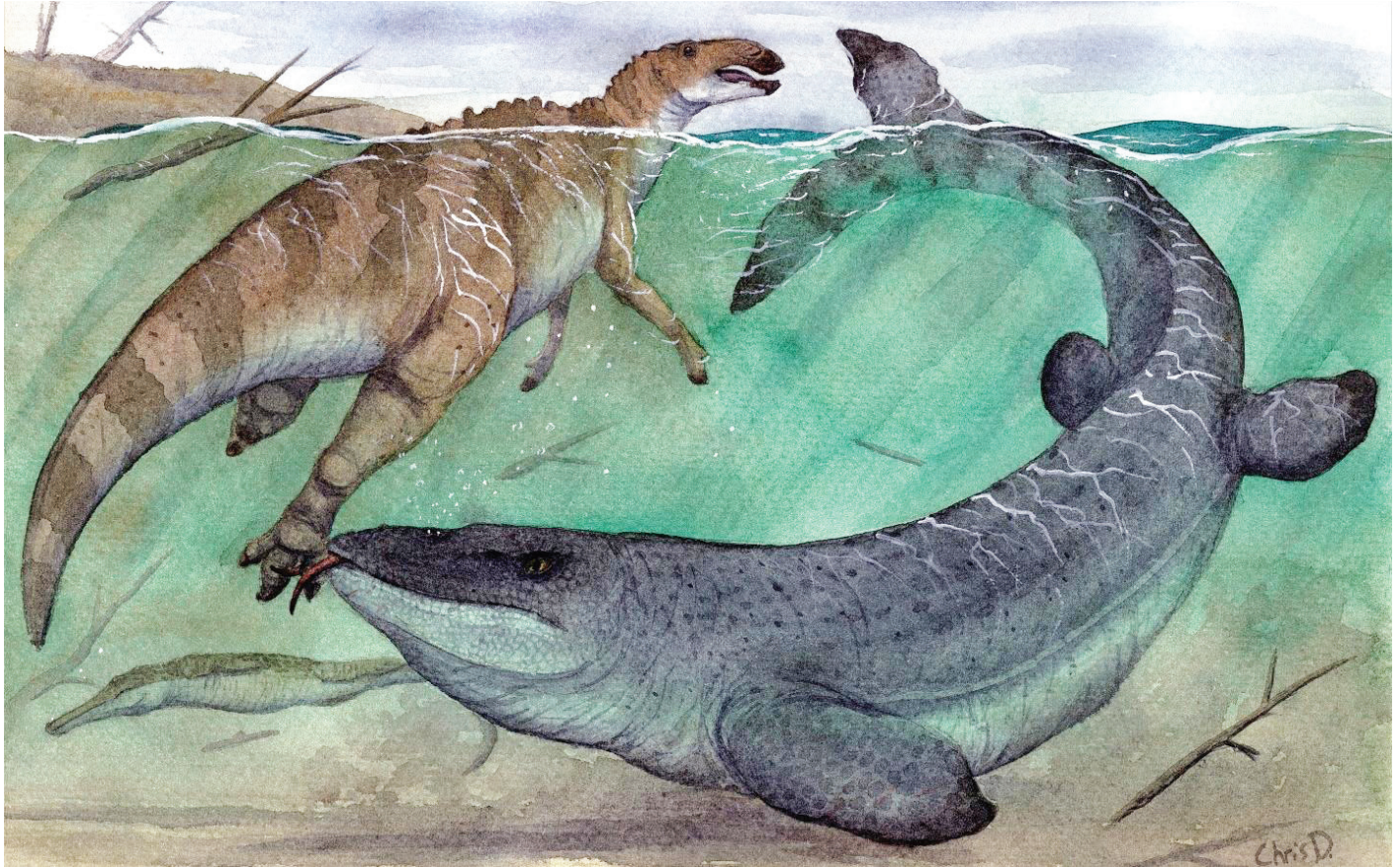


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NATHAN VAN VRANKEN & CLINT A. BOYD (2021). The first *in situ* collection of a mosasaurine from the marine Breien Member of the Hell Creek Formation in south-central North Dakota, USA.

Cover: An adult 15 m long mosasaurine mosasaur (either *Mosasaurus* or *Prognathodon*) investigates a subadult hadrosaur (*Edmontosaurus*) in its attempt to cross the deeper waters of the receding Western Interior Seaway. Artwork by Christopher DiPiazza
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The first *in situ* collection of a mosasaurine from the marine Breien Member of the Hell Creek Formation in south-central North Dakota, USA

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The upper Maastrichtian Breien Member situated within the lower portion of the Hell Creek Formation in south-central North Dakota records one of the last transgressions of the Western Interior Seaway (WIS) during the terminal Cretaceous. A fragmentary articular-prearticular complex and isolated vertebra belonging to a mosasauroid were recovered in 2016 from sandstones and mudstones deposited in a nearshore marine paleoenvironment within the southern arm of the bisected WIS. The medially-rotated retroarticular process on the articular-prearticular complex, the shape of the glenoid fossa, along with the morphology of the isolated vertebra, facilitate a conservative referral to a large-bodied mosasaurine such as *Mosasaurus* or *Prognathodon*. The rocks of the Breien Member provide paleontologists a unique glimpse of intracontinental marine ecosystems immediately prior to the end of the Cretaceous Period. This discovery provides additional evidence that the latest Maastrichtian marine fauna is a continuation of the fauna preserved in the underlying Fox Hills Formation and that the marine faunal turnover that gave rise to the subsequent Cannonball Sea fauna recorded in Paleocene rocks in North Dakota occurred at the Cretaceous-Paleogene boundary.

