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ARTICLE

FIRST OCCURRENCE OF *DOSWELLIA* CF. *D. KALTENBACHI* (ARCHOSAURIFORMES) FROM THE LATE TRIASSIC (MIDDLE NORIAN) CHINLE FORMATION OF ARIZONA AND ITS IMPLICATIONS ON PROPOSED BIOSTRATIGRAPHIC CORRELATIONS ACROSS NORTH AMERICA DURING THE LATE TRIASSIC

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ABSTRACT—*Doswellia kaltenbachi* is a long-snouted non-archosaur archosauriform known from the Late Triassic of the United States (Virginia and Texas). New material from the Chinle Formation of Arizona represents the first occurrence of *D.* cf. *D. kaltenbachi* from that formation and state. This occurrence is from the type section for the Adamanian estimated holochronozone (Late Triassic: middle Norian) in Petrified Forest National Park and firmly establishes the presence of this taxon in the Adamanian. This occurrence adds to the diverse vertebrate assemblage of the upper part of the Blue Mesa Member of the Chinle Formation (Adamanian). More broadly, the new occurrence strengthens biogeographic links to the older (latest Carnian or earliest Norian) Otischalkian from Texas and the possibly older Sanfordian/Conewagian assemblages of Virginia. The spatiotemporal distribution of *Doswellia* underscores the similarity of North American continental vertebrate assemblages across the Carnian–Norian boundary prior to the Adamanian–Revueltian boundary.

Q2 Q1 SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Convincing support for the theory of continental drift (e.g., Du Toit, 1937; Wegener, 1966) and recognition of the existence and composition of the supercontinent Pangea during the late Paleozoic and early Mesozoic was based in part on the biostratigraphy and biogeography of fossil vertebrates (Colbert, 1958, 1971; Elliot et al., 1970). The continuity of major land masses during the Triassic Period led to the hypothesis of a cosmopolitan distribution of vertebrate taxa across Pangea (e.g., Colbert, 1974; Cox, 1974; Cracraft, 1974), including the development of the first global biostratigraphic schemes for dating fossil-bearing rocks (e.g., Colbert, 1971; Romer, 1975; Cooper, 1982), some still proposed today (e.g., Lucas, 1998, 2010, 2018). These ideas also resulted in the formulation of more regional biostratigraphic frameworks (e.g., Colbert and Gregory, 1957; Bonaparte, 1966). However, recent taxonomic revisions and descriptions utilizing apomorphy-based identifications have suggested that Late Triassic assemblages are more regionally endemic and that cross-Pangean biostratigraphic ties are rarer than previously believed at the genus and species levels (e.g., Benton, 1983; Olsen and Galton, 1984; Shubin and Sues, 1991; Schultz, 2005; Irmis et al., 2010; Ezcurra, 2010).

The framework for Late Triassic biostratigraphy and biochronology in North America is based mainly on fossil terrestrial vertebrates, and four recognized biozones (estimated holochronozones *sensu* Martz and Parker, 2017) are defined by the lowest known occurrences of phytosaur taxa; Phytosauria = Otischalkian (latest Carnian? to earliest Norian?); Leptosuchomorpha = Adamanian (early to middle Norian); Mystriosuchinae (Pseudopalatinae) = Revueltian (middle to late Norian); and *Redondasaurus* = Apachean (late Norian to end Rhaetian) (Lucas and Hunt, 1993, based on earlier work by Colbert and Gregory, 1957; Martz and Parker, 2017). These estimated holochronozones, and a complementary set of 'Land Vertebrate Faunachrons' established for the Newark Supergroup (Huber et al., 1993), have been proposed to correlate Triassic strata in eastern and western North America. However, this has been hindered by the general lack of shared genus or species-level taxa between the two depositional areas. Many other taxa, although not defining these biozones, are considered diagnostic for the various assemblages that occur in each zone. One of these zone fossils is *Doswellia kaltenbachi* from the Sanfordian (= Otischalkian; Lucas, 2018) of the Newark Supergroup, until very recently the only recognized member of the Doswelliidae in North America, and recovered only from the Upper Triassic of Virginia and Texas (Weems, 1980; Long and Murry, 1995; Lucas, 1998; Dilkes and Sues, 2009; Sues et al., 2013).

Doswelliids are quadrupedal non-archosaur archosauriform diapsids known from Middle Triassic and Late Triassic strata in North America and Europe (Sues et al., 2013). The eponymous taxon *Doswellia kaltenbachi* was first described for a partial skull and skeleton that forms the holotype and paratype specimens from the Poor Farm Member of the Falling Creek Formation of the Newark Supergroup in Virginia (Weems, 1980;

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LeTourneau, 2003). Parrish (1999) and Long and Murry (1995) assigned vertebrae and osteoderms from the Chinle Formation of Utah and the Dockum Group of Texas to *D. kaltenbachi*, respectively. The Utah material consists of several osteoderms that have surface pitting similar of *Doswellia* (Heckert et al., 2012a), but has since been determined to instead belong to the diminutive suchian *Acaenasuchus geoffreyi* (Marsh et al., 2020) and therefore is not considered here further. The Dockum Group material apart from *Ankylosuchus chinlegroupensis* (TMM 31025-64, TMM 31025-153, TMM 31098-45; Long and Murry, 1995), pertains to *D. kaltenbachi*, which is accepted here, but this material and newly identified material from the same locality warrants further investigation.

Doswellia kaltenbachi was originally assigned to the 'Thecodontia' by Weems (1980) who provided detailed comparisons of *Doswellia* with the other known 'thecodontian' groups but was unable to confidently assign his specimen to one. Instead he erected the family Doswelliidae to include *Doswellia kaltenbachi* and noted that (p. 36) "it seems much more likely that *Doswellia* was derived from an animal like *Archosaurus* or *Proterosuchus*" and thus would be what is considered today a 'proterosuchid' archosauriform (Ezcurra et al., 2010). Bonaparte (1982) assigned the Doswelliidae to the Aetosauria based upon the anatomy of the osteoderms and implied similarities of the pelvis and femur. However, as initially discussed by Weems (1980), these similarities are superficial and cannot be reliably used to support a close relationship. Long and Murry (1995) assigned Doswelliidae to the Archosauriformes *incertae sedis.*

Phylogenetic analyses have recovered doswelliids as a clade of non-archosaurian archosauriforms more closely related to proterochampsids than to the paraphyletic 'Proterosuchidae' (Parker and Barton, 2008; Dilkes and Sues, 2009; Desojo et al., 2011; Schoch and Sues, 2013; Sues et al., 2013). However, more recent phylogenetic analyses of Archosauromorpha have recovered doswelliids as eucrocopod archosauriforms, notably within the Proterochampsia as the sister taxon of Proterochampsidae (Ezcurra, 2016; Wynd et al., 2019).

Recently, the Doswelliidae underwent a significant systematic revision with a number of newly reported specimens assigned to the Doswelliidae from South America (*Archeopelta arborensis*) and Germany (*Jaxtasuchus salomoni*) (Desojo et al., 2011; Hagdorn and Mutter, 2011; Schoch, 2011a; Schoch and Sues, 2013), a redescription of the type material of *Doswellia kaltenbachi* (Dilkes and Sues, 2009), and a referral of new taxa from the Chinle Formation of New Mexico (*Rugarhynchos sixmilensis*) and the Dockum Group of Texas (*Ankylosuchus chinlegroupensis*) (Heckert et al., 2012a; Lucas et al., 2013; Wynd et al., 2019). In the last couple of years, some of these taxa (e.g., *Archeopelta arborensis*, Desojo et al., 2011 and *Tarjadia ruthae* Arcucci and Marsicano, 1998) have been alternately recovered well outside of Doswelliidae within Suchia in crown Archosauria (Ezcurra et al., 2017). Nonetheless, *Jaxtasuchus salomoni*, *Rugarhynchos sixmilensis*, and *Ankylosuchus chinlegroupensis* unambiguously establish the presence of doswelliids in Europe and western North America (Heckert et al., 2012a; Lucas et al., 2013; Schoch and Sues, 2013; Wynd et al., 2019).

The holotype locality of *Doswellia kaltenbachi* in the Taylorsville basin of Virginia is the only occurrence of the taxon from the Newark Supergroup, whereas referred material is from the lower part of the Dockum Group in Texas (Long and Murry, 1995; Heckert et al., 2012a). The holotype locality of *Doswellia kaltenbachi* is in late Carnian strata (Olsen et al., 2011), which is currently the best temporal constraint for the locality. The referred *D. kaltenbachi* material from Texas as well as the holotype specimen of *Ankylosuchus chinlegroupensis* are also from purported Carnian strata (Lucas et al., 2013); however, this age assignment is controversial. The Dockum Group material has only been dated through long-distance biostratigraphic correlation and it appears a Carnian date for these strata is too old (e.g., Olsen et al., 2011; Martz et al., 2013; Lessner et al., 2018; Beyl et al., 2020). *Rugarhynchos sixmilensis* is from the Bluewater Creek Member (Chinle Formation, New Mexico), which is potentially early Norian in age (Irmis et al., 2011; Wynd et al., 2019) based on radioisotopic dating. The European doswelliid material is Middle Triassic in age and represents a stratigraphic range extension for the Doswelliidae into older rocks (Hagdorn and Mutter, 2011; Schoch, 2011a; Schoch and Sues, 2013). Thus, the present stratigraphic range for doswelliids is Anisian of the Middle Triassic to potentially the middle Norian of the Late Triassic.

