First occurrences of Poposauroidea (Archosauria: Paracrocodylomorpha) from North Carolina expand their geographic range in the Late Triassic

Authors: Fitch, Adam J., Kammerer, Christian F., and Nesbitt, Sterling J.

Source: Palaeodiversity, 18(1) : 1-9

Published By: Stuttgart State Museum of Natural History

URL: https://doi.org/10.18476/pale.v18.a1

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Palaeodiversity on 30 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

Palaeodiversity 18: 1–9; Stuttgart 30 December 2025. Published online: 7 March 2025, DOI: 10.18476/pale.v18.a1

First occurrences of Poposauroidea (Archosauria: Paracrocodylomorpha) from North Carolina expand their geographic range in the Late Triassic

Adam J. Fitch, Christian F. Kammerer & Sterling J. Nesbitt

Abstract

Poposauroids (Pseudosuchia; Paracrocodylomorpha) are one of several lineages of ecologically unique archosauriform reptiles that diversified throughout the Triassic Period. Fossils of the poposauroid lineages Shuvosauridae and *Poposaurus* are well known from Late Triassic deposits across western Pangaea, represented by abundant materials in the southwestern United States in the Chinle Formation and the Dockum Group and rarer occurrences in the Ischigualasto Formation of Argentina. However, Late Triassic records of these lineages are currently unknown in other parts of Pangaea. Here, we extend the geographic range of Late Triassic poposauroids by reporting two incomplete femora from the Newark Supergroup of the eastern United States. Both specimens are from the Chatham Group of North Carolina, the first (NCSM 27054) from a quarry near Wadesboro in Anson County (Cumnock Formation), and the second (AMNH FR 24431) from a quarry near Gulf in Chatham County (Pekin Formation). Both possess diagnostic character states of Poposauroidea and the more complete specimen, NCSM 27054, lacks character states of shuvosaurids. We conclude that these femora represent poposauroids similar (if not identical) to *Poposaurus gracilis* among known taxa in the clade. Our findings expand the Late Triassic range of Poposauroidea into the central/eastern Pangaean Atlantic rift zone. NCSM 27054 and AMNH FR 24431 may represent some of the oldest Late Triassic poposauroid fossils and help fill a gap in the stratigraphic range of Poposauroidea.

Keywords: Archosauria; Poposauroidea; Newark Supergroup; biogeography; Upper Triassic.

1. Introduction

The Triassic Period represents a time of great diversification for archosauriform reptiles (birds, crocodiles, and their closest relatives; Nesbitt 2011; Cabreira et al. 2016; Ezcurra et al. 2017, 2020). The Poposauroidea, a lineage of paracrocodylomorph stem-crocodylians, exemplify this diversity, exhibiting broad ecological and morphological variation (including hypertrophy of the neural spines, loss of teeth, and bipedalism in various taxa) throughout the Triassic (Nesbitt 2007, 2011; Butler et al. 2011; Wang et al. 2009). Two lineages of large-bodied bipedal poposauroids occur in the Late Triassic: the beaked, edentulous shuvosaurids (e.g., *Effigia*, *Shuvosaurus*) and the toothed *Poposaurus* (Long & Murray 1995; Nesbitt & Norell 2006; Parker & Nesbitt 2013; Schachner et al. 2020). Nearly all Late Triassic poposauroids are from the northwestern fringes of Pangaea (the current-day western USA; Nesbitt & Norell 2006; Parker & Nesbitt 2013) with the exception of the southwestern Pangaean (Argentinian) shuvosaurid *Sillosuchus longicervix* Alcober & Parrish 1997. This latter occurrence highlights the potential for a much more widespread presence of poposauroids in the Late Triassic. One of the primary barriers to the dispersal of these poposauroids (and all terrestrial life) was enormous arid belts across the mid-latitude of Pangaea (Whiteside et al. 2011; 2015; Griffin et al. 2022). In spite of this, several aspects of northern and southern Pangaean faunas suggest that various tetrapod clades crossed these arid belts, as indicated by the presence of closely-related taxa on both sides (e.g., aetosaurs, Desojo et al. 2013; parasuchid phytosaurs, Kammerer et al. 2016; Stocker et al. 2017; lagerpetid ornithodirans, Nesbitt et al. 2009; metoposaurid temnospodyls, Chakravorti & Sengupta 2018). *Sillosuchus* was from south of these belts, with the remainder of known Late Triassic Poposauroidea residing north of them.

There is an exception to the otherwise latitudinally-continuous barrier formed by the arid belts: the Atlantic rift zone, which formed a terrestrial northeast-southwest-trending, higher humidity zone during the Late Triassic Period that connected what is now eastern North America and northwestern Afro-Eurasia to present-day South America and western Africa prior to the origin of the central part of the Atlantic Ocean (Sellwood & Valdes 2006; Khalifa 2007; Dunne et al. 2021). Fossils from this rift zone are thus critical in filling biogeographic gaps in Late Triassic ecosystems. Archosauriform trackways are abundant throughout this region (e.g., Olsen 1980; Olsen & Baird 1986), but these are difficult to place to more specific groups due to shared plesiomorphies across the pes of archosaurs and their closest relatives (=Eucrocopoda; Demathieu & Demathieu 2004; Padian et al. 2010; Ezcurra 2016). The body fossil record of the Newark Supergroup, particularly from the Deep River Basin, has greatly expanded in recent years (Heckert et al. 2015;

