INTRODUCTION

Late Cretaceous dinosaur-dominated ecosystems from the Western Interior of North America present an unparalleled opportunity to examine evolution along a latitudinal gradient and within a relatively constrained time interval (~83 to 70 Ma). Lying along the alluvial and coastal plains of Laramidia, the differences between dinosaur assemblages of the Western Interior were noted several decades ago (e.g. Russell, 1967; 1969), and they were later divided broadly into northern and southern regions (e.g. Lehman, 1997; 2001).

Recent discoveries from underexplored regions of Laramidia, with increased attention to stratigraphic position, geochronology, and regional ecologies, have refined hypotheses regarding dinosaur distribution and evolution in Laramidia (e.g. Gates et al., 2010; Sampson & Loewen 2010; Sampson et al., 2010; Loewen et al., 2013), though some doubts persist regarding the degree and nature of these differences (e.g. Lucas et al., 2016; Fowler, 2017). Regardless, increased sampling and stratigraphic resolution reveal local and regional patterns in dinosaur evolution, including rapid turnover of megaherbivores (Mallon et al., 2012; Mallon, 2019), potential anagenetic evolution (Freedman Fowler & Horner 2015; Fowler & Freedman Fowler 2020; Wilson et al., 2020), and unexpected new forms (e.g. Brown & Henderson 2015; Wiersma et al., 2018).

Within the dinosaur ecosystems of Laramidia, the Ceratopsidae were geographically widespread and morphologically diverse, possessing highly variable cranial ornaments including horns and morphologically diverse parietosquamosal frills (Marsh, 1891a; Hatcher et al., 1907; Lull, 1933; Dodson et al., 2004; Sampson and Loewen, 2010). Two distinct clades within Ceratopsidae diverged by at least ~83 ma. These are the long-nosed, long-frilled Chasmosaurinae, characterized by *Chasmosaurus belli* (Lambe, 1902), *Pentaceratops sternbergii* (Osborn, 1923), and *Torosaurus latus* (Marsh, 1891b) and the round-nosed, relatively short-frilled Centrosaurinae, characterized by *Diablocerataops eatoni* (Kirkland & DeBlieux, 2010), *Centrosaurus apertus* (Lambe, 1904), *Styracosaurus albertensis* (Lambe, 1913) and *Pachyrhinosaurus lakustai* (Currie et al., 2008).

Centrosaurinae are an ecologically important and diverse radiation of ceratopsids, reaching peak diversity in the Campanian (~83-70 Ma). Historically known from abundant remains in Alberta, Canada and Montana, USA discoveries over the past two decades have rapidly expanded our understanding of the clade, particularly its geographic (Xu et al., 2010; Loewen et al., 2010; Fiorillo & Tykowski, 2012) and morphologic breadth with additional insights into centrosaurine ontogeny (Sampson et al., 1997; Ryan et al., 2001; Tumarkin-Deratzian 2009; Frederickson & Tumarkin-Deratzian 2014; Brown et al., 2009; 2020). Though locally abundant in some north-central localities within Laramidia (e.g. *Centrosaurus apertus* [Lambe, 1904], *Sytracosaurus albertensis* [Lambe, 1913], and *Pachyrhinosaurus canadensis* [Sternberg, 1950]), centrosaurines were previously rare or poorly known from other sites. Our expanding knowledge about centrosaurines includes new taxa from the southwestern United States and Mexico (e.g. *Diabloceratops eatoni* [Kirkland & DeBlieux, 2010], *Nasutoceratops titusi* [Sampson et al., 2013; Lund et al., 2016b], *Machairoceratops cornusi* [Lund et al., 2016a], *Yehuecauhceratops mudei* [Rivera-Sylva et al., 2016; 2017], *Crittendenceratops krzyzanowskii* [Dalman et al., 2018], *Menefeeceratops sealeyi* [Dalman et al., 2021]) and new and reinterpreted taxa from Montana and Canada (e.g. *Coronaceratops brinkmani* [Ryan & Russell, 2005; Ryan et al., 2011], *Albertaceratops nesmoi* [Ryan, 2007], *Pachyrhinosaurus. lakustai* [Currie et al., 2008], *Styracosaurus ovatus* [McDonald & Horner 2010; Wilson et al., 2020], *Spinops*

Commented [DFP1]: I study dinosaurs of the Late Cretaceous Western interior, and I don't know what "north-central Laramidia" means. Why not just say "Montana and Alberta" since that is what looks to be the intent based on extrapolating back from the taxa.

Commented [DFP2]: Do you mean "sites", "localities", or "regions" here. I'm not sure sites is the right choice.

sternbergorum [Farke et al., 2011], *Medusaceratops lokii* [Ryan et al., 2010; Chiba et al., 2017], *Pachyrhinosaurus perotorum* [Fiorillo & Tykoski, 2012], *Xenoceratops formostensis* [Ryan et al., 2012], *Wendiceratops pinhornensis* [Evans & Ryan, 2015], and *Stellasaurus ancellae* [Wilson et al., 2020]). Many of these new taxa have changed our understanding of morphological diversity of the clade. This proliferation of new taxa and occurrences has enhanced our understanding of the evolution of Centrosaurinae and provides clues regarding the mechanisms driving diversification of large vertebrates in Laramidia (Sampson and Loewen 1010; Gates et al., 2010).

The Upper Campanian deposits of the Judith River Group of Montana (Judith River Formation) and southern Alberta and Saskatchewan (Belly River Group: Foremost, Oldman, and Dinosaur Park formations) preserves a suite of parasynchronous non-marine biotas. Among the most abundant large vertebrates from these deposits are ceratopsid dinosaurs, including both chasmosaurines~~s~~ and centrosaurines. This assemblage represents one of the richest known from the Western Interior (Weishampel et al., 2004; Ryan & Evans 2005; Currie & Russell 2005), spanning sediments dated between ~82.4 and ~74.3 million years ago (Roberts et al., 2013; Rogers et al., 2017; Ramezani et al., 2022).

Commented [DFP3]: It's not a Group in Montana, it's just the Judith River Formation. It used to be called the Judith River Group in Alberta.

A new, relatively complete centrosaurine from the lower half of the McClelland Ferry Member of the Judith River Formation, in Kennedy Coulee in northern Montana, USA, is described here as a distinct genus and species, *Lokiceratops rangiformis*. The new taxon is in the same narrow stratigraphic interval and geographic area (Fig. 1) as three other centrosaurines (*Wendiceratops pinhornensis*, *Albertaceratops nesmoi*, and *Medusaceratops lokii*) and one putative chasmosaurine (*Judiceratops tigris*, though see Discussion). Morphologically, *Lokiceratops* resembles both *Albertaceratops* and *Medusaceratops*, implying rapid, sympatric diversification within a clade, a pattern not previously seen in dinosaurs. Furthermore, the possible sympatric occurrence of five distinct ceratopsids (four centrosaurines, one chasmosaurine) is unparalleled in any other known interval in Laramidia, even in more heavily sampled and documented horizons (e.g. Mallon et al., 2012). This discovery supports a novel hypothesis that some dinosaur clades saw rapid regional radiations rather than anagenesis, in geographically limited regions along the coastal and alluvial plains of Laramidia.

Commented [DFP4]: There is no formal or informal subdivision of the McCelland Ferry Mbr. You should not use language that makes it look this way here. Saying "lower half of the" avoids people thinking that "lower McCelland Ferry Mbr" has some kind of definition – it doesn't.

However, see next comment:

Commented [DFP5]: You should put in here that this is the US equivalent of the lower Oldman Fm of Alberta – this is useful information as people will want to compare with the Canadian faunas.

As you're aware – I don't think we should use McClelland Ferry Mbr or any of the subdivisions of Rogers et al (2016) for outcrop along the hi-line (border) in northern Montana. Unfortunately, Rogers et al did not demonstrate that these terms were applicable here. However, outcrop of the Foremost and lower Oldman Fms in Canada (2 miles to the north of the Lokiceratops locality) are continuous with outcrop in Kennedy Coulee. There's no question of equivalence or correlation with the Canadian units.

However, I appreciate that the authors included both sets of terminology in their figure.

But here's the problem – how do you know that Kennedy Coulee represents the "lower McClelland Ferry Mbr"? You can't see the bottom or top of the unit (as defined) in Kennedy Coulee. Moreover, since Kennedy Coulee contains the Foremost Fm equivalent, then this section (including the subsurface) is likely thicker and more time inclusive than the type section from Rogers et al (2016), which is further south and (most importantly) east. Thus, if the Foremost Fm part of the Kennedy Coulee area was say 170m thick, but the overlying Oldman Fm part was 120m thick (based on thicknesses in Canada), then in a total thickness of 0-290m Kennedy Coulee would represent #160 to ~#120 m, ie. within the upper half of the Mclelland Ferry Member. I'm confused myself now. Basically, Mclelland ferry terminology is not helpful.

Commented [DFP6]: Or anagenesis, since they do not overlap stratigraphically

(INSERT FIGURE 1 HERE FULL PAGE WIDTH)

Geological Context

The Loki Quarry producing the new specimen lies on private land in the badlands of Kennedy Coulee, north of Rudyard in Hill County, Montana, USA (Fig. 1). The proximal end of Kennedy Coulee is also known as Canadian Creek where it originates north of the US/Canada border, west of its confluence with the Milk River. In these badlands, Campanian alluvial deposits, the lower Judith River Formation (Goodwin & Deino, 1989; Rogers, 1988) crop out extensively along the drainage systems flowing toward the Milk River Valley in the north (Fig. 1).

Commented [DFP7]: What is "proximal end" for a drainage?

Commented [DFP8]: There is no "lower Judith River Fm", informally or formally. Call it the "lower part" or something like that.

Following recent stratigraphic revision of the Judith River Formation by Rogers et al. (2016), the exposed Kennedy Coulee beds correlate to the McClelland Ferry Member to the south, as well as the upper Foremost and overlying lower Oldman formations of southern Alberta to the north, including the Taber Coal Zone and the Herronton Sandstone Zone (Ogunyomi & Hills, 1977; Eberth & Hamblin, 1993; Cullen et al., 2016). The Taber Coal Zone, representing the top of the Foremost Formation in Alberta and correlative coal deposits exposed to the south, represents a datum for calibrating stratigraphic sections and associated fossil taxa (Eberth &

Commented [DFP9]: It certainly correlates with the Canadian Foremost and lower Oldman Fms, since the rock outcrop is continuous the 2 miles up to the international border. However it is not clear if there is an equivalent to the Foremost Fm in the McClelland Ferry Mbr in the type section 130miles to the SE.

Commented [DFP10]: Do you mean to the south of the border (ie, at Rudyard), or do you mean at the type section?

Hamblin, 1993; Brinkman et al., 2004; Eberth, 2005; Ryan, 2007; Evans & Ryan, 2015; Freedman Fowler & Horner, 2015; Cullen et al., 2016; Ryan et al., 2017).

The Loki Quarry lies near two other significant ceratopsian localities in the same Canadian Creek within Kennedy Coulee (Fig. 1). The Loki Quarry is 4.9 kilometers northwest of the site where the holotype of the putative chasmosaurine ceratopsid *Judiceratops tigris* (YPM VPPU 022404) was collected, and 2.6 kilometers west of the Mansfield Bonebed (*Medusaceratops lokii*). The Mansfield Bonebed that produced *Medusaceratops* occurs ~8 km southwest of the *Probrachylophosaurus bergei* quarry which produced referred material of *Judiceratops* (YPM VPPU 023262 Campbell, 2015). The Loki Quarry lies 2.8 kilometers west of the *Brachylophosaurus goodwini* (Horner, 1988) holotype locality (UCMP Locality No. V83125). Two other important ceratopsian quarries lie just north of the Montana/Alberta border. The South Side Ceratopsian *Wendiceratops* quarry (Evans & Ryan, 2015) is 10 kilometers north of the Montana-Alberta border and the *Albertaceratops* quarry (Ryan, 2007) is 3.5 kilometers north of the South Side Ceratopsian *Wendiceratops* quarry. The Loki Quarry is 22 kilometers southwest of the South Side Ceratopsian quarry (Fig. 1).

Commented [DFP11]: This could all just be a figure and caption

The Loki Quarry sits 922 meters above sea level and 12 meters above the top of the Marker A Coal (MAC) seam. The Marker A Coal seam is equivalent to the top of the Taber Coal Zone (*sensu* Goodwin & Deino, 1989) based on multiple sections measured in the Kennedy Coulee and at the *Probrachylophosaurus* (Freedman et al., 2015) locality (MOR locality JR-518). The Mansfield Bonebed producing *Medusaceratops* occurs ~10 meters above the Marker A Coal. All of these quarries occur near the top of a 10–15 meter thick interval of interbedded organic-rich mudstones with discontinuous carbonaceous seams, siltstone, and sandstones (Fig. 1).

The stratigraphic occurrence of the Loki Quarry places it above *Medusaceratops* (~10 m above the Marker A Coal) and places both taxa within equivalents of the Herronton Sandstone Zone, in the same stratigraphic interval where *Albertaceratops* and *Wendiceratops* were recovered in southern Alberta. Correlation to the top of the Taber Coal Zone (TCZ) places *Albertaceratops* slightly lower in section (~8 m above the TCZ) with respect to *Medusaceratops* (~10 m above the MAC) and places the Loki Quarry at roughly the same level as *Wendiceratops* (~12 m above the TCZ), making them virtually indistinguishable stratigraphically. Beds and channel deposits in the Herronton Sandstone Zone and its McClelland Ferry Member to the south are laterally discontinuous and variable in nature, suggesting that these four ceratopsian quarries are stratigraphically equivalent, and the relative occurrences of these taxa may be slightly inaccurate.

Commented [DFP12]: Sandstone beds?

Two bentonite ash beds that bracket the Loki Quarry (21 meters below and 16 meters above) were radiometrically dated by Goodwin and Deino (1989). The single-crystal, laser-fusion ^{40}Ar/^{39}Ar ages on biotite crystals yielded a weighted mean of 78.5 ± 0.2 Ma for bentonite 85MG7-16-1, approximately 21 meters below the quarry, and a weighted mean of 78.2 ± 0.2 Ma for bentonite 84MG8-3-4, approximately 16 meters above the quarry (Fig. 1). The ages were recalibrated by Roberts et al. (2013) and Fowler (2017). For the purposes of this study, and until additional geochronologic work is undertaken in the northern Judith River Fm near the study area, we instead prefer to use recently published high-precision U-Pb dates of Ramezani et al. (2022).

Commented [DFP13]: These were incorrectly recalibrated

Commented [DFP14]: But you don't use either of these. Do you use recalibrated dates for other taxa in your chart?

Commented [DFP15]: These dates have their own problems, which curiously enough are not raised in the Ramezani paper.

High-precision U–Pb analyses of zircons by the CA-ID-TIMS method from a bentonitic ash bed within Marker A Coal (KC061517-1) 12 meters below the Loki Quarry date to 78.549 ± 0.024 Ma (Ramezani et al., 2022). Using the median Bayesian estimate for the location of the

Loki Quarry recovers a date of roughly 78.08 Ma, with error estimates ranging from +0.3 to -0.9 Ma. This constrains the chronostratigraphic age of the Loki Quarry to between 78.38 and 77.18 Ma.

The lithology of the Loki Quarry is characterized by carbonaceous fine-grained sandstones, siltstones, and mudstones with depositional features indicating a poorly-drained fluvial system (Figs. 1-2). Gar scales and mollusks occur in the quarry. Some of the quarry matrix is in the collections of Evolutionsmuseet, Knuthenborg, Maribo, Denmark. Carbonized plant fragments are common, many attributable to Araucariales, along with beads of amber and indeterminate fragments of carbonized wood.

Many bones recovered from the quarry are broken, but there is no evidence of subaerial or subaqueous weathering of any elements. Some breakage may reflect collection techniques, as most elements were plucked from the quarry sediments and only two plaster jackets (scapulocoracoid and sacrum) were made. Many of the bones were plasticly deformed after deposition by compression of the clay-rich, fine-grained sediments. This deformation skews the bones so that the mount does not accurately represent the skull shape. Taphonomic indicators, including a high degree of association of the cranial bones (Fig. 2), indicate little to no fluvial transport after death and disarticulation.

(INSERT FIGURE 2 HERE FULL PAGE WIDTH)

Discovery and Excavational History

EMK 0012 is an associated skeleton of a mature ceratopsid. The specimen was discovered by Mark Eatman in late spring 2019 and excavated under lease on the lands of the Wolery Ranch in fall, 2019. The skull was associated, but partially disarticulated. The right jugal and squamosal were found together, dorsal side up. Portions of the parietosquamosal frill were found in close association. Both orbits and postorbital horns were found on either side of the braincase with both maxillae directly in front of them followed by the nasal, premaxillae and rostral. The synsacrum and ilia were found ventral side facing up, with the right ischium in articulation; the left ischium lay one meter away (Fig. 2). The left parietal with fused epiparietals ep1-ep7 was found dorsal side up along with the left ischium. The right scapulocoracoid was found medial side up just posterior to the pelvis. The free anterior caudal vertebra and chevron were found next to the pelvis. Ownership of EMK 0012 was permanently transferred to Evolutionsmuseet, Knuthenborg in 2021 where it is available to researchers.

Preparation and Reconstruction

EMK 0012 was delivered to Fossilogic LLC in Pleasant Grove, Utah for preparation, restoration, mounting, and reconstruction. The skull was received in multiple fragments wrapped in aluminum foil along with two blocks protected with plaster and burlap field jackets. Preparation began with removal of jackets, foil, matrix, and any stabilizing cyanoacrylate applied in the field. Hairline cracks were stabilized using a low-viscosity (2-3 centipose, roughly equivalent to the viscosity of milk) cyanoacrylate (Starbond EM-02). Larger pieces were glued together using a gel-like high-viscosity (2000 3 centipose, roughly equivalent to the viscosity of honey) cyanoacrylate (Starbond EM-2000). Some larger cracks were filled with a polyester resin (Key-Lite) that was not painted to make gap fills obvious to researchers. Finally, all bones were sealed and stabilized with a matt clear paraloid ethyl methacrylate co-polymer B-72 (Rust-Oleum). Preparation was largely performed by Jen Sellers and Estrella Gallegos over the period of several weeks during the fall of 2021.

Following preparation, each element was surrounded by silicone rubber molds prior to any restoration to preserve scientifically valuable data as research casts in a polyurethane casting plastic. These casts are available at the Natural History Museum of Utah as NHMU VP C-991. Mark Loewen, Joseph Sertich, Savhannah Carpenter, and Brock Sisson determined the identity of all recovered elements and articulated and assembled them into their proper locations in a 3D skull reconstruction. Missing elements were sculpted as mirror images of existing material from blocks of polyester resin (Key-Lite). Where plastic deformation had deformed bones, the casts were heated to allow retrodeformation and restored or cut and restored to original shapes.

Upon assembly, the restored 3D cast skull was surrounded by a silicon rubber mold enabling multiple replicas to be cast. This process included sectioning the restored skull into several major sections: the right and left face, the frill, braincase and quadrates. These sections of the skull were surrounded in clay along a parting line with corresponding keys, vents, and sprues as needed with a hard mother mold of fiberglass and polyester resin to support the flexible silicone and retain its shape. Each section was then flipped and the clay removed, excepting the vents and spues, and the process was repeated. The finished two-part molds (the braincase was a three-part mold) were then opened and the master-cast removed. The molds were then filled with a polyurethane casting plastic that is lightweight, durable, and easily painted to match the original bone. The results are accurate 3D skull replicas for research and display.

One replica was used as a base into which each original bone was mounted in a manner that would allow for its removal for examination by scientists. Custom steel brackets were bent to cradle every individual piece, holding them in their correct anatomical positions without using adhesives or drilling holes into the bones. The replica areas of the “real bone” mount were painted to a similar brown color, making the finished piece aesthetic overall but clearly highlighting the original material compared to sections of reconstruction (Fig. 3).

Mounting and restoration was performed by Ben Meredith, Ethan Storrer, Jose Muñoz, and Seth Bourgeous during the spring of 2022. Upon completion of the mount, two large solid wooden crates were constructed. One held the steel and replica material and the other was for packing of all of the original material. The packing was done using a custom spray-in-place foam system that allowed for a perfectly form fitting, reusable padding that protects the specimen during transport. Upon completion, the specimen was transported to Evolutionsmuseet, Knuthenborg, Maribo, Denmark via airfreight, where it was received by museum staff.

(INSERT FIGURE 3 HERE HERE FULL PAGE WIDTH)

MATERIALS AND METHODS

Paleontological Ethics Statement

The specimen described here (EMK 0012) is in the publicly accessible, permanent repository of Evolutionsmuseet, Knuthenborg, Maribo, Denmark. Ownership title EMK 0012 was transferred from the landowner to Montana Dinosaur Company of Belgrade, Montana and finally to Evolutionsmuseet, Knuthenborg. Casts of EMK 0012 are reposited as UMNH VP C-991 at the Natural History Museum of Utah, Salt Lake City, Utah, United States of America. Locality coordinates to the site are listed below, and notes and diagrams associated with the specimen are available from the specific repository institutions as per institutional policy. All necessary permits and or permissions were obtained for the described study, which complied with all relevant regulations.

Terminology

We employ traditional, or “Romerian,” anatomical and directional terms over veterinary alternatives (Wilson, 2006) in order to be consistent with the vast majority of ceratopsid literature. For example, “anterior” and “posterior” are used as directional terms in lieu of the veterinary alternatives “rostral”, “cranial”, and “caudal”, and human anatomical terms “inferior” and “superior”. These terms are especially unsuited to descriptions of ceratopsians that possess a rostral bone and caudal vertebrae. English equivalents of standard Latin terms are used, and directional terms follow Clark (1993).

Specifically, regarding ceratopsian anatomy, we employ the terms ectonaris and endonaris to refer to the outer and inner openings of the nasal vestibule, respectively, which are closely analogous to bony nostril, and external and internal antorbital fenestra as used by Witmer (1997; 2001). (Note: although the more familiar terms “external” and “internal naris” could be used in place of ectonaris and endonaris, respectively, the former terminology is not applied here because it has been used previously to refer to other structures. For example, external naris has been used to refer to the endonaris, and internal naris has often been applied to refer to the choana, or narial fenestra). Major openings posterior to the orbit are referred to as dorsotemporal and laterotemporal fenestrae. Anatomical nomenclature for the sinuses at the roof of the skull are modified from Farke (2006; 2010) to reflect the dorsocranial sinus complex. Anatomical nomenclature for marginal ossifications of the parietosquamosal frill follows the system first proposed by Hatcher et al. (1907) and more recently advocated by Goodwin and Horner (2008) and modified by Loewen et al. (2010). Marginal ossifications on the squamosal and parietal of ceratopsids are referred to as “episquamosals” (es) and “epiparietals” (ep), respectively. As a group, we refer to these epiossifications as “marginal ossifications of the frill” in place of the anatomically erroneous nomenclature “epoccipitals.” Where an epiossification crosses the squamosal-parietal contact, we refer to it as an “epiparietosquamosal marginal ossification” (eps). Epiossifications of the frill are numbered sequentially from the midline of the parietal; with a possible midline epiparietal (ep0) and epiparietals then sequentially numbered lateral from the midline (ep1-ep8); an epiparietosquamosal (eps) if present at the parietosquamosal suture, and episquamosals sequentially from posterior to anterior (es1 to es4 or es5). Raised bumps on the dorsal surface of the marginal parietal frill are termed dorsoparietal processes (dpp).

Phylogenetic Analysis

To assess the systematic position of EMK 0012, the specimen was coded in a matrix initiated by Scott Sampson and Cathy Forster in the 1990’s and expanded by Mark Loewen and Andrew Farke during the 2000’s and 2010’s (Forster & Sampson 2002; Loewen et al., 2010; Sampson et al., 2010; Farke et al., 2011; Knapp et al., 2018). Character scorings were based on firsthand observations of specimens. The character-taxon matrix was assembled in Mesquite v.3.70 (Maddison & Maddison 2021), and the matrix was analyzed using TNT v. 1.5 (Goloboff et al., 2008; Goloboff & Catalano 2016). Tree searching followed the parsimony criterion implemented under the heuristic search option using tree bisection and reconnection (TBR) with 10,000 random addition sequence replicates. Zero length branches were collapsed if they lacked support under any of the most parsimonious reconstructions. *Hypsilophodon foxii* was designated the outgroup, and characters were run equally weighted, except for multistate Characters 1, 51 70, 126, 130, 144, 170, 261, 262, 279, 336, and 339 which were considered ordered (additive). Character 90 regarding postorbital ornamentation in juveniles can be (but was not) excluded, as most taxa do not include immature specimens. The analysis consists of 377 characters (263 cranial, 61 postcranial, and 53 concerning frill-based ornamentation) and 86 taxa.

Comparative Material

We compared EMK 0012 with an exhaustive selection of ceratopsian taxa and accessed the ever-expanding literature focused specifically on ceratopsid dinosaurs. The authors have had the opportunity over the past 20 years to study firsthand and photograph nearly the complete range of marginocephalian material collected globally. Where published illustrations and descriptions were used to supplement data obtained through direct observation, appropriate references are cited below.

