A new leptoceratopsid dinosaur from Maastrichtian-aged deposits of the Sustut Basin, northern British Columbia, Canada

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ABSTRACT

A partial dinosaur skeleton from the Sustut Basin of northern British Columbia, Canada, previously described as an indeterminate neornithischian, is here reinterpreted as a leptoceratopsid ceratopsian, *Ferrisaurus sustutensis*, gen. et. sp. nov. The skeleton includes parts of the pectoral girdles, left forelimb, left hindlimb, and right pes. It can be distinguished from other named leptoceratopsids based on the proportions of the ulna and pedal phalanges. This is the first unique dinosaur species reported from British Columbia, and can be placed within a reasonably resolved phylogenetic context, with *Ferrisaurus* recovered as more closely related to *Leptoceratops* than *Montanoceratops*. At 68.2 to 67.2 Ma in age, *Ferrisaurus* falls between, and slightly overlaps with, both *Montanoceratops* and *Leptoceratops*, and represents a western range extension for Laramidian leptoceratopsids.

INTRODUCTION

The dense boreal forest and thrusted, folded rocks of the Canadian Cordillera present a challenging environment in which to search for dinosaurs, compared to the better exposed and more easily accessible outcrops in the badlands of the prairie provinces. Nevertheless, a dinosaur specimen (RBCM P900) consisting of articulated and disarticulated limb and girdle elements was discovered in 1971 in the remote interior mountains of north-central British Columbia (Fig. 1; Arbour and Graves 2008). These bones were collected by geologist Kenny F. Larsen, who was surveying for uranium along the then in-construction BC Rail line along the Sustut River, and were later donated to Dalhousie University (Halifax, NS) and subsequently accessioned at the Royal British Columbia Museum in Victoria, BC. Arbour and Graves (2008) described this material and identified it as an indeterminate small-bodied, bipedal neornithischian, possibly representing either a pachycephalosaur or a basal ornithopod similar to *Thescelosaurus*. Here we provide a new interpretation of this material and argue for its assignment to Leptoceratopsidae as a new genus and species. Leptoceratopsids were short-frilled, hornless ceratopsians with a maximum body length of about two-to-three meters, and form the sister group to all other coronosaurian neoceratopsians (He et al. 2015). They were present in many Campanian-Maastrictian aged dinosaur assemblages from Asia and North America, but are generally rare in the fossil record (Ryan et al. 2012, Longrich 2016).

RBCM P900 is one of the only vertebrate fossils yet described from the Sustut Basin and as such is significant for understanding the distribution and evolution of dinosaurs in western North America. A 2017 survey of the field area near the confluence of Birdflat Creek and the Sustut River recovered a fragment of the Cretaceous turtle *Basilemys* at a location closely matching Larsen's original field notes, suggesting that RBCM P900 most likely derived from the same outcrop (Fig 1; Arbour et al. in review). This work generated new stratigraphic and palynological data that allows the provenance of this important skeleton to be documented in detail for the first time. RBCM P900 is likely from the Tango Creek Formation, rather that the Brothers Peak Formation as originally reported, and the new palynological data suggest that the specimen is late Maastrichtian in age, allowing its morphology and biogeography to be understood in a more detailed temporal context and compared to more closely related leptoceratopsids.

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Institutional abbreviations: LACM, Los Angeles County Museum; MOR – Museum of the Rockies, Bozeman, Montana, USA; RBCM – Royal BC Museum, Victoria, British Columbia, Canada; RAM, Raymond Alf Museum; ROM – Royal Ontario Museum, Toronto, Ontario, Canada; TMP - Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP – University of Alberta, Edmonton, Alberta, Canada; CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada.

METHODS

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 online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) 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:D1C60A34-3632-43AD-BCE0-C93D5E26D1B0. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS. No permits were required for this study and all fossils are permanently accessioned in repositories.

RBCM P900 was compared to ceratopsian, pachycephalosaurid, ornithopodan, and parksosaurid dinosaurs in various collections (SI 1) and the literature, and comparative measurements are provided in SI 2. Photogrammetric digital models of the specimen (SI 3) were created using Agisoft Metashape. We assessed the phylogenetic position of RBCM P900 using the character-taxon matrix for ceratopsians presented by He et al. (2015), which in turn was built from the matrix presented by Farke et al. (2014). Our matrix includes 34 taxa and 165 characters (SI 1 and 4) and was compiled in Mesquite v3.04 build 725 (Maddison and Maddison 2011). We added three new characters (characters 163-165) based on observations made over the course of this study. We performed a cladistic parsimony analysis using the Traditional Search option in TNT v1.5 (Goloboff et al. 2008); all characters were treated as unordered and of equal weight, and we used the tree bisection reconnection (TBR) swapping algorithm with 1000 replications.

