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THE ALLOKOTOSAUR (REPTILIA: ARCHOSAUROMORPHA) ASSEMBLAGE FROM A MULTITAXIC BONEBED IN THE SONSELA MEMBER (JIM CAMP WASH BEDS, CHINLE FORMATION) AT PETRIFIED FOREST NATIONAL PARK, U.S.A.

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ABSTRACT — Allokotosaurian archosauromorphs (i.e., trilophosaurids and azendohsaurids) are known from Middle Triassic to Upper Triassic terrestrial deposits in Madagascar, Morocco, India, the United Kingdom, southeastern Canada, and the southwestern United States. In western Texas, trilophosaurids and malerisaurine azendohsaurids co-occur in Otischalkian sites, but numerous sites in the Chinle Formation-Dockum Group depobasin of Texas, New Mexico, and Arizona preserve either trilophosaurids or malerisaurines, blurring our understanding of the evolution of these groups and their potential biostratigraphic utility. Here we report an allokotosaurian assemblage from PFV 410 (the Kaye Quarry), a lowermost Revueltian locality in the upper Sonsela Member of the Chinle Formation at Petrified Forest National Park that preserves both trilophosaurid and malerisaurine azendohsaurid taxa, which indicates that these lineages may have co-occurred in the southwestern United States for ~10 million years during the Carnian to Norian. This locality is important because it preserves teeth of *Trilophosaurus phasmalophos* in a maxilla that may help resolve taxonomic uncertainty in that genus, and it shows that malerisaurines persisted at least for some time after the hypothesized Adamanian-Revueltian biotic turnover.

Keywords: Trilophosauridae; Malerisaurinae; Chinle Formation; Biostratigraphy.

INTRODUCTION

The Upper Triassic terrestrial assemblages from the Chinle Formation and Dockum Group of the southwestern United States include a significant number of non-archosauriform archosauromorphs, principally allokotosaurs (trilophosaurids and azendohsaurids; Gregory, 1945; Spielmann et al., 2008; Hégron et al., 2020; Nesbitt et al., 2021; Marsh et al., 2022) and tanystropheids (Pritchard et al., 2015; Lessner et al., 2018). Recently, allokotosaurs have received renewed research attention as enigmatic taxa were attributed to the group (Sues, 2003; Flynn et al., 2010, Pritchard and Sues, 2019; Chambi-Trowell et al., 2022; Foffa et al., 2023) and as new species have been discovered (Kligman et al., 2020; Marsh et al., 2022). Once considered 'cotylosaurs' or 'protorosaurs' (Case, 1928; Chatterjee, 1980), we can now recognize and identify even fragmentary remains of these extinct lineages owing to their near-global distribution in the last 40 million years of the Triassic Period as well as monodominant bonebeds that provide examples of nearly every skeletal element (Gregory, 1975; Nesbitt et al., 2015, Sengupta et al., 2017; Marsh et al., 2022).

In the southwestern United States (Fig. 1; Appendix 1), trilophosaurids are present in the Middle Triassic Holbrook Member of the Moenkopi Formation in Arizona (*Anisodontosaurus greeri* Welles, 1947; Foffa et al., 2023), the Otischalkian (*sensu* Martz and Parker, 2017) Upper Triassic of the Colorado City Formation of western Texas (*Trilophosaurus buettneri* Case, 1928; *Trilophosaurus jacobsi* Murry, 1987/*Spinosuchus caseanus* Huene, 1932), the Adamanian Upper Triassic Tecovas Formation and middle Cooper Canyon Formation of western Texas (*T. jacobsi*/*S. caseanus*; Spielmann et al., 2008; Nesbitt et al., 2015; Kligman et al., 2020; *Trilophosaurus dornorum* Mueller and Parker, 2006; Martz et al., 2013) and the Blue Mesa Member and lower part of the Jim Camp Wash beds (Sonsela Member) of the Chinle Formation of Arizona (*Trilophosaurus dornorum*, Mueller and Parker, 2006; *Trilophosaurus* spp.; Kligman, 2023), and the lowermost part of the Revueltian Upper Triassic of the Jim Camp Wash beds (Sonsela Member) in Arizona (*Trilophosaurus phasmalophos* Kligman et al., 2020). In the same region, malerisaurine azendohsaurids are absent (to date) in the Middle Triassic Moenkopi Formation, but other azendohsaurids are present in the Middle Triassic of India and potentially Madagascar (*Pamelaria dolichotrachela* Sen, 2003, *Shringasaurus indicus* Sengupta et al., 2017, and *Azendohsaurus madagaskarensis* Flynn et al., 2010), present in the Otischalkian Upper Triassic of the Colorado City Formation of western Texas (*Malerisaurus langstoni* Chatterjee, 1986/*Otischalkia elderae* Hunt and Lucas, 1991), and the Adamanian Upper Triassic Garita Creek Formation of New Mexico (Hégron et al., 2020), Tecovas Formation of western Texas (Nesbitt et al., 2021), and Blue Mesa Member of the Chinle Formation in Arizona (*Puercosuchus traverorum* Marsh et al., 2022). Malerisaurines were thought to be absent in the Revueltian holochron or were only found in one locality at Revuelto Creek, NM (Speilmann et al., 2013), potentially representing a lineage that did not survive the Adamanian-Revueltian biotic turnover (Parker and Martz, 2010; Kligman et al., 2020; Marsh et al., 2022). Here, we identify recently collected specimens belonging to indeterminate allokotosaurians, trilophosaurids (including *Trilophosaurus phasmalophos*), and malerisaurines from a multitaxic bonebed in the lowermost Revueltian strata of the Jim Camp Wash beds (Sonsela Member, Chinle Formation) at Petrified Forest National Park. This site, published previously for its shuvosaurid, drepanosauromorph, and ornithodiran fossils (Sidor et al., 2018; Goncalves and Sidor, 2019; Marsh and Parker, 2020), contains one of the few allokotosaurian assemblages preserving material referrable both trilophosaurids and azendohsaurids, as well as the only unambiguous malerisaurine azendohsaurid currently known from the Revueltian.

MATERIALS AND METHODS

Color photographs were taken using a Nikon D90 digital camera equipped with a Nikon AF-S NIKKOR 24–85 mm lens. Image stacking was performed using Adobe Photoshop (25.0.0). When possible, identifications below are made using apomorphies of the respective clade (e.g., Nesbitt and Stocker, 2008; Bell et al., 2010; Martz et al., 2013; Lessner et al., 2018). Otherwise, identifications are made here by exclusion; only a few specimens of tanystropheids and *Vancleavea* *campi* Long and Murry, 1995 have been found despite hundreds of specimens collected and prepared from PFV 410. The anatomy of the non-allokotosaurian archosauromorphs at PFV 410 is sufficiently different than what is described below that the following can be referred to the Allokotosauria until disproven with future fossil discoveries. There has yet to be a non-malerisaurine azendohsaurid found in the Chinle Formation and Dockum Group (Nesbitt et al., 2021), so we assume that specimens with azendohsaurid features are also likely malerisaurines. This is emphasized by traits found in the malerisaurine specimens of PFV 410 that are not present in non-malerisaurine azendohsaurids, as described below (Nesbitt et al., 2021; Marsh et al., 2022; Sengupta et al., 2024). The specimens discussed here were collected at Petrified Forest National Park by teams from the University of Washington under Scientific Research and Collecting permits (Study #: PEFO-00085). They are catalogued with both PEFO and UWBM specimen numbers and each is provided here, as required by U.S. National Park Service policy.

