On the Validity and Phylogenetic Position of *Eubrachiosaurus browni*, a Kannemeyeriiform Dicynodont (Anomodontia) from Triassic North America

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Abstract

The large dicynodont *Eubrachiosaurus browni* from the Upper Triassic Popo Agie Formation of Wyoming is redescribed. *Eubrachiosaurus* is a valid taxon that differs from *Placerias hesternus*, with which it was previously synonymized, by greater anteroposterior expansion of the scapula dorsally and a very large, nearly rectangular humeral ectepicondyle with a broad supinator process. Inclusion of *Eubrachiosaurus* in a revised phylogenetic analysis of anomodont therapsids indicates that it is a stahleckeriid closely related to the South American genera *Ischigualastia* and *Jachaleria*. The recognition of *Eubrachiosaurus* as a distinct lineage of North American dicynodonts, combined with other recent discoveries in the eastern USA and Europe, alters our perception of Late Triassic dicynodont diversity in the northern hemisphere. Rather than being isolated relicts in previously therapsid-dominated regions, Late Triassic stahleckeriid dicynodonts were continuing to disperse and diversify, even in areas like western North America that were otherwise uninhabited by coeval therapsids (i.e., cynodonts).

Introduction

The Triassic is generally considered a time of diminishing fortunes for the synapsid lineage [1,2]. Compared to their Permian heyday, Triassic synapsids were relatively species-poor and ecologically restricted. The canonical example of this trend is the anomalodont subclade Dicyonodontia. Once the dominant Permian terrestrial herbivores in terms of abundance, species richness, and ecological diversity, only four lineages of dicynodonts survived the Permo-Triassic extinction [3,4]. Of these four, two (Lystrosauridae and Myosauridae) were post-extinction “disaster taxa” that did not survive beyond the Early Triassic [5] and one (Kingorididae) was extremely rare (Kombuisia, the sole Triassic genus, is known from four specimens [6,7]). Only the Kannemeyeriformes underwent a significant diversification during the Triassic, with roughly 40 known species [4,8]. Unlike Permian anomalodonts, however, which are known from ~90 species spanning mouse-to-rhinoceros sizes and occupying an array of niches (including lissosaurial and arborescent forms) [9,10], all kannemeyeriforms were medium- to large-bodied [11], graviporous herbivores with relatively erect posture and gait [12,13].

Unlike cynodonts, which show a primarily Gondwanan distribution [14], kannemeyeriform dicynodonts were distributed worldwide in the Middle Triassic [4]. In addition to the well-known dicynodont records of South America and Africa, assemblages with multiple sympatric kannemeyeriform taxa are known from the Anisian of Russia and China [15,16]. Fitting the concept of progressive synapsid decline, Late Triassic kannemeyeriforms are by contrast present in low abundance, and in most assemblages where they occur only a single species is present. They are also thought to be geographically restricted: until recently only a single Late Triassic dicynodont species was known outside of South America. That species, *Placerias hesternus*, is usually listed as the only Late Triassic North American dicynodont [17,18]. *Placerias* is best known from the Placerias Quarry in eastern Arizona (Blue Mesa Member, Chinle Formation), which yielded roughly 1600 *Placerias* elements representing at least 41 individuals [19,20]. However, this is an exceptional case and may represent a drought-driven concentration of individuals [19]; outside the Placerias Quarry this taxon is extremely rare, with only a handful of isolated elements known from less than 10 other localities in the American southwest [18] and North Carolina [21,22]. Of these, the most significant specimen is a relatively complete skull (MNA V8464) that was briefly described by Lucas and Heckert [18], although they oriented the specimen upside down (Figures 1A, 1B). When the specimen is properly oriented (Figure 1C), it bears a striking resemblance to the hypothetical reconstruction of the skull developed by Camp and Welles [23] and modified by Cox [24] (Figure 1D). As such, this specimen confirms the accuracy of the Camp and Welles/Cox reconstruction, which has been used extensively in studies of the systematic position of *Placerias* [25–27].

However, *Placerias* is not the only dicynodont described from the Late Triassic of North America. Williston [28] described two
dicynodont genera from the Popo Agie Formation of Wyoming, *Eubrachiosaurus browni* and *Brachybrachium brevipes*. Lucas and Hunt [17] considered these taxa junior synonyms of *Placerias hesternus*, a position maintained in most subsequent studies (e.g., [18]). However, Long and Murry [29] questioned the synonymy of *Eubrachiosaurus* and *Placerias*, noting that the ectepicondyle of *Eubrachiosaurus* was enlarged as in *Ischigualastia*. Unfortunately, most of Williston’s dicynodont material from Popo Agie has been lost, hindering restudy of this taxon. Of the holotype of *Eubrachiosaurus browni* (FMNH UC 633), the humerus and pelvis have been lost, only the scapula remains. The holotypic partial humerus of *Brachybrachium brevipes* has been lost entirely. Searches of the Field Museum and University of Chicago (these specimens were originally housed at the University of Chicago Walker Museum) have failed to locate any of these missing specimens and it is probable that they were discarded or destroyed prior to the transfer between institutions. Fortunately, and unusually for the time period, Williston [28] published photographs of these elements, so we can be confident of their morphology. In this contribution we redescribe *Eubrachiosaurus browni* based on study of the remaining portion of the holotype and the original photographs, address its supposed synonymy with *Placerias*, and investigate the phylogenetic position of the taxon and its implications for Late Triassic dicynodont diversity.

**Materials and Methods**

We compared the surviving and photographed material of problematic North American kannemeyeriforms (*Eubrachiosaurus browni*, *Brachybrachium brevipes*, NMMNH P-13001) with kannemeyeriform postcranial material we have examined firsthand: *Angonisaurus cruickshanki* (NHMUK R9732); *Dinodontosaurus pedroanus* (MCN 3584, MCP 130, MCP 4172, MCZ 1670, 1687, 3108, 3454, UFRGS PV0115T, PV0161T, PV0161T); *Dolichuranus primaevus* (CGP/1/191A); *Ischigualastia jenseni* (MACN 18055, MCZ 3119, PVL 3807, PVSV 607); *Jachaleria canadensis* (UFRGS PV0150T, PV0151T, PV0287T); *Kannemeyeria simocephalus* (BP/1/ 4523, 4550, 5624, CAMZM T757, ELM 1, NHMUK R3740, R3741, R3758, R3760, R3761, R3762, SAM-PK-2771, 3017, UCMP 38373); *Parakannemeyeria youngi* (PIN 2422/1); *Placerias hesternus* (MNA V2713, UCMP 24782, 25093, 25361, 25373, 32393, 32394, 32459, USNM 2198); *Rhadiodromus klimovi* (PIN 159/1); *Shansiodon wangi* (IVPP V2415); *Sinokannemeyeria yingchiaoensis* (IVPP V974); *Stahleckeria potens* (GPIT/RE/8001); *Tetragonias njalilus* (CAMZM T754, GPIT/RE/7110); *Wadiasaurus indicus* (ISI R175/1); *Xiniankannemeyeria brevirostris* (IVPP V4453, 4458); and *Zambiasaurus submersus* (NHMUK R9068, 9069, 9089, 9091, 9103, 9106, 9109, 9113, 9118, 9122, 9140). We also made comparisons based on descriptions from the literature [30–36]. No permits were required for the described study, which complied with all relevant regulations.  

