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New trilophosaurid species demonstrates a decline in allokotosaur diversity across the Adamanian-Revueltian boundary in the Late Triassic of western North America

BEN T. KLIGMAN, ADAM D. MARSH, STERLING J. NESBITT, WILLIAM G. PARKER & MICHELLE R. STOCKER

Abstract

Allokotosauria, including Trilophosauridae and Azendohsauridae, is an extinct archosauromorph group that reached a near-Pangean distribution in the Middle Triassic to Late Triassic and evolved a broad range of cranial and dental morphologies. Within the Chinle Formation of western North America, allokotosaurs span the Norian-aged Blue Mesa Member (Adamanian estimated holochronozone) and Sonsela Member (Adamanian and Revueltian estimated holochronozone). The Adamanian-Revueltian faunal assemblage transition is hypothesized to represent extinction and faunal turnover in large-bodied archosauromorphs, but poor sampling of known localities has obscured any similar patterns in tetrapods <1 m long. Trilophosaurids are the most common smaller-bodied herbivorous taxa found in Adamanian microvertebrate sites, with four species previously reported (*Trilophosaurus buettneri*, *T. jacobsi*, *T. dornorum*, and *Spinosuchus caseanus*). The presence of three new allokotosaur taxa in Adamanian microvertebrate sites, including a new species of trilophosaurid described here (*Trilophosaurus phasmalophos* sp. nov.) demonstrates the high diversity of this group in the Adamanian. *Trilophosaurus phasmalophos* occurs in microvertebrate-bearing horizons in the Jim Camp Wash beds of the Sonsela Member, making it the first unambiguous trilophosaurid reported from the Revueltian estimated holochronozone. Unlike in other trilophosaurids, the teeth are bicuspid, but the cusp and cingulum structure and complexity are similar to those of *Trilophosaurus dornorum* and *T. jacobsi*. The Adamanian-Revueltian boundary marks a reduction in allokotosaur diversity from five Adamanian taxa to one Revueltian taxon. This pattern of faunal turnover and extinction is similar to those of other large-bodied archosauromorph clades across the Adamanian-Revueltian boundary in the American Southwest. Systematic sampling of microvertebrate bonebeds at stratigraphic intervals across this boundary demonstrates that this turnover in allokotosaurs may reveal similar patterns in other groups that have been missed because of collecting biases towards larger-bodied vertebrate fossils.

Key words: Archosauromorpha, *Trilophosaurus*, Chinle Formation, microvertebrate, herbivorous reptile, Upper Triassic.

1. Introduction

Archosauromorph reptiles diversified rapidly as part of the biotic recovery after the end-Permian extinction, achieving a range of shapes, sizes, and ecological roles (DILKES 1998; BRUSATTE et al. 2010; TURNER & NESBITT 2013; EZCURRA 2016; FOTH et al. 2016). Diversification of this group included the evolution of a variety of dental morphologies that indicate a shift from carnivory to more specialized diets, including herbivory (FLYNN et al. 2010). Allokotosauria, an archosauromorph clade known for its diversity of dental morphologies, hypothesized diets, and cosmopolitan distribution, includes azendohsaurids, trilophosaurids, and *Pamelaria dolichotrachela* (NESBITT et al. 2015). The global radiation of allokotosaurs in the Late Triassic is demonstrated by high taxonomic diversity, morphological disparity, and a near-Pangean biogeographic distribution. The range of body sizes and

dental morphologies in this clade possibly allowed its members to fill a variety of ecological niches left open after the end-Permian extinction (SENGUPTA et al. 2017).

Within Allokotosauria, trilophosaurids are a clade of herbivores with complex, transversely-widened, tricuspid teeth in the dentary and maxilla that are known from Upper Triassic terrestrial sediments in western North America and Nova Scotia (GREGORY 1945; ROBINSON 1957; MURRY 1987; HECKERT et al. 2001; SUES 2003; MUELLER & PARKER 2006; SPIELMANN et al. 2008; PRITCHARD & SUES 2019) and possibly from the Late Triassic of the United Kingdom (ROBINSON 1957). Frequently found as isolated teeth, trilophosaurids are the most common small- to medium-sized (<1 m in length) herbivorous tetrapods in Norian assemblages of western North America (equatorial Pangaea during the Norian), found at over 28 localities (MUELLER & PARKER 2006), compared to other smaller-bodied herbivorous taxa such as procolophonids (FRASER

1993; SMALL 1997; FRASER et al. 2005) and *Palacrodon* (KLI GMAN et al. 2018) that are known from single occurrences. *Trilophosaurus buettneri*, *Trilophosaurus jacobsi* (either a subjective junior synonym of *Spinosaurs caseanus* or its sister taxon; NESBITT et al. 2015) and *Trilophosaurus dornorum* are known from the Dockum Group of Texas and the Chinle Formation of Arizona (MUELLER & PARKER 2006; SPIELMANN et al. 2008). Trilophosaurid occurrences described from equatorial Pangaea prior to 2001 (HECKERT et al. 2001) were largely known from mass-death assemblages of *T. buettneri* in the Dockum Group of Texas (GREGORY 1945), with the exception of highly fragmentary jaws of *T. jacobsi* from a single locality in the Chinle Formation of Arizona (MURRY 1987). Recent work on microvertebrate-bearing bonebeds in the Chinle Formation and Dockum Group has expanded the data on allokotosaurs from equatorial Pangaea, significantly increasing the number of known localities, stratigraphic distribution, anatomy, and diversity for this group in western North America (HECKERT 2004; HECKERT et al. 2001, 2006; MUELLER & PARKER 2006; SPIELMANN et al. 2007; KLI GMAN 2015; MARSH et al. 2017; NESBITT et al. 2017; PARKER et al. 2018; SIDOR et al. 2018; KLI GMAN et al. 2019).

