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A long-necked tanystropheid from the Middle Triassic Moenkopi Formation (Anisian) provides insights into the ecology and biogeography of tanystropheids

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ABSTRACT

Archosauromorphs are a diverse and successful group of reptiles that radiated into a series of groups around the time of the end-Permian extinction. One of these groups of archosauromorphs, tanystropheids, consists of diverse forms, and some of the largest members of the group possessed extremely elongated cervical vertebrae (greater than five times longer than tall), resulting in a hyperelongate neck. These derived tanystropheids have been found in Tethyan marine deposits of Pangaea. Four partial cervical vertebrae from a hyperelongate-necked tanystropheid from the Middle Triassic Moenkopi Formation of Arizona and New Mexico are described in this paper. These cervical vertebrae are assigned to Tanystropheidae, specifically the clade that includes the hyperelongate-necked *Tanystropheus* based on character states, which include an elongate centrum (length to height ratio of 6.2), the presence of epipophyses, and an elongate axial centrum. The Moenkopi tanystropheid elements were found in lower latitude fluvial sequences without any marine influence, corresponding to western Pangaea, whereas *Tanystropheus*-like tanystropheids are typically associated with marginal marine environments in middle to high latitudes of eastern Pangaea. These fossils suggest that hyperelongate-necked, *Tanystropheus*-like tanystropheids were perhaps behaviorally bound to general semi-aquatic environments, both marine and freshwater, due to their unique morphology. These fossils also greatly extend the biogeographic range of large tanystropheids and increase the anatomical diversity of tanystropheids known from North America demonstrating that the clade persisted in a wide variety of environments throughout the Triassic Period.

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INTRODUCTION

The end-Permian Extinction (252 Ma) was the largest-known extinction event in Earth history, and it paved the way for subsequent diversification of the surviving fauna, particularly Archosauromorpha (including dinosaurs, birds, crocodiles, their relatives, and a diversity of extinct groups) in the Mesozoic Era starting in the Triassic Period (Romer, 1956; Benton, 2003; Shen et al., 2011; Ezcurra and Butler, 2018). Within the first half of the Triassic, archosauromorphs were incredibly diverse, demonstrated high morphological disparity, and were widespread across Pangaea (Sahney and Benton, 2008; Foth et al., 2016; Ezcurra and Butler, 2018). However, our understanding of the early diversification, biogeographic patterns, and ecologies of early archosauromorphs from the Early and Middle Triassic is limited because the fossil record of many of these clades consists of highly fragmentary, isolated elements from early-diverging members; more complete skeletons are typically only known from younger, highly disparate taxa (Gregory, 1945; Wild, 1973; Nosotti, 2007; Nesbitt et al., 2010).

Tanystropheids are a unique group of archosauromorph reptiles, which likely appeared in the Late Permian (based on inferred ghost lineages) and diversified within five million years after the end-Permian extinction (Dilkes, 1998; Reisz and Müller, 2004; Ezcurra, 2016; Pritchard and Nesbitt, 2017). Temporally, tanystropheids ranged from the Early Triassic (247 Ma) with *Augustaburiania vatagini* of modern-day Eastern Europe as the oldest known representative of the group (Sennikov, 2011), to the middle Norian with an unnamed tanystropheid from the Hayden Quarry of the Chinle Formation (~212 Ma) in New Mexico (Pritchard et al., 2015), and the Rhaetian with a tanystropheid from Italy (Wild, 1980b). All tanystropheids have some degree of neck elongation (e.g., *Amotosaurus rotfeldensis*, *Langobardisaurus pandolfii*, *Macrocnemus bassanii*, and *Tanytrachelos ahynis*) relative to other archosauromorph groups; however, some tanystropheids took neck elongation to the extreme (Olsen, 1979; Renesto, 1994; Fraser and Rieppel, 2006; Casey et al., 2007; Ezcurra, 2016). *Tanystropheus longobardicus,* the largest and best-known member of Tanystropheidae, is characterized by an incredibly long and slender neck—roughly twice the length of the trunk—achieved by a composition of 13 highly-elongate cervical vertebrae with low neural arches (Rieppel et al., 2010). The hyperelongate neck of *Tanystropheus longobardicus* was longer than the body and tail combined, and *Tanystropheus*-like tanystropheids have some of the longest proportional necks of all reptiles.

Tanystropheids geographically occur widely across Triassic Pangaea. The clade is primarily known from the mid-latitudes of eastern Pangaea, and fossils of these animals are predominantly known from modern-day Europe, China, the Middle East, and eastern North America, often associated with marine environments in these regions (Olsen, 1979; Wild, 1980b; Vickers-Rich et al., 1999; Casey et al., 2007; Borsuk–Białynicka and Evans, 2009; Sues and Fraser, 2010; Sennikov, 2011; Sues and Olsen, 2014). However, there is a growing body of evidence of a diversity of tanystropheids in Western Pangaea supported by the following finds: an incomplete *Tanystropheus*-like cervical vertebra from the Middle/Upper Triassic Economy Member of the Wolfville Formation of Nova Scotia, *Tanytrachelos ahynis* and similar taxa of Upper Triassic deposits of the eastern United States ranging from New Jersey and Pennsylvania to Virginia, tanystropheid elements from the Upper Triassic Chinle Formation of western North America, Late Triassic tanystropheid elements from the Cooper Canyon Formation of Texas, and Early Triassic tanystropheid elements from the Sanga do Cabral Formation of Brazil (Olsen, 1979; Casey et al., 2007; Sues and Fraser, 2010; Sues and Olsen, 2015; Pritchard et al., 2015; De Oliveira et al., 2018; Lessner et al., 2018). The widespread biogeographic occurrences of tanystropheids and their persistent temporal ranges suggest that tanystropheids were extremely widespread in terrestrial and marginal marine ecosystems. However, the group of *Tanystropheus*-like tanystropheids, characterized by their hyperelongate necks are previously unknown from the western-edge regions of Pangaea like the other smaller tanystropheids.

