A new centrosaurine from the Late Cretaceous of Alberta, Canada, and the evolution of parietal ornamentation in horned dinosaurs

ANDREW A. FARKE, MICHAEL J. RYAN, PAUL M. BARRETT, DARREN H. TANKE, DENNIS R. BRAMAN, MARK A. LOEWEN, and MARK R. GRAHAM

Farke, A.A., Ryan, M.J., Barrett, P.M., Tanke, D.H., Braman, D.R., Loewen, M.A., and Graham, M.R. 2011. A new centrosaurine from the Late Cretaceous of Alberta, Canada, and the evolution of parietal ornamentation in horned dinosaurs. *Acta Palaeontologica Polonica* 56 (4): 691–702.

In 1916, a centrosaurine dinosaur bonebed was excavated within the Campanian-aged deposits of what is now Dinosaur Provincial Park, Alberta, Canada. Specimens from this now-lost quarry, including two parietals, a squamosal, a skull missing the frill, and an incomplete dentary, were purchased by The Natural History Museum, London. The material was recently reprepared and identified herein as a previously unknown taxon, *Spinops sternbergorum* gen. et sp. nov. Based upon the available locality data and paleopalynology, the quarry lies in either the upper part of the Oldman Formation or the lower part of the Dinosaur Park Formation. The facial region of the partial skull is similar to putative mature specimens of *Centrosaurus* spp. and *Styracosaurus albertensis*, with short, rounded postorbital horncores and a large, erect nasal horncore. Parietal ornamentation is consistent on both known parietals and is unique among ceratopsids. Bilateral, procurved parietal hooks occupy the P1 (medial-most) position on the dorsal surface of the parietal and are very similar to those seen in *Centrosaurus apertus*. Epiparietals in the P2 or possibly P3 position (lateral to P1) manifest as extremely elongate, caudally directed spikes, unlike the condition in *C. apertus*, *S. albertensis*, or any other "derived" centrosaurine. Cladistic analysis suggests that *S. sternbergorum* is closely related to *Centrosaurus* and *Styracosaurus*. Historically, based upon the condition in *Styracosaurus* and related centrosaurines, it was assumed that the medial-most elongated spikes on centrosaurine parietals correspond to the P3 epiparietal position. The exception illustrated in the new taxon suggests that homologies of epiparietals among basal centrosaurines (e.g., *Albertaceratops* and *Diabloceratops*) and derived centrosaurines (e.g., *Styracosaurus* and "pachyrhinosaurs") should be reconsidered. The medially-placed, caudally-directed "P3" process of basal centrosaurines may, in fact, be homologous with P2.

Key words: Dinosauria, Ornithischia, Centrosaurinae, Ceratopsidae, epiparietal, Oldman Formation, Dinosaur Park Formation, Campanian, Cretaceous, Alberta, Canada.

Andrew A. Farke [afarke@webb.org], Raymond M. Alf Museum of Paleontology, 1175 West Baseline Road, Claremont, CA 91711, USA;
Michael J. Ryan [mryan@cmnh.org], Department of Vertebrate Paleontology, Cleveland Museum of Natural History, 1 Wade Oval Drive, Cleveland, OH 44106, USA;
Paul M. Barrett [p.barrett@nhm.ac.uk], Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK;
Darren H. Tanke [darren.tanke@gov.ab.ca] and Dennis R. Braman [dennis.braman@gov.ab.ca], Royal Tyrrell Museum of Palaeontology, P.O. Box 7500, Drumheller, AB T0J 0Y0, Canada;
Mark A. Loewen [mloewen@nhmu.utah.edu], Department of Geology and Geophysics, University of Utah; Natural History Museum of Utah, 301 Wakara Way, Salt Lake City, UT 84108, USA;
Mark R. Graham [m.graham@nhm.ac.uk], Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK.

Received 30 November 2010, accepted 27 January 2011, available online 6 December 2011.

Introduction

During the past four decades, Ceratopsidae (popularly known as "horned dinosaurs") has been the subject of intensive work in such diverse areas as behavior (e.g., Currie and Dodson 1984; Sampson 1997; Farke 2004; Hunt and Farke 2010), thermal physiology (e.g., Farlow and Dodson 1975; Barrick et al. 1998) and biomechanics (e.g., Dodson and Farlow 1997; Paul and Christiansen 2000; Thompson and Holmes 2007; Fujiwara 2009; Rega et al. 2010). This interest has been driven in part by the near doubling of the number of named, valid species over the past 25 years, beginning with *Avaceratops lammersi* (Dodson, 1986), which was the first new ceratopsid taxon to be named since *Pachyrhinosaurus canadensis* (Stern-

http://dx.doi.org/10.4202/app.2010.0121

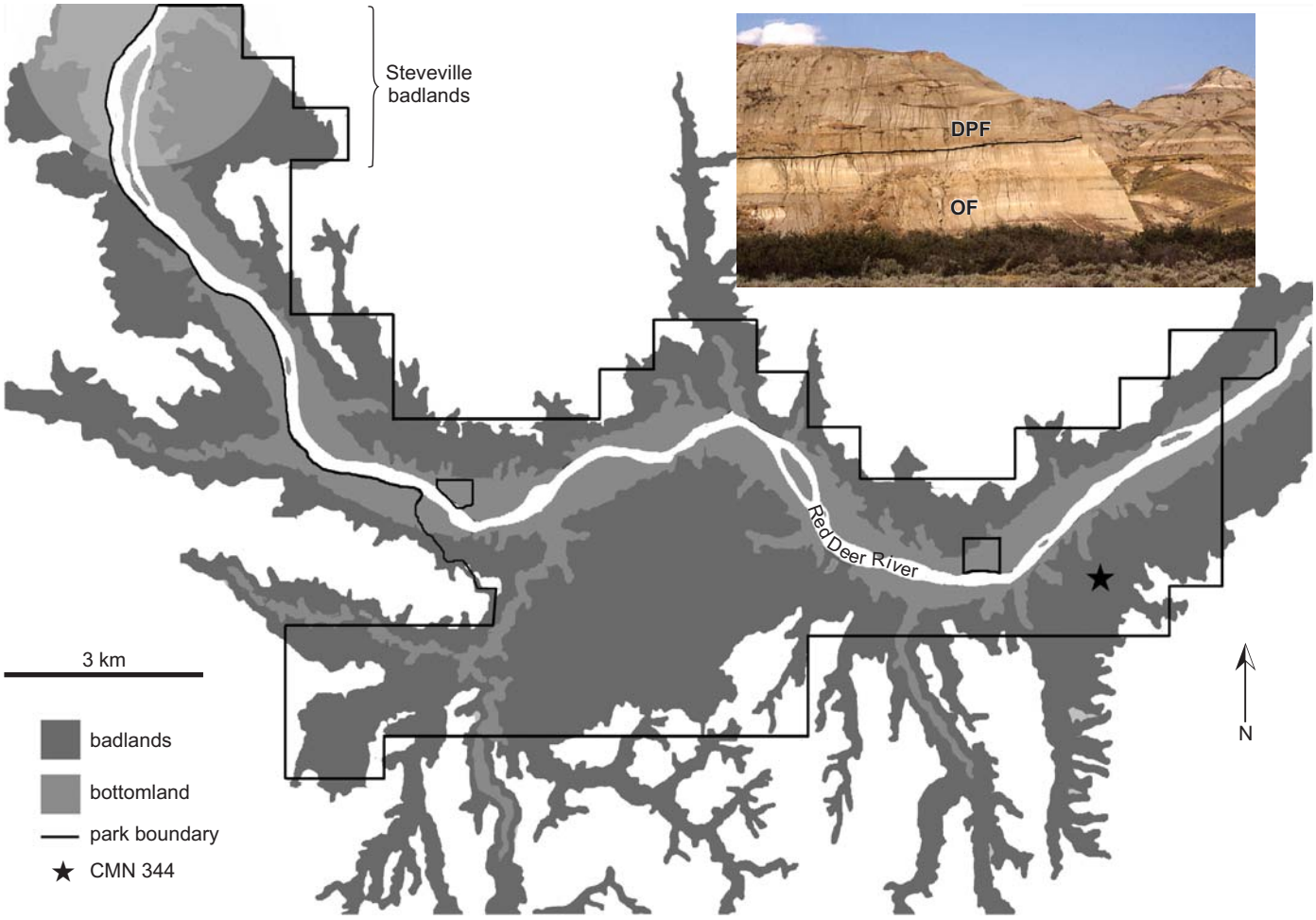

Fig. 1. Map showing the presumed location of the *Spinops sternbergorum* gen. et sp. nov. type locality within the area informally called the "Steveville badlands," Dinosaur Provincial Park, Alberta Canada. Charles Sternberg (unpublished data in NHMUK archives) indicated that the bone bed was one mile below the mouth of Berry Creek, and the estimated area that this covers is indicated by the grey semi-circle. Intense prospecting on the east side of the river has failed to relocate the quarry, and badlands on the west side are outside of the Park boundary and currently inaccessible for prospecting. The indicated southeast Park boundary does not include the margins of two major coulees in this region that are also within the Park. Note that the quarry for the holotype of *Styracosaurus albertensis* Lambe, 1913 (CMN 344) is in the southeast part of the Park. The inset photograph, courtesy of David Eberth, shows a typical view of the contact between the Dinosaur Park Formation (DPF) and Oldman Formation (OF) near the Steveville badlands.