The vertebrate assemblages of the Blue Mesa Member and Sonsela Member of the Chinle Formation comprise the Adamanian and Revueltian estimated holochronozones, which are defined by the lowest stratigraphic occurrences of various phytosaurian taxa (LUCAS & HUNT 1993; LUCAS 1998; PARKER & MARTZ 2011; MARTZ & PARKER 2017). The boundary of the Adamanian and Revueltian estimated holochronozones occurs within the lower part of the Jim Camp Wash beds of the Sonsela Member at Petrified Forest National Park (PEFO) and is marked by species- and genus-level faunal turnovers among phytosaurs and aetosaurs (PARKER & MARTZ 2011). Because of limited sampling, there has been no observed signal of extinction or faunal turnover at this boundary in medium- or small-bodied tetrapod clades in the Chinle Formation. Our recent efforts to sample microvertebrate sites spanning the Adamanian-Revueltian boundary in and around PEFO in northeastern Arizona has shed light on faunal change and diversity of small- to medium-sized tetrapods in the Blue Mesa Member and Sonsela Member (KLI GMAN 2015; KLI GMAN et al. 2017, 2018; STOCKER et al. 2019). Here we describe a new taxon of trilophosaurid from the Sonsela Member of the Chinle Formation that expands the range of trilophosaurid dental morphology and is the first definitive evidence of an allokotosaur in the Revueltian estimated holochronozone. This adds to a growing body of evidence supporting a multi-clade disruption in biodiversity across the Adamanian-Revueltian boundary in western North America (PARKER & MARTZ 2011; BARANYI et al. 2018; PARKER et al. 2018).

Abbreviations: DMNH, Perot Museum of Natural History, Dallas, Texas, U.S.A.; MNA, Museum of Northern Arizona, Flagstaff, Arizona, U.S.A.; MOTT, Museum of Texas Tech locality, Museum of Texas Tech University, Lubbock, Texas, U.S.A.; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; NSM, Nova Scotia Museum of Natural History, Halifax, Nova Scotia, Canada; PEFO, Petrified Forest National Park, Arizona, U.S.A.; TMM, Texas Vertebrate Paleontology Collections, The University of Texas at Austin, Austin, Texas, U.S.A.; UCMP, University of California Museum of Paleontology, University of California, Berkeley, California, U.S.A.; UWBM, Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, U.S.A.

2. Geologic setting and age

The specimens were collected from two microvertebrate-bearing horizons in the lower part of the Jim Camp Wash beds of the Sonsela Member, Chinle Formation (MARTZ & PARKER 2010; Fig. 1): (1) PFV 089 (the ‘Bowman Site’; type locality, see below), a ~20 cm-thick grey horizon of interfingering conglomeratic lenses with a tan-colored sandy matrix including rounded mud rip-up clasts, unionid bivalves, coprolites, charcolified wood, and an assemblage of disarticulated bones from chondrichthyans, actinopterygians, non-tetrapod sarcopterygians, and tetrapods (LONG & MURRY 1995; PARKER & IRMIS 2005; PARKER 2006; PARKER & MARTZ 2011; MARSH et al. 2019); (2) the ‘Green Layer Locality’ outside PEFO, a ~20 cm thick horizon of conglomeratic lenses with a green-colored mudstone matrix including rounded mud rip-up clasts, unionid bivalves, coprolites, charcolified wood, and a diverse assemblage of disarticulated and articulated bones from chondrichthyans, actinopterygians, non-tetrapod sarcopterygians, and tetrapods including stem-anurans (STOCKER et al. 2019). U-Pb detrital zircon ages bracket the deposition of these two horizons to between 218.017 ± 0.088 and 213.870 ± 0.078 Ma (RAMEZANI et al. 2011). A more recent U-Pb detrital zircon date (sample 182Q-1) from a stratigraphically equivalent horizon from the upper part of the Sonsela Member in a drilled core (PFNP-1A) recovered an age of 214.08 ± 0.20 Ma (KENT et al. 2018). PFV 089 occurs within the Revueltian estimated holochronozone based on the presence of the aetosaur taxa *Typothorax coccinarum* (PEFO 36722) and *Paratypothorax* (PEFO 34565) and the phytosaur *Machaeropsosopus* (PEFO 4857; PARKER 2006; MARTZ & PARKER 2017). Stratigraphically, the lowest occurrence of *Machaeropsosopus* in PEFO defining the base of the Revueltian is ~3 meters below PFV 089 (PARKER & MARTZ 2011) and ~9 meters below the ‘Green Layer Locality.’ Thus, the available evidence indicates that PFV 089 and the ‘Green Layer Locality’ are in the lower part of the Revueltian.

