NASUTOCERATOPS TITUSI (ORNITHISCHIA, CERATOPSIDAE), A BASAL CENTROSAURINE CERATOPSID FROM THE KAIPAROWITS FORMATION, SOUTHERN UTAH

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ABSTRACT—The skull and associated postcrania of Nasutoceratops titusi, a basal centrosaurine ceratopsid from the Upper Cretaceous (Campanian) Kaiparowits Formation of Grand Staircase–Escalante National Monument, southern Utah, are herein described. Autapomorphies of this taxon include: an ectonaris that comprises 75% of preorbital skull length; pneumatic nasals; a hyper-robust premaxilla–maxilla contact; a double-faceted, medial flange on the maxilla contributing to the hard palate; and unique supraorbital horncores that are anterolaterally directed, anteriorly curved, torsionally twisted, and relatively enormous. A Bayesian analysis, the first conducted for ceratopsians, is coupled with a parsimony phylogenetic analysis of Centrosaurinae, with both analyses recovering Nasutoceratops as the sister taxon to Avaceratops lammersi from the late Campanian of Montana. Nasutoceratops titusi provides insights into the origins of Centrosaurinae and suggests the existence of a previously unknown clade of short-snouted, long-horned centrosaurines that we here hypothesize have originated in the southern Western Interior Basin of North America.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

The ceratopsid dinosaur record from the southern region of the Western Interior Basin (WIB) of Cretaceous North America (i.e., Utah, Colorado, New Mexico, Texas, and Mexico) remains enigmatic and poorly understood in comparison to that in the north (i.e., Alberta, Saskatchewan, and Montana), resulting in a large latitudinal bias in the ceratopsid fossil record, most notably among centrosaurines. Centrosaurines are known from numerous skulls and skeletons from the northern WIB, many of which have been recovered from paucispecific bonebed assemblages (Ryan, 2007; Sampson and Loewen, 2010; Sampson et al., 2010). In contrast, only a limited number of isolated centrosaurine specimens are thus far known from the southern WIB (Williamson, 1997; Heckert et al., 2003; Kirkland and DeBlieux, 2010; Loewen et al., 2010; Sampson et al., 2010, 2013).

Initiated by the University of Utah in 2000, the Kaiparowits Basin Project (KBP) is a multi-institution collaboration that has undertaken the study of terrestrial and freshwater macrovertebrate fossils from two Campanian-aged geologic units within Grand Staircase–Escalante National Monument (GSENM). The GSENM encompasses ~1.9 million acres of badland terrain composed of several Upper Cretaceous formations (Roberts, 2007). These formations represent one of the most continuous Cenomanian–Campanian terrestrial records anywhere in the world (Eaton and Cifelli, 1988). Fossil discoveries resulting from the KBP to date are abundant and significant, documenting 16 nonavian dinosaur taxa within the Kaiparowits Formation alone. Seven of these taxa have been formally named: the tyrannosaurid Teratophoneus curriei (Carr et al., 2011); the oviraptorosaur Hagryphus giganteus (Zanno and Sampson, 2006); the troodontid Talos sampsoni (Zanno et al., 2011); the hadrosaurine Gryposaurus monumentensis (Gates and Sampson, 2007); and three ceratopsids. These include two chasmosaurine ceratopsids, Utahceratops gettyi and Kosmoceratops Richardsi (Sampson et al., 2010), and the recently named centrosaurine Nasutoceratops titusi (Sampson et al., 2013). Prior to the inception of the KBP, ceratopsian remains from the Kaiparowits Formation were uninformative, limited to isolated teeth (Eaton et al., 1999; Getty et al., 2010). Since 2000, the KBP, in conjunction with recent efforts by the Utah Geological Survey, has increased the known diversity of ceratopsids from the southern WIB by four genera and species, including two chasmosaurines and two centrosaurines (Sampson et al., 2004, 2010, 2013; Kirkland and DeBlieux, 2010).

Excavations conducted by the Natural History Museum of Utah during the 2006 field season in the Kaiparowits Formation led to the recovery of a nearly complete centrosaurine skull and associated postcranium, along with other material diagnosable to the new taxon. Characters distinguishing this

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new form are restricted to the skull, particularly the pre-orbital face (i.e., premaxilla and maxilla) and skull roof (i.e., supraorbital ornamentation and nasal ornamentation). Sampson et al. (2013) provided a brief description of this new taxon, naming it *Nasutoceratops titusi* and placing the animal into stratigraphic and phylogenetic context. The present contribution expounds on this previous work, elaborating on the osteology of the skull, and includes descriptions of known postcranial elements.

**Institutional Abbreviations**—AMNH, American Museum of Natural History, New York, New York; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; MOR, Museum of the Rockies, Bozeman, Montana; MTM V, Magyar Természettudományi Múzeum, Budapest, Hungary; MM, Mesa Southwest Museum, Mesa, Arizona; NMC, Canadian Museum of Nature (National Museum of Canada), Ottawa, Ontario; NMMNH, New Mexico Museum of Natural History, Albuquerque, New Mexico; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma; ROM, Royal Ontario Museum, Toronto, Ontario; SMFR, Senckenberg Naturmuseum, Frankfurt, Germany; TMM, Texas Memorial Museum, University of Texas at Austin, Austin, Texas; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; UUMP, Natural History Museum of Utah, Salt Lake City, Utah; UTEP, University of Texas, El Paso, Texas; YPM, Yale Peabody Museum, New Haven, Connecticut; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

**SYSTEMATIC PALEONTOLOGY**

**CERATOPSIA** Marsh, 1890

**CERATOPSIDAE** Marsh, 1888

**CENTROSAURINAE** Lambe, 1915

**NASUTOCERATOPS TITUSI** Sampson, Lund, Loeven, Farke, and Clayton, 2013

**Etymology**—*Nasutus* (Latin) describes the specimen as ‘large-nosed’ and ‘ceratops’ (Latinized Greek) describes the specimen as ‘horned-face’. The specific name *titusi* is an eponym in honor of GSNM paleontologist Alan Titus, who has played a pivotal role in the recovery of fossils from GSNM.

**Diagnosis**—Centrosaurus possessing the following autapomorphies: external naris that comprises 75% of the preorbital skull length; nasals pneumatic; premaxillary contact of the maxilla hypertrophied, forming an expanded contact shelf; maxilla with double-faceted, medially directed flange contributing to the hard palate; supraorbital horncores anterolaterally directed, anteriorly curved, and apically twisted (modified from Sampson et al., 1997, 2013). Two additional specimens (UMNH VP 19466, UUMHP VP 19469) referred to this taxon possess unequivocal morphological characteristics of the holotype specimen. Considered together, these materials represent approximately 80% of the craniofacial skeleton and approximately 10% of the postcranial skeleton (Fig. 2). Genus- and species-level taxonomic resolution of ceratopsids has typically been based on craniofacial characters pertaining to the skull roof (Dodson et al., 2004). Therefore, this description focuses mainly on skull characters primarily derived from the holotype specimen. The description is subdivided into three main sections—circumnarial region, circumorbit region, and parietosquamosal frill—with each section focusing on key aspects useful in resolving taxonomic relationships of centrosaurines.

**Skull—Circumnarial Region**

The nasal and premaxilla dominate the circumarial region, but for ease of description, both the rostral and maxilla are included in this section. *Nasutoceratops* possesses a remarkably tall (dorsoventrally deep) craniofacial skeleton, particularly in the circumarial region (Fig. 2). The deep facial skeleton is similar to that described for *Diabloceratops* (UMNH VP 16699; Kirkland and DeBlieux, 2010). Overall, the narial region of *Nasutoceratops* is subcircular in shape, typical of centrosaurines (e.g., *Achelosaurus* [MOR 485], *Einiosaurus* [MOR 456]). However, it differs from more derived centrosaurines and more closely resembles *Diabloceratops*, because it is dorsally expanded such that the narial region has a bulbous appearance.

**Rostral**—The rostral, a neomorphic element unique to Cera-
topsia, contacts the anterior-most portion of the premaxilla in ceratopsids and forms the upper portion of the beak. Although the rostral is not preserved in UMNH VP 16800, the general con-
formation of this element can be inferred from the preserved con-
tact on the premaxilla (Fig. 3). The contact surface is rugose, typical of other ceratopsids, and crescentic in shape, closely fol-
lowing the contour of the narial border. The dorsal extent of the nasal process of the rostral was approximately level with the mid-
dle of the narial opening, whereas the posterior extent of the pos-
terior process nearly abuts the ventral angle of the premaxilla.

**Premaxilla**—Portions of both premaxillae, preserved in con-
tact with each other as well as with the nasals, are present in UMNH VP 16800 (Fig. 3) but are damaged and transversely compressed, with the right premaxilla missing part of its ventral margin. Additionally, partial right and left premaxillae...
(UMNH VP 19466.3, UMNH VP 19466.4; not figured) similar to the holotype were recovered from another quarry and are here referred to *Nasutoceratops*. Whereas the premaxilla of centrosaurines tends to be morphologically conservative, this element in *Nasutoceratops* shows several characteristics that distinguish it from other centrosaurines. In general, the

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**FIGURE 1.** Composite measured section of the Kaiparowits Formation in Grand Staircase–Escalante National Monument. Approximate stratigraphic locations of the holotype material and referred material are shown to the right. Location and 40Ar/39Ar ages of four bentonites shown on the right (modified after Roberts et al., 2013).