We follow Nesbitt et al. (2021) in considering '*Otischalkia elderae*' Hunt and Lucas, 1991 a robust malerisaurine azendohsaurid, if not *Malerisaurus langstoni* Chatterjee, 1986 itself, when present in the TMM Otis Chalk quarries. The distal ends of humeri from the Bull Creek Formation of eastern New Mexico (UMMP 7441 and NMMNH P-4686; Spielmann et al., 2013: fig 1a–l) were referred to '*Otischalkia elderae*' when those authors considered that taxon to represent a rhynchosaur, but here we refer to them as indeterminate malerisaurines until we can observe them in person. Regardless of whether *Trilophosaurus dornorum* (Mueller and Parker, 2006) can be differentiated from *Trilophosaurus jacobsi* Murry, 1987 (e.g., Spielmann et al., 2008) or if *T. jacobsi* Murry, 1987 is a likely junior synonym of *Spinosuchus caseanus* Huene, 1932 (e.g., Nesbitt et al., 2015), we choose to differentiate these species names in the text for clarity until a future study thoroughly evaluates the taxonomy of the genus-level clade *Trilophosaurus* and its close relatives in the context of the wealth of recent data and newly-recognized trilophosaurid taxa (Pritchard and Sues, 2019; Kligman et al., 2020; Chambi-Trowell et al., 2022; Foffa et al., 2023; Kligman, 2023; Sues et al., 2022; Sues and Schoch, 2023; Marsh et al., 2024). Below, we provide catalog numbers for comparative specimens we have observed in person or via photographs and provide the appropriate citation for literature-based comparisons.

Institutional Abbreviations — **FMNH**, Field Museum of Natural History, Chicago, IL, U.S.A.; **GR**, Ruth Hall Museum of Paleontology at Ghost Ranch, Abiquiu, NM, U.S.A.; **ISIR**, Statistical Institute, Reptiles, Kolkata, India; **MNA**, Museum of Northern Arizona, Flagstaff, AZ, U.S.A.; **IITKGPR**, Indian Institute of Technology Kharagpur, Kharagpur, India; **IVPP**, Institute for Ver tebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **PEFO**, Petrified Forest National Park, Petrified Forest, AZ, U.S.A. (**PFV**, Petrified Forest vertebrate locality); **PIMUZ**, Paläontologisches Institut und Museum der Universidäd Zürich, Zurich, Switzerland; **TMM**, Texas Vertebrate Paleontology Collections, University of Texas Austin, Austin, TX, U.S.A.; **TTU**, Museum of Texas Tech University, Lubbock, TX, U.S.A., (**MOTT**, Museum of Texas

Tech locality); **UA**, Université d'Antannanarivo, Antannanarivo, Madagascar; **UCMP**, University of California Museum of Paleontology, Berkeley, CA, U.S.A.; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, MI, U.S.A.; **UWBM**, Burke Museum of Natural History and Culture, University of Washington, Seattle, WA, U.S.A.; **YPM**, Yale Peabody Museum, Yale University, New Haven, CT, U.S.A.

LOCALITY INFORMATION

Locality. — PFV 410/UWBM C2226 (Kaye Quarry), near Blue Mesa and Cedar Tank, Petrified Forest National Park (Fig. 1; Marsh and Parker, 2020: fig. 2b).

Stratigraphy. — Jim Camp Wash beds, Sonsela Member, Chinle Formation (Martz and Parker, 2010).

Age. — Late Triassic, Norian (Martz and Parker, 2010), ~213–215 Ma (Nordt et al., 2015; Ramezani et al., 2011; Rasmussen et al., 2020). Revueltian holochronozone (*sensu* Martz and Parker, 2017) based on a *Machaeroprosopus* skull (PEFO 54782/UWBM 120720) discovered in 2022 and found 0.5–1.0 m below the level of the quarry from about 30 meters away (*contra* Goncalves and Sidor, 2019). The Kaye Quarry itself is approximately 1.0–1.5 m below a silicified plant debris horizon cropping out extensively laterally known as the 'persistent red silcrete zone' that may approximate the Adamanian-Revueltian boundary at PEFO (Martz and Parker, 2010).

Sedimentology. — The locality consists of two major facies: 1) a purple overbank siltstone mottled with pale greenish yellow reduction halos that are often found around vertebrate bones; and 2) a white well-cemented conglomerate lens full of extra-basinal clasts and siltstone ripups that discontinuously incises into the purple silt stone (Sidor et al., 2018).Vertebrate bones are distributed throughout both facies, articulation is extremely rare, and most elements are disassociated.

Vertebrate assemblage. — PFV 410/UWBM C2226 is a multitaxic bonebed comprising at least 13 taxa, including metoposaurid temnospondyls, allokotosaurian and tanystropheid archosauromorphs, the archosauriform *Vancleavea campi*, phytosaurs, pseudosuchians, and ornithodirans (Sidor et al., 2018). This is the type locality of the drepanosauromorph *Ancistronychus paradoxus* Goncalves and Sidor (2019), represented by more than a dozen unguals from the second manual digit (holotype PEFO 42805/UWBM 117331). The site also includes a diverse ornithodiran fauna (Marsh and Parker, 2020), including a lagerpetid pterosauromorph (PEFO 42397/UWBM 116823), a silesaurid dinosauriform (PEFO 39373/UWBM 108379), a dinosaur in the *Chindesaurus bryansmalli* Long and Murry (1995)/*Tawa hallae* Nesbitt et al. (2009a) clade (PEFO 39273/UWBM 108212), and a neotheropod (PEFO 39421/UWBM 108881). Most notable, PFV 410/UWBM C2226 preserves hundreds of bones belonging to at least 21 individuals of a new species of shuvosaurid pseudosuchian (Sidor et al., 2018; Armour Smith et al., 2022).

SYSTEMATIC PALEONTOLOGY

ARCHOSAUROMORPHA Huene, 1946 *sensu* Benton, 1995

ALLOKOTOSAURIA

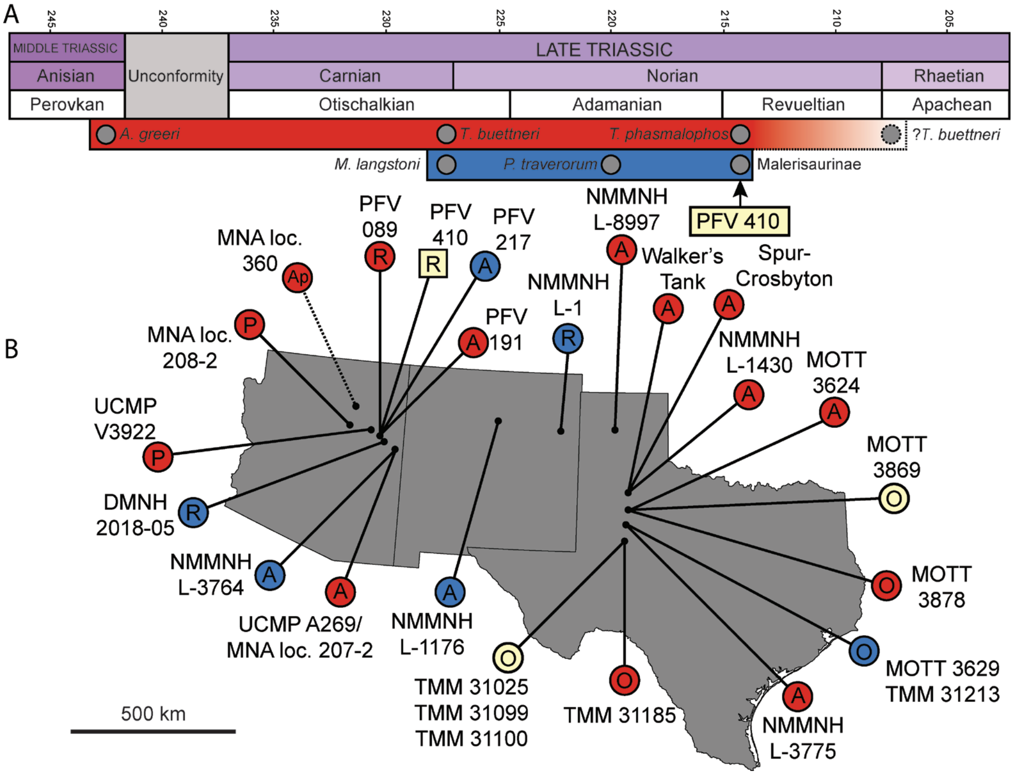

FIGURE 1. Geology and geography of selected allokotosaurians. A. Stratigraphic distribution of major localities that include trilophosaurids and malerisaurine azendohsaurids in the southwestern United States. B. Geographic distribution of major localities that include trilophosaurids and malerisaurine azendohsaurids in the southwestern United States. Red indicates trilophosaurids, blue indicates malerisaurines, and yellow indicates the presence of both at the same locality. Dashed lines indicate questioned occurrences. Map by Free Vector Maps: http://freevectormaps.com. Abbreviations: **A**, Adamanian; **Ap**, Apachean; **loc.**, fossil locality; **O**, Otischalkian; **P**, Perovkan; **R**, Revueltian.

