

Research



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Palaeontology

A new non-mammalian eucynodont from the Chinle Formation (Triassic: Norian), and implications for the early Mesozoic equatorial cynodont record


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The Upper Triassic tetrapod fossil record of North America features a pronounced discrepancy between the assemblages of present-day Virginia and North Carolina relative to those of the American Southwest. While both are typified by large-bodied archosaurian reptiles like phytosaurs and aetosaurs, the latter notably lacks substantial representation of mammal relatives, including cynodonts. Recently collected non-mammalian eucynodontian jaws from the middle Norian Blue Mesa Member of the Chinle Formation in northeastern Arizona shed light on the Triassic cynodont record from western equatorial Pangaea. Importantly, they reveal new biogeographic connections to eastern equatorial Pangaea as well as southern portions of the supercontinent. This discovery indicates that the faunal dissimilarity previously recognized between the western and eastern portions of equatorial Pangaea is overstated and possibly reflects longstanding sampling biases, rather than a true biogeographic pattern.

1. Introduction

The Triassic fossil record preserves the earliest representatives of all major extant tetrapod groups, including lissamphibians ([1,2]), mammals ([3–5]), lepidosaurs (e.g. [6,7]), turtles (e.g. [8,9]), and archosaurs (e.g. [10]). Cynodonts, which originated by the late Permian [11] and include mammals as their extant representatives, underwent a radiation in the Triassic characterized by the diversification of two sister lineages, the cynognathians and probainognathians (e.g. [12,13]). Nested within Probainognathia are the earliest mammaliaforms, including morganucodontids, kuehneotheriids and probably haramiyids, known from the Late Triassic of Europe, Greenland, India and North America [3–5,14–16]. Cynognathians were almost exclusively herbivorous and included the traversodontids, a geographically broadly distributed clade characterized by transversely expanded, multicusped postcanine teeth [12,17]. Both groups are common elements in Late Triassic tetrapod assemblages across Pangaea, with the notable exception of present-day western North America. The Chinle Formation is of critical importance as a palaeontological and chronostratigraphic benchmark for global correlations to coeval strata because of its robust palaeontological [18], radioisotopic [19–23], palaeomagnetic [24,25] and palaeoclimatic records [22,26]. Therefore, the near-absence

of Triassic-age cynodonts from western North America is problematic, hampering a unified temporal and biogeographic understanding of the group's distribution in the Late Triassic.

The cynodont record from Upper Triassic strata in western North America includes only a single unambiguous record, *Adelobasileus cromptoni*, a purported mammaliaform represented by an isolated braincase from the Tecovas Formation of the Dockum Group (Norian; [27]) of western Texas [14]. A handful of isolated bones [28,29], jaw fragments [30,31] and isolated teeth [32–35] have been attributed to cynodonts based on features that are ambiguously interpreted or are found homoplastically in other coeval tetrapod groups (electronic supplementary material, table S1).

The depauperate cynodont record from western North America stands in contrast to that of the Upper Triassic rift basins in eastern North America, which includes probainognathian [36], traversodontid [37,38] and tritylodontid [39] eucynodonts in the Deep River, Durham, Fundy and Richmond basins of the Newark Supergroup. Whiteside *et al.* [40] hypothesized that a dry, arid climate was a driving factor in the exclusion of cynodonts, which dominated Late Triassic tetrapod assemblages at lower latitudes (0–5° N), from higher latitudes (5–20° N). This hypothesis warrants re-examination given more recent reports of cynodont material from the northernmost basin in the Newark Supergroup [38,39], and the material described herein. Here, we introduce a new taxon of eucynodont from a microvertebrate-bearing horizon in the Upper Triassic Chinle Formation that reveals previously hidden cynodont diversity in western North America.

2. Methods

Field and laboratory methods. The two jaw fragments described here were collected at Petrified Forest National Park while quarrying a fossiliferous layer (PFV 456) using hand tools. Fossil preparation was conducted under magnification using pin vices, fine artist brushes and Butvar B-76 (Eastman).

Computed tomographic methods. X-ray computed microtomography (μ CT) of PEFO 43755 was conducted at the Duke Shared Materials Facility (Duke SMIF) at Duke University with a Nikon XTH 225 ST High-Resolution X-ray Computed Tomography Scanner using the following parameters: source voltage = 165 kV; source current = 163 μ A; image pixel size = 20 μ m. Digital three-dimensional models were generated in Materialize Mimics 20.0 and imaged in Meshlab 2016. Images of μ CT slices and segmented teeth were generated using Dragonfly 2020.1.0.797.