**FIGURE 2.** *Nasutoceratops titusi* (UMNH VP 16800), photographs of the holotype skull in A, dorsal and B, lateral views with reconstruction in C, dorsal and D, lateral views. Left-lateral parietal bar in dorsal view (A) is mirrored. Abbreviations: ej, epijugal; en, exconalar; ep, epiparietal; ept, ectopterygoid; es, episquamosal; f, frontal; j, jugal; l, lacrimal; ltf, lateral temporal fenestra; m, maxilla; n, nasal; oh, orbital horn; p, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; pp, palpebral; pt, pterygoid; q, quadratojugal; qj, quadratojugal; r, rostral; sq, squamosal; stf, supratemporal fenestra.

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Lund et al. — *Nasutoceratops*, a new basal centrosaurine (e1054936-3)
The anterior-most portion of the premaxilla is deep, forming a thin, rounded, median premaxillary septum within the nasal fossa that extends between the endonasal and the ectonasal. The premaxillary septum appears to be more extensive than in all other known ceratopsids, likely relating to the general dorsal expansion of the nasal region. Anteriorly, the nasals contribute to the premaxillary septum, with the premaxillae slotting into the bifurcated rostral processes of the nasals. In contrast to the septal morphology seen in other ceratocephalians (e.g., Diabloceratops eatoni Kirkland and DeBlieux, 2010; Achelosaurus horneri Sampson, 1995; Einosaurus procervicornis Sampson, 1995), the premaxillary septum of Nasutoceratops extends posteriorly to underlie the nasal cornices. Projecting into and possibly well beyond the endonasal, the premaxillae possess a robust, posteroventrally directed process that is continuous with the premaxillary septum. Unlike the chasmosaurine condition, the premaxillary septum lacks a narial strut or any secondary foramina or depressions (Forster et al., 1993). The premaxillary septum is poorly preserved in the holotype of Nasutoceratops, preventing observation of surface features such as ectonarial sulci that have been described for other ceratocephalians (Sampson, 1995; Penkalski and Dodson, 1999; Kirkland and DeBlieux, 2010). The endonasal, relatively small and elliptical as viewed laterally, is located in the posteroventral portion of the premaxillae, bordered anteriorly by the premaxillary septum, posteriorly by the ascending maxillary process (of the premaxilla), and dorsally by the nasals.

Both premaxillae of UMNH VP 16800 exhibit an unusual posterior process (Fig. 3) that ascends dorsally more than in any other ceratopsid, approaching the dorsal margin of the skull. In this conformation, Nasutoceratops closely resembles the condition in basal noenoceratopsians (e.g., Protoceratops [AMNH 6444]; Makovicky and Norell, 2006). The anterodorsal extent of the posterior process contributes to the narial spine, as evidenced by the corresponding suture, which extends the length of the anterodorsal margin of the process. The posterior process does not appear to contact the lacrimal in the holotype, but this inference cannot be confirmed due to poor preservation in the holotype specimen. The left premaxilla of UMNH VP 16800 possesses an inclined, beveled ventral edge, the posterior continuation of the rostral cutting edge, which terminates in a relatively more robust ventral angle than in all other ceratocephalians in which it is known (Fig. 3). In profile, the ventral angle drops well below the ventral margin of the maxillary tooth row. In contrast to non-ceratopsid noenoceratopsians (e.g., Magnirostris [IVPP V 12513]; Bagaceratops [ZPAL MgD-I/126]) and the ceratopsian Diabloceratops (Makovicky and Norell, 2006; Kirkland and DeBlieux, 2010), Nasutoceratops does not appear to possess an accessory antorbital fenestra.

Medially, a narrow ventromedial shelf abuts the premaxillary flange of the maxilla, forming a short hard palate. This feature is preserved on the left premaxilla of UMNH VP 16800 and otherwise appears to be present only in Pachyrhinosaurus (TMP 1986.55.153) among ceratocephalians (Sampson, 1995; Currie et al., 2008).

**Maxilla**—Only the left maxilla is preserved in the holotype of Nasutoceratops (Fig. 4), but a nearly complete referred right maxilla (UMNH VP 19466.1; Fig. 5) has been recovered from another locality. The mostly complete and apparently undistorted holotype maxilla is roughly triangular. As viewed in medial or lateral aspect the element can be divided into a dorsal ascending ramus and a ventral horizontal ramus, with the latter housing the tooth row. Anteriorly, the dorsal ramus possesses a thin-walled, well-defined contact surface for the posterior process of the premaxilla that extends the length of the ascending ramus. The condition of the premaxillary contact, which appears hypertrophed relative to that of other ceratopsids, is considered an autapomorphy of Nasutoceratops (Sampson et al., 2013) and it is deeply excavated ventrally and shallows dorsally. As

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**FIGURE 3.** Photograph (A) with reconstruction (B) of the circumnarial region of *Nasutoceratops titusi* (UMNH VP 16800) with preserved material in dark gray. **Abbreviations:** aof, antorbital fossa; ept, ectopterygoid; j, jugal; l, lacrimal; m, maxilla; n, nasal; na, naris; nh, nasal horn; o, orbit; pf, prefrontal; pm, premaxilla; pp, palpebral; pt, pterygoid; r, rostral; va, ventral angle.
preserved, the posterolateral branch of the ascending ramus has a well-developed contact surface for the jugal. As is typical of ceratopsids, the antorbital fenestra shows minimal development, situated in a deep, crescentic excavation between the two branches of the ascending ramus (Sampson, 1995; Kirkland and DeBlieux, 2010).

Based on comparisons with the more complete specimen (UMNH VP 19466.1, Fig. 5), approximately 40 mm of the horizontal ramus is absent in the holotype maxilla. The holotype preserves 22 tooth positions and 20 in situ teeth at various stages of wear and replacement. The more complete UMNH VP 19466.1 contains 29 alveoli, and this is the estimated total number of maxillary tooth positions. At present, it has not been ascertained whether the teeth are double-rooted, as in other ceratopsids, or single-rooted, as in neoceratopsians. As is typical of ceratopsids, the lingual surfaces of the maxillary teeth exhibit nearly vertical wear facets (Ryan, 2007; Kirkland and DeBlieux, 2010).

Specimen UMNH VP 19466.1 preserves the entire horizontal ramus, demonstrating that the posteriormost portion of this process forms a large, rounded shelf that includes contacts for pterygoid (medially) and the ectopterygoid (laterally). A similar conformation has been noted in neoceratopsians (e.g., Protoceratops [AMNH 6466]; You and Dodson, 2004) and Diabloceratops (UMNH VP 16699; Kirkland and DeBlieux, 2010). The palatine contacts the internal surface of the maxilla along a well-defined medial shelf that arches above the dental battery immediately anterior to the pterygoid. The anterior portion of the medial shelf is nearly horizontal, occurring well above (~80 mm) the dental battery, whereas the posterior portion curves distinctly ventrally. The contact for the pterygoid in UMNH VP 19466.1 is

FIGURE 4. Holotype left maxilla of *Nasutoceratops titusi* (UMNH VP 16800) in A, lateral view; B, medial view; C, interpretive drawing of lateral view; and D, interpretive drawing of medial view. Abbreviations: aof, antorbital fossa; ascr, ascending ramus of maxilla; df, dental foramina; ept, ectopterygoid contact; hr, horizontal ramus of maxilla; idp, interdental plate; j, jugal contact; l, lacrimal contact; n, nasal contact; nvf, neurovascular foramina; pa, palatine contact; pm, premaxilla contact; ppm, palatal process of maxilla; pt, pterygoid contact; tr, tooth row.
Deeply excavated, forming a well-defined trough. The pterygoid contact on the holotype maxilla is similarly well defined but not as deeply excavated; however, this variation may be due at least in part to postmortem crushing and abrasion in this area.

Viewed posteriorly and medially, an elliptical, deeply excavated medial maxillary cavity is evident, formed medially by the maxilla, palatine, and pterygoid and dorsally by the lacrimal, palatine, and maxilla. This cavity lies directly beneath the antorbital fenestra and occurs largely within the ventral half of the dorsal ascending ramus. Anteriorly, a medially directed maxillary flange with a double socket abuts its counterpart, slotting into the premaxilla to contribute to an abbreviated hard palate (Fig. 5). The long axes of the sulci on this flange are oriented anteroposteriorly. The double-faceted conformation of this flange is autapomorphic for *Nasutoceratops* (Sampson et al., 2013).

Externally, the maxilla is perforated on both the dorsal ascending ramus and the horizontal ramus by a number of variably shaped and irregularly distributed foramina. The foramina are anteroventrally directed and likely transmitted neurovascular supply to the cheek region. There is no evidence in either the premaxilla or the maxilla of an accessory antorbital fenestra. Posteriorly, the maxilla has a moderately well-developed buccal excavation that appears less well defined than in other ceratopsids (Sampson, 1995; Ryan, 2007).