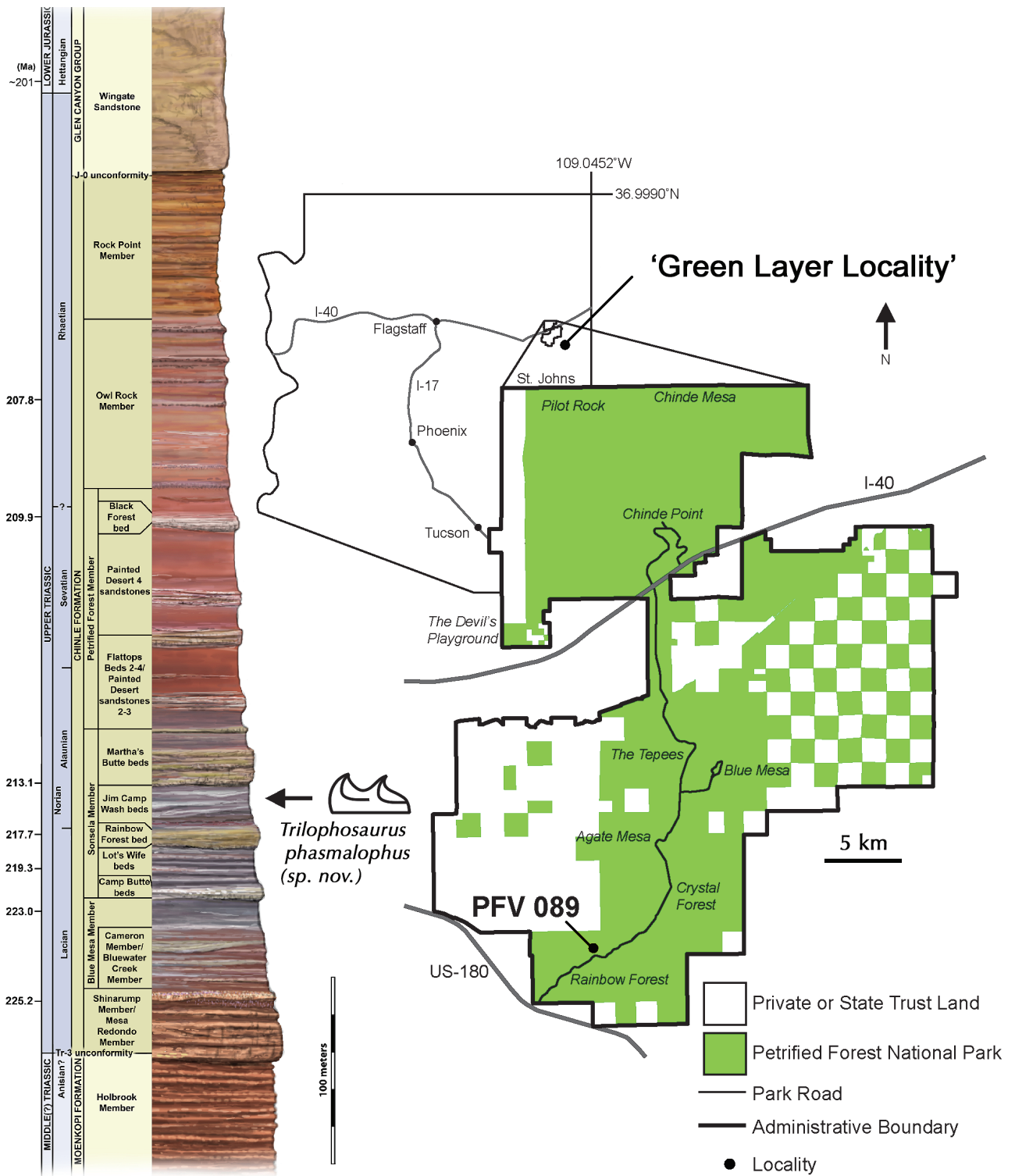


Fig. 1. Stratigraphic column of the Chinle Formation and map showing placement of PFV 089 and the 'Green Layer Locality', showing the approximate horizon of *Trilophosaurus phasmalophus* sp. nov. in the Sonsela Member (modified from KLIGMAN et al. 2017, 2018; MARSH et al. 2019).

3. Material and methods

Specimens were collected by visually inspecting split rocks in the field and by screen-washing fossiliferous sediments in the laboratory as described by KLIGMAN et al. (2017, 2018) and STOCKER et al. (2019). PEFO 42082 and specimens from the ‘Green Layer Locality’ (i.e., DMNH PAL 2018-05-0012, DMNH PAL 2018-05-0013) were prepared by hand under stereomicroscope using a 1/32-inch chisel-pointed carbide needle in a pin vise. Consolidation of fractures in the specimens was achieved with a 1:2 solution (by volume) of Paraloid B-72 in acetone. Photography of PEFO 42082 was performed using a Leica MZApro stereomicroscope and a Sony NEX-5T digital camera. Photography of DMNH PAL 2018-05-0012 was performed using a Leica MZ67 stereomicroscope and a Sony NEX-5T digital camera. PEFO 42082 was μ CT scanned using a Skyscan 1172 Microfocus X-radiographic Scanner at Virginia Tech under the following parameters: aluminum and copper filters, source voltage (kV) = 79, source current (uA) = 125, Image Pixel Size (um) = 17.42. Scan data was subsequently processed in Materialize Mimics 20.0 and imaged in Meshlab 2016. A digital surface reconstruction of PEFO 42082 is available online on Morphosource (morphosource.org) under project P926.

To test the evolutionary relationships of the new trilophosaurid species, we used a recent archosauromorph dataset (PRITCHARD et al. 2015) with subsequent additions (NESBITT et al. 2015) because this dataset sampled within *Trilophosaurus* (compared to another recent archosauromorph dataset, EZCURRA et al. 2016). Moreover, this dataset includes dental character states that separate *Trilophosaurus* from other allokotosaurians. We added the new species and *T. dornorum* (terminal taxa = 32) but did not add any new characters (total characters = 247). We performed a parsimony analysis replicating previous parameters (PRITCHARD et al. 2015; NESBITT et al. 2015) in PAUP* version v4.0b10 (SWOFFORD 2002) using heuristic searches with 10,000 random addition replicates; consistency (CI) and retention (RI) indices were calculated in PAUP*; characters 2, 5, 10, 11, 20, 32, 52, 72, 204, and 212 were ordered. *Trilophosaurus phasmalophos* sp. nov. was scored as follows: 90(0), 91(0), 93(1), 98(2). The holotype of *T. dornorum* was scored as follows: 7(0), 89(0), 90(0), 91(0), 92(0), 93(1), 94(0), 95(0), 96(0), 97(1), 98(2), 211(0).

In the context of trilophosaurid teeth, the term ‘cingulum’ was first used in the description of *Tricuspisaurus thomasi* (ROBINSON 1957), referring to apically-facing flat shelves with acute-to-obtuse margins, and subsequently has been followed by authors describing trilophosaurid teeth. This usage is followed herein.

4. Systematic paleontology

Diapsida OSBORN 1903 sensu GAUTHIER et al., 1988

Archosauromorpha v. HUENE, 1946 sensu BENTON, 1985

Trilophosauridae ROMER, 1956 sensu NESBITT et al., 2015

Trilophosaurus CASE, 1928a

Trilophosaurus phasmalophos sp. nov.

Fig. 2

E t y m o l o g y : Named derived from ‘phasma’ (Greek for phantom or ghost), and ‘lopho’ (Greek for crest), referring to the unique two cusped condition of this trilophosaurid taxon.

H o l o t y p e : PEFO 42082, isolated tooth from the maxilla or dentary.