Keywords: biogeography, youngest occurrence, morphology, squamate, marine

INTRODUCTION

Swimming in the epeiric Western Interior Seaway (WIS) and along the continental margins of North America during the Late Cretaceous (Turonian to Maastrichtian) were diverse members of the clade Mosasauroida (hereafter referred to as mosasaurs), a group of marine-adapted, carnivorous squamates with a world-wide distribution (Bardet et al. 2014). This clade of marine reptiles displays a 30 Ma evolutionary history, during which they adapted to different marine (and non-marine: Makádi et al. 2012) environments and, for several lineages, attained large body sizes (Bardet et al. 2014, Polcyn et al. 2014, Harrell and Perez-Huerta 2015). The collapse of the marine food chain through the effects of a ‘Strangelove Ocean’ and an over-acidification of the waters along with the regression of the WIS may have caused most of the remaining Mesozoic marine megafauna, including the mosasaurs,

to become extinct at the end of the Cretaceous (Alegret et al. 2012, Slattery et al. 2015).

The mosasaur fossil record from upper Maastrichtian deposits in North America largely comes from the Atlantic and Gulf Coastal Plains and Pacific Margin (Kiernan 2002, Lindgren and Schulp 2010, Gallagher et al. 2012). Within the intracontinental region, the mosasaur fossil record from the WIS is better sampled from Campanian units, such as the Pierre Formation, whereas specimens from Maastrichtian units are comparatively rare and typically consist of highly fragmentary material (Driscoll et al. 2019). The youngest mosasaur occurrences from the WIS are mostly from the Fox Hills Formation and include a partial skull of *Mosasaurus hoffmannii* Mantell (1829) from north-central South Dakota (Harrell and Martin 2015), a single vertebrae from an indeterminate mosasaur from southeastern South Dakota (Cicimurri et al. 1999), and isolated teeth and vertebrae from North Dakota referred to *Mosasaurus dekayi* Bronn (1838)

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(=*Mo. hoffmannii* [Street 2016]) and *?Plioplatecarpus* sp. (Getman 1994, Hoganson et al. 2007).

Overlying the Fox Hills Formation in North Dakota are the largely terrestrial deposits of the Hell Creek Formation, impeding study of the latest Maastrichtian mosasaur fossil record within the WIS. Thus far only a single, indeterminate mosasaur tooth is reported from the upper-most portion of the Hell Creek Formation (DePalma et al. 2019: supplement fig. S3), but the recovery of that specimen from a putative surge deposit related to the Chicxulub impact at the K-Pg boundary raises the possibility that it was either transported to that location from a marine environment or was reworked from older rocks. In south-central North Dakota two brief, latest Maastrichtian transgressions of the WIS are recorded within the Hell Creek Formation: the lower Breien Member and the upper Cantapeta Tongue (Hoganson and Murphy 2002: fig. 13). Although vertebrate fossils are currently unknown from the latter unit, a mix of terrestrial, brackish, and marine vertebrate taxa are documented from the Breien Member (Hoganson and Murphy 2002). With one possible exception, no mosasaur fossils are currently documented from the Breien Member. Leonard (1912) reported the recovery of two mosasaur teeth, identified by C. W. Gilmore as *Mosasaurus* sp., collected loose on the surface of either the Fox Hills Formation outcrops or the overlying Lance Formation “Ceratops Beds” (=Hell Creek Formation in this study) along the Cannonball River in south-central North Dakota. Rocks of the Breien Member, which was not recognized at the time, are also exposed at that location between three and four meters above the Fox Hills-Hell Creek Formation contact (measured section 1 in Laird and Mitchell [1942]). Given that stratigraphic relationship, the possibility that those teeth were eroded from the overlying Breien Member and were subsequently collected on the surface of the Fox Hills Formation cannot be discounted. Although we consider that scenario to be unlikely, the provenance of those specimens should be treated with caution as the teeth were not collected *in situ* unlike the specimens described in this report.

In 2016, a private landowner brought an isolated vertebra collected loose on the surface of the Hell Creek Formation into the North Dakota Geological Survey for identification. Examination of the specimen (NDGS 2728) suggested it is likely a pygal vertebra from a mosasaur. Subsequent visitation of the location (NDGS L301) revealed that the specimen eroded from rocks of the Breien Member and fell several meters to the location where it was discovered. The subsequent survey of that

outcrop led to the recovery of a partial mosasaur articular-prearticular complex (NDGS 2729) *in situ* within the Breien Member, confirming the original stratigraphic position of the surface-collected vertebra. Here, we describe these first confirmed, non-dental mosasaur remains from the Breien Member of the Hell Creek Formation and discuss their implications for the persistence of large-bodied mosasaurs within the WIS during the latest Maastrichtian in North America.

MATERIALS AND METHODS

Geologic Setting

The Breien Member is the only formal subdivision of the Hell Creek Formation recognized in North Dakota (Murphy et al. 2002). It records one of the last transgressions of the WIS into the Dakotas during the late Maastrichtian *Hoploscaphites nebrascensis* Zone (Hoganson and Murphy 2002). These fine-grained glauconitic sandstones, siltstones, and mudstones were deposited in interdistributary tidal channels, bays, and estuaries along the eastern edge of the prograded Sheridan Delta (*sensu* Gill and Cobban 1973). Recorded outcrops of the Breien Member are restricted to Morton, Emmons, and Sioux Counties in the south-central portion of North Dakota (Frye 1967, 1969, Hoganson and Murphy 2002). A type section was not identified when it was originally named (Laird and Mitchell 1942), but Frye (1969) designated a type section in the northern portion of Sioux County near the town of Breien, North Dakota based on personal communications with those latter authors. Further study revealed a high degree of lateral and vertical variability in the lithology of the Breien Member, prompting the description of three reference sections (Hoganson and Murphy 2002) to supplement the description of the type section (Frye 1969). In all, more than two dozen measured sections of the Breien Member are described across south-central North Dakota (Laird and Mitchell 1942, Frye 1964, 1969, Hoganson and Murphy 2002). Thus, the new fossil locality (NDGS L301) can be put into context relative to previously published measured sections and paleontological localities (Fig. 1). This site is situated approximately three miles southwest of the Stumpf Composite reference section (Hoganson and Murphy 2002: fig. 7) and approximately one mile southeast of the Fort Rice measured section (Hoganson and Murphy 2002: fig. 2).