berg, 1950). Although several historical taxa have been "lost" during the past 25 years (e.g., *"Brachyceratops*" and "*Monoclonius*" are now regarded as nomina dubia; Sampson et al. 1997), no fewer than 18 new taxa have been erected. Of these, only four are from Alberta: representing the ceratopsid clade Centrosaurinae, *Centrosaurus brinkmani* (Ryan and Russell, 2005) from the uppermost Oldman Formation and *Albertaceratops nesmoi* (Ryan, 2007) from the lowermost Oldman Formation; and representing the clade Chasmosaurinae, *Vagaceratops irvinensis* (Holmes, Forster, Ryan, and Shephard, 2001) and *Mojoceratops perifania* (Longrich, 2010) from the Dinosaur Park Formation.

One possible reason for the limited number of new taxa from Alberta is that most of the productive ceratopsian-bearing outcrops are restricted to the Dinosaur Park Formation within the geographically limited area (73 km^2) of Dinosaur Provincial Park. These beds have been well prospected since 1898, when Lawrence Lambe made the first major collections of fossils from this area (Currie 2005). A disconformity separates the Dinosaur Park Formation from the underlying Oldman Formation, and no more than 20 m (generally much less) of the upper part of the Oldman Formation is exposed within the park (Eberth 2005).

Recent work by Currie and Russell (2005), Eberth (2005), and others has allowed precise geographic and stratigraphic placement of many significant dinosaur skulls and skeletons collected within Dinosaur Provincial Park. Using these data for the Dinosaur Park Formation, Ryan and Evans (2005) identified three dinosaur faunal zones, each possessing a unique, stratigraphically restricted centrosaurine ceratopsid and lambeosaurine hadrosaurid. In ascending order the zones are: the *Centrosaurus–Corythosaurus* Zone (the lowest 30 m), the *Styracosaurus–Lambeosaurus* Zone (the successive ~30 m), and the "pachyrhinosaur–*Lambeosaurus magnicristatus*–*Vagaceratops irvinensis* Zone (in the uppermost Lethbridge Coal Zone). Each zone also appears to have an associated

chasmosaurine ceratopsid species (Holmes et al. 2001), these being *Chasmosaurus russelli*, *C. belli*, and *Vagaceratops irvinensis*, respectively. However the current data are not sufficiently robust to confirm that these species do not cross the proposed faunal boundaries (Ryan and Evans 2005). Both *Centrosaurus apertus* and *Styracosaurus albertensis* are known from multiple bone beds (>20 and at least two, respectively), skeletons and isolated elements, whereas an unidentified "pachyrhinosaur" (sensu Currie et al. 2008) is known from only a single specimen (Ryan et al. 2010).

Here, we describe a new centrosaurine ceratopsid, *Spinops sternbergorum*, from the northwestern region ("Steveville Badlands") of Dinosaur Provincial Park (Fig. 1). The material was collected by Charles H. Sternberg and Levi Sternberg in the summer of 1916 on behalf of the British Museum (Natural History, now the Natural History Museum, London), with funding provided by the Percy Sladen Trust. During the expedition, the Sternbergs discovered and collected fossils from a ceratopsian bonebed—the first to be systematically excavated in Alberta.

Unfortunately, no known field notes are associated with the excavation, but correspondence between Charles Sternberg and staff at the Natural History Museum indicates that the bonebed was quite dense and that the skeletal material was disarticulated and preserved within a well-indurated, iron-rich matrix. Charles Sternberg believed that the material represented a new taxon closely related to *Styracosaurus albertensis*, but Arthur Smith Woodward (then Keeper of Geology at the museum) was greatly disappointed with the quality of the specimens. An unsigned letter to C. Sternberg in the Natural History Museum archives, dated 11 January 1918, states, "There is indeed in the Sladen Collection nothing but rubbish...". Consequently, most of the material remained overlooked and unprepared for over 90 years. However, re-examination of the collection led several of the authors to conclude that the fossils might represent a new taxon, providing the impetus to prepare the specimens fully (Figs. 2–4).

Beyond expanding ceratopsid diversity counts, specimens of *Spinops sternbergorum* provide new information on the evolution of epiparietals, the marginal ossifications on the parietal bone of the frill. Epiparietal morphology varies greatly within Centrosaurinae, ranging from low, rounded crescents to elongated spikes to procurved hooks (Fig. 5). Because these ornamentations appear to have phylogenetic significance, epiparietals are central to centrosaurine systematics. Traditionally, epiparietals have been homologized on the basis of their positions relative to the midline of the parietal. The ossification immediately adjacent to the midline is termed the P1 process, the next lateral ossification the P2 process, and so forth (Sampson 1995; Fig. 5). The derived morphology for P3 in many long-known species is an elongated spike (e.g., *Styracosaurus albertensis* and *Pachyrhinosaurus lakustai*), and thus elongated spikes in a number of newly described species (e.g., *Albertaceratops nesmoi*) have likewise been identified as P3. Material of *Spinops sternbergorum* suggests that alternative homology statements are possible, with implications for centrosaurine phylogenetic hypotheses.

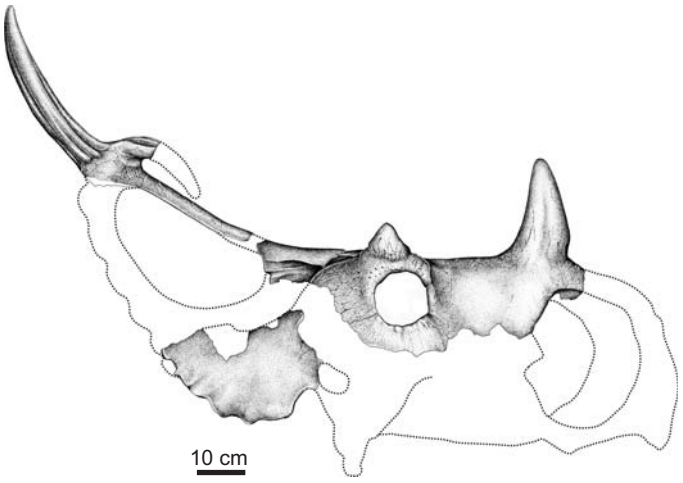

Fig. 2. Reconstruction of the skull of *Spinops sternbergorum* gen. et sp. nov. from the Campanian of Dinosaur Provincial Park, southern Alberta, in right lateral view. Preserved elements are stippled; missing portions are dotted and modeled after *Centrosaurus apertus*.

Institutional abbreviations.—CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; NHMUK, The Natural History Museum, London, England, United Kingdom; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

Other abbreviations.—CI, consistency indices; CIC, cladistic information content; MPT, most parsimonious trees; RCI, rescaled consistency indices; SRC, strict reduced consensus; TL, tree lengths.

Preparation methods

The specimens were prepared mechanically by one of the authors (MRG). Thick areas of matrix were scored with a rotary industrial diamond-edged cutter (to 12 cm on NHMUK R16308), and the matrix was removed by hand chisels and airpens. Rotary grinders were used nearer the bone surfaces, and fine removal of sediment particles was achieved by air abrasion with powdered aluminium oxide and sodium bicarbonate. A small sample of matrix from around NHMUK R16306 was processed for pollen, using standard techniques (see Supplemetary Online Material at http://app.pan.pl/SOM/app56-Farke_etal_SOM.pdf: SOM 1).

Systematic paleontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Ceratopsia Marsh, 1890

http://dx.doi.org/10.4202/app.2010.0121

Ceratopsidae Marsh, 1888

Centrosaurinae Lambe, 1915

Genus *Spinops* nov.

Etymology: From the Latin *spina*, spine; and the Greek—*ops*, face; referring to the ornamentation on the face.

Type species: *Spinops sternbergorum* sp. nov.; see below.

Diagnosis.—As for the only species.

Spinops sternbergorum sp. nov.

Figs. 2–4.

Etymology: The specific epithet honors Charles H. and Levi Sternberg, collectors of the original specimens.

