Histology of the preparietal: a neomorphic cranial element in dicynodont therapsids.

LIANNA M. MARILAO,[1] ZOE T. KULIK,[1] and CHRISTIAN A. SIDOR,*,[1]

[1]Department of Biology and Burke Museum, University of Washington, Seattle, Washington 98195, U.S.A., lmarilao@uw.edu, zkulik@uw.edu, casidor@uw.edu

*Corresponding author

RH: MARILAO ET AL.—DICYNODONT PREPARIETAL HISTOLOGY

ABSTRACT—The preparietal, a neomorphic midline ossification on the skull roof, is thought to have evolved three times in therapsids, but its development and homology remain poorly understood. Here we provide preliminary data on the histology of this element in specimens referred to *Diictodon feliceps* and an indeterminate species of *Lystrosaurus*. The preparietal has previously been noted to vary substantially in its shape on the dorsal surface of the skull in several dicynodonts and we found similar variation in thin section. In *Diictodon*, the preparietal forms a prong that embeds itself entirely within the frontals and shows evidence of a midline suture anteriorly. The sectioned specimen of *Lystrosaurus* shows histological evidence of immaturity and features a well-defined midline suture at the posterior end of the preparietal, although an anterior prong was not present. In both taxa the anteroventral portion of the preparietal forms a strongly interdigitating suture with the underlying frontals and parietals. More posteriorly, the preparietal is composed of fibrolamellar bone suggestive of rapid posteroventral growth. In large dicynodont species, the dorsal expression of the preparietal appears to show negative allometry compared to other cranial roofing elements during ontogeny, but the significance of this geometry is unclear. In addition, histological work is needed on the preparietal in gorgonopsians and biarmosuchians to determine if the features characterizing dicynodonts are also seen in the other two groups of therapsids that evolved a preparietal. The therapsid preparietal provides a rare opportunity to study the development and evolution of a neomorphic cranial element in the vertebrate fossil record.

INTRODUCTION

The reduction and eventual loss of skull bones is a well-known and repeated feature of tetrapod evolution (Williston, 1914; Gregory, 1927, 1929; Sidor, 2001). By contrast, the appearance of novel elements is a much less common occurrence (Sidor, 2001). In ornithischian dinosaurs, the neomorphic rostral and predentary evolved within ceratopsians and are beak-bearing elements with clear adaptive roles in the feeding apparatus (Nabavizadeh and Weishampel, 2016). Likewise, the incorporation of novel palpebral elements or osteoderms into the skull roof of thyreothoran dinosaurs is likely related to an overall increase in defensive structures seen throughout the skeletons of members of this clade (Sereno, 1997; Hayashi et al., 2010). Importantly, once evolved, these neomorphic elements were uniformly retained in members of both the ceratopsian and thyreothoran clades. Sidor (2001) discussed several other examples of neomorphic skull bones in tetrapods, but the handful of occurrences over the past ~350 million years points to their rarity.

The preparietal is an unpaired neomorphic ossification in some therapsids, typically presenting near the frontoparietal suture or just anterior to the parietal foramen (Fig. 1). Although a prominent feature of the skull roof, its functional significance is unknown and its development unexplored. The distribution of the preparietal suggests that this element was independently evolved in three distinct therapsid subclades during the middle Permian, even considering multiple phylogenetic hypotheses of therapsid higher-level relationships (e.g., Hopson, 1991; Rubidge and Sidor, 2001; Kammerer et al., 2013). As an initial step in assessing the ontogeny and homology of the preparietal in therapsids, we provide here the first histological assessment of this element in the dicynodonts *Diictodon* and *Lystrosaurus*.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, USA; **IVPP**, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; **NHCC**, National Heritage Conservation Commission, Lusaka, Zambia.

METHODS

Two partial skull roofs preserving the interorbital-intertemporal region (NHCC LB840 and IVPP V 22763) were histologically prepared following the hard tissue sampling techniques outlined by Lamm (2013). Specimens were embedded in Epothin Epoxy/Resin 2, sectioned to a thickness of approximately 2 mm on an Isomet 1000 saw and glued to glass slides using 2-ton epoxy. Slides were ground using a Metaserv 3000 lapidary plate until the specimen was approximately 80 μm thick or until optical clarity was reached. Both specimens were serially thin sectioned in the coronal plane to investigate their microanatomical architecture and internal sutural morphology.

Thin sections were imaged using a Nikon Eclipse LV100POL microscope. Composite images were processed using Nikon NIS-ELEMENTS BR (version 4.3) imaging software. Highresolution images of all of the thin sections are available on the online repository MorphoBank (Project Number 3636: http://morphobank.org/permalink/?P3636).

