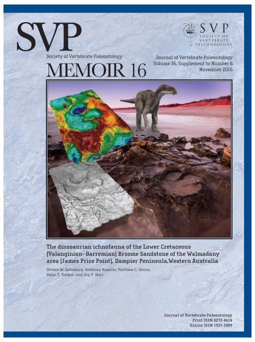

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Reevaluation of the holotypes of *Koskinonodon princeps* Branson and Mehl, 1929, and *Borborophagus wyomingensis* Branson and Mehl, 1929 (Temnospondyli, Metoposauridae)

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ARTICLE

REEVALUATION OF THE HOLOTYPES OF *KOSKINONODON PRINCEPS* BRANSON AND MEHL, 1929, AND *BORBOROPHAGUS WYOMINGENSIS* BRANSON AND MEHL, 1929 (TEMNOSPONDYLI, METOPOSAURIDAE)

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ABSTRACT—Metoposaurids are some of the most commonly occurring tetrapods in non-marine Upper Triassic sediments in the northern hemisphere of Pangea. Since the first description of a metoposaurid in 1842, nearly two dozen species have been named, but many of these have been regarded with increasing skepticism by modern workers because of minor differences used to validate novel species and sometimes novel genera. More recent comprehensive descriptions and evaluations of intraspecific variation from several presumed monospecific bonebeds of metoposaurids have prompted reevaluation of holotypes due to variation in proposed apomorphies. Four metoposaurid species were named from the Popo Agie Formation exposures of Wyoming, U.S.A., but at present, only a single species, *Anaschisma browni*, is considered valid following a recent redescription of two of these taxa (*An. browni* and *An. brachygnatha*). The other two taxa, *Borborophagus wyomingensis* and *Koskinonodon princeps*, have not been redescribed since their original description in 1929. A redescription of the holotypes of these two taxa is presented here to assess their historic synonymy with *An. browni* and to provide a detailed, updated record of the Popo Agie Formation metoposaurids in light of a historic relative lack of attention compared with other North American deposits. Our confirmation of the conspecificity of all four Popo Agie Formation metoposaurids permits a detailed discussion of potential ontogenetic variation in the Popo Agie Formation metoposaurids and latitudinal variability in *An. browni*.

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

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INTRODUCTION

History of Study of Popo Agie Formation Metoposaurids

The Metoposauridae are Late Triassic, globally distributed stereospondyls with 10 valid species in six recognized genera (Hunt, 1993; Sulej, 2007; Brusatte et al., 2015; Chakravorti and Sengupta, 2018; Buffa et al., 2019; Gee et al., 2019). The earliest description of metoposaurid material from North America was based on the posterior end of a skull roof from the Cumnock Formation of North Carolina, the holotype of *Dictyocephalus elegans* Leidy, 1856 (Colbert and Imbrie, 1956:figs. 1–2), and an ornamented fragment of either the skull or pectoral girdle from the Lockatong Formation of Pennsylvania, the holotype of *Eupelor durus* Cope, 1866 (Cope, 1868; Colbert and Imbrie, 1956: figs. 3–5). However, both taxa are now considered nomina dubia due to the absence of diagnostic characters below the family level (Hunt, 1993). A third taxon, *Metoposaurus fraasi* Lucas, 1904 (pl. 3), was named for an interclavicle from Arizona but can only be associated with other North American metoposaurids based on the relative size of the circular pitted region and was regarded as an indeterminate metoposaurid by Hunt (1993). The earliest described metoposaurid cranium of a presently valid North American species is thus the holotype of *Anaschisma browni* Branson, 1905 (figs. 1, 3, 7–8, 10.2, therein) from the Popo Agie Formation of Wyoming.

Three other species were described from the Popo Agie Formation: *Anaschisma brachygnatha* Branson, 1905 (fig. 9), *Borborophagus wyomingensis* Branson and Mehl, 1929 (fig. 10; pls. 10–11), and *Koskinonodon princeps* Branson and Mehl, 1929 (fig. 8; pls. 4–6). The four species of Popo Agie Formation metoposaurids were long suspected to be synonymous based on their overall similarity of proportions, stratigraphic position, geographic proximity, and the possibility that purported diagnostic features were attributable to ontogeny, such as the relatively thin skull roof and palate of *B. wyomingensis* (Romer, 1947; Colbert and Imbrie, 1956). Colbert and Imbrie (1956) were the first to formalize this synonymy, uniting the Popo Agie Formation taxa under a single taxon, *Eupelor browni*, and contrasted *Eupelor* with *Metoposaurus* Lydekker, 1890 (fig. 35) from western Europe and *Buettneria* Case, 1922 (pls. 1, 2a–b; fig. 1) from Arizona, New Mexico, and Texas, on the basis of a relatively wide and shortened posterior skull table, a relatively long antorbital region, and a square, rather than an anteroposteriorly elongate, postparietal. Colbert and Imbrie (1956) used biometry as a taxonomic tool for statistically distinguishing metoposaurid taxa. This technique has since largely been ignored for taxonomy, but geometric morphometrics has been used in more recent studies to quantify intraspecific cranial and pectoral girdle allometry and growth trajectory in metoposaurid populations (Sulej, 2007; Lucas et al., 2016; Antczak and Bodzioch, 2018) and for phylogenetic inference with continuous characters (Chakravorti and Sengupta, 2018).

The taxonomy of metoposaurids remained unstable for several decades after Colbert and Imbrie's (1956) study; at one point, all

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known species were placed in the genus *Metoposaurus* (Chowdhury, 1965), and subspecies, a rarely utilized concept in vertebrate paleontology, were widely applied for the North American taxa based on geographic occurrence. This also led to the uncertain status of names generally thought to be nomina dubia, some of which were revived in spite of a lack of consensus on their standing. *Anaschisma* (inclusive of *Borborophagus*) was often synonymized with other genera (*Buettneria*, *Eupelor*, *Koskinonodon*, and *Metoposaurus*) but was occasionally referenced by Gregory (1980) and Lucas et al. (1985) as a distinct possible candidate for the identity of what is now *Apachesaurus gregorii* Hunt, 1993 (figs. 12, 13a–b), a taxon represented only by small-bodied individuals from Arizona, New Mexico, and Texas (Long and Murry, 1995; Spielmann and Lucas, 2012; Gee and Parker, 2017, 2018). This conjecture was made by the purported shared absence of a deep otic notch, but in the holotypes of *Anaschisma browni* and *Anaschisma brachygnatha*, this is a taphonomic artifact that was sometimes erroneously interpreted as the biological condition (Gee et al., 2019). Hunt (1993) provided the most recent review of the Metoposauridae, a taxonomic framework that remains largely intact today. Whereas previous authors distinguished the Popo Agie Formation metoposaurids from those found in the Chinle Formation and the Dockum Group through subspecies designations (Colbert and Imbrie, 1956; Chowdhury, 1965), Hunt (1993) synonymized two of the three Popo Agie Formation genera, *Borborophagus* and *Koskinonodon*, with *Buettneria*, named for material from the Dockum Group of Texas by Case (1922) and known from Arizona and New Mexico, on the basis of a shared lacrimal contribution to the orbital margin. Although *Buettneria* was named after *Anaschisma*, Hunt argued that the latter preserved no diagnostic features and was thus a nomen dubium, rather than the preserved name by precedent. *Eupelor* (in part) was also synonymized with *Buettneria* by Hunt (1993). It was later recognized that the generic name *Buettneria* was preoccupied by a bush cricket (Mueller, 2007), leading to the use of *Koskinonodon* as the replacement based on the quality of preservation of the holotype of *Koskinonodon princeps* and page priority compared with *Borborophagus wyomingensis*. The species name of *Bu. perfecta* was also amended to *Koskinonodon perfectus* (Mueller, 2007). Most recently, Gee et al. (2019) redescribed the holotype material of *An. browni* and *An. brachygnatha* from the Popo Agie Formation, showing the holotype of *An. browni* to be diagnostic to the level of species and demonstrating both holotypes to be indistinguishable from both each other and from that of *Koskinonodon perfectus*, rendering *K. perfectus* and *An. brachygnatha* as junior synonyms of *An. browni* (the latter by page priority and quality of preservation of the holotype). This recent study in particular justifies the need to carefully reexamine historic specimens. A summary of this taxonomic history is presented in Table 1.

Intraspecific Variation in Metoposaurids

One of the fundamental challenges in morphology-based taxonomy of extinct vertebrates is the frequent paucity of specimens for a given taxon, as this confounds a clear understanding of intraspecific variation (ontogenetic, sexually dimorphic, and other forms), an understanding that is essential for robust taxonomic acts and diagnoses. There are numerous instances, including for metoposaurids, in which a new taxon was erected for a distinctly differently sized holotype whose differences were subsequently recognized as being size-related and ontogenetically variable. Metoposaurids are commonly found in mass death assemblages made up of dozens of individuals (e.g., Case, 1932; Romer, 1939; Sawin, 1945; Chowdhury, 1965; Dutuit, 1976; Sulej, 2007; Lucas et al., 2010, 2016; Brusatte et al., 2015). Crucially, with the exception of the *Dutuitosaurus*-bearing Site 13 in Morocco (Dutuit, 1976), the skulls, mandibles, and postcrania from these mass death assemblages are almost completely disarticulated and without association. Furthermore, relative abundances of elements are often preferentially skewed toward preservation of the large, plate-like skulls and ornamented pectoral elements in which those elements provide the highest estimate of the minimum number of individuals (MNI) (e.g., Sulej, 2007; Lucas et al., 2016). The metoposaurids in these bonebeds have long been interpreted as representing monospecific populations due to physical concentration, sedimentological evidence supporting contemporaneous deposition of the specimens (Colbert and Imbrie, 1956; Lucas et al., 2010), and the unlikely scenario of the coexistence of multiple highly morphologically conserved, large-bodied taxa in a restricted geographic region.

In deposits with a large number of specimens, polymorphisms have been identified in a number of features, including those that have been historically utilized for taxonomy. Arguably the best example of this conundrum is the contribution of the lacrimal to the orbital margin that was often used to differentiate *Anaschisma* (and its various junior synonyms) from the European *Metoposaurus* in which the lacrimal was thought to be excluded from the orbit (e.g., Colbert and Imbrie, 1956; Hunt, 1993). This distinction was complicated by Sulej's (2002) report of a lacrimal entering the orbit in the type species of *Metoposaurus*, *M. diagnosticus* (Meyer, 1842), from Germany, suggesting that this feature was a synapomorphy of *Anaschisma* and *Metoposaurus*. This interpretation was contested by Lucas et al. (2007b:249) but was verified by Brusatte et al. (2015), who also documented a lacrimal-orbit contact in *Metoposaurus algarvensis*, and has been accepted by most other workers. However, this conclusion is further complicated by Sulej's (2007) monographic description of dozens of skulls of *Metoposaurus krasiejowensis* from Poland, in which a few specimens with otherwise no other cranial differences clearly possess a lacrimal excluded from the orbital margin (Sulej, 2002, 2007:37). Even in populations where this character state is monomorphic (e.g., the Rotten Hill population of *Anaschisma browni* in the Dockum Group of northwest Texas), the proportion of the lacrimal contribution to the orbital margin can vary widely (Lucas et al., 2016).

The holotypes of *Koskinonodon princeps* and *Borborophagus wyomingensis* have not been redescribed in any detail since their initial description (Branson and Mehl, 1929). Figures of the

TABLE 1. Taxonomic history of the Popo Agie Formation metoposaurids.

Original taxon name	Colbert and Imbrie (1956)	Chowdhury (1965)	Hunt (1993)	Mueller (2007)	Lucas et al. (2016)	Gee et al. (2019) and this study
Anaschisma browni Branson, 1905	*Eupelor browni*	*Metoposaurus browni*	Metoposauridae indet.	Metoposauridae indet.	N/A	*Anaschisma browni*
Anaschisma brachygnatha Branson, 1905	*Eupelor browni*	*Metoposaurus browni*	Metoposauridae indet.	Metoposauridae indet.	N/A	*Anaschisma browni*
Koskinonodon princeps Branson and Mehl, 1929	*Eupelor browni*	*Metoposaurus browni*	*Buettneria perfecta*	*Koskinonodon perfectus*	*Koskinonodon perfectum*	*Anaschisma browni*
Borborophagus wyomingensis Branson and Mehl, 1929	*Eupelor browni*	*Metoposaurus browni*	*Buettneria perfecta*	*Koskinonodon perfectus*	*Koskinonodon perfectum*	*Anaschisma browni*

specimens, products of their time, are often diagrammatic reconstructions or low-resolution plates that are of little utility for modern workers. Both taxa were synonymized with '*Buettneria perfecta*' (syn. *Anaschisma browni*) by Hunt (1993) on the basis of the lacrimal contribution to the orbital margin, a purported autapomorphy that is now known to also occur in *Metoposaurus* (Sulej, 2002), although not in all specimens (Sulej, 2007), and in *Panthasaurus* (Chakravorti and Sengupta, 2018). The growing recognition of intraspecific variation in features historically utilized to differentiate metoposaurid taxa emphasizes the need for further study of this variation at all scales, both geographically and taxonomically. In addition, the various Popo Agie Formation metoposaurids were not collected from the same locality, and without good constraints on local stratigraphy, their stratigraphic relationships are also unknown. This warrants a full redescription of the historic name-bearing type specimens to properly assess the longstanding synonymy of all of these taxa, which cannot be assumed simply by their restricted spatial occurrence, as there is evidence of succession of one metoposaurid species by a second taxon in Texas, Germany, and Morocco (e.g., Hunt, 1993; Milner and Schoch, 2004; Khaldoune et al., 2016). Lastly, the Popo Agie Formation is far separated from the main deposits from which junior synonyms of *An. browni* have been primarily studied, namely the Dockum Group of Texas, the Garita Creek Formation of New Mexico, and the Chinle Formation of Arizona. If the synonymy can be substantiated, the Popo Agie Formation specimens would represent the northernmost occurrence of the taxon and thus provide an excellent opportunity to examine potential intraspecific variation or lack thereof in widely segregated populations. Conversely, a careful exhaustive review of the vast majority of published material from the Popo Agie Formation might recover support for taxonomic distinction at some scale from other North American metoposaurids, following Colbert and Imbrie (1956), given the substantial changes in metoposaurid systematics in the past two decades alone. A final impetus for this study is the recent excavation of a new metoposaurid bonebed in the Popo Agie Formation by the University of Wisconsin–Madison (Lovelace et al., 2017; Kufner and Lovelace, 2018). This bonebed is the first new temnospondyl material to be recovered from the region in nearly a century, and a well-established framework developed from historic specimens will be important for that work. Our objectives here are thus to: (1) provide a detailed redescription of the holotypes of *Borborophagus wyomingensis* and *Koskinonodon princeps* to validate their proposed synonymy with *Anaschisma browni*; (2) to assess variation among the Popo Agie Formation metoposaurids; and (3) if their synonymy is validated, to assess intraspecific variation among *Anaschisma browni* across a relatively wide paleolatitudinal range.

Institutional Abbreviations—**MU**, University of Missouri, Columbia, MO, U.S.A.; **UC** (=FMNH), Field Museum of Natural History, University of Chicago Collection, Chicago, IL, U.S.A.; **UCMP**, University of California Museum of Paleontology, Berkeley, CA, U.S.A.; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, MI, U.S.A.; **WT** (=PPHM), Panhandle Plains Historical Museum, Canyon, TX, U.S.A.

TABLE 2. List of specimens examined and described in this study. Taxonomic identification is based on the original designations by Branson and Mehl (1929).