Comparative material included the nonmarginocephalian taxa *Hypsilophodon foxii* (NHM 28707; NHM 9560-1; and NHM R 2477) and *Lesothosaurus diagnosticus* (BMNH R8501; BMNH R11956; BMNH RU B17; and BMNH RU B23). Pachycephalosaurs included: *Stegoceras valdensis* (TMP 99.62.1; CMN 8816; TMP84.5.1; and UALVP 2), *Homalocephale calathocercos* (IGM 100/51), and *Prenocephale prenes* (Zpal MgD-I/104). Basalmost ceratopsians included: *Yinlong downsi* (IVPP V14530), *Hualianceratops wucaiwanensis* (IVPP V12722), *Xuanhuaceratops niei* (IVPP V18642), and *Chaoyangsaurus youngi* (IGCAGS V 371). Psittacosaurs included: *Psittacosaurus lujiatunensis* (IVPP V14341; IVPP V12617; LH PV1; JZMP-V-11; CAGS-IG-VD-004), *Psittacosaurus mongoliensis* (AMNH 6254), *Psittacosaurus sinensis* (IVPP V738; BNHM BPV149), *Psittacosaurus meileyingensis* (IVPP V7705), and *Psittacosaurus sibiricus* (PM TGU 16/4-20). Other basal ceratopsians included: *Mosaiceratops azumai* (ZMNH M8856), *Beg tsi* (IGM 100/3652), *Liaoceratops yanzigouensis* (CAGS-IG-VD-002; NMNH 58749; PMOL-AD00058; PMOL-AD00078; IVPP V12738; and IVPP V12633), *Aquilops americanus* (OMNH 34557), *Archaeoceratops yujingziensis* (CAGS-IG-VD-003), *Yamaceratops dorngobiensis* (IGM 100/1315), *Auroroceratops rugosus* (CAGS-IG-VD-001), and *Archaeoceratops oshimai* (IVPP V11114). Leptoceratopsids included: *Cerasinops hodgskissi* (MOR 300; USNM 13863), *Montanaceratops cerorhynchus* (AMNH 5464; AMNH 5244; MOR 542), *Udanoceratops tschizhovi* (PIN 3907/11), *Prenoceratops pieganensis* (MNHCM material; TCM material), *Zhuchengceratops inexpectus* (ZCDM V0015), and *Leptoceratops gracilis* (CMN 8887; CMN 8889). Derived non-ceratopsid taxa included: *Protoceratops hellenikorhinus* (IMM 95BM1/1; IMM 96BM1/4), *Protoceratops andrewsi* (AMNH 6251,6408, 6414, 6418, 6425, 6429, 6430, 6438, 6441, 6443, 6444, 6447, 6449,6451, 6466, 6473, 6477, 6480, 6483, 6485, 6486, 6487 6637, 6638; BMNH R6640; R10060; IGM 100-500, 100-502, 100-522, 100-581), *Protoceratops* sp. (IGM 100-1246), *Breviceratops kozlowskii* (Zpal MgD-I/116; Zpal MgD-I/117), *Bagaceratops rozhdestvenskyi* (Zpal MgD-I-126; ZPAL MgD-I/123; ZPAL MgD-I/124; ZPAL MgD-I/125; ZPAL MgD-I/127; ZPAL MgD-I/128; ZPAL MgD-I/129 (Czepinski 2019)), *Ajkaceratops kozmai* (MTM V2009.192.1; MTM V2009.193.1; MTM V2009.194.1; MTM V2009. 195.1; MTM V2009.196.1), *Graciliceratops mongoliensis* (ZPal MgD-I/156), *Turanoceratops tardabilis* (CCMGE 251/12457), and *Zuniceratops christopheri* (MSM P2101; MSM P2107; MSM P 2110). Centrosaurine taxa included: *Diabloceratops eatoni* (UMNH VP 16699), *Machairoceratops cronusi* (UMNH VP 20550), *Crittendenceratops krzyzanowskii* (NMMNH P-34906), *Menefeeceratops sealeyi* (NMMNH P-25052), *Yehuecauhceratops mudei* (CPC 274), *Avaceratops lammersi type* (ANSP 15800), *Avaceratops sp.* (MOR 692 (Ryan et al 2016)), *Avaceratops sp.* (CMN 8804 (Ryan et al 2016)), *Nasutoceratops titusi* (UMNH VP 16800; UMNH VP 19466), *Xenoceratops foremostensis* (CMN 53282), *Lokiceratops rangiformis* (EMK 0012), *Albertaceratops nesmoi* (TMP 2001.26.01), *Medusaceratops lokii* (TMP 2002.69.1–10; TMP 2002.28–38; WDCB-MC-001; FDMJ-V-10; WDCB unnumbered specimens), *Wendiceratops pinhornensis* (TMP

2011.051.0009 and ~240 other TMP specimens from the South Side Ceratopsian bonebed), *Sinoceratops zhuchengensis* (ZCDM V0010; ZCDM V0011; ZCDM V0012), *Coronosaurus brinkmani* (TMP 2002.68.1), *Spinops sternbergorum* (NHMUKR16307; NHMUKR16308; NHMUKR16309), *Centrosaurus apertus* (CMN 348; CMN 8795; CMN 8798; UAL VP 11735), *Styracosaurus albertensis* (CMN 344), *Styracosaurus ovatus* (USNM 11869), *Stellasaurus ancellae* (MOR 492), *Einiosaurus procurvacornis* (MOR collection), *Iddesleigh pachyrhinosaur* (TMP 2002.76.0), *Achelousaurus horneri* (MOR 485), *Pachyrhinosaurus lakustai* (TMP 86.55.285; TMP 87.55.156; TMP 89.55.1234), *Pachyrhinosaurus perotorum* (DMNH 21200; DMNH 22558), *Pachyrhinosaurus canadensis* (CMN 8860, CMN 8866, CMN 8867, CMN 9485, CMN 10645, CMN 10663, CMN 21863, CMN 21864, TMP 82.52.1). Chasmosaurine taxa included: *Mercuriceratops gemini* (UALVP 54559), *Regaliceratops peterhewsi* (RTMP 2005.55.1), *Kosmoceratops richardsoni* (UMNH VP 17000; UMNH VP 16878), *Vagaceratops irvinensis* (NMC 41357; TMP 87.45.1; TMP 98.102.8), *Spiclypeus shipporum* (CMN 58071), *Chasmosaurus belli* (AMNH 5402; BMNH R4948; CMN 2245; ROM839; ROM843; YPM 2016), *Mojoceratops kaiseni* (AMNH 5401; AMNH 5656; TMP 79.11.147; TMP 81.19.175; TMP 83.25.1), *Agujaceratops mavericus* (TMM 43098-1), *Agujaceratops mariscalensis* (TMM 46500-1; UTEP P37.7.065; UTEP P.3737.046), *Chasmosaurus russelli* (CMN 8800; CMN 8801; TMP 2013.19.38), *Utahceratops gettyi* (UMNH VP 12198; UMNH VP 16671; UMNH VP 16784), *Pentaceratops sternbergii* (NMMNH P-27468; NMMNH P-50000; PMU R200), *Anchiceratops ornatus* (CMN 8535; TMP 83.01.01), *Arrhinoceratops brachyops* (ROM 796), *Eotriceratops xerinsularis* (TMP 2002.57.7), *Torosaurus latus* (AMNH 5116; ANSP 15192; EM P16.1; MOR 981; MOR 1122; MPM VP 6841; YPM 1830), *Torosaurus utahensis* (USNM 15583), *Triceratops prorsus* (LACM 27428; YPM 1822), *Triceratops horridus* (AMNH 5116; YPM 1820). Some comparative taxa that were considered but not included in the phylogenetic analysis: *Helioceratops brachygnathus* (JLUM L0204-Y-3), *Koreaceratops hwaseongensis* (KIGAM VP 200801), *Gryphoceratops morrisoni* (ROM 56635), *Unescoceratops koppeihusi* (TMP 95.12.6), the *Agujaceratops sp.* Terilingua exemplar (TMM 45922), *Terminocavus sealeyi* (NMMNH VP 27468), *Navajoceratops sullivani* (SMP VP 1500), *Coahuilaceratops magnaquerna* (CPC 276; CPC 277), *Bravoceratops polyphemus* (TMM 46015-1), "*Judiceratops tigris"* revised (YPM VPPU 022404 contra Longrich, 2013 and Campbell, 2015 see discussion), *Sierraceratops turneri* (NMNNH P-76870), *Ojoceratops fowleri* (SMP VP-1865), and *Nedoceratops hatcheri* (USNM 2412).

Commented [DFP16]: This is the holotype of Terminocavus sealeyi

Commented [DFP17]: This is now the holotype of Bisticeratops, if you think that is a defensible taxon

Commented [DFP18]: SO this does not include the holotype or hypodigm material of Pentaceratops? All of these specimens have been referred to other taxa. The holotype of Penta has thin struts for the parietal, NMMNH P-27468 has thick posterior bars and is from higher in section.

P-50000 is from even higher in section, however it unfortunately lacks the diagnostic posterior parietal, so I do not think it is very useful as a new taxon (Bisticeratops).

Commented [DFP19]: Any reason why?

Nomenclatural Acts

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank. The ZooBank Life Science Identifiers (LSIDs) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub:77A46B79-9BA1-4764-9AF6-14C69C2B8C8F. The LSID for *Lokiceratops* is: urn:lsid:zoobank.org:act:4640DFB2-63D2-483A-93ED-4EF405285CAC. The LSID for *Lokiceratops rangiformis* is: urn:lsid:zoobank.org:act:548AA668-EE62-49DA-8CA2-939A00223B92. The online version of this work is archived and available from the following digital repositories: CLOCKSS, Zenodo and PubMed Central.

RESULTS

Systematic Paleontology

Dinosauria Owen, 1842; *sensu* Padian & May, 1993
Ornithischia Seeley, 1887; *sensu* Sereno, 1998
Ceratopsia Marsh, 1890; *sensu* Dodson, 1997
Ceratopsidae Marsh, 1888; *sensu* Sereno, 1998
Centrosaurinae Lambe, 1915; *sensu* Dodson et al., 2004
Albertaceratopsini clade nov.
urn:lsid:zoobank.org:act:4640DFB2-63D2-483A-93ED-4EF405285CAC

Diagnosis— Albertaceratopsini is defined as a stem-based clade (tribe that consists of all taxa more closely related to *Albertaceratops nesmoi* than to *Centrosaurus apertus*.

Lokiceratops gen. nov.
urn:lsid:zoobank.org:act:4640DFB2-63D2-483A-93ED-4EF405285CAC
(THE ABOVE SECTION SHOULD BE CENTERED)

Diagnosis—Monotypic, same as for species.

Lokiceratops rangiformis gen. et sp. nov.
urn:lsid:zoobank.org:act:548AA668-EE62-49DA-8CA2-939A00223B92
(THE ABOVE SECTION SHOULD BE CENTERED)

Etymology— The generic name refers to the god Loki from Norse mythology, and *ceratops*, (Greek) meaning “horned face.” The species name refers to the bilateral asymmetry of frill ornamentations, similar to the asymmetry in antlers of the reindeer/caribou genus *Rangifer*.

Holotype—EMK 0012 is an associated, disarticulated skull and partial skeleton (Figs. 2-4). The skull is represented by the rostral, premaxillae, maxillae, nasals, lacrimals, jugals, frontals, palpebrals, postorbitals, squamosals and parietals. It includes the left pterygoid and a partial braincase. Postcranial elements include a cervical vertebra; the right scapula and coracoid; both ischia and the sacrum with attached sacrodorsals and sacrocaudals, an anterior free caudal vertebra and a chevron from the proximal tail. EMK 0012 is reposited at the Evolutionsmuseet, Knuthenborg, Maribo, Denmark.

(INSERT FIGURE 4 HERE HERE FULL PAGE WIDTH)

Holotype Locality—EMK 0012 was recovered from the Loki Quarry in Kennedy Coulee, south of the Milk River in Hill County, northern Montana (Fig. 1). The quarry is 3.6 kilometers from the Montana-Alberta border. Exact coordinates are 48.961955, -110.660213, 922 meters above sea level.

Holotype Horizon—EMK 0012 was recovered from lower Judith River Formation beds that correlate to the McClelland Ferry Member 200 km to the south, and the lower Oldman Formations of southern Alberta 3.6 kilometers to the north. EMK 0012 is 12 meters above the Marker A Coal equivalent to the Taber Coal Zone and just above sandstones equivalent to the Herronton Sandstone Zone at the top of the Foremost Formation 3.6 kilometers to the north in Alberta.

Commented [DFP20]: I suppose it doesn’t matter all that much what a taxon is named, but there is already medusaceratops lokii, so this might be slightly confusing.

Commented [DFP21]: I suppose I will just interject to say that, again, it’s never been demonstrated that this is the McClelland Ferry Mbr.

Age—High-precision U–Pb analyses of zircons by the CA-ID-TIMS method in a bentonite within the Marker A Coal (KC061517-1; which is 12 meters below the Loki Quarry quarry) date to 78.549 ± 0.024 Ma (Ramezani et al., 2022). Using the median Bayesian estimate for the location of the Loki Quarry recovers a date of roughly 78.08 Ma, with error estimates ranging from +0.3 to -0.9 Ma. This constrains the chronostratigraphic age of the Loki Quarry to between 78.38 and 77.18 Ma.

Commented [DFP22]: Please explain this.

Commented [DFP23]: Do you mean the stratigraphic position? "location" is geographic, ie. on a topo map.

Commented [DFP24]: There is only 300ky between the two Ar/Ar ash dates. So this amount of error is not very good really.

Diagnosis— *Lokiceratops rangiformis* is an albertaceratopsin centrosaurine ceratopsid distinguished from other centrosaurines by the following autapomorphies: presence of unadorned nasal; elongate, uncurved ep1 epiossification directed in plane of frill along posterior margin of parietosquamosal frill; and hypertrophied, lateral curving epiparietal ep2 directed in plane of frill. The hypertrophied ep2 is relatively larger than any other parietal epiossification within Centrosaurinae. Both ischia are distinctly kinked distally about two-thirds of the length the shaft at the point where the two ischia contact medially. Postorbital horncore bases are deeply excavated by pneumatic cornual sinuses penetrating distance equivalent to two orbit radii into horncore to an extent unknown in other long horned centrosaurs.

Commented [DFP25]: Unnecessary to say "pneumatic", because we don't know that they were full of air. Plus I don't think I've ever read them being called this before. They're just cornual sinuses.

Differentia— *Lokiceratops rangiformis* differs from *Zuniceratops* and all known chasmosaurines in possessing an abbreviated, fan-shaped squamosal typical of most centrosaurines. Differs from *Zuniceratops* and all known centrosaurines in the distinct kink in the ischium.

Medusaceratops lokii differs from the stratigraphically similar *Lokiceratops rangiformis* in a number of key features including: presence of nasal ornamentation; a lesser extent of postorbital pneumaticity; presence of four episquamosals (three in *Lokiceratops*); presence of multiple, raised undulations on midline ramus of parietal between the parietal fenestrae; lack of a narrow, medially restricted embayment on the midline of the posterior edge of the parietal; a reduced, rather than elongate, posteriorly directed ep1 epiossifications along the posterior margin of the parietosquamosal frill; the length of the largest curving epiparietal ep2; and the presence of five bilateral epiparietals (seven in *Lokiceratops*).

Albertaceratops nesmoi differs from the stratigraphically similar, but possibly slightly younger *Lokiceratops rangiformis*, in key features including: presence of nasal ornamentation; presence of four episquamosals (three in *Lokiceratops*); presence of multiple raised undulations on midline ramus of parietal between the parietal fenestrae; reduced, rather than elongate posteriorly directed, ep1 epiossifications along the posterior margin of the parietosquamosal frill; the length of the largest curving epiparietal ep2; and presence of five bilateral epiparietals (vs. six or seven in *Lokiceratops*).

Commented [DFP26]: What does this mean? Ambiguous language.

Commented [DFP27]: According to your strat chart, Loki is from higher in section, so it is stratigraphically younger.

Commented [DFP28]: Figure 21 shows the largest epi being ep1 not ep2. Thus the long epis of medusaceratops (ep2) and Albertaceratops (ep1) are not homologous. Either that or change your figure.

Wendiceratops pinhornensis differs from the likely stratigraphically equivalent *Lokiceratops rangiformis*, in key features including: presence of nasal ornamentation; lack of a medially restricted embayment on the midline of the posterior edge of the parietal; presence of five dorsally recurved epiparietals; lack of a hypertrophied laterally curving epiparietal; and presence of five bilateral epiparietals (seven in *Lokiceratops*).

Judiceratops tigris, a fragmentary putative chasmosaurine, differs from the stratigraphically similar *Lokiceratops rangiformis* in its elongated, sickle-shaped chasmosaurine squamosal; the lack of a medially-restricted midline embayment on the posterior parietal bar; and the lack of elongated epiparietals on its parietal (Campbell, 2015). Questions about the taxonomic identity and validity of *Judiceratops* are evalutated in the discussion (below).

Description and Comparative Anatomy

Present condition of the skull

The skull of *Lokiceratops rangiformis* (EMK 0012) is exhibited at Evolutionsmuseet, Knuthenborg, Maribo, Denmark. The skull is presently reconstructed into a steel supported mount (Fig. 3) with each individual bone articulated into a 3D cast skull reconstruction. Each bone is removable from the mount for study. A cranial osteograph illustrates the missing parts of each element of the skull (Fig. 5). As a result of elements being removable, there are slight gaps in the real bone mount to accommodate removal. For this reason, measurements were taken from the reconstructed cast skull which more accurately reflects the actual dimensions of the specimen. These data are presented in Table 1, and cranial measurements are explained in Figure 6. The measurements in Table 1 and Figure 6 are inspired by the measurement table of Mallon et al. (2016). The skull outlines in anterior, dorsal and ventral views were reconstructed using 3D surface scans and lack parallax.

(INSERT FIGURE 5 HERE FULL PAGE WIDTH)

(INSERT TABLE 1 HERE FULL PAGE WIDTH)

(INSERT FIGURE 6 HERE FULL PAGE WIDTH)

General Cranial Morphology

The narial region of *Lokiceratops rangiformis* (EMK 0012) closely resembles other centrosaurines in being roughly subcircular, with a well-developed premaxillary septum, a ventrally projecting ventral angle, and a narial spine on the posterior margin of the endonaris (Figs. 3-6). There is no evidence of nasal ornamentation either in a change in texture from the ventral surface of the nasal to the dorsal surface, or in the shape of the dorsal surface of the nasals. The anterior process of the nasal lacks the rugosity present on the rostral and dorsal premaxilla. The orbits bear dorsally elongated, anterolaterally oriented horncores and a well-developed antorbital buttress formed by the prefrontal, palpebral and lacrimal as in most basal centrosaurines, and unlike the reduced horncores of eucentrosaurines. The suborbital region is similar to that of all centrosaurines. The parietosquamosal frill is elongated compared to *Centrosaurus* with typical fan-shaped, stepped squamosals, and elongate, fenestrated parietals. Epiossifications include short epijugal horns, three episquamosals, and seven epiparietals.

Major Cranial Fenestrae*, *Foramina*, *Fossae*, *and Passageways

Nasal Vestibule—The nasal vestibule is the outermost anterior expression of the nasal cavity and is made up of the endonaris and ectonaris. This area is small in most dinosaurs including the basal ceratopsian *Yinlong downsi* (Xu et al., 2006; Han et al., 2016), but is larger in many ceratopsians including psittacosaurs (Sereno, 2010; You et al., 2008); leptoceratopsids (Brown & Schlaikjer, 1940; Chinnery, 2004), and protoceratopsids (Czepiński, 2020); it is hypertrophied in *Zuniceratops* and all ceratopsids.

Nasal Cavity—The nasal cavity proper is the main chamber of the nasal cavity, likely containing both olfactory and respiratory ~~epithelium~~epithelia. It extends between the nasal vestibule anteriorly and the nasopharynx posterorly, which in turn opens into the pharynx via the choanae.

Ectonaris—The external narial fossa (Figure 7), or ectonaris, represents the maximum inferred extent of soft-tissue associated with the narial region, expressed on the lateral surface of the premaxilla and the anterior surface of the nasal. The overall shape of the ectonaris in lateral view is hemicircular, as in all centrosaurine ceratopsids. The anterodorsal, anterior, and ventral portions of the ectonaris extend over the lateral surface of the premaxilla. The posteroventral portion of the ectonaris lies on the dorsal surface of the posteroventral process of the premaxilla, transitioning posteriorly from the lateral surface of the premaxilla to the anterior edge of the premaxillary contribution to the narial spine. The posterior part of the ectonaris is formed by the nasal contribution to the narial spine, and the dorsal portion of the ectonaris is formed by the anteroventral surface of the nasal. EMK 0012 is missing a few millimeters of the contact between the dorsal portion of the premaxilla and the anterodorsal process of the nasal, but as in other centrosaurines, the ectonaris likely transitioned from the premaxilla directly onto the lateral edge of the anterior process of the nasal. The round overall shape of the ectonaris in *Lokiceratops* is similar to the condition in all centrosaurines and contrasts with the elongated, oval ectonaris in *Zuniceratops* and all chasmosaurines.

(INSERT FIGURE 7 HERE FULL PAGE WIDTH)

Endonaris—The external narial opening (Figure 7), or endonaris, is formed by the open space between the nascent narial flange along the posterior edge of the narial septum, the posteroventral process of the premaxilla, and the narial spine and anterodorsal process of the nasal. The endonaris forms an elliptical “B” shape in lateral view, with the long axis oriented roughly at 15° from vertical. The dorsal end of the ectonaris extends almost to the dorsal surface of the ectonaris similar to the condition in *Diabloceratops*. The endonaris forms about 35% of the area of the entire ectonaris. Within basal centrosaurines the endonaris of *Diablocertops* comprises around 45% of the ectonaris, compared to the condition in *Avaceratops lammersi*, *Nasutoceratops*, *Centrosaurus*, *Styracosaurus albertensis*, *Einiosaurus*, *Achaeolosaurus*, and the Iddsleigh pachyrhinosaur where the endonaris makes up only makes up 25% or less of the ectonaris (mainly because the endonaris is ventrally displaced from the dorsal premaxilla contact with the nasal in these specimens). In *Pachyrhinosaurus canadensis*, *P. lacustai*, and *P. perotorum*, the endonaris makes up less than 20% of the ectonaris.

Oral Vault—The anterior portion of the oral vault is formed in the ventral space between the ventral rami of the rostral and the cutting surface of the ventral premaxillae and is dorsally bound by the palatal shelf of the premaxilla (Figure 7). The posterior portion of the oral vault is formed between the tooth bearing portions of the maxillae and dorsally bounded by the vomers and palatines.

Buccal Vault—The medially inset tooth bearing portions of the maxillae presumably formed pouches for cheeks between the anterior maxillary diastema, the dorsal ridge confluent with the anterior process of the jugal, the lateral ridge of the dentary ventrally, and the coronoid process of the dentary and its’ adductor musculature posteriorly (Figure 7). It is likely that a “cheek” muscle M. pseudomasseter originated on the maxillary ridge and inserted on the lateral ridge of the dentary (Sereno et al., 2009). The buccal region is similar in all centrosaurines.

Coronoid Fossa—As in all other ceratopsids, the jugal is ventrolaterally expanded over the coronoid process of the mandible, creating a slot-like adductor chamber between the posterodorsal margin of the posterior process of the maxilla and the jugal. Here, the jugal bears a smooth fossa on its medial surface, extending dorsally to the ventral margin of the orbit and anterodorsally to a ridge separating it from the posterior lacrimal fossa (Figure 7). This fossa was presumably for accommodation of the coronoid process during occlusion and passage of adductor musculature inserting on the coronoid process of the mandible.

Antorbital Fenestra—As in other ceratopsids, the antorbital fenestra consists of a small, slot-like opening in the posterior rostrum, bordered anteriorly, anterodorsally, and ventrally by the maxilla, posteroventrally by the jugal, and posterodorsally by the lacrimal (Figure 7). A groove on the bifurcated ascending process of the maxilla, extending anteroventrally from the contacts for the anteroventral process of the jugal and the anteroventral margin of the lacrimal. The jugal may contribute to a small part of the posteroventral margin of the antorbital fenestra and then extends posterodorsally to form the base of the orbit. The small slit shaped nature of the antorbital fenestra is similar to the condition in all centrosaurines including *Diabloceratops*. *Lokiceratops* lacks the accessory antoribial fenestra between the premaxilla, nasal, and maxilla present in *Bagaceratops, Ajkaceratops, Zuniceratops,* and *Diabloceratops*.

Orbit—The external margins of the orbit are formed by the lacrimal and palpebral anteriorly, the jugal ventrally, and the postorbital dorsally and posteriorly (Figs. 3-7). The lacrimal and palpebral form the antorbital buttress of the anterior portion of the orbit, elevated substantially from the surface of the rostrum. The jugal and postorbital form the ventral and posterior portions of the orbit, with its rim being moderately expressed laterally. Dorsally, the postorbital ornamentation is confluent with the margin of the orbit. The overall shape of the orbit is round as in most centrosaurines, but in contrast with the ovoid orbit of some chasmosaurines. The orbits are parallel to each other and laterally directed, implying no overlapping field of vision. The parasphenoid would have been visible in the posterior part of the orbit. The orbit is~~n~~ similar to most centrosarines but differs from *Sinoceratops*, *Coronosaurus*, *Einiosaurus*, *Acheolosaurus*, the Iddsleigh pachyrhinosaur, and *Pachyrhinosaurus* in the presence of a well-developed antorbital buttress.

Adductor Chamber—The adductor chamber housed the jaw closing muscles that originate on the around the dorsotemporal fenestra, and pass deep to the laterotemporal fenestra and the ventral bar of the laterotemporal fenestra and the medial surface of the jugal to insert on the coronoid process of the dentary (Figure 7). This chamber, medial to the paroccipital groove on the squamosal housed the adductor muscles M. adductor mandibulae externus profundus and M. adductor mandibulae externus medialis (Holliday et al., 2019) which inserted on the coronoid process of the dentary. The adductor chamber is similar in all centrosaurines where it is visible (i.e. *Diabloceratops*, *Centrosaurus*, the Iddsleigh pachyrhinosaur, *Pachyrhinosaurus canadensis*).

Laterotemporal Fenestra—The laterotemporal fenestra (Figure 7) is ovoid, with its long axis oriented anteroventrally. The laterotemporal fenestra is bordered by the jugal and postorbital anteriorly, dorsally, and anteroventrally, and by the squamosal posteriorly and posteroventrally. While the anterior portion of the fenestra is not preserved in EMK 0012, its shape can be inferred from the shape of the jugals. Both squamosals preserve the articular facet at the posterodorsal corner of the fenestra for articulation to the posterodorsal process of the jugal. The left squamosal preserves the articulation for the posteroventral process of the jugal. The right lower bar of the laterotemporal fenestra preserves the tip of the posteroventral process of the jugal. The postorbital and quadratojugal are excluded from the laterotemporal fenestra as in all centrosaurines. The laterotemporal fenestra differs in shape across centrosauridae from subround in *Diabloceratops* to the anteroposteriorly elongate oval *in Lokiceratops*, *Albertaceratops*, *Centrosaurus*, *Styracosaurus albertensis*, to the tiny round opening in *Einiosaurus*, the Iddsleigh pachyrhinosaur, and *Pachyrhinosaurus lacustai.*

Dorsotemporal Fenestra—The dorsotemporal fenestra (Figure 7) is the dorsal opening in the skull posterior to the orbit, bordered by the parietal anteromedially and posteriorly, and by the squamosal laterally and anteriorly. In dorsal view, the dorsotemporal fenestra forms an elongated, ovoid slot bordered by the parietal medially and the squamosal laterally. Medially, a channel in the dorsal surface of the anterior parietal leads into the posterior chamber of the dorsocranial sinus, posterior to the frontal fontanelle. The dorsotemporal fenestrae of *Lokiceratops* are typical for

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Commented [DFP29]: How do you know this? It's not even half-completely preserved on either left or right sides (figs 12,13)?

Commented [DFP30]: Surely not possible to say as it is incomplete.

Commented [DFP31]: This isn't visible in the broken fossil. What is the point of saying it if it isn't observable in your material?

Commented [DFP32]: But you don't have this part of the jugals preserved, on either side?

Commented [DFP33]: Above you say "the laterotemporal fenestrae is bordered by the … postorbital"

Commented [DFP34]: You don't know this centrosaurines but are most similar in the shape of the stepped lateral margin to *Centrosaurus*, *Styracosaurus*, *Einiosaurus*, *Achelosaurus*, and *Pachyrhinosaurus*. The step is more pronounced than the low-step present in *Diabloceratops*, *Machairoceratops*, *Avaceratops*, and JRF 63 from the Judith River Formation of Malta, Montana.

Otic Notch—The otic notch is a restricted region bounded by the jugal/quadratojugal/quadrate complex anteriorly, by the jugal and squamosal portions of the ventral laterotemporal bar dorsally, and the expanding wing of the squamosal posteriorly (Figure 7). This space contained the external expression of the auditory meatus. The otic notch is unrestricted and triangular in protoceratopsids, *Diabloceratops*, and *Machairoceratops*. The otic notch is twice as anteroposteriorly long as dorsoventrally tall in *Lokiceratops* (best preserved on the left side) and rectangular, similar to *Styracosaurus albertensis*. The otic notch is sub-round and restricted in *Albertaceratops*, *Centrosaurus*, *Einiosaurus*, *Acheolosaurus*, the Iddsleigh pachyrhinosaur, *Pachyrhinosaurus canadensis* and *Pachyrhinosaurus lak~~e~~ustai*.

Internal Choanae—The internal choanae, or internal nares, are located on the posterodorsal region of the oral cavity, bounded by the maxilla and palatine laterally, the pterygoid posteriorly, and the premaxilla anteriorly. The chamber would have been partially divided by the vomers, though the vomers and palatines are not preserved in EMK 0012. Air entering from the external nares would have passed into the nasal vestibule, passing posteriorly into the nasal antrum, then entering the pharynx at the posterior end of the nasals along the pterygoids. This area is difficult to assess in many centrosaurine specimens but *Lokiceratops* seems to have had a similar expression of the internal choanae to *Centrosaurus*.

Foramen Magnum—The foramen magnum (FIGURE 15) in *Lokiceratops* is formed by the exoccipitals laterally and dorsally, and by the basioccipital ventrally. The supraoccipital is excluded from the WHAT? to the dorsal margin of the foramen magnum. The basioccipital makes up the entire ventral margin of the foramen magnum. This differs significantly from *Diabloceratops* (UMNH VP 16699), in which the exoccipitals exclude both the basioccipital and supraoccipital from the foramen magnum, but is similar to all other centrosaurines in which this region is preserved.

Cranial Pneumaticity

Dorsocranial Sinus—The postorbitals, frontals, and parietals are excavated the dorsocranial sinus (supracranial sinus of Farke, 2010), a presumably pneumatic system extending between the orbits and the base of the parietosquamosal frill (Figs. 3-7). Here, there is evidence of an anterior frontal fontanelle between the frontals and a posterior chamber formed between the frontals and the anterior end of the parietal. This complex includes the cornual diverticulae that excavate the bases of the postorbital horncores, connected to the dorsotemporal fenestra by the dorsotemporal channels in the anteriodorsal portion of the parietal. The complex is more pronounced than the condition present in *Centrosaurus apertus* (ROM 767) and *Styracosaurus albertensis* (ROM 1436). The pneumatic excavation extends into the entire base of the postorbital horncore.

