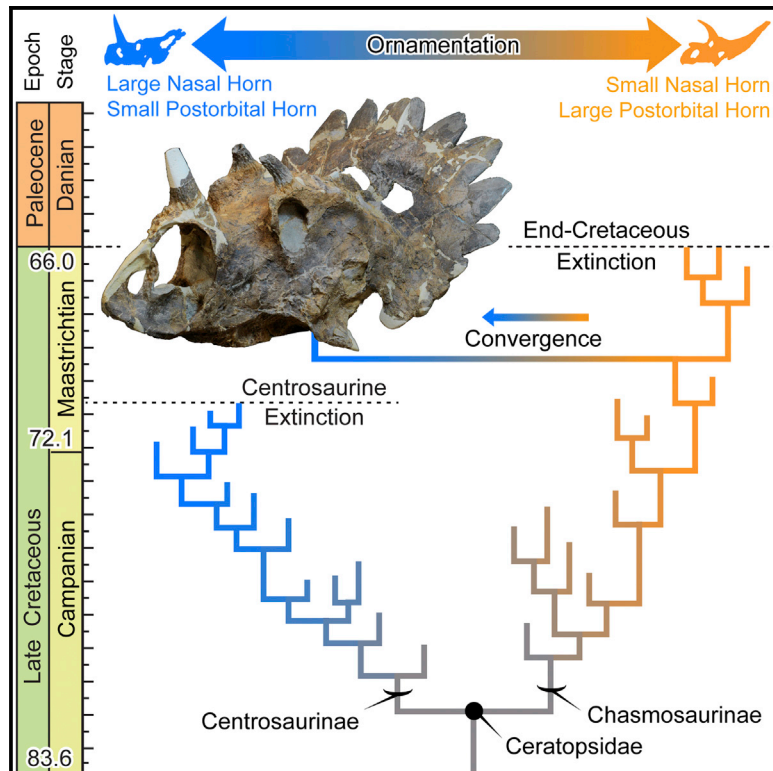


Current Biology

A New Horned Dinosaur Reveals Convergent Evolution in Cranial Ornamentation in Ceratopsidae

Graphical Abstract



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In Brief

Brown and Henderson describe a new horned dinosaur, *Regaliceratops peterhewsi*, from a nearly complete skull characterized by a large nasal horn, small postorbital horns, and large frill epioassifications. This new chasmosaurine shows display features more similar to centrosaurines and suggests evolutionary convergence in display morphology in horned dinosaurs.

Highlights

- A new horned dinosaur, *Regaliceratops*, is described based on a nearly complete skull
- It exhibits large nasal and small postorbital horns, and large frill epioassifications
- A derived chasmosaurine, the new animal shows centrosaurine-like display features
- Evidence for evolutionary convergence in horned dinosaur display is documented



A New Horned Dinosaur Reveals Convergent Evolution in Cranial Ornamentation in Ceratopsidae

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SUMMARY

Ceratopsid (horned) dinosaurs are an iconic group of large-bodied, quadrupedal, herbivorous dinosaurs that evolved in the Late Cretaceous and were largely restricted to western North America [1–5]. Ceratopsids are easily recognized by their cranial ornamentation in the form of nasal and postorbital horns and frill (capped by epioassifications); these structures show high morphological disparity and also represent the largest cranial display structures known to have evolved [2, 4]. Despite their restricted occurrence in time and space, this group has one of the best fossil records within Dinosauria, showing a rapid diversification in horn and frill morphology [1]. Here a new genus and species of chasmosaurine ceratopsid is described based on a nearly complete and three-dimensionally preserved cranium recovered from the uppermost St. Mary River Formation (Maastrichtian) of southwestern Alberta. *Regaliceratops peterhewsi* gen. et sp. nov. exhibits many unique characters of the frill and is characterized by a large nasal horncore, small postorbital horncores, and massive parietal epioassifications. Cranial morphology, particularly the epioassifications, suggests close affinity with the late Campanian/early Maastrichtian taxon *Anchiceratops*, as well as with the late Maastrichtian taxon *Triceratops*. A median epiparietal necessitates a reassessment of epioassification homology and results in a more resolved phylogeny. Most surprisingly, *Regaliceratops* exhibits a suite of cranial ornamentations that are superficially similar to Campanian centrosaurines, indicating both exploration of novel display morphospace in Chasmosaurinae, especially Maastrichtian forms, and convergent evolution in horn morphology with the recently extinct Centrosaurinae. This marks the first time that evolutionary convergence in horn-like display structures has been demonstrated between dinosaur clades, similar to those seen in fossil and extant mammals [6].

RESULTS

Systematic Paleontology

Dinosauria Owen, 1842, sensu Padian and May, 1993.
Ornithischia Seeley, 1887, sensu Sereno, 1998.
Ceratopsia Marsh, 1888, sensu Dodson, 1997.
Ceratopsidae Marsh, 1888, sensu Sereno, 1998.
Chasmosaurinae Lambe, 1915, sensu Dodson et al., 2004.
Triceratopsini Longrich et al., 2011.

Regaliceratops gen. nov.

Type species: *Regaliceratops peterhewsi* gen. et sp. nov.

Diagnosis: as per the type and only species.