Nesbitt, et al. 2015

Fig. 2

Voucher specimens. — PEFO 42757/UWBM 117283, left femur (Fig. 2A–F); PEFO 39375/UWBM 108381 (Fig. 2G–L), right tibia.

Rationale for identification. — The femur is sigmoidal in ventral view, has well-developed condyles distally, and has a prominent internal trochanter similar to other allokotosaurs like *Pamelaria dolichotrachela* Sen, 2003 (ISIR 316/55), *Azendohsaurus laaroussi* Dutuit, 1972 (MNHN-ALM 498/502, Cubo and Jalil, 2019), and *Trilophosaurus buettneri* (TMM 31025-140). The internal trochanter reaches the proximal end of the element (Fig. 2B) similar to *Malerisaurus robinsonae* (ISIR 150) and *Malerisaurus langstoni* (TMM 31099-11), some specimens of *Puercosuchus traverorum* (PEFO 44186; NMMNH P-60208), and and some *Trilophosaurus buettneri* specimens from TMM 31025 (Marsh et al., 2022). Nesbitt et al. (2021: fig. 7a) suggested that trilophosaurid and azendohsaurid femora can be differentiated on the proportion of the width of the femoral head to the maximum length of the femur, but the relatively short length (~111 mm) of PEFO 42757/UWBM 117283 occurs within the region of overlap in this proportion between the two clades.

The tibia PEFO 39375/UWBM 108381 is arched anteriorly like that of other allokotosaurs (e.g., *Azendohsaurus madagaskarensis*, FMNH PR 3814, Nesbitt et al., 2015). In proximal view, the proximal condyles are separated posteriorly by relatively deep concavity (Fig. 2K), similar to that of *Puercosuchus traverorum* (PEFO 44203) but not *Trilophosaurus buettneri* (TMM 31025-140). Unlike *Puercosuchus traverorum* (PEFO 44203), *Malerisaurus robinsonae* (ISIR 150), and *Malerisaurus langstoni* (TMM 31099-11), the tibia PEFO 39375/UWBM 108381 lacks the low tubercle on the medial side just below the proximal medial condyle (Marsh et al., 2022: fig. 16.13), similar to the tibiae of non-malerisaurine azendohsaurids (FMNH PR 2749) and *Trilophosaurus buettneri* (TMM 31025-140).

The non-allokotosaurian non-archosaur archosauromorphs at PFV 410 include tanystropheids and *Vancleavea campi*. The allokotosaur femur PEFO 42757/UWBM 117283 has a strong internal trochanter which is present in tanystropheids (TTU-P11344) but absent in *Vancleavea campi* (PEFO 2427). Unlike the allokotosaur tibia PEFO 39375/UWBM 108381 in which the proximal condyles are separated by a posterior groove, that margin is straight in *Vancleavea campi* (PEFO 2427) and is not well documented in tanystropheids. Considering that there is no unambiguous feature that would differentiate these two specimens between trilophosaurid and azendohsaurids, we can only refer these to Allokotosauria.

TRILOPHOSAURIDAE Gregory, 1945 *sensu* Nesbitt et al., 2015

Fig. 3A–J

Voucher specimens. — PEFO 39521/UWBM 109860, right postorbital (Fig. 3A); PEFO 54629/UWBM 120532, right fifth metatarsal (Fig. 3B–D); PEFO 39554/UWBM 109893, partial left calcaneum (Fig. 3E–H); PEFO 47371/UWBM 119655, cervical vertebra (Fig. 3I); PEFO 54931/UWBM 124160, five articulated posterior cervical vertebrae (Fig. 3J).

Rationale for identification. — The postorbital is triradiate and includes a prominent curved rim around the posterior margin of the orbit (Fig. 3A). In *Pamelaria dolichotrachela* (ISIR 316/1, Sen, 2003) and *Puercosuchus traverorum* (PEFO 47823), the lateral surface of the postorbital forms an isosceles triangle with the more acute apex pointing ventrally, whereas in PEFO 42365/UWBM 116791, *Trilophosaurus buettneri* (TMM 31025-140), and *Trilophosaurus jacobsi* (NMMNH P-41400) it forms more of an equilateral triangle. It lacks the bifurcated articulation with the jugal like that of *Vancleavea campi* (GR 138) and the strap-like shape found in *Tanystropheus hydroides* (PIMUZ T 2790, Spiekman et al., 2020). Like other archosauromorphs, the fifth metatarsal is hook-shaped and forms a ‘paddle’ that articulates medially with the rest of the metatarsus. The element lacks the proximal dorsal tubercle found in *Puercosuchus traverorum* (PEFO 44359) and the proximal process is relatively long like that of *Trilopho-*