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SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1842

ORNITHISCHIA Seeley, 1888

NEORNITHSICHIA Cooper, 1985

MARGINOCEPHALIA Sereno, 1986

CERATOPSIA Marsh, 1890

NEOCERATOPSIA Sereno, 1986

CORONOSAURIA Sereno, 1986

LEPTOCERATOPSIDAE Nopcsa, 1923

FERRISAURUS SUSTUTENSIS gen. et sp. nov. urn:lsid:zoobank.org:act:A7F4267C-8CC6-49B6-8E52-2C2148929B14

Diagnosis: Autapomorphic among leptoceratopsids, the penultimate pedal phalanges in digits III and IV are equal or subequal in proximodistal length compared to the length of the preceding phalanx, rather than shorter as in all other leptoceratopsids for which these elements are preserved. Astragalus and tibia coossified, unlike all other leptoceratopsids except for one specimen of *Montanoceratops*; distal end of ulna broader relative to radius length than in *Leptoceratops*. Distal end of ulna medially bowed, unlike the straight ulna of the penecontemporaneous Maastrichtian taxa *Leptoceratops* and *Montanoceratops*, but similar to *Cerasinops* and *Prenoceratops* from the Campanian.

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Etymology: "Iron lizard", from Latin *ferrum* (=iron) and Greek *sauros* (=lizard), in reference to the specimen's discovery along a railway line, and *sustutensis* in reference to its provenance near the Sustut River and within the Sustut Basin.

Holotype: RBCM P900, a partial skeleton consisting of a partial right coracoid, fragmentary left scapula, complete left radius, distal portion of the left ulna, associated distal two thirds of the left tibia and fibula and coossified astraglus and ?calcaneum, partial articulated digits III and IV of the right pes, and an unprepared block removed from the posterior surface of the tibia that appears to contain four

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metatarsals, presumably from the left pes. Previously catalogued as RBCM.EH2006.019.0001 to RBCM.EH2006.019.010 and published under RBCM.EH2006.019 by Arbour and Graves (2008).

Locality: RBCM P900 was discovered near the confluence of Birdflat Creek and the Sustut River in the Sustut Basin (Fig. 1); the bones were found loose in the rubble during construction along the BC Rail line, which has since been abandoned. Fieldwork in the Sustut Basin in 2017 provided strong support for the relocation of the original collection site a few hundred meters from the confluence of the Sustut River and Birdflat Creek (Arbour et al. in review); exact GPS coordinates are on file at the Royal BC Museum.

Formation and Age: Tatlatui Member, Tango Creek Formation, Sustut Group. Palynomorphs recovered from the presumed holotype locality included the Maastrichtian marker taxon *Pseudoaquilapollenites bertillonites*, indicating an age of approximately 68.2 to 67.2 Ma for the site (Arbour et al. in review).

LSID: urn:lsid:zoobank.org:act:A7F4267C-8CC6-49B6-8E52-2C2148929B14

DESCRIPTION AND COMPARISON

RBCM P900 includes multiple elements in articulation, including the tibia and fibula, several pedal phalanges, and potentially the metatarsals (Fig. 2). The presence of metatarsals in a block of sediment removed from the posterior face of the distal tibia suggests that the skeleton may have been fully articulated in situ. The bones do not appear to have suffered from brittle or plastic deformation, but they have been recrystallized, obscuring the original internal bone textures.

We reinterpret RBCM P900 as a leptoceratopsid based on several aspects of the preserved phalanges. The non-pedal phalanges are blockier and more robust in comparison to most orodromines (e.g. *Orodromeus* MOR 623B), parksosaurids (e.g. *Parksosaurus* ROM 804), and pachycephalosaurids (e.g. *Stegoceras* UALVP 2). The dorsal surface of the posterior articular surface in RBCM P900 is more strongly pointed, and overlaps the preceding phalanx more extensively, than in other small ornithischians with ginglymoid phalanges from similar stratigraphic and geographic ranges, such as parksosaurids (e.g. *Parksosaurus* ROM 804) and pachycephalosaurids (e.g. *Stegoceras* UALVP 2). Ginglymoid articular surfaces, and narrow, pointed unguals, also exclude identifications of this specimen as a juvenile ceratopsid (e.g. *Chasmosaurus* UALVP 52613) or hadrosaurid (e.g. *Edmontosaurus annectens*, LACM 23504 (Prieto-Marquez, 2014), RAM 7150 (Zheng et al. 2011), Lambeosaurinae indet., TMP 1998.058.0001). The relatively long and robust forelimb compared to the hindlimb, as indicated by the

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proportions of the radius and tibia, exclude RBCM P900 from being assigned to Thescelosauridae and Pachycephalosauria. The preserved elements of RBCM P900 are comparable in size to large leptoceratopsid specimens like *Cerasinops* MOR 300 and *Leptoceratops* CMN 8889.