Anatomical abbreviations. ac, canal for the inferior alveolar nerve; cr, canine tooth root; ct, canine tooth; dc, distal cusp of the postcanine tooth; ea, empty alveolus; ia, incisor alveolus; lr, lateral ridge; mc, mesial cusp of the postcanine tooth; mf, mental foramen; mg, Meckelian groove; ms, mandibular symphyseal surface; pcr, postcanine root; pct, postcanine tooth.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, New York; MNA, Museum of Northern Arizona, Flagstaff, Arizona; PEFO, Petrified Forest National Park, Petrified Forest, Arizona; TM, Ditsong National Museum of Natural History, Pretoria, South Africa; TMM, Texas Vertebrate Paleontology Collections, University of Texas at Austin, Austin, Texas; UCMP, University of California Museum of Paleontology, Berkeley, California.

3. Systematic palaeontology

Synapsida Osborn, 1903

Cynodontia Owen, 1861

Eucynodontia Kemp, 1982

Kataigidodon venetus gen. et sp. nov.

Etymology. From classical Greek 'kataigidos' (meaning 'thunderstorm'), 'odon' (meaning 'tooth') and Latin 'venetus' (meaning 'blue'). 'Thunderstorm' alludes to the name of the type locality and 'blue' refers to the Blue Mesa Member and Blue Tank at PEFO.

Holotype. PEFO 43755, anterior end of a right dentary, including I₁ alveolus, C₁, PC₁ alveolus and PC₂ (figures 1 and 2).

Paratype. PEFO 43838, anterior end of a left dentary, including I₁ alveolus, broken base of C₁, PC₁ alveolus and broken base of PC₂ (figure 2).

Type locality and horizon. PFV 456, Thunderstorm Ridge, in Petrified Forest National Park (figure 1). Upper part of the Blue Mesa Member, Chinle Formation (Late Triassic: Norian), 223.036 \pm 0.059 Ma to 220.123 \pm 0.068 Ma (approx. 221 Ma; [19,21,22]).

Diagnosis. A eucynodont that differs from all other known eucynodonts in having a unique combination of features: a large anteroposteriorly elongate mental foramen, a single large, procumbent lower incisor, and an anterior lower postcanine tooth with two mesiodistally aligned cusps of subequal size.

4. Description

The large mental foramen is anteroposteriorly longer than dorsoventrally tall. This foramen opens on the lateral side of the dentary of PEFO 43755 below the first and second postcanine teeth and opens into the Meckelian groove medially. The mental foramen occurs at the anterior end of a shallow lateral fossa above a longitudinal ridge; a corresponding longitudinal groove occurs ventral to that ridge. The large size and dimensions of this foramen differ from most eucynodonts, where the foramen is small and circular, but it bears a strong resemblance to the posterior mental foramen in the traversodontid cynodonts *Boreogomphodon jeffersoni* [37] and *Arctotraversodon plemmyridon* [38,41]. These two taxa each bear a single large elongate mental foramen, which is positioned below the second postcanine and is inset into the anterior end of an anteroposteriorly elongate fossa. Anterior to the mental foramen on the lateral surface of the dentary is a scattering of numerous tiny pits, which reflect immature bone grain. In lateral view, the preserved ventral margin of the dentary is straight. Anteriorly, the dentary is mediolaterally expanded and is widest anterior to the canine. The symphysis is incompletely preserved, and the labial alveolar wall of the incisor is missing. The Meckelian groove faces medially and is roofed by a mediolaterally wide shelf of bone housing the alveoli. The ventral margin of the groove is inset relative to the dorsal shelf. The Meckelian groove extends anteriorly to the posterior margin of the incisor alveolus.

