WINDOWS INTO SAUROPSID AND SYNAPSID EVOLUTION
Essays in honor of Prof. Louis L. Jacobs, pp. 151–165, 2023

A NEW LATE CRETACEOUS LEPTOCERATOPSID (DINOSAURIA: CERATOPSIA) FROM THE OLDMAN FORMATION (CAMPANIAN) OF ALBERTA, CANADA

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ABSTRACT Leptoceratopsid ceratopsians are poorly known from the Upper Cretaceous fossil record of the Western Interior of North America. The description of two leptoceratopsid frontals, ROMVP 66302, a left frontal from the holotype *Prenoceratops* bonebed in the Two Medicine Formation of Montana and TMP 2011.053.0027, a right leptoceratopsid frontal from the lower unit of the Oldman Formation (~77 Ma) of Alberta allows for the re-evaluation of potentially informative frontal phylogenetic characters. Straightness of the anterior margin of the frontal depression has been used to help distinguish *Cerasinops* and *Prenoceratops* from other leptoceratopsids in which the margin is rostrally convex. While the margin can indeed be considered straight in the holotype and previously referred specimens of *Prenoceratops*, this feature is distinctly crescentic in the slightly smaller ROMVP 66302. The apparent ontogenetic variability within *Prenoceratops* suggests that the condition of the margin should be carefully coded using only adult specimens. The right leptoceratopsid frontal TMP 2011.053.0027 has several unique features, including the presence of a transverse ridge that extends perpendicularly across the dorsal surface from the medial margin to the anterodorsal border of the orbit. The transverse ridge is separated from the crescentic anterior border of the frontal depression by a narrow band of smooth bone. The transverse ridge and raised anterior margin of the frontal depression both diverge from the same point on the slightly raised medial frontal margin. No other leptoceratopsid frontal presents this combination of features, leading us to assign the specimen to the new taxon *Gremlin slobodorum*.

KEYWORDS Ceratopsia, Leptoceratopsidae, Campanian, Alberta

INTRODUCTION

Leptoceratopsidae consists of non-ceratopsid, typically small-bodied neoceratopsians that are largely restricted to the Upper Cretaceous of western North America (Fig. 1) and Asia. However, a leptoceratopsid maxilla fragment (YPM-PU 24964) has been collected from the Campanian Tar Heel Formation (Black Creek Group) of North Carolina (Longrich 2016) and leptoceratopsid-like teeth and vertebrae have been found in the lower Campanian of the Kristianstad Basin of southern Sweden (Lindgren et al. 2007).

In North America, Maastrichtian strata have been the richest source of leptoceratopsids, including *Leptoceratops gracilis* Brown 1914 from the Lancian North American Land Vertebrate Age (NALVA) and *Montanoceratops cerorhynchus* Brown and Schlaikjer 1942 from the Edmontonian NALVA. *Leptoceratops* is known in Alberta from several partial or complete skeletons (i.e., AMNH 5205, CMN 8887, CMN 8888, CMN 8889) from the lower Scollard Formation (Eberth et al. 2013); in Montana from a partial skull from the upper half of the Hell Creek Formation in eastern Carter County ((UWGM-200) and an isolated tooth from ~75 m below the K-Pg boundary (UWGM-2), also from the Hell Creek Formation (Ott 2007); and in Wyoming from a partial skeleton (PU 18133) from the Lance Formation of the Bighorn Basin (Ostrom 1978) and an isolated tooth (AMNH

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2571; McKenna and Love 1970) from the Pinyon Conglomerate in the Jackson Hole area. *Montanoceratops* is known in Alberta from a braincase (AMNH 5244), from the upper Tolman Member of the Horseshoe Canyon Formation (Makovicky 2001), and in Montana from the holotype skeleton (AMNH 5464) and a referred partial skeleton (MOR 542; Chinnery and Weishampel (1998)), both from the same locality in the St Mary River Formation. A partial skeleton from the Maastrichtian lower Willow Creek Formation of Alberta (TMP 1988.011.0001) that was previously referred to *Montanoceratops* by Ryan and Currie (1998) based on its field identification, needs re-evaluation. *Ferrisaurus sustutensis* Arbour and Evans 2019 is known from a single partial skeleton (RBCM P900) from British Columbia. Although its exact stratigraphic position is unknown, it has been identified as coming from the Tatlatui Member of the Tango Creek Formation that straddles the Campanian-Maastrichtian boundary in this part of the Sustut Basin (Arbour et al. 2020).

Campanian-aged leptoceratopsids from the Judithian NALVA include *Cerasinops hodgskissi* Chinnery and Horner 2007, *Prenoceratops pieganensis* Chinnery 2004 and *Unescoceratops koppelhusae* Ryan, Evans, Currie, Brown, and Brinkman 2012. *Cerasinops* from the lowermost Two Medicine Formation of Montana (Fig. 2) is known from the holotype (MOR 300) consisting of an associated skull and skeleton from Teton County and two partial skeletons (USNM 13863 and USNM 13864) from Pondera County (Chinnery and Horner 2007). *Prenoceratops* is known from four partial skeletons collected from a bonebed from the upper Two Medicine Formation of Montana on the Blackfeet Reservation, Pondera County (Fig. 2) and acquired by Canada Fossils (CF). Some of this material was incorporated into the composite mounts MNHM 000573-00000 and TCM 2001.96.4, the latter of which includes the holotype fused articular and surangular. The remaining Montanan *Prenoceratops* material was acquired by the Royal Ontario Museum, Ontario, before Canada Fossils went out of business. The isolated frontal TMP 1987.089.0008 collected from the upper unit (Dinosaur Park Formation equivalent) of the Oldman Formation has been referred to *Prenoceratops* sp. (Miyashita et al. 2010). *Unescoceratops* is known from the Campanian middle Dinosaur Park Formation (DP Fm) from the holotype dentary (TMP 1995.012.0006) collected from Bonebed 55, Steveville region of Dinosaur Provincial Park (DPP), Alberta (Fig. 2), and a partial dentary (TMP 1974.010.031) also collected from the DP Fm of DPP.

The oldest known leptoceratopsid is *Gryphoceratops morrisoni* Ryan, Evans, Currie, Brown, and Brinkman 2012, a species only represented by the holotype dentary (ROMVP 56635) collected from the Santonian of the Deadhorse Coulee Member of the Milk River Formation, Black Coulee, Warner County, Alberta (Fig. 2).

Multiple Asian leptoceratopsid taxa are also known. *Ischioceratops zhuchengensis* He, Makovicky, Wang, Chen, Sullivan, Han, and Xu, 2015 and *Zhuchengceratops inexpectus* Xu, Wang, Zhao, Sullivan, and Chen, 2010 are both known from partially articulated skeletons from the Maastrichtian Xingezhuang Formation of Shandong, China. Taxa from outside China include the large-bodied *Udanoceratops tschizhovi* Kurzanov 1992 (Djadokhta Formation; Campanian), known from a relatively complete skull from Mongolia.

In the southern hemisphere, the problematic taxon *Serendipaceratops arthurcclarkei* is based on an isolated ulna from the Aptian Wonthangii Formation and a referred ulna from the Aptian-Albian Eumaralla Formation of Australia. These ulnae have been reported to have leptoceratopsid-like affinities (Rich and Vickers-Rich 2003), although this has been challenged (Agnolin et al. 2010).