**Institutional Abbreviations:** AMNH, American Museum of Natural History, New York, NY, USA; BP, Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa; CAMZM, University Museum of Zoology, Cambridge, UK; CGP, Council for Geosciences, Pretoria, South Africa; ELM, East London Museum, East London, South Africa; FMNH, Field Museum of Natural History, Chicago, IL, USA; ISI, Indian Statistical Institute, Kolkata, India; IVPP, Institute for Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; GPIT, Institut für Geowissenschaften, Eberhard Karls Universität Tübingen, Tübingen, Germany;
MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MCN, Museo de Ciencias Naturales, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MNA, Museum of Northern Arizona, Flagstaff, AZ, USA; NCSM, North Carolina Museum of Natural Sciences, Raleigh, NC, USA; NHCC, National Heritage Conservation Commission, Lusaka, Zambia; NHMUK, The Natural History Museum, London, UK; NMMNH, New Mexico Museum of Natural History & Science, Albuquerque, NM, USA; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PVL, Museu Mário Lillo de Ciências Naturais, San Miguel de Tucumán, Argentina; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; SAM, Iziko, the South African Museum, Cape Town, South Africa; SGU, Saratov State University, Moscow, Russia; TSK, T. S. Kemp Collection, Oxford University, Oxford, UK; UCMP, University of California Museum of Paleontology, Berkeley, CA, USA; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; US, University of Stellenbosch, Stellenbosch, South Africa; USNM, National Museum of Natural History, Washington, DC, USA.

Results

Systematic Palaeontology

Therapsida Broom, 1905 [37].
Anomodontia Owen, 1860 [38].
Dirynodontia Owen, 1860 [38].
Kannemeyeriformes Maisch, 2001 [26].
Stahleckeriidae (Lehman, 1961) [39].
Eubrachiosaurus Williston, 1904 [28].
Parakannemeyeria Williston, 1904 [28].

ZooBank Life Science Identifier (LSID). urn:lsid:zoobank.org:act:42BD6746-42DB-4F09-851E-6297F43BB3EE.

Type species. Eubrachiosaurus browni Williston, 1904 [28].

Diagnosis. As for the type and only species. Eubrachiosaurus browni Williston, 1904 [28].

Syn. Brachynychium brevipes Williston, 1904 [28].

ZooBank Life Science Identifier (LSID). urn:lsid:zoobank.org:act:BC6563A0-02E9-4CDD-884C-27EC8BE8F0B7.

Holotype. FMNH UC 633, originally a partial left scapula, left humerus, and left pelvis, of which only the scapula remains.

Type locality and Horizon. Little Popo Agie River, near Lander, Fremont County, Wyoming. Popo Agie Formation, Chugwater Group, Late Triassic (Norian).

Diagnosis. Kannemeyeriform dicynodont characterized by a unique combination of postcranial characters: well-developed scapular spine; scapula strongly constricted at level of acromion; anterior and distal edges of deltoid process more prominent than acromion; humeral ectepicondyle large, nearly rectangular, anterior iliac blade long, curving anteroventrally. An autapomorphy of Eubrachiosaurus is the extreme curvature of the anterodorsal margin of the iliac blade.

Scapula

The sole remaining element of the holotype is a left scapula (Figure 2). This specimen is badly weathered and fragmentary, with the anterior and posterior edges of the proximal portion of the scapula broken off. Several sections of the specimen down its length are reconstructed with plaster. This specimen is 48.4 cm total length along the long axis. The scapular spine is mostly reconstructed with plaster, but from the preserved sections it was clearly robust and prominent. The acromion process is worn, with only the base remaining, but the base is well developed and protrudes laterally and slightly anteriorly. The scapula is anteroposteriorly narrow (constricted) at the level of the acromion and gradually widens dorsally, although the maximum width of the dorsal portion is unknown as this region is badly damaged. Part of the lip around the glenoid fossa is preserved at the posteroverentral edge of the scapula. The anterodorsal portion of the scapula is broadly flattened and slightly concave, as in other kannemeyeriforms. The medial surface of the scapula is almost entirely obscured by plaster and a metal rod made to support the element.

The poor preservation of the scapula of Eubrachiosaurus complicates comparisons with other taxa, but several distinctions can be made. Kannemeyeriform scapulae can be divided into three general morphotypes (Figure 3): shansiodontids, which have a relatively large, robust, anteriorly-directed acromion process, no distinct scapular spine, and a short dorsal portion of the scapula (here referring to the entire scapular blade above the level of the acromion) which flares broadly dorsally (Figures 3A, 3B); “kannemeyerids”, which have a relatively small, anteriorly-directed acromion process, weak, elongate scapular spine (if present), and a tall dorsal portion of the scapula with very gradual expansion dorsally (unlike the flared condition in shansiodontids) (Figures 3D, 3E); and stahleckeriids, which have a relatively small, anterolaterally-directed acromion process, tall dorsal portion of the scapula that expands broadly dorsally, and a distinct postero-anterior slope to the dorsal margin of the scapula (Figures 3C, 3F).

The scapular spine is variable in stahleckeriids; in Stahleckeria it is well developed (Figure 3F), whereas in Jachaleria (Figure 3C) [33] and Ichigiovia (Figure 4B, 24) it is absent.

Although Placia has been recovered as a stahleckeriid in our previous phylogenies [27], its scapular morphology is distinct from other members of the clade (Figure 4A). A strong scapular spine is present, but the morphology of the dorsal portion of the scapula is more similar to the “kannemeyerid” condition: tall and only slightly expanded dorsally (although not to the degree of Kannemeryia (Figure 3D) or Parakannemeyeria (90]). The scapula of Eubrachiosaurus has a similarly tall dorsal portion as in Placia, but with more extreme dorsal expansion (especially considering that the anterior and posterior edges are broken off dorsally). The scapula is markedly more anteroposteriorly constricted at the level of the acromion process in Eubrachiosaurus than in Placia. Eubrachiosaurus is similar to Placia in having a long, robust scapular spine, but this morphology is also present in Stahleckeria. In general, the scapula of Eubrachiosaurus is most similar to that of Stahleckeria among kannemeyeriforms, although the dorsal portion is less anteroposteriorly broad than Stahleckeria (even accounting for the missing edges dorsally, compare degree of dorsal expansion in Figure 2 with Figure 3F).