Regaliceratops peterhewsi gen. et sp. nov.

Etymology

Regaliceratops, from the Latin “regalis,” meaning “royal,” combined with the Greek “ceratops,” meaning “horned face.” The adjective “royal” refers to the crown-shaped parietosquamosal frill and epioassifications and the Royal Tyrrell Museum of Palaeontology (the “Royal” appellation was bestowed on the museum in 1990 by Her Majesty Queen Elizabeth II). The species epithet honors Peter Hews, who discovered the holotype.

Holotype

The holotype and only known specimen is Tyrrell Museum of Palaeontology (TMP) 2005.055.0001, a nearly complete cranium (skull excluding lower jaw) missing only the rostral bone. Palatal and braincase regions are obscured by matrix.

Type Locality, Horizon, and Age

The holotype was recovered from Upper Cretaceous rocks along the Oldman River in the area of Waldron Flats, approximately 164 km south of Calgary, Alberta, Canada (Figure 1). The uppermost St. Mary River Formation and lowermost Willow Creek Formation are both exposed along the river in this area. Due to the strongly upthrust and faulted condition of the bedrock strata in the area and the absence of obvious outcrops of the Battle Formation and Whitemud Member marker beds in the quarry area, it has been difficult to determine the precise stratigraphic position of the specimen in relation to the contact between the St. Mary River and Willow Creek formations. Nonetheless, existing geologic maps of the area suggest that the quarry occurs within the upper 30 m of the St. Mary River Formation [9]. This stratigraphic position is supported by the presence of the angiosperm palynomorph *Scolardia trapaformis* (D.R. Braman, personal communication) in the host matrix of TMP 2005.055.0001. *S. trapaformis* is diagnostic for upper beds of both the St. Mary River Formation and the combined Carbon and Whitemud members of the

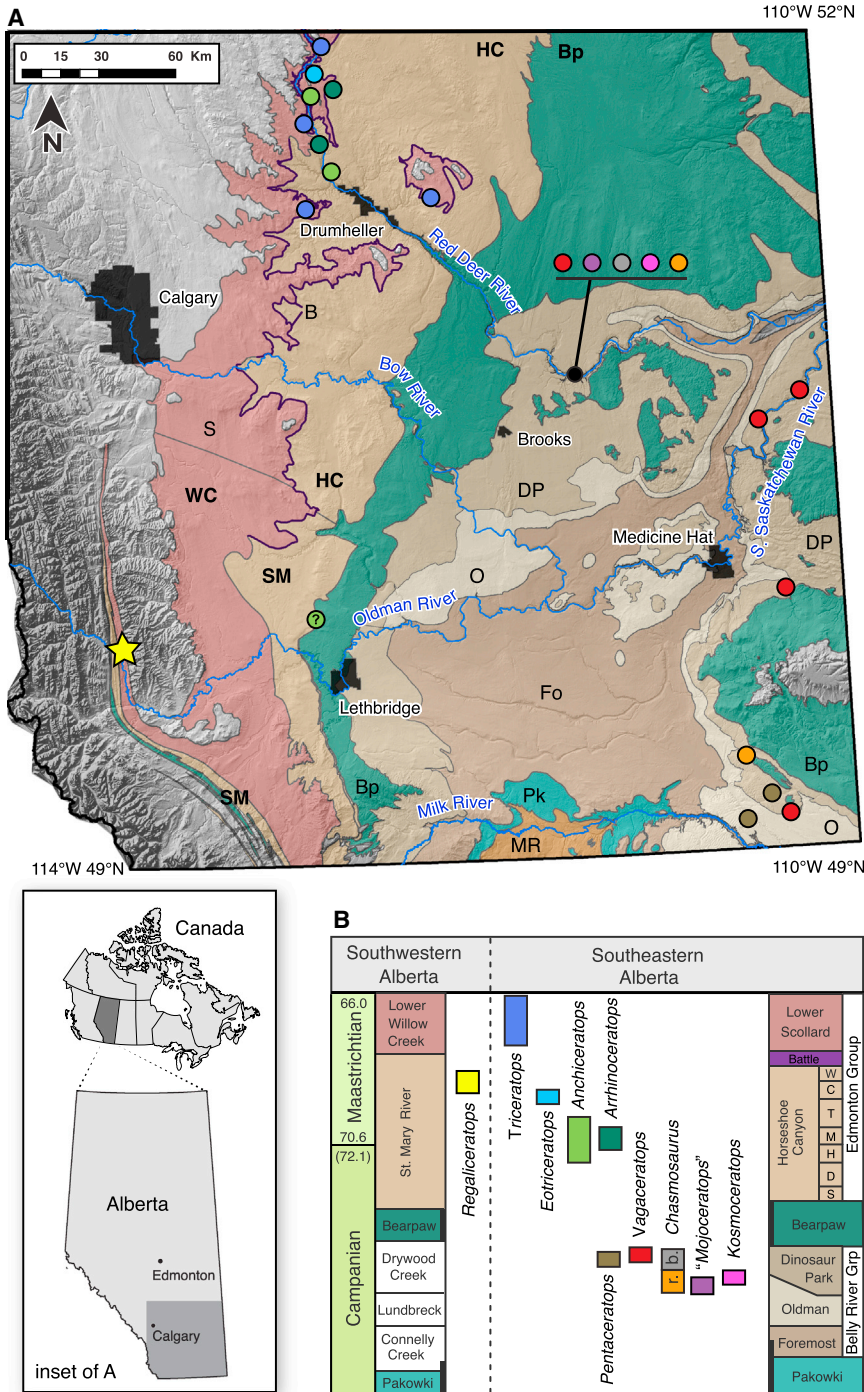


Figure 1. Geographic and Stratigraphic Occurrence of Chasmosaurinae in Upper Cretaceous Strata of Southern Alberta