Specimen	Element(s)	Taxonomic ID	Locality
MU 504	Skull	*Koskinonodon princeps*	Bull Lake Creek
MU 506	Interclavicle	*Koskinonodon princeps*	Bull Lake Creek
MU 508	Clavicle (L)	*Borborophagus wyomingensis*	Red Creek
MU 510	Clavicle (L)	*Anaschisma* sp.	Little Popo Agie Creek
MU 512	Clavicle (L)	*Koskinonodon princeps*	Bull Lake Creek
MU 513	Interclavicle, clavicles (L/R)	*Borborophagus wyomingensis*	Sage Creek
MU 514	Interclavicle	*Koskinonodon princeps*	Bull Lake Creek
MU 517	Skull	*Borborophagus wyomingensis*	Sage Creek
MU 519	Interclavicle	*Borborophagus wyomingensis*	Sage Creek
MU 521	Interclavicle	*Koskinonodon princeps*	Bull Lake Creek
MU 522	Interclavicle	*Anaschisma* sp.	Bull Lake Creek
MU 527	Skull	*Koskinonodon princeps*	Bull Lake Creek
MU 537	Skull	*Koskinonodon princeps*	Bull Lake Creek
MU 539	Mandible (R)	*Koskinonodon princeps*	Bull Lake Creek
MU 542	Interclavicle	*Anaschisma* sp.	Bull Lake Creek
MU 556	Ilium (R)	*Koskinonodon princeps*	Bull Lake Creek
MU 567	Mandible (R)	*Koskinonodon princeps*	Bull Lake Creek
MU 568	Mandible (L) and 'fang'	*Koskinonodon princeps*	Bull Lake Creek
MU 578	Intercentrum	*Koskinonodon princeps*	Bull Lake Creek
MU 583	Intercentra	*Borborophagus wyomingensis*	Sage Creek

MATERIALS AND METHODS

All specimens examined in this study are reposited in the University of Missouri (MU) vertebrate paleontology collection and are listed in Table 2. All materials are from the Popo Agie Formation of the Chugwater Group, Wyoming.

The localities of metoposaurid material collected from the Wind River Basin of Wyoming are plotted along with the outcrop area of the Chugwater Group and generalized stratigraphic column with a focus on the Popo Agie Formation in Figure 1. The holotype material of *Borborophagus wyomingensis* was collected on Sage Creek about 30 miles northwest of Lander, Fremont County, WY. An associated pectoral girdle (MU 513), the holotype cranium (MU 517), an interclavicle (MU 519), and three intercentra (MU 583) are from this locality. Branson and Mehl (1929) also referred a clavicle (MU 508) collected near Red Creek in Hot Springs County, WY to *B. wyomingensis* based on its comparable size to the type locality clavicles. One clavicle (MU 510) referred to *Anaschisma* sp. is from the Little Popo Agie Creek locality and came from the same horizon as the holotypes of *Anaschisma browni* and *Anaschisma brachygnatha* found nearby at the Willow Creek locality (Branson and Mehl, 1929). The remaining material from the Popo Agie Formation housed at MU is from the Bull Lake Creek locality in Fremont County, WY. This includes the holotype cranium of *Koskinonodon princeps* (MU 537), two referred crania (MU 504 and MU 527), three mandibles (MU 539, MU 567, and MU 568), three interclavicles (MU 506, MU 514, and MU 521), a clavicle (MU 512), an ilium (MU 556), and an intercentrum (MU 578) all referred to *K. princeps* (Branson and Mehl, 1929). Two additional interclavicles (MU 522 and MU 542) were collected from Bull Lake Creek and referred to *Anaschisma* sp. (Branson and Mehl, 1929). Several specimens were not located during our visit: cranial fragments (MU 505), three interclavicles (MU 523, MU 557, and MU 579), two clavicles, (MU 528 and MU 536), an unspecified

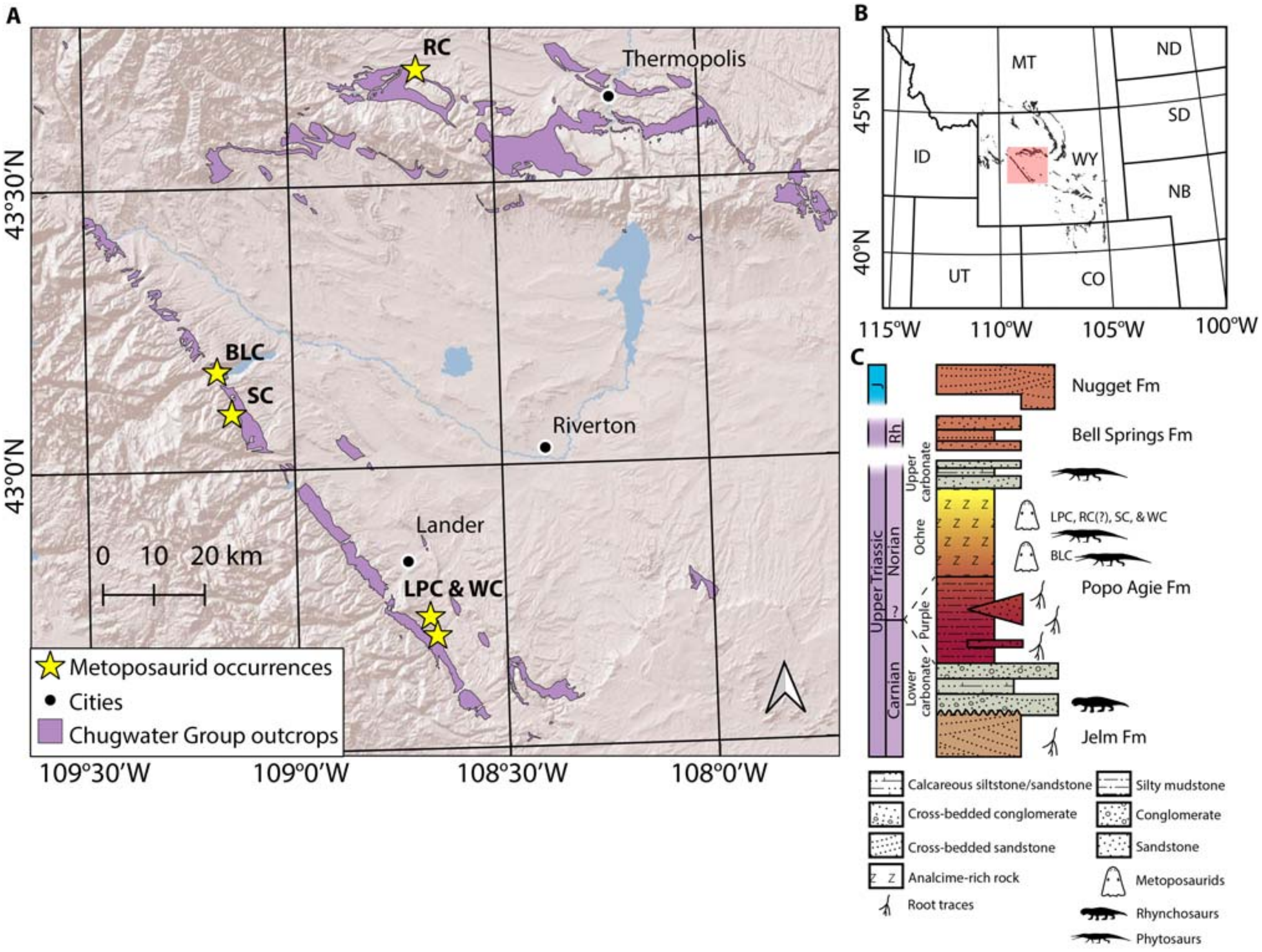

FIGURE 1. Geographic and geologic setting of Upper Triassic Chugwater Group outcrops of the Wind River Basin in Fremont County, Wyoming. Outcrop area data collected from macrostrat.org; metoposaurid fossil occurrence data collected from the Paleobiology Database; map projection: NAD27; '*Paleorhinus*' silhouette from PhyloPic, copyright Scott Hartman; rhynchosaur silhouette by Adam Fitch, modified from Benton, 1983. **A**, map of Chugwater Group outcrops in the Wind River Basin with metoposaurid occurrences; **B**, map of Rocky Mountain region Chugwater Group outcrops with area in **A** marked by bounding box; **C**, generalized stratigraphic column of the Chugwater Group in Fremont County. **Abbreviations**: **BLC**, Bull Lake Creek locality; **J**, Jurassic; **LPC**, Little Popo Agie Creek locality; **RC**, Red Creek locality; **Rh**, Rhaetian; **SC**, Sage Creek locality; **WC**, Willow Creek.

number of intercentra (MU 543), a mandible (MU 551), a putative pectoral girdle (MU 553), and a partial skull (MU 566) (Katz, 1973). None of these specimens was listed in a dated catalogue of the MU collections (Katz, 1976), so it is presumed that they were lost, although the potential that they were exchanged with another institution and the records of such a transfer being lost should also be considered (Katz, 1973).

Photographs were taken using a Panasonic DMC-LX 100 camera with a Leica F1.7–2.8 lens. The plane of each skull roof was positioned at a right angle relative to the direction of the camera shot. Figures were compiled in Adobe Photoshop and Illustrator.

SYSTEMATIC PALEONTOLOGY

TEMNOSPONDYLI Zittel, 1888, sensu Schoch, 2013
STEREOSPONDYLI Zittel, 1888, sensu Yates and Warren, 2000
METOPOSAURIDAE Watson, 1919
ANASCHISMA Branson, 1905, sensu Gee et al., 2019

Type Species—*Anaschisma browni* Branson, 1905, sensu Gee et al., 2019.

Diagnosis—As for the type species.

ANASCHISMA BROWNI Branson, 1905, sensu Gee et al., 2019
(Figs. 2–11, S1–8)

Anaschisma browni Branson, 1905:585.
Anaschisma brachygnatha Branson 1905:588.
Buettneria perfecta Case, 1922:13.
Anaschisma browni Branson and Mehl, 1929:199.
Anaschisma brachygnatha Branson and Mehl, 1929:201.
Koskinonodon princeps Branson and Mehl, 1929:203.
Borborophagus wyomingensis Branson and Mehl, 1929:217.
Eupelor browni Colbert and Imbrie, 1956:422.
Metoposaurus browni Chowdhury, 1965:42.
Buettneria perfecta Hunt, 1993.
Koskinonodon perfectus Mueller, 2007:225.

Koskinonodon perfectum Lucas et al., 2016:24.

Anaschisma browni Gee et al., 2019:4.

Holotype—nearly complete cranium, UC 447, from the Willow Creek locality near Lander, WY.

Referred Material— holotype cranium of *Borborophagus wyomingensis*; MU 537, MU 517, holotype cranium of *Koskinonodon princeps*; MU 504, nearly complete cranium covered in plaster; MU 527, partial left cranium; MU 539, partial right mandible; MU 567, right mandible; MU 568, left mandible and associated 'fang'; MU 578, partial presacral(?) intercentrum; MU 583, three intercentra: anterior(?) dorsal, presacral, and postsacral; MU 506, MU 519, MU 521, MU 522, and MU 542, interclavicles; MU 513, associated interclavicle and left and right clavicles found associated with holotype of *B. wyomingensis*; MU 508, MU 510, and MU 512, left clavicles; MU 556, ilium; UC 448, holotype cranium of *Anaschisma brachygnatha*.

Localities—All of the material redescribed here is from the Popo Agie Formation of the Chugwater Group in the Wind River Basin of Wyoming, U.S.A. The specimens were collected during the summer of 1927 by a University of Missouri field team. The majority of the specimens are from Bull Lake Creek, Fremont County, WY (*K. princeps* type locality) including: MU 504, MU 506, MU 512, MU 521, MU 522, MU 527, MU 537, MU 539, MU 542, MU 556, MU 567, MU 568, MU 578. Material from at least two individuals was collected from Sage Creek, Fremont County, WY (*B. wyomingensis* type locality), including: MU 513, MU 517, MU 519, MU 583. One clavicle was collected from Red Creek, Hot Springs County, WY: MU 508, and another clavicle was collected from Little Popo Agie Formation Creek, Fremont County, WY, the type locality of *Anaschisma browni*: MU 510.

Revised Diagnosis—Metoposaurid defined by the following differential diagnosis: differing from all other metoposaurids except *Metoposaurus* sensu Brusatte et al. (2015) (*M. diagnosticus*, *M. krasiejowensis*, and *M. algarvensis*) and *Panthasaurus* in: lacrimal that enters orbital margin; differing from *Metoposaurus* in: presence of large area of reticulate ornament on ornamented region of interclavicle, prefrontal and lacrimal terminate anteriorly at about the same level, maxilla-prefrontal contact, jugal that terminates at about level of anterior orbital margin, ossified opisthotic, absence of deep notochordal groove on caudal intercentra, and absence of convex kink along anterodorsal margin of ilium; differing from *Panthasaurus* in: frontal that tapers posteriorly, lacrimal widely separated from external naris and less elongate, absence of sensory groove on clavicle, larger area of reticulate ornamentation on clavicle, and absence of convex kink along anterodorsal margin of ilium.

Geological Setting and Age—The Popo Agie Formation is an Upper Triassic series of fluvio-lacustrine beds forming the top of the Chugwater Group primarily exposed in Wyoming (Williston, 1904; Branson, 1927; High and Picard, 1965; Picard, 1993). The base of the Popo Agie Formation is made up of lenticular beds of cross-bedded microconglomerates within calcareous, silty sandstone and typically overlies the Jelm Formation (Fig. 1C; High and Picard, 1965; Pipiringos, 1968). The purple unit of the Popo Agie Formation is predominantly made up of mudstone and siltstone with some interbedded sandstone and calcareous nodules rich in the zeolite analcime throughout; whereas the ochre unit is almost entirely made up of 'ooid-like' grains similarly rich in analcime at the top of the section in most locations (Branson and Mehl, 1929; High and Picard, 1965; Pipiringos, 1968). In some locations, the top of the Popo Agie is formed by a calcareous sandstone often called the 'upper carbonate', but this unit is typically eroded such that either the Rhaetian Bell Springs Formation, the Early Jurassic Nugget Formation, or other younger strata directly overlie the Popo Agie Formation unconformably (Pipiringos, 1968; Jensen and Kowallis, 2005; May, 2014). Based on the general descriptions of the stratigraphic occurrences documented by Branson and Mehl (1929) of the specimens redescribed here and by Gee et al. (2019), all of the described metoposaurid material from the Popo Agie Formation is from the ochre unit or the transition between the purple and ochre units. In addition, specimens from each of the localities have at least some remnants of the distinct ochre 'ooid-like' matrix (Figs. 3, S1, S8; Gee et al., 2019:fig. 6). The majority of Popo Agie Formation vertebrate fossils are reported from the purple to ochre transition or the ochre unit, but vertebrate remains have been found throughout the Popo Agie Formation (Fig. 1C).

Terrestrial vertebrate fossil occurrences offer some age constraint on the Popo Agie Formation (Hunt and Lucas, 1991), but land vertebrate 'faunachrons' (now referred to as 'estimated holochrons' in this context; Martz and Parker, 2017) have received criticism for producing tenuous global correlations of Middle Triassic and Upper Triassic strata due to dubious specimen identification, taxonomic instability, and long or unknown temporal ranges and geographically restricted occurrences of proposed index fossils (Langer, 2005; Rayfield et al., 2005, 2009; Schultz, 2005; Irmis et al., 2010). However, estimated holochrons may have some utility in determining relative regional ages of stratigraphic units (Rayfield et al., 2009) such as the non-marine Upper Triassic units of the southwestern U.S.A. (Martz and Parker, 2017).