Pectoral Girdle

Arbour and Graves (2008:Fig. 2:G, H) were unable to identify a thin, gently curved element of RBCM P900, which we reinterpret here as a fragmentary right coracoid (Fig. 3A). Most of the edges are broken, but the angle of the sternal process is complete and part of the anterior edge is complete. The morphology of this bone compares well with the complete coracoids of *Leptoceratops* CMN 8889 (Fig. 3B); the coracoids of most other Laramidian leptoceratopsids are incomplete and cannot be compared with RBCM P900. As in *Leptoceratops*, RBCM P900 had a pronounced, sharply pointed sternal process at the anterior and ventral end of the coracoid. The anterior edge of the coracoid in RBCM P900 appears straighter compared to the more curved edge in CMN 8889 (*Leptoceratops*), but without comparable material from other taxa it is difficult to assess whether or not this is within the range of intraspecific variation or a taxonomic difference.

A fragmentary flattened bone was interpreted as a possible rib by Arbour and Graves (2008: Fig. 2E,F) and is reinterpreted here as part of the left scapula (Fig. 3C, D), representing a section near the midpoint of the scapular blade. It has a teardrop-shaped cross section on one side and rapidly narrows to a thin oval cross-section on the other side. The ventral edge of the fragment is straight, and the dorsal edge is markedly concave. The scapulae of *Montanoceratops* (MOR 452) and *Prenoceratops* (TCM 2003.1.9 and TCM 2003.1.11; Fig. 3F) are relatively straight along their dorsal lengths, whereas the scapulae of *Cerasinops* (MOR 300, Fig. 3E) and *Leptoceratops* (CMN 8889) are more concave dorsally in lateral view.

Forelimb

We agree with the identification of the radius by Arbour and Graves (2008: Fig. 2C,D). The radius is a relatively simple rod-shaped bone with gently expanded proximal and distal ends and a shaft that is triangular in cross section (Fig. 4A-D. Overall, the radius of RBCM P900 is very similar to that of *Leptoceratops* (Brown 1914; Fig. 4E), and it differs only in subtle aspects. The proximal end in RBCM P900 is less cup-shaped compared to *Leptoceratops* (CMN 8889), and the shaft lacks the prominent

protuberance present near the midpoint in *Leptoceratops (*AMNH 5205; Brown 1914), although a light distal tuberosity is present as in AMNH 5205. The preserved radii of *Cerasinops* (MOR 300; Fig. 4F) lack distal and proximal ends, but preserve straight shafts lacking any bulges or tuberosities.

We reinterpret the bone previously identified by Arbour and Graves (2008: Fig. 2) as the proximal half of a humerus as a partial right ulna including the distal end (Fig 5A,B). The ulna is incomplete proximally, but the shaft is expanded towards the broken proximal end. Based on the proportions of the radius length to ulna length in *Leptoceratops*, *Montanoceratops*, and to a lesser extent *Cerasinops* (SI 2) where the radius is 75-80% of the length of the ulna, the ulna of RBCM P900 may have been 170-180 mm in total length. Comparing the width of the distal ulna to the length of the radius, the ulna of RBCM P900 was proportionately wider compared to other leptoceratopsids (Fig 5, SI 2), giving it a stouter appearance.

The ulna shaft is a flattened oval in cross-section, and the distal end is flat and only moderately expanded. A diagnostic character for *Cerasinops* proposed by Chinnery and Horner (2007) is the strong medial bend of the distal part of the ulna. The distal ulna of RBCM P900 is also medially deflected (Fig. 5G), with the posterior edge more strongly curved than the anterior edge. The postcrania of the bonebed material of *Prenoceratops* was not previously described by Chinnery (2004), but examination of TCM 2003.1.8, a right ulna (Fig. 5H), indicates that *Prenoceratops* also had a medial bend to the distal ulna. The ulna is straight in this region in *Leptoceratops* (CMN 8889) and *Montanoceratops* (MOR 542; Fig. 5I).