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905

DICYNODONTIA Owen, 1859

DIICTODON FELICEPS (Owen, 1876)

Referred Material—NHCC LB840, incomplete interorbital and intertemporal region of skull roof.

Locality and Horizon—L398, an outcrop of the upper Madumabisa Mudstone Formation approximately 2.5 kilometers southwest of the Mulondoshi River, near the southern border of North Luangwa National Park, Northern Province, Zambia. Biostratigraphic correlation to the *Cistecephalus* Assemblage Zone of South Africa suggests these Zambian rocks are

Lopingian in age (late Permian; Angielczyk et al., 2014; Viglietti et al., 2016). Detailed locality information is available from the NHCC or by contacting the authors.

Identification—The specimen described here was collected at L398 along with more complete cranial material of four other specimens pertaining to *Diictodon* (NHCC LB837, LB838, LB872, LB873). While the latter four can be confidently identified on the basis of the cranial features considered diagnostic for the taxon (e.g., caniniform notch), the isolated cranial roof under consideration here lacks diagnostic characters. Nonetheless, we are confident in our proposed referral because the specimen conforms nicely to the anatomy seen in *Diictodon,* and *Diictodon* was the only small dicynodont found at L398.

DESCRIPTION

Gross Anatomy

NHCC LB840 is an incomplete skull roof (Fig. 2). As preserved, it is 37.75 mm in anteroposterior length, suggesting a total skull length of approximately 120 mm, based on comparisons to more complete specimens (e.g., Angielczyk and Sullivan, 2008). This inferred size is near the maximum reported for the taxon, indicating that this individual is likely mature (Angielczyk and Sullivan, 2008). The skull roof preserves the intertemporal and interorbital regions and is made up of incomplete frontals, a preparietal, incomplete parietals, postfrontals, and incomplete postorbitals. Sutures are distinguishable on the dorsal and ventral skull surfaces with coronal thin sections further clarifying the sutural arrangements between the individual cranial elements.

In dorsal view, the median preparietal is long and narrow. It forms the anterior margin of the parietal foramen and extends between the parietals with roughly parallel sides until it tapers to a point between the frontals. On the ventral surface, the preparetial is circular and does not appear to extend between the frontals. Previous descriptions of *Diictodon* have demonstrated that the shape of the preparietal can vary widely among individuals (Sullivan and Reisz, 2005). Broom (1913) described the type specimen of *D. feliceps* (AMNH FARB 5308) with a preparietal that completely encircles the pineal foramen, an unusual condition only known from one other specimen described as *D. sesoma* by Watson (1960). A more recent re-examination of AMNH FARB 5308 by Sullivan and Reisz (2005) suggested that the dorsal surface of the skull was overprepared, causing the preparietal to appear to expand posteriorly around the pineal foramen, when in reality, this occurs only at depth. In addition to the type specimen, Sullivan and Reisz (2005) also summarized morphological variation in preparietals of South African *Diictodon* as being generally rectangular, but with a highly variable anterior shape. For example, some specimens showed a sharply pointed anterior suture (e.g., Fig. 2), others have a rounded point, while still others have a transverse suture with the frontals (Sullivan and Reisz, 2005). Keyser (1975) noted similar variation in *Oudenodon*.

Histology

Five coronal thin sections were made from NHCC LB840. What follows is a description of the major differences in bone tissue organization from anterior to posterior regions of the skull cap, with special attention given to the preparietal bone.

The most anterior thin section captures the frontal, postfrontal, and postorbital bones. Unexpectedly, the preparietal appears not superficially on the skull roof, but as two fan-like projections, completely surrounded by the frontal bones (Fig. 3). Here, the preparietal is primarily formed of compact bone with little vascularization. A midline suture separates the frontals and preparietal projections and widens to a crack ventrally (Fig. 2A). In more posterior sections, the preparietal lacks any indication of a midline suture and the ventral contact between the preparietal and parietal is deeply interdigitated unlike the more typical sutures seen throughout the rest of the skull cap (Fig. 2B). Moving more posteriorly to where the preparietal is thickest dorsoventrally, the vascular organization changes. Here, the ventral portion of the preparietal is composed of stacked layers of fibrolamellar bone (Fig. 3). These highly organized layers of longitudinal canals are unlike the vascular organization of the surrounding elements suggesting that the preparietal grew rapidly posteroventrally (Fig. 2C, D). The remainder of the skull bones are composed of vascularized compacta with cancellous interiors. In coronal section, the compact tissue largely consists of longitudinal canals that occasionally become more obliquely or radially oriented, especially in the laterally extending postorbital bars (Fig. 2A). Throughout the skull, osteocyte lacunae densely surround primary osteons (see supplemental images on Morphobank).