Here we describe the new leptoceratopsid frontals TMP 2011.053.0027 (Fig. 3A-C) from the lower Oldman Formation (upper Campanian) in southern Alberta and ROMVP 66302 (Fig. 4I-K) from the *Prenoceratops* bonebed in Montana. These specimens provide us with an opportunity to re-evaluate frontal characters previously considered taxonomically informative for leptoceratopsids. The recognition of TMP 2011.053.0027 as representing a new taxon also helps to narrow the temporal gap between *Gryphoceratops* and *Unescoceratops* in Alberta.

LOCALITIES

TMP 2011.053.0027 was collected from the Herronton SS zone, within 15 m of the top of the Taber Coal zone underlying the lower unit of the Campanian Oldman Formation (Fig. 1) in southern Alberta at 49°04'43"N 110°51'19"W (Fig. 2). The locality is along a southern tributary of the Milk River located on the southern Pinhorn Grazing Reserve adjacent to the Montana border (Fig. 2).

ROMVP 66302 was collected from the *Prenoceratops* bonebed in the Two Medicine Formation on the Blackfeet Indian Reservation in Pondera County, Montana (Fig. 2), approximately 50 m below the Bearpaw-Two Medicine contact (Fig. 1) (Chinnery 2004).

REGIONAL GEOLOGY

The Upper Cretaceous Belly River Group of southern Alberta is composed of, in ascending stratigraphic succession, the conformable Foremost, Oldman, and Dinosaur Park formations (Fig. 1). The Dinosaur Park Formation (76.7-74.3 Ma; Ramezani et al., 2022) preserves a transgressive sequence of up to 70 m in Dinosaur Provincial Park of channel sandstones and overbank mudstones capped by a series of coals (Lethbridge Coal Zone) that grade into the overlying marine Bearpaw Formation (Eberth 2005). The Oldman (76.7 Ma; Ramezani et al., 2022 to ~77 Ma) and Foremost (~77 to ~80.2 Ma) formations are, respectively, up to 100 and 170 m in thickness (Eberth 2005) (Fig. 1). The Oldman Formation is informally divided into the upper, middle (Comrey Sandstone) and lower units. The upper unit, as exposed in southeastern Alberta, is time equivalent to the lower Dinosaur Park Formation in Dinosaur Provincial Park (Eberth and Hamlin 1993). Overall, the middle and lower units comprise lightly colored sandstones and mudstones deposited in a regressive setting, whereas the upper unit documents the beginning of a transgressive cycle that ended with the Bearpaw Sea covering much of southeastern Alberta (Eberth 2005). The lower unit represents a time of high basin-ward extension of the sediments that make up the Belly River Group, indicating a continuing regression of the nearby Western Interior Seaway, a trend that had begun as the upper Foremost Formation was being deposited (Eberth 2005).

Many fewer diagnostic dinosaur specimens are known from the Oldman Formation than from the Dinosaur Park Formation, partly due to the fact that the former has received much less prospecting attention (Evans and Ryan, 2015). While the upper unit of the Oldman Formation preserves taxa also found in the lower Dinosaur Park Formation of Dinosaur Provincial Park, only the tyrannosaurid *Daspletosaurus torosus* Russell 1970 and the hadrosaurine hadrosaurids *Brachylophosaurus canadensis* Sternberg 1953 and *Maiasaura* sp. (McFeeters et al. 2021) are known from skeletal material from the Comrey Sandstone, and only the centrosaurine ceratopsids *Albertaceratops nesmoi* Ryan 2007 and *Wendiceratops pinhornensis* Evans and Ryan 2015, the hadrosaurine *Gryposaurus* sp. (Scott et al. 2022), and the pachycephalosaur cf. *Stegoceras* Sternberg 1945 (Scott et al. 2022), are known from diagnostic, non-tooth skeletal remains from the lower unit.

The Campanian Two Medicine Formation (82.4 to ~75.2 Ma; Ramezani et al., 2022) in northwestern Montana is time equivalent to portions of the Belly River Group of Alberta (Fig. 1). The formation can be informally split into three portions. The lower portion is about 100 m thick, records a brief transgression of the Western Interior Seaway (Rogers et al. 1993), and overlies the Virgelle Sandstone which is composed of nearshore sandstone deposits (Trexler 2001). The middle portion is approximately 225 m thick and was deposited during a transgression of the Bearpaw Sea (a portion of the Western Interior Seaway). It is characterized by siltstones and mudstones with occasional sandstone inclusions (Rogers et al. 1993). The upper portion composes about half of the entire formation, being approximately 275 m thick (Rogers et al. 1993).

The Two Medicine Formation is well known for containing a large and diverse suite of fossil taxa (You and Dodson 2004), including the leptoceratopsid ceratopsians *Cerasinops hodgskissi* Chinnery and Horner 2007 and *Prenoceratops pieganensis* Chinnery 2004, and the centrosaurine ceratopsids *Achelousaurus horneri* Sampson 1995, *Einiosaurus procurvicornis* Sampson 1995, *Stellasaurus ancellae* Wilson, Ryan and Evans 2020, and *Styracosaurus ovatus* Gilmore 1930. In the context of this study, it is notable that *Prenoceratops* was described based on material collected from the uppermost portion of the Two Medicine Formation (Chinnery 2004) (Fig. 1), approximately time equivalent to the Bearpaw Formation in Alberta. The holotype and referred specimens of *Cerasinops* were collected from the lowermost Two Medicine Formation beds that are not far above the 80 Ma ash layer reported by Chinnery (2004) (Fig. 1), and approximately time equivalent to the Foremost Formation of the Belly River Group in Alberta.

MATERIALS AND METHODS

TMP 2011.053.0027 and ROMVP 66302 were photographed using an Apple iPhone 10, measured with a standard 30-cm ruler and Vernier 150 mm digital calipers, and described following standard anatomical terminologies for ceratopsians (e.g., You and Dodson 2004; Miyashita et al. 2010). Comparative measurements for other leptoceratopsid specimens were