Holotype: NHMUK R16307, a partial parietal bone, preserving most of the midline bar and a portion of the lateral rami (Fig. 3C).

Type locality: Exact locality unknown but collected in the vicinity of the Red Deer River, Steveville Badlands, Dinosaur Provincial Park, Alberta, Canada (Fig. 1). Attempts to relocate the quarry have been unsuccessful so far.

Type horizon: Unfortunately, only limited stratigraphic data are available. The locality was estimated to be at least 90 m stratigraphically below the quarry that yielded the type specimen of *Styracosaurus albertensis* (C. H. Sternberg, 9 July 1916 letter to A. Smith Woodward, NHMUK archives; see also Tanke 2010). The *S. albertensis* locality is approximately 42 m above the contact between the Dinosaur Park Formation and the underlying Oldman Formation. Because the Oldman Formation is only 40 m thick in Dinosaur Provincial Park (Eberth 2005), this would place the type locality for *Spinops sternbergorum* in the Foremost Formation (which underlies the Oldman Formation). However, the Foremost Formation is not exposed in the immediate region, so Sternberg's estimation of the stratigraphic position of the quarry is almost certainly incorrect. Palynological analysis of the matrix from the *Spinops* bonebed is most consistent with location of the quarry within either the upper few meters of the Oldman Formation or at any level in the Dinosaur Park Formation (see SOM 1). Sternberg described the quarry as at floodplain level near Berry Creek; the pattern of exposures in this vicinity suggests that the quarry is no higher than the lower Dinosaur Park Formation and quite possibly in the upper Oldman Formation, which is exposed at floodplain level there.

Definition and diagnosis.—A centrosaurine ceratopsid characterized by the following unique combination of characters: a procurving hook as the most medial-most epiparietal (P1) on the caudal margin of the parietal, with a straight, caudally-projecting spike (presumed P2 or possibly P3) with gentle dorsal curvature immediately lateral to the hook; short postorbital horncores that project dorsally; nasal horn core longer than the postorbital horncores. The prominence of the P1 hooks and their proximity to the caudally-projecting spike distinguish *Spinops sternbergorum* from *Styracosaurus albertensis* and other centrosaurines exclusive of *Centrosaurus* spp., and the caudally-projecting spike distinguishes *S. sternbergorum* from *Centrosaurus* spp.

Referred material.—NHMUK R16308, a partial parietal bone, preserving portions of the midline bar and lateral rami, with adhered partial dentary and unidentifiable limb elements. NHMUK R16306, an incomplete skull, preserving the dorsal portion of the skull from the rostralmost portion of the midline parietal bar to the caudalmost portion of the premaxillae, lacking all elements ventral to the ventral border of the orbit. NHMUK R16309, a partial right squamosal. Although none of this material was found in articulation, it was all closely associated in the same bone bed and no evidence suggests that any other ceratopsid taxon was present. None of the isolated elements can be assigned confidently to the individual represented by the partial skull.

Description

Parietal (Fig. 3B, C).—The following description is based primarily upon the holotype and most complete specimen, NHMUK R16307, supplemented by information from the referred specimen NHMUK R16308. In nearly all details, the two specimens are remarkably similar.

The midline bar of the parietal is smooth and unornamented, with only extremely subtle dorsal undulations. In cross section, the bar is roughly triangular in outline, with a rounded dorsum and lateral edges that thin to a point. The bar is 119 mm wide in NHMUK R16307. The ventral surface is gently and convexly rounded, similar to the condition seen in other centrosaurines. Only a portion of the margin of the parietal fenestra is preserved on the right side of NHMUK R16307 (Fig. $3C_1$); although this is complete enough to indicate the presence of fenestrae, it does not allow any details of their morphology to be determined.

The lateral rami of the parietal have a broad, V-shaped embayment (253 mm wide between the bases of epiparietals P2), as seen in most other centrosaurines (e.g., *Centrosaurus apertus*). Well-developed epiparietals ornament this portion of the frill. Following the numbering scheme of Sampson (1995), only epiparietals P1 and P2 are preserved in each specimen (see discussion below for more on establishing homology of the processes in *Spinops*; the epiparietal adjacent to P1 may instead represent P3). The remainders of the lateral rami, and the associated epiparietals, are not preserved.

A procurving bony hook (P1) occurs on both sides of the midline, similar to those seen in *Centrosaurus apertus*. The base of the hook projects directly dorsally, and the bone curves rostrally towards its distal end (Fig. $3C_3$). The distal ends of both processes in the holotype were broken and lost during collection, as indicated by the cancellous bone texture visible along fresh breaks. The left hook, which is 120 mm in mediolateral width and 47 mm in craniocaudal length, is more completely preserved than the right. The ventral surface of the hook is smooth, but the dorsal surface has a very deep sulcus laterally (approximately 15 mm deep), with a second, shallower sulcus (5 mm deep) positioned immediately lateral to this. The remainder of the hook was abraded post-collection.

In the referred specimen (NHMUK R16308; Fig. 3B) the right hook is approximately 90 mm in width, but its length cannot be reliably measured as other bones cover this area. The hook on the left side projects at least 80 mm from the dorsal surface of the parietal and measures at least 115 mm in length along the outer curve (approximately 100 mm straight length). A portion of the cross section is preserved, allowing estimation of the degree of taper for the hook, which suggests the complete hooks might have been up to 200 mm long.

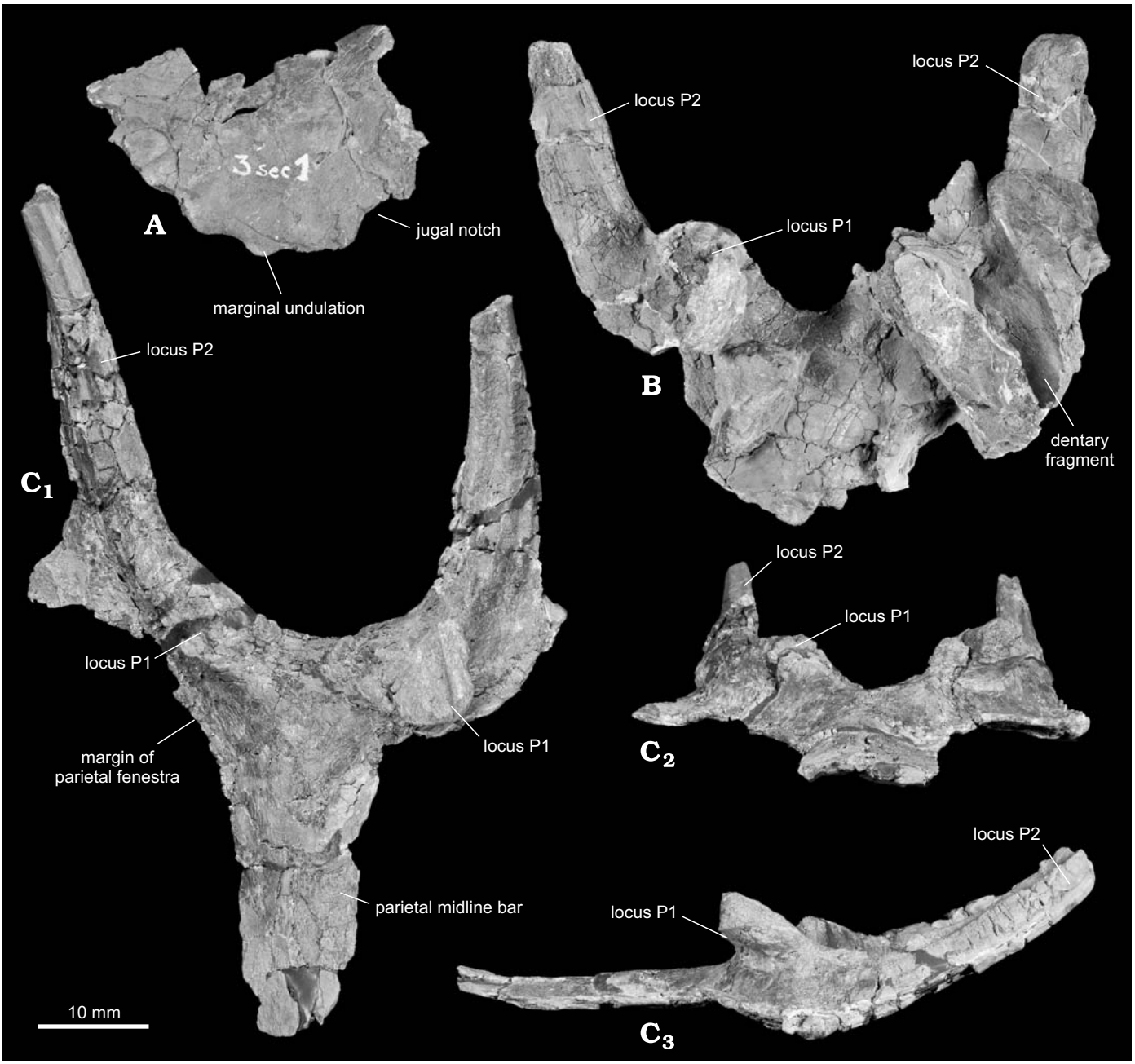

Fig. 3. Centrosaurine ceratopsid *Spinops sternbergorum* gen. et sp. nov. from the Campanian of Dinosaur Provincial Park, southern Alberta. **A**. Partial right squamosal in lateral view, NHMUK R16309. **B**. Partial parietal with adherent bone fragments in dorsal view, NHMUK R16308. **C**. Partial parietal in dorsal (C_1), rostral (C_2), and left lateral (C_3) views, holotype NHMUK R16307.