Several phytosaur occurrences including the holotype of *Parasuchus bransoni* Williston, 1904 (sensu Kammerer et al., 2016) have been documented within the Popo Agie Formation in the purple to ochre unit transition (Williston, 1904; Lucas et al., 2007a), the ochre unit (Mehl, 1928), and the upper carbonate unit (Eaton, 1965). The presence of *Parasuchus*-grade phytosaurs and the phytosaur *Angistorhinus* in both the Popo Agie Formation and the lower Dockum Group (e.g., the Santa Rosa Sandstone, Camp Springs Formation, and Colorado City Formation) may indicate that these units are coeval (Colbert, 1957; Hunt and Lucas, 1991; Lucas et al., 2010). The absence of *Parasuchus*-grade phytosaurs and *Angistorhinus* and the presence of more derived phytosaurs in the Chinle Formation may indicate that the Popo Agie Formation and the lower Dockum Group are older than the lowest fossiliferous units of the Chinle Formation (Colbert, 1957; Hunt and Lucas, 1991; Martz, 2008; Lucas et al., 2010; Martz and Parker, 2017). The occurrence of the rhynchosaur *Hyperodapedon* sp. in the lower carbonate unit has been used to argue for a late Carnian age of the Popo Agie Formation (Lucas et al., 2002); however, hyperodapedontine rhynchosaurs are known to cross the Carnian–Norian boundary in Brazil (Desojo et al., 2020). Placing the Popo Agie Formation and *Parasuchus*-grade phytosaurs into a chronostratigraphic context is complicated by uncertain relation with the Camp Springs Formation of the Dockum Group and a dearth of vertebrate fossils that can be assigned to alpha taxa from the potential correlative units in the lower part of the Chinle Formation (Shinarump Member and Mesa Redondo Member) (Martz and Parker, 2017). In addition to vertebrate biostratigraphy, the Popo Agie Formation has been suggested to correlate to the *Eoginkgoites* macrofloral assemblage zone, but the macroflora of the Popo Agie Formation are preserved as impressions of uncertain taxonomic affinity and are thus of limited utility (Berry, 1924; Ash, 1980).

Recent high-precision radioisotopic ages from the Chinle Formation (Rasmussen et al., 2020) broadly agree with previous findings (Irmis et al., 2011; Ramezani et al., 2011, 2014) that the Chinle Formation encompasses the Norian. The youngest single crystal age obtained from the Blue Mesa Member, the oldest Chinle Formation member bearing body fossils, is middle Norian (~221 Ma; Rasmussen et al., 2020) suggesting that Chinle Formation deposition is younger than previously thought although within the earlier established range of uncertainty (Blue Mesa Member, ~225–220 Ma; Irmis et al., 2011; Ramezani et al., 2011, 2014). No radioisotopic ages of the Popo Agie Formation are available for comparison, but if a stratigraphically lower position of this formation to that of the lowest body-fossil-bearing unit of the Chinle Formation (Blue Mesa Member) is accepted, then the Popo Agie Formation is no younger than the middle Norian. This is not intended to be a comprehensive reevaluation of the stratigraphic position of the Popo Agie Formation in relation to other North American Upper Triassic deposits, and work is ongoing to correlate the terrestrial Triassic units of the western U.S.A. and develop a chronostratigraphic framework that incorporates new information from the Chugwater Group of Wyoming (Lovelace pers. comm.). In the absence of proxies independent of vertebrate biostratigraphy (e.g., radioisotope ages), the best current estimate for the age of the Popo Agie Formation and potentially the earliest occurrences of *Anaschisma browni* is early Norian.

DESCRIPTION

Dorsal Surface of the Cranium

The description is considered representative of all specimens, with deviations noted where relevant. For the purposes of this redescription, all specimens will be referred to using the original taxonomic assignments of Branson and Mehl (1929). One cranium referred to *Koskinonodon princeps* (MU 504) is not described in detail here because it was evidently badly weathered and then extensively reconstructed such that the sutures are all but impossible to even guess at (Fig. S2); contrary to other specimens, it was also not reconstructed with a level of surficial detail to match the original fossil components. The extent of reconstruction of both the holotypes of *K. princeps* and *Borborophagus wyomingensis* is not evident in the original description (Branson and Mehl, 1929:pls. 4, 5, 10, 11) but is illustrated here (Figs. 2, 3). The right posterior portion of the *K. princeps* holotype cranium was largely reconstructed based on the corresponding left counterparts, as are minor portions of the anterior palate. A portion of the left cranial margin bordering the orbit of the *K. princeps* holotype is reconstructed, but the original fragment is present in the collection (Fig. 2). Reconstruction of the anterior region of the skull roof of the holotype of *B. wyomingensis* obscures many of the antorbital sutures; reconstruction on the posterior skull roof and palate is relatively minor (Fig. 3). Features of the dorsal surface of the cranium of metoposaurids, e.g., the lacrimal contribution to the orbital margin, have historically been regarded as the most taxonomically informative aspect of their morphology (Colbert and Imbrie, 1956; Chowdhury, 1965; Hunt, 1993; Chakravorti and Sengupta, 2018; Gee et al., 2019; Buffa et al., 2019), in spite of a high degree of conservatism of the skull roof between metoposaurid taxa (Romer, 1947; Chowdhury, 1965). Most of the polymorphic character states from presumably monospecific metoposaurid populations are from the dorsal surface of the cranium (Gee et al., 2019), so the following description includes more detailed discussion of variation of the skull roof with differences between specimens.

The premaxilla contacts the maxilla posterolaterally and the nasal posteromedially. The premaxilla-nasal suture is only defined in the *Koskinonodon princeps* holotype (Fig. 2A, B). An alary process projects posteriorly from the premaxilla to contact the nasal along the medial margin of the naris. The nares of the *K. princeps* holotype are relatively wide, being subequal to the diameter of the orbits (Fig. 2A, B). The narial margins of the *Borborophagus wyomingensis* holotype are largely reconstructed but appear to be narrower than the diameter of the orbits (Fig. 3A, B).

The maxilla forms the majority of the lateral border of the skull roof. The maxilla contacts the premaxilla anteriorly, the lacrimal and the jugal medially, and tapers posteriorly to underlie the jugal in dorsal profile. The maxilla does not contribute to the orbital margin as it does in *Duituitosaurus ouazzoui* (Dutuit, 1976). The posterior portion of the maxilla of the referred cranium of *K. princeps*, MU 527 (Fig. 4A, B), does not underlie the jugal due to deformation of the palate posterodorsally and the maxilla dorsolaterally. The maxilla contains the majority of the lateral marginal tooth row, but damage and reconstruction in various regions of all of the examined specimens prevents a confident count or estimation of the marginal dentition.

The nasal contacts the premaxilla anteriorly, the maxilla anterolaterally, the prefrontal posterolaterally, and the frontal posteriorly. It is approximately sub-rectangular with an anterior projection to meet the premaxilla at about the midlength of the naris.

The lacrimal contacts the maxilla anterolaterally, the jugal posterolaterally, and the prefrontal medially. The lateral edge of the lacrimal of the *Borborophagus wyomingensis* holotype is difficult to identify due to a loss of much of the surface texture during preparation and reconstruction on the right side, so the description is based largely on the lacrimal of the holotype and a referred specimen, MU 527, of *Koskinonodon princeps*. However, the lacrimal clearly contributes to the orbital margin in all specimens (Figs. 2–4) as it does in the holotype of *Anaschisma browni* (UC 447; Gee et al., 2019:fig. 2) compared with the exclusion observed in other North American metoposaurids (Case, 1931:fig. 1; Hunt, 1993; Gee et al., 2019). The position of the lacrimal in relation to the orbit and naris is a long-standing character for diagnosing metoposaurid genera and is the only character that currently distinguishes '*Metoposaurus*' *bakeri* from *An. browni* (Gee et al., 2019). An ongoing study of '*M.*' *bakeri* will provide an updated taxonomy and diagnosis of this taxon.

The prefrontal is a square element with irregular edges that contacts the maxilla anteriorly, the nasal anteromedially, the lacrimal anterolaterally, the frontal medially, and the postfrontal posteriorly. It forms the majority of the anterior orbital margin. The prefrontal of the *Borborophagus wyomingensis* holotype (Fig. 3) is more elongate than that of the *Koskinonodon princeps* holotype (Fig. 2). The prefrontal-maxilla contact is broad and well defined in the *K. princeps* holotype. The prefrontal-maxilla contact of the *B. wyomingensis* holotype is poorly defined due to damage and reconstruction in the anterolateral regions of the skull roof.

The postfrontal forms the posteromedial margin of the orbit and contacts the prefrontal anteriorly, the frontal anteromedially, the parietal posteromedially, the supratemporal posteriorly, and the postorbital laterally. The postfrontal is elongate and sub-rectangular and posteriorly comes to a point between the anterior projections of the parietal and the supratemporal. The left postfrontal of the *Borborophagus wyomingensis* holotype has a slender posterolateral projection between the supratemporal and the postorbital. The prefrontal-postfrontal sutures are asymmetric in both complete crania (Figs. 2, 3).

The frontal is a slender element that contacts the nasal anteriorly, the prefrontal anterolaterally, the postfrontal posterolaterally, and tapers posteriorly to contact the parietal. The frontal is markedly asymmetric in the *Koskinonodon princeps* holotype (Fig. 2), with the posterior projection of the right frontal terminating about 2 cm anterior to that of the left, and the anterior portion of the right frontal being wider than that of the left. The frontal-parietal suture is thus asymmetric in this specimen (Fig. 2), with one of the sutures forming a W-shape and the other directed posteromedially to the midline. Similar asymmetry of the frontal-parietal suture can be seen in several specimens

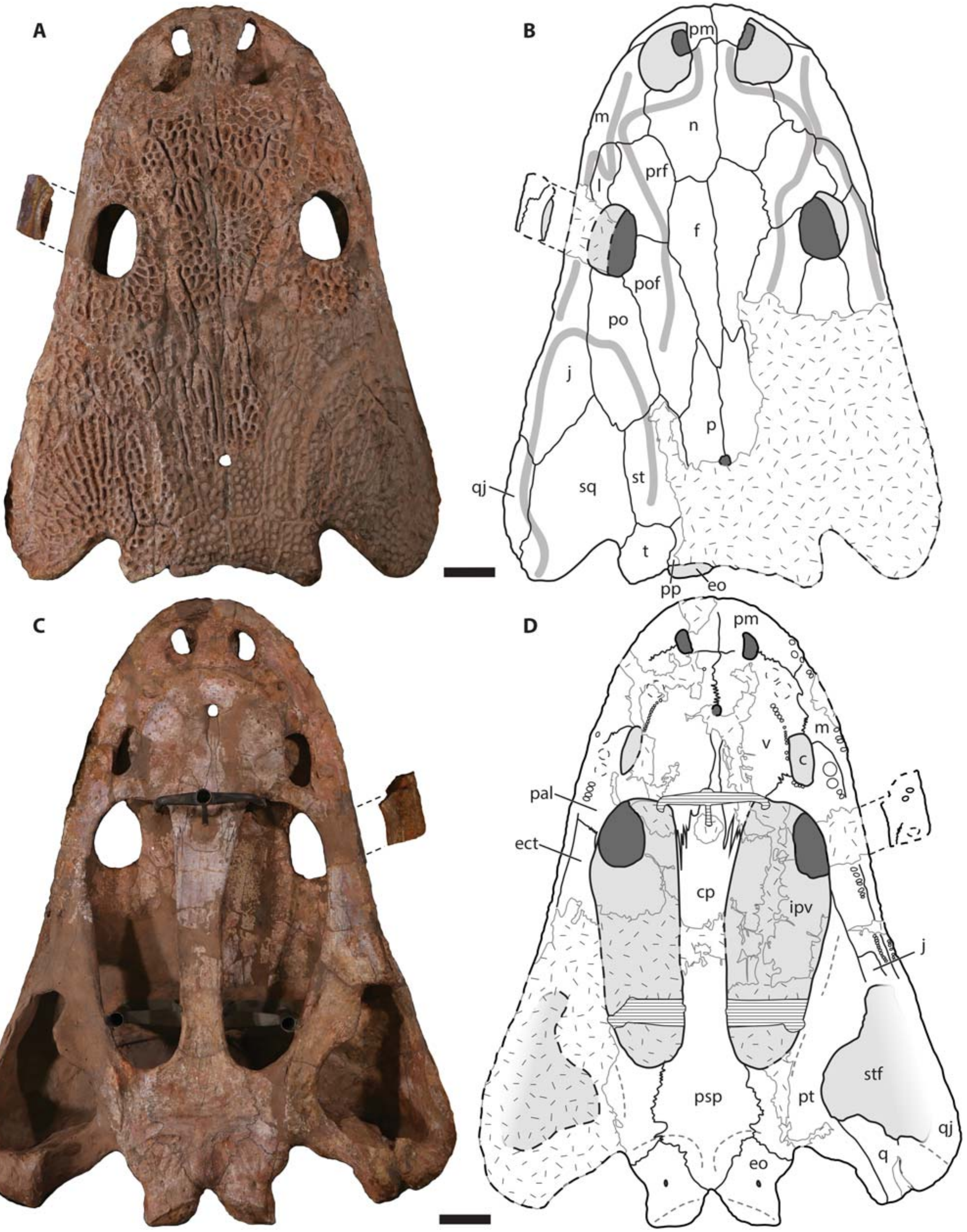

FIGURE 2. Holotype cranium (MU 537) of *Koskinonodon princeps* (syn. *Anaschisma browni*). Hatching represents reconstruction; horizontal lines represent metal mounting armature; gray dashed lines represent contours/ridges. **A**, photograph in dorsal view; **B**, interpretive drawing in dorsal view; **C**, photograph in ventral view; **D**, interpretive drawing in ventral view. **Abbreviations**: **c**, choana; **cp**, cultriform process of the parasphenoid; **ect**, ectopterygoid; **eo**, exoccipital; **f**, frontal; **ipv**, interpterygoid vacuity; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **p**, parietal; **pal**, palatine; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pp**, postparietal; **prf**, prefrontal; **psp**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sq**, squamosal; **st**, supratemporal; **stf**, subtemporal fenestra; **t**, tabular; **v**, vomer. Scale bars equal 5 cm.

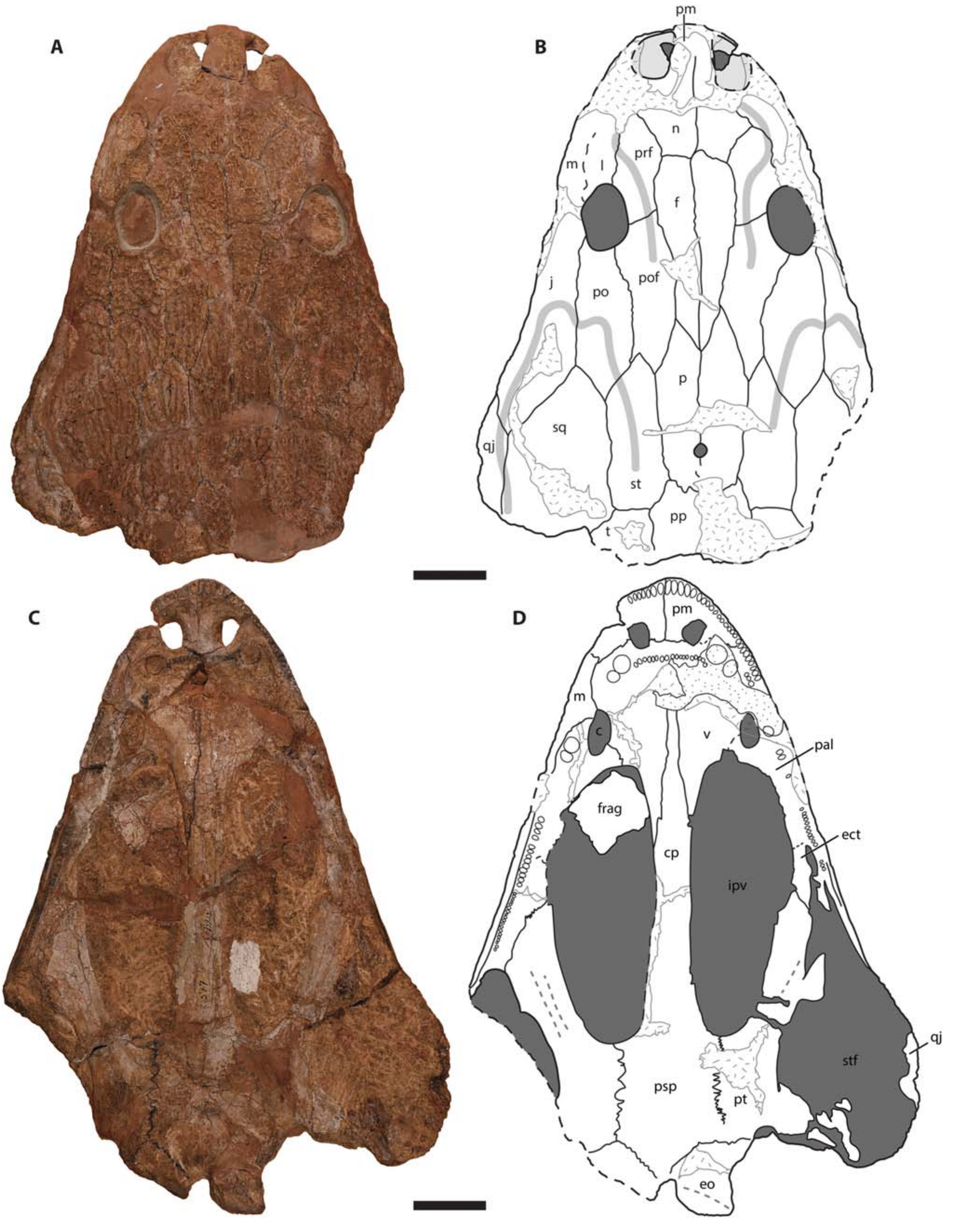

FIGURE 3. Holotype cranium (MU 517) of *Borborophagus wyomingensis* (syn. *Anaschisma browni*). Hatching represents reconstruction; stippling represents matrix; gray dashed lines represent contours/ridges. **A**, photograph in dorsal view; **B**, interpretive drawing in dorsal view; **C**, photograph in ventral view; **D**, interpretive drawing in ventral view. **Abbreviations**: **c**, choana; **cp**, cultriform process of the parasphenoid; **ect**, ectopterygoid; **eo**, exoccipital; **f**, frontal; **frag**, bone fragment; **ipv**, interpterygoid vacuity; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **p**, parietal; **pal**, palatine; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pp**, postparietal; **prf**, prefrontal; **psp**, parasphenoid; **pt**, pterygoid; **qj**, quadratojugal; **sq**, squamosal; **st**, supratemporal; **stf**, subtemporal fenestra; **t**, tabular; **v**, vomer. Scale bars equal 5 cm.