Hindlimb

Approximately the distal two thirds of the right tibia and fibula are preserved, with the tibia and fibula in articulation (Fig. 6A-D). Using more complete specimens of similar size as a guide (SI 2), we estimate that the tibia in RBCM P900 was likely between 310 and 330 m in length originally. The astragalus and possibly the calcaneum are coossified to the tibia but the boundaries between these elements are difficult to discern. The tibia and astragalus are not coossified in *Leptoceratops* (CMN 8889; Fig. 6F,G), *Cerasinops* (MOR 300; Fig. 6H-J) or *Montanoceratops* (MOR 542) and in these specimens the boundary between these elements is clearly discernible. Makovicky (2010) notes that the astragalus is partly coossified with the tibia in *Montanoceratops (*AMNH 5465). It is unclear whether this an ontogenetic phenomenon, and if it is phylogenetically significant.

In medial and lateral views (Fig. 6A,D) the tibia of RBCM P900 has a pronounced distal curvature that was not observed in any other leptoceratopsid specimens and which does not seem to represent taphonomic deformation, based on the absence of crushing or fractures on the tibia. In distal view (Fig. 6B), the lateral and medial malleoli are offset at a distinct angle, giving the distal face of the tibia/astragalus a triangular cross section; RBCM P900 has a more pronounced edge marking the confluence between the malleoli compared to the condition in *Leptoceratops* (CMN 8889), *Cerasinops* (MOR 300), or *Montanoceratops* (MOR 542). The tibia of RBCM P900 is straight-sided in anterior and posterior view and tapers towards the midpoint in anterior or posterior view, similar to the condition in *Leptoceratops* (CMN 8889; Fig. 6F,G), and *Montanoceratops* (MOR 542), and unlike the strongly kinked morphology observed in *Cerasinops* (MOR 300; Fig. 6H-J). The tibia narrows significantly along the shaft and has an oval cross section at its broken proximal end. The fibula is narrow, with an oval cross section. A portion of matrix removed from the anterior side of the distal tibia contains what appear to be the remains of four metatarsals in cross section (Fig. 6E), but little can be said about their morphology without further preparation.

RBCM P900 preserves a large number of pedal phalanges: III-2, III-3, and III-4, and IV-2, IV-3, IV-4, and IV-5 (Fig. 7A-C). Pedal digit III was preserved in articulation on a piece of matrix (Fig. 7A,B); digit IV includes IV-2 and IV-3 preserved in articulation and IV-4 and IV-5 can be 'snapped' back into articulation based on the presence of some remaining matrix on these elements (Fig. 7C). The non-ungual phalanges are somewhat longer than wide, but blocky rather than elongate, and ginglymoid. The distinctly ginglymoid nature of the interphalangeal joints is distinct from the non-ginglymoid pedal phalangeal joints in Hadrosauridae (e.g., Zheng et al. 2011).

In *Leptoceratops* (CMN 8889, CMN 8887), *Cerasinops* (MOR 300), and *Montanoceratops* (MOR 542) the penultimate pedal phalanx of each major digit is markedly shorter in length compared to the preceding phalanx (~75%-90% the length of the preceding phalanx); in RBCM P900 the penultimate and preceding phalanx on digits III and IV are similar in size, with the penultimate phalanx actually being slightly longer than the preceding phalanx (SI 2). *Leptoceratops (*AMNH 5205; Brown 1914) and *Cerasinops (*USNM 13863; Gilmore 1939, Chinnery and Horner 2007) are both illustrated with penultimate phalanges subequal in length to the preceding phalanx, but these are both illustrated as line drawings rather than photographs, measurements were not provided by the authors, the digits in AMNH 5205 were not part of an articulated pes, and neither of these specimens were measured for this study. As such, it is unclear if the illustrations accurately reflect the actual morphology of the pedal digits in these two specimens.

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The figured pes of *Udanoceratops* PIN 4046/11 (Tereschenko 2008) appears to show penultimate phalanges subequal in length to the preceding phalanx in digits II-IV, but measurements were not provided, and no rationale was provided for why this specimen is referred to *Udanoceratops* rather than *Protoceratops*. RBCM P900 can, however, be differentiated from *Udanoceratops* by the morphology of the pedal unguals, if PIN 4046/11 (Tereschenko 2008) is referable to *Udanoceratops* rather than *Protoceratops*.