The scapula of Placia bears a well-developed, mound-like tubercle for attachment of the triceps (Figure 4A); this type of tubercle also occurs in Zambiasaurus (Figure 4C). A distinct tricipital tubercle is absent in most kannemeyeriforms. A weak tubercle occurs in Kannemeryia (Figure 3D) and a sharply pointed tubercle quite unlike the broad mound of Placia occurs in Jachaleria (Figure 3C). The relevant region is mostly reconstructed with plaster in Eubrachiosaurus, but there is no sign of such a tubercle at the edges, suggesting that if this feature was present it was not the mound-like structure as in Placia.
Humerus

The recovered forelimb material of *Eubrachiosaurus browni* was a largely complete left humerus, although Williston’s ([28]:Fig. 3) figure of this specimen shows that part of the proximal portion was reconstructed with plaster (see Figure 5A). Williston [28] only figured the dorsal view, and although he provided information on the ventral side, its degree of reconstruction is uncertain. The shaft of the humerus was narrow and the deltopectoral crest was massive and flared, with a distinct perpendicular angle between its proximal and distal margins. According to Williston [28], the humerus was 44.0 cm long, with 23.7 cm greatest width of the proximal portion, 6.8 cm least width of the shaft, and 26.3 cm greatest width of the distal portion.

The morphology of the humerus in *Eubrachiosaurus* differs strongly from that of *Placerias* (Figure 5A, 5D). The shape of the deltopectoral crest is similar in these two taxa, but this morphology is common among kannemeyeriiforms (also present in, e.g., *Ischigualastia, Stahleckeria*) (Figure 5B). *Placerias* also exhibits an unusual condition, otherwise known only in *Zambiasaurus* (Figure 6) and the unnamed Polish dicynodont [35]: a short ectepicondyle with a very tall, subvertical supinator process close to the shaft. In *Eubrachiosaurus*, the ectepicondyle is long, massive, and roughly rectangular, with an enlarged, nearly horizontal supinator process extending far out on the ectepicondyle. This morphology is closest to the condition in *Ischigualastia* (Figure 5B), as noted by Long and Murry [29], although similar ectepicondyles are also present in *Sinokannemeyeria* [30] and *Dimodontosaurus* [40]. *Stahleckeria* has a massive ectepicondyle as well, but with a more sloping dorsal edge and somewhat weaker supinator process [40]. In both *Eubrachiosaurs* and *Ischigualastia*, the rim of the trochlea is very pronounced dorsally, forming a prominent ridge beneath the attachment of the M. triceps humeralis medialis (Figures 5A, 5B). Development of this ridge (and size of the trochlea in general) is ontogenetically variable in kannemeyeriiforms (with weak development on the bone in juveniles, see Figures 5E, 5F). But even in specimens of similar size, this ridge is more weakly developed in *Stahleckeria* and *Placerias* (e.g., Figure 6A) than *Eubrachiosaurus* and *Ischigualastia*.

Although the humerus of *Eubrachiosaurus* is very similar to that of *Ischigualastia*, there are distinctions between them. The attachment site for the M. subcoracoscapularis is rounder and less pronounced in *Eubrachiosaurus* than *Ischigualastia*, and *Eubrachiosaurus* has a less acute angle at the proximal end of the deltopectoral crest (Figures 5A, 5B). The entepicondylar process of *Eubrachiosaurus* is larger and located more distally than in *Ischigualastia*. The humeral shaft of *Ischigualastia* is more massive than that of *Eubrachiosaurus*, although it is possible this is a preservational artifact in *Eubrachiosaurus*.

Pelvis

Williston’s description [28] indicates that the pelvis of *Eubrachiosaurus* was fragmentary, missing most of the posterior part of the ilium and the anterior tip of the iliac blade (also known as the anterior iliac process) (Figure 7A). The acetabulum was intact, with fragmentary antero- and posteroverentral portions of the pubis and ischium (respectively). According to Williston [28], the dorsoventral width of the anterior iliac process was 17.0 cm, and the lengths of the pubis and ischium from the rim of the acetabulum were 14.5 cm and 20.0 cm (respectively). What was present of these bones was similar to the morphology seen in other kannemeyeriiforms (Figure 8). Kannemeyeriiforms generally have a long, anteroventrally curving anterior iliac process and short posterior iliac process. In some taxa the anteroventral curvature of the anterior iliac process is slight (e.g., *Shansiodon, Angoniasaurus*) (Figures 7D, 8A). *Stahleckeria* has an extreme version of this morphology in which the anterior iliac process begins curving anteriorly immediately above the acetabulum and is particularly
Triassic kannemeyeriiforms, had a posterior iliac process. Placerias (Figures 8B, 8D). No unbroken iliac material is known for Jachaleria and ulum (giving the appearance of an iliac 'shaft') and in this taxon Ischigualastia a more weakly curved, shorter anterior process (Figure 8C). In comparative purposes.

B, C, D, and F are right scapulae that have been reversed for phylogenetic purposes. Williston's [28] hypothetical outline of the pelvis of Eubrachiosaurus browni (dashed lines in Figure 7A) roughly similar to Ischigualastia, Jachaleria, and Kannemeyeria. Eubrachiosaurus had a distinctly elongate, strongly anteroventrally curving anterior iliac process (Figure 7A). Although incomplete, enough of this process was preserved to show that it had extreme downward curvature of the anteroventral margin of the blade above the acetabulum, differing from the typical Kannemeyeria-like condition. Williston's [28] hypothetical outline of the pelvis of Eubrachiosaurus (dashed lines in Figure 7A) was made before kannemeyeriform pelves were known from the Middle Permian of Brazil and three Triassic eccentricus (see Appendix S1), our analysis remains focused on anomodont interrelationships, not global therapsid relationships, and we did not include many general therapsid characters (see, e.g., [42]).