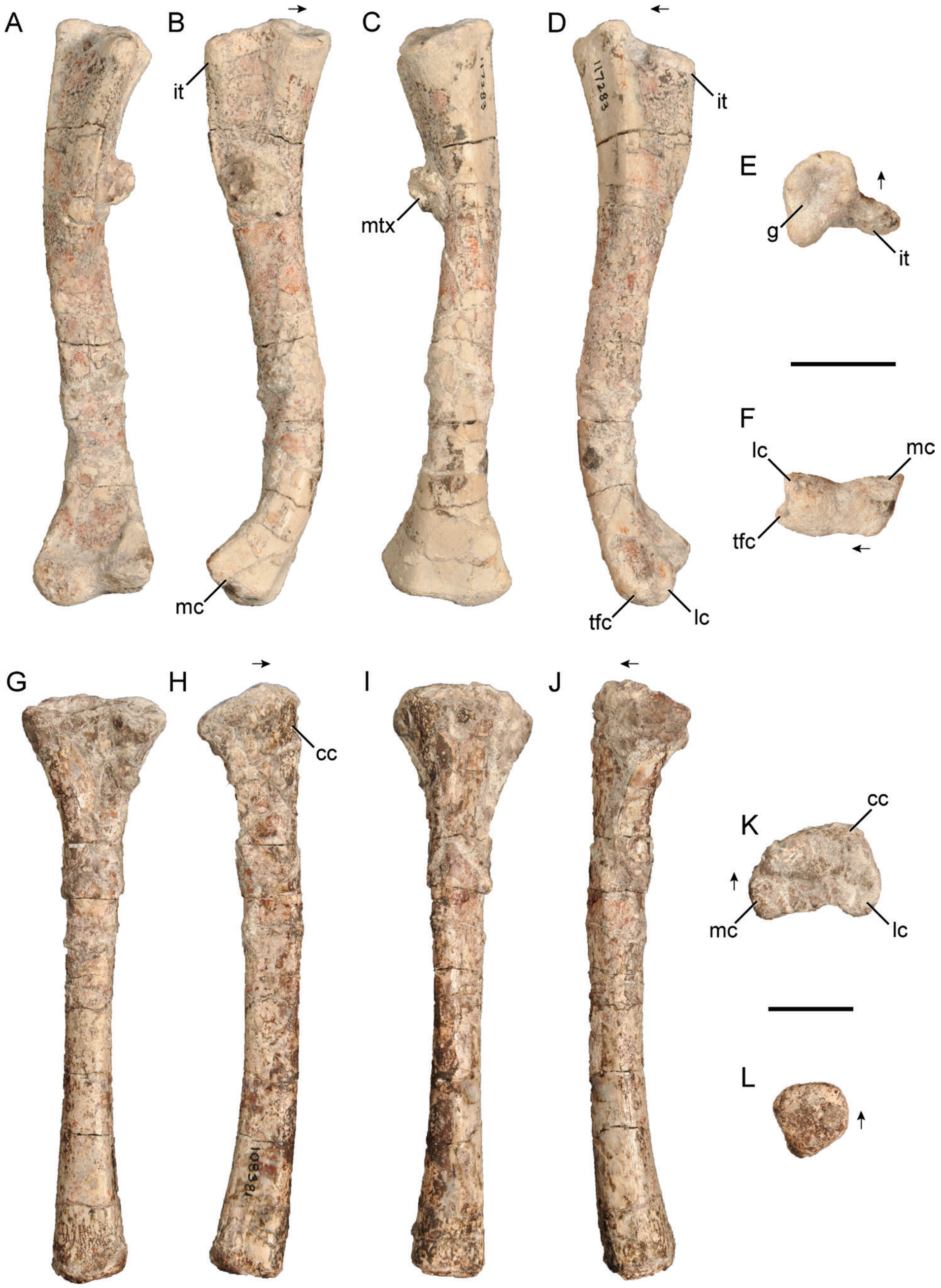

FIGURE 2. Allokotosauria specimens from the Kaye Quarry (PFV 410). A–F. PEFO 42757/UWBM 117283, left femur in A, posteroventral, B, ventral, C, anterodorsal, D, dorsal, E, proximal, and F, distal view; G–K. PEFO 39375/UWBM 108381, right tibia in G, posterior, H, lateral, I, anterior, J, medial, K, proximal, and L, distal view. Arrows point in anterior direction. Scale bars = 2 cm. Abbreviations: **cc**, cnemial crest; **g**, groove; **it**, internal trochanter; **lc**, lateral condyle; **mc**, medial condyle; **mtx**, matrix; **tfc**, tibiofibular crest.

saurus buettneri (TMM 31025). It has a ridge on the dorsolateral margin of the distal end (Fig. 3B) like that in *Trilophosaurus buettneri* (TMM 31025-140), *Azendohsaurus madagaskarensis* (FMNH PR 2776), and *Puercosuchus traverorum* (PEFO 44359).

Like metatarsal V of *Trilophosaurus buettneri*, in which the ratio of the mediolateral width to proximodistal length is 0.66, that of PEFO 54629/UWBM 120532 is 0.67, unlike the relatively shorter fifth metatarsal of *Puercosuchus traverorum* (0.88; PEFO 44359). This specimen is proximodistally shorter compared to its mediolateral width in *Vancleavea campi* (GR 138) and the tanystropheid *Macrocnemus fuyuanensis* (IVPP V 15001, Scheyer et al., 2020).

The calcaneum PEFO 39554/UWBM 109893 only preserves the proximolateral portion, so the shape of the distal and medial edges cannot be estimated. In proximal view (Fig. 3G), both articular surfaces for the astragalus are present. In ventral view (Fig. 3F), the angle formed by the articular surface for distal tarsal 4 and the dorsal articular surface for the astragalus is similar to that of *Trilophosaurus buettneri* (TMM 31025-140) in that it is much less acute than that of *Puercosuchus traverorum* (PEFO 44141) and the tanystropheid *Macrocnemus fuyuaensis* (IVPP V 15001, Spiekman et al., 2020). The calcaneum of *Vancleavea campi* is a more simple paddle-shaped element (GR 138, Nesbitt et al., 2009).

The middle cervical vertebra PEFO 47371/UWBM 119655 (Fig. 3I) is similar to other allokotosaurs in that the diapophysis and parapophysis are situated close to one anther on the anterior end of the centrum, and the latter has a longitudinal ridge extending posteriorly. The neural spine is tall (unlike the middle to posterior cervical vertebrae of the tanystropheid *Tanytrachelos ahynis*, YPM 7496, Olsen, 1979) and inclined anterodorsally but lacks the lateral dorsal expansion found in the malerisaurines *Puercosuchus traverorum* (PEFO 43992) and *Malerisaurus robinsonae* (ISIR 150, Sengupta et al., 2024). The posterior articular surface of the centrum has a shallow concave center surrounded by a raised rim and is not as convex as the cervical vertebrae of *Trilophosaurus buettneri* (TMM 31025-140) or *Trilophosaurus jacobsi* (NMMNH P-44274).

The articulated vertebrae PEFO 54931/UWBM 124160 (Fig. 3J) are considered posterior cervical vertebrae because the parapophysis is on the centrum in each of the vertebrae and the diapophysis moves from being on a short process near the parapophysis on the anterior portion of the centrum to a laterally-projecting stalk near the midpoint of the centrum. The anteriormost centrum is similarly shaped to PEFO 47371/UWBM 119655 described above (Fig. 3I), and it exhibits the same anatomical features that identify it to the Trilophosauridae. In cross section near the dorsal end of the neural spine, the anteriormost vertebra is blade-like, but in each successive posterior the spine expands slightly such that the posteriormost vertebra is cruciform in shape (Fig. 3J). This shape is different than that found in the same region of the malerisaurine *Puercosuchus traverorum* (e.g., PEFO 44265, Marsh et al., 2022) in which the lateral expansions are separated from the main body of the neural spine by sharp clefts. Dorsal expansions of the posterior cervical neural spines are not documented in any species of *Trilophosaurus*, but they are found in *Azendohsaurus madagaskarensis* (e.g., UA 8-30-98-349, Nesbitt et al., 2015) and *Shringasaurus indicus* (ISIR 803, Sengupta and Bandyopadhyay, 2022). Unaccounted-for elaboration of trilophosaurid neural spines is possible, however, as those of *Spinosuchus caseanus* (Spielmann et al., 2009) are known for a radical anatomical departure from the plesiomorphic archosauromorph condition.

TRILOPHOSAURUS PHASMALOPHOS Kligman et al., 2020

Figs. 3K–N

Voucher specimens. — PEFO 47420/UWBM 119740, isolated tooth (Fig. 3K–L); PEFO 42365/UWBM 116791, left maxilla (Fig. 3M–N).

Rationale for identification. —Previously, the only specimens known from this taxon were isolated teeth, diagnosed by a unique combination of characters and autapomorphies (the latter are marked with an asterisk below; Kligman et al., 2020: p. 28): "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*." All these features are present in PEFO 47420/UWBM 119740 (Fig. 3K) and the posterior two teeth of PEFO 42365/UWBM 116791 (Fig. 3M), allowing the specimen to be referred to *Trilophosaurus phasmalophos*. However, the three anterior partially preserved teeth clearly have three cusps (Fig. 3M) and some of the apomorphies listed above. It seems that moving anteriorly, the central ridge extending lingually from the lingual cusp becomes more prominent apically, eventually forming an additional, more lingual cusp. This specimen will be important in understanding serial variation in some trilophosaurid teeth, especially with similar variation present in earlier-diverging members of the clade (Chambi-Trowell et al., 2021; Foffa et al., 2023).

AZENDOHSAURIDAE Nesbitt et al., 2015

MALERISAURINAE Nesbitt et al., 2021

Figs. 4–5

Voucher specimens. — PEFO 46902/UWBM 118796, right premaxilla (Fig. 4A); PEFO 39376/UWBM 108382, left maxilla (Fig. 4C); PEFO 47450/UWBM 119770, right prefrontal (Fig. 4E); PEFO 39556/UWBM 109895, ventral end of left quadrate (Fig. 4F–G); PEFO 39558/UWBM 109897, ventral end of left quadrate (Fig. 4H–I); PEFO 39429/UWBM 108889, left humerus (Fig. 5A–F); PEFO 39436/UWBM 108896, proximal end of left ulna (Fig. 5G–H); PEFO 39544/UWBM 109883, partial right astragalus (Fig. 5I–K); PEFO 47459/UWBM 119779, ungual (Fig. 5L–O).