(A) Map of southern Alberta (inset below shows location of A relative to Alberta and Canada) showing occurrences of chasmosaurine taxa (colored circles) and major rivers and cities. Colors of circles correspond to labeled taxa in the center panel of (B). Colored areas of the map correspond to stratigraphy of (B) and illustrate the surface exposure of Cretaceous formations in the region. Position of TMP 2005.055.0001 is indicated by the yellow star. “?” indicates purported occurrence of *Anchiceratops* at Scabby Butte, north of Lethbridge [8]. (B) Stratigraphy of southern Alberta indicating the occurrence of chasmosaurine taxa in both southwestern and southeastern regions (incorporating data from [7]). Colors of formations correspond to surface exposure in (A).

Diagnosis

Chasmosaurine ceratopsid characterized by the following autapomorphies (*) and unique suite of synapomorphies: single, midline epiparietal ossification (P0) rostrocaudally offset from plane of frill and other epiparietals, projecting caudal to parietal and with a roughly triangular transverse cross-section*; prominent midline ridge on parietal confluent with median epiparietal (P0 locus)*; paired epiparietal ossifications (P1-2) long, flat, and roughly pentagonal or spade shaped*; prominent postorbital ridge running diagonally from supraorbital horncore to base of squamosal; parietal fenestrae small or subequal in size to orbit (shared with *Kosmoceratops*); nasal horncore larger than postorbital horncores (shared with *Chasmosaurus belli* and *Vagaceratops*).

Abbreviated Description

The skull is nearly complete, missing only the rostral bone and lower jaws, and has a maximum sagittal length of approximately 1,570 mm. Although the cranium is nearly complete and three-dimensionally preserved, it has experienced post-depositional deformation affecting some aspects of the cranial morphology,

Horseshoe Canyon Formation (southern and central Alberta) [10, 11]. Carbon Member strata north of Drumheller have yielded the chasmosaurine *Eotriceratops xerinsularis* [10: Figure 3] and are assigned an age of 67.5–68.5 mega-annum (Ma) [10–12]. Given that well-established chronostratigraphic correlations across southern Alberta equate the upper Horseshoe Canyon Formation with the upper St. Mary River Formation (see Figure 9 in [13]), the holotype likely shares this same middle Maastrichtian age.

including rostrocaudal compression of the entire cranium, dorsal shear of the narial region, and dorsal deflection of the parietosquamosal frill. For a more complete discussion of the deformation, see [Supplemental Results and Discussion, “Post-Depositional Deformation.”](#) The description below highlights the most salient and diagnostic features. For a complete osteological description, as well as discussion of ontogenetic status, see [Supplemental Results and Discussion, “Description,” “Ontogenetic Status of TMP 2005.055.0001,”](#) and [Table S1.](#)

Narial Region

The narial region is completely preserved, with the exception of the rostral bone and the apex of the nasal horncore. The premaxillary septum, formed by the appressed premaxillae, is permeated rostrally by an interpremaxillary fenestra characteristic of Maastrichtian chasmosaurines (Figure 2). The caudal margin of the interpremaxillary fenestra is bounded by a narial strut, which is sinuous in shape (not broad and triangular as in *Triceratops* and *Titanoceratops* [14]) and lacks the thin septal flange seen in the Campanian chasmosaurines. The caudoventral process of the premaxilla projects caudodorsally from the laterally flared ventral aspect of the premaxilla and is of constant thickness. This process abruptly tapers caudally without forking (Figure 2) and inserts between the nasal and maxilla laterally, both features shared with Maastrichtian taxa (e.g., *Anchiceratops*, *Triceratops* [15]) but not Campanian taxa (e.g., *Chasmosaurus*, *Utahceratops* [16, 17]). The external naris extends caudally to overlap the maxillary tooth row, as seen in other Maastrichtian chasmosaurines (e.g., *Anchiceratops*, *Anchiceratops*, *Triceratops* [15, 18]) and is not restricted to the area rostral to the tooth row as in Campanian taxa [16] (Figure 2).

The most obvious feature of the narial region is a large, steeply sided nasal horncore, which is situated at the caudal margin of the external naris as in *Chasmosaurus* [16], in contrast to the more rostral position seen in *Triceratopsini* [14, 19] (Figure 2). The apex of the horncore was lost to erosion (preserved height is 148 mm) but would have had an estimated height of 240–280 mm, making it one of the tallest nasal horncores in Chasmosaurinae (see Supplemental Results and Discussion, “Description: Narial Region: Nasal” and Table S2). The nasal horncore is straight, projects dorsally and slightly rostrally, and is teardrop shaped in cross-section, with a broad rostral margin and tapered caudal margin.