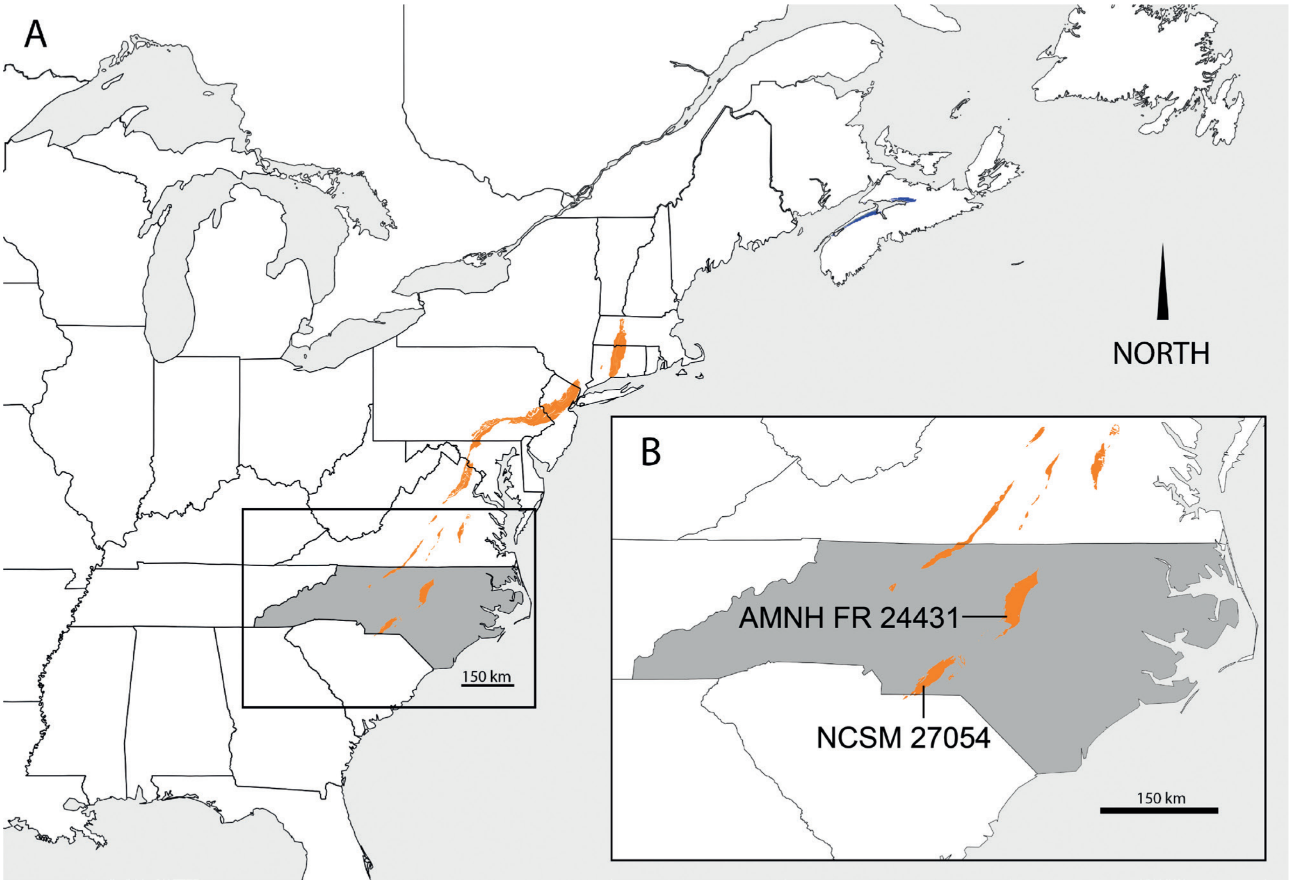

Fig. 1. Map of eastern North America, with highlighted box (B) showing North Carolina and the places of discovery of the poposauroid specimens NCSM 27054 and AMNH FR 24431. Orange represents the Newark Supergroup depositional basins; AMNH FR 24431 was found within the Durham Sub-basin while NCSM 27054 was found within the Wadesboro Sub-basin, together making up the larger Deep River Basin. Map constituent references: Newark depositional basins (marcostrat.org), US map ('USA_States_Generalized': https://www.arcgis.com/home/item.html?id=8c2d6d7df8fa4142b0a1211c8dd66903&sublayer=0), Canada map ('Territorial_Evolution_1867_-2003_TE_': https://www-tlstest.arcgis.com/home/item.html?id=c705639d23e34f8691d97edc653a29a7)

Sues et al. 2003; Zanno et al. 2015), filling out and clarifying the diversity of these low-latitude faunas.

Here we add to this diversity and document the first occurrences of Poposauroidea from the Late Triassic Chatham Group of the Deep River Basin, an Atlantic rift basin located in current-day North Carolina. We further explore its biogeographic implications for Late Triassic corridors prior to the split of Pangaea.

Abbreviations: AMNH FR, Fossil Reptile Collections at the American Museum of Natural History, New York City, USA; NHMUK (formerly BMNH), Natural History Museum, London, U.K.; GR, Ghost Ranch Ruth Hall Museum of Paleontology, Abiquiu, USA; MCP, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; NCSM, North Carolina Museum of Natural Sciences, Raleigh, USA; NMT, National Museums of Tanzania, Dar es Salaam, Tanzania; PVL, Paleontología de Vertebrados, Instituto "Miguel Lillo", San Miguel de Tucumán, Argentina; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TTU-P, Paleontological Collections at Texas Tech University Museum, Lubbock, USA; UCMP, University of California Museum of Paleontology, Berkeley, USA; YPM, Yale Peabody Museum of Natural History, New Haven, USA; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

2. Geologic setting and age

Both femora were collected in exposures attributed to the Upper Triassic Chatham Group. More specifically, AMNH FR 24431 was collected from the Pekin Formation and NCSM 27054 was collected from the overlying Cumnock Formation. The sediments in these formations represent terrestrial deposits within the Deep River Basin (NCSM 27054 from the Wadesboro sub-basin, AMNH FR 24431 from the Sanford sub-basin), a rift basin that formed along with several others across eastern North America and Afro-Eurasia with the initiation of spreading between the North American and African tectonic plates in the late Permian Period (Campbell & Kimball 1923; Olsen et al. 1991; Clark et al. 2001). Radioisotopic ages are absent for this basin and nearly all circum-Atlantic rift basins, but correlations with the absolutely-dated deposits of the Newark Basin were employed (Olsen & Whiteside 2008; Olsen et al. 2011). Correlation of the Newark Basin was accomplished when Olsen (1997) demonstrated a series of four tectonostratigraphic sequences (TS) that can be found throughout circum-Atlantic rift basin deposits of eastern North America and Morocco referred to as, from lowest to highest, TS I, TS II, TS III, and TS IV. The depositional initiation of each TS is thought to have occurred as a result of an extensional event associated with the aforementioned break-up of Pangaea and the opening of the Atlantic Ocean. Olsen et al. (2000) demonstrated extraordinarily similar sequence stratigraphy between the only two basins known to preserve all four TS, the western-Atlantic Fundy Basin (Nova Scotia) and the eastern-Atlantic Argana Basin (Morocco), further supporting the existence of the four TS proposed by Olsen (1997). The units of the Fundy Basin had previously been correlated with those of the absolutely-dated Newark Basin, and so the newly-identified boundary between TS II and TS III was subsequently dated to 228.5 Ma (Olsen & Whiteside 2008; Olsen et al. 2010), making this an intercontinentally-locatable age constraint on early Late Triassic strata of the Atlantic rift basins.