Based on their morphology, as well as the marine environments from which their fossils are known, *Tanystropheus* has been thought to be at least semi-aquatic with numerous interpretations of it being fully aquatic. A fully aquatic lifestyle was originally thought to have been able to support the unique morphology of *Tanystropheus*' highly elongate necks, which were likely quite stiff because of the elongate structure of the cervicals and overlapping cervical ribs (Wild, 1973; Tschanz, 1988; Nosotti, 2007). Based on limb proportions and tail structure, Renesto and Saller (2018) hypothesized that *Tanystropheus* lived a shore-dwelling, semi-aquatic lifestyle using hind limb propulsion in water, but frequently spent time on land (Renesto and Saller, 2018). Previously, Renesto (2005) inferred a semi-aquatic lifestyle based on tail and limb structure in a well-preserved *Tanystropheus* specimen from Valle Serrata in Switzerland (Renesto, 2005). Paleohistology and taphonomy have also recently been used to support a semi-aquatic existence for *Tanystropheus* (Jaquier and Scheyer, 2017; Beardmore and Furrer, 2018). These recent studies support the prevailing notion that *Tanystropheus* had morphological constraints that restricted it to at least semi-, but not fully-aquatic lifestyles (e.g., Wild, 1973) in marine and marginal environments of the Tethys Sea.

A new occurrence of a *Tanystropheus*-like taxon from the Moenkopi Formation of New Mexico and Arizona, which was deposited on the far western portion of equatorial Pangaea during the Middle Triassic, is described in this paper. We identify this hyperelongate-necked taxon based on four partial cervical vertebrae that share a number of synapomorphies with tanystropheids, specifically the highly disparate *Tanystropheus,* and we show that this occurrence adds new biogeographic and ecological information for this clade of a broader western Pangaean range and freshwater occurrence, respectively.

GEOLOGICAL SETTING

The described vertebral elements were found in the Holbrook and Anton Chico members of the Moenkopi Formation in northeastern Arizona and north-central New Mexico, respectively (Morales, 1987; Schoch et al., 2010). The Moenkopi Formation, spanning the Early to Middle Triassic, extends throughout the southwestern United States in Utah, Arizona, New Mexico, Nevada, southeastern California, and Colorado.

The Holbrook and Anton Chico members are thought to be Middle Triassic (Anisian; 247-242 Ma) in age, and both are correlative members with each other as determined by vertebrate fossil evidence (Lucas and Hunt, 1987; Schoch et al., 2010). These members were formed from continental deposits predominantly consisting of cross-stratified reddish-brown sandstones and siltstones, trough-stratified litharenites, beds of conglomerates, and freshwater limestone indicating that these particular members have no marine influence (McKee, 1954; Lucas and Hunt, 1987; Morales, 1987; Lucas and Schoch, 2002).

The Moenkopi Formation preserves a diverse assemblage of vertebrates including temnospondyl amphibians, dicynodonts, early actinopterygians, sarcopterygian fishes, chondrichthyans, non-archosauriform archosauromorphs, archosaurs, and other amniotes of undetermined affinities, as well as invertebrates including arthropods, mollusks, and annelid trace fossils, and plants (Welles, 1947; Hunt et al., 1993; Morales, 1987; Nesbitt, 2003; 2005).

The cervical vertebrae described here (NMMNH P-80482, NMMNH P-80483, and NMMNH P-80484) were found in the Anton Chico Member, just north of the Pecos River, east of the town of Anton Chico, New Mexico, in fluvial conglomerate beds.

Specimen DMNH 2018-05-0003 was recovered in the Holbrook Member in the Little Colorado River valley, just southeast of Woodruff, Arizona, also in fluvial conglomerate beds (Figure 1). Specific locality information is on file at the New Mexico Museum of Natural History and Science and the Perot Museum of Nature and Science, respectively.

MATERIALS AND METHODS

Measuring Methods

The Moenkopi tanystropheid cervicals were measured using EZ Cal digital calipers. Centrum length was measured between the ventral margins of the outer rims of the centrum articular surfaces, or to the end of the preserved centrum if the element was broken. Centrum articular surface height was taken as a dorsoventral measurement from

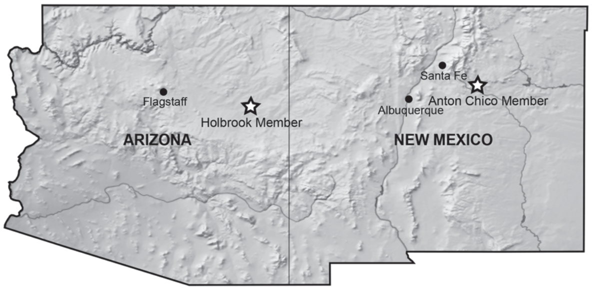

FIGURE 1. Holbrook and Anton Chico Member locations within the Moenkopi Formation of New Mexico and Arizona (National Geologic Map Database, USGS).

the outer rims of the anterior and/or posterior centrum articular surfaces.

Preparation Methods

Matrix was removed using a fine-tipped Microjack 1 (www.paleotools.com) air scribe under a Wild 9 dissection microscope to clear the matrix away from the cervical vertebrae. Broken pieces were glued using Loctite super glue. Fossils were prepared in the Virginia Tech Fossil Preparation Laboratory.

Institutional Abbreviations

DMNH, Perot Museum of Nature and Science, Dallas, TX, USA; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, NM, USA.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903
SAURIA MacCartney, 1802 (sensu Gauthier, 1984)
ARCHOSAUROMORPHA von Huene, 1946
(sensu Benton, 1985)
TANYSTROPHEIDAE Gervais, 1858
Figures 2-6

Referred specimens. An axis (DMNH 2018-05-0003) and three postaxial cervical vertebrae (NMMNH P-80482, NMMNH P-80843, NMMNH P-80844). All specimens were found isolated.