The maxilla of *Nasutoceratops* is distinguished from that of other ceratopsids by several features including: an expanded premaxillary contact with a deeply excavated sulcus; a double-faceted, medially directed flange that slots into the premaxilla and contributes to the hard palate; and an elevated horizontal medial shelf. Moreover, the maxilla is distinguished from the typical ceratopsid condition in exhibiting a steeply angled dorsal ascending ramus, a symplesiomorphic character observed in neoceratopsians (e.g., *Protoceratops* [AMNH 6414]). The maxilla is further distinguished from the standard ceratopsid condition in that the entire tooth row is displaced ventrally relative to the anterior-most portion of the maxilla (i.e., maxilla–premaxilla contact flange; Figs. 2–5). Such ventral displacement of the tooth row is similar to that present in *Diabloceratops* (UMNH VP 16699) and *Avaceratops* (MOR 692), although this character has

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**FIGURE 5.** Referred right maxilla of *Nasutoceratops titusi* (UMNH VP 19466.2) in A, lateral view; B, medial view; C, interpretive drawing of lateral view; and D, interpretive drawing of medial view. **Abbreviations:** aof, antorbital fossa; ascr, ascending ramus of maxilla; df, dental foramina; ept, ectopterygoid contact; hr, horizontal ramus of maxilla; idp, interdental plate; j, jugal contact; l, lacrimal contact; n, nasal contact; nvf, neurovascular foramina; pa, palatine contact; pm, premaxilla contact; ppm, palatal process of maxilla; pt, pterygoid contact; tr, tooth row.
not previously been noted for either taxon (Penkalski and Dodson, 1999; Kirkland and DeBlieux, 2010). Displacement of the tooth row in *Nasutoceratops* (best preserved in UMNH VP 16800) differs slightly from that of *Diabloceratops* (UMNH VP 16699) in that the latter taxon exhibits a greater external exposure of the maxilla anterior to the tooth row. A ventrally displaced maxillary tooth row also occurs in many neoceratopsians (e.g., *Bagaceratops* [ZPAL MgD-I/126], *Protoceratops* [AMNH 6438]) and is thus inferred here to be symplesiomorphic.

**Nasals**—The paired nasals of UMNH VP 16800 are nearly complete, preserving the full extent of the contact with the premaxillae (Fig. 6). A second disarticulated right nasal recovered from another quarry (UMNH VP 19466.1) exhibits similar morphology and is referred to *Nasutoceratops* (Fig. 7). The holotype nasals are almost completely fused along the midline, forming the anterodorsal portion of the facial skeleton. Anteroposteriorly, the nasals are short (~248 mm in UMNH VP 16800, 32% of basal skull length) relative to other, more derived
centrosaurines, contacting the premaxillae anteriorly and ventrally, the maxillae ventrally, and the lacrimals and prefrontals posteriorly. The extremely abbreviated nasal and maxilla of *Nasutoceratops* result in an exceptionally short preorbital facial skeleton relative to other centrosaurines, arguably the shortest known for any centrosaurine (Table 1). The nasal horncore, positioned anterodorsal to the nasal opening, is low, long, and blade like. It is pinched transversely along the posterior portion, with a slightly raised, teardrop-shaped anterior expansion formed in part by contributions from the premaxillae. There is no evidence of an accessory epinarial ossification, as occurs in many chasmosaurines. The surface texture of the horncore in UMNH VP 16800 is moderately obscured due to surface weathering, but overall it appears typical of other ceratopsids, being highly rugose and vascularized. Anteroventral to the base of the horncore, the nasals protrude laterally and posterodorsally, forming much of the roof and sides of the ectonarial fossa. The protruding sides are thin and blade like along the ventral margin, thickening dorsally to form a hood that roofs over much of the endonaris. Internally, the dorsal ‘roof’ of the nasal cavity is similar to that observed in other centrosaurines (e.g., *Centrosaurus* [TMP 93.36.117], *Achelousaurus* [MOR 591]). In contrast to more derived centrosaurines (e.g., *Centrosaurus* [TMP 93.36.117], *Achelousaurus* [MOR 591]), the posterior portion of the nasals forms a deep, convex, saddle-shaped margin that contributes to a steeply inclined ‘forehead’ (Figs. 2, 3, 6). Similarly, posterior to the nasal horncore and ventral to the lacrimal and prefrontal contacts, the external surface of the nasals is deeply concave, forming bilateral, symmetrical pneumatic excavations separated by a thin septum (Fig. 6E, F).

The posterodorsal margin of the nasal, including the lacrimal and prefrontal sutures, is well preserved in the holotype specimen; however, the ventral portion has been obscured by prepositional breakage. The prefrontal and lacrimal sutures are also well preserved in the referred nasal (UMNH VP 19466.1). The nasal–premaxilla contact resembles that of other centrosaurines, with the nasal bifurcating anterior to the nasal horncore to clasp the dorsal processes of the premaxillae (Lambe, 1904, 1913; Sternberg, 1950; Dodson, 1986; Sampson, 1995; Ryan, 2007;

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**FIGURE 7.** Referred right nasal of *Nasutoceratops titusi* (UMNH VP 19466.4) in A, lateral view; B, medial view; C, interpretive drawing of lateral view; and D, interpretive drawing of medial view. **Abbreviations:** bf, bifurcated process of nasal to contact the premaxilla; ins, internarial suture; l, lacrimal contact; na, naris; nh, nasal horn; np, nasal pneumaticity; ns, narial spine; pf, prefrontal contact; pm, premaxilla.
TABLE 1. Skull measurements of select centrosaurine taxa. POH, maximum preorbital skull height; POL, maximum preorbital skull length; POL/POH, maximum preorbital skull height.

| Taxon                     | Specimen         | POH (mm) | POL (mm) | POL/POH |
|---------------------------|------------------|----------|----------|---------|
| Diabloceratops eatoni     | UMNH BP 16699    | 260      | 400      | 1.54    |
| Nasutoceratops titusi     | UMNH VP 16800    | 450      | 410      | 1.09    |
| Avaceratops lamersi       | ANSP 15800       | 180?     | 280?     | 1.56?   |
| Centrosaurus apertus      | YPM 2015         | 350      | 580      | 1.76    |
| Styracosaurus albertensis | NMC 344          | 300?     | 530      | 1.77?   |
| Einiosaurus procurvicornis| MOR 456 8-9-6-1  | 280?     | 440?     | 1.57?   |
| Achelosaurus horneri      | MOR 485          | 275?     | 410?     | 1.49?   |
| Pachyrhinosaurus lakustai | TMP 86.55.258    | 420      | 575?     | 1.37?   |

*Estimated.

Currie et al., 2008; Kirkland and DeBlieux, 2010; McDonald and Horner, 2010). A posterovertrally directed semicircular excavation leads into a nasal cavity at the junction of the nasal and premaxilla (Fig. 6E, F).

As is typical of centrosaurines, a narial spine is formed by contributions from both the nasal and premaxilla (Fig. 3). This feature is deflected medially into the nasal cavity, resulting in a roughly hourglass-shaped opening into the nasal cavity proper as viewed anteriorly (Sampson, 1995). Viewed laterally, the endoloph in Nasutoceratops is relatively small and slightly crescentic, with a dorsally arched anteromedial border. In lateral view, the nasal ‘hood’ arches posterovertrally to become confluent with the narial spine protruding into the posterior portion of the ectornaris. The long axis of the endoloph is oriented almost horizontally, whereas it is subvertically oriented in most centrosaurines. The long axis of the endoloph is 160 mm long, comprising approximately 40% of the premaxillary facial skeleton.

Both nasal specimens known for Nasutoceratops possess well-developed, posteriorly positioned internal cavities in the nasal body posterior to the horncore. When combined with the transverse and dorsoventral crushing of the nasal horncore in the referred right nasal (UMNH VP 19466.1), these features suggest that the nasals were hollow, presumably pneumatized by prefrontal–frontal pneumaticity extending anteriorly into the nasals (Figs. 6E, F, 7). Pneumatic nasals are otherwise unknown in ceratopsians, and this feature is regarded as autapomorphic for Nasutoceratops (Sampson et al., 2013). Medially, the dorsal portion of the contact surface for the opposing nasal is rugose with anteriorly arcing ridges and troughs. The ventral portion of this contact is similarly rugose, but the ridges and troughs are more pronounced and oriented subhorizontally. Ventrally, a triangular excavation is present on the internal surface of the nasal immediately beneath the horncore, presumably related to the lateral and ventral extension of this element. Posteriorly, contacts with the lacrimal and prefrontal are well preserved.

**Skull—Circumorbital Region**

**Postorbital**—Along with the relatively abbreviated facial cranium and dorsally expanded narial region, the most notable feature of *Nasutoceratops* is the supraorbital horncores (Fig. 2). As in all ceratopsids, the supraorbital horncores of the holotype occur as outgrowths of the postorbital and comprise the majority of this element, with a nominal contribution from the palpebral (Sampson et al., 1997). However, the supraorbital horncores of *Nasutoceratops* differ from those of all other ceratopsids in both orientation and, to a lesser extent, shape. The horncores exhibit a strong curvature, with the bases directed anterolaterally and the distal portions directed anteromedially. The distal portion also exhibits a pronounced torsion whereby the dorsal surface, at the midpoint of the horncore, rotates laterally. This torsion leads into a counterclockwise rotation of the distal tip of the left horncore and a clockwise rotation of the distal tip of the right horncore (as evidenced by longitudinal groves and ridges externally when viewed from the horncore base). In addition to their unusual orientation, these structures are highly elongate (~457 mm in the holotype, approximately 59% of basal skull length), exceeding relative and maximum supraorbital horncore length in any other centrosaurine (Table 2). Indeed, when viewed dorsally or laterally, the horncores extend anteriorly almost to the tip of the snout, superficially resembling a ‘Texas Longhorn’ bull. As is typical in ceratopsids, the horncores are subcircular in cross section, tapering distally to a point, with numerous longitudinal ridges and grooves externally.