There is an empty but dorsoventrally deep alveolus for a large procumbent incisor, similar to traversodontids (e.g. *Arctotraversodon plemmyridon* [38, Fig. 15a]; *Exaeretodon*

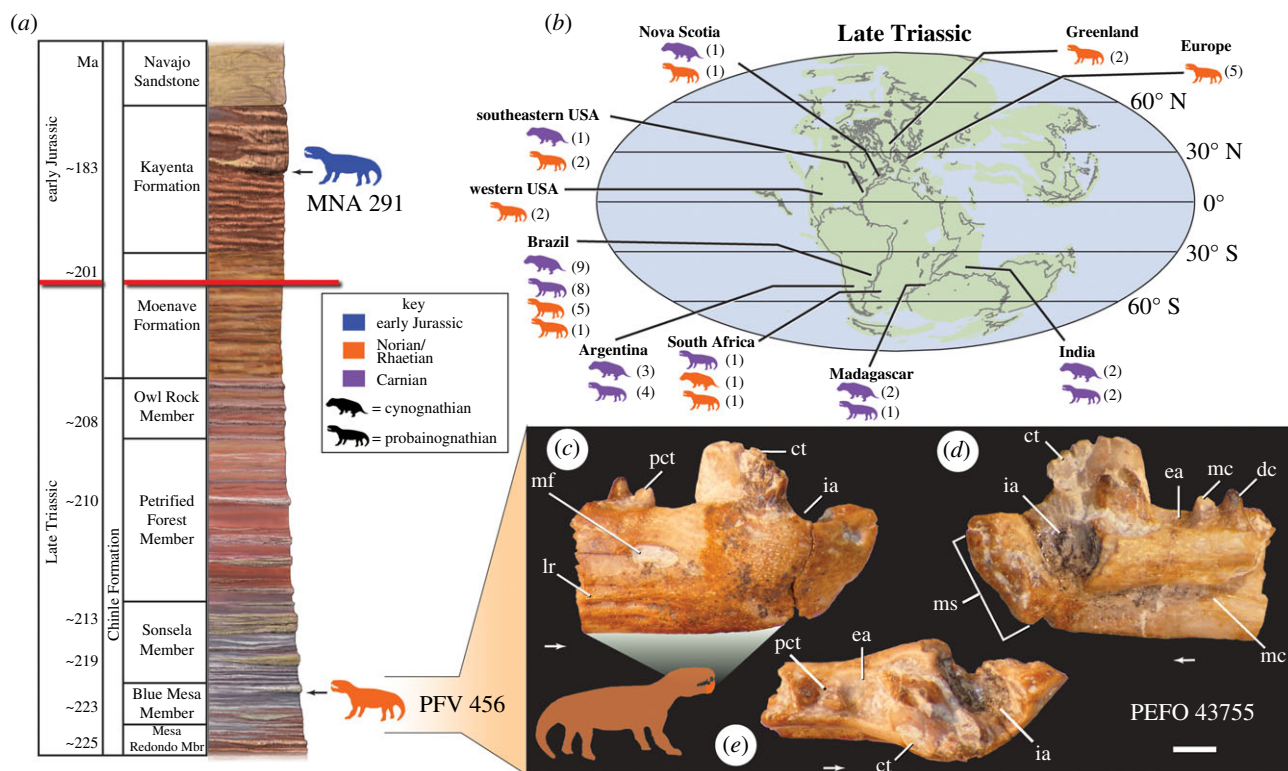


Figure 1. Stratigraphic occurrence of cynodonts in the early Mesozoic strata of the Colorado Plateau, biogeographic distribution of Late Triassic eucynodonts, and morphology of PEFO 43755 (holotype of *Kataigidodon venetus* gen. et sp. nov.). (a) Time-calibrated stratigraphic column of Upper Triassic and Lower Jurassic strata exposed on the Colorado Plateau in southwestern USA with stratigraphic positions of cynodont occurrences, including the holotypic locality of *Kataigidodon venetus* gen. et sp. nov., as well as the Kayenta Formation eucynodont assemblage (MNA 291). Triassic/Jurassic boundary marked by a red line. (b) Late Triassic palaeogeography showing the distribution of cynodont occurrences. Numbers in parentheses indicate the number of named genera. Dataset of cynodont biogeography sourced from [17]. Right dentary of *Kataigidodon venetus* gen. et sp. nov. (holotype, PEFO 43755) in lateral (c), medial (d), and dorsal (e) views. Arrows indicate anterior direction. Scale bar, 1.0 mm. Figure adapted from [1] with permission from the Royal Society.