Rationale for identification. — Unlike *Trilophosaurus buttneri* (TMM 31025-207), the premaxilla bears teeth and lacks a 'beak.' It is very similar to those of malerisaurines (e.g., PEFO 43914, TTU-P11212) and other azendohsaurids (e.g., *Shringasaurus indicus*, ISIR 793, Sengupta and Bandyopadhyay, 2022) in that the posterodorsal process is relatively long and it lacks an anterodorsal process (Nesbitt et al., 2021; Marsh et al.,

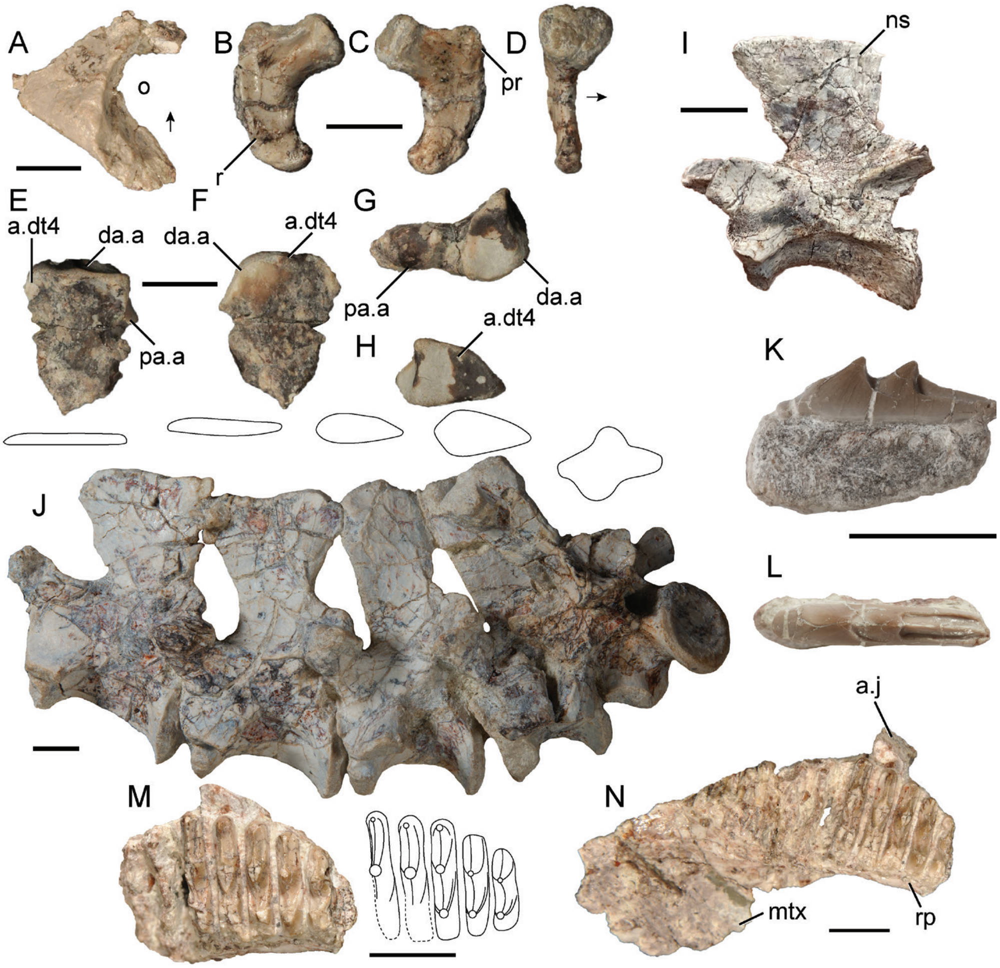

FIGURE 3. Trilophosaurid specimens from the Kaye Quarry (PFV 410). A. PEFO 39521/UWBM 109860, trilophosaurid right postorbital in lateral view; B–D. PEFO 54629/UWBM 120532, trilophosaurid right metatarsal V in B, dorsal, C, ventral, and D, proximal view; E–H. PEFO 39554/UWBM 109893, partial trilophosaurid left calcaneum in E, dorsal, F, ventral, G, proximal, and H, medial view; I. PEFO 47371/UWBM 119655, trilophosaurid middle cervical vertebra in left lateral view; J. PEFO 54931/UWBM 124160, five posterior neck vertebrae in lateral view with interpretive drawings of the dorsal cross sections of the each neural spine; K–L; PEFO 47420/UWBM 119740, *Trilophosaurus phasmalophos* tooth in K, distal and L, occlusal view; M–N. PEFO 42365/UWBM 116791, *Trilophosaurus phasmalophos* left maxilla in M, occlusal view with interpretive line drawing and N, ventral view. Arrows point in dorsal direction. Scale bars = 1 cm. Abbreviations: **a.j**, articular surface with jugal; **a.dt4**, articular surface for distal tarsal 4; **da.a**, distal articular surface for astragalus; **mtx**, matrix; **ns**, neural spine; **o**, orbit; **pa.a**, proximal articular surface for astragalus; **pr**, proximal process; **rp**, resorption pit.

2022). The premaxilla in tanystropheid *Tanystropheus hydroides* also lacks an anterodorsal process, but the element is anteroposteriorly longer compared to its dorsoventral height in that taxon (PIMUZ T 2790, Spiekman et al., 2020). The archosauriform *Vancleavea campi* has an anterodorsal process that separates the external nares medially (GR 138). The single tooth preserved in PEFO 46902/UWBM 118796 is slightly procumbent like that of *Azendohsaurus madagaskarensis* (FMNH PR 2751) and *Puercosuchus traverorum* (PEFO 43914). The angle formed by the ventral margin of the element and the posterodorsal process is relatively steep in PEFO 46902/UWBM 118796 (33°; Fig. 4A) compared to the more acute angle present in *Puercosuchus traverorum* (14°, PEFO 43914; Fig 4B).

The maxilla preserves a prominent posterodorsal process with a posteroventral concavity (Fig. 4C), shared in *Azendohsaurus laaroussii* (MNHN-ALM 355-3, Dutuit, 1972), *Azendohsaurus madagaskarensis* (FMNH PR 2751), and malerisaurines (e.g., PEFO 43914).

The overall shape of the maxilla is more similar to that of tanystropheids (e.g., PIMUZ T 2790) than that *Vancleavea campi* which lacks a long anterior process (GR 138), but the teeth of tanystropheids are not ankylothecodont like those of allokotosaurs. Unlike trilophosaurids and non-malerisaurine azendohsaurids, PEFO 39376/UWBM 108382 preserves triangular, labiolingually compressed teeth with fine serrations and apical recurvature, like other malerisaurines (Nesbitt et al., 2011). However, unlike in *Puercosuchus traverorum* (PEFO 43914; Fig. 4D), the teeth in PEFO 39376/UWBM 108382 are all the same basic shape (Fig. 4C). Whether this indicates an autapomorphy of a new taxon or a plesiomorphy of malerisaurines is uncertain, as the holotype specimen of *Malerisaurus langstoni* (TMM 31099-11) and hypodigm of *Malerisaurus robinsonae* (ISIR 150, ISIR 151) do not preserve maxillary teeth.

The prefrontal is triradiate and forms the anterodorsal margin of the orbit, like in other reptiles (Fig. 4E). Like *Azendohsaurus madagaskarensis* (FMNH PR 2751) and *Puercosuchus traverorum* (PEFO 43991), the dorsolateral margin is thickened and slightly rugose, unlike the relatively smooth but still thickened margin found in *Trilophosaurus buettneri* (TMM 31025-143) and *Trilophosaurus jacobsi* (NMMNH P-41400). The orbital rim of the prefrontal of some tanystropheids (e.g., PIMUZ T 2790, Spiekman et al., 2020) and *Vancleavea campi* (GR 138) is sharp rimmed rather than thickened. The two ventral ends of the quadrate are typical of those of azendohsaurids (e.g., *Azendohsaurus madagakarensis*, FMNH PR 2751, *Pamelaria dolichotrachela*, ISIR 328/1, Sen, 2003; Nesbitt et al., 2021) in that they are asymmetrical (unlike *Trilophosaurus buettneri*, TMM 31025-140), such that the posterior condyle is offset ventrally from the rest of the articular surface (Fig. 4F–I).