P a r a t y p e s : PEFO 42231, PEFO 42261, PEFO 42271, PEFO 42117, PEFO 42278, PEFO 42167, PEFO 42292, PEFO 42209, isolated teeth

R e f e r r e d M a t e r i a l : DMNH PAL 2018-05-0012, DMNH PAL 2018-05-0013, isolated teeth.

T y p e l o c a l i t y a n d h o r i z o n : PFV 089 (the Bowman Site), a microvertebrate-bearing layer in the lower part of the Jim Camp Wash beds of the Sonsela Member, Chinle Formation, Petrified Forest National Park, Arizona, U.S.A. (PARKER 2006; PARKER & MARTZ 2011).

A g e : Late Triassic, Norian, between 218.017 ± 0.088 Ma and 213.870 ± 0.078 Ma (RAMEZANI et al. 2011), Revueltian land vertebrate holochronozone (MARTZ & PARKER 2017). A more recent U-Pb detrital zircon date (from sample 182Q-1) from a stratigraphically equivalent horizon from the upper Sonsela Member in a drilled core (PFNP-1A) recovered an age of 214.08 ± 0.20 Ma (KENT et al. 2018).

D i a g n o s i s : We refer the new taxon to the genus *Trilophosaurus* based on the following shared apomorphies: nonserrated marginal dentition (PRITCHARD et al. 2015 [Character] 90 – [state] 0); morphology of crown base of the marginal teeth a flattened platform with pointed cusps (93–1); tooth shape at crown base of the marginal teeth labiolingually wider than mesiodistally long (98–2). *Trilophosaurus phasmalophos* differs from all known trilophosaurids in possessing the following unique combination of characters and autapomorphies (marked with an asterisk): a crown base labiolingually wider than mesiodistally long (a 1:5 mesiodistal length to labiolingual width ratio) with two distinct cusps instead of three*; the tips of the cusps are slightly recurved lingually*; both cusps bear apicolingually-facing cingula on their mesial and distal margins, with two symmetrical cingula on the mesial and distal sides of the lingual cusp, one cingulum on the mesial margin of the labial cusp, and two superimposed cingula on the distal margin of the labial cusp, totaling five cingula per tooth*.

D e s c r i p t i o n : The holotype, PEFO 42082, is a complete unworn tooth from the maxilla or dentary, and its position is based on comparisons with teeth of other trilophosaurids (e.g., *T. buettneri*). Isolated trilophosaurid teeth cannot be confidently assigned to upper or lower jaws, and therefore the holotype is herein described as a tooth from the right dentary for ease of description. The tooth of *Trilophosaurus phasmalophos* is trans-

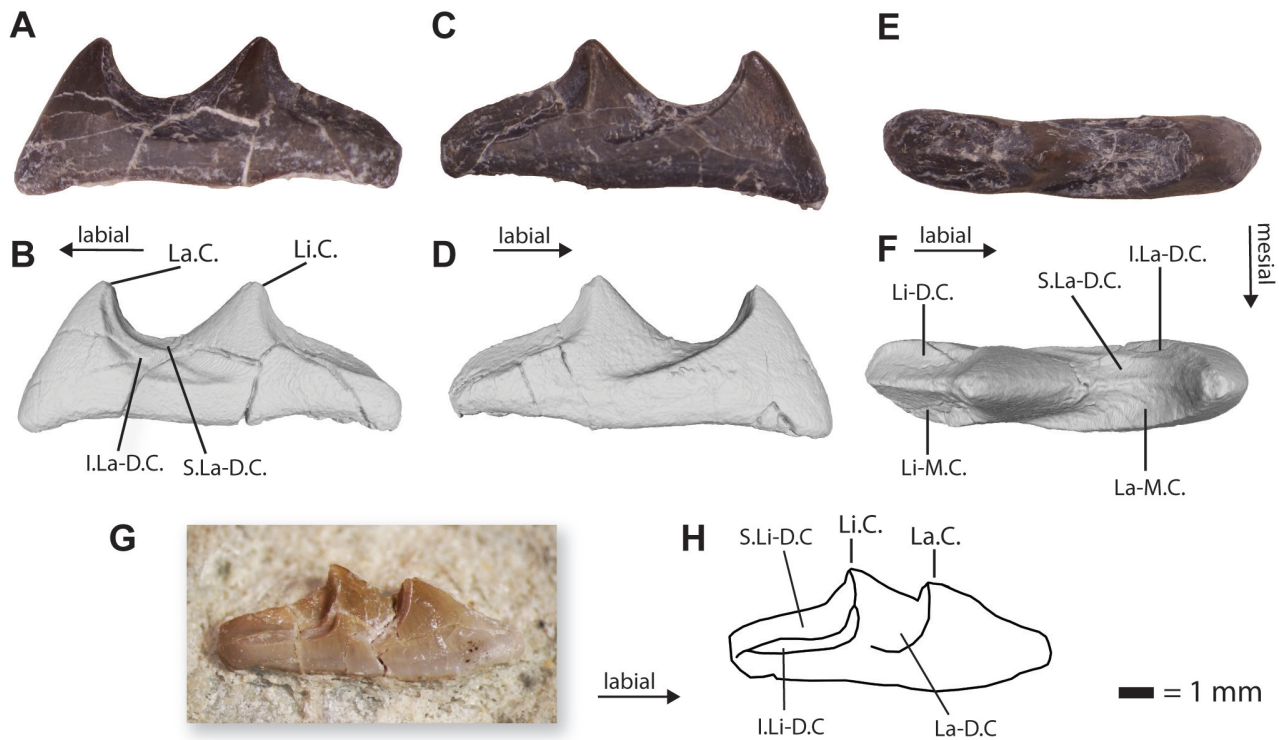


Fig. 2. Holotype tooth of *Trilophosaurus phasmalophos* sp. nov. PEFO 42082 (A–F). Photograph in mesial view (A) and surface reconstruction based on μ CT data ‘Green Layer Locality’ from Mimics (V20) (B). Photograph in in distal view (C) and virtual reconstruction based on μ CT data (D). Photograph in occlusal view (E) and virtual reconstruction based on μ CT data (F). Photograph of referred *Trilophosaurus phasmalophos* sp. nov. tooth DMNH PAL 2018-05-0012 in distal view (G) and line drawing (H). Abbreviations: I.D.-Li.C., inferior linguodistal cingulum; I.La-D.C., inferior labiodistal cingulum; La.C., labial cusp; La-M.C. labiomesial cingulum; Li.C., lingual cusp; Li-D.C., linguodistal cingulum; Li-M.C., linguomesial cingulum; S.Ca-D.C., superior labiodistal cingulum. – Scale bar equals 1 mm.

versely widened (a 1:5 mesiodistal length to labio-lingual width ratio) along its labiolingual axis and bears two cusps of equal apicobasal height (Fig. 2B).

