in turn from Rollot et al. (2021), Joyce and Rollot (2020), and ultimately Lyson and Joyce (2011). A parsimony analysis was performed in TNT 1.6 (Goloboff et al., 2008; Goloboff et al., 2016), with *Proganochelys* as the outgroup. Parameters were set to 10,000 maximum trees, Wagner trees as the starting trees with 100,000 replications, a random seed of 1, TBR (tree bisection reconnection) swapping algorithm, and 1,000 trees saved per replication. Following Rollot et al. (2022), characters 4, 8, 12, 14, 16, 24, 25, 28, 31, 36.38, 43, 45, 57, 60, 77, 85, 92, 94, 95, and 98 were set as ordered. The TNT file with codings is available online (Farke 2023a).

## Results

### **Systematic Paleontology**

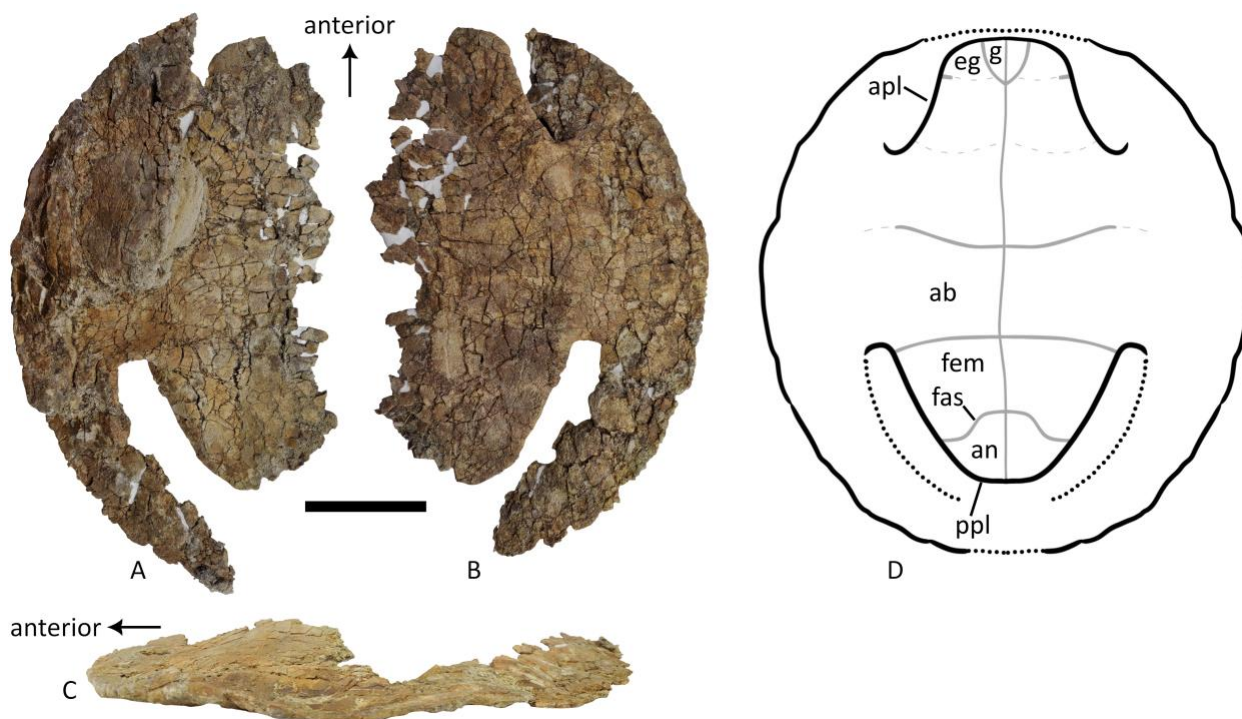
Testudines Batsch, 1788

Baenidae Cope, 1873

*Neurankylus* sp. Lambe, 1902

*Material.* RAM 28750, an articulated but incomplete carapace and plastron.

*Locality and horizon.* RAM locality V2021009, located within Oregon Basin, Park County, Wyoming. Detailed locality data are available to qualified individuals upon request. The site is in the lower third of the Mesaverde Formation, 96 meters above the base as measured from the lowest visible sandstone bed in the area; the formation in this part of the Oregon Basin is approximately 350 m to 420 m thick (Farke, personal observation; Hewett, 1926). RAM V2021009 is situated within a 1 meter thick gray siltstone with small (~1 cm diameter) clay clasts, scattered vertebrate bone fragments, and carbonaceous plant debris, overlying a 1 meter thick coal seam. The siltstone was overlain by a grey mudstone, which was capped by a resistant brown sandstone ledge.



**Figure 2** - RAM 28750, partial shell of *Neurankylus* sp., in A) dorsal; B) ventral; and C) left lateral views. D) Interpretive reconstruction showing major features on the plastron in ventral view, mirrored to present both halves. Preserved sulci are shown with solid gray lines; dashed gray lines depict sulci that are not visible in the specimen but have been depicted to help provide context. Scale bar equals 10 cm. Abbreviations: ab, abdominal scute; an, anal scute; apl, anterior plastral lobe; eg, extragular scute; fas, femoral-anal sulcus; fem, femoral scute; g, gular scute; ppl, posterior plastral lobe.