Here, we document new material referrable to *Doswellia* cf. *D. kaltenbachi* from the upper part of the Blue Mesa Member (middle Norian) of Petrified Forest National Park, that represents the second occurrence of a doswelliid from the Chinle Formation, however, it is the first from Arizona and Petrified Forest National Park. More importantly, this new occurrence of *Doswellia* cf. *D. kaltenbachi* represents a higher stratigraphic occurrence than the New Mexico doswelliid *Rugarhynchos sixmilensis* and is the youngest occurrence of a doswelliid in North America.

Institutional Abbreviations— **NCSM**, North Carolina State Museum, Raleigh, North Carolina, U.S.A.; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.; **PEFO**, Petrified Forest National Park Museum Collections, Arizona, U.S.A.; **PFV**, Petrified Forest National Park Vertebrate Locality; **SMNS**, Stuttgart State Museum of Natural History, Stuttgart, Germany; **TMM**, Vertebrate Paleontology Collections, Jackson School Museum of Earth History, University of Texas at Austin, Austin, Texas, U.S.A.; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

SYSTEMATIC PALEONTOLOGY

ARCHOSAUROMORPHA sensu Benton, 1985
ARCHOSAURIFORMES sensu Gauthier, Kluge, and Rowe, 1988
DOSWELLIIDAE sensu Desojo, Ezcurra, and Schultz, 2011
DOSWELLIA Weems, 1980
DOSWELLIA CF. *D. KALTENBACHI* Weems, 1980
(Figs. 2–7)

Newly-referred Specimen—Specimen PEFO 36739, a partial right ilium, a partial cervical vertebra, one trunk vertebra, five nearly complete osteoderms, ten osteoderm fragments, and a rib fragment.

Assignment to Doswelliidae—Specimen PEFO 36739 can be referred to the Doswelliidae based on the presence of the following combination of character states (see Phylogenetic Analysis below): angle between head and shaft in anterior dorsal ribs low, gentle posteroventral bowing of the base of the shaft; sculpturing present on external surface of osteoderms; and dorsal prominence on paramedian osteoderms blunted, anteroposteriorly restricted eminence.

The dorsoventrally thickened osteoderms of PEFO 36739 have a 'honeycombed' surface ornamentation of deep, closely spaced pits and possess a dorsal keel (Weems, 1980; Long and Murry, 1995; Dilkes and Sues, 2009; Desojo et al., 2011; Sues et al., 2013). A trunk centrum associated with this material is mediolaterally broad and subrectangular in ventral view. It possesses articular faces that are mediolaterally wider than dorsoventrally tall, unlike the more spool-shaped centra of phytosaurs and aetosaurs that have nearly circular articular faces. This centrum is very similar to those of TMM 31025-64

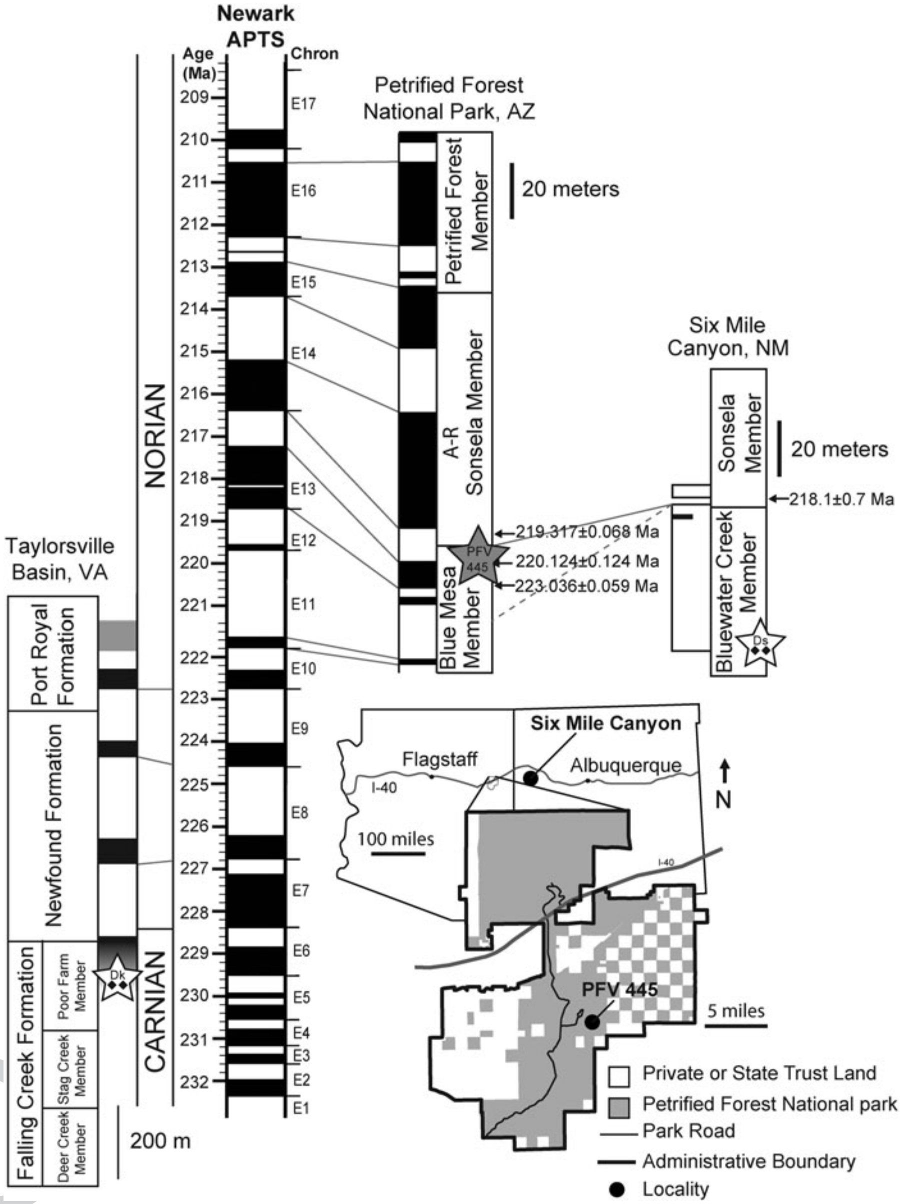

FIGURE 1. Stratigraphic occurrences of *Doswellia* (Dk) in the Taylorsville Basin, Virginia, PFV 445 at Petrified Forest National Park, Arizona, and *Rugarhynchos sixmilensis* at Six Mile Canyon, New Mexico, and geographic locations of doswelliids in Arizona and New Mexico. Modified from Weems, 1980; LeTourneau, 2003; Irmis et al., 2011, Ramezani et al., 2011; Zeigler and Geissman, 2011; Heckert et al., 2012a; Atchley et al., 2013; Kent et al., 2017, 2019; Marsh et al., 2019. **A-R** indicates the approximate temporal position of the Adamanian–Revueltian boundary at PEFO.

assigned to *Doswellia kaltenbachi* by Long and Murry (1995) and vertebrae assigned to *Ankylosuchus chinlegroupensis* (NMMNH P-16723; Lucas et al., 2013). The rib fragment is consistent in its anatomy with the trunk ribs of *Doswellia kaltenbachi* and *Jaxtasuchus solomoni* and represents the mid-sectional bend of a doswelliid trunk rib. Trunk vertebrae and ribs are unknown for *Rugarhynchos sixmilensis* (NMMNH P-61909; Wynn et al., 2019).

Referral to *Doswellia kaltenbachi*—PEFO 36739 possesses the following apomorphies of *Doswellia kaltenbachi*: abrupt change in cross-sectional shape of rib cage from narrow to wide between anterior and posterior dorsal vertebrae; ilium with a strongly laterally deflected iliac blade; three sacral ribs; medial surface of the ilium with a large oval, rugose articular surfaces for the second and third sacral ribs (Dilkes and Sues, 2009). The ilium is unknown for *Rugarhynchos sixmilensis* (NMMNH P-61909), *Jaxtasuchus solomoni*, and *Ankylosuchus chinlegroupensis* (NMMNH P-16723), therefore it is possible that the characters uniting PEFO 36739 and *D. kaltenbachi* have a wider distribution within Doswelliidae.

PEFO 36739 and *Doswellia kaltenbachi* share: osteoderms with a surface ornamentation of densely packed deep pits that are randomly distributed, differing from that of *Jaxtasuchus solomoni* where the pits have more of a radiating pattern from a dorsal eminence (Schoch and Sues, 2013); deeper and smaller pits than found in *Rugarhynchos sixmilensis* (NMMNH P-61909) and *Ankylosuchus chinlegroupensis* (NMMNH P-16723), and lacking the blunted spike-like dorsal eminence of the posterior dorsal osteoderms of *R. sixmilensis* (Lucas et al., 2013; Wynd et al., 2019); trunk ribs with a flattened, slightly expanded dorsal surface ornamented with numerous ridges as in the *D. kaltenbachi* holotype (Dilkes and Sues, 2009; unknown in *Rugarhynchos sixmilensis*, NMMNH P-61909) and *Ankylosuchus chinlegroupensis*, NMMNH P-16723). However, because of the incomplete nature of the PEFO material and the unknown character states in *R. sixmilensis* and

A. chinlegroupensis we assign this material to *Doswellia* cf. *D. kaltenbachi*.

Locality and Horizon—The fossil locality is situated in a laterally extensive 'blue' paleosol horizon in the upper part of the Blue Mesa Member, Chinle Formation (Parker and Martz, 2011), near Billings Gap at Petrified Forest National Park, Arizona, U.S.A. (PFV 445, the *Doswellia* Quarry; Fig. 1). Similar facies are found in other fossiliferous sites in the upper part of the Blue Mesa Member at PEFO, such as PFV 122 (Dinosaur Wash; Therrien and Fastovsky, 2000). Dominated by pedogenic mudstones, these sites are thought to represent preserved A horizon paleosols deposited in an abandoned channel complex (Therrien and Fastovsky, 2000); the characteristic 'blue' coloration of the paleosols represents gleying conditions from a poorly drained water table. The fossils represent an attritional, time-averaged assemblage typical for this type of depositional setting. PFV 445 is situated 3.6 m above PFV 396 (the Coprolite Layer) on the same badland hill (Kligman et al., 2017, 2018; Stocker et al., 2019).