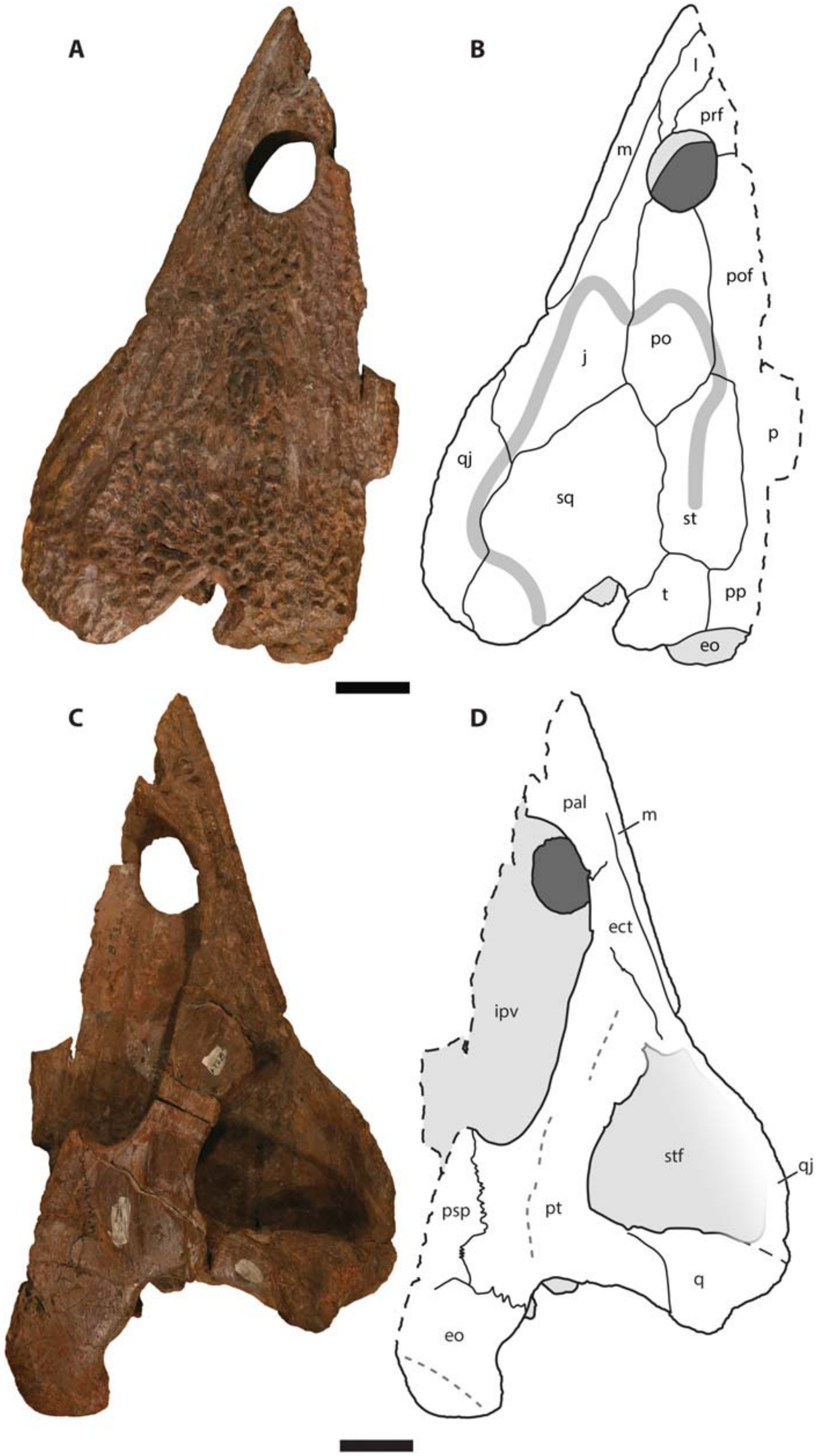

FIGURE 4. Referred partial left cranium (MU 527) of *Koskinonodon princeps* (syn. *Anaschisma browni*). Stippling represents matrix; gray dashed lines represent contours/ridges. **A**, photograph in dorsal view; **B**, interpretive drawing in dorsal view; **C**, photograph in ventral view; **D**, interpretive drawing in ventral view. **Abbreviations**: **ect**, ectopterygoid; **eo**, exoccipital; **ipv**, interpterygoid vacuity; **j**, jugal; **l**, lacrimal; **m**, maxilla; **p**, parietal; **pal**, palatine; **po**, postorbital; **pof**, postfrontal; **pp**, postparietal; **prf**, prefrontal; **psp**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sq**, squamosal; **st**, supratemporal; **stf**, subtemporal fenestra; **t**, tabular. Scale bars equal 5 cm.

of *Metoposaurus krasiejowensis* (Sulej, 2007:figs. 6, 9, 15), but many specimens of *M. krasiejowensis* also have more symmetrical frontal-parietal sutures without a W-shape on either side (Sulej, 2007:figs. 12, 13, 14). One specimen of the Rotten Hill population of *Anaschisma browni* from the Dockum Group of northwest Texas (Lucas et al., 2016:fig. 30a) has similarly asymmetrical frontal-parietal sutures, but most of the specimens have relatively symmetrical frontal-parietal sutures in comparison to the *K. princeps* holotype (Fig. 2). The right and left frontal of the *Borborophagus wyomingensis* holotype are approximately symmetrical (Fig. 3).

The parietal is a sub-rectangular element that contacts the frontal anteriorly, the postfrontal anterolaterally, the supratemporal posterolaterally, and the postparietal posteriorly. The pineal foramen lies along the midline suture in the posterior third of the length of the parietal. The post-pineal region of the parietal is reconstructed in the *Koskinonodon princeps* holotype but is present in the *Borborophagus wyomingensis* holotype. The anteromedial portion of the parietal forms a process that separates the frontal and the postfrontal as it does in most metoposaurids with the exception of *Metoposaurus algarvensis* (Brusatte et al., 2015:figs. 2a, b).

The postorbital is elongate and sub-rectangular similar to the postfrontal. It contacts the postfrontal medially, the jugal laterally, the squamosal posterolaterally, and the supratemporal posteromedially. The sutures shared with the jugal and the postfrontal are long, nearly the anteroposterior extent of the postorbital. The postorbital-postfrontal suture is slightly convex toward the midline. The postorbital tapers posteriorly to a point to form short sutures with the squamosal and the supratemporal as is typical in metoposaurids with the exception of some specimens of *Dutuitosaurus ouazzoui* (Dutuit, 1976:fig. 2, pl. 5) and *Arganasaurus lyazidi* (Dutuit, 1976:pl. 49).

The postparietal contacts the parietal anteriorly, the supratemporal anterolaterally, and the tabular laterally and forms the posteromedial margin of the skull roof. Colbert and Imbrie (1956) found that the postparietal of the Popo Agie Formation metoposaurid specimens was less anteroposteriorly elongate than other North American and European metoposaurids. The left postparietal of the *Borborophagus wyomingensis* holotype is the most complete example of all the MU specimens, and it is longer than it is wide. Proportions of the postparietal range from those seen in this specimen to more equant, as seen in *Metoposaurus krasiejowensis* of Poland (Sulej, 2007) and *Anaschisma browni* specimens from the Dockum Group of Texas (Lucas et al., 2016). The morphology of the postparietal of *Koskinonodon princeps* is inconclusive due to the fragmentary nature of this region in both the holotype and referred specimens (Figs. 3, 4, S2).

The squamosal is approximately pentagonal and contacts the jugal anterolaterally, the postorbital anteromedially, the supratemporal medially, the tabular posteromedially, and the quadratojugal laterally. The dorsal surface of the squamosal is ornamented with the exception of the region posterior to the falciform crest. The posterior margin of the squamosal forms an S-shaped curve due to the presence of an incised otic notch as is typical of metoposaurids with the exception of *Apachesaurus gregorii* (UCMP 63845; Hunt, 1993). The lateral margins are slightly convex and laterally expanded, resulting in a triangular, medially offset anterior process that is typical for large-bodied metoposaurids but unlike *Ap. gregorii* (UCMP 63845) in which the squamosal is more mediolaterally symmetrical.

The supratemporal is an elongate, pentagonal element that contacts the parietal medially, the squamosal laterally, and the postparietal and the tabular posteriorly and sends out an anterior triangular process to contact the postorbital laterally and the postfrontal medially. The supratemporal of the *Borborophagus wyomingensis* holotype (Fig. 3A, B) is subequal to the length of the postorbital, but the supratemporal of *Koskinonodon princeps* is about two-thirds the length of the postorbital (Fig. 2A, B, 4A, B). Similarly to the squamosal, the anterior triangular process of the supratemporal is medially offset.

The jugal is an elongate element that forms much of the lateral margin of the posterior skull roof and the lateral margin of the orbit. It contacts the lacrimal anteromedially, the maxilla anterolaterally, the postorbital medially, the squamosal posteromedially, and the quadratojugal posterolaterally. The long contact with the maxilla begins anterolaterally and continues ventrally as the maxilla comes to underlie the jugal. Much of the lateral orbital margin of the *Borborophagus wyomingensis* holotype is reconstructed, and the anterior extent of the jugal is not preserved (Fig. 3). The anterior extent of the jugal is preserved in the *Koskinonodon princeps* holotype (Figs. 2, 4) showing that it contacts the lacrimal as in most metoposaurids except for *Dutuitosaurus ouazzoui* (Duituit, 1976:fig. 2) and does not contact the prefrontal as it does in *Apachesaurus gregorii* (UCMP 63845; Spielmann and Lucas, 2012:figs. 9a, 10a), *Arganasaurus lyazidi* (Dutuit, 1976:pls. 49–50), '*Metoposaurus*' *bakeri* (UMMP 13055; Case, 1931:fig. 1, 1932:figs. 2–5), and some variants of *Metoposaurus krasiejowensis* (Sulej, 2007:fig. 12).

The quadratojugal appears as a sub-rectangular element in dorsal profile that forms part of the posterolateral margin of the skull roof and that contacts the jugal anteromedially and the squamosal medially. The posterior extent of the postorbital canal often follows the suture between the quadratojugal and the squamosal. The dorsal exposure of the quadratojugal in *Borborophagus wyomingensis* (Fig. 3) and *Koskinonodon princeps* (Figs. 2A, B, 4A, B) is similar in shape and proportion, but the quadratojugal appears more laterally expanded in the referred cranium of *K. princeps.* This appearance of lateral expansion is likely due to dorsoventral compression of the specimen as was previously mentioned regarding the dorsal exposure of the maxilla.

The tabular is a small, square element that forms part of the posteromedial skull margin lateral to the postparietal. It contacts the postparietal medially, the supratemporal anteriorly, and the squamosal anterolaterally. Both the holotype, MU 537 (Fig. 3A, B), and the well-preserved referred specimen of *Koskinonodon princeps*, MU 527 (Fig. 4A, B), possess the distinct tabular horn and incised otic notch typical of most metoposaurids with the exception of *Apachesaurus gregorii* (UCMP 63845; Hunt 1993:fig. 12; Spielmann and Lucas, 2012:fig. 9), *Arganasaurus lyazidi* (Dutuit, 1976:pls. 49–50), and *Arganasaurus azerouali* (Dutuit, 1976:pl. 35; Buffa et al., 2019: fig. 1), but tabular horn size and shape are known to be variable in *Metoposaurus krasiejowensis* (Sulej, 2007) and could be influenced by ontogeny (Gee and Parker, 2018). Both the left and right tabular of the *Borborophagus wyomingensis* holotype are weathered at the posterior margin and are reconstructed with plaster putty on the posteroventral margins (Fig. S3); thus, the size and shape of the tabular horns and depth of the otic notch cannot be determined for this specimen.

Contrary to the majority of metoposaurids, the occiput of all specimens redescribed here does not project posteriorly beyond the skull roof (is not clearly visible) in dorsal profile (Figs. 2–4). The only other metoposaurid in which the occiput is not clearly visible in dorsal profile is *Apachesaurus gregorii* (UCMP 63845), represented only by much smaller specimens (Hunt, 1993; Spielmann and Lucas, 2012). The palate of the referred partial cranium of *Koskinonodon princeps* is clearly broken and dorsally displaced (Fig. 4), but the occiput still does not project as relatively far posteriorly as it does in most large-bodied metoposaurids. The holotypes of *K. princeps* and *Borborophagus wyomingensis* show no evidence of crushing or displacement of the palate relative to the skull roof (Fig. 5, S3) that would suggest a taphonomic influence.

Ornamentation

The ornamentation of all the specimens is typical for metoposaurids with sub-circular pits and restricted zones of elongate grooves and ridges on the posterior portions of the postfrontal and the postorbital, anterior portions of the parietal and the supratemporal, minor portions of the anterior and posterior regions of the frontal, and on the quadratojugal. The quality of preservation of ornamentation is inconsistent among the skulls. The surface of the poorly preserved referred cranium of *Koskinonodon princeps* (MU 504) has some patches of preserved ornamentation, but the damage to the specimen is too extensive to draw any conclusions on the morphology of surface features (Fig. S2). The dorsal surface of the *Borborophagus wyomingensis* holotype was damaged during preparation (Branson and Mehl, 1929) removing some portions of ornamentation and any unambiguous infraorbital sulcus morphology. The remaining lateral line sulci are visible but shallow and narrow when compared with the lateral line sulci of *K. princeps* (Branson and Mehl, 1929). The relatively shallow and narrow lateral line sulci of *B. wyomingensis* have been suggested to be attributable to ontogenetic variation (Branson and Mehl, 1929; Colbert and Imbrie, 1956), but the relatively shallow state of the sulci compared with the rest of the ornamentation may be partially due to overpreparation. The supraorbital canal forms an S-shaped curve that is laterally deflected between the orbits and the nares and that reaches the medial margin of the lacrimal in *B. wyomingensis* but not in *K. princeps*. The infraorbital canal of the *K. princeps* holotype (Fig. 2) is preserved almost completely, beginning at the lateral margin of the naris with the S-shaped flexure onto the lacrimal on the left side and the minor medial projection onto the lacrimal on the right side; it terminates about 6 cm posterior to the orbit on the jugal. The full extent of the temporal canal is preserved on all specimens and forms an inverted U-shape on the posterior skull roof with a slight posterior deflection on the transverse portion of the canal at the jugal-postorbital suture. There is no commissure between the infraorbital canal and either the supraorbital or temporal canals (Figs. 3, 4).