The supraorbital horncores in *Nasutoceratops* differ markedly from those of all other ceratopsids. Chasmosaurines tend to possess relatively elongate horncores in the supraorbital region but without a strong anterior orientation or torsion. Within Centrosaurinae, the vast majority of taxa possess relatively short supraorbital horncores (e.g., *Centrosaurus* [TMP 93.36.117], *Einiosaurus* [MOR 456 8-9-7-3]) or pachyostotic bosses (*Achelosaurus*, *Pachyrhinosaurus*; Sampson, 1995; Currie et al., 2008). Only three centrosaurines, all from the base of

TABLE 2. Basal skull length versus supraorbital ornamentation length in select centrosaurines. SBL, skull basal length; SHL, supraorbital horncore length.

| Taxon                     | Specimen         | SBL (mm) | SHL (mm) |
|---------------------------|------------------|----------|----------|
| Diabloceratops eatoni     | UMNH VP 16699    | 590      | 230      |
| Alberceratops nesmoi      | TMP 2001.26.01   | ?        | 400      |
| Nasutoceratops titusi     | UMNH VP 16800    | 770      | 457      |
| Avaceratops lamersi       | MOR 692          | ?        | 258      |
| Centrosaurus apertus      | ROM 767          | 677      | 100      |
| Coronosaurus brinkmani    | TMP 2002.68.05   | 530*     | 62       |
| Styracosaurus albertensis | NMC 344          | 760*     | 60       |
| Einiosaurus procurvicornis| MOR 456 8-9-6-1  | 670      | 85       |

*Estimated.
the centrosaurine tree, have been described with elongate supraorbital horncores: *Diabloceratops*, *Avaceratops*, and *Albertaceratops* (Dodson, 1986; Ryan, 2007; Kirkland and DeBlieux, 2010). Zuniceratops, *Diabloceratops*, and *Albertaceratops* possess supraorbital horncores similar to those of *Nasutoceratops* in length and cross section, but these structures have a stronger dorsal (as opposed to anterior) component to their orientation and lack any evidence of torsion. The supraorbital horncores of *Nasutoceratops* are situated anterodorsal to the orbit, as in the centrosaurines *Diabloceratops* [UMNH VP 16699] and *Albertaceratops* [TMP 2002.26.1], as well as the chasmosaurines *Pentaceratops* [OMNH 10165], *Agujaceratops* [TMM 43098-1], *Utahceratops* [UMNH VP 12198], and *Chasmosaurus* [CMN 2245], but in contrast to the condition in all other ceratopsians.

The postorbital comprises a major portion of the dorsal skull roof, forming most of the dorsal margin of the orbit. Sutural contacts are with the lacrimal, palpebral, and prefrontal anteriorly, the frontal medially, the parietal posteriorly, the squamosal posteroventrally, and the jugal ventrally; however, the contacts are mostly obscured in the study sample due to a combination of fusion and breakage. The lacrimal and palpebral form most of the anteroventral and anterior margins of the orbit, respectively, whereas the ventral and posterior margins of the orbit are formed by the dorsal margin of the jugal. The nearly complete right orbit preserved in the holotype (UMNH VP 16800) indicates that *Nasutoceratops* had an elliptical orbit, as is typical of ceratopsids.

Medially, the postorbital of *Nasutoceratops* displays a smooth-walled cornual sinus dorsal to the orbit that protrudes (106 mm) into the horncore shaft on UMNH VP 16800 (23% of total horncore length). Because cornual sinuses are an internal feature, they are typically observed only on isolated postorbitals or fragmentary skulls. The holotype specimen of *Nasutoceratops* is broken in the orbital region, allowing this structure to be observed on both the right and left sides, although the morphology is better preserved on the left. Like other ceratopsids with relatively elongate supraorbital horncores (e.g., *Triceratops* [AMNH 5116]), the cornual sinus of *Nasutoceratops* invaginates the center of the proximal horncore interior. This is in contrast to those ceratopsids with relatively short supraorbital horncores (e.g., *Centrosaurus*, *Anchiceratops*) in which the cornual sinuses may occupy a position in the posterior half of the horncore (Farke, 2006).

The preserved cranial material of UMNH VP 16800 reveals that *Nasutoceratops* possesses a prounced, vaulted skull roof in the interorbital region, formed largely by the prefrontals, frontals, palpebrals, and postorbitals (Fig. 2). These elements together give the impression of the animal having a prounced, anteriorly facing ‘forehead,’ as noted above. A similar feature has been noted for *Diabloceratops* and *Albertaceratops*, as well as for several chasmosaurines (e.g., *Pentaceratops*, *Utahceratops*, and *Kosmoceratops*; Ryan, 2007; Kirkland and DeBlieux, 2010; Sampson et al., 2010). The vaulted forehead spans the entire breadth of the skull and is laterally constrained by well-developed antorbital buttresses. In *Nasutoceratops*, this character is only preserved on the right side of the holotype skull. Complete fusion of the bones forming the skull roof in this region (e.g., frontals and prefrontals) obscures all sutures; however, the prefrontals and frontals are presumed to have similar morphology to those noted for other well-known centrosaurines (Sampson, 1995), with the frontal forming the anterior-most margin of the frontal fontanelle, as well as a substantial portion of the supracranial cavity (Fig. 2). Positioned medially and posteriorly to the postorbitals, the well-developed fontanelle forms an elongate oval with straight sides, a conformation typical of centrosaurines (Dodson et al., 2004).

**Jugal**—The holotype, UMNH VP 16800, preserves a small (~50 mm) fragment of the dorsal margin of the left jugal and a larger portion of the dorsal margin of the right jugal that forms the ventral and posterior margins of the right orbit (Fig. 2). The preserved orbital margin of the jugal is thickened and rugose. The incomplete jugals are presumed to have exhibited morphology typical of other centrosaurines (e.g., *Centrosaurus* [ROM 767]; *Albertaceratops* [TMP 2001.26.1]), contacting the lacrimal dorsally, the maxilla anteriorly, the postorbital postero-dorsally, and the squamosal posteriorly.

**Epipidal**—A single, disarticulated right epipidal (UMNH VP 16800) is preserved with the holotype skull (Fig. 8). The epipidal is roughly trihedral in shape, possessing a flattened anterior surface and a deeply excavated rugose facet along the medial (internal) surface for articulation with the jugal and quadratojugal. Relative to other centrosaurines (e.g., *Centrosaurus* [AMNH 5239], *Styracosaurus* [TMP 2005.42.58]), the epipidal measures approximately 85 mm in length and 78 mm in width at the base and represents the largest example known among centrosaurines. Compared to that of *Diabloceratops* (UMNH VP 16699), the epipidal is very similar, being relatively large with a flattened anterior surface. Large epipidals are typical of most chasmosaurines and may represent a basal feature of Ceratopsidae. Similar to other epiossifications found in ceratopsids, the external surface is highly vascularized and rugose and likely bore a keratinous sheath during life.

**Quadratojugal**—A partial, disarticulated right quadratojugal (UMNH VP 16800), damaged along its dorsal and anterior edges, is preserved in the holotype specimen (Fig. 9). The quadratojugal closely resembles that described for other ceratopsids, being thin anteriorly and thick posteriorly, with an overall wedge shape and well-developed, rugose articular facets along the anterior and medial surfaces for contacting the jugal (anterolateral), epipidal (lateral), and quadratojugal (medial). The contact facet along the rostral surface is slightly concave and scored by a series of rugose grooves and ridges that accommodate the jugal. The thickened posteroventral portion possesses a raised, rugose, semirounded peak that lies between the jugal and quadratojugal. Medial to this raised peak, the quadratojugal possesses a well-defined excavation for the articulation with the quadratojugal.

**Quadratojugal**—A partial left quadratojugal (UMNH VP 16800) is preserved in the holotype specimen (Fig. 10). The element is pre-dominantly broken through the mid-shaft and is missing nearly all of the pterygoid flange and the proximal head for contact with the squamosal. Additionally, much of the medial condyle has been lost to erosion. The preserved ventrolateral surface is thickened and rugose for contact with the quadratojugal. Overall, the quadratojugal closely resembles those described for other ceratopsids and, as in other centrosaurines, does not provide any diagnostic morphology at the genus or species level.

**Skull—Parietosquamosal Frill**

**General**—As in other ceratopsids, the frill is formed by the fused parietals and paired squamosals. Although the squamosals are only partially preserved in UMNH VP 16800, the entire midline parietal bar and much of the transverse parietal bar are present. The frill is subcircular in overall shape, with the widest point located along the midline coronal axis of the frill (Figs. 2, 12). The total length of the frill in UMNH VP 16800 is approximately 610 mm, with a total estimated width of 800 mm (based on mirroring). Frill length is approximately equal to basal skull length (i.e., premaxilla to occipital condyle length). In overall shape, the parietosquamosal frill of *Nasutoceratops* resembles that of *Centrosaurus* (ROM 767), *Achelosaurus* (MOR 485), and *Einiosaurus* (MOR 456 8.9-6-1), although it differs greatly in morphology and organization of both episquamosals and
epiparietals (see below). As in centrosaurines generally, the frill is perforated by two large, bilaterally symmetric, oval fenestrae contained entirely within the boundary of the parietal (Figs. 2, 12). The major axis of each parietal fenestra is approximately 350 mm long, anteroposteriorly oriented, and comprises about 57% of total frill length. The transverse axis is approximately 260 mm in maximum width and comprises about 33% of total frill width. The frill is typical of centrosaurines in being saddle shaped, with the dorsal surface convex transversely and concave anteroposteriorly.