Localities. Holbrook and Anton Chico members, correlative members, of the Moenkopi Formation of Arizona and New Mexico, U.S.A.

Age. Early, but not earliest Anisian Stage (244-242 Ma) of the Middle Triassic (Morales, 1987).

DIAGNOSIS AND DESCRIPTION

Assignment to a *Tanystropheus*-like Tanystropheid Clade

The referred cervical vertebrae are justified as tanystropheid cervicals based on the following character states. The neural spine of the axis is dorsoventrally short, being lower than the height of the axial centrum, which is a character state shared with *Tanystropheus longobardicus*, *Amotosaurus rotfeldensis*, and *Macrocnemus bassanii* (Ezcurra, 2016). The complete centrum of a postaxial cervical, NMMNH P-80482, exhibits a centrum length that is more than five times anteroposteriorly long than it is dorsoventrally tall, a character shared with the hyperelongate-necked tanystropheids (Pritchard et al., 2015; Ezcurra, 2016).The post-axial cervicals, NMMNH P-80482 through P-80483, have a flattened ventral surface of the anterior half of the centrum (excluding the keel) and this is also shared with tanystropheids (Pritchard et al., 2015). Epipophyses are present on NMMNH P-80484, which is a characteristic of Tanystropheidae. In spite of the limits posed by the preservation of the post-axial cervicals, the flattened ventral surface of the centrum, presence of epipophyses and hyperelongate axial centrum suggest that the Moenkopi cervicals are from a tanystropheid more closely related to *Tanystropheus longobardicus.* We do not know if there is one or multiple species of a Moenkopi *Tanystropheus*-like taxon, so we are hesitant to name the taxon.

Axis

The axis (DMNH 2018-05-0003) is identified by its inverted subtriangular anterior centrum surface in anterior view (Figure 2.5), as well as non-projecting prezygapophyses (identification criteria from Nesbitt et al., 2015). The centrum has an anteroposterior length to dorsoventral height at centrum midpoint ratio of 4.02. This value exceeds the approximate proportional length to height ratios of the axis in tanystropheids *Macrocnemus bassanii* (1.3), *Amotosaurus rotfeldensis* (2.8), and *Dinocephalosaurus orientalis* (2.2) (Fraser and Rieppel, 2006; Rieppel et al., 2008; Jaquier et al., 2017). This proportionally elongate axis relative to the axes in other taxa is similarly seen in the tanystropheids *Tanytrachelos ahynis* and *Tanystropheus longobardicus* (Olsen, 1979; Nosotti, 2007). In the Moenkopi form, there is a thin, shallow, ventral keel-like ridge present on the axis centrum which trends anteroposteriorly, and which is a very

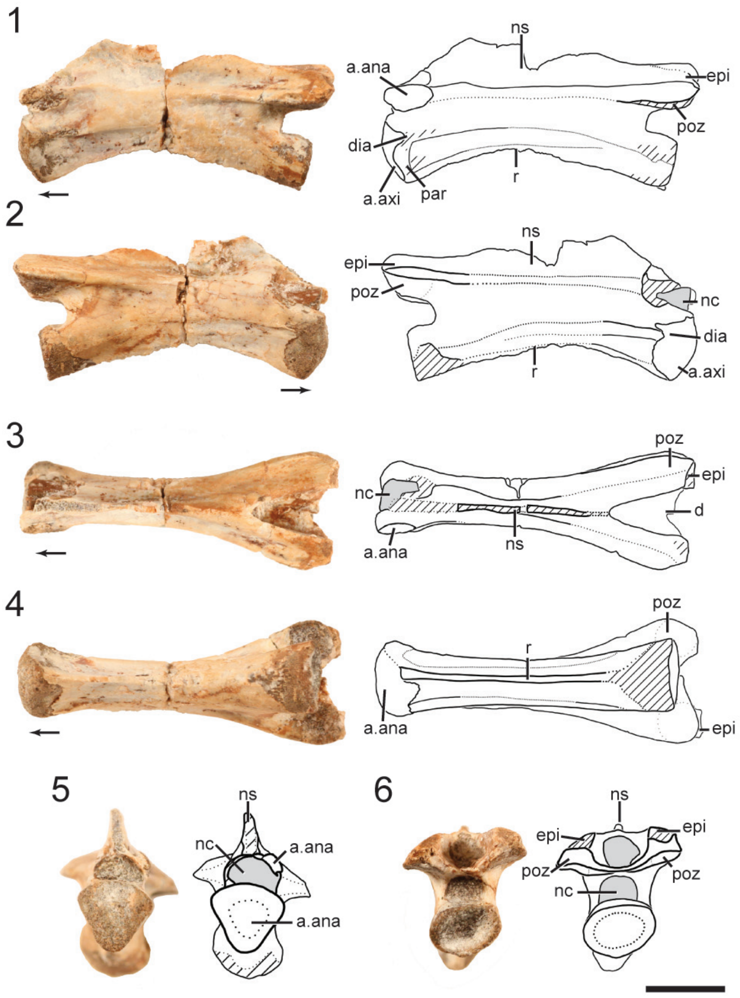

FIGURE 2. DMNH 2018-05-0003, axis of the Moenkopi tanystropheid, in **1**, left lateral; **2**, right lateral; **3**, dorsal; **4**, ventral; **5**, anterior; and **6**, posterior views. Arrows indicate anterior direction. Hatched areas indicate incomplete surface preservation and gray color indicates where matrix is exposed. Abbreviations: **a.**, articulates with; **ana**, atlas neural arch; **axi,** axis intercentrum; **dia**, diapophysis; **epi**, epipophysis; **nc**, neural canal; **poz**, postzygapophysis; **r.** ridge. Scale bar equals 1 cm.

widespread character state shared among diapsids and archosauromorphs and present in tanystropheids (Nesbitt et al., 2015; Ezcurra, 2016).