In contrast to *Centrosaurus apertus* and *Styracosaurus albertensis*, *Spinops sternbergorum* lacks an inward-curving or projecting P2 epiparietal. The fact that both known parietals for *Spinops* exhibit excellent preservation of the frill in this region, and that both specimens consistently lack this process, indicates that this is a genuine feature of the taxon.

An elongated spike, here identified as P2 (although also possibly homologous to P3; see Discussion) occurs just lateral to the procurving hook at P1 (Fig. 3B, C). Unlike other centrosaurines that possess large parietal spikes (e.g., *Styracosaurus albertensis*) the spikes in both known specimens of *Spinops sternbergorum* show a gentle dorsal curvature along their entire lengths. The consistency of the morphology between the specimens, as well as the generally uncrushed preservation of the parietals, indicates that this morphology is not a result of post-burial distortion. The left spike of NHMUK R16307 has a deep longitudinal sulcus inscribed dorsally and a shallower one just lateral to this. Another sulcus is on the medial surface, but the ventral surface is unsulcated. The left and right spikes are 275 mm and 260 mm long, respectively (as preserved), but the distal ends are missing, which would add up to an additional 10% to the overall lengths of the processes.

http://dx.doi.org/10.4202/app.2010.0121

Each spike is approximately 100 mm wide at its base. In NHMUK R16308, the left and right spikes are 290 and 245 mm long as preserved, with basal widths of approximately 90 mm. The medial edges of their bases are separated by 270 mm.

The P2 spike changes in cross-sectional morphology along its length. It is much wider than deep at the base (93 mm wide by 62 mm deep on the right P2 spike of NHMUK R16307), with a roughly flat dorsal surface, strongly rounded ventral surface, and a flattened medial surface. Distal to the base, this process deepens dorsoventrally and narrows mediolaterally (49 mm deep and 39 mm wide on the right P2 spike of NHMUK R16307). This occurs bilaterally. The medial sulcus deepens distally. The P2 morphologies are consistent between the two known parietal specimens. In specimen NHMUK R16308, the right spike has two sulci parallel to the long axis dorsally, each no more than 10 mm deep, and at least one sulcus laterally on the left side (incomplete preservation obscures the rest of the morphology).

The surface texture of the bone on the holotype is difficult to discern, because the adhering ironstone matrix is hard to remove. Towards the distal end of the midline parietal bar, some faint neurovascular impressions are visible, and other eroded impressions are visible elsewhere. In all, the texture is consistent with this being an adult individual (Sampson et al. 1997).

Squamosal (Fig. 3A).—The isolated right squamosal (NHMUK R16309) preserves nearly the complete "blade" of the element, but the rostral portion that would have articulated with the facial bones is not preserved. Five marginal undulations ornament the lateral margin of the squamosal, but the parietal-squamosal contact is not sufficiently well preserved to determine whether an ossification spanned this suture. The overall shape, proportions, and ornamentation of the element are similar to those in other centrosaurines. The squamosal measures 280 mm from the distal end of the parietosquamosal contact to the rostral corner of the free blade just caudal to the jugal notch.

Skull roof (Fig. 4).—NHMUK R16306 preserves much of the skull roof, from the region rostral to the nasal horn to the rostralmost portion of the parietal bar. The skull is well preserved, but is skewed slightly to the left by post-burial deformation (Fig. 4B). Sutures between individual elements were not visible even after detailed preparation, so some structural relationships cannot be described. Based on bone surface texture, the morphology of the postorbital horncores, and the fusion of cranial elements, the animal was an adult. The specimen cannot be articulated with either parietal or the squamosal; because the specimens were collected from a bonebed, it is possible that none of the elements belongs to the same individual.

The prominent, caudally recurved nasal horncore is complete and centered just over the caudal margin of the ectonaris (Fig. 4A). The horn's base measures 115 mm long and 45 mm wide, and it extends 251 mm above the top of the external naris, or 201 mm above the dorsum of the nasal bones.

A portion of the premaxillary septum is preserved, indicating that the septum extended for the full distance to the top of the nasals, as is typical for centrosaurines (Fig. 4A). The distance from the front of the orbit to the caudal margin of the external naris is 231 mm. A complete *Centrosaurus apertus* skull, ROM 767, measures 223 mm at this point, suggesting that NHMUK R16306 came from an individual of similar skull size (ROM 767 measures 724 mm in basal skull length).

The postorbital horncores are short (69 mm tall above the orbit on the right side) and have relatively blunt tips, as is typical of many adult individuals of *Centrosaurus apertus* and *Styracosaurus albertensis* (Fig. 4A, B). A small, broad resorption pit occurs on the rostral surface of the left horncore, also similar to pits in adult individuals of *C. apertus* and *S. albertensis*. The lateral surfaces of the horns are flattened and the medial surfaces are convex. Despite the slight crushing of the specimen, there is no evidence that the horncores curved laterally (as in *Centrosaurus brinkmani*; Ryan and Russell 2005). The horns are centered just caudal to the midpoint of the orbits, which are roughly circular (98 mm tall by 112 mm long on the right side). An antorbital buttress projects over the rostrodorsal quadrant of the orbit (Fig. 4A).

The narrow and elongate frontoparietal fontanelle (126 mm long by 22 mm wide, as preserved; Fig. 4C) is typical for centrosaurines. The margins leading to the opening taper gently. The fontanelle extends up to the plane defining the rostral third of the orbit and the caudal end extends approximately 5 to 10 cm caudal to the orbit. The supracranial sinus complex extends laterally to the medial base of the postorbital horncores. This condition is typical for *Centrosaurus* and *Styracosaurus*, but less extensive than the condition in *Pachyrhinosaurus lakustai* (Farke 2010).

Bilaterally positioned dorsotemporal channels, lined by smooth bone, extend into the caudal end of the frontoparietal fontanelle from the dorsotemporal fenestrae. The channels join at their rostral ends to form a common channel that then slopes ventrally into the caudal margin of the fontanelle. A midline pocket into the dorsum of the parietal is placed just caudal to the common channel.

The entire medial margins and portions of the dorsal margins of the dorsotemporal fenestrae are preserved, showing the sharp emargination typical of ceratopsids. The median bar of the parietal, where preserved, is unremarkable and shows typical adult centrosaurine bone texture.

Dentary (Fig. 3B).—The rostral end of a left dentary, preserving the articular surface for the predentary, adheres to the partial parietal NHM R16308. The morphology of this fragment does not differ markedly from that of other centrosaurine dentaries.