The unguals of RBCM P900 are long and narrow, with a gently curved ventral surface (Fig. 7A-C, E), differing from the broad, hoof-shaped unguals of ceratopsids or the wide triangular unguals of protoceratopsids (Sternberg 1951). Their overall shape is similar to the unguals of most other leptoceratopsids, with the possible exception of *Udanoceratops* based on specimen PIN 4046/11 where the proximal articular surface of the ungual is much wider than the distal articular surface of the penultimate phalanx (Tereschenko 2008). Lateral grooves on the unguals of RBCM P900 are shallow. The unguals of *Leptoceratops* specimen CMN 8889 have a longitudinal furrow on the ventral surface, but these are absent in the smaller *Leptoceratops* specimen CMN 8887, and ventral furrows were not observed on any other leptoceratopsid unguals examined for this study. No ventral furrows are present on the unguals of RBCM P900. The unguals of RBCM P900 appear slightly deeper in lateral view compared to other leptoceratopsids, but it is unclear how much this is influenced by taphonomic factors (e.g. the pedal elements of *Cerasinops* MOR 300 are severely crushed), ontogeny, or body size (e.g. *Montanoceratops* MOR 542 is substantially smaller and presumably ontogenetically younger than RBCM P900).

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RESULTS OF THE PHYLOGENETIC ANALYSIS

The phylogenetic analysis recovered 7 most parsimonious trees, each with a tree length of 328, a consistency index of 0.60, a retention index of 0.80, and a best tree-bisection reconnection score of 326 (Fig. 8). The strict consensus tree (Fig. 8) is nearly identical to that presented by He et al. (2015), with a basal grade of small-bodied ceratopsians and two derived clades, Coronosauria and Leptoceratopsidae. Within Leptoceratopsidae, the recovered relationships are similar to those found by He et al. (2015), with *Asiaceratops* and *Cerasinops* recovered as successive sister taxa to all other leptoceratopsids, *Montanoceratops* and *Ischioceratops* as sister taxa, and *Prenoceratops* as the sister taxon to an unresolved clade of the six remaining leptoceratopsids, including *Ferrisaurus*. Within this

clade, *Ferrisaurus* has an unresolved relationship with the North American taxa *Leptoceratops*, *Gryphoceratops* and *Unescoceratops* and the Asian taxa *Udanoceratops* and *Zhuchengceratops*. Poor resolution of this group is most likely because of the low number of characters that could be coded for *Ferrisaurus*. In two of the seven trees, *Ferrisaurus* and *Udanoceratops* were sister taxa; the position of *Ferrisaurus* differs in the other five trees.

DISCUSSION

The fact that RBCM P900, the first dinosaur specimen recovered from the Sustut Basin, is a leptoceratopsid rather than one of the more commonly encountered groups in many coeval formations in western North America, such as hadrosaurs, ceratopsians, or tyrannosaurs, is surprising, especially given well-documented preservational biases against small-bodied dinosaurs in more fossiliferous areas (Brown et al. 2013a, b; Evans et al., 2013). Most leptoceratopsid taxa are distinguished on the basis of cranial morphology, especially aspects of the lower jaw anatomy (e.g., Ryan et al. 2012). However, excellent postcranial material is known for many taxa, making it possible to identify diagnostic features in RBCM P900 despite the absence of cranial material for this specimen. *Leptoceratops*, *Montanoceratops*, and *Cerasinops* are all known from multiple partial or complete skeletons (Chinnery and Weishampel 1998, Chinnery and Horner 2007, Ostrom 1978, Brown and Schlaikjer 1942, Sternberg 1951, Brown 1914), and *Prenoceratops* specimens described by Chinnery (2004) come from a single mixed bonebed from which multiple composite skeletons have been assembled.

Digit proportions have been used to distinguish caenagnathids (e.g. Zanno and Sampson 2005), oviraptorids (Longrich et al. 2010), and ornithomimids (Kobayashi and Barsbold 2006) at low taxonomic levels, and we show that they can also be used to distinguish among leptoceratopsids. In all specimens preserving partial or complete articulated pedes, the penultimate phalanx (preceding the ungual) for each major digit is shorter in length than the immediately preceding phalanx. In other words, pedal phalanx length decreases distally in the digit, except for the unguals (Fig. 7). In *Ferrisaurus*, the penultimate phalanx is subequal in length to the preceding phalanx in digits 3 and 4, and phalanx length does not decrease distally within each pedal digit. This appears to be unique to *Ferrisaurus* within leptoceratopsids; it may be present in a referred specimen of *Udanoceratops* (PIN 4046/11, Tereschenko 2008, although it is not clear that this specimen is not referable to *Protoceratops*), and may also be

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present in more basal ceratopsian taxa such as *Archaeoceratops* (You and Dodson 2003) or *Yinlong* (Xu et al. 2006), although phalangeal measurements were not provided in the descriptions of these taxa.