Cornual Diverticulae—The cornual diverticulae (Farke, 2004) are a portion of the dorsocranial sinus that extends into the base of the postorbital horncores to a length twice that of the radius of the orbit, and extend more than 120 mm dorsally into the horns. Part of the ventral surfaces of the cornual diverticulae are preserved on the braincase and extended from the frontal fontanelle into the postorbital horncores. The condition in *Lokiceratops rangiformis* differs from *Diabloceratops eatoni* (UMNH VP 16699), *Machiroceratops cronusi* (UMNH VP 20550), and *Maltaceratops lokii* (WDCB 12 1CA 2), in which the diverticulae only shallowly excavate the

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Commented [DFP37]: If you had reconstructed the jugal differently, the Lokiceratops notch would look the same as Albertaceratops.

Commented [DFP38]: What does this mean? This entire paragraph is uninformative.

Commented [DFP39]: This is a lot of text considering all you have is a really small fragment of a postorbital-frontal (it's the tiny brown square at the bottom of figure 14). Morphology of the sinus in this fragment is impossible to assess since it isn't figured. However, it doesn't look like you really say anything here anyway. Delete.

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base of the horncores. The deeply excavated condition in *Lokiceratops rangiformis* is most closely approximated in the extended curved horns of *Diabloceratops eatoni* (UMNH VP 16800), excavated 106 mm into the base of the preserved horncore.

Frontal Fontanelle—The frontal fontanelle is a distinct midline opening between the frontals and lies just posterior to the base of the postorbital horncores (Figs. 3-7). The frontal fontanelle opens ventrally into the cornual diverticulae at the base of the horncores. In EMK 0012, the medial region of the frontal fontanelle and cornual diverticulae is crushed anteroposteriorly on the right horncore and dorsoventrally on the left horncore. Based on the edges of the crushed frontals, the frontal fontanelle in *Lokiceratops* is reconstructed as large and sub-circular. Much of the ventral floor of the frontal fontanelle is preserved on the braincase.

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Dorsotemporal Channels–The dorsotemporal channels (Farke, 2010) are smooth-floored grooves connecting the dorsotemporal fenestrae anteriorly to the posterior chamber of the dorsocranial sinus complex (Figs. 3-7). The right channel is partially preserved in EMK 0012. The smooth, wide channel floor is similar to the condition present in *Centrosaurus* (ROM 767).

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Parietal Channels–The parietal channels are a smooth, relative untextured area between the posteroventral edge of the laterotemporal fenestra that extend posteriorly to the anterior portion of the parietal fenestrae. The dorsotemporal channel exits laterally into this area and the parietal channel is bounded medially by the anterior portion of the midline parietal bar posterior to the dorsocranial sinus and laterally by the "step" at the lateral edge of the dorsotemporal fenestra (Figs. 3-7). The parietal channels are similar to those in all other centrosaurines.

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Dorsal Narial Sinus—The internal airway from the endonaris passes into two chambers posteriorly inside the snout, demarked by the narial ridge, a distinct horizontal line on the medial surface of each~~the~~ nasal (Figure 7). Multiple smaller ridges extend caudoventrally from the narial ridge, suggesting an attachment surface for soft tissues. This narial ridge is confluent with the nasal contribution to the narial spine and the dorsal narial sinus occurs dorsal to this feature. The dorsal narial sinus is triangular in *Lokiceratops* and more similar in shape to *Medusaceratops*, *Wendiceratops*, *Avaceratops* sp. MOR 692, and *Nasutoceratops*, than to elongate rectangular chamber in *Sinoceratops* (ZCDM V0010), *Coronosaurus* (TMP 2002.68.07) and *Centrosaurus* (TMP 93.36.117).

Ventral Narial Sinus—The ventral narial sinus extends below the narial ridge on the medial surface of the nasal onto the medial surfaces of the posterior process of the premaxilla, lacrimal, and dorsal surface of the maxilla and is floored by the vomers and palatines (Figure 7). The two narial sinuses may have been a single chamber with an "hourglass" or "8" shaped cross-section in anterior view. The shape of the ventral narial sinus in *Lokiceratops* resembles the shape in *Avaceratops* sp. MOR 692, *Nasutoceratops*, and *Centrosaurus*.

Commented [DFP43]: I rather suspect that a lot of this has to with taphohistory. Whether a specimen is preserved on its side, or disarticulated, or fragmentary. It isn't helpful to atomize a specimen into as many little features as you can – you do have to demonstrate that they have utility. Or something – I'm just not convinced by this at all. You're looking at, effectively, how triangular the snout is in the nasal area.

Anterior Lacrimal Fossa—Two chambers are associated with the posterior end of the ventral narial sinus on the medial surface of the lacrimal. The anterior lacrimal sinus is restricted to the medial surface of the lacrimal and is excluded from the posteromedial surface of the nasal (Figure 7). No distinct demarcation separates the anterior portion of this fossa and the posterior end of the ventral narial sinus. The anterior lacrimal fossa may be analogous to the pneumatic sinus in *Nasutoceratops titusi (*UMNH VP 19466) that invaginates the posterior portion of the nasal (Lund et al., 2016b), but there is no evidence for nasal pneumaticity in EMK 0012. The anterior lacrimal fossa in *Lokiceratops* is similar to the condition in *Avaceratops* sp. (MOR 692) in which it is subequal in size to the posterior lacrimal fossa. The anterior lacrimal fossa in EMK 0012 is much smaller than in *Sinoceratops zhuchengensis* (ZCDM V0010, ZCDM V0010); *Centrosaurus apertus* (ROM 43214) or the Iddesleigh pachyrhinosaur (TMP 2002.78.1).

Posterior Lacrimal Fossa—The posterior lacrimal fossa is located just ventral to the anterior border of the orbit and separated from the anterior lacrimal fossa by a thin posteroventrally oriented ridge (Figure 7). The posteroventral edge of the posterior lacrimal fossa extends ventrally onto the dorsal portion of the medial surface of the jugal. This fossa is separated from the adductor chamber by a medially directed fin of bone on the medial surface of the jugal. The posterior lacrimal fossa is oriented in line with the ascending ramus of the maxilla and resembles the posterior lacrimal fossa in *Avaceratops* sp. (MOR 692), *Sinoceratops zhuchengensis* (ZCDM V0010); *Centrosaurus apertus* (ROM 43214); the Iddesleigh pachyrhinosaur (TMP 2002.78.1); and *Pachyrhinosaurus lak~~e~~ustai* (TMP 89.55.1).

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Circumnarial Region

The narial region of *Lokiceratops rangiformis* (EMK 0012) closely resembles those of other centrosaurines in having a subcircular ectonaris with a well-developed premaxillary septum and a posteriorly positioned narial spine projecting into the endonaris produced by the premaxilla and nasal. The subtriangular rostral, the ventral angle of the ventral premaxilla, and the anterior edentulous section of the maxilla form the buccal cutting surface anterior to the maxillary teeth (Figs. 3-5,7-10).

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Rostral– The rostral is single median element that caps the premaxillae anteriorly. The overall surface texture of the anterior and lateral surfaces of the rostral is rugose with multiple elongate two to three mm wide channels and pits all roughly trending toward the anteroventral tip of the element. It is a tri-partite element in lateral view, with a squared anteroventral tip, two short posteroventral processes, and a tall dorsal process bordering the anteroventral margins of the premaxillae (Figs. 3-5,7-9). The posteroventral process is short, approximately one third the length of the dorsal process. In lateral view, the overall arcuate, concave posterior margin of the rostral is interrupted by a modest convexity positioned just ventral to the midpoint, dividing the posterior margin into two concave segments. In lateral view, the anterior margin of the rostral is nearly straight for approximately half of its ventral length before arcing dorsally along the premaxilla. The ventral margins of the rostral form sharp cutting edges, which converge anteriorly in a narrow arc. The rostral is triangular with a ventral process that is much shorter than the element height, morphologically similar to all centrosaurines including *Diabloceratops* (UMNH VP 16699), *Centrosaurus* (AMNH 5259), and *Pachyrhinosaurus* (CMN 9845), differing from the sub-equal dorsal and ventral processes of the rostrals of *Zuniceratops* (MSM P2101) and all known Chasmosaurinae.

Premaxillae– The majority of both premaxillae are preserved in EMK 0012 (Figs. 3-5,7-9), recovered in contact with each other, although slightly displaced, and fused to the rostral. As in other centrosaurines, the premaxilla is a crescentic element, consisting of a primary ventral body from which emanates a laminar anterior portion circumscribed by a thickened anterior and ventral margin, and a dorsally expanded posteroventral process. The laminar central portion, or premaxillary septum, is broad and smooth, forming the medial wall of the anterior narial fossa. The posterior half of the septum is marked with a moderately thickened and anterodorsally inclined nascent narial strut, itself bordered posteriorly by a laminar septal flange along the anterior border of the endonaris (narial fenestra).

Anterior to the nascent narial strut, smooth margins indicate the presence of an ovoid depression, or nascent narial fossa. Anteriorly and anteroventrally, the thickened rim of the premaxilla is sharply offset laterally from the smooth endonarial recess. Externally, the ridge contacts, and is tightly sutured to, the rostral. Anterodorsally, the thickened rim of the premaxilla forms the margin of the rostrum between the rostral and nasal. Here, it is relatively rugose, ornamented with deep fissures and grooves, possibly related to keratinous or adherent tissues between the keratinous coverings on the rostral and tissues on the smoother nasal.

As in all ceratopsids, the premaxillae are edentulous, and ventral surfaces of the premaxillae contribute to a posteroventral cutting surface. These surfaces form an inclined, beveled ventral edge, the caudal continuation of the cutting edges of the rostral, which terminates in a robust 'ventral angle' (Fig. 9). This ventral angle occludes with the angled lateral cutting surface of the predentary which is characteristic of centrosaurines. In lateral view, the ventral angle drops well below the ventral margin of maxillary tooth row, in contrast to the slightly developed ventral angle in *Diabloceratops* (UMNH VP 16699), but as in all other centrosaurines.

The posterior processes of the premaxillae diverge in ventral view (Fig.10). Posteriorly, the posteroventral process of the premaxilla meets the maxilla along a posterodorsally inclined suture, ascending dorsally to a laminar, externally exposed contribution to the narial spine. Dorsally, the nasal contacts the premaxilla to form the ventral portion of the narial spine, projecting anteriorly and lateral to the narial opening. Posteriorly, the dorsal portion of the posteroventral process meets the lacrimal along a dorsoventrally directed suture, excluding contact between the nasal and maxilla as in *Wendiceratops* (TMP 2014.029.0074), *Styracosaurus* (CMN 344) and *Achelousaurus* (MOR 591), and contrasting with the condition in *Diabloceratops* (UMNH VP 16699), *Centrosaurus* (AMNH 5259), and *Nasutoceratops* (UMNH VP 16800 and UMNH VP 19466.1). Both the nasal and the premaxilla contribute to a narial spine at the posterior edge of the ectonaris. Medially, the palatal processes of the premaxillae are not preserved but the broken edges of these platforms are preserved and form the demarcation between the buccal vault and the endonaris.

(INSERT FIGURE 10 HERE FULL PAGE WIDTH)

Maxillae— Both maxillae are preserved in *Lokiceratops* (EMK 0012), though the right maxilla is missing its teeth, and the left maxilla exhibits post-depositional plastic deformation (Figs. 3-5,7-10). The maxilla contacts the posteroventral surface of the premaxilla anteriorly, the nasal dorsally, the lacrimal posterodorsally and the jugal posteriorly. The palatine and ectopterygoid contact the maxilla medially. The maxilla is generally similar to other centrosaurines, being trapezoidal in shape, and nearly as tall dorsoventrally as long anteroposteriorly. It consists of a dentigerous horizontal ramus from which a bifurcating dorsal process emanates. The external surface of the horizontal ramus is moderately rugose, pierced obliquely by several foramina associated with anteroventrally directed neurovascular grooves. This ridge is inclined moderately anterodorsally in lateral view and curves laterally from the toothrow to the premaxillary shelf, for contact with the posterior occlusal surface of the premaxilla posterior to the ventral angle. A similar shelf occurs in *Diabloceratops*, *Nasutoceratops*, and *Wendiceratops*, but not in *Centrosaurus*. The "cheek" muscle, the M. pseudomasseter, likely originated on this shelf on the maxilla and inserted on the lateral ridge of the dentary lateral to the dentary tooth row (Sereno et al., 2009).

Medially, the maxillary cavity is a well-developed internal chamber formed largely within the medial surface of the ventral portion of the ascending maxillary ramus. The medial wall of this space is formed by the maxilla, palatine, and pterygoid, and the roof is formed by the lacrimal, palatine, and maxilla. The maxillary cavity, posited here to be of pneumatic origin and interconnected with the antorbital sinus, is distinct from the “intramaxillary sinus” of some basal neoceratopsians (e.g. *Bagaceratops*, *Protoceratops*). The maxillary cavity ~~forms~~ occurs within the body of the maxilla on the medial side and was likely sourced from above by the antorbital pneumatic system. The internal maxillary fossa is a broad, shallow trough that extends along the internal surface of the ascending maxillary ramus from the lacrimal posteriorly to the premaxilla anteriorly and is also bounded medially by the palatine. The interdental plate of the right maxilla is missing at the line of the dental foramina, the teeth are missing, and the toothrow is inset from the lateral surface of the maxilla, bearing 22 alveolar grooves and extending anteriorly to a short edentulous ridge.

Posteriorly, the toothrow continues along the maxillary body onto the posterior process, which bears the last five alveoli ventral to the anterior extension of the postmaxillary fenestra. The dorsal process is divided into a laminar anterodorsal portion and a robust posterodorsal portion by the antorbital fenestra and anteriorly extending, slot-like antorbital fossa. The anterior body and anterior edge of the anterodorsal process meet the premaxilla along a continuous, posterodorsally directed suture. The dorsal margin of the anterodorsal process forms the anteroposteriorly directed suture with the lacrimal. The posterodorsal process originates from the lateral body of the maxilla as a thickened, laterally expanded, posterodorsally inclined jugal ridge, passing below the antorbital fenestra to meet the anterior process of the jugal along a broad sutural surface. Laterally, the main body of the maxilla is medially inset from the ridge confluent with the anterior process of the jugal forming the buccal vault or “check space”. Internally, a vaulted oral cavity is outlined by a thin palatal process that extends anteriorly to form the medial portion of the premaxillary shelf (Figure 11). Posteriorly, the palatal process blends into the surface at the level of the suture for the palatine. This suture continues posteriorly onto the medial surface of the posterior ramus for contact with the pterygoid.

(INSERT FIGURE 11 HERE FULL PAGE WIDTH)

Nasal— The anterior portion right nasal is preserved in EMK 0012, broken just lateral to the midline suture with its counterpart (Figs. 3,4,7-11). Generally, the nasals form much of the proximodorsal rostrum anterior to the orbits and forms the dorsal and posterodorsal borders of the external nares. Anteriorly, the nasal forms the smooth, arcuate posterodorsal margin of the external nares, interrupted about halfway down its extent by the acute anterodorsal extension of the contribution of the nasal to the narial spine. The narial spine is a distinct bony process that extends from the posterior ectonarial margin anteromedially into the nasal vestibule. This process, a derived feature of Centrosaurinae, arises from the nasal but often includes a ventral contribution from the premaxilla. The narial spine occurs in conjunction with a bilateral narrowing of the nasal cavity, effectively forming an “hourglass” or “8” shaped opening (as viewed anteriorly) into the nasal cavity proper. Chasmosaurines exhibit a similar “pinching” of this portion the nasal cavity, associated with a medial thickening of the nasal that is likely homologous to the narial spine of centrosaurines. In centrosaurines, however, this process is distinct and projects anteriorly into the nasal vestibule.

Ventrally, the nasal meets the dorsal lamina of the posteroventral process of the premaxilla along an anteroventrally directed suture. The ventral margin of the nasal posterior to the premaxilla meets the anterior extent of the lacrimal, excluding contact with the anterodorsal portion of the dorsal process of the maxilla. Internally, the nasal is domed forming an~~d~~ internal nasal vault similar to the configuration in *Nasutoceratops* (UMNH VP 19466.1) but different from *Medusaceratops lokii* (WDCB-MC-001) in which the entire dorsal surface of the internal narial vault is flat from anterior to posterior. The narial ridge is an internal horizontal ridge that

Commented [DFP45]: If you put something in quotes, usually you reference whatever it is that you are quoting.

Commented [DFP46]: That’s not really the right language. I know it feels like a flowing river, but it isn’t one. Maybe “… has its origination in the antorbital…”

Commented [DFP47]: So what is the point of all this text? Is the narial spine preserved?

In a lot of these descriptive sections, there is a little introduction to general ceratopsid or centrosaurine morphology, then you describe specifically the Lokiceratops morphology.

Now, sometimes Lokiceratops actually doesn’t preserve much or any of the particular morphology being discussed, in which case, why include it in the paper? Other times (including here) you seem to start with this general introduction, then at some point you switch from generality into describing Lokiceratops specifically, but it isn’t made clear where this occurs.

Commented [DFP48]: Generally, or in Lokiceratops specifically?

Commented [DFP49]: This could also be preservational. I don’t know, I’m not very convinced by these sorts of characters.

extends from the nasal contribution of the narial spine posteriorly along the medial surface of the preserved right nasal (Fig. 11). Multiple smaller ridges extend posteroventrally from the narial ridge, suggestive of an attachment surface for soft tissues. Even though the dorsocranial sinus complex is more extensive in *Lokiceratops* than any other centrosaurine, there is no indication of pneumatic chambers in the posterodorsal region of the nasal as seen in *Nasutoceratops* (UMNH VP 16800 and UMNH VP 19466.1).

No evidence of nasal ornamentation is visible. The convex lateral external surface is moderately ornamented with deep, branching neurovascular grooves and a generally rough, interwoven texture. This texture is similar those present on the dorsal surfaces of the lacrimals, squamosals, and parietals, but unlike the texture of the postorbital horncores. There is no change in nasal surface texture from the ventral surface of the nasal to the dorsal surface. The anterior process of the nasal lacks the rugosity present on the dorsal surface of the premaxilla or the rostral just anterior to the dorsal surface of the premaxilla. There is no evidence that the nasal ornamentation formed a pachyostotic boss as in pachyrhinosaurs that appear in the sediments along the northeastern coast of Laramidia at least three million years later (Sampson, 1995). This evidence, in addition to the overall shape of the preserved dorsal margin and the preserved surface texture on the dorsolateral surface, strongly indicates an absence of nasal ornamentation in *Lokiceratops*, differentiating it from the well-developed nasal horns in *Albertaceratops, Medusaceratops*, and *Wendiceratops*. *Zuniceratops* also lacks nasal ornamentation and *Diabloceratops* has a very limited nasal ornamentation.

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Commented [DFP51]: What is the texture of the nose horns of Medusa and Alberta? How does it compare?

Commented [DFP52]: I’m skeptical. It’s not strong evidence because you lack the essential area of the bone. And besides, the nasal horns in Alberta and Medusa are really not extensive. Medusa is a small bump; Alberta is weak too.

Commented [DFP53]: That’s pretty generous – Medusa and Alberta have really small nasal horns, bumps really.

Circumorbital Region

The circumorbital region in *Lokiceratops rangiformis* (EMK 0012) closely resembles those of most basal centrosaurines in having orbits with dorsally elongated postorbital horns and a well-developed antorbital buttress formed by the prefrontal, palpebral and lacrimal. Formed by the jugal and quadratojugal, the suborbital region is as in all other centrosaurines (Figs. 12-13).

(INSERT FIGURE 12 HERE FULL PAGE WIDTH)

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Lacrimal— Portions of both lacrimals are preserved *in Lokiceratops* (EMK 0012), the right consisting of most of the circumorbital region and a portion of the anterodorsal region tightly sutured to the right nasal, the left consisting of most of the posterior half of the element including the circumorbital region (Figs. 3-5,7-9,11-13). The lacrimal contacts the nasal and premaxilla anteriorly, the maxilla and jugal ventrally, the prefrontal and palpebral dorsally. The lacrimal forms the anteroventral portion of the orbit below the palpebral and above the jugal. Overall, the lacrimal is a laminar, anteroventrally oriented element that contributes to the lateral surface of the posterior region of the rostrum, contacting the dorsal portion of the posteroventral process of the premaxilla anteriorly, the anterodorsal portion of the dorsal process of the maxilla anteroventrally, the nasal anterodorsally, the prefrontal dorsally, and the jugal posteroventrally. Sutures with the nasal are not visible in external or internal surface view, though sutures with the maxilla, premaxilla, and jugal indicate that the main axis of the lacrimal was oriented anteroventrally. The lacrimal contributes to the ventral half of the anterior margin of the orbital opening, contributing a moderately elevated rim ventrally. Dorsally, the ventral half of the palpebral is sutured to the external surface of the lacrimal to form the pronouncedly robust anterior rim of the orbital opening. Internally, the surface of the lacrimal is excavated the anterior and posterior lacrimal fossae (Fig. 7) bounded by sharply pinched crests.

Jugal— Sections of both jugals are preserved in *Lokiceratops* (EMK 0012), each consisting of portions of the orbital margin and the ventral complex with the epijugal and quadratojugal (Figs. 3-5,7-9,11-13). As in other ceratopsids, the jugal of *Lokiceratops* is a tripartite, laminar element, consisting of an anterior process that would have contacted the lacrimal and maxilla, a posterior process contacting the postorbital and squamosal, and a ventral process contacting the quadratojugal and hornlike epijugal. The jugal forms the ventral margin of the orbit and contributes to the dorsal, anterior, and ventral margins of the lateral temporal fenestra, though the latter two portions are not preserved in EMK 0012. Anteriorly, the jugal contact with the maxilla is preserved on the posterodorsal portion of the dorsal process of the maxillae where it transitions into the lateral ridge of the maxilla. The suture with the lacrimal is likely preserved on the left side of EMK 0012, though the surface evidence for the suture is not visible. Posteriorly, the jugal is deeply inset into the anterior lamina of the squamosal along a deeply anastomosing suture, extending posterodorsaly from the posterolateral margin of the lateral temporal fenestra to a sharp point, then along an anterodorally directed suture to the posterior margin of the orbit. The external surface of the jugal is moderately rugose, ornamented with shallow neurovascular grooves. The dorsal contribution to the orbital margin is elevated as a subtle rim, ornamented with deeper grooves radiating from the orbit. Ventrally, the jugal terminates as a triangular process, its anteroventral margin forming the lateral margin of the entrance to the coronoid fossa for reception of the coronoid process of the occluded mandible and associated musculature. At the ventral and posterior portions of the ventral process, the jugal is tightly sutured to the quadratojugal in an overlapping scarf joint, the jugal laterally overlapping the posteriorly exposed quadratojugal. Both the jugal and quadratojugal contribute equally to the suture for the laterally directed epijugal horn. Internally, a rounded crest extends anteroventrally from the posteroventral margin of the orbit to the posterodorsal portion of the dorsal process of the maxilla, creating a continuous boundary between the posterior lacrimal fossa and the posterior, internal smooth surface of the coronoid fossa (Figure 7).

Epijugal— Both epijugals are preserved in ~~*Lokiceratops* (~~EMK 0012~~)~~ and form short, laterally directed epijugal horns (Figs. 3-5,7-13). The quadratojugal sits on both the jugal and quadratojugal laterally. Overall, the epijugal horns extend ~~seven~~ 7 cm laterally from the jugal surface and are triangular in cross-section, with a slight anteriorly directed flat facet. The external surface of the epijugal horn is ornamented with deep laterally directed grooves and pits with an overall rugose texture indicative of a keratinous covering.

Quadratojugal— The left quadratojugal is preserved and visible in ~~*Lokiceratops* (~~EMK 0012~~)~~ articulated onto the jugal (Figs. 10-13). In general form, the quadratojugal is a laminar, triangular element with a thickened ventral process and thin anterior lamina. As in other ceratopsids, the quadratojugal is mediolaterally compressed between the ventral process of the jugal and the lateral articulation with the quadrate. The anterior lamina medially underlaps the jugal in a broad scarf joint, thinning to an anteriorly convex termination on the posteromedial half of the jugal. Ventrally, the quadratojugal thickens to form a robust contribution to the suture for the epijugal horn laterally and a broad butt suture with the distal quadrate medially, a small ventral projection of the quadratojugal extending beyond the epijugal to cover the lateral quadrate. The posteroventral margin of the quadratojugal forms the free border of the skull in lateral view, overlapping the lateral margin of the quadrate. Dorsally, it would have extended to meet the squamosal, contributing to the strut posterior to the lateral temporal fenestra.

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Commented [DFP55]: So… if a bone is absent because it is broken off or lost due to taphonomy or preservation, then you should use the specimen number. If you are describing the morphology or lack of a bone (e.g. nose horn) in the taxon, then use the taxon.

Palpebral— Both palpebral elements are preserved in *Lokiceratops* as ovoid protrusions tightly sutured to the anterior margins of the orbits (Figs. 12-13). In overall shape, the palpebral is blocky, steep sided, and forms the main portion of the antorbital buttress ventral to the postorbital horn. Even though we consider this individual to be of adult maturity, based on many other osteological criteria, the palpebral sutural lines are visible where it contacts the prefrontal and lacrimal, over which it sutures.

Prefrontal—Both prefrontals are preserved in *Lokiceratops* (EMK 0012), the left as a fragmentary portion firmly sutured to the medial surface of the palpebral, the right as a moderately larger portion sutured to the postorbital and medial to the palpebral (Figs. 3-5,11-13). The prefrontal forms the dorsal half of the anterior orbital margin where it is entirely covered by the palpebral. Dorsally, the prefrontal is firmly sutured to the postorbital ventral to the postorbital horn. The prefrontal meets the nasal anteriorly and the frontal medially. The prefrontals are medial to the palpebrals and form the anterodorsal part of the internal orbit between the postorbital dorsally and the lacrimal anteroventrally. The prefrontals also form part of the antorbital buttress and contacts the nasal anteriorly, and the lacrimal ventrally.

Frontal— Only small fragments of the frontals are preserved in ~~*Lokiceratops* (~~EMK 0012), fused indistinguishably to the medial portions of the postorbitals on the dorsal skull roof and on the dorsal surface of the braincase. One large portion, fused to the posterior lamina of the right postorbital, preserves a portion of the lateral margin of the frontal fontanelle. The frontal would have contacted the nasal and prefrontal anteriorly, the postorbital laterally, and the parietal posteriorly. Internally, the frontals are deeply excavated by pneumatic recesses associated with internal pneumatic tissues continuous into the postorbital and the frontal fontanelle (described above).

Postorbital— Both postorbitals are preserved in ~~*Lokiceratops* (~~EMK 0012), forming distinctive, elongate horns over the orbits, and contributing to the dorsal and posterior margins of the orbit (Figs. 3-5,7,11-13). Each postorbital is moderately distorted by crushing, largely effecting the morphology of the horns. The left is compressed dorsoventrally and the right is compressed mediolaterally. In overall form, the postorbital of Lokiceratops is similar to other ceratopsids with elongate postorbital horns, including centrosaurines like *Albertaceratops, Wendiceratops, Nasutoceratops, Avaceratops*, and *Diabloceratops*, with a laterally facing orbital portion, a distinct postorbital horncore, and a broad posterior lamina. The orbital portion of the postorbital meets the prefrontal and frontal anteriorly and is laterally capped by the dorsal extent of the palpebral. Posteroventrally, the postorbital meets the jugal at the midpoint of the orbital wall. Dorsally, the orbital portion of the postorbital is continuous with the lateral surface of the postorbital horn, its surface textured with distinct grooves and rugosity. The postorbital horn projects anterolaterally with a moderate ventral curvature in anterior view. Though both postorbital horns are crushed, the postorbital horn would have been subcircular to elliptical in cross section, tapering gradually distally to a rounded point. The external surface of the postorbital horn is ornamented with deep longitudinal grooves and an overall rugose texture indicative of a keratinous covering. Posteriorly, the dorsal surface of the horn is continuous with the posterior lamina, a rugose, dorsally convex extension of the postorbital that meets the frontal and parietal medially, the squamosal posterolaterally, and the jugal laterally. Unlike in many other centrosaurines, the postorbital is deeply excavated internally by pneumatic recesses, with a deep pneumatic recess extending distally over 120 mm into each postorbital horncore.