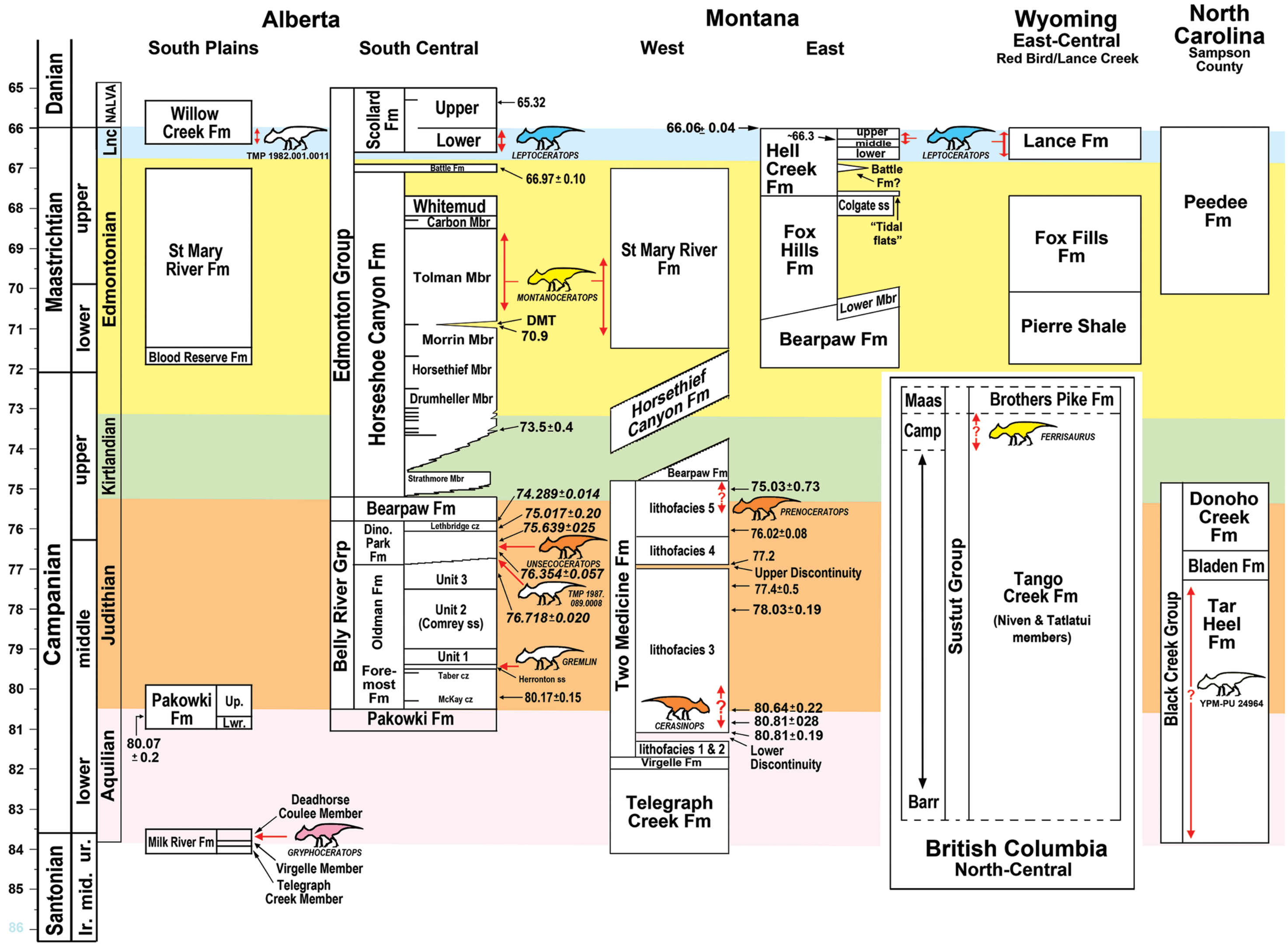

FIGURE 1. Stratigraphic and geographic distribution of North American leptoceratopsids. Chart and dates are adapted from Fowler (2017), except the British Columbia column that is adapted from Arbour et al. (2019); dates in italics for the Belly River Group of Alberta are from Ramezani et al. (2022). Note that Ramezani et al. (2022) report a more recent date from near the base of the Two Medicine Formation (CB061417-1) of ~82.42 Ma. Red arrows with question marks indicate that the range of a taxon is uncertain or that more than one specimen is known from a given formation. Note that the stratigraphic column for British Columbia (BC) is shown in an inset with its own time scale; see Evenchick and Thorkelson (2005) and Arbour et al. (2020) for discussion of the age and boundaries of the Sustut Group of BC. **Abbreviations**: **Barr**, Berriasian; **Camp**, Campanian; **cz**, coal zone; **Fm**, Formation; **Lnc**, Lancian; **lr**, lower; **Maas**, Maastrichtian; **mbr**, member; **mid**, middle; **ss**, sandstone; **ur**, upper

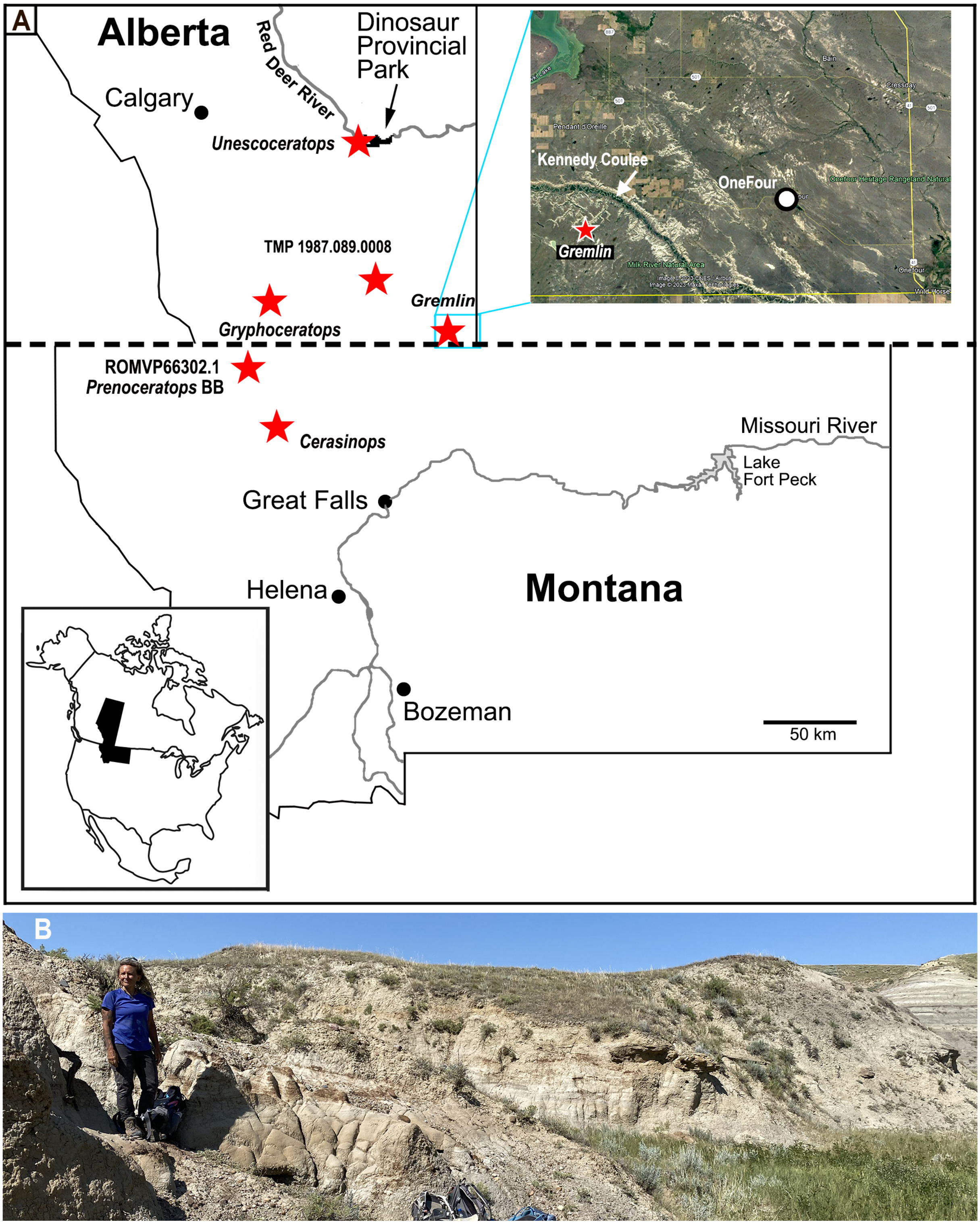

FIGURE 2. **A**, Locality map for *Cerasinop*s from Teton County, MT; *Unescoceratops* from Dinosaur Provincial Park, AB; ROMVP 66302 from the holotype *Prenoceratops* bonebed, Blackfoot Reservation, Pondera County, MT; TMP 2011.053.0027 from the South Pinhorn Grazing Reserve, AB; TMP 1987.089.0008 from Devil's Coulee, AB; and *Gryphoceratops* from Black Coulee, AB. **B**, photograph of the *Gremlin* locality with collector, Wendy Sloboda, standing where she found TMP 2011.053.0027. Map modified from Ryan et al. (2012). Southern Alberta municipal districts and counties inset photograph: Google, image © 2023 Maxar Technologies; image © 2023 CNES/Airbus; accessed March 24, 2023.