The astragalus and tibia in RBCM P900 are coossified (Fig. 6), an unusual condition among leptoceratopsids that is otherwise present in only one specimen of *Montanoceratops* (AMNH 5465). Coossification of the astragalus and tibia could indicate advanced skeletal maturity in RBCM P900, but this specimen is smaller than specimens in which the tibia and astragalus remain separate (e.g. *Leptoceratops* CMN 8889, *Montanoceratops* AMNH 5205), suggesting that size alone does not explain the differences in coossification patterns in leptoceratopsids. It is unclear what the ontogenetic or taxonomic significance of this coossification represents in *Ferrisaurus*. Fusion of the ankle (distal tibia and fibula) has been proposed as a diagnostic character of the small bodied thescelosaurid *Albertadromeus syntarsus* from the Campanian of Alberta (Brown et al. 2013b).

Commented [S22]: I totally agree; this is the same in *Prenoceratops* elements. But again, if so then maybe it shouldn't be used as a taxonomic character.

Ferrisaurus shares with *Cerasinops* a medially bent distal ulna (originally proposed as a diagnostic character for *Cerasinops* by Chinnery and Horner 2007), a feature that is also present in *Prenoceratops* (TCM 2003.1.8). This feature is not present in the Maastrichtian-aged leptoceratopsids *Montanoceratops* and *Leptoceratops*, which are penecontemporaneous with *Ferrisaurus*. Chinnery and Horner (2007) suggested that the medial deflection of the ulna in *Cerasinops*, as well as the proportions and histology of the limb elements, may indicate that *Cerasinops* was primarily bipedal rather than quadrupedal. Although limb proportions are more difficult to determine in *Ferrisaurus*, if the complete tibia was between 310-330 mm (estimated based on more complete tibiae in *Leptoceratops* and *Montanoceratops*, SI 2), then the radius of *Ferrisaurus* would have been no more than 40-43% of the length of the tibia. This is less than other comparable leptoceratopsids: the radius is 50% the length of the tibia in *Leptoceratops* CMN 8889, 48% in *Leptoceratops* AMNH 5205, and 47% in *Leptoceratops* CMN 8888, and much more than 45% in the incomplete radii of *Cerasinops* MOR 300. *Ferrisaurus* thus may have had a more robust distal ulna (Fig. 5), but a shorter forelimb overall compared to *Cerasinops*, suggesting that it too may have been at least facultatively bipedal. Alternately, the robusticity of the ulna may be related to another aspect of its ecology, such as digging, which has been suggested in the orodromine *Oryctodromeus* (Fearon and Varricchio 2015) and *Protoceratops* (Longrich 2010).

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Although the precise relationships of *Ferrisaurus* are unresolved, we found it to be more closely related to *Leptoceratops* than *Montanoceratops* (Fig. 8). Despite their stratigraphic and geographic proximity, *Leptoceratops* and *Montanoceratops* are not recovered as close relatives in recent phylogenetic analyses. *Montanoceratops* occupies a relatively basal position within Leptoceratopsidae (Makovicky

2010, Ryan et al. 2012, Farke et al. 2014, He et al. 2015), and was found to be the sister taxon to *Ischioceratops* from Asia by He et al. (2015). *Leptoceratops* typically occupies a more derived position and has been recovered as the sister taxon to the Asian *Udanoceratops* (He et al. 2015). *Ferrisaurus* was thus recovered in a more derived position within Leptoceratopsidae relative to *Montanoceratops*.

Stratigraphic and palaeobiogeographic implications

Leptoceratopsids are known from the Santonian through Maastrichtian of Laramidia (Ryan et al. 2012), and the Campanian-Maastrichtian of Mongolia and China (He et al. 2015); fragmentary putative leptoceratopsids have also been reported from the Cenomanian of Uzbekistan (Nessov et al. 1989), the ?Coniacian-Santonian of Belgium (Godefroit et al. 2007, Longrich 2016), the Campanian of North Carolina (Longrich 2016), and the Campanian of Sweden (Lindgren et al. 2007). *Gryphoceratops*, the oldest taxon, derives from the Deadhorse Coulee Member of the Milk River Formation, with a minimum age of about 83.7 Ma. Campanian Laramidian taxa include *Cerasinops* from the lower Two Medicine Formation, *Prenoceratops* from the upper Two Medicine Formation of Montana and Oldman Formation of Alberta, and *Unescoceratops* from the lower Dinosaur Park Formation. Only two genera are known from the Maastrichtian of Laramidia: *Montanoceratops* from the St Mary River and Horseshoe Canyon formations, and *Leptoceratops* from the Scollard and Hell Creek formations and the Pinyin Conglomerate. RBCM P900 was most likely collected from approximately 68.2 to 67.2 Ma sediments of the Tatlatui Member of the Tango Creek Formation (Arbour et al. in review). This places it between the stratigraphic ranges for *Montanoceratops* (71.939 – 68 Ma) and *Leptoceratops* (66.97 – 66 Ma), and slightly overlapping with the known range of *Montanoceratops* (Fowler 2017).