### Description

RAM 28750 preserves the left half of the plastron and the attached peripheral portions of the carapace (Figure 2), with the remainder of the specimen weathered away prior to discovery. The midline sulcus on the plastron is relatively easily visible, so the dimensions and overall shape of the shell can be estimated with a high degree of confidence by simple reflection of the shell. Thus, the complete carapace would have had a maximum width of approximately 380 mm and a length of 450 mm.

The total length of the plastron in RAM 28750 is 390 mm along the midline. As reconstructed in ventral view (Figure 2B, 2D), the plastron has a blunt, slightly trapezoidal anterior plastral lobe with a squared-off anterior border and a more rounded posterior plastral lobe, similar to the conditions found in many *Neurankylus*, such as *Neurankylus baueri* (e.g., USNM 8344), *Neurankylus eximius* (e.g., TMP 1999.055.0134 and 2003.012.0171), *Neurankylus torrejonensis* (NMMNH P-9049; Lyson et al., 2016), and *Neurankylus lithographicus* (fig. 5 in Larson et al., 2013; Gaffney, 1972; Joyce & Lyson, 2015; Sullivan et al., 2013). This contrasts with the narrower and triangular anterior plastral lobe and a more trapezoidal posterior plastral lobe of taxa such as *Plesiobaena antiqua* (e.g., TMP 1985.058.0045; Brinkman, 2003b) and *Thescelus insiliens* (e.g., AMNH 1108; Hay, 1908) or and the rounded, roughly identical anterior and posterior plastral lobes of *Eubaena hatcheri* (CM 115; Joyce & Lyson, 2015). The anterior lobe of the plastron in RAM 28750 has a length of 110 mm, and the posterior plastral lobe has a length of 125 mm. The anterior plastral lobe would have been obscured by the carapace and not visible in dorsal view, unlike the condition in *Thescelus* spp. (e.g., USNM 12818, AMNH 1108; Gaffney, 1972, Sullivan et al., 2013). The posterior plastral lobe in RAM 28750 is larger than the anterior plastral lobe, although the proportions are variable within

*Neurankylus* (Lichtig & Lucas, 2018). The axillary and inguinal buttresses on RAM 28750 are relatively well developed and contact the costals, as is typical of Baenidae (Joyce & Lyson, 2015).

Due to weathering, sulci and patterns on the plastron and carapace were difficult to identify, but some details are visible under low angle illumination (Figure 2D). When mirrored, RAM 28750 has an omega-shaped femoral-anal sulcus on the plastron, a defining trait seen in many Baenodda (Smith et al., 2017, Brinkman, 2003b, Joyce & Lyson, 2015, Adrian et al., 2023), whereas described specimens of *Neurankylus* spp. have straight or v-shaped femoral-anal sulci (Joyce & Lyson, 2015; Larson et al., 2013). We do note that because the sulcus is preserved only on one side in RAM 28750 and parts are somewhat difficult to see, that a definitive bilateral omega-shaped sulcus cannot be verified. Furthermore, the sulcus may have an element of asymmetry and sinuousness even in *Neurankylus* (e.g., *N. eximius*, TMP 1999.055.0134; see figure 3 in Larson et al., 2013). The gular scutes (*sensu* Joyce & Lyson, 2015) are relatively large compared to the overall anterior plastral lobe (Figure 2D). Unfortunately, only the most lateral portion of the extragular scute border is preserved, and it is not possible to determine if the extragular scutes contacted each other along the midline. None of the sutures between plastral bones is visible.

The carapace has a relatively uniform oval profile in dorsal view, with a slight narrowing just anterior to the carapace's anteroposterior midpoint. The carapace is 450 mm in maximum length as preserved, which matches smaller *Neurankylus* specimens, typically measuring over 500 mm in length. The relatively large size differs from the condition in many species in Baenodda, which (excepting *Chisternon undatum* and *Boremys grandis*) typically are around half the size of most *Neurankylus* specimens (Joyce & Lyson, 2015).

The surface of the carapace and associated carapace fragments is relatively smooth, with no observable sulci and lacking distinct ornamentation. This distinguishes it from *Boremys* spp., *Scabremys ornata* (e.g., USNM 13229), and *Denazinemys nodosa* (e.g., USNM 8345), which have prominent tubercles (Sullivan et al., 2013; Joyce & Lyson, 2015). Portions of the lateral margin of the carapace are slightly upturned, to form a dorsolateral gutter as also seen in *Neurankylus* spp. (Lively, 2016). The axillary notch is narrow, with a gap of 10 mm compared to a larger inguinal notch with a gap of 30 mm. The carapace of the specimen extends 60 mm beyond the anterior end of the plastron. The anterior outline of the carapace is uncertain. The preserved posterior outline of the carapace in dorsal view lacks significant scalloping or spines, unlike the condition in *Eubaena hatcheri* (e.g., CM 115), *Scabremys ornata* (USNM 13229), and others, although subtle scalloping is possible but not verifiable due to preservation. Similar to the condition in RAM 28750, many other *Neurankylus* specimens also lack scalloping (Larson et al., 2013), but the trait can be variable within species (Lichtig and Lucas, 2018).