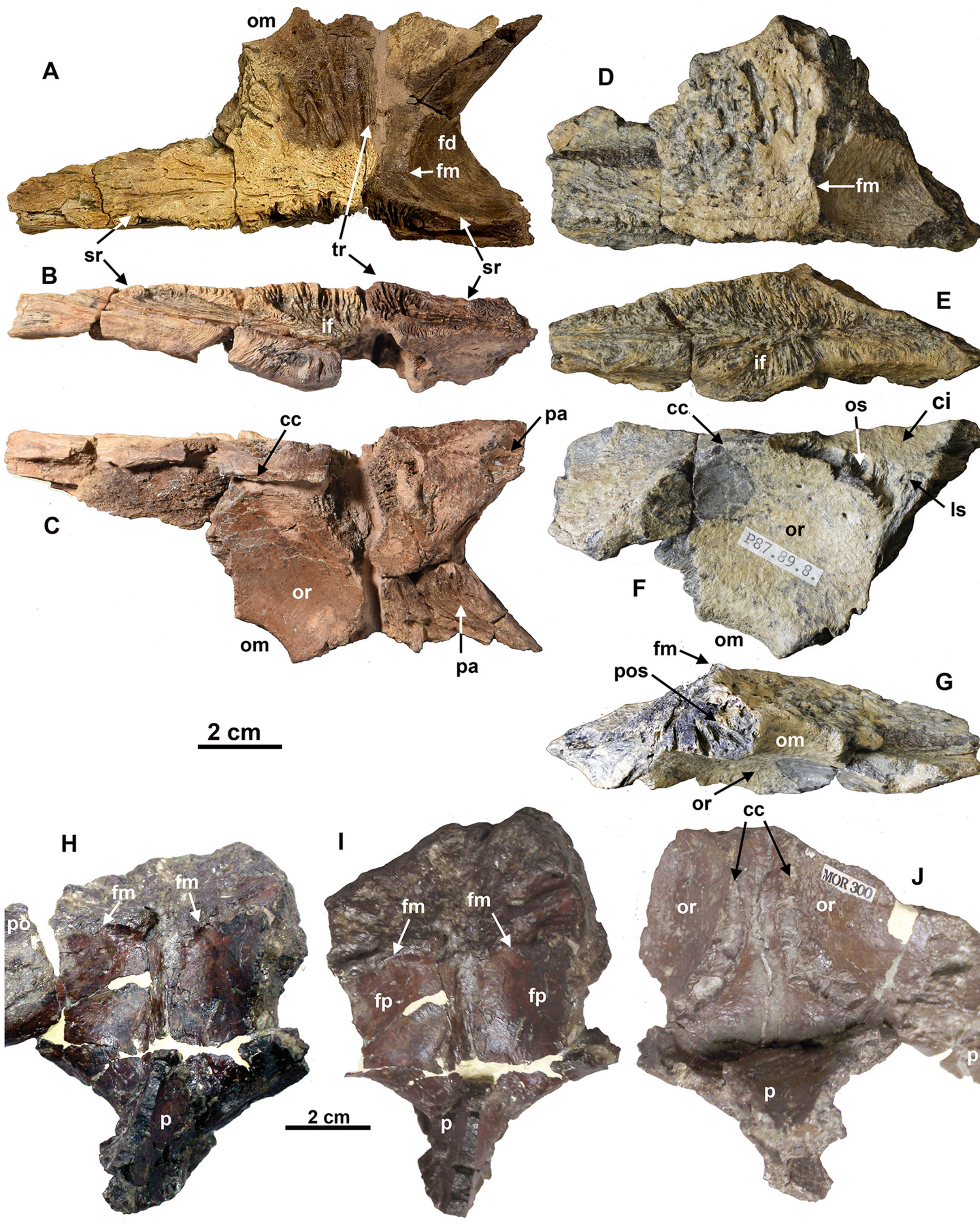

FIGURE 3. Leptoceratopsid frontals. *Gremlin slobodorum* (holotype) TMP 2011.053.0027 right frontal in **A**, dorsal; **B**, medial; and **C** ventral views. TMP 1987.089.0008 right frontal in **D**, dorsal; **E**, medial; **F**, ventral; and **G**, lateral views. *Cerasinops hodgskissi* (holotype) MOR 300 frontals in **H**, dorsal; **I**, anterodorsal; and **J**, ventral views. **Abbreviations**: **cc**, crista cranii; **ci**, impression of cerebrum; **fd**, frontal depression; **fm**, anterior margin of frontal depression; **if**, interfrontal suture; **ls**, laterosphenoid suture; **om**, orbital margin; **or**, roof of orbit; **os**, orbitosphenoid suture; **p**, parietal; **pa**, parietal suture; **po**, postorbital; **pos**, postorbital suture; **sr**, sagittal ridge; **tr**, transverse ridge.