Ventral Surface of the Cranium and Palate

The palate of metoposaurids is highly conserved with only one feature suggested to be taxonomically informative, the width of the cultriform process of the parasphenoid (Hunt, 1993). The cultriform process is wide and flat in all metoposaurids, differing from most other temnospondyls, except for *Apachesaurus gregorii* (UCMP 63845; Spielmann and Lucas, 2012:figs. 9b, 10b) in which it is narrower and more rod-like. However, the narrow cultriform process of *Ap. gregorii* only serves to distinguish it from large-bodied metoposaurids, and a paucity of complete, described small-bodied metoposaurid crania complicates comparison between taxa (see Davidow-Henry, 1987, 1989; Gee and Parker, 2017; Gee et al., 2019).

The palatal exposure of the premaxilla is sub-rectangular (Fig. 2) to sub-triangular (Fig. 3) and contacts the maxilla laterally and the vomer posteriorly. It forms the anterior margin of the anterior palatal fenestra and bears the anterior portion of the lateral marginal tooth row. In palatal profile of the *Borborophagus wyomingensis* holotype, the premaxillae form a more pointed profile than the typical rounded parabolic shape of other metoposaurids (Fig. 3).

In palatal view, the maxilla forms the majority of the lateral margin of the skull and contacts the premaxilla anteriorly, the vomer, the palatine, and the ectopterygoid medially, and the jugal posteromedially. With the exception of *Dutuitosaurus ouazzoui* (Dutuit, 1976:fig. 3), the presence of a maxilla-vomer contact is conserved among metoposaurids. The maxilla sends out a medial projection to contribute to the anterolateral margin of the choana and bears most of the lateral marginal tooth row and its posterior termination.

The vomer is a rounded sub-rectangular element that sutures to the premaxilla anteriorly, the maxilla laterally, the palatine posterolaterally, and the parasphenoid posteromedially. It forms the anteromedial margin of the interpterygoid vacuity, the anterior and medial margins of the choana, and the posterior margin of the anterior palatal fenestra. The intervomerine canal lies at the apex of the cultriform process of the parasphenoid between the left and right vomer. The vomer bears portions of two tooth rows, the entire transverse tooth row and the anterior termination of the parachoanal tooth row. None of the crania retain both tooth rows in their entirety, but the *Koskinonodon princeps* holotype retains most of the parachoanal tooth rows and a ridge along the transverse tooth row with one visible tooth base (Fig. 2C, D) whereas the *Borborophagus wyomingensis* holotype possesses a clear transverse tooth row (Fig. 3C, D). The transverse tooth row is separated from the parachoanal tooth row by the paired vomerine 'fang' (often referred to as 'tusk') sockets.

The parasphenoid is a long unpaired element with two regions visible in palatal view, the basal plate and the anteriorly projecting cultriform process. In all specimens examined here, the cultriform process is mediolaterally expanded, dorsoventrally flattened, and forms a projection that sutures to the vomer anterolaterally with the intervomerine canal at its anterior apex. The dorsal surface of the cultriform process bears two longitudinal ridges, the sphenethmoidal crests, which can be seen only in occipital view of the *Koskinonodon princeps* holotype (Fig. 5A, C). The basal plate of the parasphenoid is semi-elliptical and sutures to the pterygoid laterally and the exoccipital posterolaterally. The adjoining region between the cultriform process and the muscle scars on the basal plate of the parasphenoid is ornamented in the holotypes of *Borborophagus wyomingensis* (Fig. 3C, D) and *K. princeps* (Figs. 2C, D, 4C, D). This ornamentation is present in other metoposaurids such as *Anaschisma browni* (Sawin, 1945:fig. 3; Lucas et al., 2016:figs. 29b, h); '*Metoposaurus*' *bakeri* (UMMP 13055; Case, 1932:fig. 6); and *Metoposaurus krasiejowensis* (Sulej, 2007: figs. 6b, 10a), but the presence or absence of palatal ornamentation appears to be polymorphic in *M. krasiejowensis* and *An. browni* without a clear size-related pattern that would, for example, suggest ontogenetic influence.

The palatine is sub-triangular and forms part of the anterior and lateral margins of the interpterygoid vacuity and the posterior and lateral margins of the choana. It shares a long anterolateral suture with the maxilla, an anteromedial suture with the vomer, and a posterior suture with the ectopterygoid. The palatine bears portions of two tooth rows, the anterior termination of the medial marginal tooth row, and the posterior termination of the parachoanal tooth row. The anterior termination of the medial tooth row ends with two palatine 'fang' sockets. The parachoanal tooth row is best represented in the *Koskinonodon princeps* holotype (Fig. 2C, D); some slight depressions along the posterior border of the left choana of the *Borborophagus wyomingensis* holotype likely represent the parachoanal tooth positions (Fig. 3C, D). The position of the palatine-ectopterygoid suture is poorly defined in the *B. wyomingensis* holotype due to fractures along the lateral margin of the palate, but there is no reason to believe it differs from the typical position in metoposaurids.

The ectopterygoid is a sub-rectangular element that contacts the palatine anteriorly, the maxilla laterally, the pterygoid medially, and the jugal posteriorly. It forms part of the lateral margin of the interpterygoid vacuity along with the palatine and bears the posterior termination of the medial tooth row. The ectopterygoid-jugal suture is consistent among metoposaurids although it was rarely identified and described by earlier workers (Gee et al., 2019). The ectopterygoid-jugal suture can only be confidently identified in the *Koskinonodon princeps* holotype (Fig. 3D) due to poor definition of the sutures in this region in the referred cranium of *K. princeps*, MU 527 (Fig. 4), and the *Borborophagus wyomingensis* holotype (Fig. 3).

A ventral exposure of the jugal was identified on the holotype of *Koskinonodon princeps* that sutures to the pterygoid medially and the ectopterygoid anterolaterally (Fig. 2C, D). This exposure of the jugal is often misidentified as part of an exclusively palatal element in metoposaurids, including the type specimens of *Anaschisma browni* (Branson, 1905:fig. 2; Branson and Mehl, 1929:fig. 6) and *Anaschisma brachygnatha* (syn. *An. browni*) (Branson and Mehl, 1929:fig. 7), prior to their redescription because a ventral exposure of the jugal is uncommon in other temnospondyls (Gee et al., 2019).

The pterygoid is a triradiate element with three distinct processes, a transverse process, a posterolateral process, and a posteromedial process (the palatine ramus, quadrate ramus, and basipterygoid ramus, respectively). The transverse process of the pterygoid contacts the ectopterygoid and the jugal laterally and is the largest of the three processes, contributing to most of the posterolateral margin of the interpterygoid vacuity and the anterior margin of the subtemporal fenestra. As in other metoposaurids, a small ventrolaterally directed flange extends from the transverse process into the subtemporal fenestra. The quadrate ramus overlaps the quadrate laterally and varies in length between the crania of *Koskinonodon princeps* (Figs. 3, 4) in which the process is preserved. The basipterygoid ramus is the shortest of the three processes and extends medially to abut the parasphenoid in a long, interdigitated suture and posteriorly to contact the exoccipital. The pterygoid-exoccipital suture is typically perpendicular to the midline in metoposaurids (see Sulej, 2007), but the angle of this suture can vary from perpendicular to the midline (Fig. 3) to oblique to the midline (see Figs. 2, 4; Sulej, 2007; Lucas et al., 2016). The pterygoid-exoccipital sutures of one specimen of *Metoposaurus krasiejowensis* are perpendicular on one side and angled on the other (Sulej, 2007:fig. 8). The pterygoid bears several ridges extending along the margin of the subtemporal fenestra from the posterolateral process onto the palatine ramus, similar to what has been described for other metoposaurids, such as ‘*Buettneria howardensis*’ (Sawin, 1945:fig. 3), which is often considered synonymous with *Anaschisma browni* (Hunt, 1993; Sulej, 2002; Gee et al., 2019), and *Metoposaurus algarvensis* (Brusatte et al., 2015:figs. 2c, d).

The quadrate of *Koskinonodon princeps* (Figs. 2C, D, 4C, D) is sub-triangular in palatal view and underlies the quadrate ramus of the pterygoid medially and sutures to the quadratojugal dorsolaterally. The quadrate is poorly ossified relative to the rest of the cranium and made up of highly porous, trabecular bone. The quadrate of the *Borborophagus wyomingensis* holotype is only partially freed from matrix and is uninformative in its current state (Fig. 2C, D).

The exoccipital is a rectangular element that contacts the pterygoid anteriorly and the parasphenoid medially in palatal view. Posteriorly the exoccipitals form the convex occipital condyles that are angled medially to meet the anterior condyles of the atlas. A ventrally facing foramen is present on the exoccipital of the *Koskinonodon princeps* holotype (Fig. 2C, D) which is typical among metoposaurids although the position of the foramen is variable among metoposaurids. For example, the foramen of *Metoposaurus algarvensis* is located laterally compared with other metoposaurids (Brusatte et al., 2015:fig. 6).

Cranial Dentition

Portions of the ventral surface of the maxilla have been reconstructed and are also obscured by matrix in the *Koskinonodon princeps* holotype, making identification of distinct tooth positions problematic (Fig. 2C, D). Where it is possible to identify them, the tooth bases are oval and transversely broadened. Much of the ventral surface of the *Borborophagus wyomingensis* holotype is damaged from overpreparation as evidenced by the smoothed surfaces of round, ooid-like matrix grains retained over the vomer and lateral margins of the palate and thus some of the tooth bases are either unnaturally elongated or difficult to identify (Fig. 3C, D). In addition to overpreparation, some of the tooth bases are obscured by ink used to trace the inferred outline of adjacent positions; any tooth base only identified by an outline and without the distinctive labyrinthine tooth cross section was not included in the interpretive drawings.

Occiput

Very few taxonomically informative characters of the occiput have been identified within the Metoposauridae. The foramen magnum is typically keyhole-shaped in metoposaurids owing to the absence of an ossification of the synotic tectum dorsal to and confluent with the foramen magnum proper. Consequently, the lamellose process of the exoccipital projects medially such that the entire opening is subdivided into dorsal and ventral regions (Sulej, 2007). The margins around the foramen magnum of *Apachesaurus gregorii* (UCMP 63845) are more smoothly confluent compared with other metoposaurids due to a lack of prominent lamellose processes (Spielmann and Lucas, 2012:figs. 9f, 11), but this may reflect ontogeny or taphonomy (Gee et al., 2019). The crania redescribed here all have inconclusive contours of the foramen magnum due to reconstruction (Fig. 5A), lack of preparation (Fig. S3), or incompleteness (Fig. 5C). The synotic tectum of the foramen magnum of the *Koskinonodon princeps* holotype is infilled with plaster apparently meant for reconstruction, but the ventral portion of the lamellose processes of the exoccipitals are visible (Fig. 5A, C), and they project into the foramen magnum, which would probably have produced the subdivided opening typical of large-bodied metoposaurids. This differs from the *Anaschisma browni* holotype (UC 447), which has an oval shaped foramen magnum similar to *Ap. gregorii* (UCMP 63845), but this has been suggested to be a taphonomic artifact (Gee et al., 2019). The ascending lamina of the pterygoid sutures with the squamosal dorsally and bears the prominent oblique crest which is broken on the holotype (Fig. 5A) but intact on the referred specimen of *K. princeps* (Fig. 5C). The oblique crest has previously been referred to as the oblique ridge (Warren and Black, 1985) and the otic flange (Watson, 1962), but the earliest term, oblique crest (Bystrow and Efremov, 1940), is retained here. Both the holotype and referred cranium of *K. princeps* exhibit a large and elongate paraquadrate foramen typical of large-bodied metoposaurids (Fig. 5).

The parotic process of the tabular of both specimens of *Koskinonodon princeps* bears a laterally directed, semi-circular flange (Fig. 5) that is not developed to the same extent in other metoposaurids. This flange is positioned ventral to the external tabular crest that extends dorsally to support the tabular horn. The flange encompasses a concave margin between it and the tabular horn. One figured specimen of *Metoposaurus krasiejowensis* bears a minor flange off of the parotic process (Sulej, 2007:fig. 16a), but it is not as prominent as those described here. The ‘*Buettneria perfecta*’ holotype (syn. *Anaschisma browni*) possesses a lateral flange in this region (Fig. S4; Case, 1922:fig. 1c), but this flange is more ventrally situated and protrudes from the lateral margin of the vertical column of the exoccipital. One referred cranium of ‘*Metoposaurus*’ *bakeri* (Case, 1932:fig. 8) from the Dockum Group of Texas has a similar flange of the parotic process of the tabular, but this flange is much less pronounced, and the skull roof of this specimen of ‘*M.*’ *bakeri* is about half the midline length (30.6 cm) of the *K. princeps* holotype (54.0 cm). A cranium of *Dutuitosaurus ouazzoui* (Dutuit, 1976: pl. 46, fig. b) also has a small flange of the parotic process of the tabular, but the size of the specimen is unclear, though it appears small.

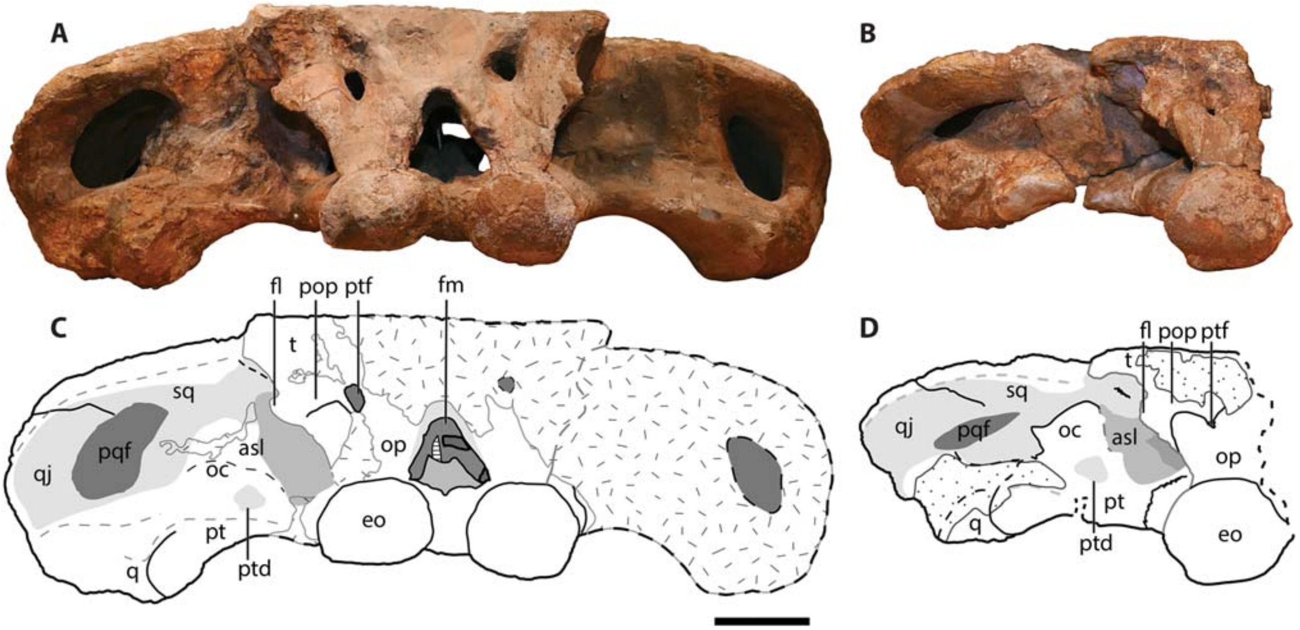

FIGURE 5. The occiput of the holotype cranium (MU 537) and a referred cranium (MU 527) of *Koskinonodon princeps* (syn. *Anaschisma browni*). Hatching represents reconstruction; stippling represents matrix; horizontal lines represent metal mounting armature; gray dashed lines represent contours/ridges. **A**, photograph (MU 537) in posterior (occipital) view; **B**, photograph (MU 527) in posterior (occipital) view; **C**, interpretive drawing (MU 537) in posterior (occipital) view; **D**, interpretive drawing (MU 527) in posterior (occipital) view. **Abbreviations**: **asl**, ascending lamina of the pterygoid; **eo**, exoccipital; **fl**, flange of the parotic process of the tabular; **fm**, foramen magnum; **oc**, oblique crest of the pterygoid; **op**, occipital pillar; **pop**, parotic process of the tabular; **pqf**, paraquadrate foramen; **pt**, pterygoid; **ptd**, pterygoid depression; **ptf**, posttemporal foramen; **q**, quadrate; **qj**, quadratojugal; **sq**, squamosal; **t**, tabular. Scale bar equals 5 cm.