At the study site the contact between the underlying Fox Hills Formation and the overlying Hell Creek Formation is not exposed, and the lower 4.75 meters of

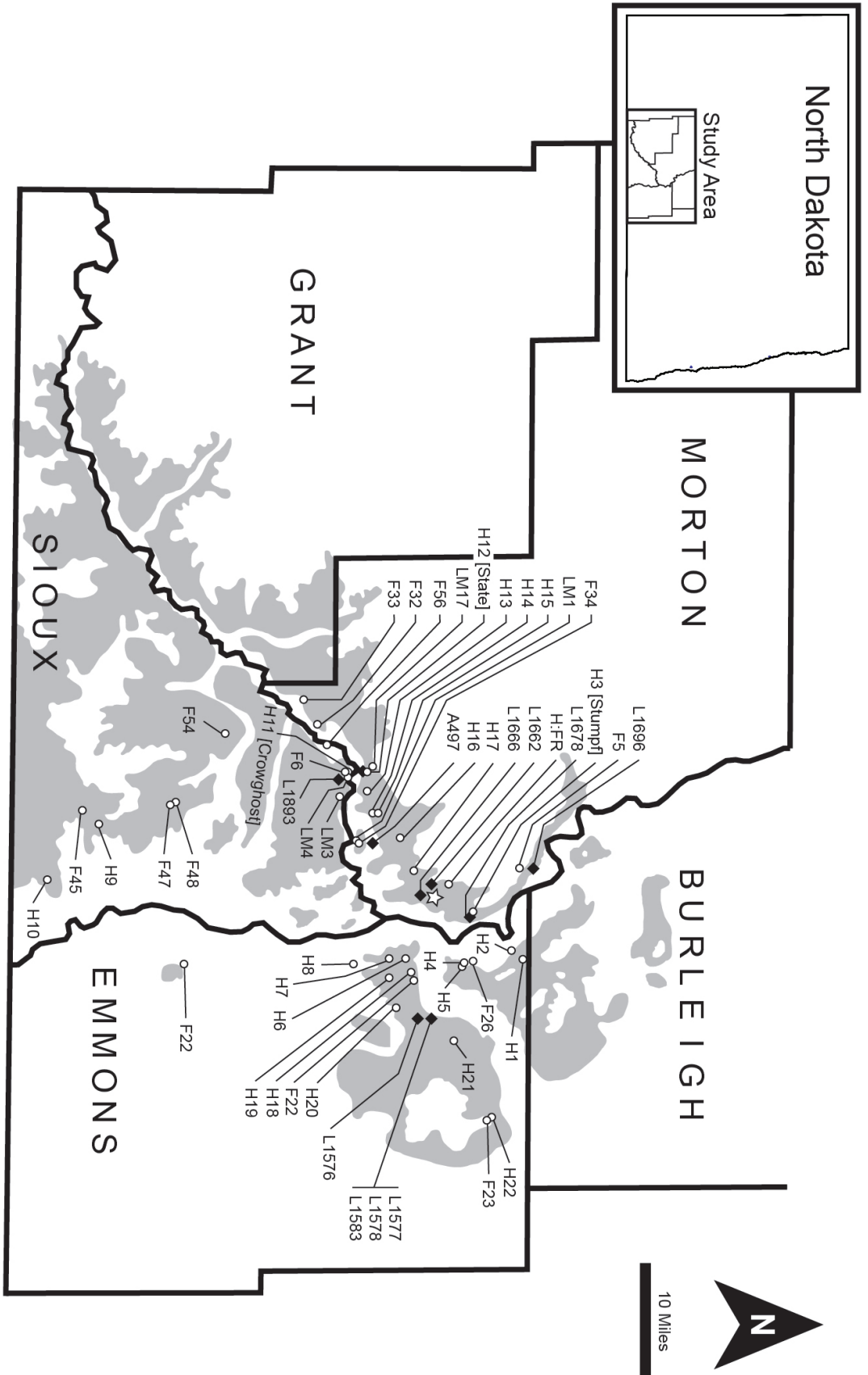


Figure 1. Geographic distribution of outcrops of the Breien Member of the Hell Creek Formation in south-central North Dakota. Surficial outcrops of the Hell Creek Formation shaded gray. Locations of measured sections shown by open circles, while published fossil localities are indicated with black diamonds. Study site is marked by a white star. Abbreviations: A, University of North Dakota paleontological locality number; **Crowghost**, Crowghost Cemetery Reference Section (Hoganson and Murphy 2002); F, measured section from Frye (1969); **FR**, Fort Rice reference section; H, measured section from Hoganson and Murphy (2002); L, North Dakota Geological Survey (NDGS) paleontological locality number (Hoganson and Murphy 2002); **LM**, measured section from Laird and Mitchell (1942); N, north; **State**, State Butte Reference Section (Hoganson and Murphy 2002); **Stumpf**, Stumpf Composite Reference Section (Hoganson and Murphy 2002).