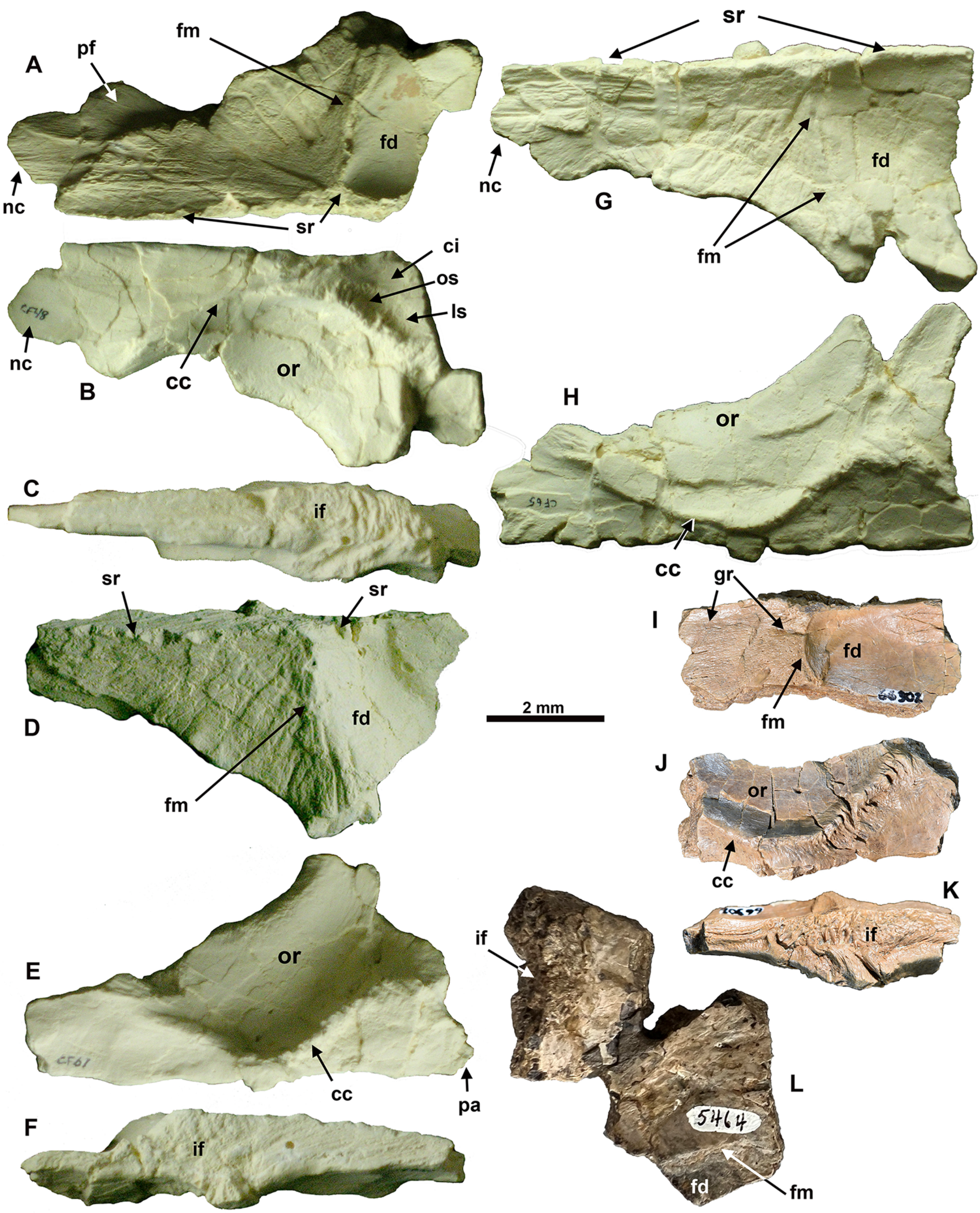

FIGURE 4. Leptoceratopsid frontals. *Prenoceratops pieganensis* CF48 (cast) right frontal in **A**, dorsal; **B**, ventral; and **C**, medial views. CF61 (cast) left frontal in **D**, dorsal; **E**, ventral; and **F**, medial views. CF65 (cast) left frontal in **G**, dorsal; and **F**, ventral views. The original frontals were incorporated into the composite mounts MNHM 000573-00000 and TCM 2001.96.4, but it is unknown which mount has which elements. ROMVP 66302 left frontal in **I**, dorsal; **J**, ventral; and **K**, medial views. *Montanoceratops cerorhynchus* (holotype) AMNH 5464 frontal in **L**, dorsal view. **Abbreviations**: **cc**, crista cranii; **ci**, impression of cerebrum; **fd**, frontal depression; **fm**, anterior margin of frontal depression; **gr**, groove; **if**, interfrontal suture; **ls**, laterosphenoid suture; **nc**, nasal contact; **or**, roof of orbit; **os**, orbitosphenoid suture; **pa**, parietal suture; **pf**, prefrontal articulation; **sr**, sagittal ridge.

obtained from the collections of the Canadian Museum of Nature, a cast of a *Leptoceratops* frontal (ROMVP 64223), and the literature. A phylogenetic analysis was conducted using the in the data matrix of Arbour and Evans (2019) with the TNT software package (Goloboff and Morles 2023).

Institutional Abbreviations — **AMNH**, American Museum of Natural History, New York, New York; **CF**, Canada Fossils, Calgary, Alberta; **CMN**, Canadian Museum of Nature, Ottawa, Ontario; **MOR**, Museum of the Rockies, Bozeman, Montana; **MNHM**, Mokpo Natural History Museum, South Korea; **PU**, Princeton University, Princeton, New Jersey; **ROM**, Royal Ontario Museum, Toronto, Ontario; **TCM**, Children's Museum of Indianapolis, Indiana; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; **USNM**, Smithsonian Institution, Washington, D.C; **UWGM**, University of Wisconsin-Madison, Madison, Wisconsin; **YPM-PU**, Yale Peabody Museum, Princeton University collection, New Haven, Connecticut.

PERMITS — TMP 2011.053.0027 was collected following the Historical Resources Act of Alberta (Canada) under the Government of Alberta Permits to Excavate Palaeontological Resources Nos. 3951-E03 (DCE) and 3950-R03 (MJR).

NOMENCLATURAL ACTS

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information is viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/".

SYSTEMATIC PALAEONTOLOGY

Dinosauria Owen, 1842
Ornithischia Seeley, 1887
Ceratopsia Marsh, 1890
Neoceratopsia Sereno, 1986
Leptoceratopsidae Makovicky, 2001
Gremlin gen. nov.
urn:lsid:zoobank.org:act:74B2D4AC-09A7-49EB-A2E6-18CDB59BF738
Diagnosis. Monotypic, as for species.
Gremlin slobodorum, gen. et. sp. nov.
urn:lsid:zoobank.org:act:698361A5-68ED-474D-91E5-6AC0D24950B0
(Fig. 3A-C)

Type and only species — *Gremlin slobodorum*

Holotype — TMP 2011.053.0027, an incomplete frontal lacking a portion of the anterolateral margin (Fig. 3A-C).

Etymology — The generic name refers to a small, troublesome, imaginary creature blamed by early 20th century aviators for mysterious mechanical faults (Massinger 1944). The specific epithet honors Ed and Wendy Sloboda for their contributions to Albertan palaeontology, and Wendy for having discovered the holotype.

Diagnosis — Leptoceratopsid ceratopsian that exhibits the following features, each of which is autapomorphic within Leptoceratopsidae: transverse ridge of the frontal that extends across the dorsal surface from the medial margin to the anterodorsal border of the orbit; the transverse ridge is separated from the raised, crescentic anterior border of the frontal depression by a narrow band of smooth bone that continues as the smooth surface of the depression; transverse ridge and anterior margin of the frontal depression both diverge from the same point on the slightly raised medial frontal margin. No other leptoceratopsid has a transverse ridge developed separately from the margin of the frontal depression. In all other leptoceratopsids, the dorsum of the frontal either has a rugose portion that contacts the margin the frontal depression (*Cerasinops*, *Prenoceratops*), or is relatively smooth (*Leptoceratops*, *Montanoceratops*).

Locality, Horizon and Age — TMP 2011.053.0027 was collected from an outcrop of the lower unit of the middle Campanian Oldman Formation (Fig. 1), located in southern Alberta at 49°04'43"N 110°51'19"W (Fig. 2).

DESCRIPTIONS

TMP 2011.053.0027

TMP 2011.053.0027 (Fig. 3A-C) is an isolated right frontal. Portions of the anterolateral margin have been lost to erosion. A mediolaterally oriented gap immediately posterior to the transverse ridge has been infilled with epoxy putty, but very little bone has been lost. As preserved, the frontal is approximately triangular in dorsal outline, with the deep,