We added four anomodont taxa to the analysis of Kammerer et al. [27]: the recently described basal anomodont Tiaraaudens eccentricus from the Middle Permian of Brazil and three Triassic kannemeyeriforms (Eubrachiosaurus browni from Wyoming, Shambakannemeyera from China, and Zambiasaurus submersus from Zambia). Two nominal species of Shambakannemeyera exist (S. xilongouensis Cheng, 1980 [43], the type, and S. buerdongia Li, 1980 [44]), but because they are extremely similar and probably synonymous we coded them as a single taxon here. Codings were based on personal examination of the type (for Eubrachiosaurus and S. buerdongia) and referred (for Zambiasaurus) specimens, examina-

**Figure 3. Kannemeyeriform scapulae in lateral view.** (A) IVPP V2415, Shansiodon wangi (dotted line indicates anterior edge of scapular blade, broken off in this specimen but restored based on the condition in Tetragonias and Rhinodicyonodon); (B) MCN PV 3584, Dinodontosaurus pedroamum; (C) UFRGS PV-0151T, Jachaleria candelariensis (acromion process broken off in this specimen, arrow indicates base of process); (D) NHMUK R3740, Kannemeyeria simocephalus; (E) IVPP V974, Sinokannemeyeria yingchaoensis; (F) GPIT/RE/8001, Stahleckeria potens. The specimens in A and E are left scapulae, the specimens in B, C, D, and F are right scapulae that have been reversed for comparative purposes. Abbreviations: ac, acromion process; ss, scapular spine; tri, tricipital tubercle. Scale bars equal 5 cm. (formatted for 2 column width).

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**Figure 4. Stahleckerid scapulae in lateral view.** (A) UCMP 24782, left scapula of Placerias hesternus (partially reconstructed, plaster is light brown); (B) PVL 3807, distal portion of left scapula of Ischigualastia jenseni; (C) NHMUK R9068, distal portion of left scapula of Zambiasaurus submersus (acromion process broken off in this specimen, arrow indicates base of process). Abbreviations: ac, acromion process; tri, tricipital tubercle. Scale bars equal 5 cm. (formatted for 1.5 column width).

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**Newly Included Taxa**

The analysis of Kammerer et al. [27] used the most basal known anomodont, Biseridentis gilavicus [41], as the outgroup. For this analysis we included non-anomodont outgroups, adding representatives of the other major therapsid groups: Biarmosuchia (represented by Biarmosuchus tener and Hipposaurus boonstraian), Dinocephalia (Archaeosodon praeventor and Titanophones potens), Gorgonopsia (Gorgonops torvus), and Eutheriodontia (the basal theriocephalians Lycosuchus zanderi and Glanosuchus macrops). These taxa were included to provide more robust polarity for anomodont characters, as Biseridentis is known from fragmentary material and could not be coded for many characters (including all postcranial characters). It should be noted that although we added several characters to the analysis of Kammerer et al. [27] (see Appendix S1), our analysis remains focused on anomodont interrelationships, not global therapsid relationships, and we did not include many general therapsid characters (see, e.g., [42]).

To determine the relationships of Eubrachiosaurus browni, we used a modified version of the anomodont matrix of Kammerer et al. [27]. Changes to that analysis (new taxa, new characters, and character state/coding revisions) are detailed below.
tion of specimen casts (for the holotypes of Z. submersus and T. eccentricus), and reference to the literature (for S. xilougouensis and the lost elements of Eubrachiosaurus [28,43]) (see Appendix S1 for specimen list).

Excluded Kannemeyeriiform Taxa

Although we attempted to sample kannemeyeriiform dicynodonts as comprehensively as possible in the current analysis, some taxa necessarily required exclusion. We did not include a number of nominal Russian kannemeyeriiforms that are based on extremely fragmentary remains, several of which may represent nomina dubia. Calleonasus furvus, Elatosaurus facetus, and Plantodonistr pechoriensis are known only from isolated nasals [45–47]. Nasoplanites danilovi and Putillosaurus sennikovi are known from premaxillary tips and partial palates [46,48]. Parvobestiola bashkiriensis is known from a partial snout roof comprising the left nasal, prefrontal, and part of the frontal [46]. Cristonasus koltsaeensis is known from an isolated left fragment of premaxilla [46]. The diagnoses of these taxa rely heavily on bone surface ornamentation, which is problematic given that this feature varies both as a result of preservational artifact and ontogenetic change in kannemeyeriiforms (pers. obs. of Dinodontosaurus pedroanum and Kannemeyeria simocephalus growth series). The majority of these taxa (Calleonasus, Cristonasus, Nasoplanites, and Parvobestiola) are from the Middle Triassic Donguz Formation of Bashkortostan and their validity relative to each other and the more completely known Donguz kannemeyeriiforms (Rabidosaurus, Rhadiodromus, Rhinodicynodon, and Uralokannemeyeria) is suspect. Few of these taxa can be coded for any characters in our phylogenetic analysis. Cristonasus is notable for having the palatal surface of the premaxilla exposed in lateral view, a character state restricted to non-shansiodontid kannemeyeriiforms albeit variable within this group. Among Donguz taxa known from nearly complete skulls, this feature is only present in Uralokannemeyeria. Surkov [46] distinguished Cristonasus from Uralokannemeyeria based on relative snout width and premaxillary surface ornamentation, but this distinction is uncertain as the premaxilla is not completely preserved in either taxon. It is possible that these taxa are synonymous, but the holotype of Cristonasus is too incomplete to be sure.

Edaxosaurus edentatus was described based on an isolated left caniniform process (SGU D-104/4–1) from the Middle Triassic Donguz Formation of Orenburg [45]. Other than lacking a tusk, this caniniform process is very similar to that of Uralokannemeyeria from the same locality. In particular, the strongly-developed ridge curving anterolaterally down the length of the caniniform process is unique to Uralokannemeyeria and the Indian Rechnisaurus among kannemeyeriiforms. Intraspecific tusk presence/absence is well known in Permian dicynodonts: in some taxa

Figure 5. Kannemeyeriiform humeri in dorsal view. (A) lost element from the holotype of Eubrachiosaurus browni (modified from [28]); (B) PVL 3807, Ischigualastia jenseni; (C) NHMUK R3741, Kannemeyeria simocephalus; (D) USNM 2198, Placerias hesternus; (E) IVPP V4457, Xiyukanannemeyeria breviostris; (F) IVPP V2415, Shansiodon wangi. The specimens in A, C, and F are left humeri, the specimens in B, D, and E are right humeri that have been reversed for comparative purposes. Hatched areas indicate plaster reconstruction, dotted lines indicate missing portions of specimen. Abbreviations: dpc, deltopectoral crest; ect, ectepicondyle; ent, entepicondyle; h, humeral head; scs, attachment site for M. subcoracoscapularis; su, supinator process; thm, attachment site for M. triceps humeralis medialis; tr, trochlea. Scale bars equal 5 cm. [formatted for 2 column width]. doi:10.1371/journal.pone.0064203.g005
representing sexual dimorphism (e.g., *Dictodon*, *Pristerodon*) [49,50] whereas in others it may represent individual variation (e.g., *Odontocylops*, *Tropidostoma*, *Dicynodontoides*) [51–53]. Only tusked individuals are known for most dicynodontoids (the many known skulls of *Deptosuchus*, *Dicynodon*, *Kanunneryia*, and *Lystrosaurus* are all tusked), indicating that both sexes were tusked in these taxa, but there are exceptions. Bandyopadhyay [31] described a tusked specimen of *Wadiasaurus indicus* (ISI R176), previously known from the tuskless holotype (ISI R38), arguing that these specimens represent the male and female of the species (respectively). Tusk development is also variable in *Placerias* [23]; they are present in some isolated maxillae (UCMP 27553), and absent in others (UCMP 137369). Given that the type specimens of *Edaxosaurus edentatus* and *Uralokannemeyeria vyaschikov* are from the same locality, share several unique features among kannemeyeriforms, and differ only in a character that is intraspecifically variable in at least some kannemeyeriform species, we consider the most parsimonious interpretation to be that these specimens are conspecific, with *Edaxosaurus* representing a junior synonym of *Uralokannemeyeria*.