With this established, the upper part of the Pekin Formation is the lowest unit in TS III of the Deep River Basin, having been correlated with the Stockton Formation of the well-studied and magnetostratigraphically-dated Newark Basin. This provides us with an estimated age restriction between 222.5–228.5 Ma for the material described here.

3. Systematic paleontology

Archosauria Cope, 1869 sensu Gauthier & Padian, 1985

Pseudosuchia Zittel, 1890 sensu Gauthier & Padian, 1985

Poposauroidea Nopcsa, 1923 sensu Nesbitt, 2011
Fig. 2A–E

Specimen: NCSM 27054, left femur with complete proximal and distal ends missing a ~3 cm section.

Locality and horizon: NCPALEO 0401 (precise location on file at NCMNS), near Wadesboro, Anson County, North Carolina. Cumnock Formation, Chatham Group, Newark Supergroup. SJN visited the quarry with Vince Schneider (who discovered the specimen) and determined it was from the southwestern side of the deepest side of the pit, stratigraphically high on the quarry wall. Although the exact position of the femur was not recorded during collection, these strata consist entirely of Cumnock exposures, per Schneider.

Age: Late Triassic, Carnian or early Norian, between 222.5–228.5 Ma (see Geological Setting and Age above).

Description: NCSM 27054 is comprised of two pieces representing much of the left femur. The proximal piece is represented by the proximal portion (=head) and the proximalmost section of the shaft, just distal to the transition between the head and the shaft (Fig 2A, upper images of 2B–E), whereas the distal portion is represented by ~2/3 of the length of the element (lower images of 2B–E). Measurements include a maximum proximal width (trending anteromedially) = 37.7 mm, a maximum distal width (trending mediolaterally) = 32.8 mm and an estimated length of ~190 cm. The preservation of both pieces is excellent and clear muscle scars are present.

The proximal surface possesses a transverse groove that trends anteromedially-posterolaterally parallel to the long axis of the surface (see Nesbitt 2011 [character 31], to understand the complex distribution of this feature), a feature common in poposauroids (Nesbitt 2011). As in other archosaurs, the proximal end of the femur features three prominent tubera easily viewed proximally: the anteromedial tuber, the posteromedial tuber, and the anterolateral tuber. The anteromedial tuber is about the same size as the posteromedial tuber, a character state shared among suchians (Nesbitt 2011). The anteromedial tuber possesses a distinct posteromedial expansion to form a head, like that in other poposauroids as well as saurischian dinosaurs (Nesbitt 2011). The medial surface of the anteromedial tuber is rounded, unlike the straight surface in silesaurids (e.g., *Asilisaurus kongwe*, NMT RB159; *Silesaurus opolensis*, ZPAL AbIII/457). The ventral margin of the tuber is well defined and a ridge at the distal margin can be traced posterolaterally to just distal of the posteromedial tuber. The bone surface distal to this ridge is a porous surface consisting of pits and small ridges (in contrast to smooth compacta), similar to *Poposaurus gracilis* (YPM 57100), *Shuvosaurus inexpectatus* (TTU-P9001), and saurischians (e.g., *Tawa hallae*, GR 244). In posteromedial view, the anteromedial tuber of NCSM 27054 is rounded, rather than hooked as in early pterosauromorphs (e.g., *Dromomeron romeri*, GR 218; *Arcticodactylus cromptonellus*, Jenkins et al. 2001).

The posteromedial tuber is separated from the anteromedial tuber by a concave depression visible in proximal view (Fig. 2A). The distal margin of the posteromedial tuber is defined by a change in bone surface texture from proximally compact to distally more porous bone, like that distal to the anteromedial tuber. An anterolateral tuber is present on the proximal end of the femur (Fig. 2A) as

Fig. 2. NCSM 27054, a left poposauroid femur in (A) proximal, (B, upper two) anterolateral, (B, lower) distal, (C) lateral, (D) posteromedial, and (E) medial views. Scale bar is 5 cm. alt = anterolateral tuber, amt = anteromedial tuber, ctf = crista tibiofibularis, 'ft' = 'fossa trochanterica', gr = groove, mc = medial condyle, lc = lateral condyle, pit = pit, pmt = posteromedial tuber, r = ridge, rs = rugose surface.

a slightly rounded ridge extending proximodistally along the anterolateral surface, as is typical of many archosaurs (e.g., *Tawa hallae*, GR 244; *Poposaurus gracilis*, YPM 57100). However, a homologous ridge is absent in *Shuvosaurus inexpectatus* (TTU-P9001; Nesbitt 2011) and *Effigia okeeffeae* (AMNH FR 30588; Nesbitt 2007).

The posterolateral portion of the proximal articular surface descends distally from the rest of this surface (Fig. 2D), resulting in a gradually depressed area often referred to as the 'fossa trochanterica' in ornithodirans (e.g., *Dromomeron romeri*, GR 218; *Tawa hallae,* Nesbitt 2011), but which is also present in poposauroids (e.g., *Poposaurus gracilis*, Schachner et al. 2020; *Shuvosaurus inexpectatus*, TTU-P9001). This sloped articular surface originates at the posteromedial tuber and extends posterolaterally to the end of the proximal surface. In anterolateral view, the profile of the proximal end is arched like that of other pseudosuchians (e.g., *Poposaurus gracilis*, YPM 57100) and this is in contrast to the more flattened morphology of dinosauriforms (e.g., *Silesaurus opolensis*, Dzik 2003; *Saturnalia tupiniquim*, Langer 2003).