Phylogenetic analysis

Methodology.—In order to investigate the phylogenetic relationships of *Spinops sternbergorum* relative to other centrosaurine ceratopsids, a data matrix including 18 taxa

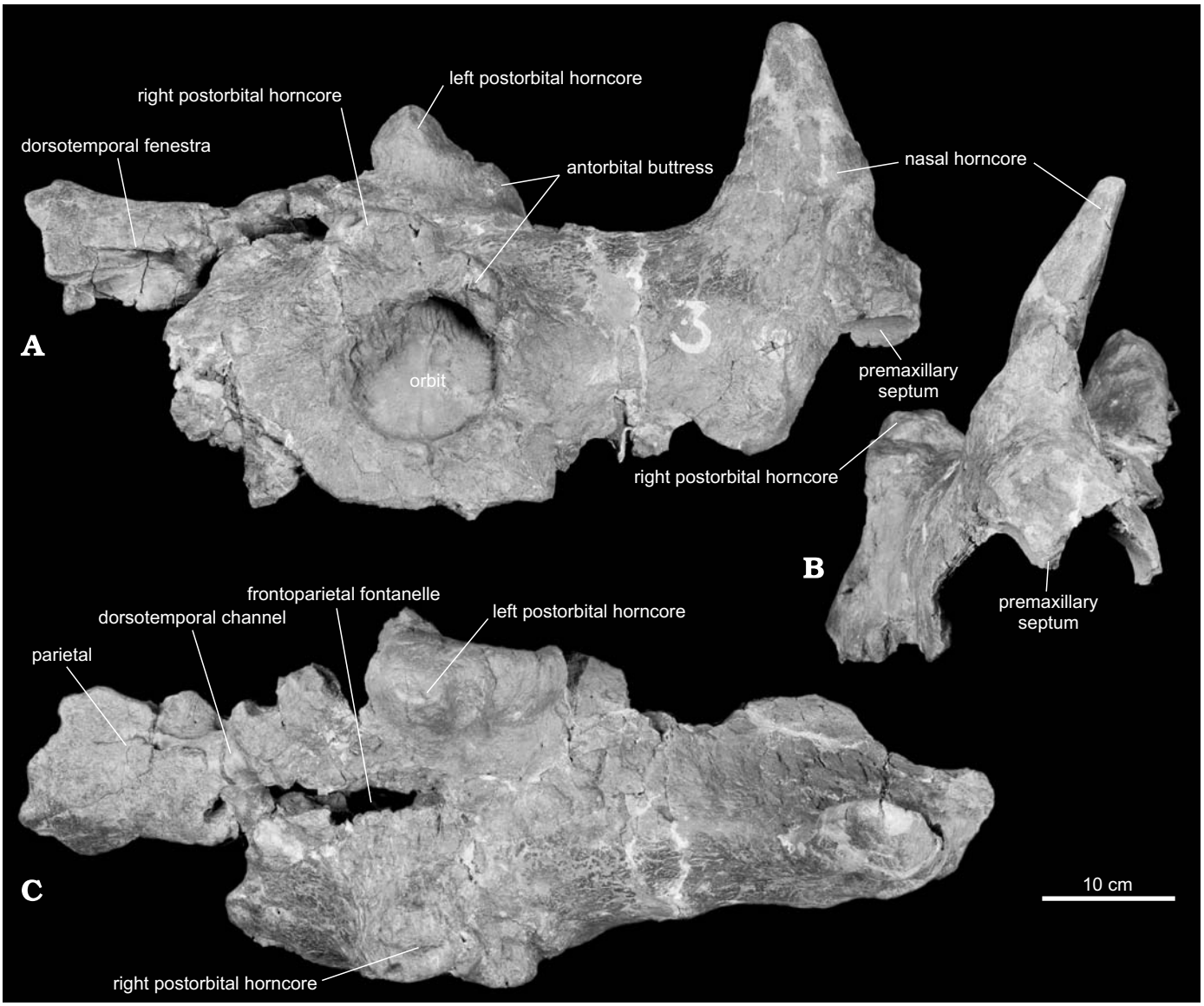

Fig. 4. Partial skull of the centrosaurine ceratopsid *Spinops sternbergorum* gen. et sp. nov. from the Campanian of Dinosaur Provincial Park, southern Alberta, NHMUK R16306; in right lateral (**A**), rostral (**B**), and dorsal (**C**) views.

(*Protoceratops andrewsi* as the outgroup, *Turanoceratops tardabilis*, *Zuniceratops christopheri*, two chasmosaurine ceratopsids, and 13 centrosaurine ceratopsids) and 97 morphological characters was assembled (see Appendix 1, SOM 5). Because cranial characters are the most useful for elucidating phylogenetic relationships among these taxa, the matrix focused on this character subset. *Spinops sternbergorum* was coded on the basis of all available bonebed material. With the exception of *Turanoceratops*, which was coded from the literature, all other taxa were examined firsthand.

The matrix was analyzed using a heuristic search within PAUP* 4.0b10 (Swofford 2003); all characters were equally weighted and most were unordered (with the exception of ordered characters 20 and 38, which were polarized using ontogenetic data). The analysis was conducted with TBR branch swapping and branches with minimum lengths of zero set to collapse. Both bootstrap (with 1,000 replications) and Bremer support values were calculated, using TNT 1.1 (Goloboff et al. 2008), in addition to strict consensus and 50% majority rule consensus trees. In order to evaluate the effects that different interpretations of epiparietal homology would have upon the results, two matrices were generated. The first assumed, based upon the positions of the ossifications, that the large spike-like processes in *Spinops*, *Albertaceratops*, and *Diabloceratops* were homologous to the P2 position of other centrosaurines (see Discussion and Fig. 5, character codings 58–68 in Appendix 1 and SOM 5). The second assumed, based upon morphology of the ossifications, that the elongated, spike-like process in the aforementioned taxa was homologous to the P3 position of other centrosaurines (as traditionally homologized, e.g., Ryan 2007; Fig. 5, character codings 98–108 in Appendix 1 and SOM 5). The strict reduced consensus (SRC) method was also applied in order to identify "wildcard" taxa that were causing lack of

http://dx.doi.org/10.4202/app.2010.0121

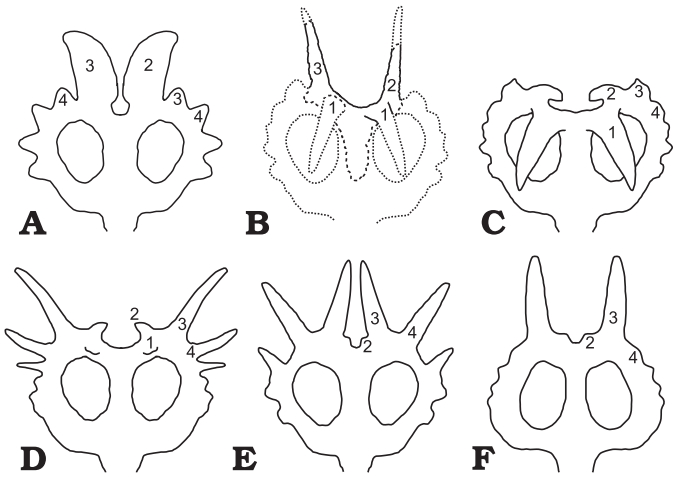

Fig. 5. Schematized parietals of centrosaurine ceratopsids in dorsal view, showing possible homologies for the first four epiparietal loci. **A**. *Albertaceratops nesmoi* Ryan, 2007. **B**. *Spinops sternbergorum* gen. et sp. nov. **C**. *Centrosaurus apertus* Lambe, 1902. **D**. *Styracosaurus albertensis* Lambe, 1913. **E**. *Rubeosaurus ovatus* Gilmore, 1930. **F**. *Einiosaurus procurvicornus* Sampson, 1995. Numbers indicate locus positions. For A and B, the numbers on the right side of the parietal indicate numbering under the "traditional" scheme; numbers on the left side indicate numbering under the revised scheme proposed here. Locus numbering is the same in both the traditional and revised schemes for C, D, E, and F, and are thus presented only on the left side of the parietal for those taxa. Not to scale.

resolution within the tree (Wilkinson 1995). These analyses were implemented using RadCon (Thorley and Page 2000), which generated a number of SRC trees that each pruned various unstable taxa. Preferred SRC trees were selected on the basis of their cladistic information content (CIC).

Results.—The first analysis (using new interpretations of epiparietal homology) yielded 90 most parsimonious trees (MPTs) with tree lengths (TL) of 130 steps, consistency indices (CI) of 0.7615, and rescaled consistency indices (RCI) of 0.5905. The second analysis (using traditional interpretations of epiparietal homology) yielded 4,536 MPTs with TL of 128 steps, CI of 0.7578, and RCI of 0.5798.

Resolution for the strict consensus tree is poor in both analyses. Centrosaurinae are not resolved in either analysis, and *Spinops sternbergorum* either forms a polytomy with *Styracosaurus albertensis* and *Centrosaurus* spp. ("new" codings) or forms a polytomy with other centrosaurines and chasmosaurines ("traditional" codings; SOM 2). Bremer support and bootstrap values are comparatively low for all clades. In the 50% majority rule trees (SOM 3), *S. sternbergorum* belongs to a clade including *Centrosaurus* spp. and *Styracosaurus albertensis* (in 100% and 67% of the trees using "new" and "traditional" codings of epiparietals, respectively). These clades are nested well within Centrosaurinae.