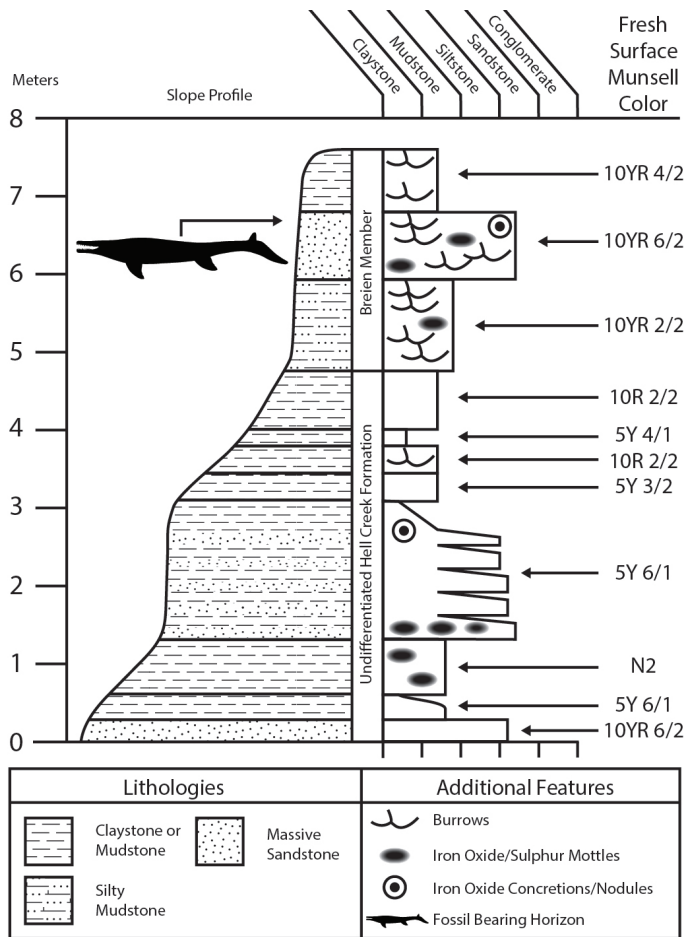


Figure 2. Stratigraphic description of the study site, NDGS L301. The original thickness of the Breien Member is not preserved at the site, with the upper prairie surface situated within the upper portion of the Breien Member. Burrows within the Breien Member are largely referable to *Ophiomorpha* sp., while those in the underlying “Undifferentiated Hell Creek Formation” are small (~3.0–4.0 mm thick) terrestrial burrows and root traces within an organic-rich paleosol.

the outcrop is formed by a series of alternating beds of bentonitic mudstones and fine-grained sandstones of the Hell Creek Formation (Fig. 2). The Breien Member is reported elsewhere to be situated between 1.5 and 9.0 meters above that contact, so it is not unexpected that the contact between these formations is not exposed at the study site. In many locations the Breien Member is underlain by a carbonaceous mudstone, and a 1.31 meter-thick bed of very dusky red carbonaceous mudstone that forms a distinct, vegetated break in the slope is present at the study site (Fig. 2). Horizontally-oriented pedotubules (either root casts or terrestrial burrows) are present within that carbonaceous mudstone and are infilled with a buff-colored sediment, making them easily discernible on fresh surfaces. Large pieces of coalified plant matter are present throughout that carbonaceous

mudstone but are especially concentrated at the upper surface. The extensive presence of pedotubes and coalified plant material identify this unit as a paleosol, indicating a period of non-deposition or erosion after the deposition of these rocks and before those of the overlying Breien Member.

When present, the Breien Member ranges in reported thickness from 1.5 to 8.5 meters (Hoganson and Murphy 2002). At the study site the observed thickness of the Breien Member is 2.83 meters, but the upper contact with the terrestrial beds of the Hell Creek Formation is not preserved, obscuring the original thickness of the Breien Member at this site. The Breien Member at this location consists of three distinct units. The lower unit is a dusky yellowish-brown mudstone containing large (>5.0 cm) gypsum crystals near the base, a typical feature of the Breien Member (Laird and Mitchell 1942). This mudstone is highly bioturbated, obscuring much of the original bedding structure, and the burrows are infilled with a sandy sediment. Most of the burrows do not conform with *Ophiomorpha* Lundgren (1891), which are crustacean burrows, in that they are smaller in size than typical *Ophiomorpha* burrows, and do not display the nodose texture of the outer wall typically seen in *Ophiomorpha* burrows (Frey et al. 1978). There is a gradual contact with the overlying unit of pale yellowish-brown sandstone. That unit is poorly cemented at the base but is moderately cemented near the top. *Ophiomorpha* burrows are present throughout the unit but are better cemented and more clearly discernible in the upper portion, some of which are infilled with a gray, fine-grained sandstone. There are irregular intervals containing carbonate or gypsum blebs 1.0 to 3.0 millimeters in diameter and reddish-orange sesquioxide mottles (weathering products of iron- and aluminum-rich silicates that form within paleosols via oxidation [e.g., goethite, hematite]: Retallack 1988, 2001). The lithology of this sandstone bed resembles the lower sandstone units described by Frye (1967) at his measured section 24 in Emmons County and at measured sections 48, 54, and 56 in Sioux County (Fig. 1). A single tooth from the sand tiger shark *Carcharias Rafinesque* (1810) was collected from the middle of this unit at the study site (NDGS 5749). Near the top of the unit is an interval of sesquioxide nodules, concretions, and chips (some >10 cm) that marks the vertebrate fossil-bearing horizon. Similar limonite staining and sesquioxide nodules and chips were noted by Frye (1967) at section 5 in Morton County and sections 6 and 45 in Sioux County and by Hoganson and Murphy (2002) at the State Butte reference section (Fig. 1: H12)

in Morton County and the Crowghost Cemetery reference section (Fig. 1: H11) in Sioux County. There is a gradual contact between the middle sandstone unit and an overlying dark yellowish-brown mudstone unit that forms the local topographic high at the study site. This transition occurs at or just above the vertebrate fossil-bearing horizon. Small carbonate blebs (1.0–3.0 mm) and *Ophiomorpha* burrows are present throughout both units. However, *Ophiomorpha* burrows are less abundant in the underlying sandstone unit.