Two symmetrical, parabolic ridges extend down the mesial and distal margins of the tooth from the apex of the lingual cusp to the lingual-most edge of the tooth. These ridges have apically concave-up profiles with their labial arm oriented vertically from the cusp apex, and the lingual arm oriented horizontally. The ridges form the mesial and distal margins of two symmetrical apicolingually-facing cingula.

Three apicolingually-facing cingula emarginated by ridges with apically concave-up profiles and labial arms oriented vertically from the labial cusp apex and the lingual arm oriented horizontally occupy the labial side of the tooth. These ridges terminate directly basal to the lingual cusp where they grade into the flat surface of the medial and distal sides of the tooth. One of these cingula occupies the mesial side of the tooth (labiomesial cingulum; Fig. 2F), and the other two superimposed cingula occupy the distal side of the tooth (inferior labiodistal cingulum, superior labiodistal cingulum; Fig. 2B, F). Therefore, a single tooth from *Trilophosaurus phasmalophos* bears five total cingula.

A central ridge descends lingually from the apex of the lingual cusp along the mesiodistal midline of the tooth terminating at the lingual end of the tooth, forming the mesial margin of the

linguodistal cingulum and the distal margin of the linguomesial cingulum. A central ridge of similar structure descends lingually from the apex of the labial cusp along the mesiodistal midline of the tooth forming the mesial margin of the apical-most of the labiodistal cingulum and the distal margin of the labiomesial cingulum (Fig. 2F). The apex of the labial central ridge has an acute angle from the apex of the labial cusp to the apicobasal low point between the labial and lingual cusps, where its apex becomes rounded until it terminates at the apex of the lingual cusp.

In DMNH PAL 2018-05-0012 (Fig. 2G, H), an additional cingulum is present basal to the linguodistal cingulum (inferior linguodistal cingulum; Fig. 2H). Both specimens from DMNH 2018-05 have a slightly apically-taller lingual cusp than labial cusp, whereas both cusps are of equal height in the holotype (PEFO 42082). This variation in cingula and cusp structure may be a factor of variation within the marginal dentition of the upper and lower jaws in *Trilophosaurus phasmalophos*.

Comparisons: The teeth of *Trilophosaurus phasmalophos* are similar to those of other species of *Trilophosaurus* in that they are labiolingually widened and bear prominent cusps connected by a transverse occlusal ridge. *T. buettneri*, *T. jacobsi*, and *T. dornorum* all bear three distinct labiolingually-oriented cusps including the lingual, central, and labial cusps. *Trilophosaurus phasmalophos* lacks a lingual cusp, with the lingual

central ridge descending without interruption to the lingual edge of the tooth from the lingual cusp (Fig 2). Therefore, *Trilophosaurus phasmalophos* is the only known trilophosaurid that possesses two rather than three cusps on its teeth.

Cingular structure and complexity are commonly used to distinguish *Trilophosaurus* species (MURRY 1986; HECKERT et al. 2006; MUELLER & PARKER 2006; SPIELMANN et al. 2008). No distinct cingula are present in the teeth of *T. buettneri* (Fig. 3A), whereas at least four distinct cingula are present on the teeth of *T. jacobsi* and *T. dornorum* (MUELLER & PARKER 2006; HECKERT et al. 2006; SPIELMANN et al. 2008). The exact cingula structure of *T. jacobsi* is uncertain due to the difficulty of observing tooth morphology in the fragmentary holotype material and crushed cranial material referred to this taxon, where teeth are still attached to the jaws, and the few isolated teeth known from these taxon are too fragmentary to assess their structure in detail, unlike isolated teeth known from *T. buettneri* and *T. phasmalophos*. The use of CT scanning and 3D reconstruction technology on material from *T. jacobsi* is likely to yield a better understanding of its dental morphology and will allow for more robust comparison of dental structure across trilophosaurid taxa.

Trilophosaurus jacobsi was described from a tooth-bearing fragment of a maxilla (MNA V3192) as well as several isolated teeth from the Placerias Quarry (MNA 207-2; MURRY 1987; HECKERT et al. 2006) and referred dentigerous material from the Kahle *Trilophosaurus* quarry (NMMNH L-3775; HECKERT et al. 2006). *Trilophosaurus dornorum* was described based on an associated maxilla and dentary fragments (PEFO 31165) from PFV 191 at PEFO (MUELLER & PARKER 2006). SPIELMANN et al. (2007, 2008) argued that differences in the number of cingula between *T. jacobsi* (two) and *T. dornorum* (three) were associated with the larger size of the latter and that an increase in cingulum count was a size-related character. The presence of five cingula in *T. phasmalophos*, the known specimens of which are much smaller than the holotype of *T. dornorum*, refutes this hypothesis of a simple relationship between number of cingula and specimen size in trilophosaurids. For these reasons we follow MARTZ et al. (2013) in treating *T. jacobsi* and *T. dornorum* as distinct taxa.