Circumorbital Region

The rostradorsal margin of the orbital rim is characterized by a prominent antorbital buttress, formed by the rugose, and swollen palprebral (Figure 2). The postorbital horncores are small relative to the cranial proportions and are smaller than the nasal horncore (being ~140 mm in height and 110 mm rostrocaudal length at base). The horncores taper distally, with the apex of each replaced by a distinct resorption pit (Figure 2). The postorbital horncores are positioned slightly caudal to the orbit, in contrast to the more rostral position seen in the short-horned taxa *Chasmosaurus* and *Kosmoceratops* [16, 17], yet share the narrow base seen in these but not other chasmosaurine taxa (e.g., *Anchiceratops*, *Triceratops* [18, 19]). The horncores are dorsally directed and straight in the parasagittal plane (Figures 2C and 2D) and are rostrally procurved (Figures 2A and 2B). A prominent postorbital ridge, bearing two peaks on each side, extends caudomedially from the horncores across the postorbital. The ventrolateral extremity of the jugal is triangular, with the apex capped by a large, conical epijugal (Figure 2C). The base of the epijugal is circular to subcircular in cross-section and only slightly smaller than the postorbital horncore bases.

Parietosquamosal Frill

Although the frill is a nearly perfect semicircle in rostradorsal view, it shows signs of post-depositional deformation resulting in a shortening along the rostrocaudal axis and deflection dorsally (see Supplemental Results and Discussion, “Post-

Depositional Deformation”). Similar to *Triceratops*, the epioassifications are uniformly spaced along the circumference (Figure 2C), with no medial embayment caudally as seen in *Chasmosaurus* and *Utahceratops* [16, 17]. Relative to other chasmosaurines, but shared with *Triceratops* and *Nedoceratops*, the frill is short—less than preorbital length and less than 70% basal skull length (but see Supplemental Results and Discussion, “Post-Depositional Deformation”).

The dorsal midline of the parietal preserves a prominent sagittal keel that runs from the rostralmost point of the parietal to the base of the large midline epioassification (P0) near the caudal margin. Small, paired parietal fenestrae are situated entirely within the parietal and do not contact the squamosal laterally (in contrast to the condition in *Chasmosaurus*, *Aguja-ceratops*, and *Pentaceratops* [16, 20]). A single, large epiparietal (P0) is located at the caudal midline of the parietal, is rostradorsally offset from the caudal margin, and projects caudally (Figure 2). This epioassification is confluent with the median ridge of the parietal and is triangular in cross-section, with a sharp rostral edge and rounded caudal margin.

The remaining caudolateral periphery of the frill is adorned with a series of seven flat, distally attenuated epioassifications on each side, decreasing in size from largest caudomedially to smallest rostrolaterally. Two paired epioassifications (P1 and P2) are fused with the caudal parietal exclusively (epiparietals) and are large (larger than the postorbital horncores) and roughly pentagonal or spade shaped. These epiparietals represent the largest (maximum length 201 mm) frill epioassifications in Chasmosaurinae. Four epioassifications (S1–S4) are fused to the lateral margin of the squamosal (episquamosals). The rostralmost three episquamosals (S2–S4) are roughly triangular in shape and decrease slightly in size rostrally, while the caudalmost (S1) is pentagonal or spade shaped and distinctly larger than the rostralmost three. One paired epioassification (PS) articulates along the parietosquamosal suture (epiparietosquamosal) and is transitional in both shape and size between the epiparietals and episquamosals.

DISCUSSION

Homology of Frill Epioassifications

The pattern of homology of the parietosquamosal epioassifications is integral to an understanding of both taxonomy and phylogeny of Ceratopsidae. A homology scheme numbering the epioassifications from medial to lateral was derived initially for the diverse array of spike- and horn-like epioassifications seen in centrosaurines [21–24] and was subsequently applied across Ceratopsidae [25, 26] and modified to include more basal taxa (K.E. Clayton et al., 2009, 2010, Soc. Vertebrate Paleontol., abstracts). These studies have shown that for the parietal of Centrosaurinae, the number of epioassifications is relatively constant, but with more medial loci showing more variation in development and more phylogenetic signal than lateral ossifications [22, 27]. Contrasted with Centrosaurinae, epioassification homology in Chasmosaurinae is less well established and has featured less prominently in inferring phylogeny. New data derived from the epioassifications of *Regaliceratops* have prompted a review of epioassification homology across Chasmosaurinae, specifically those taxa with a median epiparietal (Figure S3).