The medial expansion of the head of the femur of NCSM 27054 is not as medially-expanded as that of *Shuvosaurus inexpectatus* (TTU-P9001; Nesbitt 2011) and *Effigia okeeffeae* (AMNH FR 30588), but it is nearly identical to that of *Poposaurus gracilis* (YPM 57100). The femur possesses a smooth transition between the head and the shaft on the medial portion of the bone, as is typical of early archosaurs and differs from the distinct notch or concave emargination found in ornithodirans (e.g., *Dromomeron romeri*, GR 218; *Asilisaurus kongwe*, NMT RB159).

The anterolateral surface of the proximal portion of the femur is largely smooth and featureless, lacking the ridge often referred to as the dorsolateral trochanter found in this location in some crocodylomorphs (*Terrestrisuchus gracilis*, NHMUK PV R 7562; Nesbitt 2011; *Kayentasuchus walkeri*, UCMP 131830; Clark & Sues 2002) and most dinosauriforms (e.g., *Silesaurus opolensis*, ZPAL Ab III/460/1; *Saturnalia tupiniquim*, Langer 2003). At the distal part of the preserved portion of the proximal end, slight rugosities are present (Fig. 2C). Slight rugosities are present in the same place in shuvosaurids (e.g., *Effigia okeeffeae*, AMNH FR 30588; *Shuvosaurus inexpectatus*, TTU-P18309) and in other pseudosuchians such as ornithosuchids (*Riojasuchus tenuisceps*, PVL 3827) and some early diverging crocodylomorphs (*Kayentasuchus walkeri*, UCMP 131830). This area bears the anterior trochanter in avemetatarsalians (e.g., *Teleocrater rhadinus*, NHMUK PV R6795; *Saturnalia tupiniquim*, MCP 3846-PV). A proximal condylar fold, as is found in some loricatans (*Fasolasuchus tenax*, PVL 3851; Nesbitt 2011), including some crocodylomorphs (e.g., *Hesperosuchus agilis*, AMNH FR 6758), is absent in NCSM 27054.

Based on comparisons with other poposauroids (e.g., *Poposaurus gracilis*, YPM 57100; *Effigia okeeffeae*, AMNH FR 30588; *Shuvosaurus inexpectatus*, TTU-P9001), the gap between the preserved proximal and distal portions of NCSM 27054 should represent approximately 3 cm of missing bone. Breaks in both the proximal and distal pieces show that the bone was largely hollow, with a large medullary cavity that has a cortex thickness varying from 2.14 mm to 4.24 mm across a diameter of 14.9 mm at its shortest, to 22.14 mm at its longest. This cortical thickness is only found in the crocodylomorph *Terrestrisuchus gracilis*, Ornithodira, and Poposauroidea among early members of Archosauria (see character 323 of Nesbitt 2011). It is not clear if NCSM 27054 lacked a ridge for the attachment of the M. caudifemoralis as in *Shuvosaurus inexpectatus* (TTU-P9001; Nesbitt 2011) and *Effigia okeeffeae* (AMNH FR 30588). A deep pit lies on the medial portion of the distal portion of the femur and is likely homologous with the deep pit associated with the attachment of the M. caudifemoralis in most archosaurs (Fig. 2E). If homologous, this pit is deeper in NCSM 27054 and shuvosaurids (*Shuvosaurus inexpectatus*, TTU-P18309) and the medial border of the shaft is slightly medially bowed at the proximodistal level of (and thus medial to) this pit, a character state exclusive to poposauroids (Nesbitt 2005; 2007; 2011). Just lateral to the pit, the surface of NCSM 27054 is slightly rugose, a feature that is absent in a well-preserved femur of *Shuvosaurus inexpectatus* (TTU-P18309). The slightly rugose surface of NCSM 27054 swells and forms the posterolateral edge of the femur. This rugosity is also present in *Poposaurus gracilis* (YPM 57100) and is likely the attachment for the M. iliofemoralis externus (Nesbitt et al. 2017; 2018). From this swollen area, a ridge that defines the posterolateral border emerges and extends to the crista tibiofibularis (Fig. 2C–E).

Distally, the posterior portions of a crista tibiofibularis and the fibular condyle are broken off. However, enough of the bases of the lateral condyle and crista tibiofibularis are preserved to demonstrate that these structures form roughly a right angle to each other in distal view, a feature differing from the obtuse angle in Dinosauriformes (Nesbitt 2011) but shared with *Effigia okeeffeae* (AMNH FR 30587; Nesbitt 2007), *Poposaurus gracilis* (YPM 57100), and some loricatans (e.g., *Batrachotomus kupferzellensis*, Gower & Schoch 2009; *Postosuchus kirkpatricki*, TTU-P9000; *Dromicosuchus grallator*, NCSM 13733). In distal view, the lateral condyle tapers posterolaterally and the distal surface of this condyle extends more distally than any of the other condyles. A small groove is present between the lateral condyle and the crista tibiofibularis in distal view. Anteriorly, there is a proximodistally oriented fossa that separates the medial and lateral sides of the distal end.