LYSTROSAURUS CF. *L. HEDINI*

Referred Material—IVPP V 22763, incomplete interorbital and intertemporal region of skull roof of a small, presumably juvenile, individual.

Locality and Horizon—Middle portion of the Lower Triassic Jiucaiyuan Formation at west Taodongguo, Xinjiang Uygur Autonomous Region (Yang et al., 2010; Thomas et al., 2011).

Identification—We refer this specimen to *Lystrosaurus* because the anatomy it preserves conforms to what is seen in that genus and because, besides a single specimen ascribed to the kannemeyeriiform *Sungeodon kimkraemerae*, *Lystrosaurus* is the only other dicynodont reported from the Jiucaiyuan Formation (Yang et al., 1982; Lucas, 2001; Maisch and Matzke, 2014) and represents by far the most common fossil taxon encountered during fieldwork at west Taodongguo.

Gross Anatomy

IVPP V 22763 is inferred to represent a juvenile individual based on its small size and histological features (see below). We estimate a skull length of about 10 cm when complete, which is quite small compared to other specimens of *Lystrosaurus* from China, which can be over 25 cm in anteroposterior length (Cheng, 1986). IVPP V 22763 measures 31.10 mm anteroposteriorly and is thus nearly the same size as NHCC LB840. However, in the former specimen, only the intertemporal region is preserved. In dorsal view, incomplete frontal bones are easily distinguishable from an oval-shaped preparietal that tapers to a point anteriorly. In ventral view, the preparietal has a pointed anterior margin but the overall shape of the bone is pentagonal rather than elongate.

The parietal, postfrontal, and postorbital bones are especially fragmentary on the left side of the skull, leaving the margins of the parietal foramen largely incomplete. Sutures clearly separate the skull roofing elements on both the dorsal and ventral sides. Interestingly, the preparietal has what appears to be a midline suture at its caudal end in dorsal view. This suture is clearly distinguishable in thin section (see below) but does not appear on the ventral surface of the bone. We were unable to make a thin section in the same location of NHCC LB840, but to our knowledge a midline suture on the preparietal has not been previously reported in the literature on dicynodonts.

Histology

Five coronal thin sections were made from IVPP V 22763 in similar locations as NHCC LB840. Here, the preparietal does not penetrate into the frontal bones, as seen in *Diictodon*. Instead, it appears as a dorsally located sliver of bone between the frontal bones (Fig. 4A). More posteriorly, the preparietal expands ventrally with a complex and interdigitated suture pattern similar to that seen in *Diictodon* (Fig. 3B). The preparietal contacts the frontal bone ventrally, unlike in NHCC LB840, which has a ventral contact with the parietal (Fig. 2B). As in *Diictodon*, in more posterior thin sections, stacked layers of organized fibrolamellar bone suggest rapid growth ventrally. A middle region of cancellous tissue is maintained in the thickest region of the preparietal but the majority of the bone is highly vascularized cortical bone tissue (Fig. 4D). In the most posterior thin section, a small, vertical midline suture is present in the preparietal (Fig. 4E).

The remaining cranial elements consist of well-vascularized cortical bone with scarce trabeculae restricted to the innermost regions of each bone. In comparison to *Diictodon* thin sections, *Lystrosaurus* consists predominantly of fibrolamellar bone tissue. Indeed, the only highly vascularized fibrolamellar bone seen in *Diictodon* is in the preparietal. This suggests a young ontogenetic stage for the *Lystrosaurus* skull cap where little of the cortical bone has developed into compact tissue.

DISCUSSION

Preparietal Comparison

There are several osteohistological similarities in the preparietal of *Diictodon* and *Lystrosaurus*. In both, the bone forms a strongly interdigitated suture with the bones deep to it anteriorly (viz. frontals and parietals). In both specimens, highly vascularized, longitudinally oriented fibrolamellar bone tissue makes up the majority of the preparietal suggesting a relatively rapid rate of growth. In addition to the similarities, there are also some differences in the bone between the two specimens. In *Diictodon*, vascularized fibrolamellar tissue is restricted to the ventral surface of the preparietal but that tissue type appears on dorsal and ventral regions of the preparietal in *Lystrosaurus*. Another difference is where the preparietal first appears in the anterior thin section. In *Diictodon,* the preparietal appears in the middle of the frontal bone (Figs. 2A, 3A) whereas it appears superficially in *Lystrosaurus* (Fig. 4A). Another significant difference is that a midline suture is present anteriorly in *Diictodon* but posteriorly in *Lystrosaurus*. Due to its young ontogenetic stage, it is possible that this midline suture represents separate ossification centers that fuse later in ontogeny. However, we cannot make definitive conclusions about whether the posterior suture was present in *Diictodon* because an appropriate thin section is not available for NHCC LB840. Future histological work should investigate the occurrence of a midline preparietal suture in other dicynodonts (as well as in biarmosuchians and gorgonopsians).