5. Discussion

5.1. Relationships of *Trilophosaurus phasmalophos* and trilophosaurid dental evolution

Our phylogenetic analysis places *T. phasmalophos* in a polytomy with all other species of *Trilophosaurus* (*T. buettneri*, *T. dornorum*, *T. jacobsi*), *Spinosuchus caseanus*, and *Teraterpeton hrynewichorum* within Trilophosauridae (Fig. 3; MPT = 5; Length = 618 steps; CI = 0.422; RI = 0.637). The character state that supports *T. phasmalophos* as a species in the genus *Trilophosaurus* is a crown base of the marginal teeth labiolingually wider than mesiodistally long (character 98, state 2). The bicuspid morphology of the teeth of *T. phasmalophos* allows for two hypotheses for the evolution of trilophosaurid teeth: 1) a bicuspid dental morphology as the plesiomorphic state for trilophosaurids; or 2) a derived loss of the

third (lingual) cusp in *T. phasmalophos*. Given the similarity of the cusp/cingula structure in *T. phasmalophos* to that of *T. dornorum* and *T. jacobsi*, the bicuspid morphology of *T. phasmalophos* is likely a result of a derived loss of the third cusp.

Teraterpeton hrynewichorum, the earliest diverging member of the Trilophosauridae, possesses transversely-widened teeth like all members of the clade (SUES 2003). Each tooth in *Ter. hrynewichorum* bears two cusps oriented mesiodistally (unlike the labiolingually-arranged cusps in the teeth of members of the genus *Trilophosaurus*); in the teeth of the dentary one apically tall cusp is present at the mesial end of the tooth separated by a basally concave 'heel' from a less apically prominent cusp at the distal end of the tooth, and in the maxilla and palatine the mesio-distal arrangement of the cusp height is reversed (SUES 2003; Figs. 5, 6). Although the teeth of *Ter. hrynewichorum* bear two cusps like those of *T. phasmalophos*, we suspect this bicuspid morphology is not due to homology because the teeth in *Ter. hrynewichorum* have mesiodistally arranged cusps and lack cingula, supporting a derived loss of the third cusp in *Trilophosaurus phasmalophos*.

5.2. Trilophosaurid biostratigraphy

We considered the highest and lowest stratigraphic occurrences of trilophosaurid taxa to analyze their biostratigraphic ranges and diversity through the Late Triassic (Fig. 3). Reported trilophosaurids from the Late Triassic of the United Kingdom (*Variodens inopinatus* and *Tricuspisaurus thomasi* of the Ruthin Quarry fissure fill deposit) are not considered in this analysis because of questionable phylogenetic affinities to the Trilophosauridae (ROBINSON 1957; SUES & OLSEN 1993), uncertain time-averaging in fissure fill deposits like the Ruthin Quarry, and a lack of geochronologic and biostratigraphic constraints on that deposit (WHITESIDE et al. 2016). The earliest-branching trilophosaurid, the long-snouted *Teraterpeton hrynewichorum* (NESBITT et al. 2015; SENGUPTA et al. 2017), was recovered from a fallen block of the Evangeline Beach Member of the Wolfville Formation in Nova Scotia (NSM unnumbered locality; SUES 2003; PRITCHARD & SUES 2019). That unit most likely is Carnian in age because of the presence of the metoposaurid temnospondyl '*Metoposaurus*' *bakeri* (SUES & OLSEN 2015).

SPIELMANN et al. (2007) argued that the biostratigraphic range of the various species of *Trilophosaurus* extended into the Revueltian based on their presence in three quarries in the Cooper Canyon Formation of the Dockum Group, MOTT VPL 3878, MOTT VPL 3624 (the Post Quarry), and MOTT VPL 3869. That Revueltian assignment was based on the erroneous hypothesis that