Squamosal—Only small portions of the left and right squamosals are preserved in the holotype (UMNH VP 16800), in particular the anterior-most portions associated with the postorbital contact (Fig. 2). This description is augmented by a referred specimen (UMNH VP 19469), an isolated right squamosal also recovered from the lower portion of the middle unit of the Kainarowits Formation of GSENM (Fig. 11). Referral of the latter to *Nasutoceratops* is based on overall conformation, including the presence of a pronounced, anteroposteriorly directed transverse ridge. UMNH VP 19469 appears to represent a subadult individual based on bone surface texture (Sampson et al., 1997) and exhibits a complete transverse ridge. This squamosal ridge is similar to that observed on an isolated squamosal (NMMNH P34906) from the Fort Crittenden Formation of Arizona (Williamson, 1997) and exhibits a strong anteroposterior dorsal convex curvature. Otherwise, this
specimen is relatively robust and characteristically centrosaurine, being anteroposteriorly short and subrectangular, with a slightly undulating, fan-shaped posterolateral margin and a stepped anteromedial margin representing the dorsal continuation of the quadrate groove (Dodson et al., 2004).

In most respects, the squamosal of *Nasutoceratops* is typical of other centrosaurines and is squared off anteromedially and shares an overlapping joint with the lateral edge of the postorbital. Although the surrounding contacts are incompletely preserved in the holotype specimen and therefore not directly observable, it is presumed that the squamosal of this taxon resembled that of other ceratopsids, contacting the jugal and postorbital anteromedially, parietal medially and posteriorly, and the quadrate and paroccipital process anteroventrally.

The squamosal abuts the parietal anterolaterally and posteromedially, forming approximately one third of the parietosquamosal frill. The squamosal can be subdivided into two portions as viewed laterally: a convex anteromedial portion supporting a pronounced transverse ridge and a protruding jugal process forming the posteroventral portion of the latero-temporal fenestra (almost absent in UMNH VP 19469) and a broad, fan-shaped, concave posterolateral portion. Although most of the jugal process in UMNH VP 19469 has been lost to erosion, the morphology of the jugal notch is preserved and appears similar to that of other centrosaurines. The pronounced transverse ridge in the juvenile squamosal has two almost undulating protuberances along the apex (Fig. 11B).

Although UMNH VP 19469 lacks episquamosals, it does possess four to five marginal undulations. It is presumed that, as in other centrosaurines, the squamosal of *Nasutoceratops* did possess epi-ossifications attached to these undulations.

Additionally, the morphology of the episquamosals is presumed to closely match that of the parietal due to the relatively uniform conformation of epi-ossifications preserved on the parietal (see below). The presence of an epi-ossification across the squamosal-parietal contact cannot be determined on UMNH VP 19469 because of breakage to the posterolateral margin of the element. Although the anteroventral-most portions of both the holotype and the referred squamosal have been lost to erosion, the anteriorly projecting jugal process contributed to the posteroventral margin of the latero-temporal fenestra, as is typical of other ceratopsids. As in centrosaurines generally, the ventral surface includes a pronounced groove for the head of the quadrate and an adjacent
one for the paroccipital process of the exoccipital. These grooves are lined with a series of interfingering troughs, concave to semi-triangular in cross section. Slightly posterior to the quadrateslot are two shallow, subcircular depressions of uncertain function.

For the most part, the centrosaurine squamosal is highly conservative and exhibits little variation within the clade, thereby minimizing the role of this element for resolving ingroup relationships (Sampson, 1995). In this respect, the squamosal of *Nasutoceratops*, with its distinctive ridge on the dorsal surface, is unusual.

**Parietal**—The fused parietals of centrosaurines form approximately two thirds of the parietosquamosal frill. The parietal contacts the squamosals anterolaterally, the frontals, and postorbitals anteriorly, and the supraoccipital anteroventrally. In contrast to the taxonomic conservatism of the squamosal, the parietal of centrosaurines is typically unique to the species level and arguably the most diagnostic element for resolving genera and species relationships within the clade. The holotype right parietal of *Nasutoceratops* (UMNH VP 16800) is nearly complete, preserving the entire median bar and most of the transverse bar, together with most of the lateral parietal ramus (Figs. 2, 12). It appears to pertain to a subadult individual, being relatively thin and fragile, with the surface texture consisting of a mosaic of striated subadult and mottled adult texture (Sampson et al., 1997; Brown et al., 2009). However, epiparietal ossifications are almost completely fused onto the marginal undulations, a feature typically associated with adults. This combined with other features (e.g., near-complete midline fusion of nasal horncore, fusion of the prefrontals and frontals, and fusion of the postorbitals) suggests that this animal was approaching adult status at the time of death.

The right parietal includes seven marginal undulations per side, as well as a midline undulation, all but one of which is capped by an epiparietal. A midline epiparietal is otherwise present only in the chasmosaurines *Triceratops* (Marsh, 1889), *Torosaurus* (Marsh, 1891), and the centrosaurine *Avaceratops* (Dodson, 1986). Though Xu et al. (2010) mentioned a midline parietal bony bump on the dorsal surface in *Sinoceratops*, this bony protrusion is likely more comparable to the dorsal parietal processes described by Clayton et al. (2009) and is therefore not considered a midline (p0) epiparietal. Also in contrast to the standard centrosaurine condition, the frill is rounded postero-medially, with no evidence of a pronounced median embayment. *Nasutoceratops* lacks imbrication of the epiparietals on the lateral margin, a wave-like appearance present in most centrosaurines (Sampson et al., 1997; Ryan et al., 2001).

The median bar is dorsoventrally thin (~4 mm in UMNH VP 16800) near the margins and thick toward the midline (~15 mm), with an overall strap-like conformation similar in morphology to the midline parietal bar in *Achelosaurus* (e.g., MOR 485). Anteriorly, the median bar is dorsally convex, forming a low, rounded, median ridge bearing five midline undulations of varying height; this latter feature is highly variable within centrosaurines and is the locus for horns in *Pachyrhinosaurus lakustai* (Currie et al., 2008). The bar widens posteriorly near the apex of the parietal frill to transition into the transverse parietal bar, which is similarly broad and strap-like. As is typical of other centrosaurines, the midline parietal bar splits anteriorly into a pair of projecting prongs that form the posterior margin of the frontal fontanelle.

The anteriorly directed lateral parietal ramus, best preserved on the right side, rounds out the frill and encloses the parietal fenestrae. The lateral ramus is thickest near the lateral edges, where it is associated with the marginal undulations and epiparietals, and thinnest medially toward the aperture of the fenestrae. The holotype parietal (UMNH VP 16800) is approximately 19 mm thick along the lateral margins between the epiparietals, thinning to approximately 4 mm medially along the fenestral border.

The parietal of *Nasutoceratops* differs considerably from most other centrosaurines, excluding *Avaceratops*, in: (1) lacking a distinct postmedian embayment; (2) possessing a midline epiparietal; and (3) lacking any indication of the well-developed hooks or spikes typical of other centrosaurines (e.g., *Centrosaurus* [TMP 1982.18.790], *Styracosaurus* [TMP 66.10.28], *Pachyrhinosaurus* [TMP 1987.55.141], including animals from the base of the tree (e.g., *Diabloceratops* [UMNH VP 16699], *Albertaceratops* [TMP 2002.26.1])). Although it is conceivable that these processes could have developed into larger structures had this animal reached full maturity, this alternative is considered

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**FIGURE 12.** Parietal of *Nasutoceratops titusi* (UMNH VP 16800) in **A**, posterior view; **B**, dorsal view (photo reversed); and **C**, ventral view. Abbreviations: dpp, dorsal parietal processes; ep0–ep7, epiparietals; mb, median parietal bar; pf, parietal fenestra.
unlikely given the presence of fused epiparietals on the frill margins together with a mosaic of indicators related to subadult and adult maturity (e.g., midline fusion of the nasal horncore, fusion of the prefrontals and frontals, and fusion of the orbital horncores).

The epiparietals are low, roughly crescentic, asymmetric and wedge shaped, with a slightly concave ventral surface. The ossifications project outward in the same plane as the underlying parietal, although with a slight ventral flexion. They are subequal in size around the posterolateral margins of the frill but are slightly smaller anteriorly. The external surfaces of the epiparietals are highly vascularized and rugose.

**Skull—Braincase**

The braincase of *Nasutoceratops* preserved in articulation with the skull is typical of adult ceratopsians. The sutures of the preserved elements are completely fused, making morphological description impossible. Portions of the occipital region of the braincase were lost to erosion prior to discovery, such that all of the occipital condyle, basioccipital region, both basipterygoid processes, parasphenoid, and much of the exoccipitals are not preserved. However, the location of the foramen magnum can be observed and it is elliptical to round in shape.

**Lower Jaw**

The preserved elements of the mandible known for the holotype specimen of *Nasutoceratops* (UMNH VP 16800) are fragmentary and consist of the anterior portion of the left coronoid process and a posterior portion of the ventral margin of the dentary (not figured). Overall, the coronoid process is typical of ceratopsids, although it does possess a highly rugose and pinched dorsal margin. Similarly, the dentary fragment is typical of other ceratopsids.

**Vertebrae**

Together with a nearly complete syncervical, multiple fragments of two dorsal vertebrae and one mostly complete dorsal vertebra are preserved from UMNHVP 16800. As is typical of all ceratopsids, the atlas and axis plus cervical 3 completely coalesce in *Nasutoceratops* to form the syncervical (Lull, 1933; Langston, 1975; Dodson et al., 2004; Campione and Holmes, 2006). The syncervical is nearly complete, missing only portions of the neural spines and fragments of the coalesced centra (Fig. 13). The cranial end of the first cervical preserves the characteristic deep cotyle for articulation with the occipital condyle. Although the syncervical in *Nasutoceratops* is fragmentary and crushed transversely, the element exhibits typical ceratopsid morphology and is most similar to that of the centrosaurine *Styracosaurus* [CMN 344].