At the type section of the Breien Member a gray bentonite is present in the middle of the member, separating the upper and lower sandstone units (Frye 1967, 1969). A similar bentonite is also present at the State Butte reference section and at sections 5, 6, and 56 of Frye (1967), but is absent at the Crowghost Cemetery and Stumpf Site Composite reference sections (Fig. 1: H3, Hoganson and Murphy 2002). No bentonite bed is noted at the study site; however, it is possible a bentonitic bed could have been present higher in the section and was lost to erosion.

Completeness metrics TCM, QCM, and ICM of the Breien mosasaur

Driscoll et al. (2019) studied the impacts that the completeness of individual mosasaur specimens has on our understanding of the mosasaur fossil record based on a dataset of over 4,000 specimens. That study scored individual specimens for three completeness metrics: the Taphonomic Completeness Metric (TCM: scores range from 0.0 to 36.0), the Qualitative Completeness Metric (QCM: scores range from 1.0 to 9.0), and the Informal Completeness Metric (ICM: scores range from 1.0 to 5.0). The Breien mosasaur, has a TCM score of 1.0, a QCM score of 3.0, and an ICM score of 4.0. The relatively high ICM score for the Breien mosasaur resulted from the fact that a single bone was recovered from both the skull (score of 3.0) and axial skeleton (score of 1.0), with only the appendicular skeleton (possible score of 1.0) not represented.

Sampling

Geologic backgrounds such as relative age dates for relevant mosasaur-bearing formations listed in the discussion were cross referenced against the literature. This information was taken from Macrostrat.org.

Institutional abbreviations

IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; **MOR**, Museum of the Rockies, Bozeman, Montana, USA; **NDGS**, North Dakota State Fossil

Collection, North Dakota Geological Survey, Bismarck, North Dakota, USA.

SYSTEMATIC PALEONTOLOGY

REPTILIA LINNAEUS, 1758

SQUAMATA OPPEL, 1811

MOSASAURIDAE GERVAIS, 1852

MOSASAURINAE GERVAIS, 1852

INCERTAE SEDIS

FIGS. 3, 4.

Referred material—NDGS 2728: isolated vertebra; NDGS 2729: incomplete right articular-prearticular complex.

Locality—NDGS L301: Morton County, North Dakota, USA; Township 135 North, Range 79 West, Section 17. Detailed locality information available to qualified researchers upon request.

Stratigraphic unit—Specimens collected from the Breien Member of the Hell Creek Formation.

Description—Both the surface-collected vertebra and the articular-prearticular complex collected *in situ* display poorly preserved surface texture. Three factors are proposed that may have either individually or jointly impacted the preservation of these specimens. First, subaerial erosion undoubtedly impacted these specimens given that the vertebra was completely exposed having fallen a few meters down the outcrop surface and that portions of the ventral and posterior margins of the articular-prearticular complex were lost to erosion prior to discovery. Second, the fossil-producing horizon is located several centimeters below the upper prairie surface and the rocks were extensively invaded by modern plant roots, including some that penetrated through fractures in the articular-prearticular complex. Finally, the rocks forming the fossil-bearing horizon are highly bioturbated, indicating the bones may have been negatively impacted by taphonomic processes either prior to or shortly after burial during the period where the bones were shallowly buried and remained within the bioturbation zone.

The articular-prearticular complex (NDGS 2729) is incomplete along the anteroventral margin, a short portion of the anterodorsal margin, and ventrolateral to the glenoid fossa and retroarticular process owing to subaerial erosion (Fig. 3). It is preserved in two main pieces along with some associated fragments that cannot be placed at this time. There is some anteroposterior overlap between these two pieces, resulting in an estimated total length of at least 38.0 cm, though a portion of the posterior border

of the retroarticular process is missing so the original length may have been slightly longer. Some distortion is present, mostly transverse crushing of the posterodorsal portion of the anterior piece, preventing the two pieces from being confidently reunited.

The anterior portion of the articular-prearticular complex consists of the transversely- narrow and dorsoventrally-tall blade that extended medial to the surangular and dorsal to the angular. The maximum preserved length of the anterior portion is 26.54 cm. The medial surface is nearly flat along much of its length, but transitions to slightly convex anteriorly. The dorsal margin is sinuous in medial view (Fig. 3B) with the posterior-most portion steeply dorsally inclined leading to the glenoid fossa. A similar steep incline in the dorsal margin of the prearticular-articular complex anterior to the glenoid fossa as seen in *Mosasaurus hoffmannii* (Street and Caldwell 2017: fig. 14f). The dorsoventrally narrowest portion of the articular-prearticular complex is just anterior to that dorsally-inclined surface, where the minimum thickness is 4.46 cm. That narrow portion of the articular-prearticular complex is the only part that preserves the ventral margin, and at that location it was broadly rounded and thickened relative to the rest of the anterior portion of the articular-prearticular complex. Much of the lateral surface is deeply concave owing to the presence of a thickened ventral margin (where preserved) and a prominent anteroposteriorly-directed

ridge situated near the dorsal margin. That ridge arises posteriorly on the lateral surface of the dorsal incline, though its posterior extent is unknown owing to damage, and continues anteriorly along approximately two-thirds the length of the anterior portion of the articular-prearticular complex. The dorsal surface of this ridge contacted a medially-directed wing on the surangular and formed the floor of the adductor fossa (Street and Caldwell 2017).