Stratigraphically, *Montanoceratops* and *Leptoceratops* are the most likely taxa to which RBCM P900 could be referred, but multiple anatomical features distinguish RBCM P900 from both *Leptoceratops* and *Montanoceratops*, including the proportions of the pedal digits, the proportions of the ulna, and the medially bowed morphology of the distal ulna. RBCM P900 is unlikely to represent an individual of *Cerasinops* or *Prenoceratops. Ferrisaurus* can be distinguished from *Cerasinops* based on the proportions of the pedal digits, and from both *Cerasinops* and *Prenoceratops* based on the proportions of the ulna. These morphological differences are reinforced by the stratigraphic position of *Ferrisaurus* relative to the latter taxa (latest Maastrichtian, vs. middle to Upper Campanian; Chinnery and Horner 2007, Chinnery 2004), given that no other dinosaur species with temporally well-resolved specimens spans the

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middle Campanian to latest Maastrichtian elsewhere in Laramidia (e.g. Eberth et al. 2013, Fowler 2017). An enigmatic specimen, TMP 1982.11.1, from the Maastrichtian Willow Creek Formation (Miyashita et al. 2010) has been referred to *Montanoceratops* by several authors (Ryan and Currie 1998), but was considered neither a representative of *Montanoceratops*, *Leptoceratops*, or *Cerasinops* by Makovicky (2010). Several additional as-yet undescribed specimens in the collections of the TMP (Tanke 2007) may represent examples of either *Montanoceratops*, *Leptoceratops*, or *Ferrisaurus* and their description may help clarify the differences between these three taxa or provide new anatomical information for *Ferrisaurus*.

Leptoceratopsids are uncommon components of the dinosaurian faunas of Laramidia: even in the well-sampled Dinosaur Park Formation of Alberta only a handful of leptoceratopsid specimens are known. Ryan and Evans (2005) hypothesized that leptoceratopsids may have avoided the wet coastal environments favoured by ceratopsids. Elsewhere in North America, *Leptoceratops* appears to be present primarily in piedmont and alluvial plain palaeoenvironments and is largely absent in coastal plain settings (Lehman 1987, although see Ott 2007). The Tatlatui Member of the Tango Creek Formation represents an alluvial plain palaeoenvironment (Bustin and McKenzie 1989), consistent with the palaeoenvironmental association documented for other Maastrichtian leptoceratopsids. Interestingly, the intermontane basin occurrence of *Ferrisaurus* also supports one hypothesis outlined by Lehman (1987, 2001), that leptoceratopsids, along with a few other large-bodied herbivorous taxa, were inhabitants of Cordilleran highlands and adjacent piedmonts, which, in part, explains their rarity in the fossil record.

Although today the holotype locality for *Ferrisaurus* is found at approximately 56°N today, the unusual and complex translational history of the Intermontane Superterrane means its palaeolatitude may have lain as much as 1600 km to the south of its current position with respect to cratonic North America, and may have had approximately the same palaeolatitude (~48°N) as the southern border of Oregon and Idaho (Enkin et al. 2003, van Hinsbergen et al. 2015). Despite its current apparent northern latitude, the holotype of *Ferrisaurus* may actually represent one of the southernmost occurrences of Leptoceratopsidae in western North America, and at minimum would have been within the currently known latitudinal range of Laramidian leptoceratopsids. Regardless, RBCM P900 represents a western range extension for Laramidian leptoceratopsids, and a unique occurrence within a restricted intermontane basin palaeoenvironment. The identification of RBCM P900 as a unique leptoceratopsid distinct from other known Laramidian taxa supports previous conclusions by Makovicky (2010) and Ryan

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et al. (2012) that Leptoceratopsidae was a diverse but currently poorly sampled lineage of Late Cretaceous ceratopsians.