riograndensis [42, Fig. 1a], tritheledontids (e.g. *Riograndia guai-bensis* [43, Fig. 5]; *Pachygenelus monus* [44, Fig. 1] and tritylodontids (e.g. *Kayentatherium wellsi* [45, Fig. 13]; *Dimnebitodon amarali*, MNA V3222 [45]). PEFO 43755 is more similar to some tritylodontids in having a single lower incisor, than to traversodontids and tritheledontids that typically have more than one. The labiolingually compressed canine of PEFO 43755 is broken and crushed apically. The long root of the canine extends deep into the dentary. We interpret a small hollow behind the canine as the location of a first postcanine tooth, which is represented by an alveolus floored by smooth, finished bone. The crown of the second postcanine bears two prominent cusps aligned mesiodistally, with a slight labial offset such that the mesial cusp is situated closer to the labial side of the jaw. The mesial cusp is more blade-like, and the distal cusp is more conical, with breakage truncating its apex lingually. Little of the tooth crown is visible below the cusp bases, likely because the tooth was in the process of eruption. The root of this postcanine is poorly developed, similar to those of the posterior lower molariforms of a perinate tritylodontid (TMM 43690–5.035b; [46]) or the ‘open root’ in a subadult specimen of *Thrinaxodon liorhinus* (TM 180; [47]). The anterior margin of the alveolus of the third postcanine is present. Unlike in many eucynodonts, there is no diastema between the canine and postcanine, but this condition is present in immature individuals and the diastema grows during ontogeny. The mesiodistal alignment of the canine and postcanines of PEFO 43755 is common among probainognathian eucynodonts. The canine is significantly larger than the second postcanine tooth, a condition seen in many eucynodonts, and exemplified by the extreme example

of *Trucidocynodon riograndensis* [48], but also seen in *Probainognathus jensei*, *Probesosodon* spp. and *Thrinaxodon liorhinus* [49].

Prominent lower caniniform teeth are also present in ‘sphe-nosuchian’ crocodylomorphs in the Chinle Formation such as *Hesperosuchus agilis* (AMNH FR 6758) and an unnamed PEFO taxon (PEFO 23327/UCMP 129470). However, in those specimens, the anteroventral margin of the dentary is expanded ventrally, there is a more dorsal row of mental foramina rather than a single large opening, and the Meckelian groove is not as deeply inset into the medial side of the dentary. Those specimens also preserve interdental plates, which are structures apomorphic for archosauromorphs [50] and absent in cynodonts.

5. Discussion

Prior to the discovery of *Kataigidodon venetus*, the only other unambiguous cynodont fossil from the Late Triassic of western North America was the basicranium of *Adelobasileus cromptoni* from the lower part of the Tecovas Formation (Dockum Group) in Crosby County, Texas ([14; see electronic supplementary material, data S1 and S2] for discussion on other putative cynodonts). The age of that locality is not well constrained, but the Tecovas Formation is equivalent to the lower unit of the Cooper Canyon Formation in Garza County, Texas [27], which overlies the Boren Ranch sandstone, which has been dated to approximately 225 Ma [51–53]. As such, *Adelobasileus cromptoni* is no older than 225 Ma, which is within a few million years of *Kataigidodon venetus* from the Chinle Formation at