The posterior portion consists of the articular contribution to the glenoid fossa and the dorsomedial portion of the retroarticular process and measures 12.74 cm in total length. The articular contribution to the glenoid fossa is anteroposteriorly longer than transversely wide. The glenoid surface is roughened and unfinished, indicating it was covered by cartilage in life. We do not think this roughened surface is the result of taphonomic processes as it is restricted to the glenoid surface and does not extend onto the surrounding bone surface. In dorsal view, the glenoid fossa is ovate, being broader anteriorly and pointed posteriorly, though the anterior-most portion is not completely preserved. The glenoid surface was gently dorsolaterally inclined and is anteroposteriorly concave. The medial surface immediately ventral to the glenoid slopes ventrolaterally, indicating a pronounced transverse thinning of the bone ventral to the glenoid. Lateral to the glenoid is a broad articulation surface for the surangular that is dorsomedially concave and appears to have connected to the medial ridge on the anterior

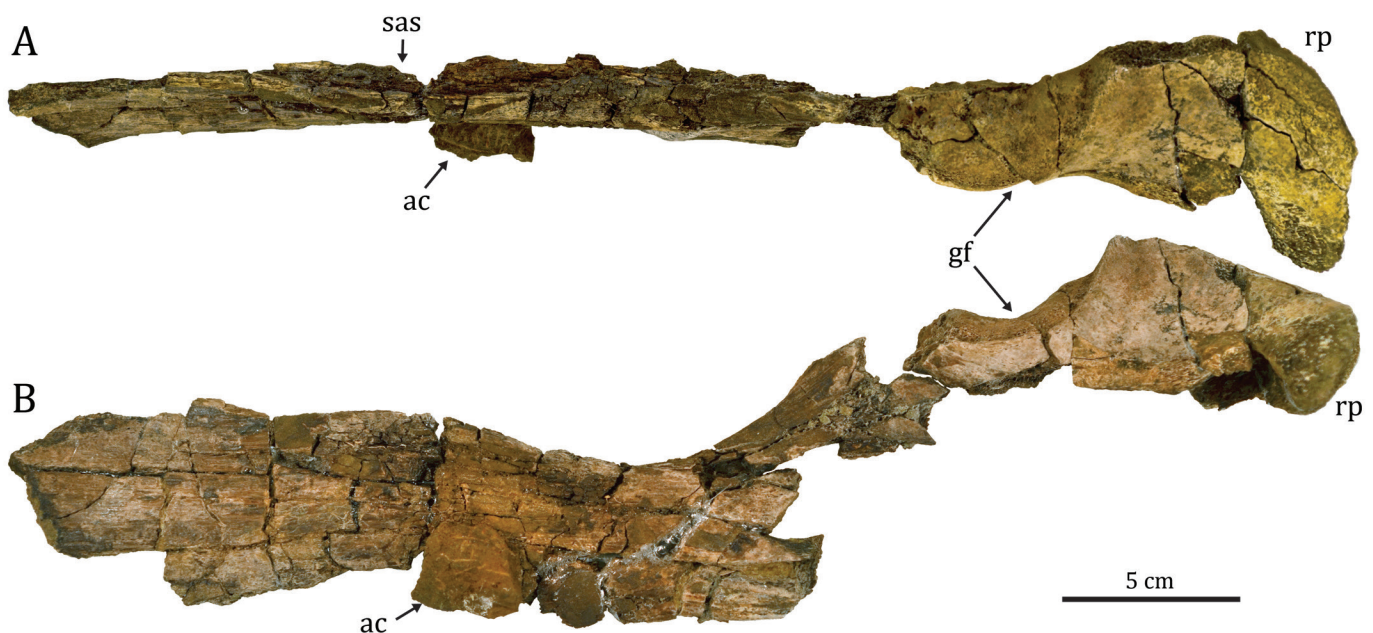


Figure 3. Right articular-prearticular complex, NDGS 2729. **A.** Dorsal view. **B.** Medial view. Specimen oriented anterior to the left. Abbreviations: **ac**, adhered concretion; **gf**, glenoid fossa; **rp**, retroarticular process; **sas**, articulation surface for the surangular.