Of the Russian kannemeyeriform ‘fragment taxa’, the only species that we recognize as clearly valid is *Elephantosaurus jachimovitschi*, known from a partial skull roof (PIN 525/25, preserving part of the frontals and the left prefrontal) and heavily worn tusks from the Middle Triassic Bukobay Formation of Bashkoria. This taxon has a unique prefrontal morphology: a large, smooth, rounded boss is present near the anterodorsal edge of the orbit and distinctly separated from a second, highly rugose prefrontal boss located anteriorly. *Elephantosaurus* is usually considered a stahleckeriid [15,54], mostly on account of its large size (interorbital width estimated ~20 cm), but the broad frontal contribution to the dorsal rim of the orbit in *Elephantosaurus* suggests that it falls outside of Stahleckeriidae. Although often described as an ‘enormous’ dicynodont, a very broad interorbital region is known in other kannemeyeriforms: both *Sinokannemeyeria* and *Stahleckeria* exceed 20 cm interorbital width in some specimens, although the individual roofing bones in these taxa are not as thick as in *Elephantosaurus*. *Elephantosaurus* was certainly a large dicynodont, but its size cannot be securely estimated given the known material and may not have exceeded that of *Stahleckeria*. Although we consider *Elephantosaurus* valid, we did not include it in the current analysis, as it could only be coded for three characters in the data set.

With regards to taxa outside of Russia, we did not include *Azarifeneria*, known from two species (*A. barrati* and *A. robustus*) from the Triassic of Morocco [55,56]. These species are based on extremely fragmentary, poorly-preserved material and their distinction from the sympatric *Mogreberia* is suspect. Finally, we excluded the gigantic dicynodont from the latest Triassic of Poland briefly described by Dzik et al. [35], as a complete description of this taxon is currently in progress (Sulej, pers. comm.).

**Character Additions and Emendations**

We added one character and ten discrete state characters to the analysis of Kammerer et al. [27]. Seven of the discrete state characters are phalangeal characters derived from previous analyses [42], three are new to this analysis. We emended a character concerning pterygoid dentition to address the unusual condition described for *Tiarajudens* and also recognized in *Anomocephalus* [57]. Finally, we recoded some character states for *Biseridens*, *Anomocephalus*, *Proictodon*, *Syops*, *Rechnisaurus*, *Wadiasaurus*, *Uralokannemeyeria*, *Rhodiodromus*, *Stahleckeria*, and *Jachaleria* based on new examination of the material and fixed some typographic errors in the data matrix of Kammerer et al. [27]. Please refer to Appendix S1 for full details.

**Phylogenetic Methods**

Our final data set includes 174 characters (see Appendices S2 and S3). One hundred fifty three of these characters are discrete binary or multistate characters, and we treated these characters as unordered and of equal weight. The remaining 21 characters are continuous. To code the continuous characters, we added a small number of new measurements to the database of Kammerer et al. [27]. Details of our measurement procedures and data processing for individual characters can be found in Kammerer et al. [27] and in Appendix S1, and the data matrix can be found as supporting information (S4). We treated the continuous characters as additive using the method of Goloboff et al. [58], and used mean values as the codings for the OTUs except in cases when only a single measurement was available for an OTU. We coded unknown and inapplicable discrete state and continuous characters as '?' [59].

We analyzed the data set using TNT 1.1 (October 2010 version) [60], and we employed two search strategies. For the first search, we used the new technology methods. We performed a driven

**Figure 6. Placerine distal humeri in dorsal view.** (A) UCMP 25361, *Placerias hesternus* (right humerus reversed for comparative purposes); (B) NHMUK R9140, *Zambiasaurus submersus* (left humerus). **Abbreviation:** su, supinator process. Scale bars equal 5 cm. [formatted for 2 column width]. doi:10.1371/journal.pone.0064203.g006
search with the initial search level set at 65, which was checked every three hits. The initial number of addition sequence replicates was 5,000, and we required the search to find the trees of shortest length ten times. We started the analysis with default settings for tree fusing, tree drifting, parsimony ratchet, and sectorial searching. In the second analysis, we used the traditional search method of TBR branch swapping with 10,000 replicates, with 10 trees held per replicate. We used *Biarmosuchus* (see above) to root the most parsimonious cladograms from both analyses. To measure support for the most parsimonious cladograms, we utilized symmetric resampling [61] and decay analysis [62, 63]. Our symmetric resampling results are based on 15,000 replicates, with 10 replicates of TBR branch swapping with two trees held per replicate for each resampling replicate. The decay analysis results are based on a sample of 596,251 suboptimal cladograms with lengths up to seven steps longer than the most parsimonious cladograms. Following the recommendations of Goloboff et al. [60], we generated the suboptimal trees through a series of traditional searches in which we incrementally increased the length of suboptimal cladograms retained as well as the number of suboptimal cladograms. The resulting cladograms were filtered to remove duplicates before the decay analysis, so the 596,251 cladograms in the sample are all unique.

**Results of Phylogenetic Analysis**

Both the new technology searches and the traditional searches discovered the same most parsimonious cladogram (986.211 steps; CI = 0.244; RI = 0.713), and the topological results are summarized in Figure 9. Of particular importance in the current context is the fact that *Eubrachiosaurus* is reconstructed within the clade Stahlekeriinae (see below for the definition of this taxon) and not as a close relative of *Placerias*. There are also some differences between the current topology and that of Kammerer et al. [27], particularly in the arrangement of basal dicynodontoid species and among kannemeyeriiforms. In part, this likely stems from our inclusion of new characters and taxa in the analysis, as well as our revised coding for *Syops vanhoepeni*. At the same time, it is important to note that most nodes in Dicynodontoida are weakly supported, and we expect there to be continued instability for some time as additional alpha taxonomic and phylogenetic work on this group proceeds.

Because this analysis is expanded from that of Kammerer et al. [27], it understandably agrees with it in most regards. In this section we will detail the novel results; for a more thorough description of all branches on the tree please refer to [27].