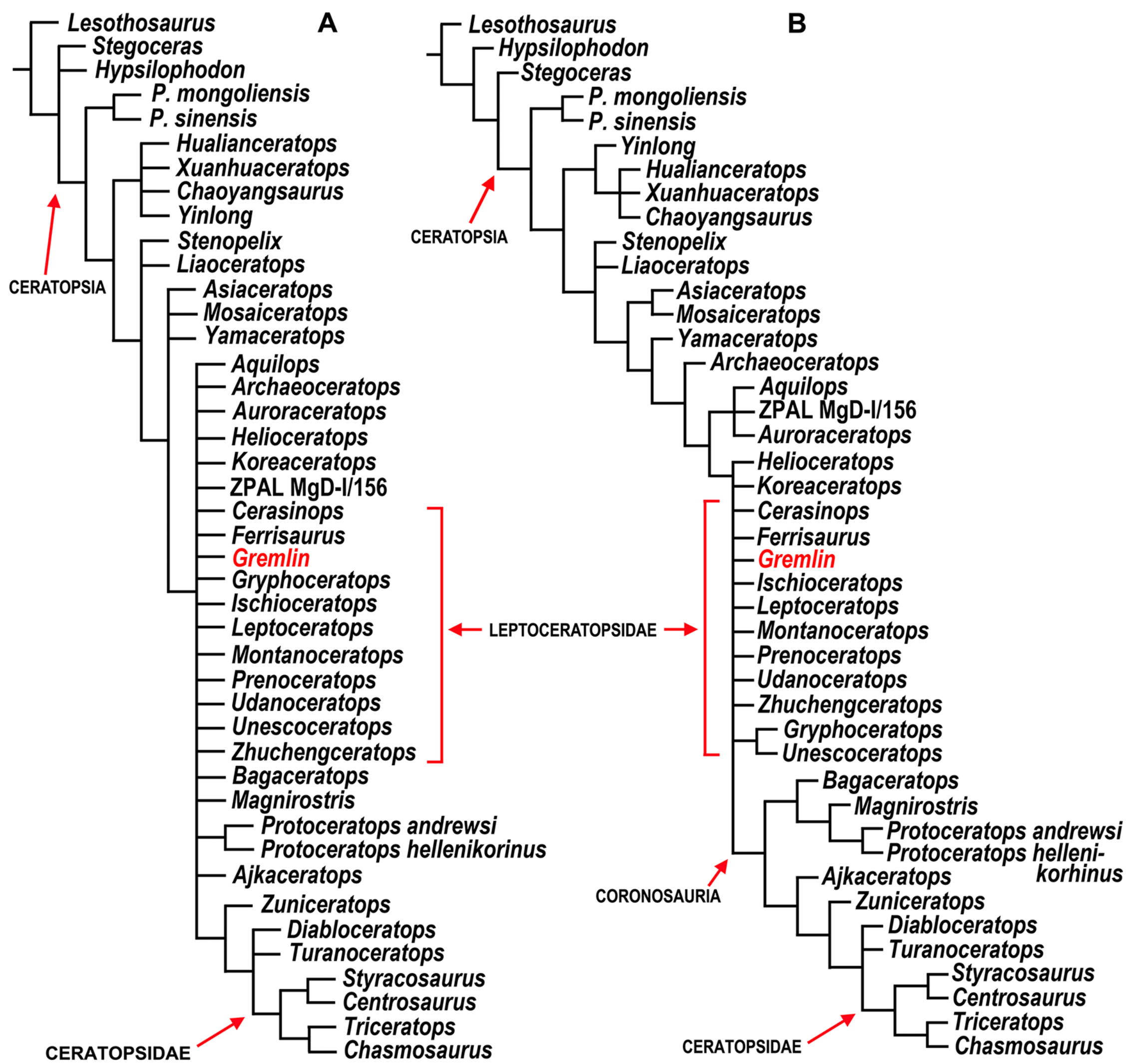

FIGURE 5. Results of a phylogenetic analysis of Ceratopsia using a matrix modified from Arbour and Evans (2019) to test rescored characters discussed in this paper. **A**, strict consensus cladogram of 746 most parsimonious trees, with a best tree length of 688 steps; consistency index (CI) of 0.45, and retention index (RI) 0.67; **B**, 50% majority rule cladogram. The taxa traditionally comprising Leptoceratopsidae are indicated in red brackets, but were not recovered as a monophyletic clade in this analysis.

almost sagittally oriented crenulated area for the left frontal. The frontal would have contacted the nasal anteriorly, the left frontal medially, the parietal posteriorly, the postorbital posterolaterally, and the prefrontal anterolaterally. The frontal forms approximately one-half of the dorsal orbital margin, as it does in *Leptoceratops* (Sternberg 1951).

The maximum preserved length of TMP 2011.053.0027 is approximately 120 mm and the maximum thickness is 24.1 mm, occurring at the medial margin of the transverse ridge. A fan of grooves and pits emanates from this high point to cover the dorsal surface of the bone, except for the frontal depression and a 10 mm-wide band of smooth bone along the depressions crescentic anterior margin. A portion of the orbital rim (Fig. 3A) emargination is visible, and the well-preserved roof of the orbit forms the adjacent part of the ventral surface (Fig. 3C).

The frontal depression occupies approximately the posterior third of the preserved length of the element's dorsal surface. The medial and anterior margins of the depression are formed by a crescentic raised, smoothly rounded rim, which diminishes in prominence posterolaterally. The interior of the depression is smooth.

The subtle transverse ridge and the anterior margin of the frontal depression both arise in a bifurcation of the medial margin.

The dorsal surface is slightly deflected dorsally at the midline, and when in articulation with the left frontal would have contributed to a weak sagittal crest which would have continued onto the parietal. The otherwise vertical medial sutural surface for the left frontal is laterally deflected in dorsal view in the region of the transverse ridge which would have resulted in the sagittal ridge being asymmetrical; a similar asymmetry is seen in most articulated leptoceratopsid skulls.

Much of the ventral surface is occupied by the smooth roof of the orbital cavity. This is bordered medially by the crista cranii, most of which is broken away. The posteromedial and posterolateral corners of the frontal bear sutural surfaces for contact with overlapping processes of the parietal. In most leptoceratopsid frontals the sutural areas for the laterosphenoid and orbitosphenoid, as well as the impression of the olfactory bulb, and the nasal cavity are all clearly seen, but the present specimen is broken in the regions where those features would be expected. However, an ovoid cerebral fossa is present anterior to the posteromedial contact area for the parietal.

ROMVP 66302

ROMVP 66302 (Fig. 4I-K) is a fragment of an isolated left *Prenoceratops* frontal from a small individual based on its estimated original length (110 mm; approximately 75% of the estimated reconstructed length of TMP 2011.053.0027). Much of the lateral and anterior margins have been lost to breakage. Its preserved maximum length is approximately 44 mm, and it has a maximum thickness of 14 mm measured at the anteromedial margin of the frontal depression. From this point, the frontal thins gradually in the anterior direction and more sharply in the posterior direction. The dorsal surface, excluding the frontal depression, is ornamented with small, closely packed pits which give way to shallow, narrow grooves on the anteriormost preserved part of the frontal. In the region where the pits begin their transition into grooves, the dorsal surface is marked by an approximately transverse fracture that appears to be the result of dorsoventral crushing. The crescentic, slightly elevated anterior margin of the smooth frontal depression is accentuated in its lateralmost preserved portion by a narrow depression (approximately 0.5 cm in anteroposterior width) adjacent to its anterior edge. The dorsal surface of the frontal has a lightly inscribed groove, possibly a vascular impression, that extends anteriorly from the margin of the depression to the preserved anterior margin of the element.

The frontal depression occupies slightly more than one-half of the anteroposterior length of the dorsal surface of the preserved part of the frontal and thins to a minimum thickness of 4 mm at its posterior margin. The morphology of the medial surface of the bone indicates the sutural surface that would have formed an interdigitating contact with the right frontal, and the contact does not appear to be asymmetrical in dorsal view as it is in other *Prenoceratops* frontals (Fig. 4A-H) from the same bonebed. As in TMP 2011.053.0027, the medial margin of the frontal is deflected slightly dorsally, reaching its maximum height where it intersects the anteromedial margin of the frontal depression, and would have contributed to a very low sagittal ridge.