### Phylogenetic analysis

Due to poor resolution, the parsimony analysis terminated when the tree buffer was full, retaining a total of 75,282 equally parsimonious trees with lengths of 360 steps. RAM 28750 was recovered within Baenidae, preserving the synapomorphies of a robust inguinal buttress (character 85) and lack of an epiplastral process (character 45). The strict consensus tree (Farke, 2023b) was poorly resolved for Baenidae, with *Lakotemys* and *Trinitichelys* as sister taxa to a polytomy comprising the rest of the clade, including RAM 28750. This "wildcard" status for RAM 28750 is unsurprising given its incomplete nature, being scored for only seven out of 105 characters.

## Discussion

We posit that RAM 28750 likely represents *Neurankylus*, based on the combination of features observed here. This includes relatively large size compared to most other baenids, an unornamented carapace, presence of shallow channels (gutters) on the rim of the carapace, a slight increase in the width of the

carapace halfway between the posterior and anterior extremes, and a trapezoidal anterior plastral lobe with a squared-off anterior border. However, the potentially omega-shaped femoral-anal sulcus on RAM 28750 differs from the condition in *Neurankylus* spp., presenting an interesting difference (Joyce & Lyson, 2015). Given the mix of features, RAM 28750 may be a species that bridges the phylogenetic gap between *Neurankylus* and *Baenodda*, but this hypothesis cannot be tested with the material at hand. Alternatively, RAM 28750 may represent a previously unknown species of *Neurankylus* or an aberrant member of an existing species. The shape of the femoral-anal sulcus, the primary differentiating feature here, does show some individual variation within baenid species (e.g., Smith et al., 2017), and thus is not sufficient to separate RAM 28750 with confidence from *Neurankylus* spp.

RAM 28750 represents the first report of Baenidae and of *Neurankylus* sp. from the Mesaverde Formation in the Bighorn Basin of Wyoming (see faunal lists of DeMar & Breithaupt, 2006, 2008). DeMar and Breithaupt (2006, 2008) reported cf. *Neurankylus* sp. from the Wind River Basin, but did not illustrate the material or list voucher specimens.

The presence of Baenidae is consistent with a freshwater environment for the locality RAM V2021009 (Joyce & Lyson, 2015), and also augments other reports of Baenidae in the Mesaverde Formation for the Wind River Basin (DeMar & Breithaupt, 2006, 2008). If correctly assigned to *Neurankylus*, the occurrence of RAM 28750 in a presumed non-fluvial depositional environment would be consistent with an inferred preferred habitat of standing water for this taxon (Hutchison & Archibald, 1986; Sullivan et al., 1988). Although this is the first definitive report of Baenidae and *Neurankylus* in the Mesaverde Formation of the Bighorn Basin, the occurrence is not terribly surprising given the broad distribution of the clade in equivalent strata throughout the Western Interior. Nonetheless, RAM 28750 illustrates the strong potential for significant new discoveries in the Mesaverde Formation. We are hopeful that ongoing fieldwork will reveal more complete specimens, in order to more precisely characterize the turtle assemblage of the Mesaverde Formation in Wyoming and allow comparison with those of penecontemporaneous formations.

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We thank Alex Maya-Romero for first discovering RAM 28750 along with FJV. Bailey Jorgensen (with JH) skillfully headed up final collection of the fossil, with assistance from high school students at The Webb Schools. RAM 28750 was collected under permit from the US Bureau of Land Management, Wyoming State Office permit PA19-WY-276. We gratefully acknowledge Brent Breithaupt (Wyoming State Office) and Gretchen Hurley (Cody Field Office) for support in permitting and fieldwork. Conversations with Brent Adrian, Brent Breithaupt, Don Brinkman, Walter Joyce, Tyler Lyson, and Heather Smith were useful in better understanding this fossil, and comments from Brent Adrian and Heather Smith improved the final manuscript. Jérémy Anquetin is gratefully acknowledged for editorial handling of this manuscript. Charon Henning skillfully prepared the line drawing of RAM 28750. Preprint version 5 of this article has been peer-reviewed and recommended by Peer Community In Paleontology (<https://doi.org/10.24072/pci.paleo.100216>; Anquetin 2023).

### Data, scripts, code, and supplementary information availability

Supplemental data including phylogenetic data matrix, high resolution image of specimen, and the strict consensus tree are available online (Farke, 2023a,b,c):

Data matrix: <https://doi.org/10.6084/m9.figshare.21897225>

Strict consensus tree: <https://doi.org/10.6084/m9.figshare.21897432>

High resolution version of Figure 2: <https://doi.org/10.6084/m9.figshare.21897258>

### Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article. A. Farke is a recommender for PCI Paleontology.

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