Phylogenetic Distribution of the Preparietal in Therapsids

The preparietal was first described by Huxley (1865) in a dicynodont specimen from India (likely *Lystrosaurus*) and it has since been recognized in three groups of therapsids, but with a complex phylogenetic distribution (Fig. 1). In biarmosuchians, which are often considered the most basal group of therapsids (Hopson and Barghusen, 1986; Day et al., 2016), the preparietal is absent in the most basal member of the group, *Biarmosuchus*, but present in other taxa such as *Hipposaurus* and *Herpetoskylax* as an arrowhead-shaped feature just anterior to the parietal foramen. The occurrence of a preparietal in the burnetiamorph biarmosuchians was, until recently, subject to dispute. Burnetiamorphs are characterized by thickened and spongy skull roofs, which often obliterates sutural detail and made the recognition of a preparietal ambiguous (Rubidge and Sidor, 2002). However, a preparietal was recognized in *Pachydectes* by Rubidge et al. (2006) and more recently shown in several other taxa as well (Kammerer, 2016b; Day et al., 2018). Kulik and Sidor (2019) confirmed the occurrence of a preparietal in thin sections and CT scans of isolated burnetiamorph skull caps from Zambia, but found no evidence for a midline suture in even the smallest individual they sampled.

In dicynodonts, the preparietal is positioned as in biarmosuchians, forming the anterior border of the parietal foramen. In several taxa it tapers anteriorly in between the frontals, but the preparietal also shows a wide range of morphologies including forms in which it broadens anteriorly. A preparietal is present in most dicynodonts (King, 1988), but not in some of the most basal non-dicynodont anomodonts (e.g., *Biseridens*, *Suminia*, *Ulemica*; Rybczynski, 2000; Liu et al., 2010) and sometimes not in derived Triassic taxa (e.g., *Ufudocyclops*; Kammerer et al. 2019). It is also absent in cistecephalids, a group of small-bodied species that are typically considered specialized burrowers (Angielczyk et al., 2019).

Gorgonopsians often also present a preparietal, although when it occurs it typically has a rhomboidal or diamond-shaped outline in dorsal view and is located at the intersection of the paired frontals and parietals (i.e., more anteriorly than in the other two groups previously discussed; Fig. 1). As in biarmosuchians and dicynodonts, the phylogenetic distribution of the preparietal among gorgonopsians is also somewhat complicated, but it should be recognized that this clade has long been hampered by less phylogenetic work than most other major groups of therapsids. A preparietal is present in the oldest member of the clade (*Eriphostoma*; Kammerer et al., 2015a) and occurs in most small and medium-sized species from southern Africa, where the richest fossil record of the group occurs (Sigogneau-Russell, 1989). However, a preparietal is absent in many of the latest occurring and largest species, many of which are members of the subclade Rubidginae (Kammerer, 2016a). It is unclear if this absence is congenital (perhaps due to fusion to an adjacent element) or if other cranial bones overgrow or otherwise obscure the preparietal in dorsal view. Although Kammerer (2015) suggested the former scenario for *Arctognathus curvimola*, additional histological work would be useful to distinguish between these alternatives.

Homology of the Preparietal

The homology of the preparietal has never been seriously questioned in the therapsid literature. However, there are reasons to doubt that the three instances of a preparietal (viz. biarmosuchians, dicynodonts, and gorgonopsids) stem from a common evolutionary origin. First, as noted above, the complicated distribution of the preparietal among the therapsid groups suggests that it fails the test of congruence (Patterson, 1982). That said, higher-level therapsid phylogeny is far from uncontroversial (Kemp, 2009) and so it is possible that future hypotheses of relationship would find the preparietal to be a synapomorphy of a novel clade (e.g., biarmosuchians + gorgonopsians; Sidor 2000).

A second reason to doubt that the preparietal is homologous across Therapsida is that the gorgonopsian preparietal fails the test of detailed similarity: its external outline and position on the skull roof is different than those of biarmosuchians or dicynodonts. More research on the anatomy of the preparietal in gorgonopsians and biarmosuchians is needed to determine if any of the morphological details described here for dicynodonts occur in those other therapsid groups (e.g., highly interdigitated ventral margin anteriorly). In burnetiamorphs, the preparietal has a highly modified internal structure consisting of four zones that is related to the massive thickening that occurs in it and other bones of the skull table (Kulik and Sidor, 2019).