Mandible

Three mandibles are present in the University of Missouri collection, all from the Bull Lake Creek (*Koskinonodon princeps*) locality. A right mandible (MU 567; Fig. 6A–D) and a left mandible (MU 568; Fig. 6E–H) are nearly complete and were associated with the *K. princeps* holotype, and the anterior portion of a right mandible (MU 539; Fig. S5A, B) was found in the same horizon (Branson and Mehl, 1929). The nearly complete mandibles were both figured by Branson and Mehl (1929), and their description is largely upheld here. A large portion of the dorsal margin of the right mandible (MU 567) was reconstructed as well as portions of the lingual surface, primarily obscuring the coronoid series and defining the dorsal margin of the Meckelian foramen (Fig. 6A–D). The left mandible (MU 568) is more complete than the right but also has some reconstruction defining the dorsal margin of the Meckelian foramen and obscuring some of the sutures, primarily of the lingual surface, although partial contacts are present (Fig. 6G, H). The reconstructed portions of each mandible were not evident or noted in the original description (Branson and Mehl, 1929).

The dentary is a large element that forms much of the dorsal and anterior portions of the mandible as is typical for most temnospondyls. On the labial side, it contacts the splenial, the postsplenial, and the angular ventrally and the surangular posteriorly, and on the lingual side, it contacts the splenial, the precoronoid, the intercoronoid, and the coronoid ventrally and tapers dorsally from anterior to posterior. A single disarticulated symphyseal 'fang' was found associated with MU 568 near the anterior lingual side of the mandible according to Branson and Mehl (1929) (Fig. S6). Branson and Mehl (1929) noted an additional row of symphyseal teeth on the dentary, but this was not observed upon further inspection; it may have been present on the missing mandible (MU 551).

Three coronoids are typical for metoposaurids and for temnospondyls more broadly, but the full contours of each coronoid are not discernible in any given specimen, and the identification of all three in MU 568 (Fig. 6G, H) is based on partially preserved contacts between each of the three elements. These coronoids are sometimes numbered anteroposteriorly (coronoid 1 to coronoid 3) or by their position (anterior, middle, posterior), but some authors also define the posteriormost coronoid as the 'true' coronoid, the middle coronoid as the intercoronoid, and the anteriormost coronoid as the precoronoid (e.g., Sulej, 2007). All three are restricted to lingual exposures and lack dentition. The posteriormost coronoid frames the adductor chamber anteriorly and contributes to the coronoid process.

The splenial forms the anteroventral margin of the mandible. On the labial side, it contacts the dentary dorsally and the postsplenial posteriorly, and on the lingual side, it contacts the precoronoid dorsally. The splenial contributes to the mandibular symphysis (Fig. 6C, D, G, H) which is typical among metoposaurids with only *Dutuitosaurus ouazzoui* (Dutuit, 1976:fig. 30b; pl. 17, fig. b; pl. 18, fig. b) and *Arganasaurus azerouali* (Dutuit, 1976:fig. 75b; pl. 37, fig. b; pl. 38, fig. c; pl. 39, fig. b; Buffa et al., 2019:figs. 5c, d) lacking this feature.

The postsplenial is sub-rectangular in lingual view, tapers posteriorly in labial view, and contributes to the ventral margin of the mandible and the anteroventral margin of the Meckelian foramen. In labial profile, the postsplenial contacts the splenial anteriorly, the dentary anterodorsally, and the angular posterodorsally. In lingual profile, it contacts the intercoronoid anterodorsally and likely the coronoid posterodorsally, although this suture is not preserved.

The angular forms much of the labial side of the mandible and contributes to a large part of the ventral and posterior margins of the mandible and the posteroventral margin of the Meckelian

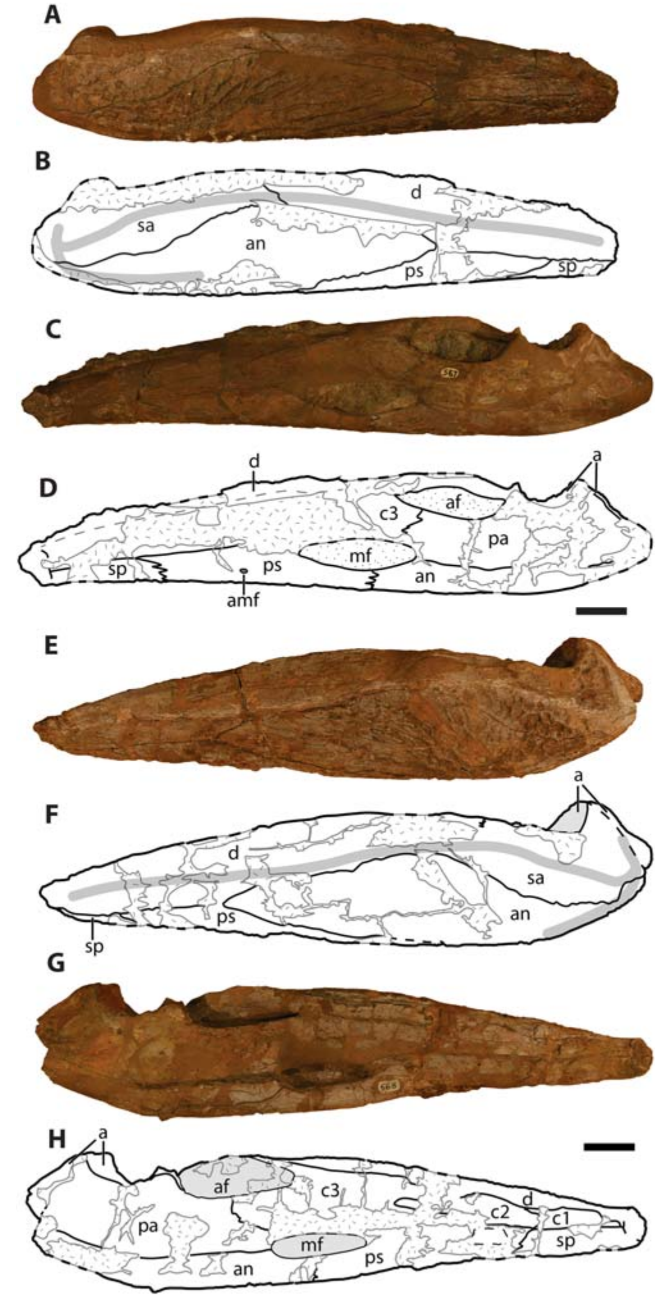

FIGURE 6. Nearly complete right (MU 567) and left (MU 568) metoposaurid mandibles associated with the holotype cranium of *Koskinonodon princeps* (syn. *Anaschisma browni*). Hatching represents reconstruction; stippling represents matrix; gray dashed lines represent contours/ridges. **A**, photograph of labial view of right mandible (MU 567); **B**, interpretive drawing of same; **C**, photograph of lingual view of right mandible (MU 567); **D**, interpretive drawing of same; **E**, labial view of left mandible (MU 568); **F**, interpretive drawing of same; **G**, lingual view of left mandible (MU 568); **H**, interpretive drawing of same. **Abbreviations**: **a**, articular; **af**, adductor fossa; **amf**, anterior Meckelian foramen; **an**, angular; **c1**, coronoid 1 (precoronoid); **c2**, coronoid 2 (intercoronoid); **c3**, coronoid 3 (coronoid); **d**, dentary; **mf**, Meckelian fenestra; **pa**, prearticular; **ps**, postsplenial; **sa**, surangular; **sp**, splenial. Scale bars equal 5 cm.

foramen. On the labial side, the angular contacts the dentary anterodorsally, the postsplenial anteroventrally, and the surangular posterodorsally; on the lingual side, it contacts the postsplenial anteriorly and the prearticular dorsally.

The surangular contributes to the posterodorsal region of the mandible and has both labial and lingual exposures. The labial exposure is mostly unornamented save for a small region of large pits along the ventral contact with the angular. The oral groove extends for the length of the surangular dorsal to this ornamented region. The surangular has a smaller lingual exposure where it contributes to the coronoid process to frame the adductor chamber.

The prearticular is a long element on the lingual surface at the posterior end of the mandible. It partially frames the adductor chamber with the posteriormost coronoid and the Meckelian foramen with the angular and the postsplenial. At the posterior end of the adductor chamber, the prearticular forms a short dorsal projection (the hamate process) that is positioned just anterior to the glenoid region. The mandibles described here are damaged in the region dorsal to the foramen, but the prearticular can at least be seen to contact the foramen along the posterior margin (Fig. 6G, H). Posteriorly, the prearticular meets the articular to partially frame the chorda tympani foramen and the glenoid region.

The articular forms the jaw articulation, with a developed glenoid region posterior to the hamate process of the prearticular. The glenoid region is triangular, expanding posteriorly and with a longitudinal ridge (the ‘postglenoid ridge’ of Sulej, 2007) extending along the labial margin above the surangular. Posterior to the glenoid, the articular slopes posteroventrally, where it partially frames the chorda tympani foramen.

Postcrania

As with other metoposaurid deposits, the large ornamented elements of the pectoral girdle and the robust intercentra are the best represented postcranial elements. Nearly all of the interclavicles lack the more delicate anterior process but are otherwise well-preserved (Figs. 7, S7). Ornamentation at the center of the elements consists of a large region of circular pitting, as with other large-bodied North American metoposaurids and in contrast to the European *Metoposaurus* (e.g., Sulej, 2007; Lucas et al., 2016). This has been a long-standing character used to differentiate the North American and European taxa (e.g., Colbert and Imbrie, 1956; Hunt, 1993; Sulej, 2002), although there may be some plasticity in the feature as suggested by the identification of a *Metoposaurus*-like interclavicle (Lucas et al., 2016:fig. 49c) in the Rotten Hill bonebed, which otherwise preserves an extremely large amount of material diagnostic for *Anaschisma browni* (Lucas et al., 2016). The clavicles are relatively complete but often lack the plate-like ascending crest and the dorsal process for the cleithrum (Figs. 8, 9, S8). As with the interclavicles, the region of circular ornamentation, situated at the posterolateral margin on the ventral surface, is relatively large like that seen in other North American specimens. A set of right and left clavicles and an interclavicle (Fig. 9) was associated with the holotype cranium of *Borborophagus wyomingensis* (Branson and Mehl, 1929). The ventral surface of the interclavicle (Fig. 9A) is largely unprepared, but a referred interclavicle from the same locality displays a large area of pitted ornamentation (Fig. S7).

The four intercentra present in the MU collection are typical for large-bodied metoposaurids, forming anteroposteriorly shortened cylinders as opposed to the elongate cylinders proposed to be diagnostic of *Apachesaurus gregorii* (UCMP 63845; Hunt, 1993; Spielmann and Lucas, 2012) but also reported for *Dutuitosaurus ouazzoui* (Dutuit, 1976). The three intercentra from Sage Creek associated with *Borborophagus wyomingensis* are representative of different positions of the axial column identified: anterior(?) dorsal (Fig. 10A–C), presacral (Fig. 10D–F), and postsacral (Fig. 10G–I). The intercentrum from Bull

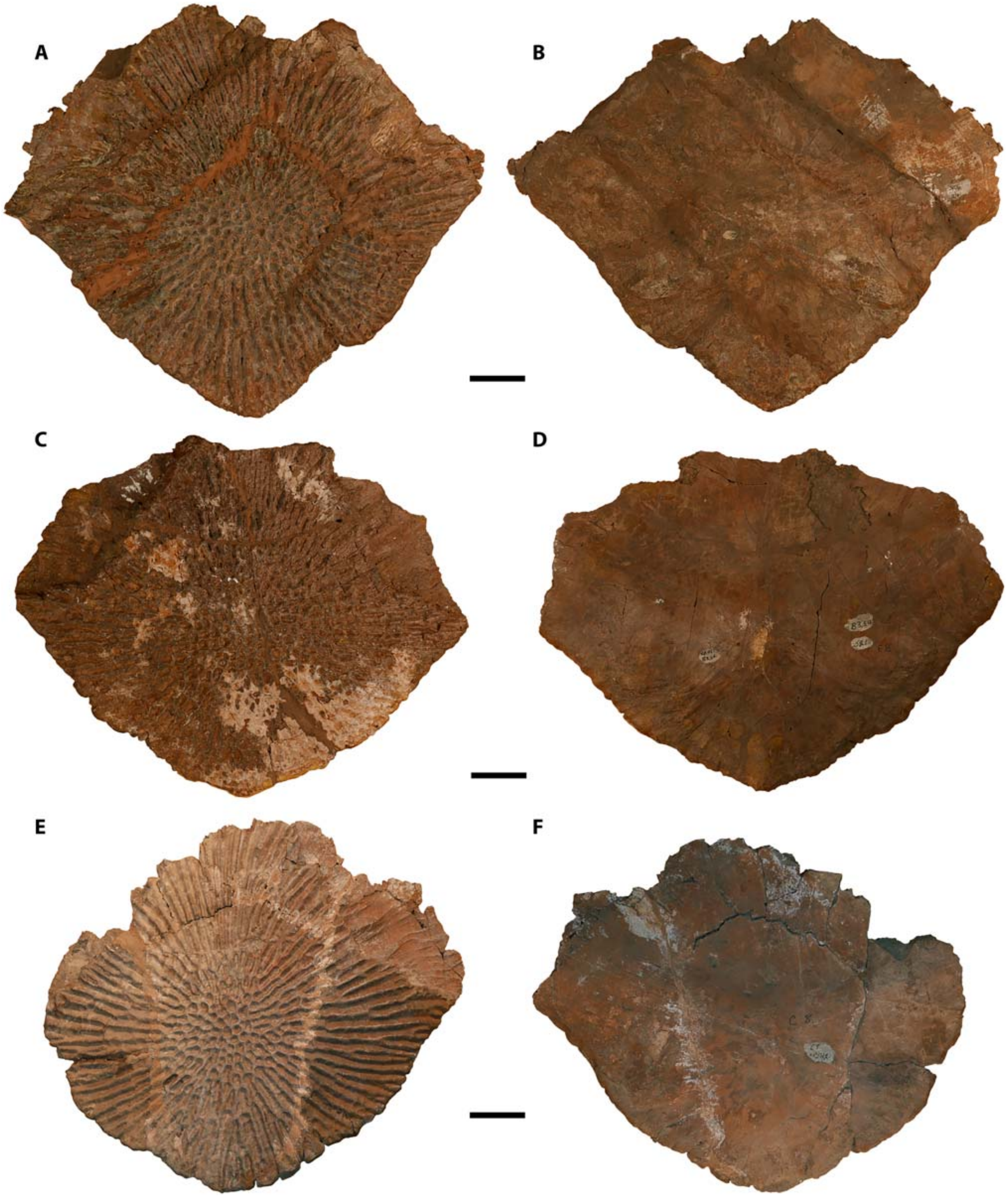

FIGURE 7. Photographs of select metoposaurid interclavicles from the Bull Lake Creek locality referred to *Koskinonodon princeps* (syn. *Anaschisma browni*). **A**, interclavicle (MU 506) ventral view; **B**, interclavicle (MU 506) in dorsal view; **C**, interclavicle (MU 521) in ventral view; **D**, interclavicle (MU 521) in dorsal view; **E**, interclavicle (MU 542) in ventral view; **F**, interclavicle (MU 542) in dorsal view. Scale bar equals 5 cm.