Epipophyses are present on the dorsal surface of the postzygapophyses but do not extend past their posterior edges, a character state shared with tanystropheids as well as other archosauromorphs like *Azendohsaurus* (Nesbitt et al., 2015). There are clear depressions on the anterolateral end of the centrum, ventral to the parapophyses and posterior to the lateral sides of the articular surface. An interzygapophyseal lamina connects the ventral portion of the bases of the zygapophyses at the midline, a feature also described in the post-axial cervical vertebrae from the Hayden Quarry tanystropheid (Pritchard et al., 2015). The full anterior portion of the neural spine of the axis was originally preserved—as seen in Figure 3, a preliminary photograph of the specimen—although it was unfortunately broken and lost during handling, but was used to assess critical tanystropheid character states. The axial neural spine is anterodorsally expanded with an inclined dorsal margin (Nesbitt, 2011: character 244-state [1]; Nesbitt, 2015: character 179- state [1]; Ezcurra, 2016: character 329- state [1]). Though much of the posterior end of the axial neural spine is missing, it appears to have been dorsoventrally shorter than the centrum, a character state shared by the tanystropheids *Tanystropheus longobardicus*, *Amotosaurus*

FIGURE 3. DMNH 2018-05-0003, axis of the Moenkopi tanystropheid with intact anterior portion of neural spine present. Scale bar equals 1 cm.

rotfeldensis, and *Macrocnemus bassanii* (Ezcurra, 2016: character 328- state [1]). This dorsoventrally short neural spine and anterodorsal expansion are synapomorphies of Tanystropheidae in the analysis of Ezcurra (2016).

Post-axial Cervical Vertebrae

In the post-axial cervicals, only NMMNH P-80482 (Figure 4) has the complete amphicoelous centrum preserved, but it is missing the majority of its neural arch including the neural spine. The centrum is highly elongate and greater than five times anteroposteriorly long than dorsoventrally tall. This extreme length-to-height ratio is a unique character state present in *Tanystropheus longobardicus* (Ezcurra, 2016: character 331- state [2]). In lateral view, the centrum is parallelogram-shaped, where the anterior portion is inclined about 15° dorsal to the posterior portion. The centrum is waisted in ventral view and has the smallest proportional diameter at mid-length. The centrum articular surfaces are dorsoventrally compressed in the postaxial cervicals and deeply concave (Figures 4.5-6, 5.5, 6.5). The centrum articular faces are oval-shaped in anterior and posterior views, with the long axis oriented transversely. A longitudinally oriented lamina extends the full length of the lateral centra posteriorly from the base of the parapophyses. This lamina results in a sharp change in slope between the ventral and lateral surfaces of the centrum which in anterior and posterior views is shown by the dorsoventral compression. This dorsoventral compression is shared in the tanystropheids *Macrocnemus bassanii* and *Tanystropheus longobardicus* and is a tanystropheid synapomorphy as determined by Ezcurra, 2016 (character 340- state [1]).

Although NMMNH P-80483 and P-80484 are partially preserved, being broken through the transverse plane near midpoint (Figures 5, 6), the centra are complete enough to discern the morphology of the centrum articular surfaces (anterior and posterior), parapophyses and diapophyses, and ventral surfaces. The morphology of these two specimens is nearly identical to that of NMMNH P-80482, but NMMNH P-80483 and P-80484 contain more anatomical information. The postaxial cervicals of the Moenkopi tanystropheid all have a flattened ventral surface lacking a ventromedial keel near the anterior and posterior ends, which is a character state shared by *Tanystropheus longobardicus* and *Tanytrachelos ahynis* (Dalla Vecchia, 2005). The cross section in the broken cervical vertebrae reveal a hollow core of the centrum of the cervicals, which was previously recognized in the cervicals of *Tanystropheus longobardicus* (Wild, 1973). In NMMNH P-80483, the neural canal is wider than tall (Figure 5.5), and the prezygapophyseal attachments overhang the canal slightly. In NMMNH P-80482 the neural canal is flat ventrally and convex, forming a D-shape in cross-section (Figure 4.6).

Prezygapophyses and postzygapophyses are partially preserved in NMMNH P-80483 and NMMNH P-80484, respectively. There are epipophyses present on the postzygapophyses of NMMNH P-80484, though their posterior tips are broken (Figure 6). The presence of epipophyses on NMMNH P-80484 suggests that this cervical can be placed somewhere between the third to fifth cervical in the neck column constrained by comparisons with other members of Tanystropheidae (Ezcurra, 2016). Using NMMNH P-80482, we determine that the postzygapophyses are elevated dorsal to the prezygapophyses, which is a character seen in the geographically close Hayden Quarry tanystropheid fossils (Pritchard et al., 2015). Additionally, the dorsal border of the prezygapophyses is inclined approximately 45° above the horizontal when viewed laterally (Figure 4.1-2). A shallow groove is present in NMMNH P-80483 on the lower lateral surface of the centrum that extends anteriorly along the represented centrum length (Figure 5.1-2).

All of the postaxial cervicals lack complete neural spines. In NMMNH P-80483 the dorsal margin of the neural spine is present anteriorly and indicates that the neural spine was dorsoventrally shorter than the dorsoventral height of the centrum. The broken surfaces of the neural spine in NMMNH P-80482 and NMMNH P-80484 (Figures 4.3, 6.3) indicate that the neural spine extended