Application of strict reduced consensus to the analysis using the "new" set of epiparietal character codings generated three SRC trees: of these SRC 3 had the highest CIC value (45.38) and also retained 17 of the original 18 taxa. This tree (SOM 4A) excludes only *Sinoceratops*, and this one deletion results in a substantial increase in the resolution of centrosaurine interrelationships. A "pachyrhinosaur" clade (*Achelousaurus*, *Einiosaurus*, and *Pachyrhinosaurus*) sister to *Rubeosaurus* is recovered, which is in turn sister to an unresolved clade comprising *Centrosaurus* spp., *Spinops*, and *Styracosaurus*. SRC 2 has the next highest CIC (37.53) and excludes *Centrosaurus brinkmani* only (SOM 4B). SRC 2 also recovers the "pachyrhinosaur" + *Rubeosaurus* clade and a "centrosaur" clade containing *Centrosaurus apertus*, *Styracosaurus*, and *Spinops*. However, these clades and other ceratopsids together form an unresolved polytomy. SRC 1 (CIC = 38.58) is identical to the strict consensus tree. *Sinoceratops* and *C. brinkmani* were identified as the most unstable taxa, so the original analysis was re-run with the same settings, but these two "wildcards" were deleted a posteriori. The strict consensus tree obtained (Fig. 6B) following their deletion is much better resolved and recovers the "pachyrhinosaurs" (inclusive of *Rubeosaurus*) as the sister-group of the "centrosaurs," and *Spinops* was recovered as sister to *Styracosaurus* + *C. apertus*. *Albertaceratops* and *Avaceratops* are outgroups to this "derived centrosaur" clade and more basal nodes within the analysis are also more highly resolved, including a monophyletic Centrosaurinae.

Strict reduced consensus generated five SRC trees on the basis of the "traditional" epiparietal character codings. Of these, SRC 5 has the highest CIC value (40.52) and excludes *Sinoceratops* and *Rubeosaurus*. This tree (Fig. 6A) recovers the "pachyrhinosaur" clade and a "centrosaur" clade that includes *Centrosaurus* spp., *Spinops* and *Styracosaurus*. In all other respects the tree topology is identical to that of the modified strict consensus tree described above for the analysis based on "new" epiparietal codings.

Discussion

Homology of epiparietal ossifications.—For the purposes of phylogenetic analysis, the marginal ossifications on the parietals of ceratopsids (often called epoccipitals, but more correctly termed epiparietals; Hatcher et al. 1907, Horner and Goodwin 2008) have been numbered starting from their most medial position (Sampson 1995, Sampson et al. 1997). Process P1 occurs in *Centrosaurus apertus* as a strongly procurved hook, but is typically manifested as a more muted knob or bump of bone in *Styracosaurus albertensis* and other taxa (Sampson et al. 1997). Homology across taxa is inferred on the basis of its unique position (dorsal surface of the parietal) relative to other epiparietal positions. Position P1 unambiguously occurs in *Spinops sternbergorum*.

In all "derived" centrosaurines (exclusive of *Avaceratops, Albertaceratops*, and *Diabloceratops*), position P2 is a medially directed hook or small tab of bone in the plane of the frill, emanating from the caudal margin of the frill just lateral to the midline of the parietal. In taxa with P1 hooks, the P2 epiparietals occur immediately lateral to the P1 position. No

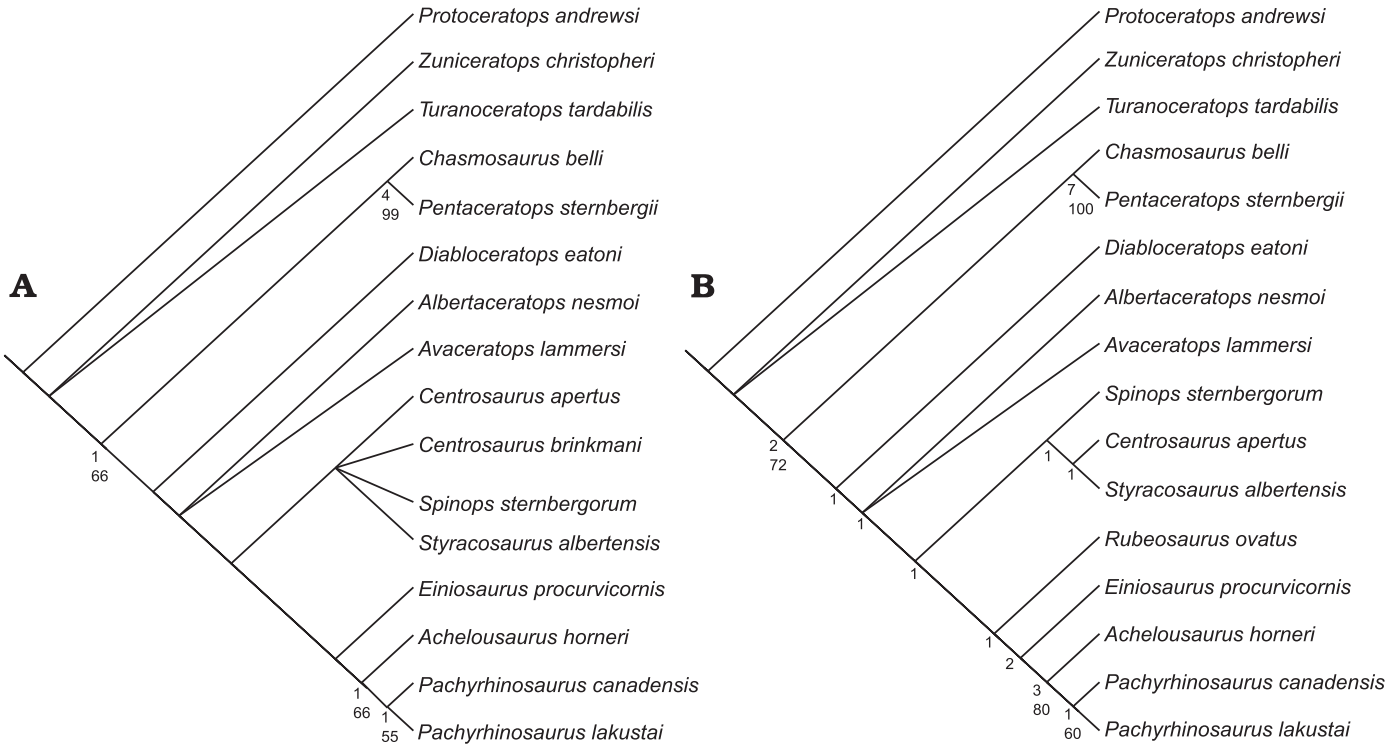

Fig. 6. Phylogenetic hypotheses for relationships within Ceratopsidae, focusing on Centrosaurinae. **A**. Strict reduced consensus tree using "traditional" codings for the epiparietal homologies in selected centrosaurines (see text), with *Sinoceratops zhuchengensis* and *Rubeosaurus ovatus* removed. **B**. Strict consensus tree using "new" codings for epiparietal homologies, following a posteriori deletion of *Sinoceratops zhuchengensis* and *Centrosaurus brinkmani*. At selected nodes, the top number indicates Bremer support and the bottom number indicates bootstrap support values above 50%.

epiparietal consistent with this pattern occurs in *Spinops*, and some centrosaurines (*Albertaceratops* and *Diabloceratops*) were previously assumed to lack P2 (e.g., Ryan 2007; Kirkland and DeBlieux 2010). It should be noted that the P2 process is variable in *Styracosaurus albertensis*, developed as either a medially recurved P2 process or a small, dorsoventrally depressed, medially oriented, tab-shaped process similar to that seen in *Achelosaurus* and *Einiosaurus*. When present as a hook (e.g., the right side of ROM 1436; TMP 86.126.1) the process tends to be shorter, more gracile and more lightly textured than P2 hooks in *C. apertus*. The tab-like P2 morphology occurs in many specimens of *S. albertensis*, including the holotype, CMN 344, and on isolated partial parietals such as TMP 66.10.4, TMP 81.19.157, TMP 81.19.160, TMP 81.19.209, TMP 91.36.254, and TMP 99.55.2. In the last specimen, the small right P2 process is positioned at what appears to be the base of the P3 spike (see Ryan et al. 2007: fig. 9D).

Finally, many centrosaurines (*Styracosaurus*, *Pachyrhinosaurus*, *Achelousaurus*, and *Einiosaurus*) possess an elongated spike at the P3 position, immediately lateral to P2. For taxa lacking clear epiparietals positioned more medially (e.g., *Albertaceratops*, *Diabloceratops*) it is typically assumed that medially placed, prominent epiparietals are homologous to P3 (Ryan 2007; Kirkland and DeBlieux 2010). However, new data provided by *Spinops* suggest an alternative set of epiparietal homologies (see also Clayton et al. 2009). If confirmed, this new information would have important consequences for the homology statements that form a core component of most phylogenetic analyses of ceratopsid dinosaurs.