Other taxa from this locality and horizon include the aetosaur *Desmatosuchus spurensis* (PEFO 38611), a non-desmatosuchine aetosaurian (PEFO 38612), the suchian *Acaenasuchus geoffreyi* (PEFO 46323); phytosaurids, and metoposaurids. Screenwashing of the fossiliferous layer produced microvertebrate fossils including the archosauriform *Vancleavea campi* (PEFO 38615), the reptilian tooth taxon *Crosbysaurus harrisae* (PEFO 38616), a tanystropheid (PEFO 38619), as well as xenacanthid sharks (PEFO 38622), dipnoan toothplates (PEFO 38610), and actinopterygian scales (PEFO 38623). The microvertebrate assemblage is broadly similar to others from the upper part of the Blue Mesa Member including PFV 396 (Kligman et al., 2017, 2018; Stocker et al., 2019) and PFV 456 (Thunderstorm Ridge; Jenkins et al., 2020; Kligman et al., 2020). These slightly (~2 m) stratigraphically lower sites are hypothesized to represent shallow lakes with anoxic bottoms (Kligman et al., 2017); however, the lack of coprolites and the presence of aetosaurians in the slightly higher *Doswellia*-bearing strata (PFV 445) suggest that this younger horizon alternately represents proximal channel floodplain deposits (Therrien and Fastovsky, 2000). The assemblage is also very similar to that of PFV 122 (Dying Grounds) and PFV 124 (Crocodile Hill) also from the upper part of the Blue Mesa Member, which are the type assemblages for the Adamanian holochronozone (Murry, 1989; Long and Murry, 1995; Parker, 2002; Heckert, 2004; Parker and Martz, 2010).

Age—The most recent age model estimate for the upper part of the Blue Mesa Member based on U-Pb ages from detrital zircons in a geological core is about 219-217 Ma (Rasmussen et al., 2020). Conversely, outcrop studies utilizing U-Pb ages bracket the site between 223 and 220 Ma (Ramezani et al., 2011; Atchley et al., 2013; but see discussion in Rasmussen et al., 2020, Gehrels et al., 2020, and Vermeesch, 2020). Both are consistent with the proposed range of ages (224-215 Ma) for the Adamanian estimated holochronozone (Martz and Parker, 2017). Thus, fossil evidence and geochronology place the locality solidly in the middle Norian and in the Adamanian.

Taphonomic and Collection Notes—The initial discovery consisted of several of the larger osteoderm fragments situated on top of the weathered surface of a small hill of highly bentonitic claystone. The specimens were found around an 'erosional pipe,' a common drainage feature in badland topography formed by standing water percolating down into the hill. Initial investigation of the weathered surface around the original find resulted in collection of additional large osteoderm fragments as well as the trunk centrum. Excavating the erosional pipe produced only the ilium fragment. A radius of 1.5 m was excavated around the initial find to a depth of 0.3 m resulting in the recovery of another large osteoderm fragment. Using a pick on the surface and screening the disturbed matrix resulted in the recovery of the small osteoderm fragments and the rib fragment. The specimens were cleaned using tap water and a bristled brush. Paraloid B-72 dissolved in acetone was used as the adhesive to combine fragments. The similar size, preservation, the close association in the ~1 m^2 surface, and lack of duplicate elements in PEFO 36739 suggests that the material belongs to a single individual.

DESCRIPTION

Cervical Vertebra

A partial posterior cervical centrum (split coronally) (Fig. 2) shows more surface wear than the other elements. The centrum is morphologically consistent with *Doswellia kaltenbachi* and *Rugarhynchos sixmilensis* (NMMNH P-61909) in having closely situated diapophyses and parapophyses separated by a deep groove and a low ridge (keel) on the ventral surface (Dilkes and Sues, 2009:fig. 3C; Wynd et al., 2019:fig. 10D). Only the anterior face of the centrum is preserved, and it is round, as described for the holotype specimen (Weems, 1980), and equant, measuring 17 mm wide and 17 mm tall (Fig. 2A). The left diapophysis is missing (Fig. 2B). The neural arch is also missing but shows that the neural canal is mediolaterally wide as described for USNM 244214 (Dilkes and Sues, 2009). In right lateral view, the diapophysis and parapophysis are closely situated (Fig. 2C) and on the left side (Fig. 2B), a short and sharp ridge extends from the posterior margin of the parapophyses as in the holotype specimen (Dilkes and Sues, 2009:fig. 3C). This ridge forms the lower border of a concavity between the diapophysis and parapophyses as seen in the holotype specimen (Fig. 2B).

The ventral surface (Fig. 3D) bears a ridge on the midline (i.e., a keel). A ventral keel was described as not present in the holotype (Weems, 1980; Sues et al., 2013), but is common for other archosauriforms (Nesbitt, 2011). However, Dilkes and Sues (2009) describe a low ridge along the ventral surface of the

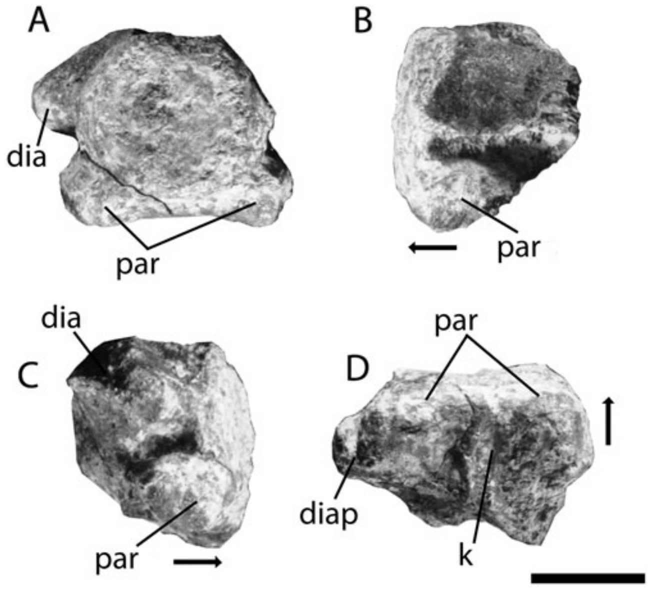

FIGURE 2. Cervical centrum (PEFO 36739) referred to *Doswellia* cf. *D. kaltenbachi* in **A**, anterior; **B**, left lateral; **C**, right lateral; and **D**, ventral views. **Abbreviations**: **dia**, diapophysis; **k**, keel; **par**, parapophysis. Arrows point in anterior direction. Scale bar equals 1 cm.

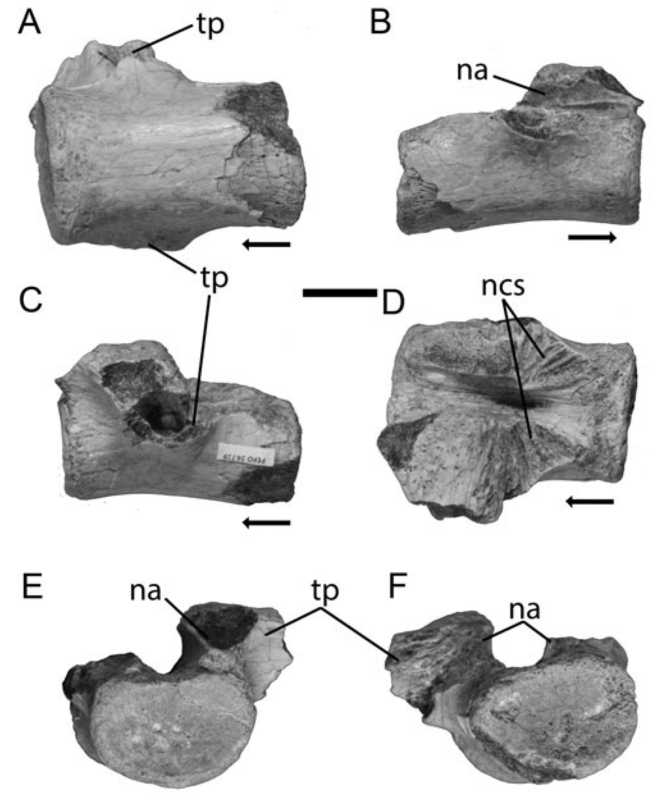

FIGURE 3. Trunk vertebral centrum (PEFO 36739) referred to *Doswellia* cf. *D. kaltenbachi* in **A**, ventral; **B**, right lateral; **C**, left lateral; **D**, dorsal; **E**, anterior; and **F**, posterior views. **Abbreviations**: **na**, neural arch; **ncs**; neural arch suture; **tp**; transverse process. Arrows point in anterior direction. Scale bar equals 1 cm.