The dorsal vertebrae are also typical of ceratopsids, with the centra being anteroposteriorly abbreviated and the neural arches relatively tall (Dodson et al., 2004). The articular faces of the preserved centra are subcircular to pear shaped, most closely resembling the dorsal vertebrae of *Styracosaurus*. The transverse processes associated with the nearly complete dorsal vertebrae are strongly elevated, with prominent zygapophyses, as is typical for ceratopsids.

**Pectoral Girdle and Forelimb**

A nearly complete left forelimb—including coracoid, scapula, humerus, and radius and ulna but lacking the carpal elements and manus—is preserved in the holotype (Figs. 4–7). Additionally, this specimen includes portions of the right forelimb, including the posterodorsal blade of the scapula, proximal end of the humerus, fragments of the radius, and a nearly complete ulna.

The left scapula, coracoid, humerus, ulna, and radius were all recovered in articulation. Several patches of integumentary impressions were preserved in association with the left humerus and scapula (see below). Long bone measurements from the left forelimb are presented in Table S1.

**Scapula**—The left scapula of UMNH VP 16800 is nearly complete, missing only a portion of the posterodorsal blade (Fig. 14). Conversely, only the posterodorsal blade of the right scapula is preserved (not figured). The scapula resembles that of other centrosaurines (Dodson et al., 2004), being long and relatively slender (~280 mm as preserved), with a flared and flattened posterior end and a scapular spine that extends from the posterior margin of the supraglenoid ridge along the posterodorsal blade. The scapula forms approximately two thirds of the glenoid fossa. If the scapula is oriented with the glenoid fossa in the horizontal plane; the posterodorsal blade is flattened transversely along the posterior end as well as being dorsoventrally expanded. The posterior margin of the posterior posterodorsal blade bears prominent muscle attachment scars. The thickest portion of the scapula is located immediately dorsal to the glenoid fossa. Overall, the scapula of the *Nasutoceratops* holotype (UMNH VP 16800) closely resembles that described for other centrosaurines (e.g., *Centrosaurus*, AMNH 5351).
Coracoid—As often occurs in ceratopsids, the left coracoid of UMNH VP 16800 is fused onto the proximal end of the scapula, and this element forms approximately one third of the glenoid fossa (Fig. 14; Dodson et al., 2004). The nearly complete coracoid is roughly square, lacking the prominent posterior process typical of other ceratopsids; however, this unusual conformation appears to be the result of postmortem breakage. The coracoid is ventrally flexed, giving the element a slight concavity on the ventral surface. As is typical of ceratopsids, a large neurovascular coracoid foramen is present on the postero-medial portion of the coracoid immediately cranial to the scapular contact. Overall, the coracoid of *Nasutoceratops* is similar in morphology to that of other centrosaurines (e.g., *Centrosaurus*, AMNH 5351).

Humerus—The complete left humerus in UMNH VP 16800 is 475 mm in overall length, with a minimum diaphyseal circumference of 199 mm, and exhibits typical ceratopsid morphology, possessing a hemispheric and eccentric humeral head and a
prominent deltopectoral crest (~215 mm in length) that comprises nearly half the total length of the humerus (Fig. 15). The deltopectoral crest possesses a curved lateral margin, closely resembling the condition in *Centrosaurus* (e.g., TMP 2002.068.0083). As is more typical of centrosaurines than chasmosaurines, the distal end is less rugose and only modestly expanded (Dodson et al., 2004). The right humerus in the holotype is fragmentary, lacking most of the distal end. Overall the humerus is relatively long and slender but is otherwise typical of ceratopsids.

**Ulna**—An articulated left ulna (figured) and disarticulated right ulna were recovered with UMNH VP 16800 (Fig. 16A, B). The left ulna is 400 mm in length and, as is typical of ceratopsids, has a pronounced olecranon process for insertion of the triceps. However, the olecranon process in UMNH VP 16800 compares closely with that of chasmosaurines, more closely resembling the condition in *Agujaceratops mariscalensis* (UTEP P.37.7.086) than in *Centrosaurus apertus* (Lehman, 1989; Lucas et al., 2006). The most robust portion of the ulna occurs proximally, whereas the distal end is transversely narrow.

**Radius**—Together with a complete left radius (figured), fragments of the right radius are preserved with UMNH VP 16800 (Fig. 16C). The radius is thin overall, with expanded ends typical of other ceratopsids, and is 335 mm long. The expanded proximal end is semicircular in expression, whereas the distal end dorsoventrally expands and transversely narrows.

**Integument and Skin Impressions**

Three patches of integumentary impressions are preserved in association with the scapula and humerus of UMNH VP 16800 (Fig. 17). This is the only occurrence of ceratopsid integumentary impressions from GSENM and one of only a handful known worldwide (Lambe, 1914; Brown, 1917; Sternberg, 1925; Mayr et al., 2002; Larson et al., 2007). The skin impressions occur as both casts and molds and exhibit three different tubercle patterns.

FIGURE 15. Left humerus of *Nasutoceratops titusi* (UMNH VP 16800) in A, lateral view; and B, medial view. Abbreviations: dpc, deltopectoral crest; hh, humeral head; lc, lateral condyle; mc, medial condyle.
The tubercles differ from those described for ornithopod (e.g., hadrosaur) integument impressions, which are considerably more common finds (Osborn, 1911; Brown, 1916; Lull and Wright, 1942; Hall et al., 1988; Anderson et al., 1999; Davis, 2014).

The preserved integumentary impressions are described here in three ‘patches’: A, B, and C. These patches cover an area of 120, 84, and 25 cm², respectively, and only patches B and C are preserved as both cast and mold (Fig. 17). Integument patch A is an array of tightly packed, oval to subcircular tubercles, varying in diameter from 2 to 8 mm, arranged in irregular rows and associated with the left humerus just below the humeral head along the posterior margin of this element (Fig. 17B). Integument patch B is an array of larger, loosely packed, subcircular tubercles varying in diameter from 5 to 11 mm, similarly arranged in irregular rows but associated with the left humeral head, adjacent to the glenoid fossa (Fig. 17C). The most notable integument impression associated with *Nasutoceratops*, however, is Patch C, composed of raised hexagonal tubercles measuring 8–11 mm in diameter, which are framed by prominent triangular grooves (Fig. 17D). Integument patch C is associated with the left humeral head between patches A and B.

Integument patches A and B from *Nasutoceratops* are similar to other known ceratopsian integument (i.e., *Psittacosaurus* [SMF R 4970], *Chasmosaurus* [CMN 2245], and *Centrosaurus* [AMNH 5351]), with variably sized round to elliptical pavement tubercles similarly arranged in irregular rows (Brown, 1917; Sternberg, 1925; Mayr et al., 2002). However, integument patch C is distinct in consisting of relatively equal-sized, hexagonal tubercles delineated from surrounding tubercles by triangular creases an integumentary pattern not observed in any other occurrence of ceratopsian skin impressions. Additionally, unlike the integument patches noted for *Chasmosaurus* (CMN 2245) and *Centrosaurus* (AMNH 5351), there is no evidence in *Nasutoceratops* for the larger, round ossicle-like scales surrounded by pavement tubercles.

**PHYLlogenetic Analysis**

**Methods**

Ceratopsid dinosaurs have been the focus of several cladistic analyses (Sereno, 1986; Dodson et al., 2004), with the most recent analysis of all ceratopsids published by Ryan (2007). The majority of these analyses have been limited in breadth to a particular subset or portion of the clade (e.g., basal ceratopsians: Makovicky and Norell, 2006; Centrosaurinae: Sampson, 1995; Penkalski and Dodson, 1999; Currie et al., 2008; Farke et al., 2011; Ryan et al., 2012; Sampson et al., 2013; Chasmosaurinae: Forster et al., 1993; Forster, 1996; Lehman, 1996; Holmes et al., 2001; Sampson and Loewen, 2010), and none have incorporated Bayesian techniques. The parsimony analysis presented here is a brief summary of the analysis in Sampson et al. (2013); for a detailed discussion refer to that paper. A species-level, parsimony-based cladistic analysis of Centrosaurinae was conducted in order to resolve the phylogenetic relationships of *Nasutoceratops titusi*. The analysis utilized 97 characters (76 cranial and 21 postcranial) across 18 ceratopsid ingroup taxa and six outgroup taxa; refer to supplementary Appendix S1 for specific specimen sources used for character scorings.