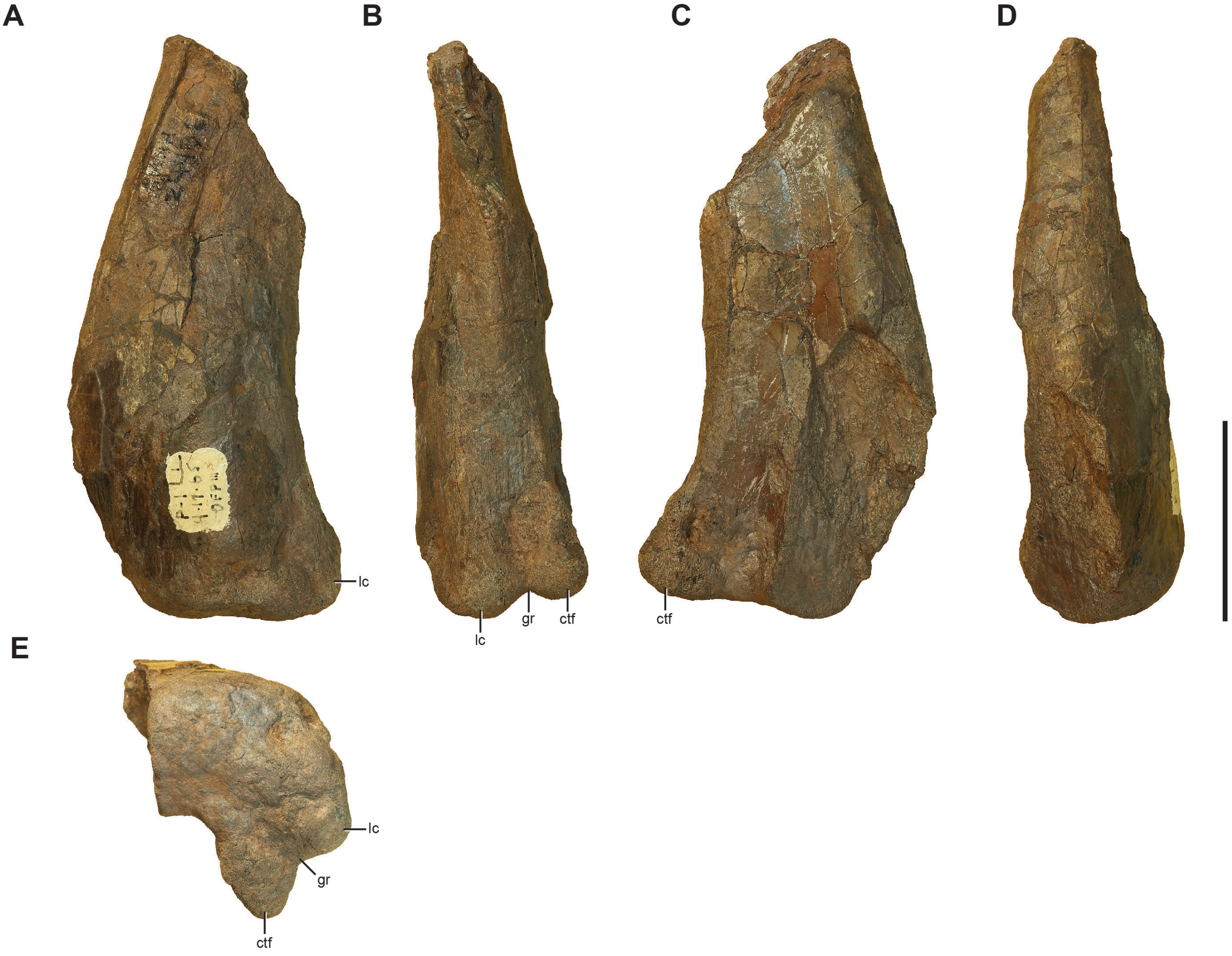

Fig. 3. AMNH FR 24431, a distal left poposauroid femur in (A) anterolateral, (B) lateral, (C) posteromedial, (D) medial, and (E) distal views. Scale bar is 5 cm. ctf = crista tibiofibularis, gr = groove, mc = medial condyle, lc = lateral condyle.

Poposauroidea indet.
Fig. 3

Specimen: AMNH FR 24431, distal ~25% of the left femur (Fig. 3).

Locality and horizon: Pekin Formation, Pomona Pipe Products Pit, near Gulf, Chatham Co., North Carolina. Collected April 17th, 1965.

Age: Late Triassic, Carnian or early Norian, between 222.5–228.5 Ma (see Geological Setting and Age above).

Description: The lateral condyle and crista tibiofibularis are preserved, whereas the medial condyle is missing. The shaft has thin walls (~5 mm or less) and is caved in (Fig. 3). We estimate the length of the femur to be ~24 cm based on the width (estimated at 55 mm) of AMNH FR 24431 and comparisons to *Poposaurus gracilis* (YPM 57100). The lateral condyle is posterolaterally directed, rounded and separated from the crista tibiofibularis by a groove on both its medial and distal surfaces (Fig. 3E). The crista tibiofibularis tapers posterolaterally to a blunt point and the distal surface is slightly more proximal than the rest of the distal end.

The shape of the distal end is consistent with that of *Poposaurus gracilis* (YPM 57100) and *Effigia okeeffeae* (AMNH FR 30587) in that the crista tibiofibularis is pointed and separated from the lateral condyle by a groove, the lateral condyle is tapered posterolaterally and rounded, and that there is a 90°–100° angle between the posterior portion of the lateral condyle and the lateral side of the crista tibiofibularis (Fig. 3B, E). However, some of these character states are also present in other pseudosuchians. For example, the 90°–100° angle between the posterior portion of the lateral condyle and the lateral side of the crista tibiofibularis is also present in some loricatans (e.g., *Batrachotomus kupferzellensis*, Gower & Schoch 2009;

Postosuchus kirkpatricki, TTU-P9000; *Dromicosuchus grallator*, NCSM 13733).

4. Discussion

4.1. Identification

The nearly complete femur NCSM 27054 preserves a combination of poposauroid character states previously tested in phylogenetic analyses (Nesbitt 2011, and iterations of the same dataset, e.g., Butler et al. 2011; Nesbitt et al. 2020; Smith et al. 2024). This combination includes the following character states: a proximal surface with a transverse groove that trends anteromedially-posterolaterally parallel to the long axis of the surface (broadly present in Paracrocodylomorpha); three prominent tubera clearly visible proximally (the anteromedial tuber, the posteromedial tuber, and the anterolateral tuber); the posterolateral portion of the proximal articular surface is depressed (='fossa trochanterica'); a low or absent ridge for the attachment of the M. caudifemoralis; absence of a distinct ridge in the anterolateral surface of the proximal end (= anterior trochanter area); thin cortex with an open medullary cavity; a medially-bowed border of the femur adjacent to a pit for the attachment of the M. caudifemoralis medially; approximately a 90° angle in distal view between the lateral condyle and crista tibiofibularis; and a small groove present between the lateral condyle and the crista tibiofibularis in distal view. Similarly, AMNH FR 24431 preserves character states consistent with those of the distal end of NCSM 27054. The combination of character states listed above supports a placement within Poposauroidea for both specimens. The lack of clear shuvosaurid character states (e.g., an enlarged and hooked anteromedial tuber of the proximal end, a less arched proximal profile in posterolateral view; Nesbitt 2011; Nesbitt & Chatterjee 2023) indicates that NCSM 27054 does not belong to that clade, but a more precise and well-supported position within Poposauroidea is not inferable based on this material alone. However, we do note that the character state combination in NCSM 27054 is consistent with that of *Poposaurus gracilis* (e.g., YPM 57100), although NCSM 27054 and *Poposaurus gracilis* do not appear to possess any clear synapomorphies exclusively. Therefore, we identify the Chatham Group poposauroid only as a non-shuvosaurid poposauroid, albeit noting the possibility that it could be a close relative of or even referable to *Poposaurus*.