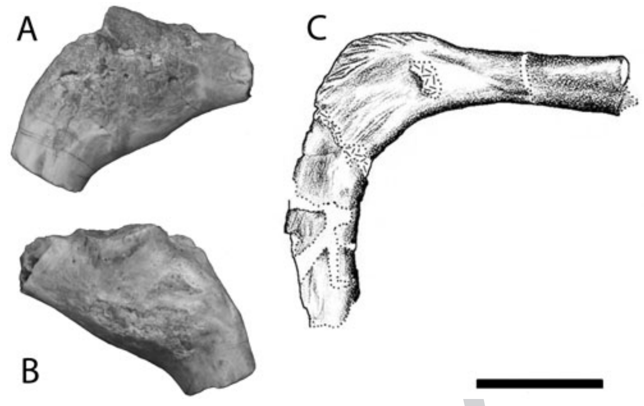

FIGURE 4. **A**, **B**, Trunk rib fragment (PEFO 36739) assigned to *Doswellia* cf. *D. kaltenbachi* in **A**, anteroventral and **B**, posterodorsal views. **C**, Interpretive drawing of a trunk rib from the holotype of *Doswellia kaltenbachi* (Dilkes and Sues, 2009:fig. 7F). Scale bar equals 1 cm.

cervical centrum in *D. kaltenbachi*. A ventral keel is also found in *Vancleavea campi* (Parker and Barton, 2008), which is also present at the locality, but this specimen differs from *V. campi* in lacking the strongly concave anterior face of the centrum. A partial cervical vertebra of *Rugarhynchos sixmilensis* (NMMNH P-61909; Heckert et al., 2012a:fig. 4n; Wynd et al., 2019:fig. 10d) is nearly identical to PEFO 36739 in bearing a very low ridge on the midline of the anterior portion of the centrum. This contrasts with a more ventrally extended keel in, what is based on size, presumably a more posterior cervical centrum in *R. sixmilensis* (Wynd et al., 2019:fig. 10b), suggesting the size of the keel varies in size along the cervical series.

Trunk Vertebra

The preserved centrum is anteroposteriorly longer than mediolaterally wide, amphicoelous, and subrectangular in ventral view (Fig. 3A). The anterior centrum face is 12 mm tall dorsoventrally. The centrum body is only slightly constricted relative to the articular faces, which lack strongly laterally flaring rims. Dilkes and Sues (2009:64) described the resultant shape found in the holotype specimen of *Doswellia kaltenbachi* as "cylindrical" and this morphology is consistent with PEFO 36739. The lack of a strong mediolateral constriction of the centrum suggests it is an anterior trunk vertebra and not a posterior trunk vertebra, the latter of which are more constricted in ventral view (Dilkes and Sues, 2009: fig. 4). The ventral surface of the trunk centrum of PEFO 36739 is smooth and featureless lacking a ventral keel, consistent with *Doswellia kaltenbachi* (Dilkes and Sues, 2009) and *Ankylosuchus chinlegroupensis* (NMMNH P-16723), unlike the keeled trunk centra of *Jaxtasuchus solomoni* (Dilkes and Sues, 2009). Trunk vertebrae are unknown for *Rugarhynchos sixmilensis* (NMMNH P-61909; Wynd et al., 2019).

In lateral view (Fig. 3B–F), the centrum is dorsoventrally compressed, and the oval articular faces are significantly wider than tall (30 mm long mediolaterally and 18 mm wide dorsoventrally) in anterior and posterior views, identical to the condition in *Doswellia kaltenbachi* (Dilkes and Sues, 2009). The ventral margin of the centrum differs significantly from that of *Jaxtasuchus solomoni* which is markedly concave in lateral view (Dilkes and Sues, 2009:fig. 4f). In dorsal view (Fig. 3D), the neural canal is wide anteriorly and posteriorly and constricted at the midpoint of the centrum giving the canal a narrow hourglass shape that is also present in *Ankylosuchus chinlegroupensis* (NMMNH P-16723). An elongate incised groove floors the mid-part of the neural canal. Distinct neurocentral sutures are present on the posterior portion of the dorsal surface, demonstrating that the centrum and neural arch were not co-ossified. Although the anterior portions of the neurocentral suture are covered by fragments of the neural arch, the suture is still clear especially on the right side (Fig. 3D). The neurocentral sutures expand laterally underlying the proximal portions of the transverse processes, and do not extend posteriorly to contact the posterior margin of the centrum. A very similar condition is present in *Ankylosuchus chinlegroupensis* (NMMNH P-16723; Lucas et al., 2013: fig. 3). The anteriorly positioned transverse processes on the trunk vertebra of PEFO 36739 (see Dilkes and Sues, 2009:figs. 4a, b) are broken away except for a small remnant of the left process. Ventral to this process is a distinct rounded pit surrounded by edges of broken bone (Fig. 3C). The surfaces within this pit are slightly striated suggesting that it represents an articular surface, probably for the capitulum of the associated rib, which is similarly grooved in the holotype specimen of *Doswellia kaltenbachi* (Dilkes and Sues, 2009:fig. 7). A similar pit found on the right side of PEFO 36739 demonstrates that this is a biological feature and not a preservational artifact.

Trunk Rib

A fragment in PEFO 36739 represents the middle section of a right dorsal rib (Fig. 4). The fragment location and identification can be determined by the presence of a pronounced, raised tubercle that has a slightly raised posterior margin that is

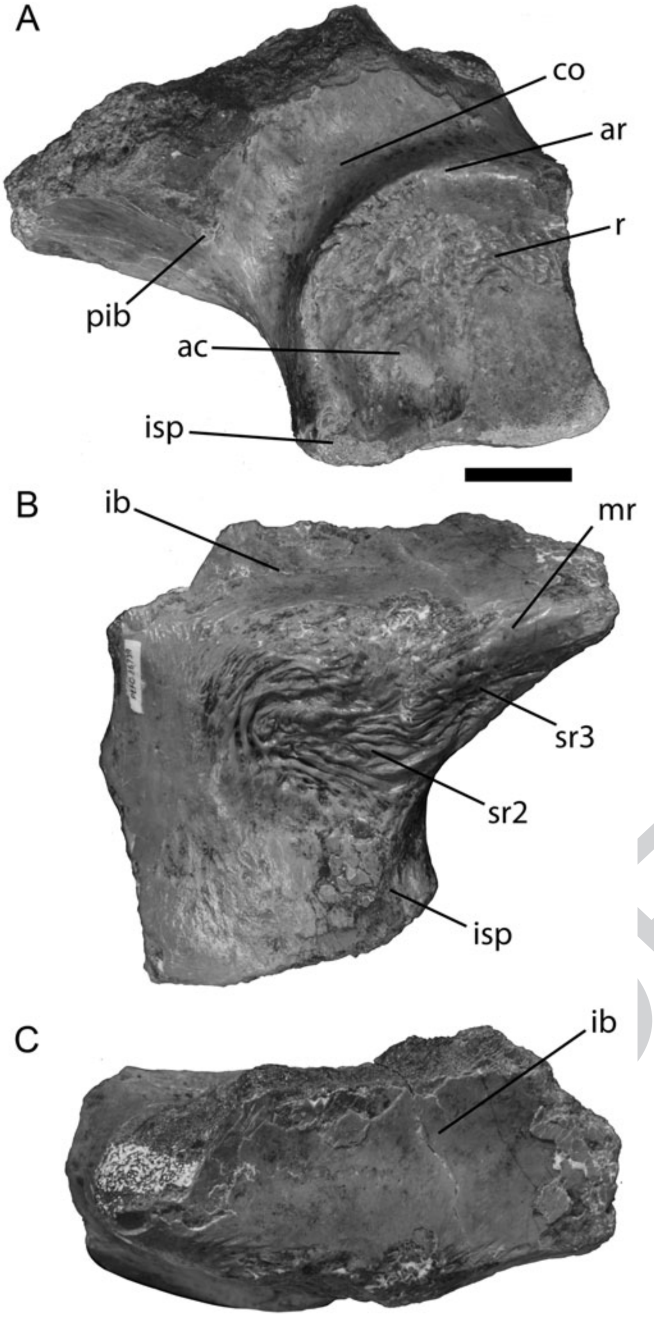

FIGURE 5. Right ilium (PEFO 36739) assigned to *Doswellia* cf. *D. kaltenbachi* in **A**, ventrolateral; **B**, dorsomedial; and **C**, dorsal views. **Abbreviations**: **ac**, acetabulum; **ar**, acetabular rim; **co**, concavity; **ib**, iliac blade; **isp**, ischiadic peduncle; **mr**, medial ridge; **pib**, posterior portion of the iliac blade; **r**, rugose surface; **sr2**, sacral rib 2 articulation area; **sr3**, sacral rib 3 articulation area. Arrows point in anterior direction. Scale bar equals 1 cm.

Q4

present at the bend in the rib shaft, similar to that of doswelliids such as *Doswellia kaltenbachi* (USNM 214823) and *Jaxtasuchus solomoni* (SMNS 91352); the element of PEFO 36739 was probably identical to those in *Doswellia kaltenbachi*, with the autapomorphic 90° flexion in the dorsal rib (Fig. 4; Weems, 1980; Dilkes and Sues, 2009:fig. 7) based on the preserved portion. Trunk ribs are unknown for *Rugarhynchos sixmilensis* (NMMNH P-61909) and *Ankylosuchus chinlegroupensis* (NMMNH P-16723).