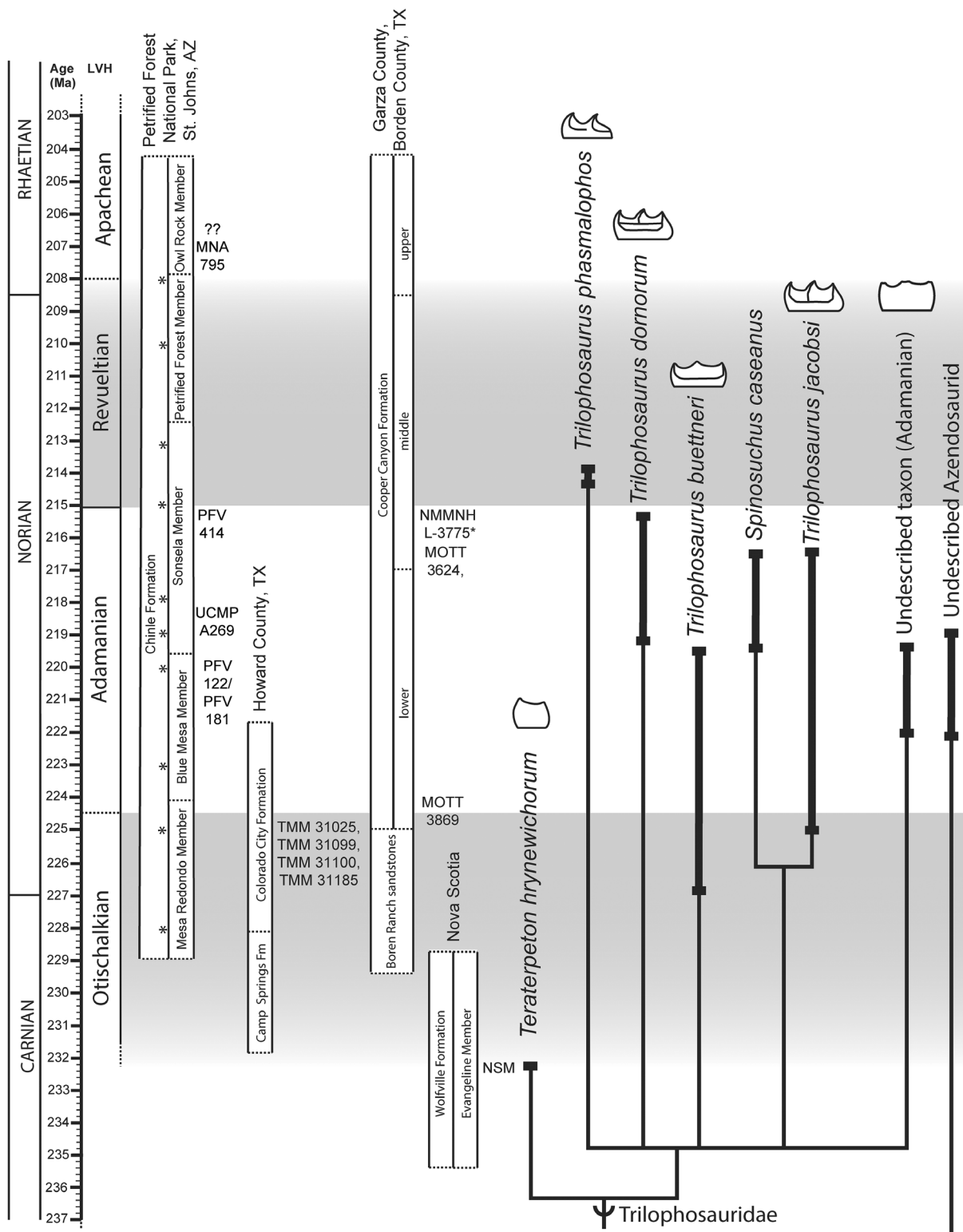


Fig. 3. Stratigraphic ranges of the Trilophosauridae and other allokotosaurs in North America, U-Pb geochronologic dates shown as asterisks (RAMEZANI et al. 2011, 2014; ATCHLEY et al. 2013), with topological results of the phylogenetic analysis (modified from MARSH 2018). Black bars represent highest and lowest stratigraphic occurrence of each taxon, which may underestimate the total stratigraphic range. Asterisk represents uncertainty as to the exact stratigraphic location of NMMNH L-3775 within the Middle Member of the Cooper Canyon Formation.

the entirety of the Cooper Canyon Formation in Texas is equivalent to the Bull Canyon Formation of New Mexico (e.g., LUCAS et al. 1993; LEHMAN 1994). Detailed stratigraphic work demonstrated that only the upper portion of the Cooper Canyon Formation is equivalent to the Bull Canyon Formation (MARTZ 2008), and vertebrate biostratigraphy now places the Post Quarry (MOTT 3624) and other Cooper Canyon sites producing trilophosaurid taxa in the Adamanian (MARTZ et al. 2013).

The type species of *Trilophosaurus*, *T. buettneri* (CASE 1928a, b), is likely the lowest-occurring species of the genus. The type specimen (UMMP 2338) is from the Tecovas Formation, and referred skeletal material (e.g., TMM 31025-140) is from the four main Otis Chalk localities in the Colorado City Formation (Dockum Group) of Howard County, Texas (Quarry 1, TMM 31025; Quarry 2, TMM 31099; Quarry 3, TMM 31100; and Quarry 3A, TMM 31185; STOCKER 2013a). Although the exact stratigraphic relationships between those quarries are uncertain (see discussions by GREGORY 1945; ELDER 1978; HECKERT 2006; STOCKER 2013a), the assemblages within them have been treated as contemporaneous. Those *Trilophosaurus buettneri* localities occur in the type Otischalkian strata, which are characterized by the non-Myrstriosuchinae phytosaurian *Parasuchus* (= *Paleorhinus*; STOCKER 2010, 2013a, 2013b; BUTLER et al. 2014; KAMMERER et al. 2015). *Trilophosaurus buettneri* occurs in other places within the Dockum Group of Texas and the Chinle Formation of Arizona (see SPIELMANN et al. 2007, 2008 for a discussion and also MARTZ 2008; MARTZ et al. 2013; STOCKER 2013a; SARIGÜL 2016, 2017a, 2017b; LESSNER et al. 2018; MARSH 2018 for revisions and synthesis of the stratigraphic relationships of the Dockum Group). However, the highest occurrence of isolated teeth of *Trilophosaurus buettneri* occurs at sites within the upper part of the Blue Mesa Member at PEFO, including PFV 122/PFV 181 (the Dying Grounds), that are Adamanian due to their occurrence above the lowest occurrence of the non-Myrstriosuchini leptosuchomorph phytosaurs (PARKER & MARTZ 2011; STOCKER 2012; MARTZ & PARKER 2017). High-resolution U-Pb detrital zircon geochronology suggests that these sites can be dated to ~220 Ma (RAMEZANI et al. 2011; ATCHLEY et al. 2013; KLIGMAN et al. 2017, 2018).

NESBITT et al. (2015) tested the hypothesis that *T. jacobsi* is a subjective junior synonym of *Spinosuchus caseanus*, a trilophosaurid known largely from the axial skeleton without associated dental remains (VON HUENE 1932; SPIELMANN et al. 2009). They pointed out that the two taxa co-occur at several localities, and that very little overlap exists with respect to the preserved elements of each taxon. *Trilophosaurus jacobsi* is commonly found throughout the Dockum Group of Texas, and its lowest stratigraphic occurrence is found near the bottom of the Cooper Canyon Formation at the Boren Quarry (MOTT 3869) in Garza

County (SPIELMANN et al. 2007, 2008), which is most likely still Otischalkian (MARTZ et al. 2013). The highest stratigraphic occurrence of *T. jacobsi* is found at the Kahle Quarry (NMMNH L-3775; HECKERT et al. 2004), possibly in the Trujillo Formation-equivalent middle unit of the Cooper Canyon Formation (MARTZ 2008: 310–311). *Spinosuchus caseanus* is found at the *Placierias* Quarry within the Lot's Wife beds of the Sonsela Member (Chinle Formation) in Arizona (UCMP A269, which also contains *T. jacobsi*; SPIELMANN et al. 2007, 2008; NESBITT et al. 2015) as well as the Kahle Quarry (see above), both of which are Adamanian. Another species of *Trilophosaurus*, *T. dornorum* (MUELLER & PARKER 2006), is found at the Post Quarry (MOTT 3624) in the top of the lower unit of the Cooper Canyon Formation of Garza County, Texas (MARTZ 2008; MARTZ et al. 2013), and at Lott Hill (MOTT 3878) and the Boren Quarry (MOTT 3869) in the lower part of the Cooper Canyon Formation (MUELLER & PARKER 2006; MARTZ 2008). Chinle Formation occurrences of *T. dornorum* include its type locality in the Lot's Wife beds of the Sonsela Member at PEFO (PFV 191; MUELLER & PARKER 2006; PARKER & MARTZ 2011) and a locality in the lower part of the Jim Camp Wash beds of the Sonsela Member at PFV 414 (PEFO 42365/UWBM 116791; SIDOR et al. 2018).