The humerus is expanded mediolaterally both proximally and distally like that of azendohsaurids (Nesbitt et al., 2021); unfortunately, the midshaft is missing, preventing the calculation of the ratio of the proximal width to the total length to better differentiate it between a malerisaurine and a trilophosaurid (sensu Nesbitt et al., 2021: fig. 7b). Luckily, the specimen preserves features found only in azendohsaurids (e.g., *Azendohsaurus madagaskarensis*, FMNH FR 3816; ‘*Otischalkia elderae*’, TMM 31025-263; *Puercosuchus traverorum*, PEFO 38627) like a prominent supinator crest distally

(Fig. 5A), prominent proximal lateral tuberosity (Fig. 5C) that reaches the proximal extent of the humeral head TMM 31099-11, ISIR 150), and a pyramidal process on the dorsal surface next to the ectepicondyle (FMNH PR 3816, PEFO 38627, TMM 31099-11), best seen in distal view (Fig. 5F). The humeri of tanystropheids (e.g., IVPP V 15001, Scheyer et al., 2020; YPM 7496, Olsen, 1979) and *Vancleavea campi* (PEFO 34035) are much more gracile than those of allokotosaurs.

In proximal view, the ulna has a prominent concavity between the olecranon process and the anteromedial process (Fig. 5H), unlike the relatively flat margin found in *Trilophosaurus buettneri* (TMM 31025-140) and *Azendohsaurus madagaskarensis* (FMNH PR 3816), but more similar to what is found in the malerisaurines *Puercosuchus traverorum* (PEFO 44131, NMMNH P-63289). PEFO 39436/UWBM 108896 lacks the secondary ossification of the olecranon process found in some malerisaurines (Marsh et al., 2022), but the proximal surface of that process is rugose and likely had a cartilaginous articular surface. The olecranon process is much more prominent in malerisaurines than that of tanystropheids (e.g., *Macrocnemus fuyuanensis*, IVPP V 15001, Scheyer et al., 2020) and *Vancleavea campi* (PEFO 34035).

The partial astragalus only preserves the proximal half of the element, including the articular surface with the tibia and the dorsal articulation with the calcaneum (Fig. 5I–K). In distal view (Fig. 5J), the dorsal articular surface for the calcaneum is rounded like that of *Azendohsaurus madagaskarensis* (FMNH PR 2776) and *Puercosuchus traverorum* (PEFO 44140) whereas it is subtriangular in *Trilophosaurus buettneri* (TMM 31025-140). The astragalus of *Vancleavea campi* only has one articular surface for the calcaneum (GR 138, Nesbitt et al., 2009). The anterior hollow (Fig. 5I) is relatively deep like that of *Puercosuchus traverorum* (PEFO 44140) compared to that of *Trilophosaurus buettneri* (TMM 31025-140).

The ungual (Fig. 5L–O) is highly mediolaterally compressed, flat along its ventral surface, and has bilateral grooves extending down the lateral and medial sides of the element. It is unclear as to whether it represents an ungual from the manus or pes, however it likely belongs to an allokotosaurian because it is much more mediolaterally compressed than those found in the ornithodiran taxa present at PFV 410 (Nesbitt et al., 2011; Marsh and Parker, 2020). In addition, it is similar to unguals in *Trilophosaurus buettneri* (TMM 31025-140) and *Azendohsaurus madagakarensis* (UA 9-8-98-497), and it clearly lacks the unique dorsoventrally compressed anatomy found in shuvosaurid pedal unguals (Nesbitt, 2007). PEFO 47459/UWBM 119779 has a prominent flexor tubercle like that of *Trilophosaurus buettneri* (TMM 31025-140), but like that of *Azendohsaurus madagaskarensis* (UA 9-8-98-497) the tubercle is positioned more distal to the proximal articular surface (Nesbitt et al., 2015). The angle of curvature (*sensu* Feduccia, 1993) of PEFO 47459/UWBM 119779 is 100°, which is more similar to that of *Azendohsaurus madagaskarensis* (95°–125°; Nesbitt et al., 2015) than *Trilophosaurus buettneri* (106°–155°; Spielmann et al., 2008). At the time of publication of Marsh et al. (2022), no unguals were known from *Puercosuchus traverorum*, but a few have now been recovered and prepared from the type locality (PEFO 44138, PEFO 44139, PEFO 44343, PEFO 47777, PEFO 52337). These range in angle of curvature from 60°–105° (overlapping with that of PEFO 47459/

UWBM 119779), and like what was noted for *Azendohsaurus madagaskarensis* (Nesbitt et al., 2015), the angle tends to be higher in larger unguals of *Puercosuchus traverorum*. The angle of curvature is much less in tanystropheids (e.g., *Macrocnemus fuyuanensis*, IVPP V 15001, Scheyer et al., 2020) but is not documented for *Vancleavea campi*.

DISCUSSION

Prior to the discovery of both trilophosaurids and malerisaurine azendohsaurids in PFV 410 at Petrified Forest National Park, both clades were only found together in two Otischalkian localities in western Texas (Fig. 1B; Appendix 1): 1) three of the Otis Chalk quarries in Howard County (Quarry 1: TMM 31025; Quarry 2: TMM 31099; Quarry 3; TMM 31100), which preserve both *Trilophosaurus buettneri* (e.g., TMM 31025-140) and *Malerisaurus langstoni* (i.e., TMM 31099-11) in the Colorado City Formation; and 2) MOTT 3869 (Boren Quarry) in the lower part of the Cooper Canyon Formation in Garza County, which preserves *Trilophosaurus dornorum* (e.g., TTU-P10413) and a malerisaurine (e.g., TTU-P10515). Depending on whether or not *Trilophosaurus jacobsi* is a junior synonyn of *Spinosuchus caseanus* (Nesbitt et al., 2015), each trilophosaurid-only locality contains a single trilophosaurid taxon (with the exception of NMMNH L-1430 in the Tecovas Formation of Crosby County, Texas, which preserves both *Trilophosaurus buettneri* and *Trilophosaurus jacobsi*; Spielmann et al., 2018), a pattern that seems to be paralleled in malerisaurine-only localities, again, depending on if '*Otischalkia elderae*' is a large morph of *Malerisaurus langstoni* in the Otis Chalk quarries of Howard County, Texas (Nesbitt et al., 2021).

Thus, PFV 410 represents only the third place in the southwestern United States in which trilophosaurids and malerisaurine azendohsaurids co-occur in the same locality. Not only that, but PFV 410 is Revueltian in age, meaning malerisaurines persisted after the hypothesized Adamanian-Revueltian biotic turnover (Parker and Martz, 2010) and that the two allokotosaurian lineages may have co-occurred for more than 10 Ma across the Chinle Formation-Dockum Group depobasin (Fig. 1A). Both clades seem to disappear early in the Revueltian as they are present in a handful of sites in the upper part of the Jim Camp Wash beds of the Sonsela Member (Chinle Formation; Kligman et al., 2020; this study). However, there is a disputed occurrence of a fragmentary *Trilophosaurus buettneri* tooth (MNA V7064) from the Apachean Owl Rock Member on Ward Terrace, Arizona (MNA loc. 360; Kirby, 1991). Some authors question the trilophosaurid affinities of this specimen and its collection methodologies (e.g., Heckert et al., 2006), but given the regional Middle Triassic occurrences (Foffa et al., 2023) and high recovery of trilophosaurid teeth through much of the Chinle Formation (Mueller and Parker, 2006; Spielmann et al., 2008; Kligman et al., 2022), only increased microvertebrate sampling of Owl Rock Member localities will help to determine if trilophosaurids persisted into the Apachean.