Preparietal Histology and Allometry

The thin sections described here are a substantial contribution to what has been previously reported regarding the histology of the dicynodont cranium. Indeed, most previous studies featuring thin sections of dicynodont skulls have focused on understanding the sutural connections among the bones of the skull roof, and not on the microanatomy of the individual bones themselves (e.g., Sollas and Sollas, 1914; Cluver, 1971; Keyser, 1975). That said, several papers by Jasinoski and colleagues examined cranial histology in two dicynodonts in the context of feeding mechanics and sutural strength (Jasinoski et al., 2009, 2010, 2014; Jasinoski and Chinsamy-Turan, 2012). A median, neomorphic element was reported from subabults of at least two species of *Lystrosaurus* (*L. declivis* and *L. murrayi*). This diamondshaped bone, located between the nasal and frontal bones, appears to be unpaired in some individuals but paired in others (Jasinoski et al., 2014:table 8.1). These authors suggest that intraspecific variation in the number of cranial elements could be ontogenetic, as no adult *Lystrosaurus* appears to have supernumerary bones, but clear sutural margins are difficult to discern in this region of the snout of adult individuals (Jasinoski et al., 2014). The presence of a naso-frontal neomorphic element in the *Lystrosaurus* cranium could be attributed to its drastic reorganization and down-turning of the snout as suggested by Jasinoski et al. (2014), but function does not as easily explain the presence of the more dorsally located preparietal. Evidence for variability in the number of cranial elements is apparent across dicynodonts and strongest in juvenile

Lystrosaurus. Additional histologic sampling, especially in a growth series, will help clarify whether currently described neomorphic elements represent centers of ossification of typical cranial bones (e.g., frontals) that have failed to coalesce.

Our data suggest that dicynodonts are characterized by a stereotyped preparietal histology including, 1) a highly interdigitated ventral suture anteriorly followed by, 2) horizontally oriented fibrolamellar bone more posteriorly. Additional histological work will be necessary to determine if this combination of features should be considered a dicynodont synapomorphy, but their occurrence in both relatively basal (i.e., *Diictodon*) and derived (i.e., *Lystrosaurus*) taxa suggests that these characters have a wide phylogenetic distribution within the group. The presence of fibrolamellar bone indicates rapid growth in the posterior portion of the preparietal, closest to the parietal foramen, in both the adult specimen of *Diictodon* as well as the juvenile specimen of *Lystrosaurus*. It seems likely, therefore, that the preparietal grew mostly posteroventrally in life. It is also interesting to note that in relatively large-bodied dicynodont species like *Pelanomodon moschops*, the preparietal is relatively large in juveniles (compared to other elements of the skull roof) and that it becomes proportionately much smaller in adults (Kammerer et al., 2015b). A similar pattern seems to occur within gorgonopsians as a whole, with smaller species having proportionately larger preparietals than large-bodied species. These allometries beg for future research to investigate the possibility that the neomorphic appearance of the preparietal ossification was related to rapid growth of the pineal region of the brain in therapsids.

ACKNOWLEDGMENTS

Analysis of NHCC LB840 and support of LMM was provided by NSF EAR-133759 (to CAS). Fieldwork in Zambia in 2018 was supported by NGS-158R-18 (to B. Peecook) and NSF

EAR-133759 (to CAS) and we thank team members J. Museba, B. Peecook, S. Tolan, P. Viglietti, and M. Whitney for their assistance and companionship in the field. We gratefully acknowledge the NHCC for granting permits since 2009. Collection and analysis of IVPP V 22763, as well as support of ZTK was provided by NSF EAR-1713787 (to CAS). We thank J. Liu, K. Angielczyk, and W. Yang, as well as the rest of the 2019 field team for assistance in Xinjiang. We thank C. Sullivan, J. Liu, and K. Angielczyk for comparative supplementary images and data as well as P. Viglietti, C. Kammerer, and an anonymous reviewer for their helpful suggestions on the manuscript.

LITERATURE CITED

Angielczyk, K. D., and C. Sullivan. 2008. *Diictodon feliceps* (Owen, 1876), a Dicynodont (Therapsida, Anomodontia) Species with a Pangaean Distribution. Journal of Vertebrate Paleontology 28:788–802.

Angielczyk, K. D., J. Benoit, and B. S. Rubidge. 2019. A new tusked cistecephalid dicynodont (Therapsida, Anomodontia) from the upper Permian upper Madumabisa Mudstone Formation, Luangwa Basin, Zambia. Papers in Palaeontology 2019:1–42.

Angielczyk, K. D., S. Huertas, R. M. H. Smith, N. J. Tabor, C. A. Sidor, J. S. Steyer, L. A. Tsuji, and N. J. Gostling. 2014. New dicynodonts (Therapsida, Anomodontia) and updated tetrapod stratigraphy of the Permian Ruhuhu Formation (Songea Group, Ruhuhu Basin) of southern Tanzania. Journal of Vertebrate Paleontology 34:1408–1426.