The topographic relationship between the procurving hook (P1) and the elongate spike of *Spinops* is compatible with the elongate spike representing position P2, rather than P3 (but, see below for an alternative interpretation favored by some of the authors). In *Centrosaurus apertus,* the base of process P2 (a medially-curving hook in the plane of the parietal) partially overlaps the base of the procurving P1 process. Even in species that substitute a prominent P1 hook with a subtle swelling on the dorsum of the parietal, such as *Styracosaurus albertensis*, the swelling is immediately rostral to the medial edge of the relatively short P2 process (Ryan et al. 2007). In *Spinops sternbergorum*, the same topographic relationship occurs between the procurving P1 process and the spike-like process. Thus, based on positional criteria, the spike may represent the P2 epiparietal rather than the P3 epiparietal.

Assuming that this hypothesis of homology is correct, it then motivates a re-evaluation of previously published homology statements for epiparietals in other centrosaurine ceratopsids. For instance, Ryan (2007) hypothesized that the most medially placed, laterally hooked process on the parietal of *Albertaceratops nesmoi* represented epiparietal P3. Under the new scheme, it is then possible that the process actually represents P2, as in *Spinops*. Thus, the true P3 is a short, triangular process. Similarly, Kirkland and DeBlieux (2010) hypothesized that a spike-like, medially placed epi-

http://dx.doi.org/10.4202/app.2010.0121

parietal in *Diabloceratops* also represents P3. Again, an alternative interpretation holds that the elongated epiparietal represents P2, with the consequence that P3 is a rather short, unremarkable process in this taxon also.

We posit that the medially placed spikes on the parietals of centrosaurine ceratopsids might represent P2 and P3 in different taxa. Given the extremely plastic nature of ceratopsid epiparietals throughout their evolution, this hypothesis is not entirely unexpected.

Alternatively, it is possible that the elongated spike in *Spinops sternbergorum* (as well as in *Albertaceratops* and *Diabloceratops*) is indeed homologous to the P3 process of *Styracosaurus*. This would imply that the P2 process is missing, or that a frame shift in the gene expression of the epiparietal morphology occurred. The discovery and description of additional specimens is necessary in order to further clarify and revise these hypotheses of homology. Pending resolution of this issue, we recommend that phylogenetic analyses should consider the effects of both coding schemes on reconstructions of centrosaurine relationships.

Comparison with other centrosaurines.—The facial region, including both the nasal and postorbital horns, is nearly identical to that of *Centrosaurus apertus* and *Styracosaurus albertensis* (Sampson et al. 1997; Ryan et al. 2007). Within the frill, *Spinops sternbergorum* displays a mosaic of features seen in the latter two species. The elongated P1 hooks are virtually identical to those in *C. apertus*, whereas the elongate spike is similar to the condition in *S. albertensis*. Based on this anatomy, it is arguable that *S. sternbergorum* represents an anagenetic intermediate between *C. apertus* and *S. albertensis*. This hypothesis is unlikely, however, assuming that *Spinops* is indeed from low in the Dinosaur Park Formation or high in the Oldman Formation (thus predating or coincident with the occurrence of *C. apertus*). Alternatively, *Spinops* could represent the sister taxon to *Centrosaurus*, *Styracosaurus*, or both, as suggested by some consensus trees (Fig. 6B; SOM 2B, 3B). Unfortunately, the lack of stratigraphic constraint for the *Spinops* bonebed as well as poor phylogenetic resolution and weak support for most of the nodes within Centrosaurinae prevents definitive evaluation of these conflicting hypotheses. Furthermore, the limited nature of the *S. sternbergorum* material does not allow an investigation of how ontogenetic changes or sexual dimorphism may differ in this taxon versus other centrosaurines.

Interestingly, the putative Chinese centrosaurine *Sinoceratops zhuchengensis* was not consistently recovered as a centrosaurine by our analyses (in contrast to the analysis presented by Xu et al. 2010). This may be driven at least in part by the taphonomic loss of the premaxilla in the known specimens, which is an important diagnostic element for Centrosaurinae, as well as poor differentiation of sutures on the material that prevents coding of many critical characters. Clearly, additional research is needed here. As more species are discovered, achieving satisfactory resolution within the phylogeny of ceratopsids has become increasingly difficult. The higher degree of resolution presented by previous centrosaurine phylogenies probably resulted from a general consensus on epiparietal homologies (now undermined by the condition in *Spinops*) in addition to the completeness of the included taxa. Many new taxa are based on more fragmentary material, increasing the proportion of missing data in the data matrices.

Conclusions

Regardless of its evolutionary affinities, or the homologies of its cranial structures, *Spinops sternbergorum* is an unexpected addition to the Campanian fauna of Alberta, particularly given the intensive collecting of ceratopsids there in recent years. A total of six centrosaurine taxa are now recognized from the Oldman/Dinosaur Park Formation sequence, representing a variety of morphologies. Much additional work is needed, inside and outside Dinosaur Provincial Park, to address a number of remaining unanswered questions. Do the ceratopsians preserved here document anagenesis or cladogenesis? How are the taxa of Alberta related to those from elsewhere? Was *Spinops* a rare element of the Campanian fauna, or will more remains be recognized?

Acknowledgements

Discussions with William Blows (City University, London, UK), David Eberth (TMP), and Scott Sampson (Natural History Museum of Utah, Salt Lake City, Utah, USA) were helpful. We thank Sandra Chapman (NHMUK) for facilitating collections access, Phil Hurst (NHMUK Image Resources) for taking photographs for publication and Polly Parry (NHMUK archives) for access to archival material. Brenda Chinnery-Allgeier (University of Texas, Austin, USA) and Peter Dodson (University of Pennsylvania, Philadelphia, USA) are gratefully acknowledged for their insightful reviews. This work was funded in part by NSF grant EAR 0819953 to AF and ML, with Scott Sampson (Utah Museum of Natural History) and Catherine Forster (George Washington University, Washington, D.C., USA), and the TNT software was made available with the sponsorship of the Willi Hennig Society. Lukas Panzarin (Venice, Italy) prepared the reconstruction in Fig. 2. Ben Creisler (Seattle, Washington, USA) offered etymological assistance.

References

Barrick, R.E., Stoskopf, M.K., Marcot, J.D., and Russell, D.A. 1998. The thermoregulatory functions of the *Triceratops* frill and horns: Heat flow measured with oxygen isotopes. *Journal of Vertebrate Paleontology* 18: 746–750.

Clayton, K., Loewen, M., Sampson, S., Farke, A., and Irmis, R. 2009. Epiparietal homology within Centrosaurinae (Ornithischia, Ceratopsidae): a re-evaluation based on newly discovered basal taxa. *Journal of Vertebrate Paleontology* 29 (Supplement to No. 3): 80A.

Currie, P.J. 2005. History of research. *In*: P.J. Currie and E.B. Koppelhus (eds.), *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed*, 3–33. Indiana University Press, Bloomington.

Currie, P.J., and Dodson, P. 1984. Mass death of a herd of ceratopsian dinosaurs. *In*: W.E. Reif and F. Westphal (eds.), *Third Symposium of Mesozoic Terrestrial Ecosystems*, 52–60. Attempto Verlag, Tübingen.

Currie, P.J., and Russell, D.A. 2005. The geographic and stratigraphic distribution of articulated and associated dinosaur remains. *In*: P.J. Currie and E.B. Koppelhus (eds.), *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed*, 537–569. Indiana University Press, Bloomington.

Currie, P.J., Langston, W. Jr., and Tanke, D.H. 2008. A new species of *Pachyrhinosaurus* (Dinosauria, Ceratopsidae) from the Upper Cretaceous of Alberta. *In*: P.J. Currie, W. Langston, Jr., and D.H. Tanke (eds.), *A New Horned Dinosaur from an Upper Cretaceous Bone Bed in Alberta*, 1–108. NRC Research Press, Ottawa.

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

Dodson, P. and Farlow, J.O. 1997. The forelimb carriage of ceratopsid dinosaurs. *In*: D.L. Wolberg, E. Stump, and G.D. Rosenberg (eds.), *Dinofest International: Proceedings of a Symposium Held at Arizona State University*, 393–398. Academy of Natural Sciences of Philadelphia, Philadelphia.

Eberth, D.A. 2005. The Geology. *In*: P.J. Currie and E.B. Koppelhus (eds.), *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed*, 54–82. Indiana University Press, Bloomington.

Farke, A.A. 2004. Horn use in *Triceratops* (Dinosauria: Ceratopsidae): Testing behavioral hypotheses using scale models. *Palaeontologia Electronica* 7: 1–10.

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

Farlow, J.O. and Dodson, P. 1975. The behavioral significance of frill and horn morphology in ceratopsian dinosaurs. *Evolution* 29: 353–361.