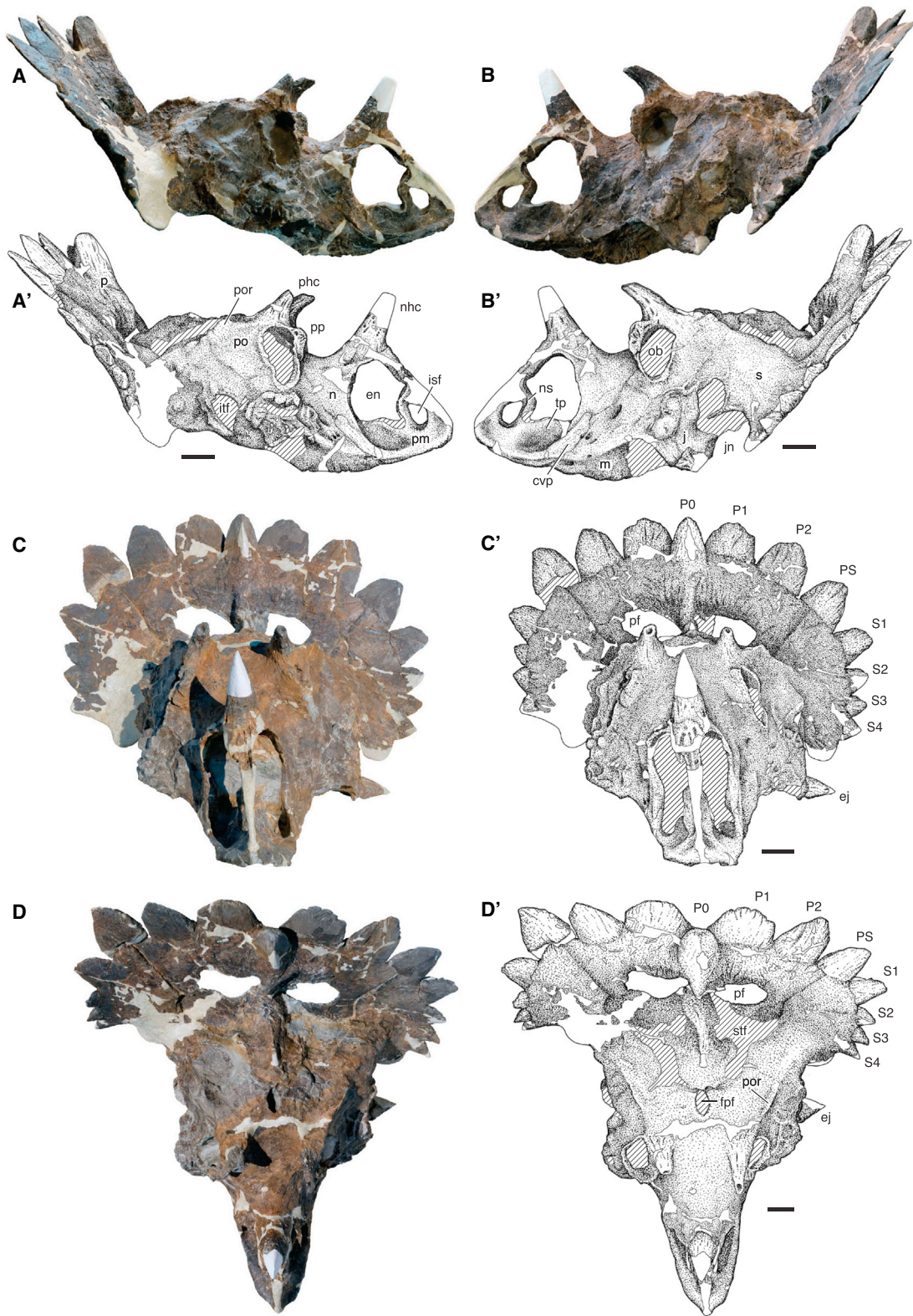
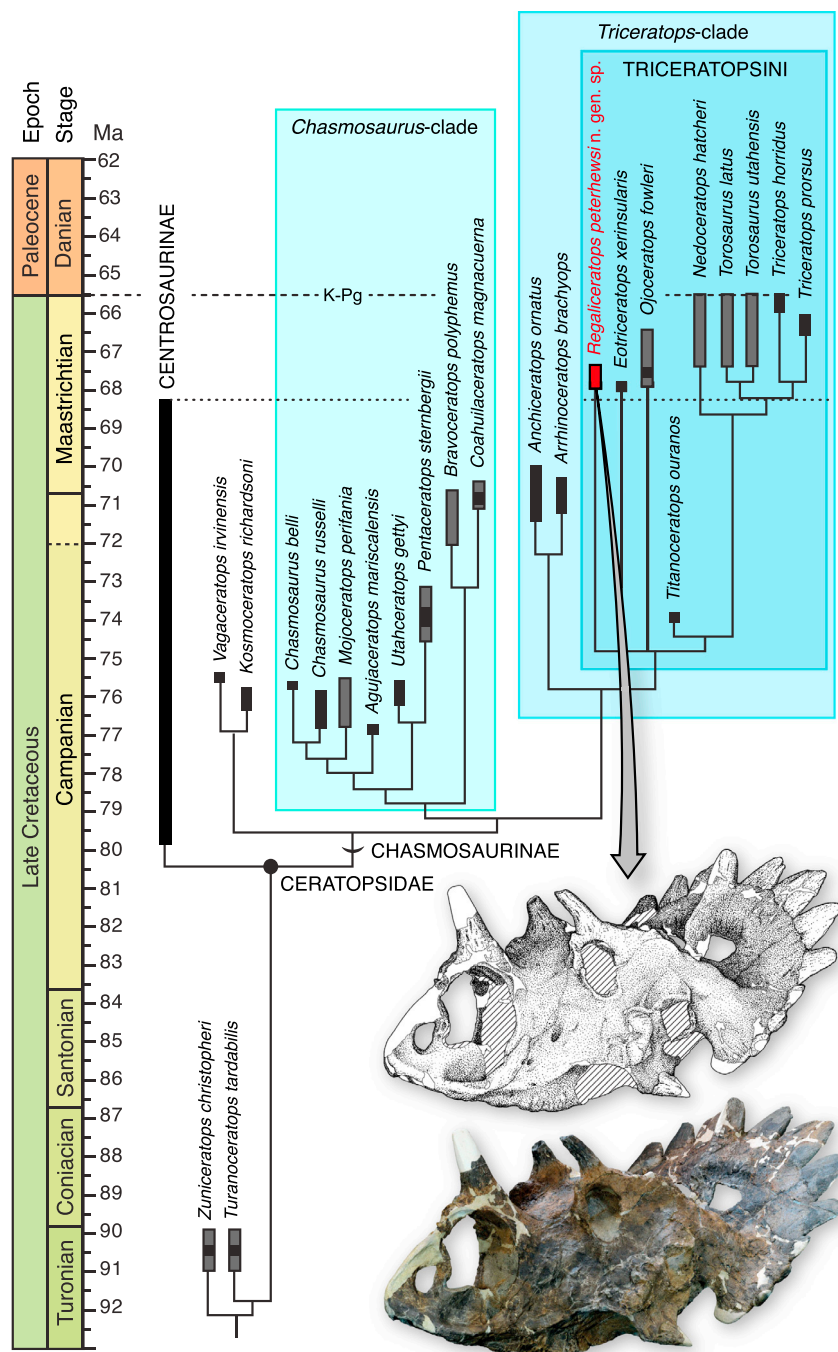