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Parietosquamosal Frill

The parietosquamosal frill of *Lokiceratops* closely resembles those of other basal centrosaurines in having crescentic, fan-shaped squamosals and an elongated asymmetrical frill as in *Diaboloceratops*, *Albertaceratops*, and *Medusaceratops* and differs from the rounder parietals in *Avaceratops*, *Nasutoceratops*, *Wendiceratops*, and *Sinoceratops*. The main differences in the frill of *Lokiceratops* and other centrosaurines is in its seven epiparietal ornamentations and their orientations (Figs. 3-5,6,11,14).

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Squamosal—Both squamosals are preserved in *Lokiceratops*, with the left squamosal nearly complete (Figs. 3-5,7,11,14). As in other ceratopsids, the squamosal can be divided into a distally expanding posterior process contributing to the formation of the anterolateral frill, an anteroventrally directed temporal process, and a broad, sheet-like anterior blade. The squamosal contacts the jugal anteroventral and anterodorsal to the laterotemporal fenestra, the postorbital dorsally, and the parietal posteriorly. Medially, at the point where the three processes of the squamosal converge, the squamosal contacts the quadrate anteroventally and the paroccipital process of the otoccipital along an arcuate suture. From this point anteriorly, the temporal and anterior processes diverge around the laterotemporal fenestra, forming its posteroventral and posterior borders. At the posterodorsal margin of the laterotemporal fenestra, the suture for the posterodorsal ramus of the jugal is present as a shallow, tapering groove. Dorsal to the jugal suture, the anterior process contacts the posterior extent of the postorbital along an anastomosing scarf joint, the squamosal passing deep to the postorbital. The squamosal forms the anterolateral boarder of the dorsotemporal fenestra and anteriorly contacts the parietal lateral to the dorsotemporal channels. Overall, the posterior process of the squamosal forms the “fan-shaped” sub-rectangular blade of the anterolateral portion of the frill. The “fan-shape” of this blade expands from a constricted otic notch ventrally. The anterior blade and temporal processes of the squamosal are subequal in length and are demarked by a distinct stepped-up margin at the lateralmost portion of the laterotemporal fenestra. This pronounced “step” is a continuation of the ventrally positioned, perpendicularly oriented, paroccipital groove on the dorsal surface. The dorsal surface of the anterior squamosal blade lacks a prominent rounded ridge or a sharp peaked ridge. The ventral surface of the squamosal has a medial suture for the quadrate on the tip of the anteroventral temporal process, and a subtriangular facet for the medial wing of the quadrate anterolateral to a “slot-like” facet or groove for the lateral paroccipital process of the exoccipital. Part of this quadrate wing scar is the likely origin site for the jaw opening muscle the M. depressor mandibulae (Sereno et al., 2009). Anteromedial to the paraoccipital groove is the smooth adductor chamber that housed M. adductor mandibulae externus profundus, and M. adductor mandibulae externus medialis (Holliday et al., 2019).

The dorsal surface texture of the squamosal transitions from a more heavily rugose texture at the anterodorsal contact with the postorbital to a rugose texture with a number of other variably inscribed vascular grooves on the dorsal surface of the squamosal, most originating from points adjacent to the preserved anterior and anteromedial margins. Overall, the dorsal surface texture is heavily rugose and covered by numerous fine pits that characterize adult centrosaurines (see below). Ventrally, the squamosal is thickened through the contacts for the quadrate and the exoccipital flange. The ventral surface is generally smooth and gently concave. Ventrally a thin groove traces the medialmost margins of the episquamosals, but this arcuate line does not follow the crenulations of each episquamosal.

The squamosal differs from the elongated, “sickle-shaped” form of chasmosaurines; the rectangular shape of *Protoceratops andrewsi*, *Diabloceratops eatoni* (UMNH VP 16699), and *Machairoceratops cronusi* (UMNH VP 20550). The “fan-shaped” subtriangular form of the lateral squamosal in *Lokiceratops* conforms to the general morphology of other centrosaurines (e.g. *Yehuecauhceratops mudei*, *Crittendenceratops krzyzanowskii*, *Menefeeceratops sealeyi*, *Nasutoceratops titusi*, *Avaceratops lammersi*, *Albertaceratops nesmoi*, *Medusaceratops lokii*, *Wendiceratops pinhornensis*, *Coronaceratops brinkmani*, *Spinops sternbergorum*, *Centrosaurus apertus*, *Sytracosaurus albertensis*, and *Pachyrhinosaurus lakustai* [see Maiorino et al., 2013]). The restricted otic notch is similar to the condition where present in all centrosaurines except *Diabloceratops eatoni*, and *Machairoceratops cronusi.*

We recognize two conditions regarding the nature of the step associated with the dorsotemporal fenestra in centrosaurines. There is both an anteroposterior and dorsoventral nature to this stepped-up suture which has been long recognized (Dodson, 1986; Sampson, 1995; Sampson et al., 2013). We recognize a “step” as being present when the lateral portion of the squamosal forming the lateral border of the dorsotemporal fenestra extends farther posteriorly than the area just posterior to the dorsotemporal fenestra. We quantify the step as being “slightly-stepped” when the posterior extension laterally is less than the dorsoventral thickness of the dorsotemporal fenestra but more than in chasmosaurines. We recognize a “slightly-stepped” parietosquamosal suture in *Protoceratops andrewsi*, *Diabloceratops eatoni*, *Machairoceratops cronusi*, *Menefeeceratops sealeyi*, *Xenoceratops formostensis*, *Nasutoceratops titusi*, and *Avaceratops lammersi*. *Crittendenceratops krzyzanowskii*, *Albertaceratops nesmoi*, *Medusaceratops lokii*, *Wendiceratops pinhornensis*, *Coronaceratops brinkmani*, *Spinops sternbergorum*, *Centrosaurus apertus*, *Sytracosaurus albertensis*, and *Pachyrhinosaurus lakustai* all have a large-stepped parieosquamosal suture with lateral posterior expansion greater than the anteroposterior thickness of the parietosquamosal suture.

The dorsal surface of the lateral squamosal blade *Lokiceratops* lacks the prominent rounded ridge that is typical for basal centrosaurines, such as *Avaceratops*, *Albertaceratops*, and *Wendiceratops*. This is the same ridge that forms a peaked ridge in *Nasutoceratops.* It also lacks the more ventrally placed pronounced dorsal otic ridge present in *Menefeeceratops sealeyi*, *Crittendenceratops krzyzanowskii*, and *Yehuecauhceratops mudei.*

Parietal—As in all other ceratopsids, the parietal is an unpaired median element. Representative parts of the parietal are preserved in *Lokiceratops* including all of the lateral left portion, most of the lateral right portion, most of the midline bar, parts of the parietal between the dorsotemporal fenestra, part of the right dorsotemporal channel and part of the proximal (anterior) right portion bordering the frontal fontanelle (Figs. 3-5,7,14). The parietal contacts the frontal anteriorly, the postorbital anterolaterally, a small portion of the squamosal at the anteromedial corner of the dorsotemporal fenestra, and the squamosal lateral to the dorsotemporal fenestra. The suture between the parietal and squamosal lateral to the dorsotemporal fenestra is visible on both sides but the right side preserves the posterior portion of the squamosal fused to it. The parietal forms the ventral floor of the dorsotemporal fenestra medial to the adductor chamber on the ventral squamosal. Both parietals are fused at the midline and the overall shape of the parietal is probably elongated rather than round with the widest part of the parietal excluding epiparietals is at the anterolateral contact with the squamosal. The midline bar is broad and rounded dorsally in transverse section with a lenticular transverse cross-section. A distinct medial embayment separates the epiparietal positions ep1 from each other. The posteriormost extent of each parietal is at the suture at the base of each ep2. The overall parietal has a slightly concave dorsal surface when viewed laterally and a gently convex when viewed posteriorly. Much of the borders of the parietal fenestra are preserved indicating a posteriorly elongate shape that is 348 mm long by 160 mm wide on the left side and 340 mm long by 185 mm wide on the right side.

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The dorsal surface texture of the parietal is heavily rugose with lightly-to-deeply inscribed vascular grooves (many oriented longitudinally), and numerous fine pits that are characteristic of adult centrosaurines (see below). The broad midline bar exhibits the most rugose surface texture compared to the lateral and transvers bars. The ventral surface also relatively rugose with many vascular grooves. The texture of the area around the parietal fenestrae is smooth and continuous with the dorsal floor of the dorsotemporal fenestrae anteriorly and the dorsotemporal channels medially.

Epiossifications of the Frill—The left side of the frill of *Lokiceratops* preserves a full complement of three epiossifications on the squamosal and seven epiossifications on the parietal (Figs. 3-5,12). The right side of the frill preserves two epiossifications (the section where es1 should be is missing, and there is space for three positions in life) on the squamosal and six epiossifications on the parietal (ep3 is interpreted as missing).

The left squamosal has three episquamosals on the margin of the posterior (distal) process. Each is low and crescentic. The proximal most episquamosal es3 is 123 mm long and one cm to its apex on the dorsal surface and six cm to its apex on the ventral surface, es2 is 106 mm long by one cm wide to its apex on the dorsal surface and four cm to its apex on the ventral surface, and the distalmost episquamosal es1 is cm long by one cm wide to its apex on the dorsal surface and three cm to its apex on the ventral surface. The right squamosal preserves es3 and half of es2. Es3 is 113 mm long by four cm wide on the dorsal surface and five cm to its apex on the ventral surface, es2 is 102 mm long. All of the episquamosals are completely fused to the margin of the squamosal. Each of the episquamosals is directed in the general plane of the frill, but the ventral edge of the squamosal is slightly curved and the episquamosals are positioned more on the edge of the squamosal, are barely distinguished from the squamosal on the dorsal surface. and are much better demarked on the ventral surface, suggesting that part of the episquamosal is wrapping ventrally onto the ventral surface of the squamosal. The episquamosals are faintly imbricated with the posterior edge each episquamosal more dorsally positioned than the anterior edge of eposquamosals in the distalmost episquamosals es1 and es2.

There is no evidence of the presence of an epiparietosquamosal on either side of the frill of *Lokiceratops*. The anterior edge of ep7 barely touches the parietosquamosal suture but does not cross the suture. *Machairoceratops* and *Medusaceratops* also lack evidence of an epiparietosquamosal. An epiparietosquamosal occurs in *Diabloceratops*, *Avaceratops*, *Xenoceratops*, *Wendiceratops*, *Centrosaurus*, *Styracosaurus*, *Stellasaurus*, *Einiosaurus*, and *Pachyrhinosaurus lakustai*.

The left parietal preserves seven epiparietals and the right parietal preserves a total of six epiparietals. The lateral edge preserving 5 epiparietals (ep3 through ep7) on the left side of the frill is subequal in length to that preserving 4 epiparietals on the left side, presenting some uncertainty whether the right ep3 is missing or whether there are only six epiparietals on the right side of the frill. In this alternate interpretation, the relatively long right ep4 is represented on the left side as the smaller ep3 and ep4 ossifications, a level of bilateral variability not uncommon in ceratopsids (e.g., *Styracosaurus* UALVP 55900 [Holmes et al., 2020]). Since the left parietal is complete from the parietosquamosal suture to the posterior midline embayment, we reconstruct both sides to have the seven epiparietal positions preserved on the left parietal. The following description of individual epiparietals assumes that the right ep3 is missing.

Lokiceratops lacks a midline epiparietal (ep0). On the left parietal, ep1 is an uncurved, posteriorly directed epiossification directed in the plane of the parietal along the posterior margin of parietosquamosal frill. The apex of ep1 is broken, and it likely extended longer that the preserved epiossification. Ep1 is 110 mm wide at the base, 132 mm long from the base of the epiossification to its preserved apex on the dorsal surface of the frill, and 164 mm long on the ventral surface of the frill. The surface of ep1 is moderately rugose, ornamented with shallow

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Commented [DFP60]: Is ep3 on the left side of parietal not possibly a part of ep2, just broken? It is an odd shape, and it does look like part of the base of ep2 is missing.

neurovascular grooves. In contrast, the right ep1 is complete and much smaller measuring 53 mm wide at the base, 67 mm long from the base of the epiossification to its preserved apex on the dorsal surface of the frill and eight cm long on the ventral surface of the frill.

Each ep2 forms a large blade-like ornamentation solidly fused into the posterior surface of the parietal. Both ep2 blades are oriented in the plane of the frill and extend posterolaterally. The right ep2 is complete and extends over 518 mm in curvilinear length, with a base that forms 310 mm of the posterior portion of the frill. The right ep3 is 142 mm wide at its narrowest point about midway along blade of ep3. The left ep2 is incomplete distally and what is preserved extends over 284 mm in curvilinear length and 265 mm of the posterior portion of the frill along its proximal base. The right ep3 is 142 mm wide at its narrowest point about midway along blade of ep3. The maximum thickness of the blade of ep3 is 47 mm.

Epiparietal ep3 is preserved on the left side of the frill and forms a laterally elongated triangular spike oriented in the plane of the frill. The distal tip is broken. Ep3 is 54 mm wide at the base, 92 mm long from the base of the epiossification to its preserved apex on the dorsal surface of the frill and 108 mm long on the ventral surface of the frill.

Epiparietal ep4 is preserved on both sides of the frill and forms a moderately elongated triangular spike. It differs from all subsequent epiparietals which are more typical in shape to those of other general proximal epiparietals in centrosaurines. The distal tip is broken on the left ep4. The left ep4 is 81 mm wide at the base, is 116 mm long from the base of the epiossification to its preserved apex on the dorsal surface of the frill, is 64 mm long on the ventral surface of the frill and is oriented in the plane of the frill. The right ep4 is complete. The right ep4 is 104 mm wide at the base, 52 mm long from the base of the epiossification to its preserved apex on the dorsal surface of the frill and 101 mm long on the ventral surface of the frill. The right ep4 is distinctly oriented posteriorly and is not in the plane of the frill. The asymmetry between left and right may indicate that the right side only had 6 epiparietals, but given the asymmetry seen in ep1, position ep4 may just be variable.

Epiparietal ep5 is preserved on both sides of the frill and forms a ~~generally~~ crescentic shape common in centrosaurines. Generally, ep5 is oriented laterally in the plane of the frill although it is imbricated. The left ep5 is 84 mm wide at the base, is 46 mm long from the base of the epiossification to its preserved apex on the dorsal surface of the frill, is 59 mm long on the ventral surface of the frill and is oriented in the plane of the frill. The right ep5 is 93 mm wide at the base, 46 mm long from the base of the epiossification to its preserved apex on the dorsal surface of the frill and 59 mm long on the ventral surface of the frill.

Epiparietal ep6 is preserved on both sides of the frill and forms a ~~generally~~ crescentic shape common in centrosaurines. Generally, ep6 is oriented laterally in the plane of the frill although it is imbricated. The left ep6 is 59 mm wide at the base, is 37 mm long from the base of the epiossification to its preserved apex on the dorsal surface of the frill, is 24 mm long on the ventral surface of the frill and is oriented in the plane of the frill. The right ep6 is 65 mm wide at the base, 43 mm long from the base of the epiossification to its preserved apex on the dorsal surface of the frill and 43 mm long on the ventral surface of the frill.

Epiparietal ep7 is preserved on both sides of the frill, is ~~and forms a generally~~ crescentic in shape ~~common in centrosaurines~~, and~~. Epiparietal ep7~~ is oriented laterally in the plane of the frill although it is imbricated. The left ep7 is 62 mm wide at the base, is 31 mm long from the base of the epiossification to its preserved apex on the dorsal surface of the frill, is 37 mm long on the ventral surface of the frill, and is oriented in the plane of the frill. The right ep7 is 72 mm wide at the base, 28 mm long from the base of the epiossification to its preserved apex on the

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dorsal surface of the frill and 35 mm long on the ventral surface of the frill. The epiparietals are faintly imbricated with the posterior edge of each epiparietal more dorsally positioned than the anterior edge of epiparietal in positions ep3 through ep7.

The surface texture of the epiparietals ep1 and ep2 exhibit a heavily rugose texture with pits and a number of lightly-to-deeply inscribed grooves. Epiparietal ep3 has a series of grooves that follow the long axis of the epiparietal. Epiparietals ep4-ep7 are textured with rugose pits similar to other centrosaurines. Epiparietal ep7 on the left side has a deep pit in the ventral surface which could be pathologic.

Lokiceratops lacks the midline parietal epiossification (ep0) present in *Avaceratops*, *Nasutoceratops*, and *Sinoceratops*. The presence of seven epiossification loci in *Lokiceratops* is only shared with the basal centrosaurines *Diabloceratops*, and *Nasutoceratops*. *Machairoceratops* has 1 epiparietal. *Avaceratops* and *Wendiceratops* have 4 epiparietals. *Albertaceratops* and *Medusaceratops* have 5 epiparietals. *Xenoceratops*, *Sinoceratops* and *Coronoceratops* have 6 epiparietals. We interpret the more derived centrosaurines *Styracosaurus ovatus*, *Einiosaurus*, *Achelousaurus*, *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus perotorum*, and *Pachyrhinosaurus lakustai* to subsequently have lost position ep1, which independently moved to the dorsum of the frill in *Spinops* and *Centrosaurus*. This would indicate that at least *Einiosaurus*, *Achelousaurus*, *Pachyrhinosaurus canadensis*, and *Pachyrhinosaurus lakustai* had an epiparietal in the equivalent position as ep7 even though these animals only have 6 total epiparietals (Clayton et al., 2009).

Commented [DFP64]: Do you really think that the large banana-like ep2 of Lokiceratops and Medusaceratops is not homologous with the banana-like ep1 of Albertaceratops (as in your figure 21)? Is it not more likely that the more medial ep1 in Alberta is perhaps small, crushed, or enveloped by ep2? In Medusaceratops the ep1 is a barely discernible bump – it would be no surprise if this were overlooked of overgrown in the laterally crushed Albertacertops holotype.

The shape of the epiparietals in *Lokicertops* is distinct from the patterns present in other centrosaurines. Blade-like epiparietals are present in *Xenoceratops*, *Albertaceratops*, *Medusaceratops*, *Wendiceratops*, and *Sinoceratops*. Large, blade-like epiparietals at position ep2 are present in *Xenoceratops*, *Medusaceratops*, *Wendiceratops*, and *Sinoceratops* but not in *Albertaceratops*. Blade-like epiparietals at position ep2 that are oriented in the plane of the frill are present in *Xenoceratops* and *Medusaceratops*, but not in *Wendiceratops*, and *Sinoceratops* but not in *Albertaceratops*. Elongated spikes at ep1 position distinguish *Lokiceratops* from *Medusaceratops*, and their orientation in the plane of the frill differentiates *Lokiceratops* from *Wendiceratops*.

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Many centrosaurines exhibit asymmetry from side to side in epiparietal number and morphology, similar to the differences in cervids (Ditchkoff and deFreese 2010) and specifically caribou (Miller, 1986). The extreme asymmetry is ep1 and ep2 in *Lokiceratops* is unusually pronounced when compared to other centrosaurines such as *Coronoceratops brinkmani*, *Centrosaurus Styracosaurus albertensis*, *Einiosaurus procurvicornis*, and *Pachyrhinosaurus lakustai*. Without additional material it is impossible to determine if this asymmetry is characteristic of *Lokiceratops* or if it the degree of asymmetry varies within the species or across ontogeny.

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Additional Cranial Elements

Braincase—Much of the braincase is preserved in *Lokiceratops* (EMK 0012), including the basioccipital, exoccipitals, prootics, and laterosphenoids, though sutures between preserved elements are largely obliterated and distal extremities of most elements are missing (Figs. 10, 15). As in other ceratopsids, the basioccipital contributes to the floor of the braincase anteriorly, and the spherical occipital condyle posteriorly. The occipital condyle is externally smooth, offset from the main braincase by a narrowed neck. Dorsally, the exoccipitals are tightly fused to the neck of the basioccipital on each side of the posterodorsally open foramen magnum, though the exoccipitals do

Commented [DFP67]: They are in all ceratopsids. Do you really need to say this?

not appear to contribute to the formation of the articular surface of the occipital condyle, terminating at the raised border of the articular surface. Ventrally, the tubera of the basioccipital are not entirely preserved in EMK 0012, though the dorsal portions indicate their presence in *Lokiceratops*. The exoccipitals meet dorsal to the foramen magnum to complete its external borders. Laterally, the paroccipital processes are missing, though their contacts with the squamosals laterally indicate that they would have been similar in morphology to other ceratopsids. The ventral portion of the supraoccipital sits on the midline dorsal to the exoccipitals, preserving the ventral base of a wide, midline crest separating two nuchal fossae. Though the left side is badly crushed, the right side of the braincase is largely intact, consisting of the prootic posteriorly and the laterosphenoid anteriorly, and preserving the external exits for the cranial nerves. A deep fenestra ovalis is the most conspicuous opening into the braincase on this side. The dorsal contact between the braincase and the parietals is incomplete. Anteriorly, the braincase would have contacted the postorbitals dorsolaterally, and the frontals dorsally.

(INSERT FIGURE 14 HERE FULL PAGE WIDTH)

Pterygoid— The left pterygoid of *Lokiceratops* was discovered in the quarry (Figs. 10, 15). The palatine contacts the quadrate laterally and the palatines medially. The eustachian canal is present on the medial surface as in *Avaceratops lammersi* (Penkalski & Dodson, 1999). The pterygoid is missing part of the quadrate wing that articulates with the medial wing of the quadrate. The eustachian canal is kinked halfway along its length. The ascending process is mostly preserved where the pterygoids meet alongside the palatines medially. At the anterior end of the element is the process that touches the medial posterior surface of the maxilla, and the angle between this and the quadrate process forms the beginning of the eustachian canal. The medial surface of this maxillary process has an articular surface for the palatine that is interrupted by a smoother surface interpreted as the pterygopalatine foramen as in *Triceratops horridus* (YPM 1821, Hatcher et al., 1907). The surfaces for articulation with the basisphenoid process is damaged. Overall, the pterygoid is similar to that of *Diabloceratops eatoni* (UMNH VP 16699), *Avaceratops lammersi* (TMP 1989.55.249, Currie et al., 3008), *Centrosaurus apertus* (ROM 767, 43219), and *Pachyrhinosaurus lakustai* (TMP 1989.55.249; Currie et al., 3008).

Commented [DFP68]: Awkward wording. Where else would it be?

Quadrate—The right quadrate of *Lokiceratops* was discovered in the quarry but was not delivered with the specimen when it was acquired by EMK. We describe it based on a photo reposited at the EMK that was taken in the quarry. The quadrate is similar to all known quadrates in centrosaurine ceratopsids. The quadrate has an elongate shaft that is straight in lateral view with a convex anterior surface and a concave posterior surface. Two ventral condyles would have articulated with the articular on the mandible. The medial condyle extends further ventrally than the lateral condyle. The lateral surface has a scar for the articulation of the quadratojugal that spans from just dorsal to the lateral condyle to most of the height of the element. A medial wing preserves part of the contact with the pterygoid.

Commented [DFP69]: Presumably lost? You should say so if so.

Dentition—The left maxilla of *Lokiceratops* preserves teeth (Fig. 8,10-12,16). The teeth are similar to those of other ceratopsids with a wear facet on the lingual surface of the most erupted teeth. Unworn teeth are leaf-shaped with enamel present on the labial surface. Each unworn tooth preserves a central ridge on the labial surface that leads to the apex of each tooth with two or three secondary ridges anterior and posterior to this central ridge. Each tooth has 15 to 20 denticles on each side of the central ridge.

(INSERT FIGURE 16 HERE FULL PAGE WIDTH)

General Description of the Axial Skeleton

Posterior Cervical Vertebrae—A posterior cervical vertebrae is preserved in *Lokiceratops* (Fig. 17), likely Ce8 or Ce9 based on its overall morphology. This vertebra is post-depositionally deformed, but several morphologic characters can be distinguished in this element. The anterior and posterior faces of the centrum are roughly amphiplatyan and the anteroposterior length of the centrum is about one third the height of the centrum. The neural arch and the right transverse process is preserved but the neural spine is missing. The neural canal is about one third of the height of the centrum alone. The prezygapophyses and postzygaphophyses are located above the neural canal. The prezygaphophyses are directed dorsomedially and the articular facets of the postzygaphophyses are directed ventrolaterally. The parapophysis (the articular facet for the capitulum of the rib) is preserved on both sides at the base of the neural spine. The diapophysis is preserved on the left neural arch, near the lateral extent of the transverse process. The transverse process is roughly horizontal. There is some indication that the neural spine would have been posteriorly inclined. Part of the cervical rib is fused to the right side of the centrum, ventral to the parapophysis. The position of the parapophysis is similar to the position on the neural canal in *Styracosaurus albertensis* (CMN 344) for cervical ce9 or possibly ce8 (Holmes et al., 2005). *Lokiceratops* differs in the horizontal angle of the transverse process compared to the 40-degree angle present in the posterior cervicals of *Styracosaurus albertensis*.

(INSERT FIGURE 16 HERE FULL PAGE WIDTH)

Synsacral Dorsosacral Vertebrae—The centrum of the penultimate posterior dorsal vertebrae (ds1) is partially preserved and fused in the ultimate posterior dorsal vertebrae (ds2) within the fused synsacrum of *Lokiceratops* (Fig. 17). The dorsal extent of the neural spines was lost in excavation. The transverse processes of the ultimate posterior dorsal sd2 extend towards each ilium but do not extend to the ilia. The lateral extent of the transverse process is unclear as they are broken, but there is a lack of clear evidence of contact for this on the left ilium. The anteroposterior width of the transverse process is narrower than the s1-s4 sacral ribs and the transverse processes of sc1-3. The centra of both posterior dorsal vertebrae are oval in anterior view, but this is likely due to post-depostional deformation. The ventral surface of the penultimate posterior dorsal is poorly preserved. The ventral surface of the ultimate posterior dorsal is flat and lacks the ventral groove that begins just posterior to it on sacral vertebrae s1.

Synsacrum—A synsacrum is preserved in *Lokiceratops* (Fig. 17) and includes a total of ten vertebral centra fused together along with the neural spine of an eleventh (an anterior caudal). These eleven vertebrae include co-opted posterior dorsal vertebrae, true sacral vertebrae and anterior caudal vertebrae. We interpret the presence of four true sacrals as seen in basal ornithischians (Marsh, 1891a; Butler et al., 2008; Maidment & Barrett 2011).

We consider, as do others (Hatcher, 1907; Marsh, 1891a), the first two vertebrae in the synsacrum that lack sacral ribs to be posterior dorsal vertebrae here referred to as sacrodorsals sd1 and sd2. The subsequent seven centra are coossified with the ilia via sacral ribs and transverse processes. The first four of these vertebrae support the acetabulum with both ventral and dorsal connections connected by a subvertical lamina that are interpreted as sacral ribs. Sacrals s1 through s4 show evidence of co-ossified neural spines most of which were destroyed during excavation.

Four anterior caudal centra (sacrocaudals sc1-sc4) are fused to the true sacral vertebrae and a fused neural spine indicates the presence of a fifth sacrocaudal sc5 that was lost in excavation. Caudosacrals cs1-cs5 have distinct, flat-topped fused neural spines that continue as a unit across the five vertebrae. A distinct ventral groove occupies the ventral surfaces of the s1 through sc3. The ventral surfaces of sd1, sd2, sc4 and sc5 are not preserved.

The sacral ribs are fused between the sacral centra s1-s4, and transverse processes from sacrocaudals sc1-sc3 are fused to and both ilia producing a set of six oval sacral foramina on either side of the centra and medial to the ilia. The sacral ribs of the four sacral vertebrae have a dorsal and ventral component forming an "I-beam" shape in sagittal cross-section as the horizontal dorsal and ventral surfaces are connected by a subvertical sheet of bone. The dorsal surfaces of the sacral ribs are oriented posterior to the ventral surfaces, so that the ovals 2-6 between the ribs are positioned more posteriorly on the dorsal surface than on the ventral surface. Sacral ribs sr1 and sr2 are the widest anterorposteriorly on the dorsal surface compared to the subsequent sacral ribs. Ventrally, only sacral rib sr1 is considerably wider anterorposteriorly than the subsequent sacral ribs.