4.2. Biogeography

NCSM 27054 and AMNH FR 24431 narrow a significant biogeographic gap between the western North American and southern South American fossil records of poposauroids, demonstrating that this group was present in the Late Triassic of the Atlantic rift basins of eastern/central Pangaea. Their Carnian to early Norian age makes these among the oldest poposauroid fossils from the Late Triassic, coeval or near coeval with the Carnian *Sillosuchus longicervix* (Alcober & Parrish 1997; Desojo et al. 2020) and the possibly Carnian-aged holotype specimen of *Poposaurus gracilis* (Lovelace et al. 2024). Because of the fragmentary remains of these specimens, their indeterminate phylogenetic position within Poposauroidea, and the paucity of Carnian vertebrate-bearing units globally (Lovelace et al. 2024), it is difficult to say whether these specimens might represent earlier-diverging, biostratigraphically-informative forms of the *Poposaurus* lineage.

The presence of poposauroids adds to a growing record of tetrapod fossils whose geographic ranges are connected by Atlantic rift basin occurrences, including Pekin Formation aetosaurs (e.g., *Gorgetosuchus pekinensis*; Heckert et al. 2015), crocodylomorphs (*Dromicosuchus grallator*, *Carnufex carolinensis*; Sues et al. 2003; Zanno et al. 2015), dicynodonts (*Placerias hesternus*; Baird & Patterson 1968), and traversodontid cynodonts (*Boreogomphodon jeffersoni*; Sues & Olsen 1990; Liu et al. 2017). The presence of these poposauroid femora and the discovery of several well-preserved tetrapods from the Pekin Formation (e.g., *Boregogomphodon jeffersoni*; Liu et al. 2017) suggest better-represented and thus more informative amniote material likely awaits discovery within the Deep River Basin.

5. Conclusion

NCSM 27054 and AMNH FR 24431 represent the first confirmed poposauroid materials from the Chatham Group and the Atlantic rift region of Late Triassic Pangaea. Their occurrence in an Atlantic rift zone basin fills biogeographic gaps in the Late Triassic poposauroid fossil record, previously restricted to northwestern Pangaea (western North America) and southwestern Pangaea (Argentina). Their occurrence supports the continuity of faunal representation between North and South Pangaean vertebrate assemblages.

Acknowledgements

We thank Vince Schneider (NCMNS, retired) for the collection of NCSM 27054 and Sean Moran for arranging the loan of NCSM 27054. We thank Marilyn Fox and Vannessa Rue (YPM) and Patricia Holroyd at UCMP for facilitating comparisons with other *Poposaurus* material. We thank William Parker and Nate Smith for their considerate and helpful reviews of this publication. Funding for SJN was provided by NSF EAR 1943286.

6. References

Alcober, O. A. & Parrish, J. M. (1997): A new poposaurid from the Upper Triassic of Argentina. – Journal of Vertebrate Paleontology, **17**(3): 548–556.

Baird, D. & Patterson, O. F., III (1968): Dicynodont-archosaur fauna in the Pekin Formation (Upper Triassic) of North Carolina. – Geological Society of America, Special Papers, **115**: 11.

Butler, R. J., Brusatte, S. L., Reich, M., Nesbitt, S. J., Schoch, R. R. & Hornung, J. J. (2011). The sail-backed reptile *Ctenosauriscus* from the latest Early Triassic of Germany and the timing and biogeography of the early archosaur radiation. – PLOS ONE, **6**(10): e25693.

Campbell, M. R. & Kinball, K. K. (1923): The Deep River coal field of North Carolina. – North Carolina Geological and Economic Survey Bulletins, **33**: 95 pp.

Chakravorti, S. & Sengupta, D. P. (2019): Taxonomy, morphometry and morphospace of cranial bones of *Panthasaurus* gen. nov. *maleriensis* from the Late Triassic of India. – Journal of Iberian Geology, **45**: 317–340.

Clark, T. W., Gore, P. J. W. & Watson, M .E. (2001): Depositional and structural framework of the Deep River Triassic basin, North Carolina – 50th Annual Meeting, Southeastern Section, Geological Society of America, Field Trip Guidebook, 27–50.

Clark, J. M. & Sues, H.-D. (2002): Two new species of basal crocodylomorphs and the status of the Sphenosuchia. – Zoological Journal of the Linnean Society, **136**(1): 77–96.

Cope, E. D. (1869): Synopsis of the extinct Batrachia, Reptilia and Aves of North America. – Transactions of the American Philosophical Society, **14**(1): 1–252.

Demathieu, G., & Demathieu, P. (2004): Chirotheria and other ichnotaxa of the European Triassic. – Ichnos, **11**(1–2): 79–88.

Desojo, J. B., Heckert, A. B., Martz, J. W., Parker, W. G., Schoch , R. R., Small, B. J., & Sulej, T. (2013). Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds. – Geological Society, London, Special Publications, **379**(1): 203–239.

Desojo, J. B., Fiorelli, L. E., Ezcurra, M. D., Martinelli, A. G., Ramezani, J., Da Rosa, A. A. S., Belén von Baczko, M., Trotteyn, M. J., Montefeltro, F. C., Ezpeleta, M. & Langer, M. C. (2020): The Late Triassic Ischigualasto Formation at Cerro Las Lajas (La Rioja, Argentina): fossil tetrapods, high-resolution chronostratigraphy, and faunal correlations. – Scientific Reports, **10**(1): 12782.