Supplementary Information

SI 1 – Specimens examined and character statements, .docx

SI 2 – Comparative measurements, .csv

SI 3 - Photogrammetric digital models of RBCM P900 are available at Morphosource, [url/doi forthcoming]

SI 4 – Character-taxon matrix, .nex

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FIGURES

Figure 1: RBCM P900, the holotype of *Ferrisaurus sustutensis*, was collected along the BC Rail line near the intersection of Birdflat Creek and the Sustut River in 1971, in the Sustut Basin of northern British Columbia, Canada. Map modified from Evenchick et al. (2003).

Figure 2: Preserved elements of RBCM P900, holotype of *Ferrisaurus sustutensis,* in white (grey represents missing parts of incomplete bones). RBCM P900 includes a partial right coracoid, partial left scapular blade, complete left radius, partial left ulna, partial left tibia, fibula, and coossified astragalus and ?calcaneum, partial left metatarsals I-IV, and digits III (phalanges 2-4) and IV (phalanges 2-5) of the right pes.

Figure 3: Pectoral elements of RBCM P900, holotype of *Ferrisaurus sustutensis*, compared to other Laramidian leptoceratopsids. A) Fragmentary right coracoid of RBCM P900 in lateral view, compared to B) complete right scapulocoracoid of CMN 8889, *Leptoceratops gracilis*, lateral view centered on coracoid with scapula in oblique view. Fragmentary left scapular blade of RBCM P900 in C) lateral and D) medial view, compared to E) left scapula of MOR 300, *Cerasinops hodgskissi* in medial view, and F) left scapula of TCM 2003.1.9, *Prenoceratops pieganensis* in lateral view. Abbreviations: sp - sternal process.

Figure 4. Radius of RBCM P900, holotype of *Ferrisaurus sustutensis*, compared to other Laramidian leptoceratopsids. RBCM P900, *Ferrisaurus sustutensis*, left radius in A) lateral, B) medial, C) proximal, and D) distal view. E) CMN 8889, *Leptoceratops gracilis*, left radius in lateral view. F) MOR 300, *Cerasinops hodgskissi*, ?left radius in ?lateral view. Abbreviations: tb - tubercle.

Figure 5: Ulna of RBCM P900, holotype of *Ferrisaurus sustutensis*, compared to other Laramidian leptoceratopsids. RBCM P900, *Ferrisaurus sustutensis*, left ulna in A) medial and B) distal view. C) CMN 8889, *Leptoceratops gracilis*, left ulna in medial view. D) MOR 300, *Cerasinops hodgskissi*, right ulna in medial view. E) TCM 2003.1.8, *Prenoceratops pieganensis*, right ulna in medial view. F) MOR 452, *Montanoceratops cerorhynchus*, right ulna in medial view. G) RBCM P900, *Ferrisaurus* left ulna in posterior view; arrow indicates medial bend to distal ulna. H) TCM 2003.1.8, *Prenoceratops* right ulna in anterior view. I) MOR 452, *Montanoceratops* right ulna in anterior view.

Figure 6: Tibia of RBCM P900, holotype of *Ferrisaurus sustutensis*, compared to other Laramidian leptoceratopsids. RBCM P900, *Ferrisaurus* left tibia in A) medial, B) posterior, C) anterior, and D) lateral views, and E) block removed from anterior face of tibia containing four partial metatarsals. CMN 8889,

584 *Leptoceratops gracilis* left tibia in F) posterior and G) anterior view. MOR 300, *Cerasinops hodgskissi*
585 right tibia in H) anterior and I) posterior views, and J) left tibia in posterior view. Abbreviations: as -
586 astraglus, ca - calcaneum, fib - fibula, ma - matrix, mt - metatarsal.

587 Figure 7: Pedal elements of RBCM P900, holotype of *Ferrisaurus sustutensis*, compared to other
588 Laramidian leptoceratopsids. RBCM P900, *Ferrisaurus*, left digit III in A) medial and B) lateral views, and
589 C) left digit IV in lateral view. D) MOR 542, *Montanoceratops cerorhynchus*, right digit IV in lateral view.
590 Illustrations of E) RBCM P900, *Ferrisaurus*, F) CMN 8889, *Leptoceratops gracilis*, G) MOR 300, *Cerasinops*
591 *hodgskissi*, and H) MOR 542, *Montanoceratops cerorhynchus*, in dorsal view.

592 Figure 8: Results of the phylogenetic analysis, strict consensus tree showing the relationships of
593 *Ferrisaurus sustutensis* within Ceratopsia.