Figure 2. Photographs and Interpretive Line Drawings of the Holotype of *Regaliceratops peterhewsi* gen. et sp. nov.

(A–D) Nearly complete cranium, TMP 2005.055.0001, in right lateral (A), left lateral (B), rostral (C), and dorsal (D) views.

(A'–D') Interpretive drawings of photographed views in (A)–(D).

(legend continued on next page)



The median epiparietal of *Regaliceratops* is similar, and likely homologous, to the median epiparietal of *Triceratops* spp., previously termed P0 (e.g., [28] and K.E. Clayton et al., 2010, Soc. Vertebrate Paleontol., abstract), in terms of (1) a median position,

(2) being of unpaired morphology, and (3) projecting caudal to the parietal margin. Additionally, based on (1) dorsally offset position from the plane of the frill, (2) rostrally offset position from the caudal margin of the frill, and (3) roughly triangular cross-section, the median epiossification of *Regaliceratops* is likely also homologous with the laterally curved hooks of *Anchiceratops*, which have previously been termed P1 [15]. To test this homology across Chasmosaurinae, we shifted the identity of the epiparietals of *Anchiceratops*, *Pentaceratops*, and *Utahceratops* one position medially (Figure S3; see Supplemental Experimental Procedures, “Phylogenetic Methods”). The phylogenetic analysis of this revised homology scheme for the epiossifications results in a simpler and better-resolved evolutionary history (i.e., a shorter, better-resolved tree), indicating support for the revised homology hypothesis proposed here (Figure S1; see Supplemental Experimental Procedures, “Phylogenetic Methods”).

Regaliceratops and Display Evolution in Ceratopsidae

The cladistic analysis of relationships within Chasmosaurinae recovers *Regaliceratops* in a polytomy with *Eotriceratops* and *Ojoceratops*, as sister taxa to the remaining Triceratopsini (*Triceratops*, *Torosaurus*, *Nedoceratops*, *Titanoceratops*)

(Figures 3 and S1). This phylogenetic position hypothesized for *Regaliceratops* is consistent with its temporal occurrence, being roughly time equivalent to *Eotriceratops* (Figure 3). This suggests that *Regaliceratops* is part of an evolutionary trend showing both

Areas in shadow, (C) and (D) left, are fully illustrated at right. Areas in white represent reconstruction (plaster/epoxy putty), and hatched areas indicate matrix. The following abbreviations are used: cvp, caudoventral process of premaxilla; ej, epijugal; en, external naris; isf, interseptal fenestra; itf, infratemporal fenestra; j, jugal; jn, jugal notch; m, maxilla; n, nasal; nhc, nasal horncore; ns, narial strut; ob, orbit; p, parietal; pf, parietal fenestra; phc, postorbital horncore; pm, premaxilla; por, postorbital ridge; pp, palpebral; ps, epiparietosquamosal; P#, epiparietal; s, squamosal; stf, supertemporal fenestra; S#, episquamosal; tp, triangular process. Scale bar represents 10 cm.