Fujiwara, S. 2009. A reevaluation of the manus structure in *Triceratops* (Ceratopsia: Ceratopsidae). *Journal of Vertebrate Paleontology* 29: 1136–1147.

Gilmore, C.W. 1930. On dinosaurian reptiles from the Two Medicine Formation of Montana. *Proceedings of the United States National Museum* 77: 1–10.

Goloboff, P., Farris, J., and Nixon, K. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.

Hatcher, J.B., Marsh, O.C., and Lull, R.S. 1907. The Ceratopsia. *United States Geological Survey Monograph* 49: 1–300.

Holmes, R.B., Forster, C., Ryan, M., and Shephard, K.M. 2001. A new species of *Chasmosaurus* (Dinosauria: Ceratopsia) from the Dinosaur Park Formation of southern Alberta. *Canadian Journal of Earth Sciences* 38: 1423–1438.

Horner, J.R. and Goodwin, M.B. 2008. Ontogeny of cranial epi-ossifications in *Triceratops*. *Journal of Vertebrate Paleontology* 28: 134–144.

Hunt, R. and Farke, A. 2010. Behavioral interpretations from ceratopsid bonebeds. In: M.J. Ryan, B.J. Chinnery-Allgeier, and D.A. Eberth (eds.), *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*, 447–455. Indiana University Press, Bloomington.

Kirkland, J.I. and DeBlieux, D.D. 2010. New basal centrosaurine ceratopsian skulls from the Wahweap Formation (middle Campanian), Grand Staircase–Escalante National Monument, southern Utah. *In*: M.J. Ryan, B.J. Chinnery-Allgeier, and D.A. Eberth (eds.), *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*, 117–140. Indiana University Press, Bloomington.

Lambe, L.M. 1902. New genera and species from the Belly River series (mid-Cretaceous). *Contributions to Canadian Palaeontology* 3, Pt. 2: 23–81.

Lambe, L.M. 1913. A new genus and species of Ceratopsia from the Belly River Formation of Alberta. *The Ottawa Naturalist* 27: 109–116.

Lambe, L.M. 1915. On *Eoceratops canadensis*, gen. nov., with remarks on other genera of Cretaceous horned dinosaurs. *Canada Department of Mines Geological Survey Museum Bulletin* 12: 1–49.

Longrich, N.R. 2010. *Mojoceratops perifania*, a new chasmosaurine ceratopsid from the late Campanian of western Canada. *Journal of Paleontology* 84: 681–694.

Marsh, O.C. 1888. A new family of horned dinosaurs from the Cretaceous. *American Journal of Science* 36: 477–478.

Marsh, O.C. 1890. Additional characters of the Ceratopsidae, with notice of new Cretaceous dinosaurs. *American Journal of Science* 39: 418–426.

Owen, R. 1842. Report on British Fossil Reptiles. Part II. *Report of the British Association for the Advancement of Science* 11: 60–204.

Paul, G.S., and Christiansen, P. 2000. Forelimb posture in neoceratopsian dinosaurs: implications for gait and locomotion. *Paleobiology* 26: 450–465.

Rega, R., Holmes, R., and Tirbasso, A. 2010. Habitual locomotor behavior inferred from manual pathology in two Late Cretaceous chasmosaurine ceratopsid dinosaurs, *Chasmosaurus irvinensis* (CMN 41357) and *Chasmosaurus belli* (ROM 843). *In*: M. Ryan, B. Chinnery-Allgeier, and D. Eberth (eds.), *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*, 340–354. Indiana University Press, Bloomington.

Ryan, M., Eberth, D., Brinkman, D., Currie, P., and Tanke, D. 2010. A new *Pachyrhinosaurus*-like ceratopsid from the upper Dinosaur Park Formation (late Campanian) of southern Alberta, Canada *In*: M. Ryan, B. Chinnery-Allgeier, and D.A. Eberth (eds.), *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*, 141–155. Indiana University Press, Bloomington.

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

Ryan, M.J. and Evans, D. 2005. Review of the Ornithischia of Dinosaur Provincial Park. *In*: P.J. Currie and E.B. Koppelhus (eds.), *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed*, 313–348. Indiana University Press, Bloomington.

Ryan, M.J. and Russell, A.P. 2005. A new centrosaurine ceratopsid from the Oldman Formation of Alberta and its implications for centrosaurine taxonomy and systematics. *Canadian Journal of Earth Sciences* 42: 1369–1387.

Ryan, M.J., Holmes, R., and Russell, A.P. 2007. A revision of the late Campanian centrosaurine ceratopsid genus *Styracosaurus* from the Western Interior of North America. *Journal of Vertebrate Paleontology* 27: 944–962.

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

Sampson, S.D. 1997. Dinosaur courtship and combat. *In*: J.O. Farlow and M.K. Brett-Surman, (eds.), *The Complete Dinosaur*, 383–393. Indiana University Press, Bloomington.

Sampson, S.D., Ryan, M.J., and Tanke, D.H. 1997. Craniofacial ontogeny in centrosaurine dinosaurs (Ornithischia: Ceratopsidae): taxonomic and behavioral implications. *Zoological Journal of the Linnean Society* 121: 293–337.

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

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

Swofford, D.L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4b10. Sinauer Associates, Sunderland, Massachusetts.

Tanke, D.H. 2010. Ceratopsian discoveries and work in Alberta, Canada: historical review and census. *In*: M. Ryan, B. Chinnery-Allgeier, and D.A. Eberth (eds.), *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*, CD-ROM supplement. Indiana University Press, Bloomington.

Thompson, S. and Holmes, R. 2007. Forelimb stance and step cycle in *Chasmosaurus irvinensis* (Dinosauria: Neoceratopsia). *Palaeontologia Electronica* 10 (1), 5A: 1–17.

Thorley, J.L. and Page, R.D.M. 2000. RadCon: phylogenetic tree comparison and consensus. *Bioinformatics* 16: 486–487.

Wilkinson, M. 1995. Coping with abundant missing entries in phylogenetic inference using parsimony. *Systematic Biology* 44: 501–514.

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

http://dx.doi.org/10.4202/app.2010.0121

Appendix 1

Character codings used in the phylogenetic analysis of Centrosaurinae. See SOM 5 for the character states.

Protoceratops andrewsi
0------100000010000000--------000-0000-0010000-000000----------000?00000000000000000000000000----------

Turanoceratops tardabilis
??????????????0000???-?0001-??1?????0-??????????????????????????????????0??0?0??????????????????????????????

Zuniceratops christopheri
1000000???010000?00--00000010??1101100-???0?????010?0----------10010000???1?0?????????01?0??----------

Diabloceratops eatoni
011000010100100 00?00?1??000102?1101101010110010111111001101100010101 1??????????????????????????0--11010101

Albertaceratops nesmoi
?1?000??????01-101?00???00011??111111??10110010111111 0?1101100010101?1101??1??????????????????????0--11010101

Avaceratops lammersi
01?0001111?0?1?1010??1?0??????????10????001000--1--0??0?10?????????????01?1?1111?10?11???????1?1?0??????????

Centrosaurus apertus
01100011111001-1111101000000201111111101011001011111100111120001010111101111111111111111111101111111200010101

Centrosaurus brinkmani
011000111 1??01-1111101000010201111111101011001011111100111????010????1101111111?1?1????111110?111?1????010???

Rubeosaurus ovatus
01?00011?1??0??????1??000000--?1?????????????101??1?1?01?0001011?????????????????????????????????0001011????

Styracosaurus albertensis
01100011111001-1111101000000--1111111101011001011111100111(01)211111111?10??1?11?1111111111101111?1(01)211111111

Spinops sternbergorum
??1000???????1-????1??0?0000--?111???10????0?101111?1????110?????????????????????????????????????1--11??????

Einiosaurus procurvicornis
?110001??????1-111110111000---010-1111010110010111111001100010010101?11?111111?1?1??1?111??1111??00010010101

Achelousaurus horneri
0110001111 10?1-111120111100---?10-1?1101011001011111100110021101010 11?1?1111???1?????????????????00211010101

Pachyrhinosaurus canadensis
011000111 1?0?1-11112011?11----?10-111101?1100???1??1?0?1?????????????1110?????????????????????????????????????

Pachyrhinosaurus lakustai
01100011111001-111120111 11----?10-1?1101011001011111100110121101010101101111111?1?1??1111111011 1??01211010101

Chasmosaurus belli
100111000-0100111111101?000001011111111111011111110001111 0-----------1101111111?1111111111111111111-----------

Pentaceratops sternbergii
100111000-0110111111101000111101110011111011111110001111 0-----------1101111111?1111111111111?11?-----------

Sinoceratops zhuchengensis
?????????????00????1????------??0-???1010?1??10?1???1???10130201010?????????????????????????????0--12010101