A survey of the lithologies and depositional environments of global allokotosaur occurrences is beyond the scope of this contribution, but such a treatment may provide some insight on any environmental, biogeographic, or paleobio logical reasons that azendohsaurids and trilophosaurids do not co-occur more

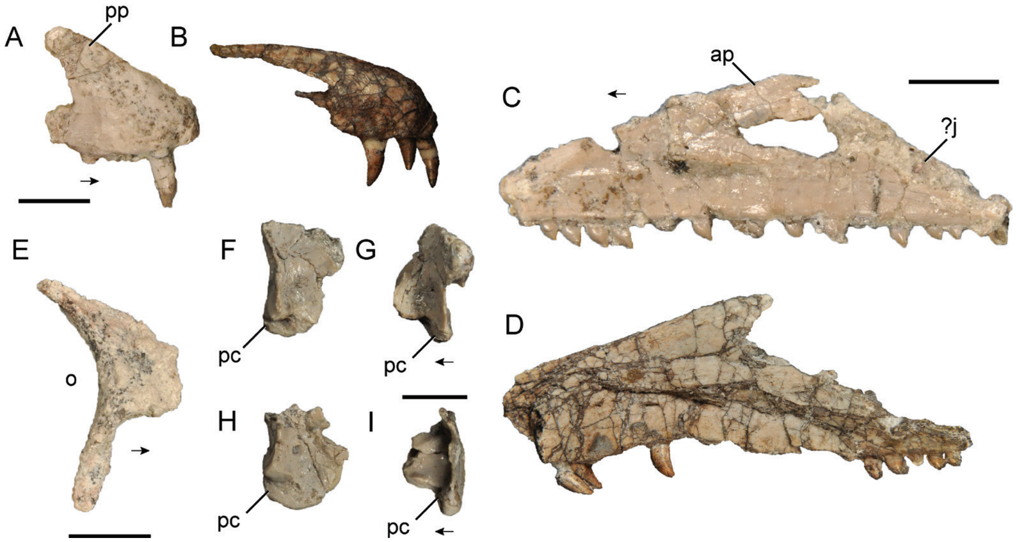

FIGURE 4. Malerisaurine cranial specimens. A. PEFO 46902/UWBM 118796, right premaxilla in lateral view; C. PEFO 39376/UWBM 108382, left maxilla in lateral view; E. PEFO 47450/UWBM 119770, right prefrontal in lateral view; F–G. PEFO 39556/UWBM 109895, ventral end of left quadrate in F, anterior and G, medial view; H–I. PEFO 39558/UWBM 109897, ventral end of left quadrate in H, anterior and I, medial view. B. Comparative holotype right premaxilla of *Puercosuchus traverorum* (PEFO 43914) in lateral view. D. Comparative holotype right maxilla of *Puercosuchus traverorum* (PEFO 43914, reversed) in lateral view. Arrows point in anterior direction. Scale bars = 1 cm labelled, B and D are not to scale. Abbreviations: **ap**, ascending process; **j**, jugal; **o**, orbit; **pc**, posterior condyle; **pp**, posterior process.

frequently in the fossil record. At present the observed lack of co-occurrences of these clades within the same locality is probably best explained by sampling methods. Important representative allokotosaur taxa have been described from monodominant bonebeds (e.g., *Trilophosaurus buettneri*, Gregory, 1945; *Trilophosaurus jacobsi*, Heckert et al., 2006; *Azendohsaurus madagaskarensis*, Flynn et al.2010; *Shringasaurus indicus*, Sengupta et al., 2017; *Puercosuchus traverorum*, Marsh et al., 2022). However, allokotosaurs are also known from microsites (e.g., Heckert et al., 2004; Cawthorne et al., 2024), but identified allokotosaurs from those sites have exclusively been trilophosaurids. This is likely because trilophosaurid teeth are more recognizable and divergent in anatomy to those of most other contemporary reptiles. Further, non-malerisaurine azendohsaurid teeth have been mistaken for ornithischian or sauropodomorph dinosaur teeth in the past (e.g., Dutuit, 1972; Gauffre, 1993), and those of malerisaurines have also been confused for ornithischian or sauropodomorph dinosaurs (Marsh et al., 2022) or have relatively plesiomorphic tooth shapes (see PEFO 39376/UWBM 108382 above; Fig. 4C). For example, Ray et al. (2016) referred isolated teeth from the Upper Triassic Tiki Formation of India to an "indeterminate theropod" (fig. 7c–d). However, IITKGPR404A looks remarkably similar to teeth in the he anterior regions of the maxillae and dentaries of the hypodigm

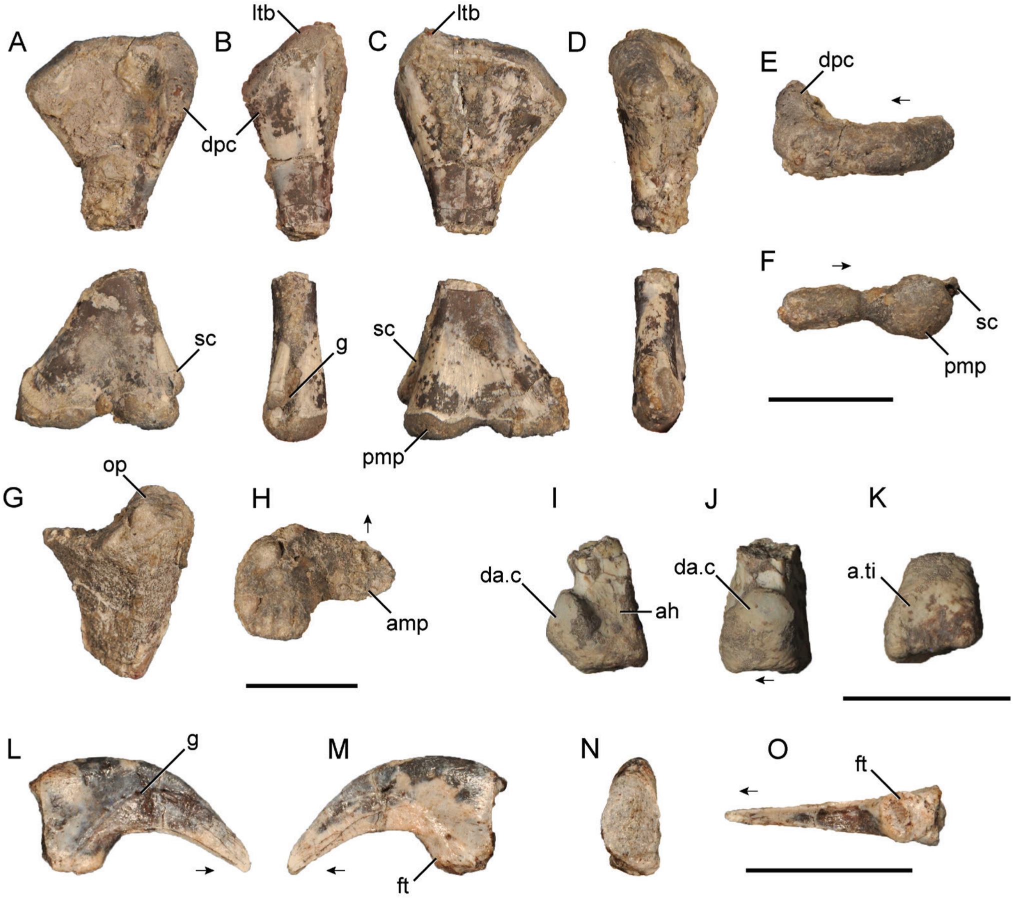

FIGURE 5. Malerisaurine postcranial specimens from the Kaye Quarry (PFV 410). A–F. PEFO 39429/UWBM 108889, left humerus in A, ventral, B, lateral, C, dorsal, D, medial, E, proximal, and F, distal view; G–H. PEFO 39436/UWBM 108896, proximal end of left ulna in G, anterior and H, proximal view; I–K. PEFO 39544/UWBM 109883, partial right astragalus in I, dorsal, J, distal, and K, medial view; L–O. PEFO 47459/UWBM 119779, ungual in L–M, medial or lateral view, N, proximal, and O, ventral view. Arrows point in anterior direction. Scale bars = 2 cm. Abbreviations: **a.ti**, articular surface for tibia; **ah**, anterior hollow; **amp**, anteromedial process; **da.c**, distal articular surface for calcaneum; **dpc**, deltopectoral crest; **ft**, flexor tubercle; **g**, groove; **ltb**, lateral tuberosity; **op**, olecranon process; **pmp**, pyramidal process; **sc**, supinator crest.