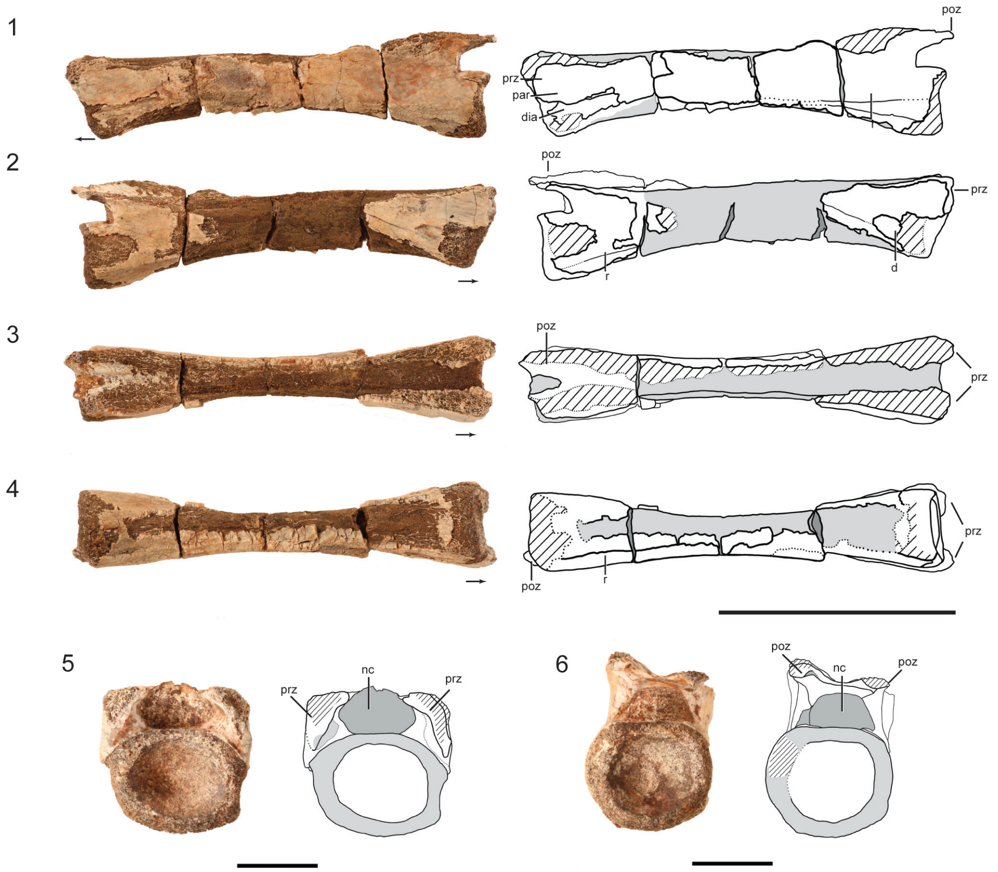

FIGURE 4. NMMNH P-80482, a post-axial cervical of the Moenkopi tanystropheid, in **1**, left lateral; **2**, right lateral; **3**, dorsal; **4**, ventral; **5**, anterior; and **6**, posterior views. Arrows indicate anterior direction. Hatched areas indicate incomplete surface preservation and gray color indicates where matrix is exposed. Abbreviations: **d**, depression; **dia**, diapophysis; **epi**, epipophysis; **nc**, neural canal; **par,** parapophysis; **poz**, postzygapophysis; **r,** ridge. Scale bar equals 1 cm.

the anteroposterior length of the neural arch, which is another consistent character state of tanystropheid cervicals (Ezcurra et al., 2014; Pritchard et al., 2015); anteroposteriorly long and dorsoventrally low cervical neural spines are present in the tanystropheids *Amotosaurus rotfeldensis*, *Macrocnemus bassanii*, *Tanystropheus longobardicus*, as well as non-tanystropheid archosauromorphs *Protorosaurus speneri* and *Prolacerta broomi* (Ezcurra, 2016: character 342 – state [1]). Because the neural spine is missing at the posterior end of NMMNH P-80484, and entirely in NMMNH P-80482, we cannot estimate the full anteroposterior extent of the neural spines in the postaxial cervicals.

The complete cervical, NMMNH P-80482, has an estimated ratio of centrum length versus height at the anterior margin of 6.20. This falls in the range of 6.09–6.80 as a synapomorphy for the tanystropheids *Amotosaurus rotfeldensis* and *Tanystropheus longobardicus* and also suggests that NMMNH P-80482 is the fourth or fifth cervical as based on *Tanystropheus longobardicus* (Ezcurra, 2016: character 331- state [2]). In measuring these cervical vertebrae, we did not take into account compression. However, these cervical vertebrae are minimally crushed and even if they were up to 15% off, they would still fall in the synapomorphic range of length to height ratio for *Tanystropheus* and *Amotosaurus*. Additionally, tanystropheids, which lack hyperelongate neck proportions have a length to height ratio in the range of 2.92–4.12 for their fourth and fifth cervicals, well below the measured range of our Moenkopi tanystropheid cervical vertebrae (Ezcurra, 2016: character 331-state [1]). We reconstructed estimated full centrum lengths of NMMNH P-80483 and NMMNH P-80484, based on centrum propor-