Synsacral Sacrocaudal Vertebrae—Four anterior caudal centra (sacrocaudals sc1-sc4) are fused to the true sacral vertebrae in *Lokiceratops* (Fig. 17) and a fused neural spine indicates the presence of a fifth sacrocaudal sc5 that was lost in excavation (see above). The transverse processes on sacrocaudal sc1-sc4 are fused to the posterior blade of the ilia. These have only a flat ventral surface (lacking the dorsal surface of the true sacral ribs) with a vertical lamina of bone dorsally forming an overall inverted "T-shape" in sagittal cross-section.

Free Proximal Caudal Vertebrae—*Lokiceratops* preserves a free anterior caudal vertebra from the proximal portion of the tail (Fig. 17). It has a round centrum that is 15 cm tall and 10 cm wide. The centrum is 3 cm wide anteroposteriorly, but the vertebrae is anteroposterally compressed by post-depositional plastic deformation. The anterior face of the centrum is slightly higher than the ventral face and both surfaces are amphiplatyan. There are lateral transverse processes on each side at about 60% up the side of the centrum. The transverse processes are 5 cm long on the left side and 7 cm long on the right side. Both transverse processes project laterally with only a slight ventral cant in orientation. The neural canal is round and two centimeters tall. The prezygapophyses jut forward just above the neural canal and the postzygapophyses tilt backwards on the back of the neural spine above the position of the prezygapophysis. The neural spine is 15 cm tall and two cm wide laterally. The neural spine is slightly posteriorly oriented and originates on the anterior half of the centrum. There is a groove on the anterior surface of the neural spine ostensibly for interosseus ligaments. A corresponding groove on the posterior surface presumably for the same purpose extends only from between the postzygapophyses to halfway up the posterior surface. In anterior view, the neural spine is generally two cm wide with a dorsal expansion to a width of three cm. Caudally, a facet for the chevrons occurs both anteriorly and posteriorly, with the anterior facet being twice as pronounced as the posterior facet and corresponding to the shape of the articular surfaces of the chevrons (see below).

Commented [DFP70]: Is this a feature of the taxon, or do you mean: "we found a caudal vertebra"

Proximal Chevron—A single chevron is preserved in *Lokiceratops* (Fig. 17). It is "V-shaped" in anterior and posterior view with no curvature laterally. It is ten centimeters long and relatively robust. It is interpreted as pertaining to the proximal third of the tail. The overall shape in lateral view has a slight anterior facet for the preceding caudal centrum and an expanded posterior tab dorsally that forms the articular surface of the subsequent caudal centrum. The ventral shaft is straight and tapers ventrally with no curvature in lateral view. The overall shape of the chevron is similar to the conformation in *Styracosaurus albertensis* (CMN 344) with no curvature or distal expansion.

Appendicular Skeleton

Lokiceratops preserves some postcranial elements, and all are comparatively similar to most known centrosaurine ceratopsids. Postcranial elements are poorly described for centrosaurines in general, with in-depth comprehensive skeletal descriptions confined to

Commented [DFP71]: What does this mean?

Centrosaurus apertus (YPM 2015; Lull, 1933) and *Styracosaurus albertensis* (CMN 344; Holmes & Ryan 2013). *Nasutoceratops titusi* (UMNH VP 16800) and *Wendiceratops pinhornensis* have some postcranial elements that have been described (Lund et al., 2016b; Evans & Ryan 2016). Other taxa *Medusaceratops lokii*, *Coronosaurus brinkmani*, and *Pachyrhinosaurus lacaustai* preserve postcrania, but these presently lack description.

Coracoid—The right coracoid is preserved in *Lokiceratops*. (Fig 18). The element is fused to the scapula with the suture running perpendicular to the overall trend of the scapular blade with the scapula forming more than half of the glenoid. The suture is thickened mediolaterally producing a change in angle from the scapula to the concave lateral surface of the coracoid. The coracoid has an arcuate overall shape from the anterior surface to the dorsal most point where it sutures to the scapula. The concave lateral surface lacks the anterolateral ridge near the confluence of anterior and ventral margins present in psittacosaurs. There is an anteroventral hook formed anterior to, and ventral to the glenoid fossa. The coracoid contributes to roughly one third of the glenoid along with the scapula. The coracoid foramen is anterior to the scapular suture and dorsal to the anterior end of the glenoid. The coracoid foramen pierces the element from medial to lateral. The entire anterior and dorsal surface of the coracoid preserves a one-centimeter rim with rugosity that is possibly for the insertion of *M. scapulocoracoideus* similar to other ornithischian dinosaurs (Maid~~e~~ment & Barrett 2011; Fearon & Varricchio 2014; Słowiak, 2019). This rugosity continues onto to acromion on the scapula posteriorly. There is a scar anterior to the coracoid foramen on the concave lateral surface that is the origin of *M. biceps*. There is depression on the ventrolateral surface of the anteroventral hook for the origin of *M. coracobrachialis brevis*. The medial surface of the coracoid is flat with some post depositional crushing. The anterior surface rugosity is pronounced on the medial surface as well. This may indicate that the whole anterior surface supported the insertion of *M. scapulocoracoideus* or it could simply represent intercoracoid ligaments. The overall medial surface of the coracoid was flat and the insertion surface for *M. subcoracoideus*.

(INSERT FIGURE 18 HERE FULL PAGE WIDTH)

Scapula—The right scapula is preserved in *Lokiceratops* and is fused to the coracoid (Fig 18). Dorsally the scapula and coracoid are medially concave, but the degree of curvature of the element as it conformed to the chest cavity is unknown as the element has been post-depositionally flattened~~ after burial~~. The overall shaft of the scapula is straight. The anterior portion of the scapula includes the suture with the coracoid that is perpendicular to the overall element above the glenoid fossa. The anterior portion is waisted just anterior to the midpoint of the element and expands anteriorly to the glenoid ventrally and towards the coracoid dorsally, this point is often referred to as the acromion. The dorsal surface from the acromion forward and continuing along to the anterior surface of the coracoid are insertions for *M. deltoideus clavicularis* and *M. supracoracoideus* but it is unclear where one ends, and the other begins. The posterior portion of the scapular blade expands distally but is not “paddle-shaped” and the distal end is “squared off”. The scapula contributes around two-thirds to the overall glenoid fossa. This is consistent with all ceratopsid dinosaurs, in which the dominant element in the glenoid is the scapula when compared to basal ornithischians. The overall glenoid is ventrolaterally directed as in all marginocephalians. The lateral shaft exhibits a scapular spine, a distinct ridge that runs from glenoid anteriorly that angles across the shaft to the dorsal surface posteriorly. The oblique orientation of the scapular spine is similar to the condition in all ceratopsids except *Torosaurus* and *Triceratops*. The scapular spine marks the separation between the origins of *M. deltoideus scapularis* and M. teres major. The ventral surface of the scapular blade ventral to the scapular spine and posterior to the major origin scar just posterior to the glenoid ridge for *M. triceps longus* is the origin for *M. scapulohumeralis caudalis*. There is a ventrolaterally directed flange on the anter~~i~~o~~r~~lateral surface of this flange that has a distinct muscle scar for the origin of *M. triceps longus*. The medial surface of the scapula exhibits some post-~~-~~depositional crushing on the proximal shaft, but the overall medial surface was flat for the insertion of *M. subscapularis*.

Ilia—Both ilia are preserved in *Lokiceratops* as part of the fused pelvis (Fig 19). The pubes and ischia were not fused into the pelvis. The right ilium is missing its anterior blade. The left ilium is complete, with a horizontally positioned anterior blade; a postacetabular lateral expansion; and a vertically oriented posterior blade. The acetabulum is positioned anteriorly on the synsacrum between sacral vertebrae s1-s3. The pubic peduncle is centered on sacral rib sr1 and the ischial peduncle is centered between sacral vertebrae and ribs sr3 and sr4. The ischial peduncle is round and is about the size of the midsacral centra in dimension. The lateral expansion of the ilium is centered on the centrum of sc1 and the posterior blade begins at this position and extends to the midcentrum of sc5.

(INSERT FIGURE 19 HERE FULL PAGE WIDTH)

Ischia—Both ischia are preserved in *Lokiceratops* (Fig 19). The right ischium was found in close association to the pelvis (Fig. 2). The shafts of both ischia are gently curved overall in a ventrally concave manner, and both are distinctly kinked about two-thirds of the length the shaft distally where the two ischia contact each other medially. Proximally the shaft is rounded and transitions to mediolaterally flattened paddle-shape distally. The ischia of *Lokiceratops* shares the rounded, flattened, paddle-shape of its distal end with *Zuniceratops* (MSM P2107 expands to a paddle-shape but is distally incomplete) and definitively with *Wendiceratops* (TMP 2011.051.0037 originally misinterpreted as right ischium with a rectangular distal end [Evans & Ryan 2015; see Scott et al., 2022]). Both of *Lokiceratops* and *Wendiceratops* differ in the overall amount of dorsal curvature in the shaft (excluding the distal kink in *Lokiceratops*) when compared to the more strongly ventrally curved ischia in *Zuniceratops* and all other known centrosaurines *Medusaceratop~~o~~s*, *Wendiceratops*, *Centrosaurus*, *Styracosaurus*, the Iddesleigh pachyrhinosaur, and *Pachyrhinosaurus lak~~e~~ustai*. Both *Lokiceratops* and *Wendiceratops* differ in their paddle-shaped distal end, compared to *Medusaceratop~~o~~s lokii* (WDCB-MC-001; FDMJ-V-10); *Centrosaurus apertus* (YPM 2015); and *Styracosaurus albertensis* (CMN 344) which have a pointed distal end that twists and shifts to an anteroposteriorally or dorsoventrally compressed tab and compared to the rounded, but not mediolaterally compressed distal ends in the Iddesleigh pachyrhinosaur (TMP 2002.76.1) and *Pachyrhinosaurus lak~~e~~ustai*. The distinct kink two-thirds of the way along the shaft on the ischia of *Lokiceratops* differ from the gently curved overall shape of the ischia in *Zuniceratops* (MSM P2107) and all known centrosaurines *Medusacertop~~o~~s*, *Wendiceratops*, *Centrosaurus*, *Styracosaurus*, the Iddesleigh pachyrhinosaur, and *Pachyrhinosaurus lackustai*

Ontogenetic Assessment

Aside from the fact that *Lokiceratops* (EMK 0012), at almost two meters long, is one of the absolutely largest centrosaurine specimens in existence, many features of the skull also confirm its maturity. The rostral is completely fused to the premaxillae, ~~compared to the situation~~whereas in juvenile specimens and many subadult ceratopsian specimens ~~in which~~ these elements are unfused or connected through a visible suture (Goodwin & Horner 2008; Kirkland & DeBlieux 2010). The sutures between the nasal, prefrontal, and lacrimal are completely obliterated, indicating skeletal maturity. These elements are unfused in juvenile subadult and specimens of both chasmosaurines and centrosaurines (Sampson et al., 1997; Goodwin et al., 2006; Goodwin & Horner 2008). Similarly, the sutures between the prefrontal, frontal,

Commented [DFP72]: Presumably you mean the skull alone postorbital, squamosal, and parietal are completely obliterated and covered with deep rugosities along the dorsum of the skull around the dorsocranial complex. Interestingly, while both palpebrals are fused to the lacrimals, the prefrontals, and the postorbitals preserve the sutures between each of these elements similar to the condition in juvenile centrosaurines (Dodson, 1990) and a juvenile chasmosaurine from the Dinosaur Park Formation (Currie et al., 2016).

Fusion of epiossifications also suggests maturity in *Lokiceratops* (EMK0012). Epiossification fusion and development can also be used to assess relative maturity (Sampson et al., 1997). Both epijugals are securely fused onto the jugals compared to the unfused situation in juvenile and many subadult ceratopsid specimens (Goodwin & Horner, 2008; Currie et al., 2008; Kirkland & DeBlieux, 2010). Epiossifications fuse from the posterior margin of the parietosquamosal frill anteriorly (Sampson et al., ~~(~~1997). Episquamosal fusion occurs only in the most mature individuals (Frederickson & Tumarkin-Deratzin 2014). The episquamosals are completely fused to the squamosals in EMK0012 and are only readily discernable from the blade of the squamosal posteriorly. All of the epiparietals are securely fused to the parietal with little indication of these being separate ossifications as seen in immature subadult specimens of more derived centrosaurines (e.g. *Centrosaurus*, *Styracosaurus*, *Einiosaurus* [Sampson et al., 1997]) and in chasmosaurines (Goodwin & Horner, 2008; Mallon et al., 2015; Currie et al., 2016). In EMK 0012, all of the epiparietals and episquamosals are present and indistinguishably fused at their respective loci. The epiossifications on the parietals of EMK0012 exhibit the subtle imbrication along their lateral margins, characteristic of adult centrosaurines that have this feature (Sampson et al., 1997).

Commented [DFP73]: Check this? In Triceratops and chasmosaurs, the anterior episquamosals fuse before the posterior episquamosals. Epiparietals can vary a bit in when they fuse, depending on the specific taxon.

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The degree of epiparietal development is variable on specimens with mottled texture that is typically associated with sub-adult individuals (Brown et al., 2009). More mature specimens exhibit a more pronounced epiparietal ornamentation (Sampson et al., 1997). The hypertrophied epiparietal ornamentation of *Lokiceratops* is also indicative of skeletal maturity. *Lokiceratops* possesses the most massive, blade-like epiparietals of any ceratopsian. These hypertrophied epiparietal ornaments ~~in *Lokiceratops*~~ resemble~~s~~ those of the basal centrosaurines *Medusaceratops* and *Albertacertatops* (considered to be mature), and the pattern seen in adult specimens of more derived centrosaurines (e.g. *Centrosaurus*, *Coronosaurus*, *Styracosaurus*, *Einiosaurus* [Sampson et al., 1997; Frederickson & Tumarkin-Deratzian 2014]).

The available postcranial elements of *Lokiceratops* (EMK0012) also indicate a high degree of skeletal maturity. The two preserved vertebrae of EMK0012 exhibit complete fusion between the centrum and the neural arch which is associated with skeletal maturity (Brochu, 1996; Irmis, 2007). The scapula and coracoid of EMK0012 are firmly fused together, compared with some juvenile ceratopsians (Słowiak et al., 2019).

The surface textures of cranial elements *Lokiceratops* (EMK0012) also exhibit evidence of maturity. Almost without exception, smaller elements of dinosaurs exhibit the characteristic striated periosteal surface bone texture typical of many other juvenile archosaurs (Bennett, 1993; Sampson et al., 1997; Carr, 1999). Juvenile bone is characterized by extremely thin, parallel ridges and grooves that are generally aligned parallel the long axis of the bone or in the direction of greatest growth. The striations are presumably attributable to rapid bone growth in juvenile animals. This pattern is also present on craniofacial elements of theropods such as maxillae, jugals, quadratojugals, and dentaries; forelimb elements such as scapulae, coracoids, humeri, radii, and ulnae; and hindlimb elements such as the pubes, ischia, femora, tibiae, fibulae, and metatarsals (Carr, 1999; Claessens & Loewen 2016; Cunningham et al., 2019). Larger elements possess a variety of textures, from rugose to mottled to smooth, all markedly distinct from the

Commented [DFP75]: There should be a reference for this if you or your coauthors know of one striated pattern of juvenile bone. Elements that fall between these sizes exhibit a mosaic between juvenile and adult patterns. These data are consistent with those noted independently in pterosaurs (Bennett, 1993) and in ceratopsians (Sampson et al., 1997). Bone surface texture varies ontogenetically on the parietosquamosal frill of numerous centrosaurines in which there is a range of sizes and has been established as an indicator of the relative maturity in the group (Sampson et al., 1997; Brown et al., 2009). This is most pronounced on the dorsal surface of the parietal posterior to the parietal fenestrae. Juvenile specimens exhibit a distinctive striated bone surface texture, whereas the largest individuals with fully developed epiparietal ornamentation completely lack this texture, exhibiting a non-porous woven bone surface texture associated with deep rugosities and well-defined vascular channels on the parietal. The parietals of subadults parietals exhibit a “mottled” transitional texture characterized by fine pitting on the bone surface and a lack of striations that characterize long-grained texture (Brown et al., 2009). EMK 0012 completely lacks any trace of striated or mottled surface texture, and exhibits only adult surface texture, suggesting that the specimen represents a somatically mature individual. This independent method of assessing relative age of specimens is consistent with the fusion of cranial elements (Sampson et al., 1997) and the degree of closure of the neurocentral sutures (Brochu, 1996; Irmis, 2007). Together, these features indicate that the holotype of *Lokiceratops rangiformis* represents an adult individual with fully developed ornamentation and can therefore be confidently diagnosed and placed in a phylogenetic analysis.

Phylogenetic Analysis

In order to formulate hypotheses of the phylogenetic relationships of *Lokiceratops rangiformis* relative to other centrosaurine ceratopsid dinosaurs, a phylogenetic analysis using cladistic parsimony was employed. The analysis comprised 86 taxa and 377 characters (263 cranial, 61 postcranial, and 53 concerning frill-based ornamentation). Characters 354-377 are scored across Chasmosaurinae and Centrosaurinae and assuming modified epiparietal homologies first proposed by Clayton et al (2009; 2010). Further discussions of this are part of a forthcoming paper. Age ranges for each taxon were taken from the literature and where possible updated to the latest calibrations. For the sources of age control for taxa see Supplemental Table S1. See Supplemental Data File (SD3 for characters used in the phylogenetic analysis, and Supplemental Data Files SD4 and SD5 for taxon scorings.

Numerous features indicate that *Lokiceratops rangiformis* was a member of the clade Centrosaurinae; therefore, selection of ingroup taxa and characters focused on this clade. Most described ceratopsid species, and several currently unnamed taxa, were included in the analysis, for a total of 27 centrosaurines, and 19 chasmosaurines.

To ensure proper character polarization and determine the position of Ceratopsidae within Ceratopsia, we sampled widely across both psittacosaur and non-ceratopsid ceratopsians. The neornithischian *Hypsilophodon foxi* was constrained as the outgroup because it is a proximate sister group of Ornithopoda and is known from nearly complete remains. Three pachycephalosaurs were included in the analysis to polarize some characters. Characters used in the analysis (SD2) were partially derived from the previous, ever-evolving data matrix initiated by Scott Sampson and Cathy Forster in the 1990’s and further fleshed out by Mark Loewen and Andrew Farke during the 2000’s and 2010’s (Loewen et al., 2010; Sampson et al., 2010; Farke et al., 2011; Knapp et al., 2018). In addition to adding several new characters and character states, close attention was paid to existing character definitions; a significant number of characters from previous analyses were deleted, combined, or otherwise revised with an eye toward improving clarity and anatomical precision.

The original character-taxon matrix was assembled in Microsoft Excel (Office Professional Plus 2019 [Supplemental Data File SD4]) imported into Mesquite v. 3.70 (Maddison and Maddison 2021) and is freely available as a NEXUS text file in Supplemental Data File SD5. The final dataset was analyzed using TNT v. 1.6 (Goloboff et al., 2008; Goloboff and Catalano 2016). Tree searching followed the parsimony criterion implemented under the heuristic search option using tree bisection and reconnection (TBR) with 10,000 random addition sequence replicates, up to 10,000 trees saved per replication, and zero length branches collapsed if they lacked support under any of the most parsimonious reconstructions. All characters were equally weighted. Characters 1, 51, 70, 126, 130, 144, 170, 261, 262, 279, 336, and 339 represent nested sets of homologies and/or entail presence and absence information. These characters were set as additive (also marked as ORDERED in highlighted bold text following character description [see Supplemental Data File SD2]). 288 most-parsimonious trees were found; we report the strict consensus of these trees here (Fig. 20; see also Supplemental Figures S1-S5 for relationships of all Ceratopsia). Tree statistics were calculated using TNT. Bootstrap proportions were calculated using 10,000 bootstrap replicates with 10 random addition sequence replicates for each bootstrap replicate.

(INSERT FIGURE 19 HERE FULL PAGE WIDTH)

With the inclusion of all 86 taxa, the analysis recovered 288 most parsimonious trees with a length of 928 steps, consistency index (CI) of 0.474, and retention index (RI) of 0.898 (Figure 20; Supplemental Figure S1,S2,S5). With the exclusion of the fragmentary taxon *Crittendenceratops krzyzanowskii*, the analysis recovered 180 most parsimonious trees with a length of 921 steps, CI=0.471, and RI=0.896. With the exclusion of the fragmentary taxa *Menefeeceratops sealeyi*, *Yehuecauhceratops mudei*, and *Crittendenceratops krzyzanowskii* the analysis recovered 60 most parsimonious trees with a length of 920 steps, CI=0.475, and RI=0.898. When analyzed with only the 27 centrosaurines and setting *Hypsilophodon foxi* as the outgroup taxon the analysis recovered 16 most parsimonious trees with a length of 364 steps, CI=1.201, and RI=1.015. When analyzed with only the 27 centrosaurines and setting *Protoceratops andrewsi* as the outgroup taxon the analysis recovered 64 most parsimonious trees with a length of 315 steps, CI=1.387, and RI=1.026. The strict consensus tree for all of these analyses is the same (Figure 20; Supplemental Figures S3-S5).

Lokiceratops rangiformis is found to be a centrosaurine ceratopsid based, in part, on the presence of a round ectonaris on the premaxilla, a fan-shaped squamosal, large flattened, bladelike epiparietals, as well as the high number (>6) of epiparietals on each side (Characters 57, 64, 66). *Lokiceratops rangiformis* is recovered as the sister taxon to *Albertaceratops nesmoi* and *Medusaceratops lokii*, and all three form the clade Albertaceratopsini. This grouping is supported by two synapomorphies; character 127, a circular or oval rather than narrow and slit-like frontoparietal fontanelle; and character 357, epiparietal 1 oriented in the plane of the frill in lateral view (note that this is a local synapomorphy, found in other clades within Centrosaurinae also); The decay index (1) and bootstrap support (<50%) for the relationships within Albertaceratopsini are low, although we note that low branch support is unsurprising—in this analysis: the confidently established clade Centrosaurinae itself has a decay index of only 2 and bootstrap support <50 percent.

Commented [DFP76]: Is this observable in EMK 0012?

This phylogeny is broadly consistent with recent phylogenies of Centrosaurinae in several aspects, such as the content of Eucentrosaura (sensu Chiba et al., 2017; seen also in Wilson et al., 2020), a monophyletic Nasutoceratopsini (sensu Ryan et al., 2016; Chiba et al., 2017; Wilson et al., 2020), and the positions of *Diabloceratops* and *Machairoceratops* as sister to most/all other Centrosaurinae (e.g. Chiba et al., 2017; Wilson et al., 2020; but note variabilities in the latter analysis for parsimony versus Bayesian methods). Variation in the positions of taxa such as *Xenoceratops*, Nasutoceratopsini, *Medusaceratops*, *Albertaceratops*, *Sinoceratops*, and *Wendiceratops* across various studies reflect missing data and likely high levels of homoplasy.

DISCUSSION

Kennedy Coulee Ceratopsid Diversity

The Milk River border region of southern-most Alberta and northernmost Montana, centered on Kennedy Coulee, provides a uniquely fossiliferous window into the lower Judith River Formation dinosaur assemblage. A single, narrow stratigraphic interval within this region preserves up to five distinct ceratopsid taxa consisting of four centrosaurines (*Albertaceratops nesmoi*, *Lokiceratops rangiformis*, *Medusaceratops lokii*, and *Wendiceratops pinhornensis*) and the putative chasmosaurine *Judiceratops tigris*. Given the rapid turnover of megaherbivorous assemblages documented in other deposits of northern Laramadia (e.g., Mallon et al. 2019), this stratigraphic interval, dated to approximately 78 Ma, is currently one of the only windows into this interval in northern Laramidia, possibly synchronous or parasynchronous with the fossils from the Two Medicine Formation of Montana (Varicchio et al., 2010) and Unit 1 of the Oldman Formation in southern Alberta (Eberth, 2005). In southern Laramidia, synchronous or parasynchronous intervals are useful for latitudinal comparisons of assemblages include the Upper Shale of the Aguja Formation of West Texas (Lehman et al., 2017) and the upper Pardner Canyon Member of the Wahweap Formation of southern Utah (Beveridge et al., 2021).

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Commented [DFP77]: This is controversial, see main review

Commented [DFP78]: Which part of the 2med? The 2med covers a very long stretch of time, basically the duration of the entire Judith River Wedge deposition, in fact longer.

Given the significance of this interval, the emerging picture of high ceratopsid diversity in the Kennedy Coulee area requires reassessment of materials previously assigned to chasmosaurine *Judiceratops tigris*, an early form based on four fragmentary cranial specimens (YPM VPPU 022404, 02341, 023261, and 023262) collected in the same region (Longrich, 2013; Campbell, 2015). The holotype of *Judiceratops tigris*, YPM VPPU 022404, consists of postorbital horncores, fragments identified as portions of a right squamosal, and a partial posterior parietal bar. Given that all four centrosaurine taxa from the Kennedy Coulee region also possess elongate postorbital horncores, the horncores alone cannot be unequivocally diagnosed as either chasmosaurine or centrosaurine.

Commented [DFP79]: It's not diversity unless the species are contemporaneous. Sampling an anagenetic lineage at different points does not constitute diversity. You need to demonstrate that part first.

The partial posterior parietal of YPM VPPU 022404 is morphologically more consistent with Centrosaurinae than Chasmosaurinae in its overall shape (rounded, extending anteriorly, well past the posterolateral corner) and its number of epiparietal positions (more than 4). In fact, the holotype parietal more closely resembles the parietal of *Wendiceratops* in having a wide posterior margin with a very weak medial embayment. Marginal parietal rugosities, interpreted as fused, low and broad epiparietals (Longrich, 2013) may in fact represent attachment sites for unfused epiparietals leaving open the possibility for dorsally curving epiparietals as in *Wendiceratops*.

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Commented [DFP80]: The pieces don't click together so the shape in the reconstruction is basically fanciful. I was always surprised that it was published.

Fragments of YPM VPPU 022404 identified as belonging to the right squamosal (Longrich, 2013; Campbell, 2015) cannot definitively be distinguished between a portion of squamosal or the anterior portion of a parietal bar. Intriguingly, one section assigned to the right squamosal of the type (Fig. 3, Longrich, 2013; Fig. 4B, D, Campbell, 2015) bears a dorsally curved epiossification similar in morphology to epiparietal ep4 of the holotype of *Wendiceratops* (Evans and Ryan, 2015). Though the holotype of *Judiceratops* (Longrich,

2013) would have priority over *Wendiceratops* (Evans and Ryan, 2015), none of the fragmentary cranial elements bear diagnostic apomophies and only compare favorably to the much more complete materials of *Wendiceratops*. We therefore consider *Judiceratops tigris* to be a nomen dubium and tentatively refer YPM VPPU 022404 to *Wendiceratops pinhornensis* subject to further, detailed investigation.

Commented [DFP81]: I expect Judiceratops is a chimaera, maybe anyway. These very fragmentary specimens don't matter very much.