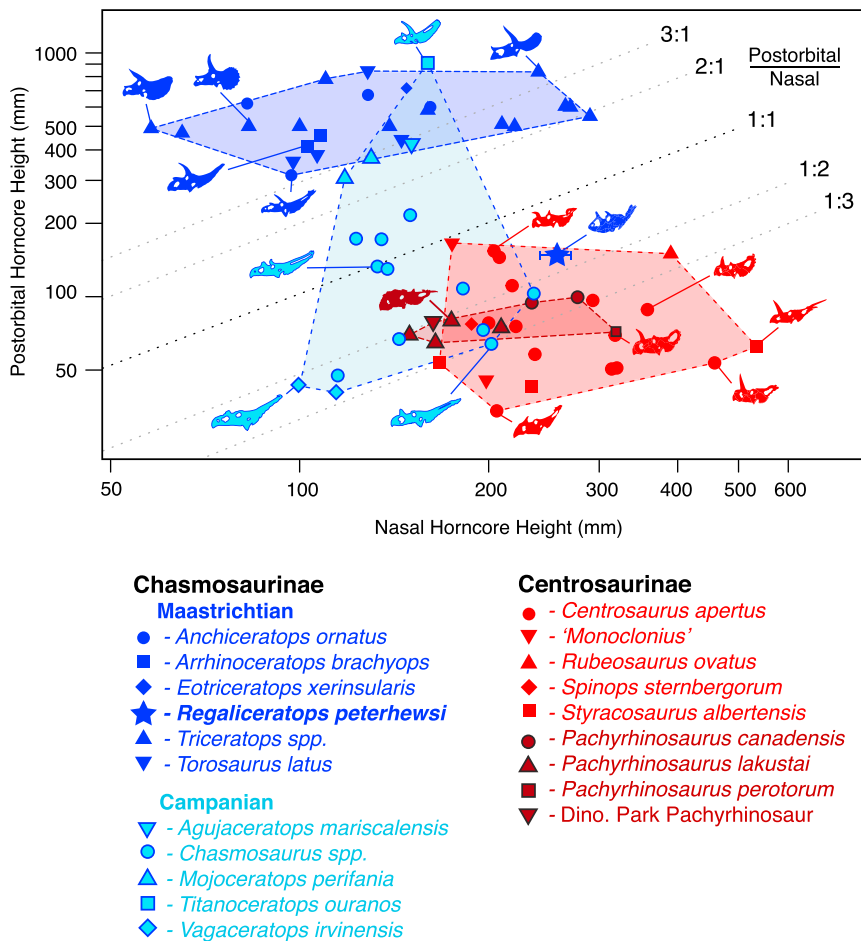


Figure 4. Plot Illustrating Morphospace within Ceratopsidae in Reference to Postorbital Horncore Length against Nasal Horncore Length

Convex hulls (colored polygons) show morphospace occupation by Centrosaurinae (red), Campanian Chasmosaurinae (light blue), and Maastrichtian Chasmosaurinae, excluding *Regaliceratops* (dark blue). Diagonal dotted lines indicate ratio of postorbital horn length to nasal horn length. Basal centrosaurines (e.g., *Albertaceratops*, *Diabloceratops*) are not plotted. Data are derived from specimen measurements (C.M.B.) as well as previously published data; see Table S2.

an increase in body size and solidification of the frill, with an extreme example being the latest Maastrichtian *Triceratops*. Despite being recovered within the Triceratopsini, *Regaliceratops* shows ornamentation morphology distinct from all other members of this clade, as well as the more inclusive clade including *Anchiceratops* and *Arrhinoceratops*. Relative to all other taxa in this clade, *Regaliceratops* has the smallest postorbital horncores (Figure S2), as well as the tallest nasal horncore relative to skull size. Campanian chasmosaurines show plasticity in the size of the postorbital horncore, with the evolution of short horncores occurring at least three times (Figure S2). However, prior to the discovery of *Regaliceratops*, Maastrichtian chasmosaurine taxa appeared to have stabilized on a long-horned postorbital, and this new taxon represents the only evolution of a short-horned postorbital within Maastrichtian chasmosaurines (Figure S2).

There has been a historical dichotomy in ceratopsid cranial ornamentation where individual species tend to emphasize either (1) the nasal horn and frill epiossification (e.g., *Styracosaurus*, *Centrosaurus*) or (2) the postorbital horns and length of the frill (e.g., *Anchiceratops*, *Chasmosaurus*, *Pentaceratops*), but not both [5, 29, 30] (Figure 4). These contrasting patterns of cranial ornamentation have been thought to be evolutionary hallmarks of two independent evolutionary lineages, Centrosaurinae (emphasizing nasal horn and frill epiossifications) and Chasmo-

saurinae (emphasizing the postorbital horns and length of the frill) [30, 31]. Recent discovery of the basal centrosaurines *Albertaceratops* [32], *Diabloceratops* [33], and *Nasutoceratops* [34] have illustrated higher disparity in cranial ornamentation than previously thought and indicate that this dichotomy evolved not at the split between Chasmosaurinae and Centrosaurinae, but within the Chasmosaurinae and Centrosaurinae lineages. Additionally, Sampson et al. [34] reported the discovery of a clade within Centrosaurinae (*Nasutoceratops* and *Avaceratops*) showing cranial ornamentation similar to those of Chasmosaurinae, i.e., an emphasis on the size of the postorbital horns and retention of a less complex frill.