Lake Creek associated with *Koskinonodon princeps* could not be confidently assigned to any position in the axial column due to damaged margins, but it is likely presacral (Fig. S5C). None of the intercentra has the distinct notochordal pit present on the anterior and posterior faces of intercentra of the European species of *Metoposaurus* (e.g., Sulej, 2007:figs. 23–30).

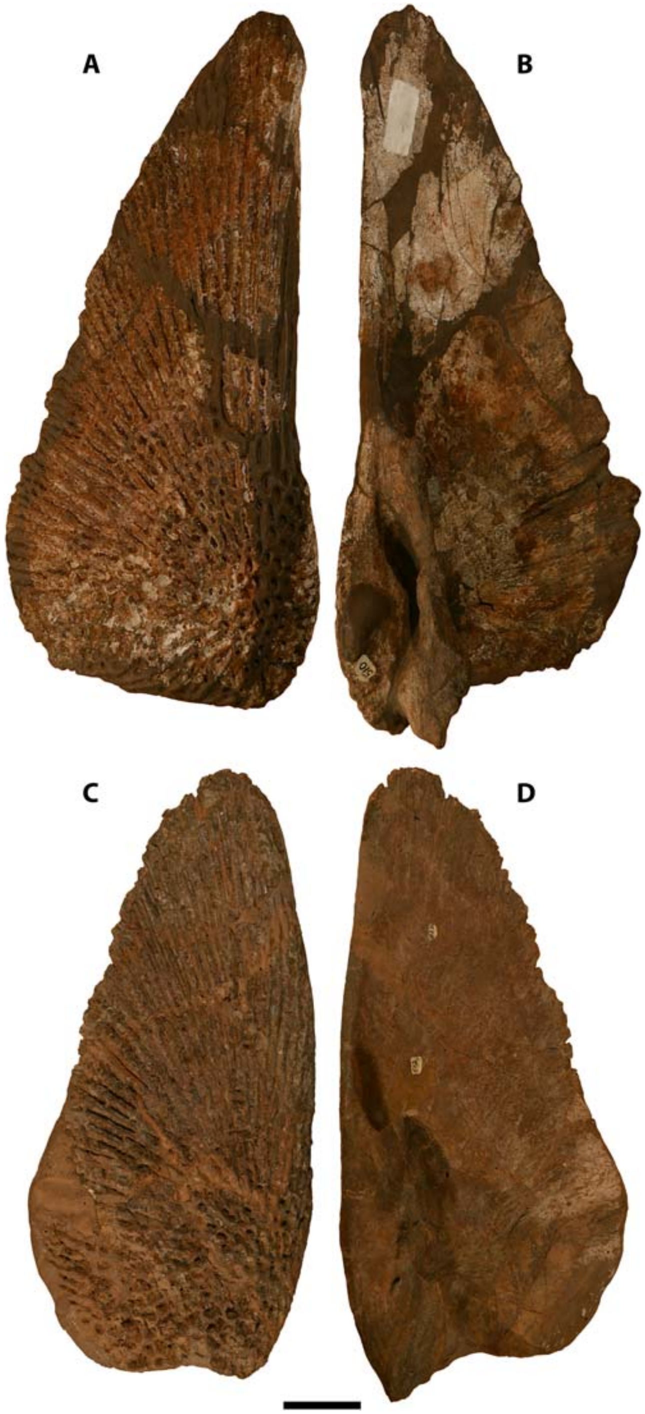

FIGURE 8. Photographs of select clavicles from the Little Popo Agie Creek locality referred to *Anaschisma* sp. (MU 510) and the Bull Lake Creek locality referred to *Koskinonodon princeps* (syn. *Anaschisma browni*) (MU 512). **A**, left clavicle (MU 510) in ventral view; **B**, left clavicle (MU 510) in dorsal view; **C**, left clavicle (MU 512) in ventral view; **D**, left clavicle (MU 512) in dorsal view. Scale bar equals 5 cm.

The pelvic girdle is often poorly represented with associated cranial material of metoposaurids, but a single right ilium (Fig. 11) from Bull Lake Creek (referred to *Koskinonodon princeps*) was recovered (Branson and Mehl, 1929). The ilium is composed of the dorsal shaft and a broadened base. The dorsal shaft is straight and is relatively robust but has a slight flexure resulting in a modestly convex anterodorsal margin, and the dorsal end of the dorsal shaft of the ilium is slightly flared. The base of the ilium has a rounded ventral margin on the medial side, and the supra-acetabular buttress overlying the sub-rectangular acetabulum has slightly rounded margins (Fig. 11A). Many specimens of *Anaschisma browni* bear a transverse pelvic ridge (sensu Pawley and Warren, 2006) anterior to the supra-acetabular buttress (e.g., WT 3085; Lucas et al., 2016:figs. 67 g, i, j, l), but the ridge is not apparent on this specimen (Fig. 11C). The process is also missing or reduced in some ilia referred to *An. browni*; it is missing on a small ilium from Texas (Lucas et al., 2016:fig. 67a, c), and it is reduced on a large ilium from Texas (Lucas et al., 2016:fig. 67d, f). The ilium of *An. browni* differs from other metoposaurids in having a straight rather than convex anterodorsal margin of the dorsal shaft (Lucas et al., 2016:fig. 67). In contrast with some of the ilia of '*Metoposaurus*' *bakeri* (UMMP 13789; Case, 1932:figs. 29, 30), *Dutuitosaurus ouazzoui* (Dutuit, 1976: pl. 27, figs. j–m, pl. 28, figs. a–b), and *Metoposaurus krasiejowensis* (Sulej, 2007:fig. 58), this ilium lacks a pronounced flexure of the dorsal shaft, but Sulej (2007:102) noted that the flexure of the dorsal shaft of *M. krasiejowensis* is variable from more straight to sinusoidal, though most of the examples of *M. krasiejowensis* are smaller than the ilium described here. Some comparably sized metoposaurid ilia from Texas (Sawin, 1945:fig. 10m–n), Poland (Sulej, 2007:fig. 58h), and Morocco (Dutuit, 1976:pl. 27, fig. i) have a straight, robust dorsal shaft with a weak flexure, similar to this specimen.

DISCUSSION

Establishing the Synonymy of Popo Agie Formation Metoposaurids

Metoposaurid taxonomy is in a state of flux, with recent revisions validating a long-standing nomen dubium (*Anaschisma browni*; Gee et al., 2019), invalidating the Malagasy taxon ('*Metoposaurus hoffmani*'; Fortuny et al., 2019), erecting a new taxon (*Panthasaurus maleriensis*; Chakravorti and Sengupta, 2018), and necessitating a novel recombination (*Arganasaurus azerouali*; Buffa et al., 2019) through reevaluation of historic holotypes. Most of these specimens had not been redescribed for decades, or, in the case of *An. browni*, for over a century. Thus, it was often unclear whether authors proposing synonymy of all four species with '*Buettneria perfecta*' had examined specimens first-hand or what shared features led to a proposed synonymy. An increased documentation of polymorphism within presumably monospecific assemblages and recognition of purported taxonomic differences as falling within a plausible range of intraspecific variation has prompted reevaluation of metoposaurid type specimens. Such reassessment is crucial for reconciling taxonomic issues of the clade, with a particular eye towards constraining the range of intraspecific variation in features that have historically been utilized for taxonomy, which in turn may inform taxonomic delimitations for other temnospondyl taxa lacking a similarly large sample size.

A suite of features unites the type specimens that we reexamined here with the holotype of *Anaschisma browni*, including: (1) a lacrimal that enters the orbital margin; (2) frontals that taper posteriorly; (3) large area of reticulate ornamentation on the dermal pectoral elements; (4) lacrimal and prefrontal that terminate anteriorly at about the same level; (5) lacrimal relatively short anteroposteriorly and widely separated from the external naris; (6) maxilla-prefrontal contact; and (7) jugal terminating at about the level of the anterior orbital margin. These additional shared features of Popo Agie Formation metoposaurids with *Anaschisma browni* provide stronger evidence for the synonymy of these taxa proposed by Hunt

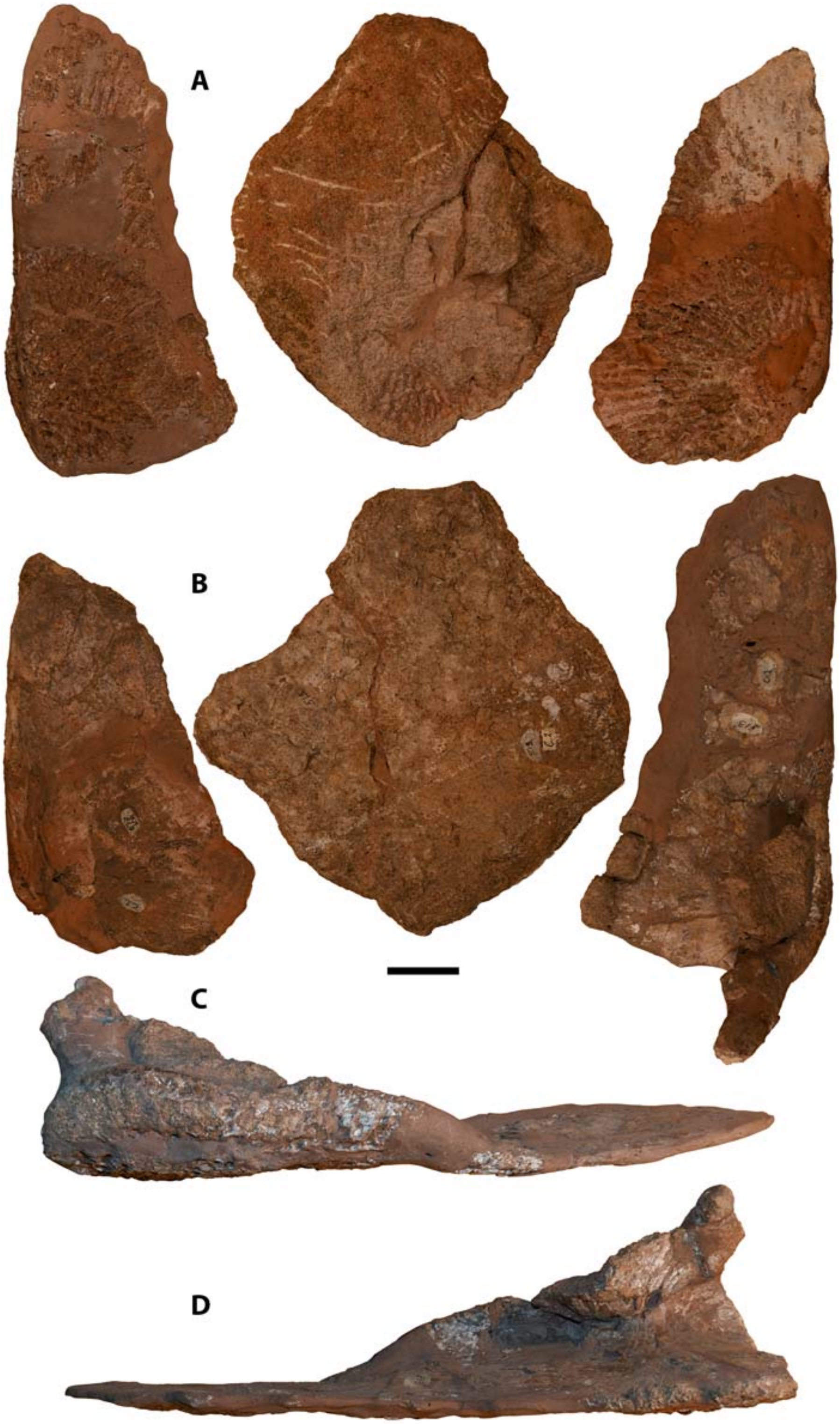

FIGURE 9. Photographs of a metoposaurid pectoral girdle (MU 513) associated with the holotype cranium of *Borborophagus wyomingensis* (syn. *Anaschisma browni*). **A**, left and right clavicles and interclavicle in ventral view; **B**, left and right clavicles and interclavicle in dorsal view; **C**, right clavicle in lateral view; **D**, right clavicle in medial view. Scale bars equal 5 cm. Top scale bar for **A**–**B**, bottom scale bar for **C**–**D**.

(1993), who did not redescribe or figure any of the specimens from this formation (save for a photograph of the holotype of *An. brachygnatha*).

In contrast to other large-bodied metoposaurids, including the holotype and referred specimens of *Anaschisma browni* previously described (Case, 1922; Sawin, 1945; Long and Murry, 1995; Lucas et al., 2016; Gee et al., 2019), but similar to the small-bodied specimens of *Apachesaurus gregorii* (UCMP 63845; Hunt, 1993; Spielmann and Lucas, 2012), two skulls (Figs. 3, S2) possess an occiput that does not project beyond the posterior

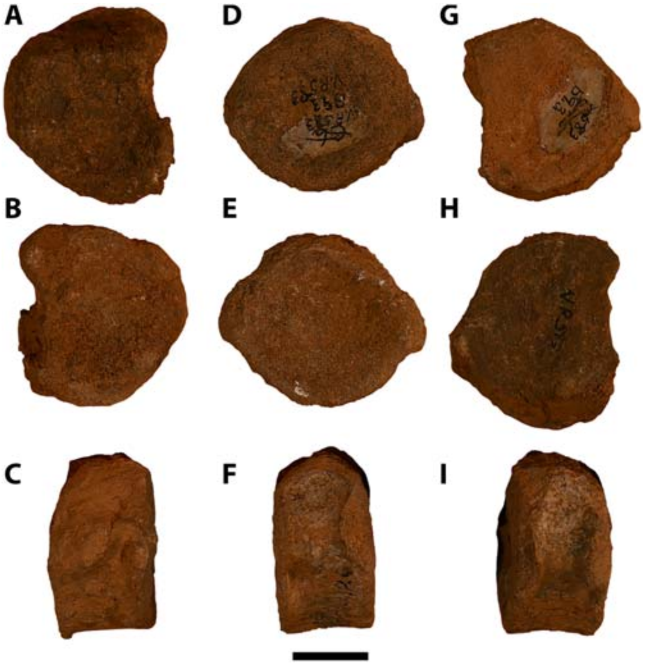

FIGURE 10. Photographs of metoposaurid intercentra (MU 583) referred to *Borborophagus wyomingensis* (syn. *Anaschisma browni*) from the Sage Creek locality. **A**, anterior(?) dorsal intercentrum in anterior view; **B**, same in posterior view; **C**, same in right lateral view; **D**, presacral intercentrum in anterior view; **E**, same in posterior view; **F**, same in left lateral view; **G**, postsacral intercentrum in anterior view; **H**, same in posterior view; **I**, same in right lateral view. Scale bar equals 2 cm.