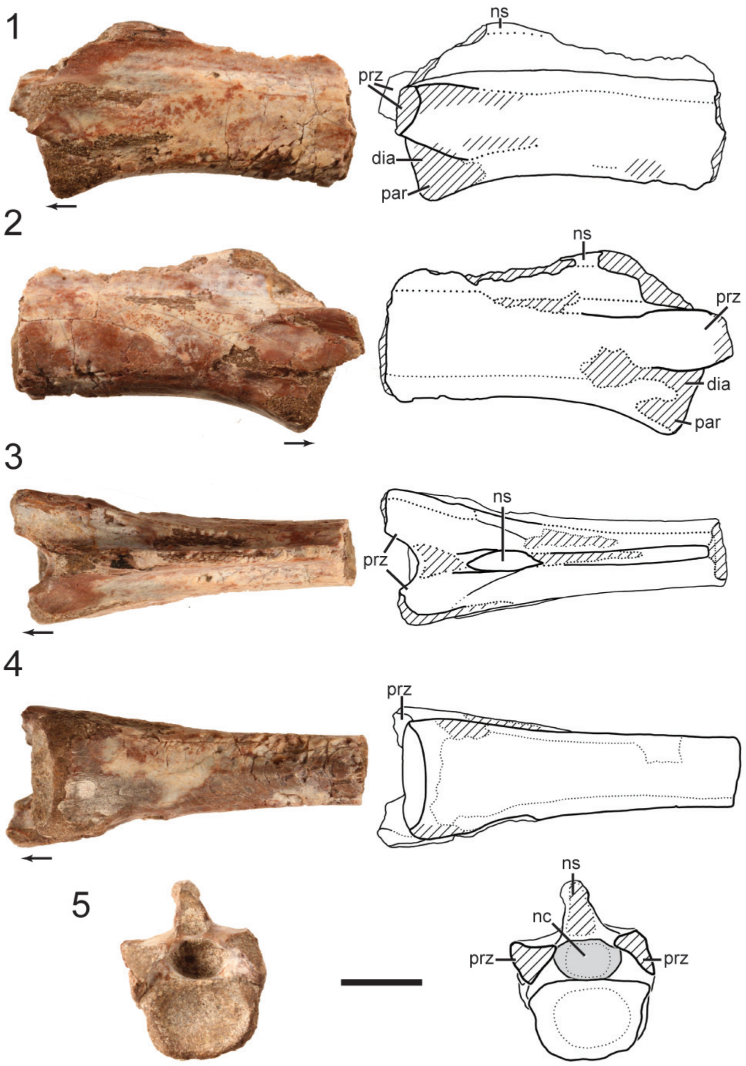

FIGURE 5. NMMNH P-80483, a post-axial cervical of the Moenkopi tanystropheid, in **1**, left lateral; **2**, right lateral; **3**, dorsal; **4**, ventral; and **5**, anterior views. Arrows indicate anterior direction. Hatched areas indicate incomplete surface preservation and gray color indicates where matrix is exposed. Abbreviations: **dia**, diapophysis; **nc**, neural canal; **ns,** neural spine; **par,** parapophysis; **prz,** prezygapophysis. Scale bar equals 1 cm.

tions in NMMNH P-80482 (Table 1). The extremely elongate cervicals are indicative of an elongated neck, though this is also dependent on the number of cervicals. *Tanystropheus longobardicus* has 13, and *Amotosaurus rotfeldensis* has eight (Wild, 1973; Fraser and Rieppel, 2006). As further comparison, *Dinocephalosaurus orientalis*, a possible tanystropheid, has at least 27 cervicals (Li et al., 2004; Rieppel et al., 2008). It is unknown at this time how many total cervicals were present in the Moenkopi tanystropheid, but the general morphology of the individual cervicals is *Tanystropheus*-like potentially alluding to a similar number of cervicals for the Moenkopi form and similar hyperelongate neck proportions.

DISCUSSION

Size Estimation

In terms of body size, *Tanystropheus longobardicus* is by far the largest-known tanystropheid at an estimated 6 m total body length (Wild, 1973; Nosotti, 2007). Our methodology for estimating the snout-vent length is based on the axis (DMNH 2018-05-0003). We used *Tanystropheus longobardicus* as our proxy for estimating the total length of

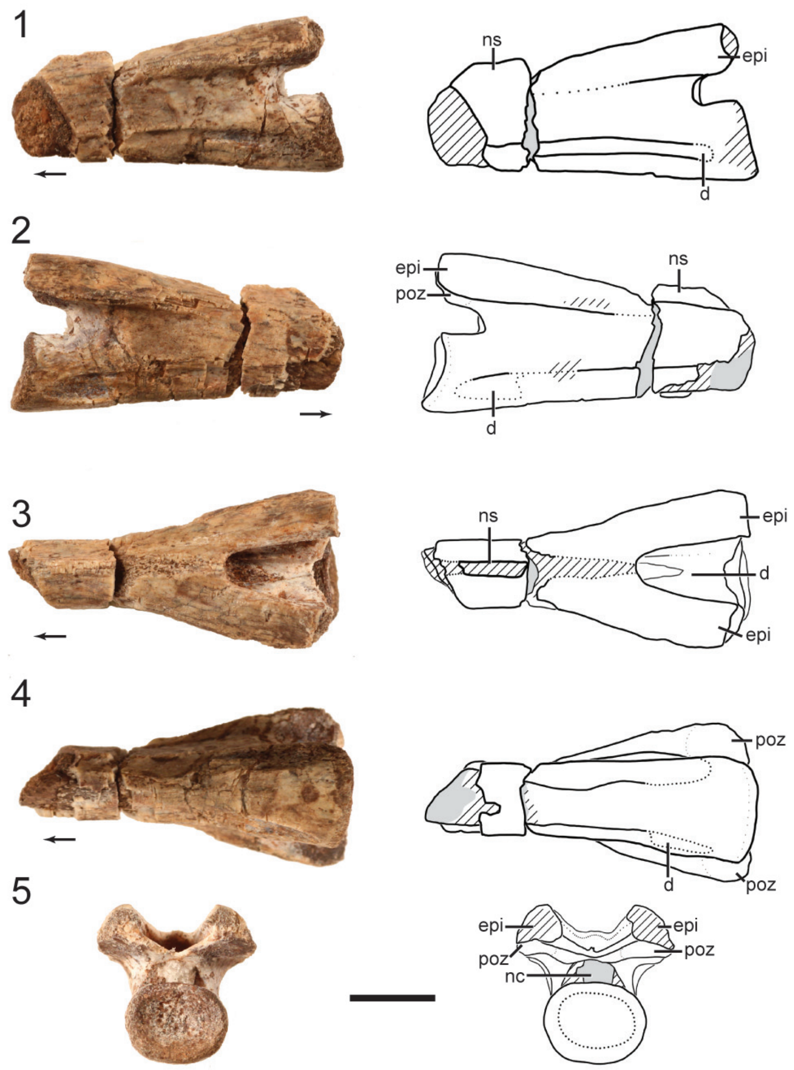

FIGURE 6. NMMNH P-80484, a post-axial cervical of the Moenkopi tanystropheid, in **1**, left lateral; **2**, right lateral; **3**, dorsal; **4**, ventral; and **5**, posterior views. Arrows indicate anterior direction. Hatched areas indicate incomplete surface preservation and gray color indicates where matrix is exposed. Abbreviations: **d,** depression; **epi**, epipophysis; **nc**, neural canal; **ns,** neural spine; **poz**, postzygapophysis; **prz,** prezygapophysis. Scale bar equals 1 cm.