Relationships among the non-anomodont outgroups should not be taken as a serious phylogenetic hypothesis for these taxa, which were included to polarize characters within Anomodontia, not to analyze higher-level therapsid relationships. The topology outside of Anomodontia is an artifact of character choice, specifically our exclusion of most general therapsid characters and the characters most applicable to the outgroups.

The newly-added basal anomodont *Tiarajudens* was strongly supported as the sister taxon of *Anomocephalus*, as found by Cisneros et al. [57]. Outside of Dicynodontoida, the only major difference between the current tree and that of Kammerer et al. [27] is the recovery of *Syops vanhoepeni* as a cryptodont rather than dicynodontoid. In the current topology this taxon is a geikiid, the sister taxon of Geikiinae (*Aulacephalodon, Pelanomodon, and Geikia*) sensu Kammerer and Angielczyk [64]. *Syops* was particularly volatile in our previous analyses, where it was coded based on the incomplete, poorly-prepared type specimens of *Dicynodon vanhoepeni* (SAM-PK-11311) and *D. roberti* (SAM-PK-11325A and B). The
discovery of a new, more complete skull and mandible of Syops from the Luangwa Valley of Zambia (NHCC LB25 [65]) has permitted this taxon to be more thoroughly coded and clearly demonstrates its cryptodontian affinities. This material is currently under study by KDA and JF and will form the basis for a redescription of Syops vanhoepeni.

Interrelationships within Dicynodontoidea varied strongly depending on the treatment of certain characters in the analyses of Kammerer et al. ([27]: compare Figs. 156, 157, and 159), and the majority of these nodes continue to be weakly supported in the present analysis. Notable features of the present topology include the recovery of “Dicynodon”-grade Karoo taxa with broad temporal bars (Basilodon and Sintocephalus) as basal dicynodontoids rather than lystrosaurids. Also close to the base of Dicynodontoidea, the Russian taxa Vivaxosaurus and Delectosaurus form a clade and Dicynodon (containing only D. lacerticeps and D. huenei) is paraphyletic, but these results are very weakly supported. A clade comprised of Daptocephalus leoniceps, Dinanomodon gilli, and Peramodon amalitzkii is recovered, as was the case in Kammerer et al. [27], but with a switch in the positions of Daptocephalus and Dinanomodon. The Chinese taxa Jimusaria and Turfanodon are found to lie outside of the Lystrosauridae-Kannemeyeriiforms split. The topology within Lystrosauridae remains problematic, with divergences opposite from the observed order of appearances in the stratigraphic record of Lystrosaurus. We believe these results are related to general instability in rooting within the Dicynodontoidea, and suggest that it may be instructive in future studies to compare the results of the current tree to an analysis focused on the Triassic dicynodontoid clades (Lystrosauridae and Kannemeyeriiformes).

Within Kannemeyeriiformes, the wildcard taxon Angonisaurus is recovered at the base of the clade. Angonisaurus exhibits a problematic mosaic of shansiodontid- and stahleckeriid-like characters [66,67], and a very basal position for this taxon was recovered in some previous trees ([27]:Fig. 157). In the current analysis Dinodontosaurus lies outside of Shansiodontidae (here containing Rhinodicynodon, Shansiodon, Tetragonias, and Vinceria) as the sister taxon of the “kannemeyeriid” assemblage. “Kannemeyeriidae” is paraphyletic in the current topology, with an array of Kannemeyeria-grade taxa leading up to Stahleckeriidae. “Kannemeyeriid” paraphyly was recovered in some previous trees [27], but a notable change is the removal of Wadiasaurus and Rhodiodromus from Stahleckeriidae and Dolichuranus and Rechnisaurus from Shansiodontidae into “Kannemeyeriidae.” More stable is the recovery of a Stahleckeriidae with two major subclades, formalized below as Placeriinae (containing Placerias, Mogherberia, and Zambiasaurus) and Stahleckeriinae (containing Stahleckeria, Ischigualastia, Jachaleria, Sangusaurus, and Eubrachiosaurus).

Discussion

Validity of Eubrachiosaurus and Brachybrachium

Eubrachiosaurus browni is clearly distinct from Placerias on the basis of humeral and scapular morphology, most notably by its massive, rectangular humeral ectepicondyle with expanded supinator process. Although their humeri are similar, Eubrachiosaurus can be distinguished from Ischigualastia (as well as Jachaleria, for which the humerus is unknown) by their strikingly different iliac morphologies (rounded blade set off from acetabulum by shaft in
Figure 9. Most parsimonious cladogram from the phylogenetic analysis. Scores: 986.11 steps, consistency index = 0.244, retention index = 0.713. Numbers at nodes represent decay index (left/top), symmetric resampling (middle), and the percentage of the 596,251 suboptimal trees in which the node is resolved (right/bottom). doi:10.1371/journal.pone.0064203.g009
Ischigualastia, elongate, anteroventrally curved blade in Eubrachiosaurus). The scapula of Eubrachiosaurus is similar to that of Stahlckeria, but narrower anteroposteriorly and more constricted at the level of the acromion. Scapular morphology also permits differentiation from Placerias (less expanded dorsally than Eubrachiosaurus) and Ischigualastia/Jachaleria (scapular spine absent, whereas it is well-developed in Eubrachiosaurus). This combination of characters, including the unique iliac curvature of Eubrachiosaurus, allows this taxon to be recognized as valid.

More problematic is Brachybrachium brevipes. Williston [28] described this taxon on the basis of a fragmentary humerus from the upper Popo Agie beds, in “almost identically the same horizon” as Eubrachiosaurus browni. This specimen, now lost, was poorly preserved with much of the proximal and distal ends missing. It shares with the humerus of Eubrachiosaurus a nearly perpendicular angle between the proximal and distal edges of the deltopectoral crest. Williston [28] distinguished Brachybrachium from Eubrachiosaurus on the basis of a more massive troclea and a more weakly-developed supinator process. However, the relative sizes of the distal processes on the humerus are intraspecifically variable in kannemeyeriiforms [23] and too little of the ectepicondyle was preserved in Brachybrachium to state with confidence that it differed appreciably from Eubrachiosaurus. Given that this specimen is from the same area and horizon as E. browni and exhibits no clear morphological differences from that taxon, it is likely that these two taxa are synonymous. However, on a strict apomorphy basis Brachybrachium brevipes must be considered a nomen dubium.