The ventral surface of the frontal preserves the smooth roof of the orbital cavity. The sutural surface for the orbitosphenoid is preserved, unlike in TMP 2011.053.0027, but that for the laterosphenoid is not.

PHYLOGENETIC ANALYSIS

To date, only three phylogenetically informative characters have been identified for the leptoceratopsid frontal: Ch 97, large caudolateral process on the frontal: absent (0), present (1); Ch 98, degree of incisure of frontal fossae/parieto-frontal contact: incisures absent (0), shallow (1), deeper (2); fronto-parietal depression present (3); invaginated by fontanelle, secondary skull roof present (4); and Ch 99 (rostral border of frontal depression: rostrally convex (0), transversely straight (1) (Morschhauser et al. 2019). Based on observations discussed below, we rescored two taxa for one character each (*Montanoceratops* Ch 98 (? → 0) and *Prenoceratops* Ch 99 (0 → 0&1)) in the matrix of Arbour and Evans (2019) derived from Morschhauser (2019) with the addition of *Ferrisaurus*, and we used this modified matrix with the inclusion of *Gremlin* to reanalyze phylogenetic relationships within Ceratopsia. The final matrix contained 44 taxa and 256 characters. *Lesothosaurus* was set as the outgroup taxon. A cladistic parsimony analysis was run under the Traditional Search option in TNT v1.5 (Goloboff and Morles 2023), using the tree bisection reconnection swapping algorithm with 1,000 replications. All characters were treated as unordered and of equal weight. Branches were collapsed if their minimum length equalled zero.

A total of 746 most parsimonious trees were obtained, each having a best tree length of 688 steps; consistency index (CI) of 0.45 and a retention index (RI) of 0.67. In the strict consensus of those trees, relationships among ceratopsians basal to Ceratopsoidea were poorly resolved, and leptoceratopsid taxa formed an unresolved polytomy outside Ceratopsoidea. A 50% majority rule tree did recover a monophyletic Coronosauria, but leptoceratopsids, together with the closely related *Helioceratops* and *Koreaceratops*, were unresolved, although *Gryphoceratops* and *Unescoceratops* were posited as sister taxa.

DISCUSSION

Our phylogenetic analysis of Ceratopsia using the matrix of Arbour and Evans (2019), with leptoceratopsid taxa rescored for one frontal character each and the inclusion of *Gremlin* yielded a similar result to that obtained by Arbour and Evans (2019). Neither the strict consensus or the 50% majority rule tree recovered Leptoceratopsidae as a monophyletic clade. Such results were not unexpected due to a large number of missing data in the matrix.

The isolated frontal TMP 2011.053.0027 is the first leptoceratopsid element to have been recovered from the lower unit of the Oldman Formation of southern Alberta. Although the frontal was clearly not coossified to its counterpart at the time of death, this condition does not necessarily indicate ontogenetic immaturity. In most dinosaurs, the interfrontal suture does close with age; however, in ceratopsians it is common for the suture to remain unfused, even in mature individuals (You and Dodson 2004).

The taxon represented by TMP 2011.053.0027 shares the general morphology characteristic of all leptoceratopsids. The only other catalogued leptoceratopsid element from the formation is also a frontal, TMP 1987.089.0008, referred to *Prenoceratops* sp. (Miyashita et al. 2010) that was collected from the upper unit of the Oldman Formation of southeastern Alberta where this unit is time equivalent to the lower Dinosaur Park Formation in Dinosaur Provincial Park.

TMP 2011.053.0027 is very similar to TMP 1987.089.0008, but differs from the latter in two features. First, the anterior margin of the frontal depression of TMP 2011.053.0027 is anteriorly convex, rather than straight. Second, TMP 2011.053.0027 has a low, narrow transverse ridge that extends across the dorsal surface of the bone from the medial margin to the dorsolateral edge of the orbit. This transverse ridge and the raised anterior margin of the frontal depression both branch off the raised medial margin of the frontal. The transverse ridge marks the posterior limit of strong rugose texturing on the dorsum of the frontal, and is separated from the raised margin of the smooth frontal depression by a narrow (approximately 10 mm wide) band of smooth bone that follows the margin of the depression. No other known leptoceratopsid has this transverse ridge situated at the posterior edge of the rugose part of the dorsum that is separated from the smooth frontal depression by a strip of smooth bone. Except for TMP 2011.053.0027, the dorsum of the leptoceratopsid frontal either bears rugose texturing that terminates only at the margin of the frontal depression (in *Cerasinops* and *Prenoceratops*) or has a relatively smooth texture that continues uninterrupted onto the surface of the depression (in *Leptoceratops* and *Montanoceratops*). It should be noted that *Leptoceratops* displays some variation in frontal texture, in that the partial skull UWGM-200 bears some radiating, groove-like, presumably vascular striations that originate at the center of each frontal. Even in this specimen, however, the dorsum cannot be characterized as rugose, and the *Leptoceratops* skeletons CMN 8887 and CMN 8889 each have smooth frontals.

The transverse ridge of TMP 2011.053.0027 also marks the frontal's point of maximum thickness, from which the frontal tapers slightly anteriorly and sharply posteriorly across the frontal depression. The maximum thickness of the frontal coincides with the anterior margin of the frontal depression in all other leptoceratopsids that have well-developed dorsal rugosites. In the stratigraphically youngest taxon, *Leptoceratops*, maximum frontal thickness occurs at approximately the same position as TMP 2011.053.0027, but *Leptoceratops* lacks a discernable transverse ridge or well-developed dorsal rugose texturing.

ROMVP 66302 is a fragment of a small frontal from the holotype *Prenoceratops* bonebed in the Two Medicine Formation of Montana. It resembles the holotype *Prenoceratops* frontals described by Chinnery and Horner (2007) and the referred specimen of Miyashita et al. (2010) in all its preserved features, apart from lacking the degree of rugose texturing seen in other *Prenoceratops* frontals and having a rostrally convex, not straight, anterior margin of the frontal depression. The crescentic form of the margin of ROMVP

66302 suggests that this character is variable in *Prenoceratops*. Given that ROMVP 66302 is approximately 25% smaller than the holotype and referred frontals (CF48, Fig. 4A-C; CF61, Fig. 4D-F; and CF65, Fig. 4G-H) and lacks the rugose texture of those specimens, it is likely that both the level of dorsal rugosity and the curvature of the anterior margin of the frontal depression changed during ontogeny.

Comments on variation in the anterior border of the frontal depression

Character 99, the straight anterior margin of the frontal depression previously has been considered a synapomorphy of *Cerasinops* and *Prenoceratops* (Morschhauser et al. 2019) However, in describing the frontals of *Cerasinops* (Fig. 3H-I), Chinnery and Horner (2007:629) described the holotype MOR 300 as having "a low ridge, curving caudolaterally [that] delineates the dorsal surface from the frontal depression." In redescribing the holotype of *Montanoceratops* (AMNH 5464), Makovicky (2010) noted that the anterior margin of its frontal depression (his supraorbital depression) was curved, and we confirm that here (Fig. 4L), but apparently this character was not coded for *Montanoceratops* in Morschhauser et al. (2019). Our observations of the fused frontals of MOR 300 indicate that the actual shape of the margin is difficult to assess. The margin appears to be rostrally convex when viewed dorsally (Fig. 3H), but when viewed anterodorsally the same margin appears to be straight (Fig. 3I), suggesting that even under optimal conditions this character is difficult to code.