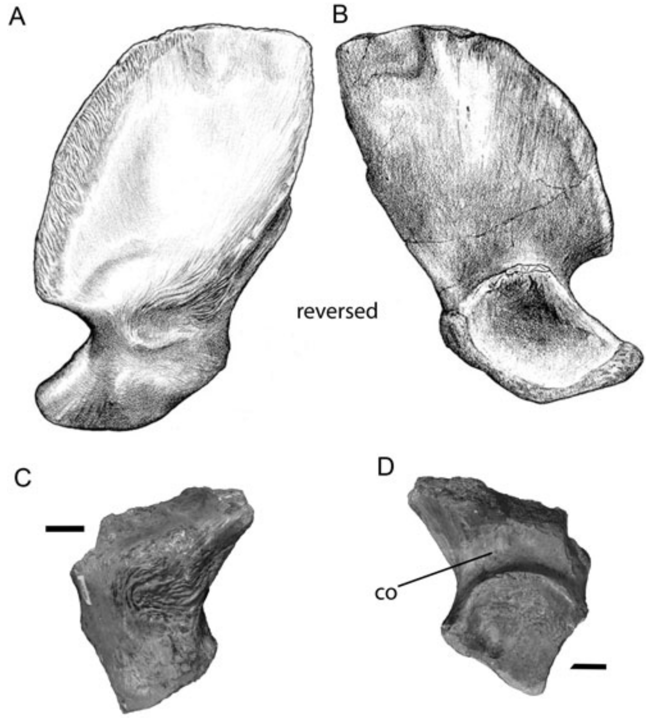

FIGURE 6. Comparison between referred specimen PEFO 36739 and the holotype of *Doswellia kaltenbachi* at the same scale. **A, B**, holotype in dorsomedial (**A**) and ventrolateral views (**B**) (Dilkes and Sues, 2009: fig. 14a, b, reversed). **C, D**, referred specimen PEFO 36739 in dorsomedial (**C**) and ventrolateral views (**D**). **Abbreviation: co**, concavity. Scale bar equals 1 cm.

Ilium

An incomplete right ilium (Fig. 5) is missing much of the iliac blade as well as the anterior portion of the acetabulum. The ilium is notably mediolaterally thick and robust for the size of the element compared with other archosauriforms. The deeply concave acetabulum is dorsally bound by a laterally expanded supraacetabular crest and the ventral margin is angled where the pubes and ischia would meet, although the pubic peduncle is missing so the exact angle cannot be determined (Fig. 5A). The surface dorsal to the acetabular crest is deeply concave. This concavity is not present in the holotype of *D. kaltenbachi* (Dilkes and Sues, 2009) where the ventral surface of the iliac blade is more confluent with the acetabular rim and represents a clear difference between the two specimens, although we feel the PEFO specimen is too incomplete to verify this as an unambiguous apomorphy and name the PEFO a separate species. Furthermore, the ilia are presently unknown in *Ankylosuchus chinlegroupensis* (NMMNH P-16723) and *Rugarhynchos sixmilensis* (NMMNH P-61909). The dorsal portion of the lateral surface of the medial wall of the acetabulum is rugose, with a complex labyrinth of grooves and ridges (Fig. 5A).

The ischiac peduncle is mediolaterally thickened (relative to the midpoint of the acetabulum) with a rugose ventral surface that is comma-shaped in posteroventral view. The medial surface of the iliac body is flat, the ventral portion is smooth, and the dorsal portion bears a rugose area of curved and anastomosing grooves and ridges (Fig. 5B). The position of this rugose area as well as the patterning of the rugosity is identical to that found on the holotype ilium of *Doswellia kaltenbachi* (USNM 244214; Dilkes and Sues, 2009:fig. 14B) and represents the

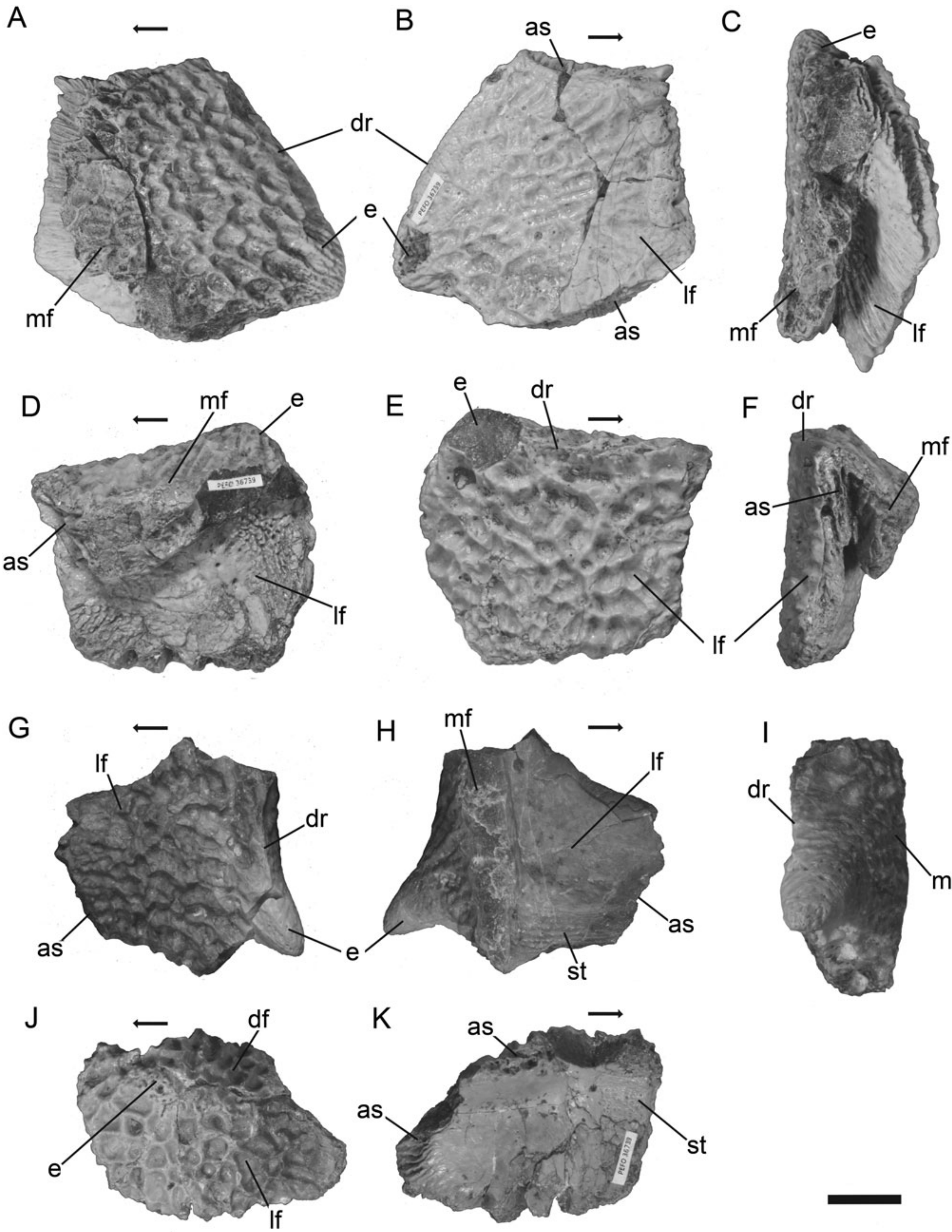

FIGURE 7. Osteoderms (PEFO 36739) referred to *Doswellia* cf. *D. kaltenbachi*. **A–C**, right pelvic osteoderm in: **A**, medial; **B**, lateral; and **C**, ventral views. **D–E**, right pelvic osteoderm in: **D**, medial; **E**, lateral; and **F**, anterior views. **G–H**, right pelvic osteoderm in: **G**, lateral; **H**, medial; and **I**, dorsal views. **J–K**, left posterior trunk osteoderm in: **J**, lateral, and **K**, medial views. **Abbreviations**: **apr**, anteroposterior ridge; **as**, articular surface; **df**, dorsal flange; **e**, eminence; **lf**, lateral flange; **mf**, medial flange; **st**, striations. Arrows point in anterior direction. Scale bar equals 1 cm.

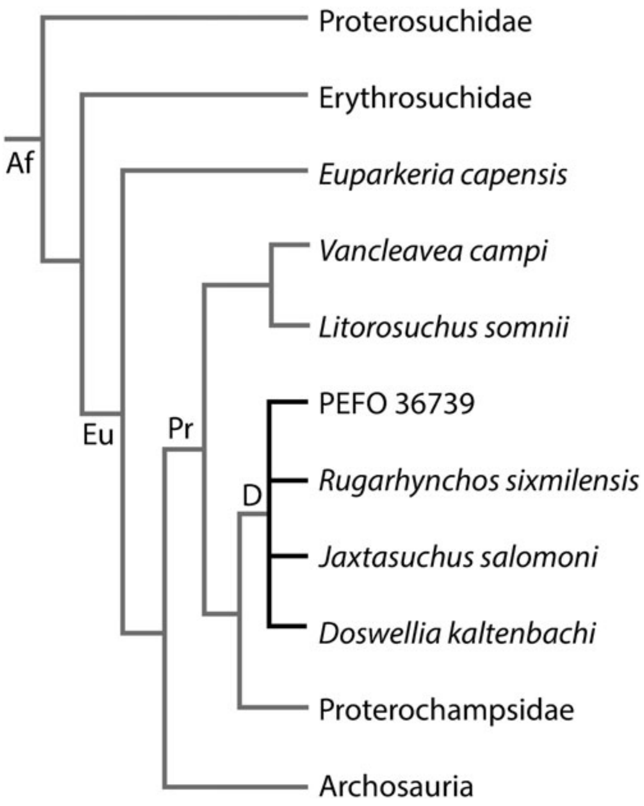

FIGURE 8. Simplified strict consensus tree of 717 MPTs found in the parsimony analysis. The black line indicates members of the Doswelliidae. **Abbreviations**: **Af**, Archosauriformes; **D**, Doswelliidae; **Eu**, Eucrocopoda; **Pr**, Proterochampsia.

articular surface for the second and third sacral ribs (Dilkes and Sues, 2009; Weems, 1980). *Doswellia kaltenbachi* is notable within Archosauromorpha in possessing three sacral vertebrae (Dilkes and Sues, 2009; Ezcurra, 2016).