Kannemeyeriiform Higher-level Taxonomy

Kammerer and Angielczyk [64] proposed a higher-level taxonomy for Permian anamodonts, but did not do the same for Triassic dicynodonts because of the lack of comprehensive phylogenetic analyses up to that point. Previous phylogenetic analyses of kannemeyeriiform taxa [26,68–70] produced conflicting topologies and included only a fraction of kannemeyeriiform diversity. Although the current analysis includes almost all valid kannemeyeriiform taxa, relationships within the clade remain weakly supported, and it is likely that they will continue to change in future studies. As such, a formalized taxonomy of most kannemeyeriiform subclades remains premature. This said, there are a few clades that have been consistently recovered in the analyses of Kammerer et al. [27] and the current study that should be formally recognized for ease of communication.

Kannemeyeriiformes Maisch, 2001 [26] was established to refer to the large clade of Triassic non-lystrosaurid dicynodontoids, breaking from taxonomies that treated this group as a subfamily of Dicynodontidae [8]. The monophyly of Kannemeyeriiformes has been recovered in all subsequent analyses [27,70]: inclusion of “Dicynodon”-grade taxa in phylogenetic analyses demonstrates that these taxa lie outside of Kannemeyeriiformes, rather than representing basal members of the kannemeyeriiform subclades. Here we define Kannemeyeriiformes as Kannemeyeria simocephalus (Weithofer, 1888) [71] and all taxa more closely related to it than to Lystrosaurus murrayi (Huxley, 1859) [72] or Dicynodon lacerticeps Owen, 1845 [73]. We use a stem-based definition for this taxon as counterpart to its sister taxon Lystrosauria. Although no Permian kannemeyeriiforms are currently known, this clade must extend back to at least the Late Permian Cistecephalus Assemblage Zone, when the first lystrosaurids appear [27]. The lengthy pre-Anisian ghost lineage of kannemeyeriiforms is one of the major mysteries of dicynodont evolution: kannemeyeriiforms are large, robust animals with a high preservation potential, suggesting that their absence in well-sampled Late Permian basins (e.g., Karoo Basin of South Africa, Russian fore-Urals) is a biogeographic issue rather than within-basin taphonomic bias. Kannemeyeriiformes is supported by the following synapomorphies in our analysis: (1) absence of the postfrontal bone on the dorsal surface of the skull (discrete state character 39:state 1); (2) postorbitals do not extend for entire length of intertemporal bar, posterior portion of bar formed only by parietals (reversal of this character is common in Kannemeyeriiformes, however) [49:1]; (3) distinct dorsolateral notch in squamosal below zygomatic arch in posterior view absent (54:0); (4) intertuberal ridge absent (90:0); (5) lateral dentary shelf present but relatively small (110:1); (6) anterolateral trough for the posterior process of the dentary absent on angular (116:0); (7) procoracoid does not participate in formation of glenoid (130:0); and (8) insertion of M. subcoracoscapularis on humerus a short, pinna-like process (132:2).

Within kannemeyeriiforms, many authors have recognized variations of Shansiodontidae, Kannemeyeriidae, and Stahleckeriidae as the primary subgroups [24], and we agree that these names correspond to common kannemeyeriiform morphotypes (see, e.g., discussion of kannemeyeriiform scapulae above). The monophyly of the first two groups is suspect, however. A group of “core shansiodontids” has been recovered in all of our analyses, but the shansiodontid-like taxa Angostusaurus and Domodontosaurus behave as walcárdids. More problematic still is the recovery of Kannemeyeria-like taxa (“kannemeyeriids”) in varying degrees of paraphyly relative to Stahleckeriidae [27] and the current analysis. Only Stahleckeriidae has retained relatively stable composition across our analyses (with the exception of occasional inclusion of Wadasaurus and Rhadiodonius). As defined here, Stahleckeriidae comprises the last common ancestor of Placerias hesternus Lucas, 1904 [74] and Stahleckeria potens Huene, 1935 [40] and all of its descendents, so long as this group does not include Shansiodon wangi Yeh, 1959 [75] or Kannemeyeria simocephalus (Weithofer, 1888) [71] (Note: Kammerer et al. [27] used the spelling Kannemeyeria simocephala for this taxon, following its wide usage in the therapsid literature. However, because this specific epithet was erected as a noun in apposition, it is undeclinable, and the original spelling simocephalus must be maintained). Stahleckeriidae is supported by one unambiguous synapomorphy in our analysis: (1) interparietal making a large contribution to the skull roof (32:2).

Stahleckeriidae contains two subfamilies with stem-based definitions to form a node-stem triplet. Placeriinae (King, 1988) [8] comprises all taxa more closely related to Placerias hesternus Lucas, 1904 [74] than to Stahleckeria potens Huene, 1935 [40]. This clade contains Placerias, Mogheberia, and Zambiasaurus. Placeriinae is supported by the following synapomorphies in our analysis: (1) distinct lateral caniniform buttress absent (27:0); and (2) origin of triceps on posterior surface of scapula developed into a distinct posterior projection (147:1). Stahleckeriinae Lehman, 1961 [39] comprises all taxa more closely related to Stahleckeria potens Huene, 1935 [40] than to Placerias hesternus Lucas, 1904 [74]. This clade contains Stahleckeria, Eubrachiosaurus, Ischigualastia, Jachaleria, and Sangusaurus. Stahleckeriinae is supported by the following synapomorphies in our analysis: (1) palatal surface of premaxilla exposed in lateral view (19:1); (2) frontal contribution to the dorsal rim of the orbit thin or absent (30:1); and (3) four sternal bosses (124:1).

Other Non-Placerias Dicynodont Material from the Triassic of Western North America

Lucas and Hunt [17] described several postcranial elements of a large dicynodont from the Los Esteros Member of the Santa Rosa Formation (Santa Fe County, New Mexico). They identified this material as cf. Ischigualastia sp., based primarily on the morphology
of a nearly-complete left femur (NMMNH P-13001). They correctly noted that the short, stout femoral shaft and prominent greater trochanter of this specimen preclude identification as *Placerias* (10C). However, this femur (Figure 10E) differs from that of *Ichigualastia*, particularly in the morphology of the greater trochanter: it is highly flared, with an acute angle between the lateral and ventral margins, unlike the low, rounded condition in *Ichigualastia* (Figure 10D). Among kannemeyeriiforms, this type of sharply-angled greater trochanter is also observed in *Stahleckeria* (Figure 10E); in most other taxa the trochanter is relatively low (Figures 10A–D). It should be noted, however, that the greater trochanter in NMMNH P-13001 is even more widely flared than that of *Stahleckeria* and also lacks the straight, vertical lateral margin of that taxon, instead curving outwards.