the Moenkopi form because other tanystropheids with similarly complete skeletons (*Macrocnemus bassanii*, *Amotosaurus rotfeldensis*,

Langobardisaurus pandolfii, and *Tanytrachelos ahynis*) do not bear the amphicoelous, hyperelongated, straight cervical vertebrae seen in *Tanystropheus longobardicus* or the Moenkopi form. They also lack an axis with such a relatively elongate centrum. These characters can be seen in PIMUZ T2791 and MCSN BES SC 265, which are the most complete skeletons of *Tanystropheus* that preserve skulls and nearly complete presacral vertebral columns. Therefore, the major assumption in this size estimate is that the Moenkopi tanystropheid is similar in proportion to *Tanystropheus longobardicus* as based on the referred cervical vertebrae.

We used the measurements of various vertebrae from Wild (1973) and Nosotti (2007) and then imported images of the complete skeletons into ImageJ. We used the known lengths of the second cervical vertebra to set the scale for the images and then measured the length of the skull and entire presacral vertebral column. We added those measurements together to estimate the total snout-vent length, then took the ratio of the snout-vent length (SV) to the total centrum length of the axis. In both specimens, the SV/Axis ratio comes out at

TABLE 1. Measurements of Moenkopi tanystropheid cervical vertebrae. N/A indicates this portion was unable to be determined with the represented material, and "e" indicates estimated length value.

Referred specimen	Anterior centrum end height (mm)	Posterior centrum end height (mm)	Mid-centrum height (mm)	Full centrum length (mm)
DMNH 201805-0003	9.11	6.41	6.49	36.63
NMMNH P-80482	13.50	13.67	12.15	83.72
NMMNH P-80483	10.28	N/A	N/A	63.73e
NMMNH P-80484	N/A	9.37	N/A	57.44e

approximately 60. Therefore, we estimate that the snout-vent length of the Moenkopi tanystropheid is equivalent to 60 times the length of the preserved axis, which is approximately 2.20 m, at maximum, based on the axial centrum length of 36.63 mm as shown in Table 1.

The Moenkopi tanystropheid cervical vertebrae belong to a considerably smaller tanystropheid than the largest *Tanystropheus*, but we determined that its body length was approximately three times larger than *Tanytrachelos ahynis* known primarily from the eastern United States (Olsen, 1979; Casey et al. 2007). Additionally, the full length cervical, NMMNH P-80482, is approximately three times longer than the cervical vertebrae of the geographically-close Hayden Quarry tanystropheid of New Mexico (Pritchard et al., 2015). Therefore, the Moenkopi tanystropheid cervical vertebrae correspond to both a larger tanystropheid and more *Tanystropheus*-like taxon compared to other biogeographically close tanystropheids.

Large-bodied, Hyperelongate-necked Tanystropheids in Western Pangaea

The Moenkopi tanystropheid cervicals belong to one of the larger known members of the clade found in western Pangaea. The lengths of these cervicals and body size estimation are indicative of an animal that was approximately three times larger than *Tanytrachelos ahynis* and the Hayden Quarry tanystropheid (Olsen, 1979; Casey et al. 2007; Pritchard et al., 2015). As suggested by the proportionally extreme centrum elongation of the referred cervical vertebrae, a synapomorphic character for *Tanystropheus*, the western Pangaean Moenkopi tanystropheid is likely closely related to the eastern Pangaean *Tanystropheus longobardicus,* which possessed some of the most extreme neck proportions of any animal (Wild, 1973; Fraser and Rieppel, 2006).

The recognition of the Moenkopi tanystropheid and its relationship to *Tanystropheus* has implications for tanystropheid paleobiogeography and ecology. First, the Moenkopi form adds to recent western North American tanystropheid discoveries further bolstering the large biogeographic range for tanystropheidae and their western Pangaean radiation. The Moenkopi tanystropheid additionally reveals a disparity in the morphologies of tanystropheids in western North America, a region where the associated tanystropheids lacked the hyperelongated neck and larger body size present in *Tanystropheus*-like taxa.

Tanystropheus is primarily known from central and eastern Pangaea of what is now Eurasia in mid to higher latitudes and associated with the Tethys coastal regions (Wild, 1873; Nosotti, 2007; Rieppel et al., 2010; Sennikov, 2011). The Moenkopi form places tanystropheids with the same body plan as *Tanystropheus* as occurring on the other side of the world at the same temporal range, the Middle Triassic. Therefore, the Moenkopi tanystropheid greatly extends the concurrent biogeographic range of the *Tanystropheus*-like taxa (Figure 7). However, these cervicals were recovered in sediments that had little to no marine influence and corresponded to an equatorial latitude. Other non-marine fauna found in these members of the Moenkopi Formation include terrestrial archosaurs and dicynodonts (Morales, 1987; Hunt et al.,1993; Nesbitt, 2003; 2005). A continental, fluvial setting is a unique environment to find hyperelongate-necked *Tanystropheus*-like tanystropheids, which are typically associated with marginal marine environments. *Tanystropheus*-like tanystropheids were a morphologically unique archosauromorph clade, and these new fluvial finds pose interesting questions about the ecology of these hyperelongate-necked tanystropheids. Were they filling different ecological roles across marginal marine to terrestrial fluvial environments, or were they filling similar ecological roles in these disparate environments? Further studies and considerations of *Tanystropheus* ecology should incorporate the Moenkopi tanystropheid fossils.