The current article augments the previous parsimony-based analysis by using a Bayesian phylogenetic approach in order to help resolve ambiguities (e.g., low Bremer support values) resulting from the parsimony-based analysis, by evaluating the phylogenetic affinities of *Nasutoceratops* within Centrosaurinae within a model-based framework. To date, only a limited number of phylogenetic analyses within vertebrate paleontology have utilized a Bayesian approach (Müller and Reisz, 2006; Evans, 2010; Prieto-Márquez, 2010; Kear and Barrett, 2011; Lee and Worthy, Lund et al. — *Nasutoceratops*, a new basal centrosaurine (e1054936-17)
The Bayesian analysis discussed herein generally follows the protocol of Lee et al. (2014) in which a morphological clock model is used to simultaneously infer phylogenetic relationships and divergence dates using morphological data in MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). The stratigraphic ages used to calibrate the morphological clock model follow the stratigraphic placement presented by Sampson et al. (2013) and are used here as either the mean age of a taxon based on the maximum and minimum stratigraphic occurrence or the most probable age of a taxon based on stratigraphic placement. The data set mirrors that used for parsimony-based analysis in Sampson et al. (2013), consisting of 97 characters (76 cranial and 21 postcranial) across 18 ceratopsid ingroup taxa and six outgroup taxa. The data matrix (Supplementary Table S2) is adapted primarily from Sampson (1995), Dodson et al. (2004), Ryan (2007), Currie et al. (2008), Farke et al. (2011), and Ryan et al. (2012). Supplementary Appendix S2 includes a complete annotated list of characters and character states modified primarily after Farke et al. (2011), many of which are from Sampson et al. (2010). Character determination for each taxon was obtained from first hand specimen observations and, where necessary, augmented with the current literature. Autapomorphies for each taxon were excluded from this analysis simply for ease of study; however, inclusion of
autapomorphies in a Bayesian analysis has a potential influence on analysis results (e.g., branch lengths; Lewis, 2001; Müller and Reisz, 2006; Prieto-Márquez, 2010). The tree was rooted on the branch between Leptoceratops and Centrosaurinae, because Centrosaurinae has long been established as monophyletic (Lambe, 1915; Sternberg, 1949; Lehman, 1990; Dodson and Currie, 1990; Sampson, 1995; Penkalski and Dodson, 1999; Dodson et al., 2004; Ryan and Russell, 2005; Ryan, 2007; Currie et al., 2008). All characters were run unordered as per Sampson et al. (2013) except character 20, which describes the nasal ornamentation type in adult individuals. This character was treated as ordered in this analysis because of detailed ontogenetic information garnered from a growth series of specimens (Forster, 1990; Sampson et al., 1997).

The Bayesian analysis was conducted using the MK likelihood model (where 'M' refers to Markov and K denotes the number of observed states; Lewis, 2001) with a gamma rates parameter, assuming variable rates of change across traits, and an uncorrelated relaxed clock model assuming variable rates of change across branches. Both of these model parameters were preferable to an equal rates model that assumes equal rates of change and a strict clock model where evolutionary rate is constant throughout the tree. The default priors in MrBayes 3.1.2 were used throughout the analysis unless otherwise specified (e.g., strict clock model). The analysis used five replicate runs of 10,000,000 iterations, sampling every 4,000 generations with five chains (one ‘cold’ chain and four incrementally ‘hot’ chains sampling the tree space). The initial 25% of sampled generations was discarded as the ‘burn-in’ phase before the analysis converges on stationarity, with the remaining samples used to calculate the summary statistics (e.g., consensus tree; Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Within the analysis, all replicate runs converged on nearly identical tree topologies (average standard deviation of clade frequencies across replicates = 0.008) and parameters (potential scale reduction factor at or close to 1.0; Gelman and Rubin, 1992). A majority-rule consensus tree was created through combination of all post-burn-in samples for all five replicate runs (Fig. 18B). Exact parameter settings in MrBayes commands are shown in supplementary Appendix S3.

Results

The parsimony-based analysis of Sampson et al. (2013) produced a single most parsimonious tree with a tree length of 140 steps, a consistency index of 0.721, and a retention index of 0.852. (Fig. 18A). Nasutoceratops is placed unequivocally within Centrosaurinae, with eight additional steps required to remove it from this clade and a subsequent 13 steps to place it within Chasmosaurinae. Nasutoceratops is the sister taxon to Avaceratops from the Judith River Formation of Montana. Bremer support for nodes is generally low, being 1 to 2 for most nodes. For a full description of the parsimony analysis results, refer to Sampson et al. (2013).

The topology generated from the Bayesian analysis is generally congruent with the parsimony analysis of Sampson et al. (2013); specifically, Nasutoceratops is recovered as the sister taxon to Avaceratops, with the posterior probability for the clade being well supported at 94%. Notable differences between the parsimony analysis and the Bayesian analysis include the positions of several taxa (i.e., Xenoceratops, Sinoceratops, and Einiosaurus). Xenoceratops and Sinoceratops are no longer sister taxa; instead, Xenoceratops is the sister taxon to a group formed by Diabloceratops + [Albertaceratops + (Avaceratops + Nasutoceratops)], and Sinoceratops is the sister taxon to a group formed by [(Einiosaurus +achelosaurus) + [(P. canadenis + (P. pentorun + P. lakustaii)])]. The placement of Einiosaurus differs between the two analyses in that Einiosaurus is positioned as the sister taxon to Achelosaurus in this Bayesian analysis, with this sister grouping generally well supported with a posterior probability of 90%. It should be noted, however, that the posterior probability support for the new positions of Xenoceratops and Sinoceratops is low, calculated as 46 and 15% respectively.

To further evaluate and compare the two topologies, the number of steps required to generate the tree for the Bayesian analysis was calculated under a parsimony framework using Mesquite v.2.75 (Maddison and Maddison, 2011) and then compared to the statistics for the parsimony topology. The parsimony analysis returned a single most parsimonious tree of 140 steps compared to 150 steps for the Bayesian majority rule consensus tree. The salient differences between the topologies of the two analyses center on the placement of several taxa as mentioned above.

DISCUSSION

Taxonomic and Phylogenetic Implications

The ceratopsid fossil record is arguably the best sampled for any major group of dinosaurs, with approximately 30 recognized species known from a relatively narrow stratigraphic and geographic range (Dodson et al., 2004; Sampson and Loewen, 2010; Dodson 2013; Sampson et al., 2013; supplementary Table S3). The exceptional fossil record of ceratopsid— including numerous monospecific bonebeds — provides researchers with insights into both inter- and intraspecific variation, including ontogeny from numerous taxa (Lehman, 1989; Dodson, 1990; Rogers, 1990; Sampson, 1995; Sampson and Ryan, 1997; Sampson et al., 1997; Ryan et al., 2001; Currie et al., 2008).

Nasutoceratops (UMNH VP 16800) can be confidently placed within Centrosaurinae on the basis of several synapomorphies, including: crescentic rostral; semicircular, hypertrophied premaxilla with expanded ventral margin and dorsal ascending ramus that slots into the nasals; narial spine formed from premaxilla and nasal; stepped squamosal (present in all centrosaurines except Avaceratops); and, compared to chasmosaurines, a relatively abbreviated parietosquamosal frill. The recovery of Nasutoceratops as a relatively basal taxon within Centrosaurinae is supported by several plesiomorphic characters. These include a ventrally displaced tooth row and elongate, robust supraorbital horns. Within Centrosaurinae, these features are otherwise present only in Avaceratops, Albertaceratops, and Diabloceratops. Both features are also present in the neoceratopsian Zuniceratops, and elongate supraorbital horncores characterize all chasmosaurines except Chasmosaurus, Vagaceratops, and Uaceratops.

The position of Nasutoceratops is important for resolving key issues surrounding the evolution of short-frilled ceratopsids. For example, a number of features present in the skull of Nasutoceratops suggest that the polarization of several characters (e.g., orientation of the dorsal ascending ramus of the premaxilla and maxilla; anteroposteriorly short maxilla) should be reversed, a finding that has potential implications for increased phylogenetic resolution of evolutionary patterns within the clade. Despite the suite of neoceratopsian (i.e., non-ceratopsid) characters retained by Nasutoceratops, a number of other features suggest that this animal is highly autapomorphic relative to other centrosaurines. Whereas the bulk of centrosaurine species are diagnosed by two or three autapomorphies (Dodson et al., 2004; Ryan, 2007), Nasutoceratops is diagnosed by five unique craniofacial characters: anteroposteriorly abbreviated and dorsoventrally deep preorbital region comprising 75% of preorbital skull length; extensively pneumatized nasals; greatly hypertrophied premaxilla—maxilla contact; maxilla possessing a double-faceted, medi ally directed flange contributing to a short hard palate; and extremely elongate and robust supraorbital horncores, the absolutely longest within Centrosaurinae. Additionally, the autapomorphies of Nasutoceratops, excluding the elongate supraorbital
FIGURE 18. Time-calibrated parsimony and Bayesian phylogenetic analyses showing the relationships of *Nasutoceratops titusi* within Ceratopsidae. **A**, single most parsimonious tree (tree length = 140, consistency index = 0.721, retention index = 0.852) based on Sampson et al. (2013) with Bremer support values at each node; **B**, resultant Bayesian topology (i.e., majority rule consensus tree of all sampled trees) with posterior probabilities of resolved nodes mapped at each node. Clade names are in bold next to the node.
horncores, do not appear to pertain to signaling and/or combat structures typically associated with mate competition and sexual selection (i.e., nasal and supraorbital horncores and parietosquamosal frill ornamentation; Farlow and Dodson, 1975; Sampson et al., 1997, 2013; Dodson et al., 2004). Instead, most occur in the facial skeleton and can be putatively associated with nonmatting features modified under natural selection (see below). This finding, coupled with a much younger geologic age than other long-horned centrosaurines (e.g., *Albertaceratops* [Ryan, 2007] and *Diacloceratops* [Kirkland and DeBlieux, 2010]; Fig. 18), suggest that *Nasutoceratops* and *Avaceratops* are members of a previously unknown radiation of short-faced, long-horned centrosaurines hypothesized to have originated in the southern WIB. This group differs from the better-known clade of northern centrosaurines not only in supraorbital and frill ornamentation but also in facial skeleton characters (e.g., short, deep preorbital facial skeleton; Sampson et al., 2013).