The discovery of *Regaliceratops*, although well nested within Chasmosaurinae, shows the reciprocal pattern to the basal centrosaurines above, where the nasal horn and epiossifications are exaggerated relative to the postorbital horns and frill length. A plot of postorbital horncore length as a function of nasal horncore length results in *Regaliceratops* falling far outside the morphospace occupied by other Maastrichtian chasmosaurines, and within the morphospace of Campanian centrosaurines (Figure 4). This is an unexpected pattern for Maastrichtian Chasmosaurinae, and one that is evolutionarily convergent with Centrosaurinae. Convergent evolution of horns, or other display/signaling structures, between sister clades or more distantly related groups has been well documented in mammals [6, 35, 36] and recently found in hadrosaurid dinosaurs [37], but this marks the first occurrence within the diverse clade of horned dinosaurs. Based on disparate patterns of cranial ornamentation, the use of these horns and frills as display or sociosexual signaling structures has been suggested to be distinct between these two subfamilies of horn dinosaurs [29, 38, 39]. Convergent horn evolution in mammals often correlates with convergent social behaviors [6]. It may be hypothesized that *Regaliceratops* converged not only morphologically with Centrosaurines but also behaviorally, following the early Maastrichtian extinction of Centrosaurinae.

Chasmosaurine Evolution

The occurrence of a chasmosaurine ceratopsid with centrosaurine-like ornamentation following the early Maastrichtian extinction of the Centrosaurinae illustrates chasmosaurine ornamentation increasing in disparity and exploration of novel morphospace previously occupied by the Centrosaurinae (Figure 4). Prior to this discovery, Maastrichtian-aged ceratopsid and hadrosaurid taxa exhibited a pattern of lower diversity and longer duration than Campanian-aged taxa [12, 40, 41] and may also have exhibited a pattern of lower morphological disparity [42] and slowing of evolutionary rates. *Regaliceratops* not only increases the diversity of Maastrichtian ceratopsids but also greatly increases the known morphological disparity.

The present study finds cladistic support for a deep split within the Chasmosaurinae into an older *Chasmosaurus* clade and a younger *Triceratops* clade based on features of the premaxilla and parietal shape (exclusive of the epiossifications). If supported by future analyses, this deep split within Chasmosaurinae has two major implications for chasmosaurine evolution. First, because these two clades are nearly non-overlapping (the *Chasmosaurus* clade being of largely Campanian age, and the *Triceratops* clade being of largely Maastrichtian age), a long (3 Ma) ghost lineage is implied at the base of the *Triceratops* clade (Figure 3). A similar (5 Ma) ghost lineage is also implied for many taxa within the Triceratopsini [14], and these ghost lineages taken together suggest that there is an undiscovered diversity of Chasmosaurine taxa in the Campanian and Maastrichtian. Much of the ghost lineage within the *Triceratops* clade is inferred due to *Titanoceratops* being well nested within Triceratopsini yet occurring in the Campanian, a combination that is stratigraphically inconsistent relative to the other taxa.

The second implication is that the *Chasmosaurus* clade appears to go extinct in the early Maastrichtian, at approximately the same time as the extinction of the Centrosaurinae. The dynamics of the centrosaurine extinction are not well understood, so whether a common mechanism may be responsible cannot be determined. We speculate that the extinction of two diverse clades of horned dinosaurs in the early Maastrichtian may have allowed for the diversification of the Triceratopsini just prior to the end-Cretaceous mass extinction.

More than 100 years of fossil collecting and stratigraphic work on the upper Campanian and Maastrichtian strata of the Red Deer River Valley, specifically the Horseshoe Canyon and Scollard formations, has revealed distinct faunal turnovers in ornithischian taxa through this interval [12]. This is perhaps best illustrated by the Chasmosaurinae, with *Anchiceratops* occurring in the Horsethief, Morrin, and Tolman members; *Anchiceratops* occurring in the Horsethief and Morrin members; *Eotriceratops* occurring in the Carbon member; and *Triceratops* occurring in the Scollard Formation [12]. This high-resolution dinosaur biostratigraphy, particularly across the Campanian-Maastrichtian boundary, is in contrast to much of the Upper Cretaceous record elsewhere in North America, where terrestrial stratigraphic sections are neither as complete and continuous nor as rich in dinosaurs (e.g., Figure 6.11 in [43]).

The unexpected discovery of *Regaliceratops* reinforces the plasticity in cranial ornamentation expressed in Ceratopsidae and highlights how much of their true diversity still remains unknown. Ongoing research will likely continue to reveal both

increased taxonomic diversity and increased morphological disparity (particularly in cranial ornamentations) within the group and may continue to blur the suite of ornamentation features between the two subfamilies.

ACCESSION NUMBERS AND NOMENCLATURE

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. ZooBank LSIDs (Life Science Identifiers) can be viewed by appending the LSID to the prefix <http://zoobank.org/>. The LSID for this publication is urn:lsid:zoobank.org:pub:9D3C353D-4422-49D7-85FD-28FFF489FA6A. The electronic edition of this work was published in a journal with an ISSN and will be archived and made available from the following digital repository: CLOCKSS (<http://www.clockss.org/clockss/Home>).

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Results and Discussion, three figures, two tables, three appendices, and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.04.041>.

AUTHOR CONTRIBUTIONS

D.M.H. assisted with collecting the specimen. C.M.B. performed the description and phylogenetic analyses. C.M.B. and D.M.H. wrote the manuscript.

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