Given the doubt cast on the validity of *Judiceratops*, other isolated materials referred to *Judiceratops tigris* by Longrich (2013) and revaluated by Campbell (2015) can be considered independently. A referred jugal, YPM VPPU 023261, can be tentatively referred to Centrosaurinae based on its wide, triangular ventral process (in contrast to the narrow ventral process in *Spiclypeus* and *Chasmosaurus belli*), and is indistinguishable from *Lokiceratops rangiformis*, *Albertaceratops nesmoi*, *Medusaceratops lokii*, and *Wendiceratops pinhornensis*. A referred midline parietal bar, YPM VPPU 23262, cannot be diagnosed confidently to any known taxon, but its broad cross-section is most consistent with a centrosaurine identity, rather than chasmosaurines. In all currently known Campanian chasmosaurines, at least a portion of the midline bar is narrow and straplike. However, the associated partial left squamosal of YPM VPPU 23262 can be confidently referred to Chasmosaurinae on the basis of its elongate, sickle-shaped morphology, concave dorsal surface, among broad episquamosals, among other features (Longrich, 2013; Campbell, 2015). However, it is far too incomplete to establish its overall morphology (see Campbell, 2015 for alternate reconstructions) and it does not bear any apomorphic features within chasmosaurinae to establish a new taxon. However, if the association between the midline parietal and squamosal is unquestioned, the combination of a wide midline parietal with a crescentic chasmosaurine squamosal would be unique and may provide clues to the plesiomorphic morphology of the earliest chasmosaurines. Regardless, based on the squamosal, YPM VPPU 23262 is unequivocal evidence for the presence of an unknown chasmosaurine ceratopsid in the Kennedy Coulee region, a fifth distinct and possibly sympatric ceratopsid taxon in the lower McClelland Ferry Member, and it also represents one of the oldest known members of the clade. The upper part of the McClelland Ferry Member also includes the chasmosaurines *Spiclypeus shipporum* (Mallon et al. 2016) and *Mercuriceratops gemini* (Ryan et al. 2014), both of which are distinct from YPM VPPU 23262.

Commented [DFP82]: I agree, and was always surprised at this initial ID

High Endemism of Centrosaurines

Among ceratopsids, Centrosaurinae show an unusual pattern of high endemism, with different species occurring differentially along the coastal plain of the Western Interior Seaway. This pattern is striking because in general, large animals tend to have large geographic ranges (Brown et al., 1996). Yet, based on current evidence and acknowledging uneven temporal and geographic sampling, all known centrosaurines species exhibit relatively small geographic ranges. This pattern is seen not only in genera and species, but above the species level as well. That is, centrosaurine subclades—including Albertaceratopsini—also show restricted geographic distributions.

Commented [DFP83]: Or maybe centrosaurines evolve rapidly anagenetically, and you are merely sampling the same lineages at slightly different spots in time. I know you won't ever acknowledge this, I just wanted to say it.

All southern centrosaurine taxa are represented either by a single specimen or limited material geographically restricted by the aerially exposed extent of their stratigraphic intervals and are currently undocumented from equivalent intervals elsewhere. For example, *Nasutoceratops titusi*, currently based on two specimens from the middle unit of the Kaiparowits Formaiton of southern Utah may have had a large range in southern Laramidia, but fossiliferous non-marine intervals of the same age are not exposed elsewhere. The same is true of northern Montana, where taxa are all known from limited specimens occurring within limited geographic

Commented [DFP84]: What constitutes a large range?

Commented [DFP85]: Well, this is the problem isn't it? Because the new dates from Ramezani et al 2022 show that the Dinosaur park Formation is actually contemporaneous with the Kaiparowits. This surprising result was not commented on in the paper because it went against all previous and current fossil and radiometric evidence. I have a lot of problems with this paper. See main review.

But anyway, I would actually agree that, based on correctly recalibrated Ar-Ar dates (Fowler 2017) only the lower Kaiparowits overlaps with the DPFm in time.

But anyway, there are no Nasutoceratopsins in the DPFm (to my knowledge), but they are present in the Judith of Montana. I suspect that these are slightly older stratigraphically than Nasuto itself.

areas (i.e. *Einiosaurus procurvicornis*, *Coronosaurus brinkmani*). However, in taxa with more extensive sampling, ranges appear relatively limited within Laramidia. *Centrosaurus*, by far one of the best represented centrosaurines, still has a geographic range spanning less than 200 km. *Pachyrhinosaurus canadensis* has a known range of 200 km (Currie et al. 2008). All other northern taxa are known from single sites or single localities. *Styracosaurus albertensis* for example is known from multiple specimens but all within Dinosaur Provincial Park. Generously, the largest range of any centrosaur (i.e. *Coronosaurus*, *Centrosaurus*, *Pachyrhinosaurus canadens*) is around 60,000 km^2.

Commented [DFP86]: This is a bit silly because the rocks are in a geographically restricted area. If you take a time slice that is conveniently exposed over a wide area, for example the lower DPFm/uppermost Oldman interval, dinosaurs like Centrosaurus apertus, or Brachylophosaurus (a hadrosaur) are present from mid Alberta down to northern Montana.

Thus, the preserved ranges of species must underestimate their true ranges. In particular, there is a lack of sampling of centrosaurines to the west of the coastal plain in upland sediments with the exception of *Crittendenceratops* in intermountain Arizona (Dalman et al., 2021). It is possible that lineages ranged further to the west, and that the geologically better represented coastal plain represents the eastern edge of many species' distributions. However, the restricted ranges seen along the coastal plain suggest endemism is not solely the result of sampling; even assuming they ranged westward all the way across Laramidia, the restricted latitudinal ranges argue for small geographic ranges.

Furthermore, if small species ranges were simply a result of poor sampling, we would predict that known species ranges would have tended to increase over time as sampling has improved since the first work in the late 19th century. Instead, better sampling has tended to reveal new species, but has resulted in only modest extensions of the ranges of known species. Trends in the data therefore corroborate the presence small geographic ranges for centrosaurines and implies that the small geographic ranges seen in centrosaurines are a real biological phenomenon.

The pattern of high endemism is not only evident at the species level, but at the clade level as well, with centrosaurine clades also exhibiting highly restricted geographic ranges. The Lokiceratopsinae (*Lokiceratops*, *Albertaceratops*, *Medusaceratops*) is so far known only from northern Montana and southern Alberta across a geographic range of 25km and ~ 490 km^2 of area. *Diabloceratops*-like animals with a single hypertrophied, elongated epiparietal ep1 have a known range distance of 30 km and a range area of ~ 700 km^2. Animals with a dorsal otic ridge (*Menefeecertops*, *Yehuecauhceratops*, *Crittendenceratops*) have a geographic range distance of 1100 km and a range area of ~ 220,000 km^2. Nasutoceratopsini (*Nasutoceratops*, *Avacertops*) have a geographic range distance of 2000 km and a range area of ~ 200,000 km^2. Basal eucentrosaurans (ie. *Coronosaurus, Centrosaurus, Spinops*) have a range extension of ~200 km and a range area of ~10,000 km^2. *Styracosaurus* (*S. albertensis* + *S. ovatus*) ranges over 225 km and a range area of ~ 12,600 km^2. Pachyrhinosaurini (*Einiosaurus, Achelousaurus*, the Iddesleigh pachyrhinosaur, and the three species of *Pachyrhinosaurus*) have the largest range at ~3,300 km and a range area of ~ 660,000 km^2 generously assuming the coastal plain averaged 200 km wide from the uplands to the coast. These patterns require that not only were lineages isolated long enough to evolve into separate species; these lineages then underwent regional diversifications producing multiple species in the same area.

Commented [DFP87]: All this paragraph really shows is the exposures of the rocks which are the right age. Some periods of time (lower Campanian) have narrow time slices only exposed in small area. Fortuitously, other periods of time have

It has previously been proposed that dinosaurs in the Late Cretaceous of North America showed relatively high levels of endemism (Lehman, 1997; Lehman, 2001), and endemism is seen in centrosaurines (Sampson et al., 2013), chasmosaurines (Sampson et al., 2010; Longrich, 2011), hadrosaurids (Gates et al., 2007), pachycephalosaurids (Williamson & Carr, 2002; Longrich et al., 2010), and tyrannosaurids (Loewen et al., 2013). Whether the faunas can be broken into discrete biogeographic provinces, or show a more complicated pattern remains

Commented [DFP88]: This has been heavily criticized in print based on the stratigraphy, even by Lehman himself! Not citing these critiques here is unacceptable.

Look, I know you think we're on opposite sides of this debate, but not even acknowledging that a debate is occurring is unscientific.

debated, but decades of fieldwork and improved stratigraphic constraint (Ryan & Evans 2005; Beveridge et al, 2022; Ramezani et al., 2022) have shown that distinct species inhabited different and relatively circumscribed regions of the coastal plain. Yet while many dinosaurs show endemism, especially at the species level, few clades are known to display endemism to the same degree seen in centrosaurines.

Commented [DFP89]: Would support if true (I very much doubt the Ramezani dates in a few places – they never discuss the problems and conflicts of the new dates in their own paper)

Commented [DFP90]: You know, I actually agree. The problem is that the Utah research group treat every species like it is its own little biogeographic region. I think there is good evidence that centrosaurines (a boreal group) get subdivided into three or four lineages, and these probably did have fairly narrow latitudinal ranges,

The hadrosaur *Parasaurolophus*, for example, is represented by different taxa in Alberta and New Mexico (Evans et al., 2009), but the genus itself has a large geographic range. Other genera with large geographic ranges include the hadrosaurine *Gryposaurus* (Gates & Sampson 2007), the pachycephalosaur *Stegoceras* (Sullivan & Lucas, 2006), and the chasmosaurs *Triceratops* and *Torosaurus* (Longrich & Field, 2012). This is not to say there are no endemic clades in other taxa; the chasmosaur *Chasmosaurus* for example is known exclusively from a small region in southern Canada (Godfrey & Holmes, 1995). Nevertheless, centrosaurines are unusual in that, thus far, none of the subclades are known to be widely distributed.

Commented [DFP91]: Pachyrhinosaurs are. I suspect that this is because they are a late Campanian-early Maastrichtian group, and that the presence of rocks of this age in Alaska gives the preservation potential for them to be found there.

The discovery of *Lokiceratops rangiformis* also suggests that, in addition to showing high endemism, the local diversity of centrosaurines was high in the Judith River area. Four distinct and coeval centrosaurine ceratopsians (*Lokiceratops rangiformis*, *Albertaceratops nesmoi*, *Medusaceratops lokii*, and *Wendiceratops pinhornensis*) occur within a small geographic area where the Milk River crosses the United States of America/Canadian border. These centrosaurines occur within a tight stratigraphic interval of four meters and range in age from a maximum of 78.28 to 78.08 + 0.2 - 0.9 Ma. This pattern is distinct from other formations, where typically only a single species existed, and is analogous to the pattern of diversity observed in sympatric lambeosaurine hadrosaurids in the Dinosaur Park Formation (Mallon et al., 2012).

Commented [DFP92]: They weren't coeval. Medusa, Loki, and Alberta are all from different levels in section. In the same way, Triceratops prorsus is not coeval with Triceratops horridus in the Hell Creek.

Endemism and Turnover

The high endemism seen here is likely connected to a pattern of rapid evolution and turnover. All known centrosaurines also have brief temporal ranges (Sampson & Loewen 2010), of 500 Ka or less. *Lokiceratops*, *Albertaceratops*, *Medusaceratops*, and *Wendiceratops* all appear and disappear in a ~200 ka window. *Styracosaurus ovatus*, *Stellasaurus*, *Einiosaurus*, and *Achelousaurus* all occur in a ~500 ka window and are not known to overlap, suggesting an average temporal range of ~125 ka. These are almost certainly underestimates of their true temporal ranges, given the Signor-Lipps Effect (Signor & Lipps, 1982; due to sampling the first occurrence and last occurrence of a fossil do not correspond to the true first and last occurrence of the species).

Commented [DFP93]: Most are known from single specimens, or single horizons. What Centrosaurines have any range at all? Styracosaurus albertensis, Centrosuaurus apertus, and Pachyrhinosaurus. That's it.

Commented [DFP94]: Not if they are sampling an anagenetic lineage. This doesn't have to be the case, but the possibility is not mentioned here.

Moreover, the appearance of e.g. *Styracosaurus* in Dinosaur Park (Evans & Ryan 2005), without any recognized ancestor lower in section may mean that its appearance marks the immigration of this species into the area, not its in-situ evolution. Some of the perceived rapid turnover observed in the record may, therefore, result from change in geographic ranges rather than speciation and extinction events. Still, as with geographic range, improved sampling over the course of the past century has largely tended to reveal new species higher and lower in section, rather than extending ranges of known species, suggesting that this rapid turnover reflects an actual evolutionary trend.

Commented [DFP95]: What does this mean? Centrosaurus is a decent candidate for an ancestor to Styracosaurus. It's a polytomy in your cladogram, which leaves that interpretation open.

Commented [DFP96]: Unless C. apertus is the ancestor.

Commented [DFP97]: Agreed, except for use of the term"turnover"

Rapid evolution may have been a key driver of high endemism. The appearance of distinct lineages in different regions of the continent suggests rapid evolution of lineages following dispersal, with adaptation to local environments, sexual selection, or both driving lineages in different directions in terms of adaptations and ornament, causing them to evolve into distinct species. However, endemism itself can also be a driver of rapid evolution. That is, if conspecific populations became isolated from one another, evolution would accelerate due to genetic drift, with mutations rapidly becoming fixed in small populations. Endemism may also increase extinction rates. Small, endemic populations have fewer individuals, making them more vulnerable to extinction. Geographic range is tightly connected to extinction rates, with widespread species being more resistant to extinction, and species with small ranges more vulnerable (Jablonski, 2008). Since wide-ranging species inhabit many different environments and regions, an environmental change has to affect all areas to eliminate the species, making their extinction more difficult.

Drivers of Dinosaurian Endemism

During the Late Cretaceous, as increased volcanic seafloor spreading in the Pacific and Atlantic Ocean basins displaced water onto the continents (Müller et al., 2022), the Western Interior Seaway connected the Gulf of Mexico to the Arctic Ocean, between around 90 Ma to about 70 Ma, with the last remnants of the seaway persisting into the Paleocene (Blakey & Ranney 2018). Laramidia, the western portion of the North American continent isolated by the creation of the Western Interior Seaway (Hay et al., 1993) hosted rich assemblages of dinosaurs on a vast coastal plain along the eastern margin of Laramidia, extending from northern Coahuila, Mexico in the south to central Alberta, Canada in the north, forming a long-lived (>10 Ma) lush coastal lowland environment seemingly lacking persistent geographic barriers. Transgression events documented by marine tongues such as the Drumheller Marine Tongue and the Bearpaw transgression would have narrowed or expanded the coastal plain, but no persistent marine barriers are known capable of preventing northern dinosaurs from dispersing south, or vice versa. This suggests that other factors were responsible for observed patterns of dinosaur distribution and evolution. These factors potentially include climatic zones, floral composition and distribution, distributions of disease and parasites, competition with other dinosaurs, or a combination of these (Linnert et al., 2014; Bergner et al., 2021).

Commented [DFP98]: There is. See Fowler and freedman Fowler, 2020. Its hard not to see this omission as unintentional

Ceratopsid dinosaurs evolved in isolation on Laramidia and are found predominantly along the eastern coast of this longitudinally restricted island landmass. It is possible that dispersal between southern and northern regions of Laramidia was physiographically restricted periodically by contemporaneous mountain building, topography, basin evolution, and high sea levels in a region between present day Utah and Montana. The central Laramidia region currently occupied by the state of Wyoming represents a unique datapoint possibly representing one of these physiographic barriers along the eastern coast of Laramidia during uppermost middle Campanian during a time in which much of the diversification of centrosaurines occurred. During this interval, shorelines fluctuated over hundreds (~300–500) of kilometers between the hogback ridges of the Wyoming Thrust belt and the Western Interior Seaway. Around ~77.5–75 Ma, the onset of the Laramide orogeny changed the nature of the basin from a back-tilted foreland basin with abundant accommodation space to a forward-tilted, irregularly-shallowed seascape across Wyoming and extending into northeastern Colorado (Bird, 1998; Steel et al., 2012). This topography led to periods of non-deposition over most of western Wyoming punctuated by rapid incursions of the seaway.

Commented [DFP99]: The mountains are not being thrust up that rapidly – at least not in the Cretaceous. It is the sea pushing right up against the foothills which causes the boundaries.

Anyway, the mountains hypothesis was really only seriously proposed by gates et al, so that should be cited here.

Commented [DFP100]: This contradicts the statement above, and well… you don't credit Fowler and Freedman Fowler 2020 with this. Not giving credit here is pretty disgraceful.

Commented [DFP101]: This is slightly beside the point, but given the size of Laramdia, what is really south, central, or northern laramidia. There's a lot of territory north of Dinosaur Provincial Park (Mid/South Alberta).

Despite this pattern, it is unclear that mountains, uplifted alluvial valleys, or rivers could explain the endemism documented here. First, mountains chains such as the Rocky Mountains and the Andes are poor barriers to dispersal for modern large mammals, especially over large timescales. Large-bodied, terrestrial mammals readily disperse around, or even across mountains. If mountains do not drive endemism in extant large terrestrial animals, it seems unlikely they would do so for Cretaceous dinosaurs. Second, in modern ecosystems, extensive endemism evolves in the absence of geographic barriers. For example, different species of mammal inhabit different regions of North America (Feldhamer et al., 2003; Qian et al., 2009) despite the absence of barriers to dispersal. Birds display high levels of endemism, especially in tropical environments (McKnight et al., 2007), despite being able to fly over geographic barriers such as mountains and rivers. The fact that extant endemism is not primarily driven by geographic barriers implies that Cretaceous endemism may not have been either. Third, the fact that, as discussed above, some dinosaur lineages (e.g. *Parasaurolophus*, *Stegoceras*, *Gryposaurus*) did manage to disperse between northern and southern regions provides strong evidence against the existence of persistent barriers to dinosaur dispersal.

Latitudinally driven gradients in climate may have played a role if different lineages were adapted to different climatic regimes. However, the Late Cretaceous greenhouse interval (Cook 2019; O'Connor et al., 2019) would have meant a weaker temperature gradient from south to north than observed today. Although high latitude environments were relatively cool (Spicer and Herman, 2010), the smaller difference in mean annual temperature between north and south (Zhang et al., 2019) may limited the ability of climate to directly drive endemism, although patterns in ectothermic squamates do show some degree of clade-level endemism (e.g., Nydam 2013; Nydam et al., 2013; Woolley et al., 2020) suggesting ecosystem level differences between high and low latitude regions. Rather than temperature, higher latitude environments would still have been highly seasonable as a result of differences in photoperiod. Differences in seasonable availability of light paired with moderate temperature gradients indicate that difference in vegetation may also have played a role. Distinct floral communities existed in Laramidia (Braman & Koppelhus, 2005), and herbivore diet specialization may have contributed to local endemism. Although diet may well have been a factor, at times dinosaurs did disperse between northern and southern floral provinces, suggesting a degree of adaptability in terms of diets, or dispersals tied to climatic fluctuations resulting in periodic homogenization or expansion of preferred floral communities. Different species are also similar in their feeding adaptations, (e.g. northern and southern *Parasaurolophus* have similar beak and jaw morphology), arguing that they probably had relatively similar feeding strategies and diets.

Lastly, resource competition between dinosaurs may have driven endemism (Mallon, 2019). Strikingly, tyrannosaurs show a pattern in which multiple large-bodied species rarely if ever co-occur. When two tyrannosaur species do co-occur, they include a larger and more robust species and a smaller and more gracile species: for example *Daspletosaurus* and *Gorgosaurus* in Dinosaur Park (Currie, 2005), *Tarbosaurus* and *Alioramus* in the Nemegt Formation (Brusatte et all, 2009), and *Tyrannosaurus* and *Nanotyrannus* in the Hell Creek Formation (Gilmore, 1946; Bakker et al., 1988). That co-existing species differed in size and morphology implies that their coexistence was made possible by niche partitioning as a means to avoid competition. Among modern birds, which are extant relatives of dinosaurs, the presence of competing species appears to exert a strong effect on geographic range. When competing species are absent, birds are able to occupy a wider range; when present, they are restricted (Freeman et al., 2022). Geographic ranges also change when competitors are eliminated; the extirpation of wolves from most of North America, for example, was followed by the rapid expansion of the coyote into areas of North America where they were previously competitively excluded (Thurber & Peterson, 1991). If the presence of multiple, closely-related dinosaur species did restrict the geographic ranges of other clade members, this might explain why lineages were sometimes endemic, and other times widely dispersed; that is, increases or decreases in diversity would restrict or permit broader

Commented [DFP102]: I'm open on Nano vs Tyranno ontogeny, but at the least, there should be mention here that this is fiercely debated. Again the authors simply ignore evidence to the contrary.

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dispersal. It is worth noting that, with the exception of the Judith River, no formation is known to have two or more centrosaurine taxa living at the same time, suggesting that competition between centrosaurine species may have been a major factor dictating geographic ranges.

Implications for dinosaur diversity.

The total diversity of a region, or gamma diversity, is a function of alpha diversity, or diversity on a local scale, and beta diversity, or turnover between localities. The dinosaurs of the eastern coastal plain of Laramidia suggest high levels of both alpha and beta diversity. The implication is that regional dinosaur diversity was probably very high, despite the limited size of the landmass. Despite the diversity of dinosaurs known from localities such as Judith River Formation of Montana, Dinosaur Provincial Park in Alberta, and Grand Staircase-Escalante National Monument in Utah, it is likely that we are significantly underestimating the total diversity of dinosaurs in North America. Our poor sampling of the West Coast, the US Southwest, Mexico, and the Arctic likely means many species remain to be discovered in these regions.

CONCLUSIONS

A centrosaur specimen recovered from the Judith River Formation of Montana, EMK 0012, can be diagnosed as a new species, *Lokiceratops rangiformis*, based on autapomorphies of the parietosquamosal frill and associated ornamentation. The new taxon is mostly closely related to *Albertaceratops nesmoi* and *Medusaceratops lokii*, both recovered in a small geographic area and in sediments that indicate overlapping temporal distributions. Together, these data imply a rapid regional radiation of five distinct sympatric ceratopsid taxa (*Albertaceratops nesmoi*, *Lokiceratops rangiformis*, *Medusaceratops lokii*, *Wendiceratops pinhornensis*, and Chasmosaurinae indet.). The clade containing *Lokiceratops*, Albertaceratopsini, is geographically restricted within northern Laramidia, a pattern documented in other centrosaurine clades across Laramidia. Endemism has been documented among other dinosaurs (Sampson et al., 2010, 2013; Loewen et al., 2013), but the pattern of multiple, regional radiations evidenced here appears to be unique so far among macroherbivorous dinosaurs, especially those with diverse cranial ornamentation putatively related to sexual selection (Evans & Reisz 2007). Centrosaurine endemism was likely driven by a combination of factors including climate-driven floral differences along a latitudinal gradient, dynamic tectonism, intense sexual selection, and interspecific resource competition, and is possibly analogous with regional radiations of sympatric lambeosaurine hadrosaurids, with the rapid speciation of dinosaurs in the Late Cretaceous of North America resulting in intense competition that restricted geographic ranges. High dinosaur endemicity implies that the diversity of dinosaurs in Laramidia was considerably higher than previously thought, because our limited geographic sampling limits our ability to recover species found in other parts of the continent.

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York, New York, USA
ANSP	Academy of Natural Sciences, Philadelphia, USA
BMNH	British Museum of Natural History, London, United Kingdom
CCMGE	Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia
CMN	Canadian Museum of Nature, Ottawa,Ontario, Canada
CPC	Colección Paleontológica de Coahuila, Saltillo, Coahuila, Mexico
DMNH	Perot Museum of Nature and Science, Dallas, USA

EMK	Evolutionsmuseet (Museum of Evolution), Knuthenborg, Maribo, Denmark
FDMU	Fukui Prefectural Dinosaur Museum, Katsuyama, Japan
GPDM	Great Plains Dinosaur Museum, Malta, Montana, USA
IGCAGS	Institute of Geology Chinese Academy of Geosciences, Beijing, China
IGM	Institute of Geology Mongolia, Ulanbaatar, Mongolia
IMM	Inner Mongolia Museum, Hohhot, China
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
JLUM	Jilin University Geological Museum, Changchun, China
JRF	Judith River Foundation, Great Plains Dinosaur Museum, Malta, Montana, USA
JZMP	Jinzhou Museumof Paleontology, Jinzhou City, Liaoning Province, China
KIGAM	Korea Institute of Geoscience and Mineral Resources, Daejeon, South Korea
LACM	Natural History Museum of Los Angeles County, Los Angeles, USA
LH	Long Hao Institute of Geology and Paleontology, Beijing, China
MNHCM	Mokpo Natural History and Culture Museum, Mokpo, South Korea
MOR	Museum of the Rockies, Bozeman, Montana, USA
MTM	Hungarian Natural History Museum, Budapest, Hungary
NHMUK	The Natural History Museum, London, United Kingdom
NMC	Canadian Museum of Nature, Ottawa, Ontario, Canada
NMMNH	New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA
OMNH	Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, USA
PCM	Phillips County Museum, Malta, Montana, USA
PIN,	Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia
PM TGU	Paleontological Museum, Tomsk State University, Tomsk, Russia
PMOL	Paleontological Museum of Liaoning, Shenyang, China
PMU	Palaeontological Collections, Museum of Evolution, Uppsala University, Uppsala, Sweden
ROM	Royal Ontario Museum, Toronto, Canada
RTMP	Royal Tyrrell Museum of Palaeontology, Alberta, USA
SMP	State Museum of Pennsylvania, Pennsylvania, USA
TMM	Vertebrate Paleontology and Radiocarbon Laboratory, University of Texas, Austin, USA
TMP	Royal Tyrrell Museum of Palaeontology, Alberta, Canada
TCM	The Children's Museum of Indianapolis, Indiana, USA
UALVP	University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada
UMNH VP	Natural History Museum of Utah, Salt Lake City, Utah, USA
USNM	Smithsonian Institution, National Museum of Natural History, Washington, D.C., USA
UTEP	University of Texas at Austin, Texas, USA
WDCB	Wyoming Dinosaur Center, Thermopolis, Wyoming, USA
YPM	Yale Peabody Museum, New Haven, Connecticut, USA
YPM VPPU	Princeton University Collection, Yale Peabody Museum, New Haven, Connecticut, USA
ZCDM	Zhucheng Dinosaur Museum, Zhucheng, China
ZMNH	Zhejiang Museum of Natural History, Hangzhou, China
ZPAL	Palaeozoological Institute, Polish Academy of Sciences, Warsaw, Poland

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REFERENCES

An W, Kuang H, Liu Y-Q, Peng N, Xu K-M, Xu H, Zhang P, Wang K-B, Chen S-Q, Zhang Y-X. 2016. Detrital zircon dating and tracing the provenance of dinosaur bone beds from the Late Cretaceous Wangshi Group in Zhucheng, Shandong, East China. *Journal of Palaeogeography* **5(10)**:1016/j.jop.2015.11.002.

Averianov A, Sues H-D. 2012. Correlation of Late Cretaceous continental vertebrate assemblages in Middle and Central Asia. *Journal of Stratigraphy* **36(2)**:462–485.

Bakker R, Williams M, Currie PJ. 1988. *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the latest Cretaceous of Montana. *Hunteria* **1**:1-30.

Bennett SC. 1993. The ontogeny of *Pteranodon* and other pterosaurs. *Paleobiology* **19**:92–106.

Beveridge TL, Roberts EM, Ramezani J, Titus AL, Eaton JG, Irmis RB, Sertich JJW. 2022. Refined geochronology and revised stratigraphic nomenclature of the Upper Cretaceous Wahweap Formation, Utah, U.S.A. and the age of early Campanian vertebrates from southern Laramidia, *Palaeogeography, Palaeoclimatology, Palaeoecology* **591**:110876, ISSN 0031-0182, https://doi.org/10.1016/j.palaeo.2022.110876.

Bird P. 1998. Kinematic history of the Laramide orogeny in latitudes 35°–49°N, western United States. *Tectonics* **17(5)**:780–801. doi:10.1029/98TC02698.

Blakey RC, Ranney WD. 2018. The Continental Arc, Sevier Orogeny, Western Interior Seaway and Flat-Slab Subduction: Cretaceous Period: Ca. 145–65 Ma. In: Blakey RC, Ranney WD, eds. *Ancient Landscapes of Western North America, A Geologic History with Paleogeographic Maps*. Cham, Switzerland: Springer (first edition), 103–130.

Bordy EM, Abrahams M, Sharman GR, Viglietti PA, Benson RBJ. McPhee BW, Barrett PM, Sciscio L, Condon D, Mundil R, Rademan Z. 2020. A chronostratigraphic framework for the upper Stormberg Group: implications for the Triassic-Jurassic boundary in southern Africa. *Earth-Science Reviews* **203**:103120.