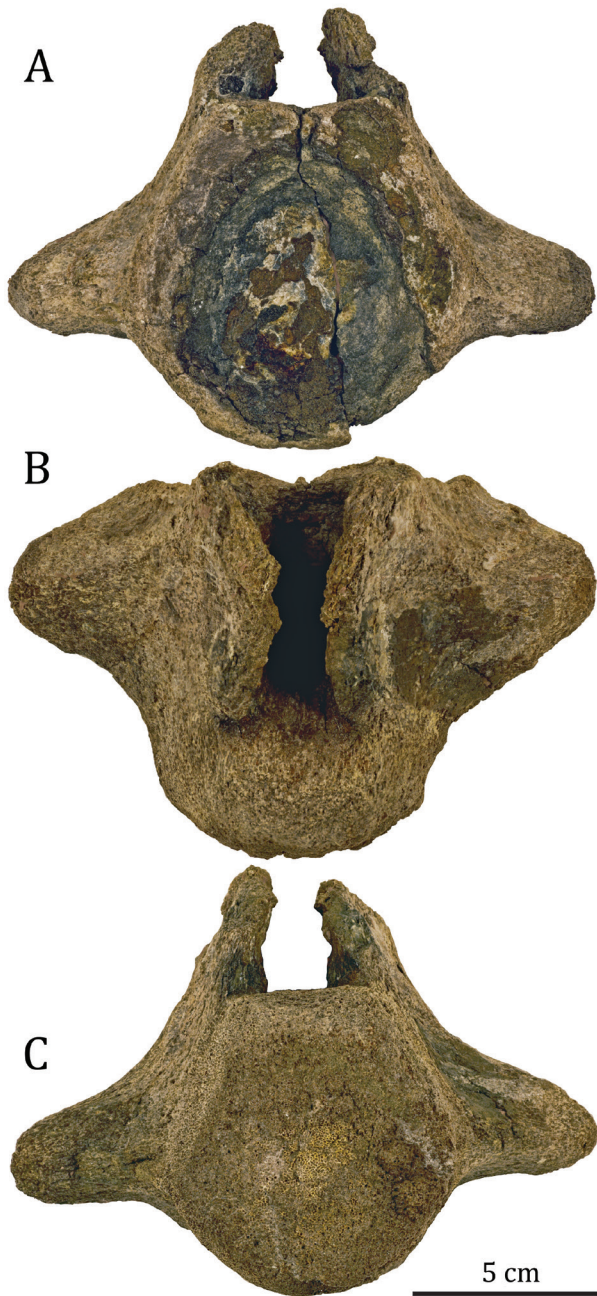


Figure 4. Pygal vertebra, NDGS 2728. **A.** Anterior view. **B.** Dorsal view. **C.** Posterior view.

portion of the articular-prearticular complex, but the connecting portion of the bone is missing. Posterior to the glenoid, the medial surface of the retroarticular process is dorsolaterally inclined, broadly concave both anteroposteriorly and dorsoventrally, and was penetrated by a prominent foramen that Russell (1967) identified as the pathway for the corda tympani. The dorsal portion of the retroarticular process curves strongly ventromedially so that the posterodorsal corner is nearly horizontal. The

surface of that horizontal portion is roughened for muscle attachment, likely by the *M. depressor mandibulae* (Lingham-Soliar 1995: fig. 24a). A small portion of the lateral surface of the retroarticular process posteroventral to the articulation surface for the surangular is preserved. That portion is relatively flat and indicates the transverse width of the retroarticular process was relatively thick and uniform throughout the preserved portion.

NDGS 2728 is a single vertebra that was surface collected a few meters away from the articular-prearticular complex (Fig. 4). The centrum is strongly procoelous, has an anteroposterior length of 9.93 cm, a posterior height of 7.66 cm, a posterior width of 7.12 cm, an anterior height of 8.89 cm, and an anterior width of 8.91 cm. The breadth across the preserved transverse processes is approximately 15.7 cm, though the original measurement would have been larger given the eroded surface texture of the bone. The transverse processes arise near the anterior margin of the centrum at or slightly below mid-height and are relatively flattened ventrally and convex dorsally. There are slight ridges arising from the middle of the dorsal surface of each transverse process that run anterodorsally up the lateral surface of the centrum and connect to the anteroventral corner of the neural arch, seemingly at the base of the prezygapophysis. Loss of the surficial bone in this area makes it difficult to determine how pronounced those ridges were in life. On the preserved left lateral surface of the centrum a ridge is clearly present extending from the posterior margin of the transverse process posteriorly to the margin of the posterior condyle. The maximum preserved height of the vertebra is approximately 11.8 cm, but most of the neural arch is missing. The base of the neural arch is situated anteriorly on the centrum, with the anterior margin arising from the anterodorsal margin of the centrum and extends posteriorly 6.55 cm, ending well anterior of the posterior margin. There is a raised lip at the anterior end of the ventral surface of the neural canal. A pair of foramina are present on the ventral surface of the centrum near mid-length.

This specimen lacks either fused chevrons or articulation facets for the chevrons, indicating it is not from the caudal series. It also lacks any evidence of ventral peduncles for the hypapophyses or midline ventral tubercles that typify the cervical series. The position of the transverse processes at or slightly below mid-height, the raised, flattened border of the neural canal above the anterior articulation surface of the centrum, and the roughly equal heights and widths of the articulation surfaces best conform with a posterior trunk vertebrae (e.g., Holmes

1996), though given the quality of preservation in this specimen it is indistinguishable from vertebrae found in the pygal region of the caudal series.

DISCUSSION

Given the absence of mosasaur remains from elsewhere in the Breien Member and the recovery of these two specimens from the same outcrop, one *in situ* and one surface collected, NDGS 2728 and 2729 are here considered to represent a single individual, hereafter referred to as the Breien mosasaur. The vertebra (NDGS 2728) displays the procoelous shape commonly found in mosasaurs (Russell 1967). Both the medial inflection of the retroarticular process and the ovate shape of the glenoid fossa confidently confirm the mosasaurine affinities of NDGS 2729. Those features are observed broadly in highly-nested members of Mosasaurinae and are not found in either early-diverging mosasaurines, *Clidastes propython* Cope (1869) or *Plesiotylosaurus crassidens* Camp (1942) (Russell 1967, Leblanc et al. 2012, Street and Caldwell 2017, Lively 2020). No further diagnostic traits were found that would permit a more precise taxonomic identification.