Although the iliac blade is incomplete, enough of the ventral portion is preserved (Figs. 5C, 6) to demonstrate that the blade was strongly deflected laterally as in *Doswellia kaltenbachi* (Weems, 1980; Dilkes and Sues, 2009). Indeed, this is one of the most characteristic traits of this taxon, although it could have a broader distribution within Doswelliidae as the ilium is not preserved in the holotype specimens of *Rugarhynchos sixmilensis* (NMMNH P-61909), *Ankylosuchus chinlegroupensis* (NMMNH P-16723), and *Jaxtasuchus solomoni*. In posterior view the angle between the body of the ilium and the iliac blade is nearly 90°. The posterior surface of the iliac blade forms a flat dorsal shelf lateral to the sacral rib attachments (Fig. 5B–C).

Osteoderms

Four nearly complete osteoderms are preserved in PEFO 36739 (Fig. 7), as well as ten smaller osteoderm fragments. The strong, acute flexion of the more complete osteoderms suggests they are from the general region of the pelvis based on those preserved in *Doswellia kaltenbachi* (Weems, 1980; Dilkes and Sues, 2009:fig.11a–b). The orientation of the pelvic osteoderms differs from those of the trunk region in that they were upright, with the large flat faces directed medially and laterally rather than dorsally and ventrally (Dilkes and Sues, 2009) and are described here using that orientation. All osteoderms bear a coarse surface ornamentation of irregular pits separated by a latticework of narrow, tall ridges consistent with the patterning found in other doswelliids such as *Doswellia kaltenbachi* (USNM 214823), *Rugarhynchos sixmilensis* (NMMNH P-61909), *Ankylosuchus chinlegroupensis* (NMMNH P-16723), and *Jaxtasuchus solomoni* (e.g., SMNS 91411).

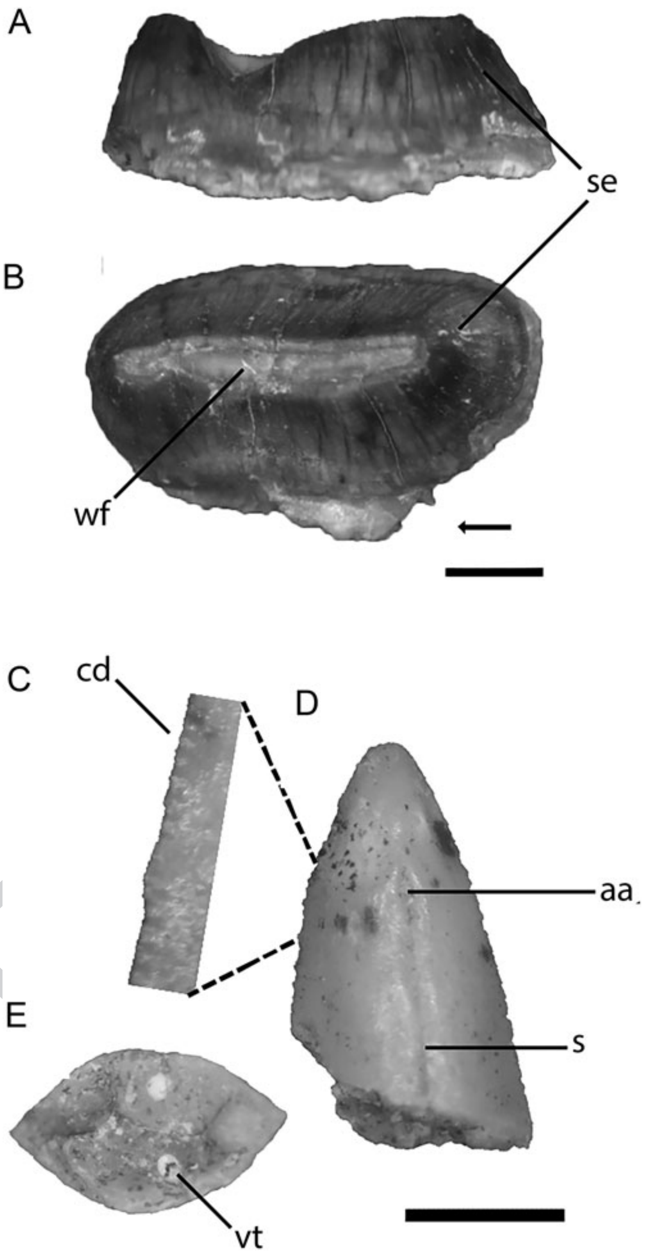

FIGURE 9. Select specimens representative of the upper part of the Blue Mesa Member (Chinle Formation) vertebrate taxa also reported from the Newark Supergroup including: **A, B**, *Colognathus obscurus* molariform tooth (PEFO 37239: PFV 396) in lingual (**A**), and occlusal (**B**) views; **C–E**, *Uatchitodon schneideri* tooth (PEFO 41989: PFV 396) magnification of compound denticles (**C**), labial(?) view (**D**), view of tooth base in cross section (**E**). **Abbreviations**: **a**, acetabulum; **aa**, apical aperture; **cd**, compound denticles; **s**, suture; **se**, striated enamel; **vt**, venom tube; **wf**, wear facet. Arrows point in anterior direction. Scale bars equal 1 mm.

The three acutely flexed osteoderms (one from the left side and two from the right side) have quadrilateral medial and lateral flanges, and the lateral flange is generally larger than the medial flange (Fig. 7A–I). Medially, these flanges are separated by a shallow groove and are oriented between 30–45° from each other. The anterior, posterior, and medial edges of the lateral flange are marked by sets of interdigitating sutures where the connecting osteoderms would have interlocked. The ventromedial edge of the medial flange also bears a sutural surface suggesting another dermal element was present along the flank of the animal (Fig. 7D). The dorsolateral surface of the osteoderm bears a sharp anteroposterior ridge along the flexural surface of the osteoderm (Figs. 7A, F, G). In two of the acutely flexed osteoderms of PEFO 36739 (Fig. 7A–F), the posterior portion of this keel is broken, but appears to have formed a very short posteriorly directed spine or eminence, similar to what is preserved in *Doswellia kaltenbachi* (USNM 214823; Dilkes and Sues, 2009:figs. 11a–b; osteoderm numbered 7 in Weems, 1980:pl. 8B). The third acutely flexed osteoderm from the right side (Fig. 7G–I) preserves this feature, which bears posterolaterally directed striations. These spines differ greatly from the dorsal eminences of *Rugarhynchos sixmilensis* (NMMNH P-61909), where a more elongate eminence projects from the center of the osteoderm (Heckert et al., 2012a:fig. 5).

The fourth osteoderm is from the right side (Fig. 7J–K). It resembles the other osteoderms in ornamentation, but it is less flexed, at about 90° and presumably was not oriented in an 'upright' position. The osteoderm consists of dorsally and laterally facing surfaces (flanges) separated by a low ridge or 'dorsal eminence' (Dilkes and Sues, 2009). The lateral flange is larger than the dorsal flange. The anterior, medial, and lateral edges bear sutural contacts, with the medial being the most pronounced. This osteoderm lacks the strongly developed keel along the flexed edge; however, a slight dorsally positioned eminence is present along the posterior portion of the flexion edge. This eminence bears the short striations found on the spines of the other osteoderms, although it is not a spine. Overall the osteoderm is very similar to the posterior trunk osteoderms of *Jaxtasuchus solomoni* (SMNS 90531; Schoch and Sues, 2013:fig. 5O, P, S) and *Doswellia kaltenbachi* (USNM 214823; Dilkes and Sues, 2009:fig. 10I–J), although the ornament in the former has a radial patterning of pits that is not present in PEFO 36739, which has a pitted ornament. It differs from *Rugarhynchos sixmilensis* (NMMNH P-61909) in that the dorsal eminence is a raised mid-line keel rather than a tall, blunt spine (Wynd et al., 2019:fig. 11H–K). The medial and ventral surfaces of this fourth osteoderm are mostly smooth, although the posterior edge bears a narrow bar of horizontal striations. There is no evidence for a thickened anterior articular surface (= anterior bar of aetosaur workers) on any of these osteoderms, such as those found on osteoderms from different regions of the carapace in other doswelliids (e.g., *Jaxtasuchus solomoni*). However, the ventral striations and lack of a posterior sutural surface in the less flexed osteoderm suggests that the posterior edge of this osteoderm overlays the anterior portion of a more posterior osteoderm in the carapace.