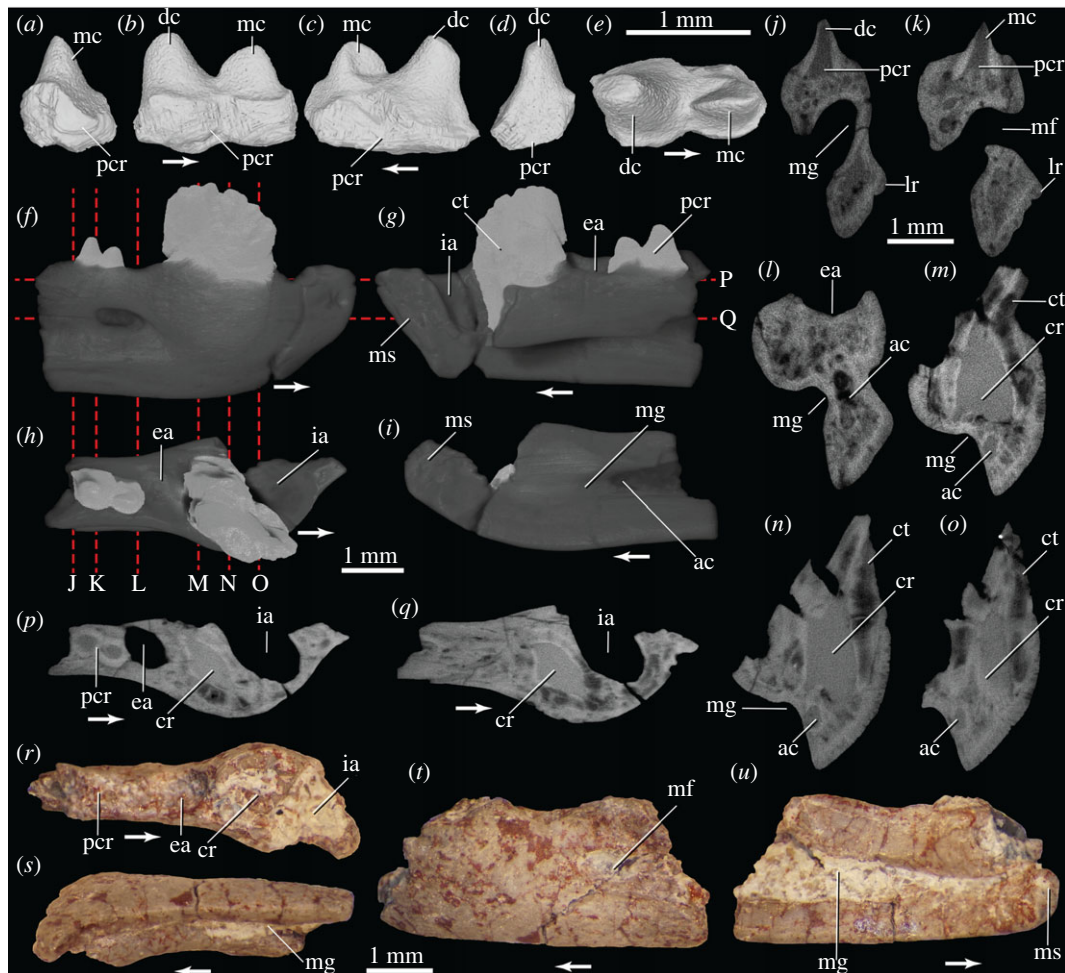


Figure 2. Images of 3D surface models and μ CT cross sections of holotypic right dentary PEFO 43755 (a–q), and photographs of paratypic left dentary PEFO 43838 (r–u). (a–e) Three-dimensional surface reconstruction of postcanine tooth in anterior (a), buccal (b), lingual (c), anterior (d), and occlusal (e) views. (f–i) Three-dimensional surface reconstruction with dentition coloured light grey and jaw tissue coloured dark grey in buccal (f), lingual (g), occlusal (h), and ventral (i) views. (j–o) Coronal μ CT cross sections. (p,q) Axial μ CT cross sections. (r–u) Jaw in occlusal (r), ventral (s), buccal (t) and lingual (u) views. Arrows indicate anterior direction. Dashed red lines indicate location of μ CT cross section.

PEFO. It should be emphasized that the Tecovas Formation is Norian in age (not Carnian, *contra* [14]), and *Adelobasileus cromptoni* almost certainly comes from the Adamanian holochron based on the presence of non-pseudopalatine leptosuchomorph phytosaurs in neighbouring localities within the Tecovas Formation [14,54,55]. The most recent phylogenetic analyses of epicynodonts suggest that *Adelobasileus cromptoni* is an early-diverging mammaliaform [56,57]. It is interesting to note that the bulk of Late Triassic cynodont fossils from eastern North America are of traversodontid cynognathians (e.g. [37]) but there is also at least one probainognathian, *Microconodon tenuirostris* [36]. In the southwestern USA, the converse is true: the only two undisputed Late Triassic cynodonts are probainognathians whereas there are as yet no unambiguous records of traversodontids (see electronic supplementary material). Whether this is a true biogeographic signal or merely an artefact of sampling is currently unclear.

Whiteside *et al.* [40] demonstrated that the Late Triassic cynodont fossil record of eastern North America bears a strong climatic overprint. Cynodonts were common in the southernmost rift basins of the Newark Supergroup, possibly owing to physiological constraints restricting them to living inside of a 6° humid equatorial band. Outside of this band, herbivorous cynodonts were largely replaced by similarly sized herbivorous procolophonid reptiles. Despite its explanatory