NMMNH P-13001 appears to represent a taxon of kannemeyeriiform dicynodont that is distinct from *Placerias* and is similar to *Stahleckeria*. Given that the only known Late Triassic stahleckeriine in western North America is *Eubrachiosaurus* (based on the phylogenetic analysis above), it is possible that the New Mexican specimen represents another individual of *Eubrachiosaurus brownii*. Unfortunately, the paucity of overlapping material between these two individuals makes it impossible at present to state whether they are conspecific. The New Mexican specimen includes a scapular fragment (NMMNH P-13003), but it is too incomplete to permit meaningful comparisons with the scapula of FMNH UC 633. The other elements of the New Mexican specimen (NMMNH P-13002, an incomplete radius; NMMNH P-13004, a phalanx; and NMMNH P-13005, an incomplete axis vertebra) preserve only the general kannemeyeriiform morphology and do not aid in lower-level identification. The discovery of more complete specimens of *Eubrachiosaurus* preserving the femur will be necessary to resolve the status of the New Mexican specimen, and it should be considered Stahleckeriidae indet. for the time being. Other than the New Mexican record, the only other western North American dicynodont material that is not referable to *Placerias* is a record from the Dockum Group of Texas [76], but this material has yet to be properly described and its possible relationships are currently unknown.

**Kannemeyeriiform Material from Eastern North America**

Kannemeyeriiform fossils are known from several localities in the Late Triassic Newark Supergroup of eastern North America. The first named North American dicynodont, *Dicyomedon rosmarus*, was described based on an isolated tooth and tooth root from Phoenixville, Pennsylvania (New Oxford Formation, Newark Supergroup) [77]. However, these teeth (now lost) may have been from a phytosaur rather than a dicynodont [27]. The first definitive dicynodont specimens from the eastern U.S. were described by Baird and Patterson [21] from the Pomona Pipe Products Pit, Pekin Formation of North Carolina. This material was referred to *Placerias* [22], operating under the idea that this taxon is the only dicynodont from the Late Triassic of North America. With the revalidation of *Eubrachiosaurus*, we have demonstrated that this is not the case. However, our reexamination of the Pomona material reveals autapomorphies that confirm identification as *Placerias hesternus*. The postorbital bones of *Placerias* exhibit a distinct pattern of rugose ornamentation, unique among kannemeyeriiforms, in which a series of deep furrows and grooves are present (Figure 11). Rugose circumorbital ornamentation is typical of many kannemeyeriiform species, and highly rugose postorbitals are also known in *Jachaleria candelatensis* (UFRGS PV0151T), but no other taxon (including *Jachaleria*) has the extremely deep furrows present in *Placerias* (Figures 11B, 11D).

Figure 10. Kannemeyeriiform femora in anterior view. (A) CAMZM T754, Tetragonias njalilus; (B) NHMUK R3740, Kannemeyeria simocephalus; (C) UCMP 32394, Placerias hesternus; (D) PVL 3807, Ichigualastia jenseni; (E) NMMNH P-13001 (modified from [17]); (F) GPIT/RE/8001, Stahleckeria potens. Dotted lines indicate unpreserved areas. The specimens in A and B are right femora, the specimens in C, D, E, and F are left femora that have been reversed for comparative purposes. Abbreviation: g tr, greater trochanter. Scale bars equal 5 cm. [formatted for 2 column width].
doi:10.1371/journal.pone.0064203.g010

Figure 11. Postorbitals of Placerias hesternus showing characteristic rugosity. AMNH FARB 2851, from the Pekin Formation of North Carolina, in lateral (A) and posterior (B) views; MNA V2950, from the Chinle Formation of Arizona, in lateral (C) and posterior (D) views. Scale bars equal 1 cm. [formatted for 2 column width].
doi:10.1371/journal.pone.0064203.g011
Green et al. [78] reported on new dicynodont material from the Upper Triassic Pekin Formation in North Carolina that seems to be distinct from *Placerias*. The material comprises a partial articulated postcranial skeleton (NCSM 21719), including the posterior dorsal and sacral regions of the vertebral column, and nearly complete pelvic girdle and hind limbs. Green [79] figured NCSM 21719, which has an anteroventrally-curved anterior iliac blade. The preserved femur, however, does not have a sharp, expanded greater trochanter as in NMNH P-13001. This suggests that at least two non-*Placerias* stahleckeriids are present in the Late Triassic of North America. More complete material is required to determine which (if either) of the North Carolina and New Mexico specimens is referable to *Eubrachiosaurus*, however.

Kannemeyeriform Diversity and Distribution in the Late Triassic

The recognition of *Eubrachiosaurus* as a valid kannemeyeriform taxon belonging to a distinct lineage (Stahleckeriinae) from *Placerias* alters our understanding of the Late Triassic fossil record of dicynodonts. Although their lower abundance and absolute richness compared to Middle Triassic faunas do attest to a clade in decline, the concept of Norian kannemeyeriforms as highly geographically-restricted relicts is no longer tenable. Instead, this is the time of highest diversity and geographic range among one of the major kannemeyeriform subclades, Stahleckeriidae, and among stahleckeriids there is evidence of continued dispersal and diversification in both recognized subfamilies. Stahleckerinines are first known from the African Middle Triassic (the Anisian *Sungasaurus* from Tanzania and Zambia) but include three taxa in the Late Triassic of South America and one (*Eubrachiosaurus*) in North America in what is most parsimoniously interpreted as trans-Pangean dispersal. Placerinines also include a taxon from the African Middle Triassic (*Zambiasaurus* from the Anisian of Zambia) but are best known from the Norian of North America (*Placerias*) and Morocco (*Magreberia*), as well as potentially including the giant Rhaetian taxon from Poland [35]. The presence of two non-*Placerias* femoral morphologies in the North American Late Triassic record (see above) suggest that at least one additional stahleckeriid other than *Eubrachiosaurus* and *Placerias* was present. Combined with other recent discoveries [90], these records suggest that large kannemeyeriforms were a component of American and European faunas throughout the Late Triassic. Intriguingly, kannemeyeriforms occur in several regions where traversodontid cynodonts are absent (e.g., western North America), complicating interpretations of synapsids as humid-belt-restricted taxa [2]. Although progressive Triassic aridification remains the primary hypothesis for synapsid decline, it is clear that arid regions were at least tolerated by stahleckeriid dicynodonts, and further research into the paleobiology and physiology of these massive herbivores is necessary.

Supporting Information

Appendix S1 Additions and emendations to the phylogenetic analysis. Details changes made between the previously published version of this data set [27] and the current analysis. (DOC)

Appendix S2 List of continuous characters used in the phylogenetic analysis. (DOC)

Appendix S3 List of discrete state characters used in the phylogenetic analysis. (NX)

Appendix S4 Data matrix used in the phylogenetic analysis. (NX)

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Author Contributions

Conceived and designed the experiments: CFK JF KDA. Performed the experiments: CFK JF KDA. Analyzed the data: CFK JF KDA. Contributed reagents/materials/analysis tools: KDA. Wrote the paper: CFK JF KDA.

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