PHYLOGENETIC ANALYSIS

We scored PEFO 36739 into the modified character-taxon matrix of Ezcurra (2016) as modified by Ezcurra et al. (2017) and Wynd et al. (2019) (Supplemental Data). The specimen was scored for 31 characters, or 4.6% of the matrix. Following Ezcurra et al. (2017) and Wynd et al. (2019) we removed ten taxa (*Eorasaurus olsoni*, *Archosaurus rossicus*, *Vonhuenia fredericki*, *Chasmatosuchus rossicus*, *Chasmatosuchus magnus*, '*Chasmatosuchus*' *vjushkovi*, *Kalisuchus rewanensis*, *Shansisuchus kuyeheensis*, *Uralosaurus magnus*, and *Koilamasuchus gonzalezdiazi*) for a final matrix of 110 taxa and 677 characters. We performed a traditional search parsimony analysis in TNT (Goloboff et al., 2008) using 1000 replications, TBR branch swapping while collapsing zero-length branches and saving ten trees per replication. The search recovered 717 most-parsimonious trees (MPTs) of 3411 steps. The strict consensus tree (Fig. 8) recovered the same topology of major clades within Archosauriformes found in the parsimony analysis of Ezcurra et al. (2017) and Wynd et al. (2019). The strict consensus tree of our analysis recovered a monophyletic Doswelliidae but resolved no sister taxa relationships within the clade. The 50% majority rules consensus tree recovered *Rugarhynchos sixmilensis* and *Doswellia kaltenbachi* as sister taxa (similar to the strict consensus tree of Wynd et al., 2019), with PEFO 36739, *Jaxtasuchus solomoni*, and *Rugarhynchos sixmilensis* + *Doswellia kaltenbachi* in a polytomy.

According to our analysis, the Doswelliidae can be diagnosed among Archosauriformes by a unique combination of eight character states: character 75(3), 15–22 maxillary tooth positions (not scored for PEFO 36739); character 222(1), one foramen for CN XII in exoccipital (not scored for PEFO 36739); character 306 (1), multiple maxillary or dentary tooth crowns with longitudinal labial or lingual striations or grooves (not scored for PEFO 36739); character 343(1), cervical and trunk vertebrae, thick, mainly vertical tuberosity immediately below the transverse process, but both structures are not connected with each other, in posterior cervical and anterior trunk vertebrae (not scored for PEFO 36739); character 367(1), dorsal ribs, angle between heads and shaft in anterior dorsal ribs low, gentle posteroventral bowing of the base of the shaft; character 589(1), osteoderms, sculpture on their external surface; character 591(2), osteoderms, dorsal prominence on paramedian osteoderms blunted, anteroposteriorly restricted eminence; and character 596(1), osteoderms, unornamented anterior articular lamina present on paramedian osteoderms (not scored for PEFO 36739).

DISCUSSION

Initially *Doswellia kaltenbachi* was known only from the Poor Farm Member of the Falling Creek Formation (Newark Supergroup) of Virginia. LeTourneau (2003) considered the Falling Creek Formation to be Carnian in age based on correlations with the Newark Supergroup astrochronology and geomagnetic polarity timescale (Newark-APTS; Olsen and Kent, 1999). These correlations place the Poor Farm Member as roughly equivalent to chrons E6r and E7n (LeTourneau, 2003). The most recent iteration of the Newark-APTS suggests an age of ∼228 Ma for these strata, which is still Tuvalian or latest Carnian (Kent et al., 2017). The stratigraphic position of the holotype locality of *Doswellia kaltenbachi* within the Poor Farm Member is not certain and there are no diagnostic biostratographic fossils found at the holotype locality. Therefore, we do concur with the latest estimate of the localities age (latest Carnian) but do note that the age constraint on the holotype locality is poorly defined.

Recovery of material of *Doswellia* cf. *D. kaltenbachi* from the upper part of the Blue Mesa Member of the Chinle Formation at PEFO extends the stratigraphic range of this taxon from the likely Carnian into the middle Norian and has important implications regarding the use of this taxon for biostratigraphy, especially regarding the global 'Land Vertebrate Faunachron' system proposed by Lucas (1998) and revisited by Lucas (2010, 2018) and Martz and Parker (2017). Most relevant for this discussion are the two oldest Late Triassic biochronological units, the Otischalkian and Adamanian, as *Doswellia* is presently considered to be an index taxon of the former based on occurrences in the Dockum Group of Texas and the Newark Supergroup of Virginia (Lucas, 2018).

Doswelliid occurrences in the Dockum Group of Texas are restricted to the Otis Chalk quarries (localities TMM 31025 and TMM 31098) and from another site just to the north (NMMNH L-3101), all from the Colorado City Formation (Long and Murry, 1995; Lucas et al., 2013). The material from Otis Chalk quarries (Long and Murry, 1995: figs. 19–21) appears very similar to that of the holotype specimen of *Doswellia kaltenbachi*, especially the osteoderms, which are rectangular (longer than wide) with pronounced pitting and a distinct rugose anterior articular laminae, and grooved lateral articular surfaces (Dilkes and Sues, 2009). However, one of the osteoderms (TMM 31098-45) bears a dorsal eminence in the form of a raised spine, which is a reported autapomorphy of *Rugarhynchos sixmilensis* (Wynd et al., 2019) suggesting the material might belong to that taxon instead. A thorough redescription of the Otis Chalk material is beyond the scope of this paper, but if *Rugarhynchos sixmilensis* is present in the Otis Chalk quarries it provides a strong biostratigraphic link between the Bluewater Creek Member of the Chinle Formation in New Mexico and the Colorado City Formation of the Dockum Group (type Otischalkian) in Texas demonstrating that the Bluewater Creek Member in New Mexico, as it has no phytosaurian material diagnostic to the genus level, might be Otischalkian rather than Adamanian (Irmis et al., 2011; Martz and Parker, 2017) or more simply that *Rugarhynchos sixmilensis* spans the Otischalkian and the Adamanian. The possibility also exists that the Otis Chalk material represents a distinct taxon bearing character states found in both *Rugarhynchos sixmilensis* and *Doswellia kaltenbachi* and may even represent *Ankylosuchus chinlegroupensis* (NMMNH P-16723) which is known solely from a nearby locality (Lucas et al., 2013).

Unfortunately, the numerical age of the Otis Chalk strata in Texas is currently unknown outside of a Rb-Sr age that has only been reported in published abstracts (<225 Ma; Long and Lehman, 1993, 1994, 2009), but the presence of non-phytosaurid phytosaurs in these strata suggest an age older than the base of the Chinle Formation, which lacks these phytosaurs (Stocker, 2013a; Martz and Parker, 2017). The base of the Chinle Formation in Arizona consists of the coarse-grained Shinarump Member and its fine-grained lateral equivalent the Mesa Redondo Member (Irmis et al., 2011:supplemental materials). Ramezani et al. (2011) recovered an age of 225.185 ± 0.079 Ma from the upper part of the Mesa Redondo Member using high precision U-Pb analysis of detrital zircons and the base of the Mesa Redondo Member has an age of 227.604 ± 0.08 Ma (Atchley et al., 2013). Recent models based on magnetostratigraphic correlations in conjunction with high precision U-Pb dates from a core drilled in Petrified Forest National Park place the base of the Chinle Formation closer to 224 Ma (Kent et al., 2018, 2019; Olsen et al., 2018; Rasmussen et al., 2020). Regardless, the Otis Chalk strata are plausibly older than this and possibly roughly equivalent in age to the Poor Farm Member in Virginia, but presently there is no definitive evidence for the Dockum to include Carnian strata (e.g., Olsen et al., 2011). The lower part of the Chinle Formation in Arizona, below the middle of the Blue Mesa Member, lacks any unambiguous claims of vertebrate fossils (Parker and Martz, 2011) and therefore are also a plausible equivalent to the Otis Chalk strata. As mentioned previously these unfossiliferous strata in Arizona are laterally equivalent to the Bluewater Creek Member in New Mexico (Irmis et al., 2011; Marsh et al., 2019), which as mentioned above may possibly be partly or even entirely Otischalkian. This is significant as all of the Chinle Formation is considered to be Norian in age (e.g., Kent et al., 2018; Rasmussen et al., 2020).

The Petrified Forest National Park locality where PEFO 36739 was recovered (PFV 445) is in the upper part of the Blue Mesa Member about 10 m above the top of the Newspaper Rock Bed, which separates the upper and lower parts of that member at least in the Tepees area of the park (Fig. 1). Atchley et al. (2013) reported an age of 220.124 ± 0.068 Ma for the upper part of the Blue Mesa Member from a location about 3 km west of PFV 445. The date is derived from a thin sandstone lens in the uppermost part of the Blue Mesa Member about 17 m above the Newspaper Rock Bed and only a few meters higher than PFV 445. This suggests an age of ~220 Ma for that locality, consistent with the age range suggested by Rasmussen et al. (2020). Thus, known occurrences of *Doswellia kaltenbachi* in North America are not isochronous and appear to span as much as six million years of time in the latest Carnian/early to middle Norian, providing a much longer range than previously recognized (Fig. 1).

Lucas (1998, 2010, 2018) considered *Doswellia kaltenbachi* to be a zone taxon of the Otischalkian estimated holochronozone (EH) based on its occurrence from the Otis Chalk quarries (type Otischalkian), and used this occurrence to correlate the Sanfordian 'Land Vertebrate Faunachron' (LVF) (Huber et al., 1993) of the eastern U.S.A. with the Otischalkian. Other purported Otischalkian relevant taxa from the Newark Supergroup (Pekin Formation, North Carolina; Wolfville Formation, Nova Scotia) are the aetosaurian genera *Desmatosuchus*, *Coahomasuchus*, and *Longosuchus*, the dicynodont *Placerias hesternus*, the temnospondyls *Anaschisma browni* (*sensu* Gee et al., 2019) and '*Metoposaurus*' *bakeri* (Lucas, 2010). The *Desmatosuchus* and *Longosuchus* material from the Newark Supergroup instead represents the aetosaur *Lucasuchus* (Long and Murry, 1995; Parker and Martz, 2011; Heckert et al., 2015), which also occurs in the Texas Otis Chalk quarries (Lucas and Hunt, 1993). *Anaschisma browni* and *Placerias hesternus* are also known from the Adamanian EH (Lucas, 1998), whereas '*Metoposaurus*' *bakeri* occurs in the Wolfville Formation (Newark Supergroup) and in the lower part of the Dockum Group in Scurry County, Texas (Case, 1931; Baird, 1986; Hunt, 1993). The Scurry County strata are considered to be Otischalkian (Lucas, 1998) owing to the presence of the non-leptosuchomorph phytosaur *Wannia scurriensis* (Stocker, 2013b; Martz and Parker, 2017).