Broom, R. 1905. On the use of the term Anomodontia. Records of the Albany Museum 1:266–269.

Broom, R. 1913. On some new genera and species of dicynodont reptiles, with notes on a few others. Bulletin of the American Museum of Natural History 32:441–457.

Cheng, Z.-W. 1986. [Permian and Triassic strata and fossil assemblages in the Dalongkou area of Jimusar, Xinjiang: 7. Vertebrates.] People’s Republic of China Ministry of Geology and Mineral Resources Geological Memoirs 2(3):207–218. [in Chinese]

Cluver, M. A. 1971. The cranial morphology of the dicynodont genus *Lystrosaurus*. Annals of the South African Museum 56(5):155–274.

Day, M. O., B. S. Rubidge, and F. Abdala. 2016. A new mid-Permian burnetiamorph therapsid from the main Karoo Basin of South Africa and a phylogenetic review of Burnetiamorpha. Acta Palaeontologica Polonica 61:701–719.

Day, M. O., R. M. H. Smith, J. Benoit, V. Fernandez, and B. S. Rubidge. 2018. A new species of burnetiid (Therapsida. Burnetiamorpha) from the early Wuchiapingian of South Africa and implications for the evolutionary ecology of the family Burnetiidae. Papers in Palaeontology 2018:1–23.

Gregory, W. K. 1927. The palaeomorphology of the human head: ten structural stages from fish to man. Part I. The skull in norma lateralis. Quarterly Review of Biology 2:267–279.

Gregory, W. K. 1929. The palaeomorphology of the human head: ten structural stages from fish to man. Part II. The skull in norma basalis. Quarterly Review of Biology 4:233–247.

Hayashi, S., K. Carpenter, T. M. Scheyer, M. Watabe, D. and Suzuki. 2010. Function and evolution of ankylosaur dermal armor. Acta Palaeontologica Polonica 55:213–228.

Hopson, J. A. 1991. Systematics of the nonmammalian Synapsida and implications for patterns of evolution in synapsids; pp. 635–693 in H.-P. Schultze, and L. Trueb (eds.), Origins of the Higher Groups of Tetrapods: Controversy and Consensus. Comstock Publishing Associates, Ithaca.

Hopson, J. A., and H. Barghusen. 1986. An analysis of therapsid relationships; pp. 83–106 in N. Hotton, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), The Ecology and Biology of the Mammal-like Reptiles. Smithsonian Institution Press, Washington.

Huxley, T. H. 1865. On a collections of vertebrate fossils from the Panchet rocks, Ranigunj, Bengal. Palaeontologia Indica 1(4):3–24.

Jasinoski, S. C., and A. Chinsamy-Turan. 2012. Biological inferences of the cranial microstructure of the dicynodonts *Oudenodon* and *Lystrosaurus*; pp. 149–176 in A. Chinsamy-Turan (ed.), Forerunners of mammals: radiation, histology, biology. Indiana University Press, Indianapolis.

Jasinoski, S.C., E.J. Rayfield, and A. Chinsamy. 2009. Comparative feeding biomechanics of *Lystrosaurus* and the generalized dicynodont *Oudenodon*. The Anatomical Record 292:862–874.

Jasinoski, S. C., E. J. Rayfield, and A. Chinsamy. 2010. Functional implications of dicynodont cranial suture morphology. Journal of Morphology 271:705–728.

Jasinoski, S. C., M. A. Cluver, A. Chinsamy, and B. Daya Reddy. 2014. Anatomical plasticity in the snout of *Lystrosaurus*; Pp. 139–149 in C F. Kammerer, K. D. Angielczyk, and J. Fröbisch (eds.), Early Evolutionary History of the Synapsida. Springer, Netherlands.

Kammerer, C. F. 2015. Cranial osteology of *Arctognathus curvimola*, a short-snouted gorgonopsian from the Late Permian of South Africa. Papers in Palaeontology 1:41–58.

Kammerer, C. F. 2016a. Systematics of the Rubidgeinae (Therapsida: Gorgonopsia). PeerJ 4:e1608.

Kammerer, C. F. 2016b. Two unrecognized burnetiamorph specimens from historical Karoo collections. Palaeontologia Africana 50:64–75.

Kammerer, C. F., K. D. Angielczyk, and J. Fröbisch. 2015b. Redescription of the geikiid *Pelanomodon* (Therapsida, Dicynodontia), with a reconsideration of ‘*Propelanomodon*’. Journal of Vertebrate Paleontology e1030408.

Kammerer, C. F., M. Jansen, and J. Fröbisch. 2013. Therapsid phylogeny revisited. Journal of Vertebrate Paleontology 33(online supplement):150.