Regarding the frontals of *Prenoceratops*, it should be noted that the condition of the anterior margin of the frontal depression has been described in at least two related, but slightly different ways. Chinnery (2004) defined the margin as a "straight, transverse border" for the *Prenoceratops* bonebed specimens that she described and they are accordingly coded as having a straight margin in the character matrix of Morschhauser et al. (2019). By contrast, Miyashita et al. (2010) renamed it as the "transverse postorbital ridge" (i.e., a straight anterior margin of the frontal depression). We confirm the presence of a straight margin on three of the *Prenoceratops* frontals (Fig. 4A-H; casts) described by Chinnery (2004). Given that the margin is clearly curved in the smaller ROMVP 66302, we propose that this character varies ontogenetically, at least within *Prenoceratops*. Until more leptoceratopsid specimens of different size classes can be evaluated, we advocate caution when coding this character in ceratopsian phylogenetic analyses.

Taxonomic assignment of ROMVP 66302, TMP 1987.089.0008, and TMP 2011.053.0027.

ROMVP 66302 — This specimen can be unequivocally assigned to *Prenoceratops hodgskissi* based on having been collected from the *Prenoceratops* bonebed that produced the holotype specimen, and the fact that no other ceratopsian taxa were found associated with the *Prenoceratops* material collected. The specimen is morphologically compatible with other *Prenoceratops* material, and we believe that it is likely that the noted differences are ontogenetic in nature given the specimen's small size.

TMP 1987.089.0008 — Miyashita et al. (2010) referred this specimen to *Prenoceratops* sp. based on what they considered to be autapomorphies for *Prenoceratops* (citing Chinnery 2004): "(1) transversely straight postorbital ridge, (2) frontal depression that is deeper than one-third the thickness of the frontal, and (3) crista cranii that coincides with the interfrontal suture" Miyashita et al. (2010:88).

Chinnery (2004) did not comment on the crista cranii of *Prenoceratops*, so it is unclear where Miyashita et al. (2010) derived the coding for this feature. Examination of TMP 1987.089.0008 and the casts of the frontals show that the crista cranii does not coincide with the interfrontal suture in the sense of being positioned at the medial edge of the frontal, but rather is stepped back from the margin by several millimetres, except for a small (~5 mm) portion anteromedial to the sutural area for the orbitosphenoid on TMP 1987.089.0008. The mediolateral position of this part of the crista cranii is rarely remarked on in ceratopsians as most described specimens are based on articulated skulls where the ventral surface of the frontal is not visible, thus its utility as a diagnostic character is questionable.

Moreover, the frontal depression's being deeper than one-third the thickness of the frontal is not a character Chinnery (2004) used in her phylogenetic analysis or her taxon diagnosis of *Prenoceratops*. A non-qualitative version of the character was used by Morschhauser (2018; Ch 98) and Arbour and Evans (2019; Ch 98), but was coded as state 2 (deeper for all leptoceratopsids in which it could be coded at all (*Cerasinops*, *Leptoceratops*, *Montanoceratops* and *Prenoceratops*), and thus was not phylogenetically informative within the clade.

Our re-evaluation of TMP 1987.089.0008 did not produce any potentially diagnostic characters beyond those listed by Miyashita et al. (2010). We agree that the anterior margin of the frontal depression of TMP 1987.089.0008 is straight, as in the putatively mature *Prenoceratops* frontals described by Chinnery and Horner (2007) (Fig. 4A-H), and does, indeed, closely resemble them in all frontal depression features, including shape and depth. The *Cerasinops* frontals (MOR 300) can also be argued to have a similarly straight anterior frontal margin, suggesting that this character is a synapomorphy for *Cerasinops* and *Prenoceratops*. Thus, although TMP 1987.089.0008 may be referable to one of those two taxa, based on its stratigraphic position we suggest that it is probably best left referred to *Prenoceratops* sp.

Another consideration is that TMP 1987.089.0008 was found in the upper unit of the Oldman Formation of southern Alberta in strata equivalent in time to the lower part of the Dinosaur Park Formation in Dinosaur Provincial Park. Given that the two sediments packages are known to share dinosaur taxa (e.g., *Centrosaurus* (Chiba et al. 2015)), and that the leptoceratopsid *Unescoceratops* is known from the middle portion of the Dinosaur Park Formation., it is also possible that TMP 1987.089.0008 may eventually prove referrable to *Unescoceratops* which is known only from partial dentaries (Ryan et al. 2012).

TMP 2011.053.0027 — Based on the data presented here, we make TMP 2011.053.0027 the holotype of the new taxon, *Gremlin slobodorum*. The recognition of *Gremlin* increases the number of dinosaur genera known from the lower unit of the Oldman Formation of southern Alberta from non-tooth skeletal material to five, with *Gremlin* joining the centrosaurine ceratopsids *Albertaceratops nesmoi* Ryan, 2007 and *Wendiceratops pinhornensis* Evans and Ryan, 2015, the hadrosaurine hadrosaurid *Gryposaurus* sp., and a pachycephalosaurid, cf. *Stegoceras*. To date, these ceratopsids are only known from this unit and geographic region, offering circumstantial stratigraphic support for the hypothesis that *Gremlin* represents a distinct new taxon within Alberta.

CONCLUSIONS

Analysis demonstrates that TMP 2011.053.0027 is a leptoceratopsid frontal that can be referred to the new taxon *Gremlin slobodorum* based, in part, on the presence of a transverse ridge that marks the posterior limit of rugose ornamentation on the dorsal surface and is separated from the margin of the frontal depression by a narrow band of smooth bone. *Gremlin slobodorum* helps to fill in a significant temporal gap in the Albertan leptoceratopsid record between *Gryphoceratops* from the Santonian Milk River Formation and *Unescoceratops* from the upper Campanian Dinosaur Park Formation. Examination of TMP 2011.053.0027, and the *Prenoceratops* frontal ROMVP 66302, and reevaluation of TMP 1987.089.0008 indicate that the shape of the anterior margin of the frontal depression varies ontogenetically in at least some leptoceratopsids.

ACKNOWLEDGMENTS

Thanks to S. Rufolo and M. Currie (CMN) for specimen access and help with loan transfers. K. Seymour (ROM) provided loans. B. Strilisky (Royal Tyrrell Museum of Palaeontology) facilitated the transfer of the loan of TMP 2011.053.0027 to the CMN. I. Morrison (ROM) expertly prepared ROMVP 66302. J. Scannella and E. Metz (Museum of The Rockies) provided photographs of MOR 300. P. Makovicky (University of Minnesota) and J. Mallon (CMN) provided photographs of AMNH 5464. A. Farke provided photographs of the *Prenoceratops* frontal casts CF48, 61 and 65. Danielle Dufault (ROM) photographed ROMVP 66302. Thanks to V. Arbour, D. Brinkman, T. Cullen, R. Holmes, J. Mallon, and T. Miyashita for providing data and helpful discussions. W. Sloboda discovered and collected TMP 2011.053.0027 while part of the 2011 field crew of the Southern Alberta Dinosaur Project jointly run and funded by DEC and MJR. We thank Rob Holmes and an anonymous reviewer, and the editor for their constructive suggestions that improved the manuscript during the review process. A Natural Sciences and Engineering Research Council of Canada Discovery Grant to DCE (NSERC Grant File Number: RGPIN 355845) supported this research, and CS acknowledges NSERC Discovery Grants RGPIN-2017-06246 and RGPIN-2023-04916.

AUTHOR CONTRIBUTIONS

MJR and DCE designed the project. LM and MJR gathered and analyzed the data. MJR and LM drafted the manuscript. All authors edited the manuscript.

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