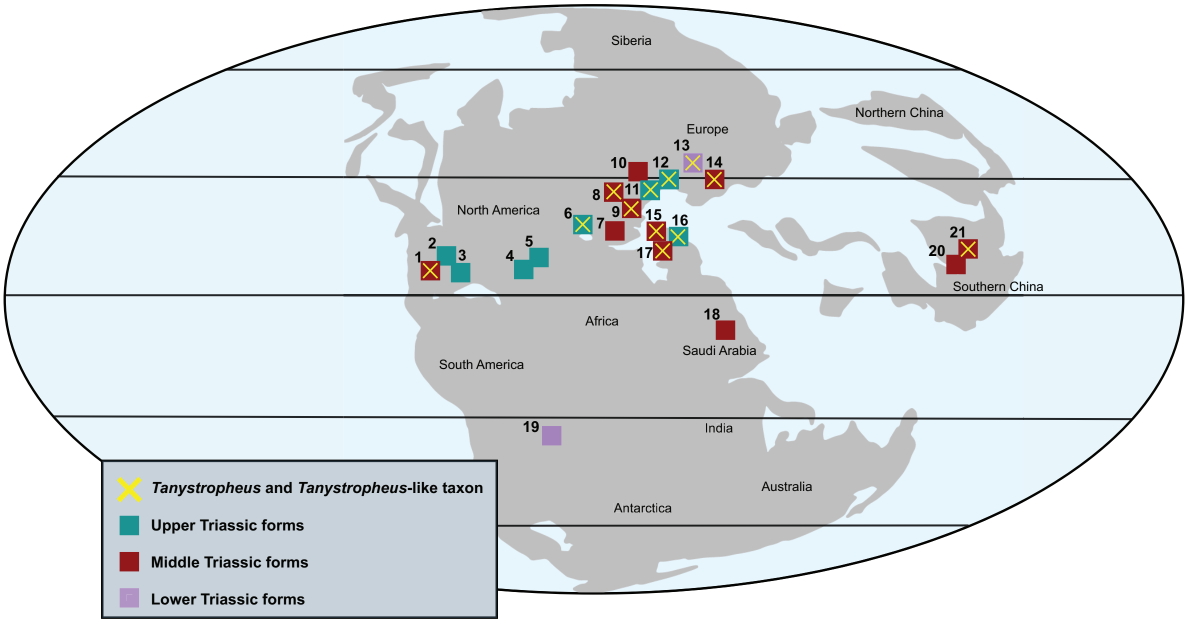

FIGURE 7. Occurrences of the family Tanystropheidae in Triassic Pangaea as indicated by squares. **1.** Moenkopi Formation, Arizona and New Mexico; **2.** Chinle Formation, New Mexico; **3.** Cooper Canyon Formation, Texas; **4.** Cow Branch Formation, Virginia; **5.** Lockatong Formation, Newark Supergroup, New Jersey and Pennsylvania; **6.** Wolfville Formation, Nova Scotia; **7.** Montral-Alcover Basin, Spain; **8.** Otter Sandstone Formation, England; **9.** Limestone Alps and Valle Serrata Locality, Switzerland; **10.** Quarry Kossig, Upper Buntsandstein of the Black Forest, Germany **11.** Bayreuth localities, Germanic Basin, Germany; **12.** Seefeld Formation, Austria; **13.** Don River Basin, Lipovskaya Formation, Eastern Europe **14.** Bihor Mountain Localities, Romania; **15.** Calcare di Zorzino, Italy; **16.** Dolomia di Forni, Italy; **17.** Besano Formation, Italy; **18.** Jilh Formation, Saudi Arabia; **19.** Sanga do Cabral Formation, Brazil; **20, 21.** Zhuganpo Member of the Falang Formation, China. (Bassani, 1886; Wild, 1973, 1980b; Jurcsak, 1975; Milner et al., 1990; Muscio, 1996; Vickers-Rich et al., 1999; Sues, 2003; Rieppel, 2004; Fraser, 2006; Renesto, 2006; Casey et al., 2007; Borsuk-Białynicka and Evans, 2009; Rieppel et al., 2010; Sennikov, 2011; Diedrich, 2012; Saller et al., 2013; Pritchard et al., 2015; Jaquier et al., 2017; De Oliviera et al., 2018; Lessner et al., 2018.)

Tanystropheus-like tanystropheids, as a clade, seem to have occupied similar, but broad ranging semi-aquatic environments during their 35 million year span in the Triassic Period. The biogeographic and environmental factors of these Moenkopi tanystropheids further refute the marine, water-restricted ecomorphological hypothesis for hyperelongate necked tanystropheids. In the past, there were preconceived limitations conferred by the extreme morphology in *Tanystropheus*-like tanystropheids and it was thought that only a full aquatic lifestyle could support their bizarre neck morphology (Tschanz, 1988; Rieppel, 1989; Nosotti, 2007). Recent studies, however, have placed *Tanystropheus* on the shoreline with specifically semi-aquatic adaptations including swimming via symmetrical strokes of the hind limbs and rowing through the water (Renesto and Saller, 2018), as well as bone histology analyzing femur density of *Tanystropheus*, which suggests an amphibious lifestyle (Jaquier and Scheyer 2017). Additionally, Beardmore and Furrer (2018) used taphonomy to infer a terrestrial or at least near-shore, shallow marine origin for preserved *Tanystropheus* carcasses (Beardmore and Furrer, 2018). The recovery of the Moenkopi tanystropheid in fluvial sediments further supports the semi-aquatic, shore dwelling ecology of *Tanystropheus*-like tanystropheids, which lacked full adaptations for continuous swimming; however, it also demonstrates that *Tanystropheus*-like taxa could occupy more than just marine shores. Recognition of these new Moenkopi fossils suggests that these highly derived tanystropheids were able to occupy a range of aquatic environments, both marine and continental freshwater, and that there were aspects of their life history which required close proximity to water.

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