Mosasaur lengths in the published literature are divided into three informal size groupings using the length estimates taken from Polcyn et al. (2014, fig. 6) and Driscoll et al. (2019, supplement tab. A), small (1.0–4.0 m), medium (4.5–7.5 m), and large (8 or more meters). Both NDGS 2728 and 2729 indicate that the Breien mosasaur was part of the large size group at approximately 11.0 m in length using the methods of Russell (1967), even accounting for some error in those size estimates. This estimate surpasses other known mosasaurines such as *Mosasaurus conodon* Cope (1881) [10.0 m, Ikejiri and Lucas (2015): table 1, MOR 006] *Plotosaurus bennisoni* Camp (1942) [8.9 m], *Mo. missouriensis* Goldfuss (1845) [8.5 m], *Ple. crassidens* [6.0 m], *Prognathodon 'rapax'* Cope (1870) [6.0 m], *Prognathodon overtoni* Williston (1897) [6.0 m], *Globidens dakotaensis* Russell (1975) [5.0 m], and *Eremiasaurus heterodontus* Leblanc et al. (2012) [4.5 m] but not 15.0 meters reported in *Mo. hoffmannii*. Size has no bearing on our taxonomic assessment. Driscoll et al. (2019) reported average scores for *Mo. hoffmannii* (n=290) of 1.4 for TCM and 1.9 for QCM, while those scores were 3.5 for TCM and 2.5 for QCM in *Mo. conodon* (n=123). These values contrast with the average values reported for the geologically older *Mo. missouriensis* (n=11; TCM=9.9; QCM=5.4), all but one specimen of which were recovered from clay-dominated rocks. Average TCM and QCM values for other large-bodied

mosasaurines include 1.9 for TCM and 1.9 for QCM in *Pr. 'rapax'* (n=12), 8.6 for TCM and 5.0 for QCM in *Pr. overtoni* (n=12), 19.0 for TCM and 7.0 for QCM in *Eremiasaurus heterodontus* (n=2), 4.6 for TCM and 2.2 for QCM in *Plo. bennisoni* (n=50), and 6.3 for TCM and 6.0 for QCM in *Ple. crassidens* (Driscoll et al. 2019). We removed *Globidens* and *Clidastes* from our study because the former's North American Maastrichtian record can be dubious and the latter did not persist into the terminal Cretaceous (Polcyn et al. 2014, Driscoll et al. 2019, supplement tabs. A and B). Driscoll et al. (2019) found significant differences in the completeness of individual specimens preserved in different lithologies, with clay-dominated rocks preserving more complete specimens than coarser-grained siliciclastic rocks (Driscoll et al. 2019: fig. 6). In fact, the authors state that in many coarser-grained rocks there appears to be an upper limit on specimen completeness that may not be possible to overcome regardless of how well-exposed or well-sampled those rocks are in the future. Given the taxonomic affinities of the Breien mosasaur and the fact that it was recovered from a muddy sandstone unit, this specimen's low TCM and QCM scores are about what would be expected. Future worker efforts focused on the discovery of more complete mosasaur specimens from the Breien Member may be best focused on the finer-grained mudstone and claystone units where specimens would be expected to be more completely preserved.

The persistence of the mosasaurine lineage through the end of the Cretaceous is documented at other sites across the planet, including specimens of both *Mosasaurus* and *Prognathodon* recovered just below the K-Pg boundary in the Upper Maastrichtian Formation in The Netherlands, the Hornerstown Formation of New Jersey, and the Prairie Bluff Chalk of Alabama (Kiernan 2002, Jagt et al. 2008, Gallagher et al. 2012). Mosasaurine fossils recovered at other localities in close association with the K-Pg boundary in North America, such as the Tanis site in southwestern North Dakota and the Owl Creek Formation in both Mississippi and Missouri, may be either reworked from underlying deposits or transported out of context by the aftereffects of the Chicxulub impact (Gallagher 2005, Farke and Phillips 2017, DePalma et al. 2019). Kiernan (2002) identified mosasaurine mosasaurs just below the K-Pg boundary in the Prairie Bluff Chalk, which has an age range of 68–67 Ma, whereas NDGS locality L301 is closer to 66 Ma. The lack of catalog numbers, stratigraphic equivalency to the Owl Creek Formation, and unclear stratigraphic position (*in situ*?) within the generalized section for the youngest occurrences precludes

it from being treated on the same level as the previously mentioned occurrences. Given those observations, the Breien mosasaur is possibly one of, if not the youngest record of the Mosasaurinae lineage preserved in its natural environment within the intracontinental region of North America.

During the late Maastrichtian the geographic extent of the WIS was greatly reduced and the formation of the Dakota Isthmus via the expansion of the Sheridan Delta severed this epeiric sea into separate southern and northern arms (Erickson 1978, Kennedy et al. 1998, Erickson 1999, Berry 2017). Within the southern intracontinental region of North America, the youngest non-dental record of the mosasaurine lineage (*Mo. hoffmannii*) is from the Trail City Member within the lower portion of the Fox Hills Formation of South Dakota from rocks deposited during the *Hoploscaphites nicolletii* Ammonite Zone (Harrell and Martin 2015). The discovery of the Breien mosasaur, which was preserved within nearshore marine facies deposited during the *Hoploscaphites nebrascensis* Ammonite Zone (Hoganson and Murphy 2002) supports the persistence of the mosasaurine lineage within the intracontinental region of North America into the latest Maastrichtian, likely up to the K-Pg boundary. This discovery supports prior inferences that the fauna preserved within the Breien Member is a continuation of that documented in the underlying Fox Hills Formation (Hoganson and Murphy 2002). Not only did the regression and division of the Western Interior Seaway not dramatically alter the composition of the latest Maastrichtian marine fauna at the species level, the productivity of the sea was sufficient to continue to support these large-bodied carnivores. Thus, the previously documented complete faunal turnover at the species level between the Cretaceous Fox Hills Formation (Hoganson et al. 1997, Hoganson and Murphy 2002, Hoganson and Erickson 2005, Hoganson et al. 2019) and the Paleocene Cannonball Formation (Cvancara and Hoganson 1993), including the extinction of the mosasaurs, resulted from an abrupt turnover at the K-Pg boundary and not from gradual change during the latest Maastrichtian.

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