of *Puerosuchus traverorum* (e.g., PEFO 43914, PEFO 38606; Marsh et al., 2020: fig. 3), and theropod postcrania from the Tiki Formation have only been mentioned in the literature anecdotally (Chatterjee and Majumdar, 1987; Ray et al., 2016; Marsh and Parker, 2020). Finally, microvertebrate sampling of fossiliferous Upper Triassic continental deposits has vastly outpaced that of Middle Triassic units, and further sampling of the latter interval in the Moenkopi Formation of the American Southwest (Foffa et al., 2023), the Economy Member of the Wolfville Formation in Nova Scotia, Canada (Sues et al. 2022), the Erfurt Formation from southwestern Germany (Sues and Schoch, 2023), the Lifua Member of the Manda beds in Tanzania (Smith et al., 2017), and the Denwa Formation, Yerrapalli Formation, and Bhimaram Formation of India (Bandyopahhyay and Sengupta, 1999) may help recover older azendohsaurids and trilophosaurids from the same localities.

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APPENDIX 1. Major occurrences of trilophosaurid and malerisaurine azendohsaurids in the southwestern United States to accompany Figure 1. Localities are arranged in approximately stratigraphic order, with oldest sites listed first. Type localities are indicated with an asterisk.

Locality	Formation, Member, Holochronozone	State, County	Trilophosaurid taxa present	Malerisaurine taxa present	References
UCMP V3922 (Holbrook Quarry)	Moenkopi Formation, Holbrook Member, Perovkan	AZ, Navajo	*Anisodontosaurus greeri**	N/A	Welles, 1947; Foffa et al., 2023
MNA loc. 208-2 (Radar Mesa)	Moenkopi Formation, Holbrook Member, Perovkan	AZ, Coconino	*Anisodontosaurus greeri*	N/A	Welles, 1947; Foffa et al., 2023
MOTT 3869 (Boren Quarry)	lower Cooper Canyon Formation, Otischalkian	TX, Garza	*Trilophosaurus dornorum*	Malerisaurinae indet.	Parker and Mueller, 2006; Spielmann et al., 2008; Sarigül, 2017; Marsh et al., 2022
MOTT 3878 (Lott Hill)	lower Cooper Canyon Formation, Otischalkian	TX, Garza	*Trilophosaurus dornorum*	N/A	Parker and Mueller, 2006; Spielmann et al., 2008
MOTT 3629; TMM 31213 (Griffin Ranch)	lower Cooper Canyon Formation, Otischalkian	TX, Borden	N/A	Malerisaurinae indet.	Nesbitt et al., 2021
TMM 31025 (Otis Chalk Quarry 1); TMM 31099 (Otis Chalk Quarry 2); TMM 31100 (Otis Chalk Quarry 3)	Colorado City Formation, Otischalkian	TX, Howard	*Trilophosaurus buettneri*	*Malerisaurus langstoni**/ *'Otischalkia elderae'*	Gregory, 1945; Chatterjee, 1986; Nesbitt et al., 2021
TMM 31185 (Otis Chalk Quarry 3A)	Colorado City Formation, Otischalkian	TX, Howard	*Trilophosaurus buettneri*	N/A	Gregory, 1945

APPENDIX 1. (*continued*)

Locality	Formation, Member, Holochronozone	State, County	Trilophosaurid taxa present	Malerisaurine taxa present	References
NMMNH L-3775 (Kahle Quarry)	middle Cooper Canyon Formation, Adamanian	TX, Borden	*Trilophosaurus jacobsi/ Spinosuchus caseanus*	N/A	Spielmann et al., 2008; Nesbitt et al., 2015
MOTT 3624 (Post Quarry)	upper part of lower Cooper Canyon Formation, Adamanian	TX, Garza	*Trilophosaurus dornorum*	N/A	Parker and Mueller, 2006; Martz et al., 2013
UMMP Walker's Tank locality	Tecovas Formation, Adamanian	TX, Crosby	*Trilophosaurus buettneri**	N/A	Case, 1928
UMMP Spur-Crosbyton locality	Tecovas Formation, Adamanian	TX, Crosby	*Spinosuchus caseanus**	N/A	Von Huene, 1932; Spielmann et al., 2009; Nesbitt et al., 2015
NMMNH L-1430 (Upper Kalgary)	Tecovas Formation, Adamanian	TX, Crosby	*Trilophosaurus buettneri*; *Trilophosaurus jacobsi*	N/A	Spielmann et al., 2008
NMMNH L-8997 (Rotten Hill)	Tecovas Formation, Adamanian	TX, Potter	*Trilophosaurus jacobsi/ Spinosuchus caseanus*	N/A	Spielmann et al., 2009; Nesbitt et al., 2015
NMMNH L-1176 (Lamy Quarry)	lower Garita Creek Formation, Adamanian	NM, Santa Fe	N/A	Malerisaurinae indet.	Hégron et al., 2020
NMMNH L-1 (Revuelto Creek)	Bull Canyon Formation	NM, Quay	N/A	Malerisaurinae indet.	Spielmann et al., 2013
UCMP A269/ MNA loc. 207-2 (*Placerias* Quarry)	Chinle Formation, lower Sonsela Member, Adamanian	AZ, Apache	*Trilophosaurus jacobsi**	N/A	Murry, 1987; Kligman et al., 2020

APPENDIX 1. (*continued*)

Locality	Formation, Member, Holochronozone	State, County	Trilophosaurid taxa present	Malerisaurine taxa present	References
NMMNH L-3764 (Krzyzanowski bonebed)	Chinle Formation, lower Blue Mesa Member, Adamanian	AZ, Apache	N/A	*Puercosuchus traverorum*	Heckert et al., 2001; Heckert et al., 2004; Marsh et al., 2022
PFV 191 (Flag Canyon)	Chinle Formation, lower Sonsela Member, Adamanian	AZ, Apache	*Trilophosaurus dornorum**	N/A	Mueller and Parker, 2006
PFV 217 (Dinosaur Wash)	Chinle Formation, upper Blue Mesa Member, Adamanian	AZ, Apache	N/A	*Puercosuchus traverorum**	Marsh et al., 2022
DMNH 2018-05 (Green Site)	Chinle Formation, upper Sonsela Member, Revueltian	AZ, Apache	*Trilophosaurus phasmalophos*	N/A	Kligman et al., 2020
PFV 089 (Bowman Locality)	Chinle Formation, upper Sonsela Member, Revueltian	AZ, Navajo	*Trilophosaurus phasmalophos**	N/A	Kligman et al., 2020
PFV 410 (Kaye Quarry)	Chinle Formation, upper Sonsela Member, Revueltian	AZ, Apache	*Trilophosaurus phasmalophos*	Malerisaurinae indet.	Sidor et al., 2018; this study.
MNA 360 (Ward Terrace)	Chinle Formation, Owl Rock Member, Apachean	AZ, Coconino	*Trilophosaurus buettneri* (questioned occurrence)	N/A	Kirby, 1991; Spielmann et al., 2008; Marsh et al., 2018

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