Dunne, E. M., Farnsworth, A., Greene, S. E., Lunt, D.J. & Butler, R. J. (2021): Climatic drivers of latitudinal variation in Late Triassic tetrapod diversity. – Palaeontology, **64**(1): 101–117.

Dzik, J. (2003): A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. – Journal of Vertebrate Paleontology, **23**(3): 556–574. doi:10.1671/a1097

Ezcurra, M. D. (2016): The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. – PeerJ, **4**: e1778. doi:10.7717/peerj.1778

Gauthier, J. & Padian, K. (1985): Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. In: Hecht, M. K., Ostrom, J. H., Viohl, G. & Wellnhofer, P. (eds.): The Beginning of Birds, 185–197; Eichstätt (Freunde des Jura Museums).

Gower, D. J. & Schoch, R. R. (2009): Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kupferzellensis*. – Journal of Vertebrate Paleontology, **29**(1): 103–122. doi:10.1080/02724634.2009.10010365

Griffin, C. T., Wynd, B. M., Munyikwa, D., Broderick, T. J., Zondo, M., Tolan, S., Langer, M. C.. Nesbitt, S. J. & Taruvinga, H. R. (2022): Africa's oldest dinosaurs reveal early suppression of dinosaur distribution. – Nature, **609**(7926): 313–319.

Heckert, A. B., Schneider, V. P., Fraser, N. C. & Webb, R. A. (2015): A new aetosaur (Archosauria, Suchia) from the Upper Triassic Pekin Formation, Deep River Basin, North Carolina, U.S.A., and its implications for early aetosaur evolution. – Journal of Vertebrate Paleontology, **35**: e881831. doi: 10.1080/02724634.2014.881831

Jenkins, F. A, Jr., Shubin, N. H., Gatesy, S. M. & Padian, K. (2001): A diminutive pterosaur (Pterosauria: Eudimorphodontidae) from the Greenlandic Triassic. – Bulletins of the Museum of Comparative Zoology, **156**: 151–170.

Kammerer, C. F., Butler, R. J., Bandyopadhyay, S. & Stocker, M. R. (2016): Relationships of the Indian phytosaur *Parasuchus hislopi* Lydekker, 1885. – Papers in Palaeontology, **2**(1): 1–23.

Khalifa, M. A. (2007): Triassic-Jurassic boundary on the southern margin of Tethys: Implications of facies, tectonics and volcanism. In: Lucas, S. G. & Spielmann, J. A. (eds.): The Global Triassic. – New Mexico Museum of Natural History and Science Bulletins, **41**: 110–119.

Langer, M. C. (2003): The sacral and pelvic anatomy of the stem-sauropodomorph *Saturnalia tupiniquim* (Late Triassic, Brazil). – PaleoBios, **23**: 1–40.

Liu, J., Schneider, V. P., Olsen, P. E. (2017): The postcranial skeleton of *Boreogomphodon* (Cynodontia: Traversodontidae) from the Upper Triassic of North Carolina, USA and the comparison with other traversodontids. – PeerJ., **5**: e3521.

Long, R. & Murray, P. (1995): Late Triassic (Carnian and Norian) Tetrapods from the Southwestern United States. – New Mexico Museum of Natural History and Science Bulletins, **4**: 254 pp.

Lovelace, D. M., Fitch, A. J., Schwartz, D. & Schmitz, M. (2024): Concurrence of Late Triassic lithostratigraphic, radioisotopic, and biostratigraphic data support a Carnian age for the Popo Agie Formation (Chugwater Group), Wyoming, USA. – Geological Society of America Bulletins, **136**(5–6): 2305–2324.

Martínez, R. N., Apaldetti, C., Correa, G. A. & Abelín, D. (2016): A Norian lagerpetid dinosauromorph from the Quebrada del Barro Formation, northwestern Argentina. – Ameghiniana, **53**(1): 1–13.

Nesbitt, S. J. (2005): Osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti*. – Historical Biology, **8**(1): 19–47.

Nesbitt, S. J. (2007): The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod-like convergence, and the distribution of related taxa. – Bulletin of the American Museum of Natural History, **302**: 84 pp.

Nesbitt, S. J. (2011): The early evolution of archosaurs: relationships and the origin of major clades. – Bulletin of the American Museum of Natural History, **352**: 1–292.

Nesbitt, S. J., Butler, R. J., Ezcurra, M. D., Barrett, P. M., Stocker, M. R., Angielczyk, K. D., Smith, R. M H., Sidor, C. A., Niedźwiedzki, G., Sennikov, A. G. & Charig, A. J. (2017): The earliest bird-line archosaurs and the assembly of the dinosaur body plan. – Nature, **544**(7651): 484–487.

Nesbitt, S. J., Butler, R. J., Ezcurra, M. D., Charig, A. J. & Barrett, P. M. (2018): The anatomy of *Teleocrater rhadi-*

nus, an early avemetatarsalian from the lower portion of the Lifua Member of the Manda Beds (Middle Triassic). – Journal of Vertebrate Paleontology, **37**(Supplement 1): 142–177.

Nesbitt, S. J., Irmis, R. B., Parker, W. G., Smith, N. D., Turner, A. H. & Rowe, T. (2009): Hindlimb osteology and distribution of basal dinosauromorphs from the Late Triassic of North America. – Journal of Vertebrate Paleontology, **29**(2): 498–516.

Nesbitt, S. J. & Norell, M. A. (2006): Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). – Proceedings of the Royal Society, B: Biological Sciences, **273**(1590): 1045–1048.

Nopsca, F. v. (1923): Die Familien der Reptilien. – Fortschritte der Geologie und Paläontologie, **2**: 1–210.

Olsen, P. E. (1980): Fossil great lakes of the Newark Supergroup in New Jersey. – 52nd Annual Meeting of the New York State Geological Association, Newark College of Arts and Sciences, Newark, Rutgers University, Field Studies in New Jersey Geology and Guide to Field Trips, 352–398.