Taken at face value, the presence of *Doswellia*, *Lucasuchus*, *Coahomasuchus*, and '*Metoposaurus*' *bakeri* from both the lower Newark Supergroup and lower Dockum Group would support proposed correlations of Lucas (1998, 2010) and the use of these genera as index taxa. However, Heckert et al. (2017) demonstrated that the Newark Supergroup *Coahomasuchus* material belongs to a different species *C. chathamensis*, with *C. kahleorum* restricted to the Dockum Group and *C. chathamensis* is only found in the Newark Supergroup. Furthermore, the recognition of the desmatosuchin *Gorgetosuchus pekinensis* from the Pekin Formation (Heckert et al., 2015) suggests that some of the aetosaur material from the Newark Supergroup previously assigned to *Lucasuchus hunti* (Long and Murry, 1995; Parker and Martz, 2010) may actually belong to that taxon. Although Heckert et al. (2015) do maintain the referral of some of that material (AMNH FARB 2797, AMNH FARB 2799, AMNH FARB 2809b) to *L. hunti*, the incompleteness of the *G. pekinensis* holotype (preserving only the anterior portion of the carapace) suggests that even those few osteoderms may actually be referable to *G. pekinensis*, especially as the dorsal eminence of the paramedian plates increases in size posteriorly in the aetosaur carapace (Heckert and Lucas, 1999; Parker and Martz, 2010). The '*Metoposaurus*' *bakeri* material requires restudy to determine its taxonomic validity and to justify previous referrals of materials, especially the Nova Scotia specimen (Gee et al., 2019).

This leaves *Doswellia kaltenbachi* and possibly *Lucasuchus hunti* as the only potential index taxa supporting not only the distinctiveness of the Otischalkian vertebrate assemblage, but also its equivalency to the Sanfordian LVF; however, this is only if the Otis Chalk quarry material is actually referable to *Doswellia kaltenbachi* (see above). Regardless, the new PEFO specimen demonstrates that *D. kaltenbachi* had a broader stratigraphic range, and therefore even *Doswellia kaltenbachi* can no longer be considered an exclusive Otischalkian zone taxon. Thus, although the Otischalkian estimated holochronozone can be defined by the presence of non-leptosuchomorph phytosaurs it lacks unambiguous zone taxa (contra Lucas, 2018). Other methods need to be employed to further test these correlations, as well as a continued review of the taxonomic affinities of fossil specimens using an apomorphy based approach (Nesbitt and Stocker, 2008; Bell et al., 2010; Lessner et al., 2018; Pritchard and Sues, 2019).

Biostratigraphic correlations should be made at the species level, not the genus level as assignments to genera are fluid and subjective (e.g., Langer, 2005; Schultz, 2005; Irmis et al., 2010; Parker, 2018a, 2018b). Unfortunately, Lucas' (2010, 2018) insistence on making global biostratigraphic correlations utilizing genera and disregarding numerous recent taxonomic revisions of many Late Triassic vertebrate genera and their referred specimens means that his correlations appear much more robust than they actually are (e.g., Irmis et al., 2010; Martz and Parker, 2017). In practice there are no unambiguous Otischalkian zone taxa and the presence of *Doswellia kaltenbachi* can only provide an assessment of an Otischalkian-Adamanian age. However, *D. kaltenbachi* is still important because it represents a rare cross-continental biogeographic tie between the Chinle Formation and the Newark Supergroup.

Besides *Doswellia kaltenbachi*, two other vertebrate species-level correlations occur between the Blue Mesa Member at PEFO and the Newark Supergroup. *Colognathus obscurus*, an amniote of uncertain affinities with a bizarre dento-mandibular morphology (Case, 1928, 1933; Sues and Schoch, 2013), is found in the upper part of the Blue Mesa Member (Fig. 9A–B: PEFO 43747, PEFO 37239) and from the Moncure locality in the Cumnock Formation of the Sanford Basin (NCSM 25165, NCSM 25186; Heckert et al., 2012b). *Colognathus obscurus* is also reported from the Tecovas Formation in Crosby County Texas and the Los Esteros Member of the Santa Rosa Formation (Heckert, 2006, 2010). Jaws referable to a *Colognathus*-like taxon are reported from the Middle Triassic of Germany (Schoch, 2011b; Sues and Schoch, 2013), revealing a distinctive spatiotemporal pattern shared with doswelliids such that: (1) their earliest representatives are found in the Anisian-aged Lower Keuper of Germany; (2) they occur in the latest Carnian–earliest Norian of the southern Newark Supergroup; (3) their latest representatives are found in the middle Norian Chinle Formation of Arizona and lower strata of the Dockum Group of Texas.

Uatchitodon schneideri, a putative archosauriform known only from distinctive isolated venom canal-bearing tooth crowns, is known from the upper part of the Blue Mesa Member (Fig. 9C–E: PEFO 41757, 45050), and the lower part of the Sonsela Member (MNA 207-2: Kaye and Padian, 1994), of the Chinle Formation, as well as at the Moncure locality in the Cumnock Formation (Mitchell et al., 2010). The age of the Moncure locality assemblage is estimated to be early Norian in age (~225 Ma: Whiteside et al., 2011; Heckert et al., 2012b), falling within the Conewagian LVF which is correlated to the Adamanian (Lucas, 2018). New interpretations of the absolute age of fossil localities in the Cumnock and Chinle Formations show that the temporal ranges of *Colognathus obscurus* (~225–220 Ma) and *Uatchitodon schneideri* (225–219 Ma) are early to middle Norian (Ramezani et al., 2011; Whiteside et al, 2011; Kligman et al., 2018), and fall within the Adamanian EH. The presence of these taxa in the Chinle Formation and Newark Supergroup provide potential key species level cross-Pangean ties that require further investigation.

Furthermore, the recovery of *Doswellia* cf. *D. kaltenbachi*, *Colognathus obscurus*, and *Uatchitodon schneideri* in the upper part of the Blue Mesa Member suggest that these taxa were impacted by the Adamanian-Revueltian faunal turnover event (Parker and Martz, 2011). Presently with the exception of the few aberrant specimens, for example the possible occurrence of *Trilophosaurus buettneri* from the Owl Rock Member (Kirby, 1989; see discussion in Heckert et al., 2006), the end of the Adamanian sees the loss, or at least a significant decline, in North America of many vertebrate groups including hybodont sharks (Murry and Kirby, 2002); large-bodied metoposaurs (Gee and Parker, 2018; Lucas, 2018), allokotosaurs (Kligman et al., 2020), non-mystriosuchine phytosaurs (Stocker, 2012; Martz and Parker, 2017), stagonolepidoid aetosaurs (Parker, 2014, 2016; Reyes et al., 2021), dicynodonts (Racki and Lucas, 2020), and now doswelliids. The causal mechanism for this turnover is presently unknown (e.g., Olsen et al., 2018), but it is becoming increasingly apparent as a significant event during the Late Triassic and may be heavily influential regarding extinctions preceding the end-Triassic extinction (ETE) event. It marks the beginnings of a step-wise reduction in clade diversity and low origination rates through the late Norian in many groups that go extinct at or by the ETE (e.g., non-crocodylomorph pseudosuchians), and an increase in other groups including dinosaurs (Parker, 2014; Lucas and Tanner, 2015; Parker et al., 2018; Lucas, 2018; Marsh and Parker, 2020).

CONCLUSIONS

PEFO 36739 represents an important extension of the stratigraphic range and geographic distribution of the non-archosaur archosauriform *Doswellia kaltenbachi*. The new specimen represents the first record of *Doswellia* cf. *D. kaltenbachi* in the Chinle Formation as well as in the Adamanian EH. The recognition of a longer stratigraphic and geochronological range for *Doswellia kaltenbachi* also limits its use as a zone taxon for a specific division of the Late Triassic as it is now found within two estimated holochronozones, the Otischalkian and the Adamanian, and thus simply implies a pre-Revueltian assignment for *Doswellia*-bearing strata. Moreover, Martz (2008) and Lucas (2010) argued that many proposed zone taxa for the Otischalkian (e.g., *Desmatosuchus spurensis*, *Stagonolepis robertsoni*, '*Metoposaurus*' *bakeri*) also are found in Adamanian assemblages. The discovery of the purported Otischalkian zone taxon *Doswellia kaltenbachi* in the Adamanian type assemblage further weakens proposed distinctiveness between the Sanfordian and the Conewagian assemblages (Langer, 2005). The presence of *Colognathus obscurus* and *Uatchitodon schneideri* in the upper part of the Blue Mesa Member and the southern Newark Supergroup further shows the spatiotemporal stability of vertebrate biodiversity during the Carnian/Norian transition in North America, and the importance of these assemblages as indicators of the continental vertebrate fauna of equatorial Pangea. Finally, the extension of *Doswellia kaltenbachi* into the Adamanian along with the discovery of other doswelliids such as *Rugarhynchos sixmilensis* demonstrates that the doswelliid lineage is longer lasting than previously recognized, but also raises the possibility that the Doswelliidae could be another clade affected by the Adamanian-Revueltian faunal turnover that occurred ~215 Ma (Parker and Martz, 2011).

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