Braman DR, Koppelhus EB. 2005. Campanian Palynomorphs. In: Currie PJ, and Koppelhus EB, eds. *Dinosaur provincial park: a spectacular ancient ecosystem revealed*. Bloomington: Indiana University Press 101-130.

Brinkman DB, Eberth DA, Ryan MJ, Chen P. 2001. The occurrence of *Psittacosaurus xinjiangensis* Sereno and Chow, 1988 in the Urho area, Junggar Basin, Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* **38(12)**:1781-1786. https://doi.org/10.1139/e01-049

Brochu CA. 1996. Closure of the neurocentral sutures during crocodilian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology* **16**:49–62.

Brown B. Schlaikjer EM. 1940. The structure and relationships of *Protoceratops. Annals of the New York Academy of Sciences* **40:**133–266.

Brown CM, Henderson DM. 2015. A New Horned Dinosaur Reveals Convergent Evolution in Cranial Ornamentation in Ceratopsidae. *Current Biology* **25(12)**:1641–1648. DOI 10.1016/j.cub.2015.04.041.

Brown CM, Russell AP, Ryan MJ. 2009. Pattern and Transition of Surficial Bone Texture of the Centrosaurine Frill and Their Ontogenetic and Taxonomic Implications. *Journal of Vertebrate Paleontology* **29**:132–141.

Brown CM, Greenwood DR, Kalyniuk JE, Braman DR, Henderson DM. Greenwood CL, Basinger JF. 2020. Dietary palaeoecology of an Early Cretaceous armoured dinosaur (Ornithischia; Nodosauridae) based on floral analysis of stomach contents. *Royal Society open* Science 7200305200305. http://doi.org/10.1098/rsos.200305

Brown JH, Stevens GC, and Kaufman DM. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual review of ecology and systematics* **27**:597-623.

Brusatte SL, Carr TD, Erickson GM, Bever GS, Norell M. 2009. A long-snouted, multihorned tyrannosaurid from the Late Cretaceous of Mongolia. *Proceedings of the National Academy of Sciences* **106:**17251-17266.

Burgener L, Hyland E, Griffith E, Mitasova H, Zanno LE, Gates TA. 2021, An extreme climate gradient-induced ecological regionalization in the Upper Cretaceous Western Interior Basin of North America. *Geological Society of America Bulletin* **133(9-10)**:2125-2136.

Burton D, Greenhalgh BW, Britt BB, Kowallis BJ, Elliott Sr WS, et al. 2006 New radiometric ages from the Cedar Mountain Formation, Utah and the Cloverly Formation, Wyoming: implications for contained dinosaur faunas. *Geological Society of America Abstracts with Programs* **38**: 52.

Campagna L, Repenning M, Silveira LF, Fontana CS, Tubaro PL, Lovette IJ. 2017. Repeated divergent selection on pigmentation genes in a rapid finch radiation. *Science Advances* **3(5)**:e1602404. doi: 10.1126/sciadv.1602404

Campbell JA. 2015. A reassessment of the horned dinosaur *Judiceratops tigris* (Ornithischia: Ceratopsidae) from the Upper Cretaceous (Campanian) of Montana, USA. *Canadian Journal of Earth Sciences* **52**: 85–95.

Carpenter K, Hayashi S, Kobayashi Y, Maryańska T, Barsbold R, Sato K, Obata I. 2011. *Saichania chulsanensis* (Ornithischia, Ankylosauridae) from the upper cretaceous of Mongolia. *Palaeontographica Abteilung A* **294(1-3)**:1-61.

Carr TD. 1999. Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria). *Journal of Vertebrate Paleontology* **19(3)**:497–520.

Caylor EA, Carrapa B, Sundell K, DeCelles PG, Smith JM. 2021. Age and deposition of the Fort Crittenden Formation: A window into Late Cretaceous Laramide and Cenozoic tectonics in southeastern Arizona. *Bulletin of the Geological Society of America* **133(9-10)**:1996-2016. https://doi.org/10.1130/B35808.1

Chiba K, Ryan MJ, Braman DR, Eberth DA, Scott EE, Brown CM, Kobayashi Y, Evans DC. 2015. Taphonomy of a monodominant *Centrosaurus apertus* (Dinosauria: Ceratopsia) bonebed from the upper Oldman Formation of southeastern Alberta. *PALAIOS* **30(9):**655

Chiba K, Ryan MJ, Fanti F, Loewen MA, Evans DC. 2017. New material and systematic re-evaluation of *Medusaceratops lokii* (Dinosauria: Ceratopsidae) from the Judith River

Formation (Campanian, Montana). *Journal of Paleontology* **92(2)**:272–288. doi: 10.1017/jpa.2017.62

Chinnery BJ, Horner JR. 2007. A new neoceratopsian Dinosaur linking North American and Asian taxa. *Journal of Vertebrate Paleontology* **27**:625-641. 10.1671/0272-4634(2007)27[625:ANNDLN]2.0.CO;2.

Chinnery BJ. 2004. Description of *Prenoceratops pieganensis* gen et sp. nov. (Dinosauria: Neoceratopsia) from the Two Medicine Formation of Montana. *Journal of Vertebrate Paleontology* **24(3)**:572–590. doi:10.1671/0272-4634(2004)024[0572:DOPPGE]2.0.CO;2. ISSN 0272-4634.

Claessens LPAM, Loewen MA, 2016. A redescription of *Ornithomimus velox* Marsh, 1890 (Dinosauria, Theropoda). *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2015.1034593.

Clark GA. 1993. *Termini situm et directionem partium corporis indicantes*. In: Baumel J, King AS, Breazile JE, Evans HE, Vanden Berge JC, eds. *Handbook of Avian Anatomy: Nomina Anatomica Avium, second edition.* Cambridge, Massachusetts: Publications of the Nuttall Ornithological Club 23, 1–6.

Clayton KE, Loewen MA, Sampson SD, Farke AA, Irmis RB. 2009. Epiparietal homology within centrosaurine (Ornithischia, Ceratopsidae): a re-evaluation based on newly discovered basal taxa. *Journal of Vertebrate Paleontology*, SVP Program and Abstracts 2009:80.

Clayton KE, Loewen MA, Farke AA, Sampson SD. 2010. A reevaluation of epiparietal homology within chasmosaurine ceratopsids (Ornithischia) based on newly discovered taxa. *Journal of Vertebrate Paleontology*, SVP Program and Abstracts 2010:73.

Conrad JE, McKee EH, Turrin BD. 1992. Age of tephra beds at the Ocean Point dinosaur locality, North Slope, Alaska based on K-Ar and ^{40}Ar/^{39}Ar analyses; U.S. Geological Survey Bulletin 1990 Chapter C:1-12.

Cook, T. 2019. Late cretaceous extreme warmth at high southern latitudes. *Eos* 100. https://doi.org/10.1029/2019EO120391.

Cullen TM, Fanti F, Capobianco C, Ryan MJ, Evans DC. 2016. A vertebrate microsite from a marine-terrestrial transition in the Foremost Formation (Campanian) of Alberta, Canada, and the use of faunal assemblage data as a paleoenvironmental indicator. *Palaeogeography, Palaeoclimatology, Palaeoecology* **444**:101-14.

Cunningham PJ. Loewen MA. Sertich JJW. 2019. The utility of periosteal aging to assess the maturity of isolated theropod cranial and femoral elements. Journal of Vertebrate Paleontology, SVP Program and Abstracts Book, 2019:26.

Currie PJ. 2005. Theropods, including birds. In: Currie PJ, and Koppelhus EB, eds. *Dinosaur provincial park: a spectacular ancient ecosystem revealed*. Bloomington: Indiana University Press, 367-397.

Currie PJ, Langston W, Tanke DH. 2008. A new species of *Pachyrhinosaurus* (Dinosauria, Ceratopsidae) from the Upper Cretaceous of Alberta, Canada. In: Currie PJ, Langston W, Tanke DH, eds. *A New Horned Dinosaur from an Upper Cretaceous Bone Bed in Alberta*. Ottawa, Ontario, Canada: NRC Research Press, 1–108.

Currie PJ. Holmes RB, Ryan MJ, Coy C. 2016. A juvenile chasmosaurine ceratopsid(Dinosauria, Ornithischia) from the Dinosaur Park Formation, Alberta, Canada. *Journal of Vertebrate Paleontology*, DOI: 10.1080/02724634.2015.1048348.

Currie PJ, Russell DA. 2005. The geographic and stratigraphic distribution of articulated and associated dinosaur remains, In Currie PJ, Koppelhus EB. eds. *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed.* Indiana University Press, Bloomington 537–569.

Czepiński L. 2020. Ontogeny and variation of a protoceratopsid dinosaur *Bagaceratops rozhdestvenskyi* from the Late Cretaceous of the Gobi Desert. *Historical Biology* **32(10)**:1394-1421, DOI: 10.1080/08912963.2019.1593404

Dalman SG, Hodnett J-PM, Lichtig AJ, Lucas SG. 2018. A new ceratopsid dinosaur (Centrosaurinae: Nasutoceratopsini) from the Fort Crittenden Formation, Upper Cretaceous (Campanian) of Arizona. *New Mexico Museum of Natural History and Science Bulletin* **79**: 141–164.

Dalman SG, Lucas SG, Jasinski SE, Lichti AJ, Dodson P. 2021. The oldest centrosaurine: a new ceratopsid dinosaur (Dinosauria: Ceratopsidae) from the Allison Member of the Menefee Formation (Upper Cretaceous, early Campanian), northwestern New Mexico, USA. *Paläontologische Zeitschrift* **95**:291–335. https://doi.org/10.1007/s12542-021-00555-w

Dashzeveg D, Dingus L, Loope DB, Swisher III CC, Dulam T, Sweeney MR. 2005. New Stratigraphic Subdivision, Depositional Environment, and Age Estimate for the Upper Cretaceous Djadokhta Formation, Southern Ulan Nur Basin, Mongolia, *Papers in the Earth and Atmospheric Sciences* 209. https://digitalcommons.unl.edu/geosciencefacpub/209

Ditchkoff SS. deFreese RL. 2010. Assessing fluctuating asymmetry of white-tailed deer antlers in a three-dimensional context. *Journal of Mammalogy* **91(1)**:27–37, https://doi.org/10.1644/09-MAMM-A-134R.1

Dodson P, Forster CA, Sampson SD. 2004. Ceratopsidae. In: Weishampel DB, Dodson P, Osmólska H, eds. *The Dinosauria, 2nd ed.* Berkeley: University of California Press, 494–513.

Dodson P. 1986. *Avaceratops lammersi*: A New Ceratopsid from the Judith River Formation of Montana. *Proceedings of the Academy of Natural Sciences* **138**:305–317.

Dodson P. 1990. On the status of the ceratopsids *Monoclonius* and *Centrosaurus*. In: Carpenter K, Currie PJ, eds. *Dinosaur Systematics: Perspectives and Approaches.* Cambridge, New York, Port Chester, Melbourne, Sydney: Cambridge University Press, 231–243.

Dodson P. 1997. Neoceratopsia. In: Currie PJ, Padian K, eds. *Encyclopedia of Dinosaurs.* San Diego: Academic Press, 473–478.

Drewes H. 1971. Mesozoic stratigraphy of the Santa Rita Mountains, southeast Tucson, Arizona: *U.S. Geological Survey*, Professional Paper 658-C:1-81.

Eberth DA. 2005. The Geology. In: Currie PJ, Koppelhus EB, eds. *Dinosaur Provincial Park: A spectacular ancient ecosystem revealed.* Bloomington: Indiana University Press, 54–82.

Eberth DA, Deino AL. 1992. A Geochronology of the non-marine Judith River Formation of southern Alberta. *Abstracts of the Society of Economic Paleontologists and Minerologists. Theme Meeting: Mesozoic of the Western Interior*, 24-25.

Eberth DA, Hamblin AP. 1993. Tectonic, stratigraphic, and sedimentologic significance of a regional discontinuity in the upper Judith River Formation (Belly River Wedge) of southern Alberta, Saskatchewan, and northern Montana. *Canadian Journal of Earth Science* **30(1)**: 174–200.

Eberth DA, Kamo SL. 2019. High-precision U–Pb CA–ID–TIMS dating and chronostratigraphy of the dinosaur-rich Horseshoe Canyon Formation (Upper Cretaceous, Campanian–Maastrichtian), Red Deer River valley, Alberta, Canada. *Canadian Journal of Earth Sciences* **57(10)**:1220-1237. https://doi.org/10.1139/cjes-2019-0019

Eberth DA, Kobayashi Y, Lee Y-N, Mateus O, Therrien F, Zelenitsky DK, Norell MA. 2009. Assignment of *Yamaceratops dorngobiensis* and associated redbeds at Shine Us Khudag (eastern Gobi, Dorngobi Province, Mongolia) to the redescribed Javkhlant Formation (Upper Cretaceous). *Journal of Vertebrate Paleontology* **29(1)**:295-302, DOI: 10.1080/02724634.2009.10010384

Eberth DA, Russell DA, Braman DR, Deino AL. 1993. The age of the dinosaur-bearing sediments at Tebch, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences*. **30(10)**:2101–2106. Bibcode:1993CaJES..30.2101E. doi:10.1139/e93-182

Eberth DA, Xing X, Clark JM. 2010. Dinosaur death pits from the Jurassic of China. *Palaios* **25(1/2)**:112–125.

Eberth DA, Braman DR. 2012. A revised stratigraphy and depositional history for the Horseshoe Canyon Formation (Upper Cretaceous), southern Alberta plains. Canadian Journal of Earth Sciences. **49(9):**1053-1086. https://doi.org/10.1139/e2012-035

Evans DC, Bavington R, Campione NE. 2009. An unusual hadrosaurid braincase from the Dinosaur Park Formation and the biostratigraphy of *Parasaurolophus* (Ornithischia: Lambeosaurinae) from southern Alberta. *Canadian Journal of Earth Sciences* **46(11)**: 791–800. doi:10.1139/E09-050.

Evans DC & Robert R. Reisz RR. 2007. Anatomy and relationships of *Lambeosaurus magnicristatus*, a crested hadrosaurid dinosaur (Ornithischia) from the Dinosaur Park Formation, Alberta. *Journal of Vertebrate Paleontology* **27(2):** 373-393. doi: 10.1671/0272-4634(2007)27[373:AAROLM]2.0.CO;2

Evans DC, Ryan MJ. 2015. Cranial anatomy of *Wendiceratops pinhornensis* gen. et sp. nov., a centrosaurine ceratopsid (Dinosauria: Ornithischia) from the Oldman Formation (Campanian), Alberta, Canada, and the evolution of ceratopsid nasal ornamentation. *PLoS ONE* **10(7)**:e0130007. DOI 10.1371/journal.pone.0130007.

Farke AA, Ryan MJ, Barrett PM, Tanke DH, Braman DR, Loewen MA, Graham MR. 2011. A new centrosaurine from the Late Cretaceous of Alberta, Canada, and the evolution of parietal ornamentation in horned dinosaurs. *Acta Palaeontologica Polonica* **56(4)**:691–702. DOI 10.4202/app.2010.0121.

Farke AA. 2006. Morphology and ontogeny of the cornual sinuses in Chasmosaurine dinosaurs (Ornithischia: Ceratopsidae). of the Supracranial Sinuses in Ceratopsian Dinosaurs. *Journal of Paleontology* **80(4)**:780–785.

Farke AA. 2010. Evolution, homology, and function of the supracranial sinuses in ceratopsian dinosaurs. *Journal of Vertebrate Paleontology* **30(5)**:1486–1500.

Farke AA. 2011. Anatomy and Taxonomic Status of the Chasmosaurine Ceratopsid *Nedoceratops hatcheri* from the Upper Cretaceous Lance Formation of Wyoming, U.S.A. *PLoS ONE* **6(1)**:e16196. doi:10.1371/journal.pone.0016196

Feldhamer GA, Thompson BC, Chapman JA. 2003. *Wild Mammals of North America*. Baltimore: Johns Hopkins University Press.

Fiorillo AR, Tykoski RS. 2012. A new Maastrichtian species of the centrosaurine ceratopsid *Pachyrhinosaurus* from the North Slope of Alaska: *Acta Palaeontologica Polonica* **57**: 561-573. doi:10.4202/app.2011.0033.

Forster CA, Sampson SD. 2002. Phylogeny of the horned dinosaurs (Ornithischia: Ceratopsidae). *Journal of Vertebrate Paleontology* **22(supplement to 3)**:54A.

Fowler DW, Freedman-Fowler E. 2020. Transitional evolutionary forms in chasmosaurine ceratopsid dinosaurs: evidence from the Campanian of New Mexico. *PeerJ* 8(e9251).

Fowler DW. 2017. Revised geochronology, correlation, and dinosaur stratigraphic ranges of the Santonian-Maastrichtian (Late Cretaceous) formations of the Western Interior of North America. *PLoS ONE* **12(11)**: e0188426. https://doi.org/10.1371/journal.pone.0188426

Frederickson JA, Tumarkin-Deratzian AR. 2014. Craniofacial ontogeny in *Centrosaurus apertus*. *PeerJ* **2**:e252. DOI 10.7717/peerj.252.

Freedman Fowler EA, Horner JR. 2015. A New Brachylophosaurin Hadrosaur (Dinosauria: Ornithischia) with an Intermediate Nasal Crest from the Campanian Judith River Formation of Northcentral Montana. *PLoS ONE* **10(11)**: e0141304. DOI 10.1371/journal.pone.0141304.

Freeman BG, Strimas-Mackey M, Miller ET. 2022. Interspecific competition limits bird species' ranges in tropical mountains. *Science* **377:**416-420.

Galton PM. 1974. The ornithischian dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight. *Bulletin of the British Museum (Natural History) Geology* London. **(5)1**:1-152.

Gates TA, Prieto-Márquez A, Zanno LE. 2012. Mountain building triggered late cretaceous North American megaherbivore dinosaur radiation. *PLoS One*. 2012;**7(8):**e42135. doi: 10.1371/journal.pone.0042135.

Gates TA, Sampson SD. 2007. A new species of *Gryposaurus* (Dinosauria: Hadrosauridae) from the late Campanian Kaiparowits Formation, southern Utah, USA. *Zoological Journal of the Linnean Society* **151(2)**:351–376. doi:10.1111/j.1096-3642.2007.00349.x

Gates TA, Sampson SD, Zanno LE, Roberts EM, Eaton JG, Nydam RL, Hutchison JH, Smith JA, Loewen MA, Getty MA. 2010 Biogeography of terrestrial and freshwater vertebrates from the late Cretaceous (Campanian) Western Interior of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* **291**:371–387.

Gilmore CW. 1946. A new carnivorous dinosaur from the Lance Formation. *Smithsonian Miscellaneous Collections* **106:**1-19.

Godfrey SJ, Holmes RB. 1995. Cranial morphology and systematics of *Chasmosaurus* (Dinosauria: Ceratopsidae) from the Upper Cretaceous of Western Canada. *Journal of Vertebrate Paleontology* **15:**726-742.

Goloboff PA, Farris JS, Nixon KC. 2003. TNT: Tree Analysis Using New Technologies. Program and documentation available from the authors and at http://www.zmuc.dk/public/phylogeny/tnt/. Accessed 2022 Dec 24.

Goloboff PA, Farris JS, Nixon KC. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* **24(5)**:774–786.

Goodwin MB, Clemens WA, Horner JR, Padian K. 2006. The smallest known *Triceratops* skull: new observations on ceratopsid cranial anatomy and ontogeny. *Journal of Vertebrate Paleontology* **26(1)**:103-112.

Goodwin MB, Deino AL. 1989. The first radiometric ages from the Judith River Formation (Upper Cretaceous), Hill County Montana. *Canadian Journal of Earth Science* **26**:1384–1389.

Goodwin MB, Horner JR. 2008. Ontogeny of Cranial Epi-Ossifications in *Triceratops*. *Journal of Vertebrate Paleontology* **28(1)**:134–144.

Haq BU, Hardenbol J, Vail PR. 1987. Chronology of Fluctuating Sea Levels Since the Triassic. *Science* **235**: 1156–1167. DOI 10.1126/science.235.4793.1156.

Hatcher JB, Marsh OC, Lull RS. 1907. The Ceratopsia. *United States Geological Survey Monograph* **49**: 300 p.

Hay WW, Eicher D, Diner R, Caldwell W, and Kauffman E. 1993. Physical oceanography and water masses in the Cretaceous Western Interior Seaway. Evolution of the Western Interior Basin: Geological Association of Canada St. John's, 297-318.

He HY, Wang XL, Zhou ZH, Wang F, Boven A, Shi GH, Zhu RX. 2004. Timing of the Jiufotang Formation (Jehol Group) in Liaoning, northeastern China, and its implications. *Geophysical Research Letters* **31(13)**:1709. Bibcode:2004GeoRL..3112605H. doi:10.1029/2004GL019790.

Hedrick BP, Dodson P. 2013. Lujiatun Psittacosaurids: Understanding Individual and Taphonomic Variation Using 3D Geometric Morphometrics. *PLoS ONE* **8(8)**:e69265. Bibcode:2013PLoSO...869265H. doi:10.1371/journal.pone.0069265.

Hejase HA, Salman-Minkov A, Campagna L, Hubisz MJ, Lovette IJ, Gronau I, Adam Siepel A. 2020. Genomic islands of differentiation in a rapid avian radiation have been driven by recent selective sweeps. Proceedings of the National Academy of Sciences **117(48)**:30554-30565. https://www.pnas.org/doi/epdf/10.1073/pnas.2015987117

Hicks FJ, Fastovsky D, Nichols DJU, Watabe M. 2001. Magnetostratigraphic correlation of Late Creta-ceous dinosaur-bearing localities in the Nemegt and Ulan Nuur Basins, Gobi Desert, Mongolia. *Geological Society of America Programs Abstracts* **A**:323.

Holliday CM, Porter WR, Vliet KA, Witmer LM. 2019. The frontoparietal fossa and dorsotemporal fenestra of archosaurs and their significance for interpretations of vascular and muscular anatomy in dinosaurs. *The Anatomical Record*, 303(4):1060-1074. DOI.org/10.1002/ar.24218.

Holmes RB, Ryan MJ, Murray AM. 2005. Photographic Atlas of the Postcranial Skeleton of the Type Specimen of *Styracosaurus albertensis* with Additional Isolated Cranial Elements from Alberta. *Canadian Museum of Nature, Syllogeus* **75**: 75 p.

Holmes RB, Persons WS, Rupal BS, Qureshi AJ, Currie PJ. 2020. Morphological variation and asymmetrical development in the skull of Styracosaurus albertensis. Cretaceous Research **107**:104308.

Holmes RB, Ryan MJ. 2013. The Postcranial Skeleton of *Styracosaurus albertensis*. *Kirtlandia, The Cleveland Museum of Natural History* **58**: 5–37. https://doi.org/10.1016/j.cretres.2019.104308

Horner JR. 1988. A new hadrosaur (Reptilia, Ornithischia) from the Upper Cretaceous Judith River Formation of Montana. *Journal of Vertebrate Paleontology* **8(3)**:314–312.

Irmis RB. 2007. Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology*, **27(2)**:350-361.

Jablonski D. 2008. Extinction and the spatial dynamics of biodiversity. *Proceedings of the Academy of Natural Sciences of Philadelphia* **105:**11528-11535.

Kauffman EG. 1977. Geological and Biological Overview: Western Interior Cretaceous Basin. *The Mountain Geologist* **14(3)**:75–99.

Kirkland J I. DeBlieux DD. 2010. New basal centrosaurine ceratopsian skulls from the Wahweap Formation (Middle Campanian), Grand Staircase– Escalante National Monument, southern Utah. In: Ryan MJ, Chinnery-Allgeier B, Eberth DA, eds. *New*

Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium. Bloomington: Indiana University Press, 117 – 140.

Knapp A, Knell RJ, Farke AA, Loewen MA, Hone DWE. 2018. Patterns of divergence in the morphology of ceratopsian dinosaurs: sympatry is not a driver of ornament evolution. *Proceedings of the Royal Society B* **285(1875)**:20180312.

Krassilov VA. 1981. Changes of Mesozoic vegetation and the extinction of dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 34:207-224.

Kurumada Y, Aoki S, Aoki K, Kato D, Saneyoshi M, Tsogtbaatar K, Windley BF, Ishigaki S. 2020. Calcite U–Pb age of the Cretaceous vertebrate-bearing Bayn Shire Formation in the Eastern Gobi Desert of Mongolia: usefulness of caliche for age determination. *Terra Nova* **32(4)**:246–252. doi:10.1111/ter.12456

Lambe, LM. 1902. New genera and species from the Belly River Series (mid-Cretaceous), Geological Survey of Canada Contributions to Canadian Palaeontology **3(2)**:25–81.

Lambe, LM. 1904. On the squamoso-parietal crest of the horned dinosaurs *Centrosaurus apertus* and *Monoclonius canadensis* from the Cretaceous of Alberta. *Proceedings and Transactions of the Royal Society of Canada 2* **10(4):**1–9.

Lambe LM. 1913. A new genus and species from the Belly River Formation of Alberta. *Ottawa Naturalist* ***27:****109–116.*

Lambe LM. 1915. On *Eoceratops canadensis*, gen. nov., with remarks on other genera of Cretaceous horned dinosaurs. *Canada Geological Survey Museum Bulletin* **12(24)**:1–49.

Lehman TM. 1997. Late Campanian dinosaur biogeography in the western interior of North America. In D. L. Wolberg DL. Stump E. Rosenburg GD. eds. *Dinofest International Proceedings*. Philadelphia: Academy of Natural Sciences 223-240

Lehman TM. 2001. Late Cretaceous dinosaur provinciality. In Tanke DH, and K. Carpenter K, eds. *Mesozoic Vertebrate Life.* Bloomington: Indiana University Press 310-328.

Lehman TM, Wick SL, Barnes KR. 2017. New specimens of horned dinosaurs from the Aguja Formation of West Texas, and a revision of *Agujaceratops*. *Journal of Systematic Palaeontology* **15(8)**:641-674. DOI: 10.1080/14772019.2016.1210683

Leshchinskiy SV, Fayngertz SC, Voronkevich AV, Maschenko AV, Averianov EN, Alexander O. 2000. Preliminary results of the investigation of the Shestakovo localities of Early Cretaceous vertebrates". In: Komarov AV, ed. *Materials of the Regional Conference of the Geologists of Siberia, Far East and North East of Russia* (in Russian). Tomsk: GalaPress, 363–366.

Leslie CE, Peppe DJ, Williamson TE, Heizler M, Jackson M, Atchley SC, Nordt L, Standhardt B. 2018. Revised age constraints for Late Cretaceous to early Paleocene terrestrial strata from the Dawson Creek section, Big Bend National Park, west Texas. *Geological Society of America Bulletin* **130(7-8)**:1143–1163. doi: https://doi.org/10.1130/B31785.1

Lijtmaer DA, Sharpe NM, Tubaro PL, Lougheed SC. 2004. Molecular phylogenetics and diversification of the genus *Sporophila* (Aves: Passeriformes). *Molecular Phylogenetics and Evololution* **33(3):**562-79. doi: 10.1016/j.ympev.2004.07.011. PMID: 15522788.

Lilligraven JA, Ostresh LM. 1990. Late Cretaceous (earliest Campanian/Maastrichtian) evolution of western shorelines of the North American Western Interior Seaway in relation to known mammalian faunas. In Bown TM. and Rose DK. eds. *Dawn of the Age of Mammals in the northern part of the Rocky Mountain Interior, North America.* Geological Society of America Special Paper 243:1-30

Linnert C, Robinson SA, Lees JA, Brown PR, Pérez-Rodríguez I, Petrizzo MR, Falzoni F, Littler K, Arz JA, Russel EE. 2014. Evidence for global cooling in the Late Cretaceous. *Nature Communications* **5**:4194. DOI 10.1038/ncomms5194.

Lockshin SN, Yacobucci MM, Gorsevski P, Gregory A. 2017. Spatial characterization of cretaceous Western Interior Seaway paleoceanography using foraminifera, fuzzy sets and Dempster–Shafer theory. *GeoResJ* **(14)**:98-120. https://doi.org/10.1016/j.grj.2017.10.001.