Kammerer, C. F., R. M. H. Smith, M. O. Day, and B. S. Rubidge. 2015a. New information on the morphology and stratigraphic range of the mid-Permian gorgonopsian *Eriphostoma microdon* Broom, 1911. Papers in Palaeontology 1:201–221.

Kammerer, C. F., P. A. Viglietti, P. J. Hancox, R. J. Butler, and J. N. Choiniere. 2019. A new kannemeyeriiform dicynodont (*Ufudocyclops mukanelai*, gen. et sp. nov.) from subzone C of the *Cynognathus* Assemblage Zone, Triassic of South Africa, with implications for biostratigraphic correlation with other African Triassic faunas. Journal of Vertebrate Paleontology e1595921.

Kemp, T. S. 2009. Phylogenetic interrelationships and pattern of evolution of the therapsids: testing for polytomy. Palaeontologia Africana 44:1–12.

Keyser, A.W. 1975. A re-evaluation of the cranial morphology and systematics of some tuskless Anomodontia. Geological Survey of South Africa Memoir 67: 1–110.

King, G. M. 1988. Anomodontia; in P. Wellnhofer (ed.), Encyclopedia of Paleoherpetology, Part 17C. Gustav Fischer, Stuttgart, 174 pp.

Kulik, Z. T., and C. A. Sidor. 2019. The original boneheads: histological analysis of the pachyostotic skull roof in Permian burnetiamorphs (Therapsida: Biarmosuchia). Journal of Anatomy 235:151–166.

Lamm, E.-T. 2013. Preparation and sectioning of specimens; pp. 55–160 in K. Padian and E.-T. Lamm (eds.), Bone Histology of Fossil Tetrapods: Advancing Methods, Analysis, and Interpretation. University of California Press.

Liu, J., B. Rubidge, and J. Li. 2010. A new specimen of *Biseridens qilianicus* indicates its phylogenetic position as the most basal anomodont. Proceedings of the Royal Society B: Biological Sciences 277:285–292.

Lucas, S. G. 2001. Chinese fossil vertebrates. Columbia University Press, New York.

Maisch, M. W. and A. T. Matzke. 2014. *Sungeodon kimkraemerae* n. gen. n. sp., the oldest kannemeyeriidorm (Therapsida, Dicynodontia) and its implications for the early diversification of large herbivores after the P/T boundary. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 272(1):1–12.

Nabavizadeh, A. and D. B. Weishampel. 2016. The predentary bone and its significance in the evolution of feeding mechanisms in ornithischian dinosaurs. The Anatomical Record 299:1358–1388.

Owen, R. 1859. On some reptilian fossils from South Africa. Quarterly Journal of the Geological Society of London 16:49–63.

Owen, R. 1876. Descriptive and illustrated catalogue of the fossil Reptilia of South Africa in the collection of the British Museum. Printed by order of the Trustees, London.

Patterson, C. 1982. Morphological characters and homology; pp. 21–74 in K. A. Joysey, and A. E. Friday (eds.), Problems of Phylogenetic Reconstruction. Academic Press, New York.

Rubidge, B. S., and C. A. Sidor. 2001. Evolutionary patterns among Permo–Triassic therapsids. Annual Review of Ecology and Systematics 32:449–480.

Rubidge, B. S., and C. A. Sidor. 2002. On the cranial morphology of the basal therapsids *Burnetia* and *Proburnetia* (Therapsida: Burnetiidae). Journal of Vertebrate Paleontology 22:257–267.

Rubidge, B. S., C. A. Sidor, and S. P. Modesto. 2006. A new burnetiamorph (Therapsida: Biarmosuchia) from the Middle Permian of South Africa. Journal of Paleontology 80:740–749.

Rybczynski, N. 2000. Cranial anatomy and phylogenetic position of *Suminia getmanovi*, a basal anomodont (Amniota: Therapsida) from the Late Permian of Eastern Europe. Zoological Journal of the Linnean Society 130:329–373.

Sereno, P.C. 1997. The origin and evolution of dinosaurs. Annual Review of Earth and Planetary Sciences 25:435–489.

Sidor, C. A. 2000. Evolutionary trends and relationships within the Synapsida. Ph.D. dissertation. University of Chicago, Chicago.

Sidor, C. A. 2001. Simplification as a trend in synapsid cranial evolution. Evolution 55(7):1419–1442.

Sidor, C. A., and B. S. Rubidge. 2006. *Herpetoskylax hopsoni*, a new biarmosuchian (Therapsida: Biarmosuchia) from the Beaufort Group of South Africa; pp. 76–113 in M. T. Carrano, T. Gaudin, R. Blob, and J. Wible (eds.), Amniote Paleobiology: Perspectives on the evolution of mammals, birds, and reptiles. University of Chicago Press, Chicago.