power, Whiteside *et al.*'s [40] biogeographic hypothesis has been difficult to extend beyond eastern North America. For example, the coeval Chinle Formation of western North America shares many of the same types of large-bodied reptile taxa with the eastern deposits regardless of palaeolatitude, and traditionally has been considered to have been deposited under a sub-arid to arid climate regime [40], but it has few procolophonids [58,59]. However, more recent isotopic data from the Blue Mesa Member and lower Sonsela Member suggest that these lower beds of the Chinle Formation were deposited in a humid climate prior to pronounced aridification at approximately 217 Ma [22], a shift likely driven by the northward drift of the North American Plate out of the humid equatorial zone [40]. Therefore, we hypothesize that the presence of *Katigidodon venetus* and *Adelobasileus cromptoni* conforms with the hypothesis of climate predictably influencing the biogeography of Late Triassic cynodonts [40]. If the pattern of procolophonid occurrence in the Triassic strata of western North America matched that of the Newark Supergroup, this group would be expected to occur in rocks deposited only after the climatic shift at approximately 215 Ma. Of the two relevant procolophonid occurrences, one is from the Rhaetian-aged Owl Rock Member of the Chinle Formation in Arizona [59], and the other from the Miller Ranch sandstone of the middle unit of the Cooper Canyon Formation in Texas

Revueltian holochron correlative to strata younger than 215 Ma in the Chinle Formation [27,55,58]. It is therefore possible that procolophonid distribution is driven by climate across the North American continent in the Late Triassic, a pattern that could be further revealed by increased examination of procolophonid-bearing beds in the upper part of the Chinle Formation.

Understanding long-term tetrapod faunal dynamics in equatorial latitudes is currently hampered by a spotty fossil record. Prior to the Late Triassic assemblages discussed above, an approximately 35 Myr gap exists before the next oldest terrestrial equatorial tetrapod assemblages, which hail from late Permian sequences in Morocco and Niger [60–64]. Synapsids are rare or absent in these African assemblages [64], which are instead dominated by temnospondyl amphibians, parareptiles and captorhinid reptiles. Unlike the Late Triassic equatorial assemblages of North America, those of the late Permian of North Africa existed under semi-arid to hyper-arid conditions [65]. However, similar to the situation in eastern North America during the Late Triassic, reptiles were the common herbivores in Permian arid environments, in stark contrast to synapsids forming tetrapod herbivore communities at higher latitudes under more temperate palaeoclimates. Additional research is needed to clarify to what degree, and under what circumstances, Permo-Triassic tetrapod community structure was influenced by climate.

The earliest post-Triassic cynodont assemblage in western North America is fairly diverse and comes from the early Jurassic (Pliensbachian) ‘silty facies’ of the Kayenta Formation in Arizona [66]. It comprises the tritylodontids *Kayentatherium welllesi* [67,68], *Dinnebitodon amarali* [45] and *Oligokyphus* sp. [69], the morganucodontid *Dinnetherium neorum* [70] and a purported haramiyid mammaliaform [70]. This assemblage (MNA 291, figure 1) post-dates the Late Triassic eucynodont reported here from the Chinle Formation by nearly 35 Myr [71].

6. Conclusion

The Blue Mesa Member of the Chinle Formation has yielded the second unambiguous cynodont record from western equatorial Pangaea and the first in the Chinle Formation, a diversity that stands to be increased by collecting efforts

focused on microvertebrate bonebeds. Sedimentological data indicate that the lowest beds of the Chinle Formation were deposited under humid, equatorial conditions [22], a climatic regime further supported by the occurrence of cynodonts, which may be restricted to humid climates in the Late Triassic of North America [40]. The Triassic is notable for the appearance of early members of the major extant tetrapod clades, and the addition of a eucynodont to the upper Blue Mesa Member assemblage, which also includes stem-anurans [1], lepidosaurs [72], dinosaurs [73] and crocodylomorphs [74], underscores the importance of these strata as a window onto the origins of modern tetrapod communities.

Data accessibility. Supplementary material referenced herein are provided as a separate electronic file. Electronic supplementary materials: S1. Table of putative cynodont occurrences from Triassic-aged sites in western North America; S2. Discussion of taxonomic affinities for specimens referenced in the table in S1. CT scan data of holotype material are available through Morphosource project 32548 (https://www.morphosource.org/Detail/SpecimenDetail/Show/specimen_id/32548).

Authors' contributions. B.T.K. carried out fieldwork, specimen preparation and CT scanning, conceived and designed the study, and drafted the manuscript. A.D.M. carried out fieldwork, designed the study and drafted the manuscript. H.D.S. contributed to design of the study and drafting of the manuscript. C.A.S. contributed to design of the study and drafting of the manuscript. All authors provided final approval for publication and agree to be held accountable for the work performed herein.

Competing interests. The authors declare no competing interests.

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