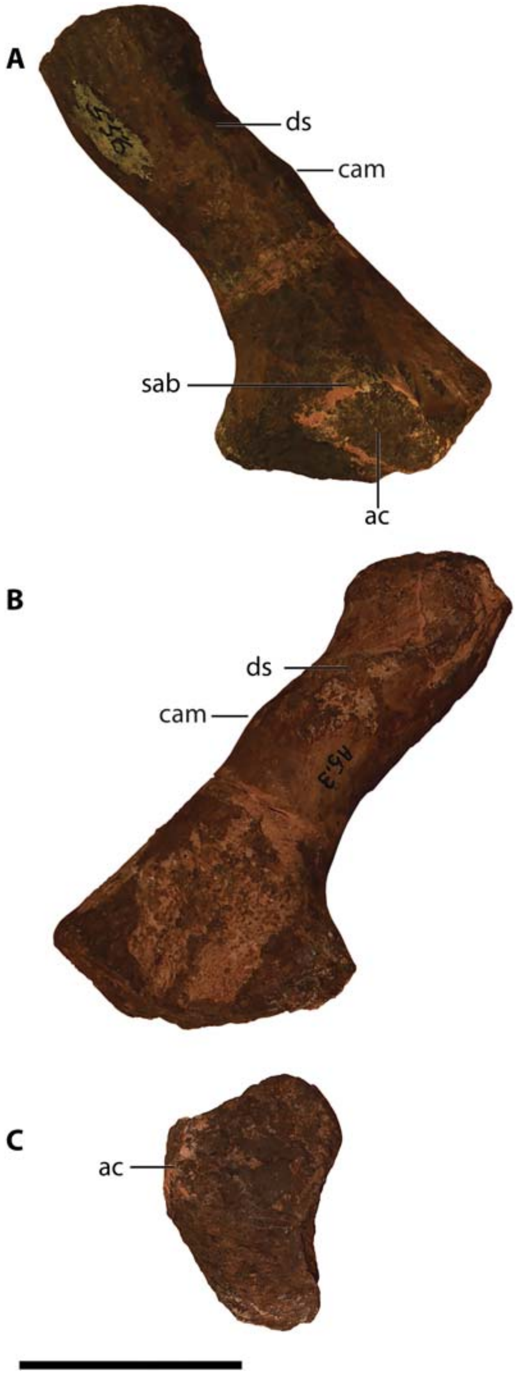

FIGURE 11. Photographs of a right metoposaurid ilium (MU 556) referred to *Koskinonodon princeps* (syn. *Anaschisma browni*) from the Bull Lake Creek locality. **A**, lateral view; **B**, medial view; **C**, distal view. **Abbreviations**: **ac**, acetabulum; **cam**, convex anterodorsal margin; **ds**, dorsal shaft; **sab**, supra-acetabular buttress. Scale bar equals 5 cm.

skull roof margin, and two other skulls (Figs. 2, 4) possess an occiput that projects slightly beyond the posterior skull roof (is visible in dorsal view beyond the margin of the postparietals). This condition warrants discussion because aspects of the occiput have been proposed to be diagnostic for two metoposaurid taxa. The condition of the specimens sampled here is indistinguishable from the purported diagnostic partial posterior projection of the (partially dorsally exposed) occiput of *Ap. gregorii* (see Spielmann and Lucas, 2012:fig. 9; but see Gee and Parker, 2018:appendix 1 for discussion of the problematic nature of this character), while Buffa et al. (2019) diagnose *Arganasaurus* by a posteriorly sloping occiput. The posterior projection of the occiput of many large-bodied specimens may be the result of displacement due to crushing (e.g., Sulej, 2007:fig. 16b–d), especially given the poor ossification of the neurocranium in pedomorphic stereospondyls. The crania described here have undergone relatively little crushing (see Fig. 5) such that only protruding condyles would appear in dorsal view. This would suggest that the condition of the Popo Agie Formation specimens is due to the absence of extensive taphonomic distortion found in numerous other specimens. However, the occiput of the type specimen of *Metoposaurus krasiejowensis* projects beyond the posterior skull margin but exhibits no evidence of dorsoventral crushing (Sulej, 2007:fig. 16a). This observation suggests that this character might be yet another feature used for taxonomic differentiation among metoposaurids that is also intraspecifically variable in at least some taxa. Alternatively, it should be considered that factors from the photographic setup (e.g., camera angle, angle of the specimen, and distance to the lens) can play a role in what features are exposed in dorsal view. Close-up photographs of the posterior region of the skull in dorsal profile do capture a larger exposure of the occipital condyles. Furthermore, the relative position of the posterior face of the occipital condyles to the quadrate condyle is the same as in other large-bodied specimens (i.e., the occipital condyles are posterior to the quadrate condyle). Taphonomic or photographic distortion can confound the use of any features like this for diagnostic purposes in certain profiles, but imaging of lateral views of metoposaurid crania could help to mitigate these issues. Features that can be influenced by any or all of these factors should be used sparingly in taxonomic diagnoses, if at all, especially when uncertainty exists about the utilized photographic methods. A refined definition of this feature could yield taxonomic utility, but in its current state, it is problematic.

A second feature is noted in the holotype and referred specimen of *Koskinonodon princeps* (MU 537 and MU 527, respectively), in which there is a prominent lateral flange from the parotic process of the tabular that has otherwise not been reported in specimens of *Anaschisma browni* to the best of our knowledge (the occiput often being figured less frequently than other profiles). Typically, the vertical column of the exoccipital and the parotic process of the tabular are of similar width where they meet (e.g., Sulej, 2007:fig. 16), but this flange projects laterally beyond the exoccipital in MU 527 and MU 537, resulting in a much wider process. However, the absence of this flange in specimens of other large-bodied metoposaurids (e.g., Sulej, 2007:fig 16; Brusatte et al., 2015:fig. 6a–b) could simply be a taphonomic artifact; it is a relatively thin projection that would be prone to breaking either during preparation or pre-burial, and the preservation is not sufficient to confidently identify a broken surface. The flange is also documented in at least some specimens of '*Metoposaurus*' *bakeri* (UMMP 13820; Case, 1932: fig. 8) and *Dutuitosaurus ouazzoui* (Dutuit, 1976:pl. 46, fig. b). Additional close inspection of this region in other metoposaurid specimens would indicate if this flange is simply lost due to taphonomic processes, or if it is truly absent in some taxa. It could potentially have resulted from taphonomic loss of the overlying external tabular crest in both MU 527 and MU 537. However, the morphology is consistent between both of the specimens, and the dorsal margin of the flange shows no clear signs of abrasion or fracture. The prominence of this flange in the largest Popo Agie Formation metoposaurids (Fig. 5) relative to smaller metoposaurids (e.g., Case, 1931:fig. 8; Dutuit, 1976:pl. 45, fig. b) may reflect increased development in larger individuals, perhaps due to increased epaxial or cranial musculature.

Variation of Popo Agie Formation Metoposaurids

Most of the observations utilized by Branson (1905) and Branson and Mehl (1929) to differentiate the four species of Popo Agie metoposaurids are proximally correct insofar as the majority do not represent misinterpretations of anatomy or conflation of taphonomic artifacts with apomorphic states. However, the validity of these observations for taxonomic differentiation has been greatly diminished by the subsequent century of research. For example, there is indeed minor variation in the respective position of the orbits and the nares between *Anaschisma browni* and '*Anaschisma brachygnatha*,' a purported pair of differential features, but this variation is so minor as to be regarded as within the feasible range of intraspecific variation by previous workers (Colbert and Imbrie, 1956; Gee et al., 2019). It also bears noting here that Branson and Mehl (1929) explicitly state an inability to confidently diagnose *Anaschisma* (p. 44 therein). Interpretations of the diagnostic features of all of the new taxa that they named are reliant on the reader parsing out their highlighted comparisons, which are often incomplete and which arguably should not always be assumed to have been regarded as taxonomically useful by the original authors. This ambiguity is reflected in the listed diagnoses for these taxa by Colbert and Imbrie (1956:414–416), which read more as summary descriptions of major features than taxonomic diagnoses. The majority of workers following Branson and Mehl (1929) have proposed or explicitly accepted that all four species were synonymous (Romer, 1947; Colbert and Imbrie, 1956; Chowdhury, 1965), and the disagreement lies primarily in whether the holotypes of all four species were sufficiently informative to be synonymized with another taxon (Hunt, 1993). With all four holotypes having been recently reexamined in close detail (Gee et al., 2019; this study), and the synonymy of all four under *Anaschisma browni* definitively proven in the current taxonomic framework, this enables us to discuss the morphological differences identified by the original workers and their significance for metoposaurid systematics.

Some of the possible diagnostic features that Colbert and Imbrie (1956) used to synonymize all the Popo Agie Formation metoposaurids under the name *Eupelor browni* warrant further investigation: (1) orbits located more posteriorly; (2) postparietal as long as wide as opposed to elongate; (3) a relatively broad posterior skull roof with a distinct transverse flare; and (4) large external nares. Similar proportional differences in the position of the orbits, length to width ratio of the postparietals, and breadth of the posterior skull roof can be seen in presumably monospecific bonebeds of metoposaurids (e.g., Sulej, 2007; Lucas et al., 2016). Specimens of *Anaschisma browni* from the Dockum Group of Texas are variable in the position of the orbits in relation to the interpterygoid vacuity (i.e., in some specimens the anterior orbital margin is anterior to the anterior margin of the interpterygoid vacuity, and in others the anterior orbital margin is posterior to the anterior margin of the interpterygoid vacuity), and the anterior orbital margin is posterior to the anterior margin of the interpterygoid vacuity (Fig. 3; Gee et al., 2019) or is at about the same level (Fig. 2) in all of the Popo Agie Formation specimens. Several specimens of *A. browni* from the Rotten Hill bonebed have postparietals with subequal length and width, but other specimens from the same bonebed have postparietals that are longer than they are wide (Lucas et al., 2016:figs. 27–34). The sutures of the postparietals of the largest Popo Agie Formation specimens are not fully defined (Figs. 2, 4), and the smallest specimen possesses postparietals that are longer than they are wide (Fig. 3). Many of the specimens of *A. browni* from the Dockum Group also have a transverse expansion of the posterior skull roof (Lucas et al., 2016). However, the presence of proportionately large external nares in Popo Agie Formation metoposaurids seems to be unique to large Popo Agie Formation specimens (see Figs. 2, S2; Gee et al., 2019:fig. 2) when contrasted with most specimens of *A. browni* from other depositional basins (e.g., Case, 1922, 1931; Long and Murry, 1995; Lucas et al., 2016) and with the small Popo Agie Formation specimen (Fig. 3). The Popo Agie Formation metoposaurids are otherwise indistinguishable from numerous specimens of *A. browni* from the Dockum Group of Texas, the Garita Creek Formation of New Mexico, and the Chinle Formation of Arizona. The occurrence of large external nares in the Popo Agie Formation specimens may reflect latitudinal variability between populations of *A. browni*, and the restriction of large nares to larger individuals may also reflect ontogenetic variability within the Popo Agie Formation population of *A. browni*. However, the small sample size of complete Popo Agie Formation metoposaurid crania in contrast with other depositional basins renders this conjecture and awaits new data from the recently excavated material mentioned in the Introduction.

While the co-occurrence of specimens that both have and lack a lacrimal contribution to the orbital margin is known for the Polish taxon *Metoposaurus krasiejowensis* (Sulej, 2002, 2007; Brusatte, 2015), this co-occurrence is unknown in North American metoposaurid bonebeds bearing *Anaschisma browni* (Lucas et al., 2010, 2016), in which the lacrimal always enters the orbital margin and '*Metoposaurus*' *bakeri*, in which the lacrimal is always excluded from the orbital margin (Case, 1932), and thus, basing either a diagnosis or a taxonomic differentiation solely on this character state alone is problematic. The proportion of the orbital margin that the lacrimal occupies is considerably variable both in the Popo Agie Formation metoposaurids and in an *A. browni* population from Texas (Lucas et al., 2016). In the largest Popo Agie Formation specimens, the lacrimal occupies a small proportion of the orbital margin (Figs. 2, 4), whereas it occupies a much larger proportion of the orbital margin in the smaller specimens (Fig. 3; Gee et al., 2019). A similarly high degree of variability in the width of the lacrimal of *M. krasiejowensis*, without an apparent correlation with skull size, was shown by Sulej (2007) using morphometric methods. Taken together with the findings of Lucas et al. (2016) and this study, this suggests that the morphology of the lacrimal exhibits high levels of plasticity within the Metoposauridae, conceivably to a degree that the contact with the orbit should be regarded skeptically in its entirety. Further analysis of bonebed populations will be essential for further assessing this hypothesis. Lucas et al. (2016) also noted variability in the vomer-parasphenoid suture of a population of *Anaschisma* with most specimens from the Rotten Hill bonebed having a diagonal suture and two having an anteroposteriorly straight suture; both of these vomer-parasphenoid suture morphologies occur in the Popo Agie Formation specimens of *A. browni* with the diagonal suture represented in this study (Figs. 2, 3) and the anteroposteriorly straight suture represented in a previous study (Gee et al., 2019:fig. 5).

Paleogeographic and Biostratigraphic Implications

The Popo Agie Formation metoposaurids represent the northernmost geographic extent and potentially the lowest stratigraphic occurrence of *Anaschisma browni*. *Anaschisma* is a common occurrence throughout the middle to upper Norian of Arizona, New Mexico, and Texas (Branson and Mehl, 1929; Hunt, 1993; Long and Murry, 1995), but if the proposed early Norian age of the ochre unit of the Popo Agie Formation is substantiated by further biostratigraphic or geochronologic work, then the stratigraphic range of *A. browni* extends back possibly to the Carnian–Norian boundary. ‘*Metoposaurus*’ *bakeri* has a similarly wide geographic range with occurrences in Texas (Case, 1931, 1932) and Nova Scotia (Sues and Olsen, 2015), but it is unknown west of Texas whereas *A. browni* is well represented in Arizona and New Mexico (Hunt, 1993; Long and Murry, 1995). Both ‘*M.*’ *bakeri* and *A. browni* overlap in geographic range in the Dockum Group of Texas, but ‘*M.*’ *bakeri* is known only from the Camp Springs Formation (historically regarded as Carnian) whereas *A. browni* is predominantly found in the younger Tecovas Formation (historically regarded as Norian). In the absence of radioisotopic ages for most localities outside of the Chinle Formation, the present data indicate that ‘*M.*’ *bakeri* is restricted to Carnian-aged sediments and that *A. browni* is restricted to Norian-aged sediments. The North American taxa have already been documented over a broader geographic range than taxa from western Europe, northern Africa, or India, some of which are restricted to a single locality. Certainly, this could suggest a far greater range than is presently recognized for the Eurasian and African taxa, although there may also have been greater competition in those regions from similarly large, aquatic non-metoposaurids. For example, the capitosauroid *Cyclotosaurus* is also found in the same horizons at Krasiejów as *Metoposaurus krasiejowensis* (Sulej and Majer, 2005), and *Metoposaurus diagnosticus* is associated with both capitosauroids and plagiosaurids at some localities (Milner and Schoch, 2004). Conversely, there is only a single definitive record of a large-bodied non-metoposaurid from the Upper Triassic of North America, the fragmentary *Calamops paludosus* from the Carnian-age Solesbury Member of the Stockton Formation in Pennsylvania (Sues and Schoch, 2013), and it does not co-occur with metoposaurid remains. An approximately 20 Ma temporal range spanning the Norian for *A. browni* would make this perhaps the most taxonomically long-lived metoposaurid, although absolute radioisotopic temporal constraints for other metoposaurid-bearing horizons are largely lacking (but see Khaldoune et al., 2016, for data on the Moroccan taxa). However, it should be considered that refined stratigraphic constraints and additional, detailed specimen-level documentation of intraspecific variation could reveal patterns that are suggestive of speciation events that are not detectable at our current resolution of biostratigraphic correlations and anatomical framework.

CONCLUSION

This is the first redescription and reevaluation of the type specimens of two Popo Agie Formation metoposaurids, *Borborophagus wyomingensis* and *Koskinonodon princeps*, since the initial description by Branson and Mehl (1929). Based on a shared suite of features with *Anaschisma browni*, the synonymy of these taxa first proposed by Colbert and Imbrie (1956) and later by Hunt (1993) and Gee et al. (2019) is upheld. The Popo Agie Formation specimens represent the northernmost extent of this wide-ranging taxon and possibly the earliest occurrence of the species, with essentially no distinguishable hard tissue differences from later Norian occurrences of this taxon in the American Southwest. Further constraints on the timing and tempo of metoposaurid origins and dispersal will help elucidate the spatial and temporal distribution of metoposaurid taxa and the progressive divergence of taxa in disparate depositional basins. Reevaluation of these specimens revealed some potentially ontogenetically (e.g., the presence of a lateral flange on the parotic process of the tabular and differences in relative proportion of posterior skull roof elements) or latitudinally variable features (e.g., the relative size of the external nares) of the metoposaurid cranium. Further description and evaluation of metoposaurid specimens, especially reevaluation of proposed type specimens, and quantitative analyses such as geometric morphometrics will be important for further assessing intraspecific and interspecific variation within this ubiquitous and morphologically conserved clade of Late Triassic stereospondyls and help to reconcile taxonomic issues of the clade.

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