Olsen, P. E. (1997): Stratigraphic record of the early Mesozoic breakup of Pangea in the Laurasia-Gondwana rift system. – Annual Reviews of Earth and Planetary Science, **25**: 337–401.

Olsen, P. E. & Baird, D. (1986): The ichnogenus *Atreipus* and its significance for Triassic biostratigraphy. In: Beginning of the Age of Dinosaurs: Faunal Change across the Triassic-Jurassic Boundary, 61–87; Cambridge, UK (Cambridge University Press).

Olsen, P. E., Froelich, A. J., Daniels, D. L., Smoot, J. P., Gore, P. J. & Horton, W. (1991): Rift basins of early Mesozoic age. In: Horton, W. (ed.): Geology of the Carolinas, 142–170; Knoxville (University of Tennessee Press).

Olsen, P. E., Kent, D. V., Fowell, S. J., Schlische, R. W., Withjack, M. O. & Letourneau, P. M. (2000): Implications of a comparison of the stratigraphy and depositional environments of the Argana (Morocco) and Fundy (Nova Scotia, Canada) Permian–Jurassic basins. In: Oujidi, M. & Et-Touhami, M. (eds.): Le Permien et le Trias du Maroc: Actes de la Première Réunion du Groupe Marocain du Permien et du Trias, 165–83; Oujda (Hilal Impression).

Olsen, P. E., Kent, D. V. & Whiteside, J. H. (2010): Implications of the Newark Supergroup-based astrochronology and geomagnetic polarity time scale (Newark-APTS) for the tempo and mode of the early diversification of the Dinosauria. – Earth and Environmental Science Transactions of the Royal Society of Edinburgh, **101**(3–4): 201–229.

Olsen, P. E. & Whiteside, J. H. (2008): Pre-Quaternary Milankovitch cycles and climate variability. In: Gornitz, V. (ed.): Encyclopedia of Paleoclimatology and Ancient Environments, Earth Science Series, 826–835; Dordrecht (Kluwer Academic Publishers).

Padian, K., Li, C. & Pchelnikova, J. (2010): The trackmaker of *Apatopus* (Late Triassic, North America): implications for the evolution of archosaur stance and gait. – Palaeontology, **53**(1): 175–189.

Parker, W. G. & Nesbitt, S. J. (2013): Cranial remains of *Poposaurus gracilis* (Pseudosuchia: Poposauroidea) from the Upper Triassic, the distribution of the taxon, and its implications for poposauroid evolution. – Geological Society, London, Special Publications, **379**: 22 pp.

Schachner, E. R., Irmis, R. B., Huttenlocker, A. K., Sanders, K., Cieri, R. L., Fox, M. & Nesbitt, S. J. (2020): Osteology of the late Triassic bipedal archosaur *Poposaurus gracilis* (Archosauria: Pseudosuchia) from western North America. – The Anatomical Record, **303**(4): 874–917.

Sellwood, B. W. & Valdes, P. J. (2006): Mesozoic climates: General circulation models and the rock record. – Sedimentary Geology, **190**(1–4): 269–287.

Smith, N. D., Klein, N., Sander, P. M. & Schmitz, L. (2024). A new pseudosuchian from the Favret Formation of Nevada reveals that archosauriforms occupied coastal regions globally during the Middle Triassic. – Biology Letters, **20**(7): 20240136.

Stocker, M. R., Zhao, L. J., Nesbitt, S. J., Wu, X. C. & Li, C. (2017): A short-snouted, Middle Triassic phytosaur and its implications for the morphological evolution and biogeography of Phytosauria. – Scientific Reports, **7**(1): 46028.

Sues, H.-D. & Olsen, P. E. (1990): Triassic vertebrates of Gondwanan aspect from the Richmond Basin of Virginia. – Science, **249**(4972): 1020–1023.

Sues, H.-D., Olsen, P. E., Carter, J. G. & Scott, D. M. (2003): A new crocodylomorph archosaur from the Upper Triassic of North Carolina. – Journal of Vertebrate Paleontology, **23**(2): 329–343.

Wang, J., Pei, R., Chen, J., Zhou, Z., Feng, C. & Chang, S.-C. (2019): New age constraints for the Middle Triassic archosaur *Lotosaurus*: Implications for basal archosaurian appearance and radiation in South China. – Palaeogeography, Palaeoclimatology, Palaeoecology, **521**: 30–41.

Whiteside, J. H., Grogan, D. S., Olsen, P. E. & Kent, D. V. (2011): Climatically driven biogeographic provinces of Late Triassic tropical Pangea. – Proceedings of the National Academy of Sciences, **108**(22): 8972–8977.

Whiteside, J. H., Lindström, S., Irmis, R. B., Glasspool, I. J., Schaller, M. F., Dunlavey, M., Nesbitt, S. J., Smith, N. D. & Turner, A. H. (2015): Extreme ecosystem instability suppressed tropical dinosaur dominance for 30 million years. – Proceedings of the National Academy of Sciences, **112**(26): 7909–7913.

Zanno, L. E., Drymala, S., Nesbitt, S. J. & Schneider, V. P. (2015): Early crocodylomorph increases top tier predator diversity during the rise of dinosaurs. – Scientific Reports, **5**: 9276.

Zittel, K. A. v. (1890): Handbuch der Palaeontologie, 1, Abteilung: Paläozoologie, Reihe 3. Oldenbourg (München & Leipzig).

Addresses of the authors:

Adam J. Fitch, Sterling J. Nesbitt, Department of Geosciences, Virginia Tech, Blacksburg, VA 24061, USA;

Christian F. Kammerer, North Carolina Museum of Natural Sciences, 11 West Jones Street, Raleigh, North Carolina 27601, USA; fitchadamjames@gmail.com; christian.kammerer@naturalsciences.org; sjn2104@vt.edu

Manuscript received: 29 October 2024; revised version accepted: 28 January 2025.

Zeitschrift/Journal: Palaeodiversity

Jahr/Year: 2025

Band/Volume: 18

Autor(en)/Author(s): Fitch Adam J., Nesbitt Sterling J., Kammerer Christian F.

Artikel/Article: First occurrences of Poposauroidea (Archosauria: Paracrocodylomorpha) from North Carolina expand their geographic range in the Late Triassic 1-9