Thus, the entire biostratigraphic ranges of *T. dornorum*, *T. buettneri*, and *T. jacobsi* are contained within the Otischalkian and Adamanian estimated holochronozones. No previously reported trilophosaurid species spans the Adamanian-Revueltian boundary (PARKER & MARTZ 2011; MARTZ et al. 2013), and *T. phasmalophos* represents the youngest and only unambiguous Revueltian trilophosaurid. A single worn tricuspid tooth was documented from the Owl Rock Member of the Chinle Formation on Ward's Terrace in Arizona (MNA V7064; KIRBY 1991) and may represent any number of coeval non-trilophosaurid taxa that exhibit similar tooth morphologies (HECKERT et al. 2006). The apparent decrease in diversity just before or at the Adamanian-Revueltian boundary likely is not an artifact of sampling because known Revueltian and later microsites lack any trilophosaurid material except for this new species, *T. phasmalophos*.

An unnamed, possible trilophosaurid taxon known from dentigerous jaw elements and isolated teeth was discovered in two Adamanian estimated holochronozone assemblages in the Blue Mesa Member in PEFO at PFV 396 (PEFO 41462) and PFV 456 (PEFO 43815, PEFO 43837) in the summer of 2019 (KLIGMAN et al. 2019). This taxon includes all of the character states of *Trilophosaurus* (see above), and description of this taxon is ongoing; however, its stratigraphic occurrence is included here. An undescribed azendohsaurid is known from several bonebeds in Adamanian estimated holochronozone assemblages from the Blue Mesa Member at PEFO (PFV 122, PFV 396, PFV 414, PFV 456). This taxon is known from

isolated teeth as well as disarticulated skeletons (MARSH et al. 2017). Its occurrence brings the total allokotosaur diversity (trilophosaurids and azendohsaurids) to six taxa in the Adamanian.

5.3. Patterns of biotic change at the Adamanian-Revueltian boundary

Allokotosaurs now add to several vertebrate clades with observed patterns of extinction and origination at the Adamanian-Revueltian boundary. Aetosaurs, a clade of large-bodied, armored, herbivorous pseudosuchian archosaurs, undergo a genus-level change at this boundary (PARKER & MARTZ 2011; PARKER 2016; PARKER et al. 2018). They are the most commonly reported large-bodied herbivorous tetrapod from the Chinle Formation. Additionally, phytosaurs, a clade of large-bodied, semi-aquatic, carnivorous archosaurs (or non-archosaur archosauriforms; see NESBITT 2011; EZCURRA 2016; STOCKER et al. 2017), exhibit a similar pattern to that of trilophosaurids and aetosaurs (PARKER et al. 2018). Leptosuchomorph phytosaurs diversified prior to the Adamanian-Revueltian turnover, with several species of *Smilosuchus* present in the Blue Mesa Member and *Pravusuchus hortus*, *Protome batalaria*, and *Smilosuchus lithodendrorum* known from the lower portions of the Sonsela Member (PARKER & MARTZ 2011; STOCKER 2012; MARTZ & PARKER 2017). Subsequent to the Adamanian-Revueltian boundary, phytosaurs solely within *Machaeroprotopus* (formerly *Pseudopalatus*; PARKER et al. 2012) are known from Revueltian strata (PARKER & MARTZ 2011; KAMMERER et al. 2015).

Trends of biotic change across this boundary have also been observed in fossil floral assemblages sampled at stratigraphic intervals throughout the Chinle Formation, characterized by a shift to xerophytic plant assemblages after the Adamanian-Revueltian boundary (REICHELGT et al. 2013; BARANYI et al. 2018). Trilophosaurids and aetosaurs, the most common herbivores known from Triassic rocks in southwestern North America, would have depended on local plant communities as a food source, and changes in the floral community may have been a causative factor in their extinction and turnover at this boundary.

The cause of biotic disruption at the Adamanian-Revueltian boundary is debated because several external factors may have acted upon the environments of southwestern North America during the Late Triassic (PARKER et al. 2018). A trend towards climatic aridification over the mid-late Norian is recorded in the Sonsela Member, possibly caused by change in the monsoonal climate systems and/or northward continental drift from the equatorial humid climate zone into the subtropical arid climate zone (KENT & TAUXE 2005; NORDT et al. 2015; BARANYI

et al. 2018). The Manicouagan bolide impact, occurring at ~215 Ma in Quebec, Canada, may have affected ecosystems across North America and has been proposed as the cause of extinctions in marine plankton in the eastern Pacific Ocean (PARKER & MARTZ 2011; ONOUE et al. 2016). Both climatic aridification and the Manicouagan bolide impact may have been concurrent with the timing of the Adamanian-Revueltian boundary and may have influenced the observed patterns of biotic change; however, a lack of direct evidence for either cause prohibits further resolution of this question. Current modeling using Bayesian statistics suggests this turnover event might have been more protracted rather than instantaneous, but does not “disqualify the impact from having influenced Chinle ecosystems” (HAYES et al. 2020: 4).

6. Conclusions

The occurrence of *T. phasmalophos* in Revueltian assemblages from the Chinle Formation is evidence of a decrease in allokotosaur diversity across the Adamanian-Revueltian boundary from six taxa known from Adamanian estimated holochronozone rocks to one in early Revueltian rocks. This pattern of change is similar to those of several large-bodied vertebrate clades across the Adamanian-Revueltian boundary in western North America, adding further evidence for a regional faunal turnover at this boundary. This evidence for biodiversity disruption at around 215 Ma in terrestrial vertebrate and plant assemblages from the Chinle Formation, in addition to that in paleo-Pacific marine invertebrates, points to a global pattern of biodiversity loss at this time (PARKER & MARTZ 2011; OLSEN et al. 2011; ONOUE et al. 2016; BARANYI et al. 2018).

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