Sigogneau-Russell, D. 1989. Theriodontia I. Pp. 1-127. *In* P. Wellnhofer, ed. Encyclopedia of Paleoherpetology, Part 17B. Gustav Fischer, Stuttgart.

Sollas, I. B. J., and W. J. Sollas. 1914. A study of the skull of a *Dicynodon* by means of serial sections. Philosophical Transactions of the Royal Society B 204:201–225.

Sullivan, C., and R. R. Reisz. 2005. Cranial anatomy and taxonomy of the Late Permian dicynodont *Diictodon*. Annals of Carnegie Museum 74:45–75.

Thomas, S. G., N. J. Tabor, W. Yang, T. S. Myers, Y. Yang, and D. Wang. 2011. Paleosol stratigraphy across the Permian-Triassic boundary, Bogda Mountains, NW China: implications for paleoenvironmental transition through earth’s largest mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology 308:41–64.

Viglietti, P. A., R. M. H. Smith, K. D. Angielczyk, C. F. Kammerer, J. Fröbisch, and B. S. Rubidge. 2016. The *Daptocephalus* Assemblage Zone (Lopingian), South Africa: a proposed biostratigraphy based on a new compilation of stratigraphic ranges. Journal of African Earth Sciences 113:1–12.

Watson, D. M. S. 1960. The anomodont skeleton. Transactions of the Zoological Society of London 29:131–208.

Williston, S. W. 1914. Water reptiles of the past and present. University of Chicago Press, Chicago.

Yang, Z. Y., Z. S. Li, L. F. Qu, Z. M. Lu, H. Q. Zhou, T. S. Zhou, G. F. Liu, B. P. Liu, and R. T. Wu. 1982. The Triassic of China. Acta Geologica Sinica 56:1–20.

Yang, W., Q. Feng, Y. Liu, N. Tabor, D. Miggins, J. L. Crowley, J. Lin, and S. Thomas. 2010. Depositional environments and cyclo- and chronostratigraphy of uppermost Carboniferous–Lower Triassic fluvial–lacustrine deposits, southern Bogda Mountains, NW China – A terrestrial paleoclimatic record of mid-latitude NE Pangea. Global and Planetary Change 73:15–113.

Submitted February 18, 2020; revisions received Month DD, YYYY; accepted Month DD, YYYY

FIGURE LEGENDS

FIGURE 1. Distribution of the preparietal in synapsids. **A,** cladogram of synapsid relationships showing the appearance of the preparietal in three clades (Biarmosuchia, Anomodontia, Gorgonopsia). Skulls of **B**, *Herpetoskylax*, **C**, juvenile of *Pelanomodon*, and **D**, *Ruhuhucerberus*, based on work Sidor and Rubidge (2006), Kammerer et al. (2015b), and Kammerer (2016a), respectively, with preparietal filled in black (skulls not to scale). Higher-level phylogenetic relationships based on Rubidge and Sidor (2001). Asterisks denote variable presence of the preparietal within the clades noted. See text for details. [Intended for column width]

FIGURE 2. Histology of the skull roof in *Diictodon feliceps* (NHCC LB840). Consecutive coronal thin sections of the skull roof (left column) with corresponding interpretive drawings (right column). Arrowheads show approximate location of sections **A–E** on skull roof prior to sectioning. **Abbreviations**: **f**, frontal; **for**, matrix infilling parietal foramen; **p**, parietal; **pf**, postfrontal; **po**, postorbital; **pp**, preparietal. Scale bar for image of skull roof equals 1 cm. [Intended for page width]

FIGURE 3. Histology of the preparietal in *Diictodon feliceps* (NHCC LB840) at higher magnification. **A**, Interfrontal suture and the ventral interdigitated suture of the preparietal. **B**, Highly organized layers of fibrolamellar bone in the ventral portion of the preparietal. **Abbreviations**: **f**, frontal; **flb**, fibrolamellar bone; **if**, interfrontal suture; **pp**, preparietal. Scale bars equal 500 μm. [Intended for column width]

FIGURE 4. Histology of the skull roof in *Lystrosaurus* cf. *hedini* (IVPP V 22763). Consecutive coronal thin sections of the skull roof (left column) with corresponding interpretive drawings

(right column). Arrowheads show approximate location of sections **A–E** on skull roof prior to sectioning. **Abbreviations**: **f**, frontal; **for**, matrix infilling parietal foramen; **p**, parietal; **pf**, postfrontal; **po**, postorbital; **pp**, preparietal. Scale bar for image of skull roof equals 1 cm.

[Intended for page width]