Loewen MA, Farke AA, Sampson SD, Getty MA, Lund ED, O'Connor PM. 2013. Ceratopsid Dinosaurs from the Grand Staircase of Southern Utah. In: Titus AL, and Loewen MA, eds. *At the Top of the Grand Staircase: The Late Cretaceous of Southern Utah.* Bloomington: Indiana University Press, 488–503.

Loewen MA, Sampson SD, Lund EK, Farke AA, de Leon C, Aguillón Martínez MC, Rodríguez de la Rosa RA, Getty MA, Eberth DA. 2010. Horned dinosaurs (Ornithischia: Ceratopsidae) from the Upper Cretaceous (Campanian) Cerro del Pueblo Formation, Coahuila, Mexico. In: Ryan MJ, Chinnery-Allgeier B, Eberth DA, eds. *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*. Bloomington: Indiana University Press, 99–116.

Longrich NR. 2013. *Judiceratops tigris*, a New Horned Dinosaur from the Middle Campanian Judith River Formation of Montana. *Bulletin of the Peabody Museum of Natural History* **54(1)**: 51–65. DOI 10.3374/014.054.0103.

Longrich NR, Field D. 2012. *Torosaurus* is not *Triceratops*: Ontogeny in Chasmosaurine Ceratopsids as a Case Study in Dinosaur Taxonomy. *PLoS ONE* **7:**e32623. doi:32610.31371/journal.pone.0032623.

Longrich NR, Sankey JT, Tanke DH. 2010. *Texacephale langstoni*, a new genus of pachycephalosaurid (Dinosauria: Ornithischia) from the upper Campanian Aguja Formation, southern Texas, USA. *Cretaceous Research* **31:**274-284.

Lowery CM, Leckie RM, Bryant R, Elderbak K, Parker A, Polyak DE, Schmidt M, Snoeyenbos-West O, Sterzinar E. 2018. The Late Cretaceous Western Interior Seaway as a model for oxygenation change in epicontinental restricted basins, *Earth-Science Reviews* **(177)**:545-564. https://doi.org/10.1016/j.earscirev.2017.12.001**.**

Lucas SG, Sullivan RM, Lichtig AJ. Dalman SG, Jasinski SE. 2016. Late Cretaceous dinosaur biogeography and endemism in the Western Interior Basin, North America: a critical re-evaluation. *New Mexico Museum of Natural History and Science Bulletin* **71**: 195-213.

Lull RS. 1933. A Revision of the Ceratopsia or Horned Dinosaurs. *Memoirs of the Peabody Museum of Natural History* **Vol III (3)**: 175 p.

Lund EK, O'Connor PM, Loewen MA, Jinnah ZA. 2016a. A New Centrosaurine Ceratopsid, *Machairoceratops cronusi* gen et sp. nov., from the Upper Sand Member of the Wahweap Formation (Middle Campanian), Southern Utah. *PLoS ONE* **11(5)**: e0154403. DOI 10.1371/journal.pone.0154403.

Lund EK, Sampson SD, Loewen MA. 2016b. *Nasutoceratops titusi* (Ornithischia, Ceratopsidae), a basal centrosaurine ceratopsid from the Kaiparowits Formation, southern Utah. *Journal of Vertebrate Paleontology* **36(2)**: e1054936-2.

Lund EK. 2011. *Nasutuceratopsi titusi*, a New Basal Centrosaurine Dinosaur (Ornithischia: Ceratopsidae) from the Upper Cretaceous Kaiparowits Formation, southern Utah. M. A. thesis. University of Utah, 161 p.

Maddison WP, Maddison DR. 2011. Mesquite: a modular system for evolutionary analysis. Version 3.02 http://mesquiteproject.org. Accessed 2022 Dec 24.

Maidment SCR, Barrett PM. 2011. A new specimen of *Chasmosaurus belli* (Ornithischia: Ceratopsidae), a revision of the genus, and the utility of postcrania in the taxonomy and systematics of ceratopsid dinosaurs. *Zootaxa* **2963**:1–47.

Maiorino L, Farke AA, Piras P, Ryan MJ, Terris KM, Kotsakis T. 2013. The evolution of squamosal shape in ceratopsid dinosaurs (Dinosauria, Ornithischia). *Journal of Vertebrate Paleontology* **33(6)**:1385-93.

Makovicky PJ. 2001. A *Montanoceratops cerorhynchus* (Dinosauria: Ceratopsia) braincase from the Horseshoe Canyon Formation of Alberta. Mesozoic Vertebrate Life, D. H. Tanke and K. Carpenter (eds.), Indiana University Press, Bloomington 243-262

Mallon JC. 2019. Competition structured a Late Cretaceous megaherbivorous dinosaur assemblage. *Scientific Reports* **9:**15447. https://doi.org/10.1038/s41598-019-51709-5

Mallon JC, Anderson JS. 2013. Skull Ecomorphology of Megaherbivorous Dinosaurs from the Dinosaur Park Formation (Upper Campanian) of Alberta, Canada. *PLoS ONE* **8(7)**: e67182.

Mallon JC, Ott CJ, Larson PL, Iuliano EM, Evans DC. 2016. *Spiclypeus shipporum* gen. et sp. nov., a boldly audacious new chasmosaurine ceratopsid (Dinosauria: Ornithischia) from the Judith River Formation (Upper Cretaceous: Campanian) of Montana, USA. *PLoS ONE* **11(5)**:e0154218.

Mallon JC, Ryan MJ, Campbell JA. 2015. Skull ontogeny in *Arrhinoceratops brachyops* (Ornithischia: Ceratopsidae) and other horned dinosaurs. *Zoological Journal of the Linnean Society* **175(4)**: 910–929. DOI 10.1111/zoj.12294.

Marsh OC. 1888. A new family of horned dinosaurs from the Cretaceous. *American Journal of Science (series 3)* **36**:477–478.

Marsh OC. 1890. Additional characters of the Ceratopsidae, with notice of new Cretaceous dinosaurs. *American Journal of Science (series 3)* **39**:418–426.

Marsh OC. 1891a. I.–The gigantic Ceratopsidæ, or horned Dinosaurs, of North America. *Geological Magazine* **8(5)**:193–199.

Marsh OC. 1891b, "Notice of new vertebrate fossils", *The American Journal of Science, series 3* **42:**265-269

McDonald AT, Horner JR. 2010. New material of *Styracosaurus ovatus* (Ceratopsia: Centrosaurinae) from the Two Medicine Formation of Montana, with a taxonomic revision and hypotheses concerning centrosaurine evolution. In: Ryan MJ, Chinnery-Allgeier B, Eberth DA, eds. *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*. Bloomington: Indiana University Press, 156–158.

McKnight MW, White PS, McDonald RI, Lamoreux JF, Sechrest W, Ridgely RS, Stuart SN. 2007. Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. *PLoS biology* **5:**e272.

Miller FL. 1986. Asymmetry in antlers of barren-ground caribou, Northwest Territories, Canada. *Rangifer Special Issue* **1**:195–202.

Miller KG, Kominz MA, Browning JV, Wright JD, Mountain GS, Katz ME, Sugarman PJ, Cramer BS, Christie-Blick N, Pekar SF. 2005. The phanerozoic record of global sea-level change. *Science* **310**: 1293–1298.

Müller RD, Mather B, Dutkiewicz A, Keller T, Merdith A, Gonzolez CM, Gorczy W, Zahirovic S. 2022. Evolution of Earth's tectonic carbon conveyor belt. *Nature* **605:**629–639. https://doi.org/10.1038/s41586-022-04420-

Nesbitt SJ, Denton RK, Loewen MA, Brusatte SL, Smith ND, Turner AH, Kirkland JI, McDonald AT, Wolfe DG. 2019. A mid-Cretaceous tyrannosauroid and the origin of North American end-Cretaceous dinosaur assemblages. *Nature Ecology and Evolution* **3**:892–899.

Nydam, R.L. 2013. Lizards and Snakes from the Cenomanian through Campanian of Southern Utah: Filling the Gap in the Fossil Record of Squamata from the Late Cretaceous of the Western Interior of North America; In, A. Titus and M. Loewen (eds) *At the Top of the Grand Staircase, The Late Cretaceous of Southern Utah.* Indiana University Press, Bloomington. pp. 370-423.

Nydam, RL, Rowe TB, Cifelli CL. 2013. Lizards and snakes of the Terlingua Local Fauna (late Campanian), Aguja Formation, Texas with comments on the distribution of paracontemporaneous squamates throughout the Western Interior of North America. *Journal of Vertebrate Paleontology* **33(5)**:1081–1099. DOI:10.1080/02724634.2013.760467

O'Connor, LK, Robinson SA, Naafs BDA, Jenkyns HC, Henson S, Clarke M, Pancost RD. 2019. Late Cretaceous temperature evolution of the southern high latitudes: A TEX86 perspective. *Paleoceanography and Paleoclimatology* **34**. https://doi.org/ 10.1029/2018PA003546.

Ogunyomi O, Hills LV. 1977. Depositional environments, Foremost Formation (Late Cretaceous), Milk River area, southern Alberta. *Bulletin of Canadian Petroleum Geology* **25**:928-968.

Osborn HF. 1923. A new genus and species of Ceratopsia from New Mexico, *Pentaceratops sternbergii*". *American Museum Novitates* **93:**1-3

Ősi A, Butler RJ. Weishampel DB. 2010. A Late Cretaceous ceratopsian dinosaur from Europe with Asian affinities. *Nature.* **465(7297)**:466–468. Bibcode:2010 Nature 465.466O. doi:10.1038/nature09019. PMID 20505726. S2CID 205220451.

Owen R. 1842. Report on British Fossil Reptiles Part II. *Report of the Eleventh Meeting of the British Association for the Advancement of Science*, Plymouth 24 July 1841:60–204.

Padian K, May CL. 1993. The earliest dinosaurs. In: Lucas SG, Morales M, eds. *The nonmarine Triassic.* Albuquerque: New Mexico Museum of Natural History and Science Bulletin Vol. 3, 379–381.

Peecook BR, Sidor CA. 2015. The first dinosaur from Washington state and a review of Pacific coast dinosaurs from North America. *PLoS ONE* **10(5)**:e0127792. doi.org/10.1371/journal.pone.0127792

Penkalski P, Dodson P. 1999. The morphology and systematics of Avaceratops, a primitive horned dinosaur from the Judith River Formation (late Campanian) of North America, with the description of a second skull. *Journal of Vertebrate Paleontology* **19**:692-711.

Qian H, Badgley C, Fox DL. 2009. The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Global Ecology and Biogeography* **18:**111-122.

Ramezani J, Beveridge TL, Rogers RR, Eberth DA, Roberts EM. 2022. Calibrating the zenith of dinosaur diversity in the Campanian of the Western Interior Basin by CA-ID-TIMS U-Pb geochronology. *Scientific Reports* 12(1):16026. doi: 10.1038/s41598-022-19896-w. PMID: 36163377; PMCID: PMC9512893.

Ree RH, Smith SA. 2008. Maximum Likelihood Inference of Geographic Range Evolution by Dispersal, Local Extinction, and Cladogenesis. *Systematic Biology* **57(1)**: 4–14.

Renne PR, Mundil R, Balco G, Min K, Ludwig KR. 2011. Joint determination of ^{40}K decay constants and ^{40}Ar/^{40}K for the Fish Canyon sanidine standard, and improved accuracy for ^{40}Ar/^{39}Ar geochronology. *Geochimica et Cosmochimica Acta* **74(18)**:5349–5367 DOI 10.1016/j.gca.2010.06.017.

Rivera-Sylva HE, Hendrick B, Dodson P. 2016. A centrosaurine (Dinosauria: Ceratopsia) from the Aguja Formation (Late Campanian) of Northern Coahuila, Mexico. *PLoS ONE* **11(4)**:e0150529

Rivera-Sylva HE, Frey E, Stinnesbeck W, Guzman-Gutirrez JR, Gonzalez-Gonzalez. 2017. Mexican ceratopsids: Considerations on their diversity and evolution. *Journal of South American Earth Sciences* **75**:66–73. doi:10.1016/j.jsames.2017.01.008.

Roberts EM, Sampson SD, Deino AL, Bowring S. 2013. The Kaiparowits Formation: a remarkable record of Late Cretaceous terrestrial environments, ecosystems and evolution in Western North America. In: Titus AL, Loewen MA, eds. *At the Top of the Grand Staircase: The Late Cretaceous of Southern Utah*. Bloomington: Indiana University Press, 85–106.

Rogers RR, Kidwell SM, Deino AL, Mitchell JP, Nelson K, Thole JT. 2016. Age, correlation, and lithostratigraphic revision of the Upper Cretaceous (Campanian) Judith River Formation in its type area (North-Central Montana), with a comparison of low- and high-accommodation alluvial records. *Journal of Geology* **124(1)**. https://doi.org/10.1086/684289

Rogers RR. 1998. Sequence analysis of the Upper Cretaceous Two Medicine and Judith River formations, Montana: nonmarine response to Claggett and Bearpaw marine cycles. *Journal of Sedimentary Research* **68 (4)**:615-631.

Rogers RR. Kidwell SM. Deino AL. Mitchell JP. Nelson K. Thole JT. 2016. Age, correlation, and lithostratigraphic revision of the Upper Cretaceous (Campanian) Judith River Formation in its type area (North-Central Montana), with a comparison of low- and high-accommodation alluvial records. *Journal of Geology* **124(1)**. https://doi.org/10.1086/684289

Ryan MJ. 2007. A new basal centrosaurine ceratopsid from the Oldman Formation, southeastern Alberta. *Journal of Paleontology* **81(2)**:376–396.

Ryan MJ, Evans DC. 2005. Ornithischian Dinosaurs. In: Currie PJ, Koppelhus E, eds. *Dinosaur Provincial Park: A spectacular ancient ecosystem revealed.* Bloomington: Indiana University Press, 312-348.

Ryan MJ, Russell AP. 2005. A new centrosaurine ceratopsid from the Oldman Formation of Alberta and its implications for centrosaurine taxonomy and systematics. Canadian Journal of Earth Sciences **42(7)**:1369. Bibcode:2005CaJES..42.1369R. doi:10.1139/e05-029

Ryan MJ, Evans DC, Currie PJ, Loewen MA. 2014. A new chasmosaurine from northern Laramidia expands frill disparity in ceratopsid dinosaurs. *Naturwissenschaften* **101(6)**:505–512. DOI 10.1007/s00114-014-1183-1.

Ryan MJ, Evans DC, Shepherd KM. 2012. A new ceratopsid from the Foremost Formation (middle Campanian) of Alberta. *Canadian Journal of Earth Science* **49(10)**:1251–1262.

Ryan MJ, Holmes R, Mallon J, Loewen M, Evans DC. 2017. A basal ceratopsid (Centrosaurinae: Nasutoceratopsini) from the Oldman Formation (Campanian) of Alberta, Canada. *Canadian Journal of Earth Science* **54(1)**:1–14.

Ryan MJ, Russell AP, Eberth DA, Currie PJ. 2001. The taphonomy of a *Centrosaurus* (Ornithischia: Certopsidae) bone bed from the Dinosaur Park Formation (Upper Campanian), Alberta, Canada, with comments on cranial ontogeny. *PALAIOS* **16(5)**:482–506.

Ryan MJ, Eberth DA, Brinkman DB, Currie PJ, Tanke DH. 2010. A New *Pachyrhinosaurus*-like ceratopsid from the Upper Dinosaur Park Formation (Late Campanian) of Southern Alberta, Canada. In: Ryan MJ, Chinnery-Allgeier B, Eberth DA, eds. *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*. Bloomington: Indiana University Press, 141–155.

Ryan MJ, Russell AP, Hartman S. 2010. A new chasmosaurine ceratopsid from the Judith River Formation, Montana. In: Ryan MJ, Chinnery-Allgeier B, Eberth DA, eds. *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*. Bloomington: Indiana University Press, 181–188.

Russel DA. 1967. A census of dinosaur specimens collected in western Canada. *National Museum of Canada Natural History Papers* 36:1-13.

Russel DA. 1969. A new specimen of *Stenonychosaurus* from the Oldman Formation (Cretaceous) of Alberta. *Canadian Journal of Earth Sciences* **6(4)**:595–612.

Sampson SD. 1995. Two new horned dinosaurs from the Upper Cretaceous Two Medicine Formation of Montana; With a phylogenetic analysis of the Centrosaurinae (Ornithischia: Ceratopsidae). *Journal of Vertebrate Paleontology* **15(4)**:743–760.

Sampson SD, Loewen MA. 2010. Unraveling a radiation: a review of the diversity, stratigraphic distribution, biogeography, and evolution of horned dinosaurs (Ornithischia: Ceratopsidae). In: Ryan MJ, Chinnery-Allgeier B, Eberth DA, eds. *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*. Bloomington: Indiana University Press, 405–27.

Sampson SD, Loewen MA, Farke AA, Roberts EM, Forster CA, Smith JA, Titus AL. 2010. New horned dinosaurs from Utah provide evidence for intracontinental dinosaur endemism. *PLoS ONE* **5(9)**:e12292.

Sampson SD, Lund EK, Loewen MA, Farke AA, Clayton KE. 2013. A remarkable short-snouted horned dinosaur from the Late Cretaceous (late Campanian) of southern Laramidia. *Proceedings of the Royal Society of London B* **280(1766)**:20131186 DOI http://dx.doi.org/10.1098/rspb.2013.1186.

Sampson SD, Lund EK, Loewen MA, Farke AA, Clayton KE. 2013. A remarkable short-snouted horned dinosaur from the Late Cretaceous (late Campanian) of southern Laramidia. *Proceedings of the Royal Society of London B* **280(1766)**:20131186 DOI http://dx.doi.org/10.1098/rspb.2013.1186.

Sampson SD, Ryan MJ, Tanke DH. 1997. Craniofacial ontogeny in centrosaurine dinosaurs (Ornithischia: Ceratopsidae): Taxonomic and behavioral implications. *Zoological Journal of the Linnean Society* **121**:293–337.

Scannella JB, Fowler DW, Goodwin MB, Horner JR. 2014. Evolutionary trends in *Triceratops* from the Hell Creek Formation, Montana. *Proceedings of the National Academy of Sciences* **111**:10245-10250. 10.1073/pnas.1313334111.

Scott, SHW, Ryan MJ, Evans DC. 2022. Postcranial description of *Wendiceratops pinhornensis* and a taphonomic analysis of the oldest monodominant ceratopsid bonebed. *The Anatomical Record*: 1–18. https://doi.org/10.1002/ar.25045.

Seeley HG. 1887. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London* **43**:165–171.

Sereno PC. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **210**:41–83.

Sereno PC. 2010. Taxonomy, cranial morphology, and relationships of parrot-beaked dinosaurs (Ceratopsia:Psittacosaurus). In: Ryan MJ, Chinnery-Allgeier BJ, Eberth DA, eds. *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium.* Bloomington and Indianapolis: Indiana University Press, 21–58.

Sereno PC, Xijin Z, Lin T. 2009. A new psittacosaur from Inner Mongolia and the parrot-like structure and function of the psittacosaur skull. *Proceedings of the Royal Society B.* **277(1679)**:199–209. doi:10.1098/rspb.2009.0691. PMC 2842669. PMID 19535376.

Sereno PC, Zhao X, Brown L, Tan L. 2007. New psittacosaurid highlights skull enlargement in horned dinosaurs. *Acta Palaeontologica Polonica* **52(2)**:275–284.

Shuvalov VF. 2000. The Cretaceous stratigraphy and palaeobiology of Mongolia. In: Benton MJ, Kurochkin EN, Novikov IV, Shishkin MA, Unwin DA, eds. *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, 256–278.

Signor PW, Lipps JH. 1982. Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. In: Silver LT, and Schultz PH, eds. *Geological Implications of Impacts of Large asteroids and Comets on the Earth*: Geological Society of America 291-296.

Slattery JS, Cobban WA, McKinney KC, Harries PJ, Sandness AL. 2015. Early Cretaceous to Paleocene paleogeography of the Western Interior Seaway: The interaction of eustasy and tectonism. In: Bingle-Davis M, ed. *68th Annual Field Conference Guidebook*. Casper, Wyoming: Wyoming Geological Association, 22–60.

Sternberg CM. 1950. *Pachyrhinosaurus canadensis*, representing a new family of the Ceratopsia, from southern Alberta. *National Museum of Canada Bulletin* **118**:109–120.

Słowiak J, Tereshchenko VS, Fostowicz-Frelik Ł. 2019. Appendicular skeleton of *Protoceratops andrewsi* (Dinosauria, Ornithischia): comparative morphology, ontogenetic changes, and the implications for non-ceratopsid ceratopsian locomotion. PeerJ, 22(7):e7324. doi: 10.7717/peerj.7324. PMID: 31367485; PMCID: PMC6657679.

Spicer RA, Herman AB. 2010. The Late Cretaceous environment of the Arctic: A quantitative reassessment based on plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* **295:**423-442.

Steel RJ, Plink-Bjorklund P, Aschoff J. 2012. Tidal deposits of the Campanian Western Interior Seaway, Wyoming, Utah and Colorado, USA. In Davis, Jr RA, Dalrymple RW. eds. P*rinciples of Tidal Sedimentology,* Springer 437-471. DOI 10.1007/978-94-007-0123-6_17,

Sullivan RM, Lucas SG. 2006. The pachycephalosaurid dinosaur *Stegoceras validum* from the Upper Cretaceous Fruitland Formation, San Juan Basin, New Mexico. *New Mexico Museum of Science Bulletin* **35:**329-330.

Swofford DL. 2002. PAUP: Phylogenetic Analysis Using Parsimony (and Other Methods), Version 4.0 Beta 10. *Sinauer Associates, Sunderland.*

Tang F, Luo Z-X, Zhou Z-H, You H-L, Georgi JA, Tang Z-L, Wang X-Z. 2001. Biostratigraphy and palaeoenvironment of the dinosaur-bearing sediments in Lower Cretaceous of Mazongshan area, Gansu Province, China. *Cretaceous Research* **22(1)**:115–129. doi:10.1006/cres.2000.0242

Thurber JM, Peterson RO. 1991. Changes in body size associated with range expansion in the coyote (*Canis latrans*). *Journal of Mammalogy* 750-755.

Tumarkin-Deratzian AR. 2009. Evaluation of long bone surface textures as ontogenetic indicators in centrosaurine ceratopsids. *Anatatomical Record* 292(9):1485-500. doi: 10.1002/ar.20972**.**

Warshaw EA, Fowler DW. 2022. A transitional species of *Daspletosaurus* Russell, 1970 from the Judith River Formation of eastern Montana. *PeerJ* **10**:e14461 DOI 10.7717/peerj.14461

Weishampel DB, Barrett PM, Coria RA, Le Loeuff J, Xu X, Zhao X, Sahni A, Gomani EMP, Noto CR. 2004. Dinosaur Distribution. In Weishampel DB, Dodson P, Osmólska H, eds. *The Dinosauria, Second Edition.* University of California Press, 517-606. ISBN 0-520-24209-2

Wiersma JP, Irmis RB. 2018. A new southern Laramidian ankylosaurid, *Akainacephalus johnsoni* gen. et sp. nov., from the upper Campanian Kaiparowits Formation of southern Utah, USA. *PeerJ* **6**:e5016.

Williamson TE, Carr TD. 2002. A new genus of derived pachycephalosaurian from western North America. *Journal of Vertebrate Paleontology* **22:**779-801.

Wilson JA. 2006. Anatomical Nomenclature of Fossil Vertebrates: Standardized Terms or Lingua Franca. *Journal of Vertebrate Paleontology* **26(3)**:511–518.

Wilson JP, Ryan MJ, Evans DC. 2020. A new, transitional centrosaurine ceratopsid from the Upper Cretaceous Two Medicine Formation of Montana and the evolution of the '*Styracosaurus*-line' dinosaurs. *Royal Society Open Publishing* **7(4)**:200284. doi:10.1098/rsos.200284

Wilson JP, Scannella JB. 2021. Comparative cranial osteology of subadult eucentrosauran ceratopsid dinosaurs from the Two Medicine Formation, Montana, indicates sequence of ornamentation development and complex supraorbital ontogenetic change. *Acta Palaeontologica Polonica* 66(4):797-814. doi:https://doi.org/10.4202/app.00797.2020

Witmer LM. 1997. The Evolution of the Antorbital Cavity of Archosaurs: A Study in Soft-Tissue Reconstruction in the Fossil Record with an Analysis of the Function of Pneumaticity. *Journal of Vertebrate Paleontology* **17(sup001):** 1–76 DOI 10.1080/02724634.1997.10011027.

Witmer LM. 2001. Nostril position in dinosaurs and other vertebrates and its significance for nasal function. *Science* doi: 10.1126/science.1062681

Wolfe DG, Kirkland JI, Smith D, Poole K, Chinnery-Allgeier BJ, McDonald A. 2010. *Zuniceratops christopheri*: the North American ceratopsid sister taxon reconstructed on the basis of new data. In: Ryan MJ, Chinnery-Allgeier BJ, Eberth DA, eds. *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium.* Bloomington and Indianapolis: Indiana University Press, 91–98.

Woolley CH, Smith ND, Sertich JJW. 2020. New fossil lizard specimens from a poorly-known squamate assemblage in the Upper Cretaceous (Campanian) San Juan Basin, New Mexico, USA. PeerJ 8:e8846. doi: 10.7717/peerj.8846.

Wu X-C. Brinkman DB. Eberth DA. Braman DR. 2007. A new ceratopsid dinosaur (Ornithischia) from the uppermost Horseshoe Canyon Formation (upper Maastrichtian), Alberta, Canada. *Canadian Journal of Earth Sciences*. **44(9):**1243–1265. Bibcode:2007CaJES..44.1243W. doi:10.1139/E07-011

Xu X. Forster CA. Clark, JM. Mo J. 2006. A basal ceratopsian with transitional features from the Late Jurassic of northwestern China. *Proceedings of the Royal Society B: Biological Sciences* **273(1598)**:2135-2140. doi:10.1098/rspb.2006.3566

Xu, X, Wang K, Zhao X, LD. 2010. First ceratopsid dinosaur from China and its biogeographical implications. *Chinese Science Bulletin*. **55:**1631–1635.

You H-L, Li D, Ji Q, Lamanna H, Dodson P. 2005. On a new genus of basal Neoceratopsian dinosaur from the Early Cretaceous of Gansu Province, China. *Acta Geologica Sinica* 79(5):593–597.

You H-L, Tanque K, Dodson P. 2010. A new species of *Archaeoceratops* (Dinosauria: Neoceratopsia) from the Early Cretaceous of the Mazongshan area, northwestern China. In: Ryan MJ, Chinnery-Allgeier BJ, Eberth DA, eds. *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium.* Bloomington and Indianapolis: Indiana University Press, 59–67. ISBN 978-0-253-35358-0.

Young CC. 1958. The dinosaur remains of Laiyang, Shantung. *Palaeontologia Sinica Series C* **16**:53–159.

Yu C. Prieto-Marquez A. Chinzorig T. Zorigt B. Norell MA. 2020. A neoceratopsian dinosaur from the early Cretaceous of Mongolia and the early evolution of ceratopsia. *Communications Biology* **3(10)**:1038/s42003-020-01222-7.

Zhang L, Hay WW, Wang C, Gu X. 2019. The evolution of latitudinal temperature gradients from the latest Cretaceous through the Present. *Earth-Science Reviews* **189:**147-158.

Zhao X, Cheng Z, Xu X. 1999. The Earliest Ceratopsian from the Tuchengzi Formation of Liaoning, China. *Journal of Vertebrate Paleontology* **19(4)**:681–691. http://www.jstor.org/stable/4524038

Zheng W, Jin X, Xu X. 2015. A psittacosaurid-like basal neoceratopsian from the Upper Cretaceous of central China and its implications for basal ceratopsian evolution. *Scientific reports* **5(14190)**:1-9; doi:10.1038/srep14190

Zhong Y, Huyskens MH, Yin Q-Z, Wang Y, Ma Q, Xu Y-G. 2021. High-precision geochronological constraints on the duration of “Dinosaur Pompeii” and the Yixian Formation. *National Science Review* **8(6)**:nwab063. doi:10.1093/nsr/nwab063. ISSN 2095-5138. PMC 8288181. PMID 34691675.