The hypothesis that *Nasutoceratops* represents a member of a previously unrecognized clade of southern centrosaurines is dependent on the placement of *Diacloceratops* (Kirkland and DeBlieux, 2010) as the basal-most centrosaurine, which is in contrast to the results of Ryan et al. (2012), whose analysis recovered *Xenoceratops*, from northern Laramida, as the basal-most member of the clade. However, ambiguity obfuscates the placement of *Xenoceratops* in both the parsimony analysis and the Bayesian analysis presented here; this ambiguity is most likely due to missing morphological data for *Xenoceratops* relative to *Diacloceratops*. Therefore, the hypothesis presented here for a southern origination and subsequent northern dispersal for the new clade depends on the placement of *Diacloceratops*. First, *Diacloceratops* possesses a facial skeleton more typical of other centrosaurines (e.g., *Albertaceratops*, *Centrosaurus*), indicating that the exceptionally deep (tall) snout of *Nasutoceratops* is apomorphic rather than plesiomorphic. Second, the significantly greater geologic age (~80 Ma) of *Diacloceratops* is also consistent with its basal position, adding support to the hypothesis that it approximates the primitive condition for centrosaurines (Jin-nah et al., 2009). Third, the geographic position of *Diacloceratops*, also found within GSENM in southern Utah, indicates that basal centrosaurines in the south were not somehow distinct from those in the north. In short, the unusual facial morphology present in the skull of *Nasutoceratops* is best interpreted as apomorphic in large part, with *Diacloceratops* representing our best understanding of basal centrosaurine morphology.

**Functional Hypotheses**

*Nasutoceratops* can be distinguished from all other centrosaurines by its extremely short, deep preorbital facial skeleton; morphologically distinct premaxilla and maxilla; highly pneumatic nasals; and extremely long and robust supraorbital ornamentation. The short preorbital region is related both to the abbreviated maxilla and to the vertically inclined posterior ramus of the premaxilla. Functional adaptations associated with this morphology are unknown; however, possession of an abbreviated preorbital region may be related to morphological changes in basal ceratopsians toward more derived masticatory functions. Such morphology would have increased the mechanical advantage during mastication by bringing the beak closer to the fulcrum (i.e., jaw joint) of the lower jaw (Ostrom, 1964, 1966). The depth of the narial region is due in large part to the morphology of the premaxilla and maxilla, with both elements exhibiting steeply rising contact surfaces (Figs. 2–5). The function of the enlarged contact surfaces between both the premaxilla and maxilla is unknown; however, given that these contacts are steeply inclined and more robust than those of more derived genera, this modification might feasibly be related to absorbing increased bite forces (Geist, 1971; Schaffer and Reed, 1972).

As described above, pneumaticity within the nasal is likely derived from a parasanal air source invaginating anteriorly. Among extant vertebrates, craniofacial pneumaticity has previously been associated with a variety of functions, including moisture exchange (O’Malley 1924; Witmer 1997b), shock absorption (Geist, 1971; Schaffer and Reed, 1972), vocalization resonance (O’Malley, 1924), and bony weight reduction (Witmer, 1990, 1995, 1997a, 1997b, 1999). At present, the function of the extensive nasal pneumaticity in *Nasutoceratops* remains unclear.

Long, robust supraorbital horncores were once thought to be diagnostic of Chasmosaurinae; however, the discoveries of *Zuniceratops*, *Avaceratops*, *Diacloceratops*, *Albertaceratops*, and now *Nasutoceratops* demonstrate that elongate supraorbital horncores are synapomorphic for the clade (Wolfe and Kirkland, 1998; Ryan, 2007; Kirkland and DeBlieux, 2010; Sampson et al., 2013). Many functions have been suggested for the supraorbital ornamentations of ceratopsids, including intraspecific combat and display (Farlow and Dodson, 1975; Spassov, 1979; Sampson, 1997; Sampson et al., 1997), predator defense (Hatcher et al., 1907), species recognition (Padian and Horner, 2010), utilitarian uses such as knocking down vegetation (Tait and Brown, 1928), and thermoregulation (Barrick et al., 1998). Of these alternatives, mate competition, involving a combination of display and combat, has been the most widely accepted interpretation in recent years (Dodson et al., 2004).

If the latter hypothesis applies to the unique supraorbital horncores of *Nasutoceratops*, the anterolateral orientation and torsional twist might have facilitated interlocking of horns with conspecific oppositee(conspecific), as in many extant bovid species (Lundri-gan, 1996). Farke (2004) considered the supraorbital horncores of ceratopsids from a functional standpoint, using scale models to examine the probability that forms with elongate supraorbital horncores, such as *Triceratops*, locked horns during agonistic interactions. Farke’s results identified three plausible horn-locking positions for *Triceratops* (i.e., single horn contact, full horn locking, and oblique horn locking) that may be relevant for *Nasutoceratops*. Additionally, Farke et al. (2009) examined cranial pathologies in adult specimens of both *Triceratops* and *Centrosaurus* that the authors postulated were related to conspecific combat in the two taxa. They concluded that periosteal bone lesions present in specimens of *Triceratops* are consistent with trauma inflicted during agonistic behavior. The results of Farke and colleagues were not as conclusive for specimens of *Centrosaurus*, but this finding in no way negates the hypothesis of an agonistic use for the supraorbital ornamentation in *Nasutoceratops*.

**Stratigraphic, Biogeographic, and Evolutionary Implications**

Biogeographic studies of Mesozoic vertebrates have emphasized intercontinental faunal comparisons. However, research involving Upper Cretaceous formations deposited in the WIB of North America offer the potential for finer-scale, intraccontinental biogeography. Extending across a temporal span of 25 million years, a Late Cretaceous epeiric sea divided continental North America into separate eastern and western landmasses, Laramidia and Appalachia, respectively (Lehman, 1997; Blakey, 2009). Although fluctuating, the total habitat area available for terrestrial and freshwater vertebrates on Laramida is estimated to have been about 16% of the total area of present-day North America (Lehman, 1997). During the final two stages of the Late Cretaceous, the Campanian and Maastrichtian, numerous fossiliferous terrestrial and marine formations were deposited east of the Sevier orogenic belt (Lehman, 1997). One such unit is the Kaiparowits Formation, deposited in the south-central region of the WIB when North America occupied a paleolatitude of approximately 45° north (Lehman, 1997). Geologic study by Roberts et al. (2013) included identification and analysis of eight
bentonitic clay (volcanic ash) layers intercalated throughout the 860-m-thick formation, yielding a late Campanian absolute age range for the Kaiparowits Formation in GSENM of ~76.6–74.5 Ma (Fig. 1). Combined with previously published radiometric dates for other fossiliferous formations of the WIB, this work shows the Kaiparowits Formation to be contemporaneous or pencontemporaneous with several of the most fossiliferous formations of North America (e.g., Dinosaur Park Formation, Alberta; upper Judith River and Two Medicine formations, Montana; Fruitland Formation and lower Kirtland Formation, New Mexico; upper Aguja Formation, Texas; Goodwin and Deino, 1989; Eberth and Hamblin, 1993; Rogers et al., 1993).

The northern portion of the WIB has been sampled extensively for ceratopsid dinosaurs. Of the 32 recognized ceratopsid species, 15 taxa (nearly one half of the total known diversity) are known only from Alberta and Montana (Sampson and Loewen, 2010). In contrast, the ceratopsid fauna, particularly centrosaurines, from the southern region of the WIB have remained relatively enigmatic. Recent finds from Utah, New Mexico, and Coahuila (Mexico) have greatly augmented our knowledge, including a previously unknown array of southern ceratopsids that may ultimately rival the horned dinosaur diversity in the north (Sweeney and Boyden, 1993; Sampson et al., 2004, 2010, 2013; Lucas et al., 2006; Loewen et al., 2010; Sampson and Loewen, 2010). Two recently described southern centrosaurines from GSENM, *Nasutoceratops titusi* from the Kaiparowits Formation and *Diabloceratops eatoni* from the underlying Wahweap Formation, challenge the long-held assumption that centrosaurines were rare or absent in the southern WIB (Lehman, 1997, 2001). *Diabloceratops* is the oldest known centrosaurine, dated at about 80 Ma (Jinnah et al., 2009), and thus predates Nasutoceratops by approximately 4 million years (Roberts et al., 2013). Morphologic data are consistent with the older age of *Diabloceratops*, which possesses several plesiomorphic characters that are absent in Nasutoceratops; examples include: an accessory antorbital fenestra, otherwise present in the basal non-ceratopsid neoceratopsians *Magnirostris* (IVPP V 12513), *Bagaceratops* (ZPAL MgD-I/126), *Ajkaceratops* (MTM V 2009.192.1), and *Zuniceratops* (MSM P2101); and a relatively straight, nonexpanded ventral margin of the premaxilla (Wolfe and Kirkland, 1998; Mackovicky and Norell, 2006). Interestingly, Nasutoceratops possesses several characters (e.g., anteroposteriorly abbreviated maxilla; near vertical posterior ramus of premaxilla) present in some basal non-ceratopsid neoceratopsians (e.g., *Lepiceratops* [NMC 8887]; and *Protoceratops* [AMNH 6425]) but that are absent in Diabloceratops. The well-supported placement of Diabloceratops at the base of Centrosaurinae (Fig. 18), combined with the relatively long snout present in the derived non-ceratopsid neoceratopsian Zuniceratops, suggests that the facial skeleton of Nasutoceratops is apomorphically short and deep. Similarly, the elaborate epiparietal spikes present in Diabloceratops (Kirkland and DeBlieux, 2010), and the predominance of elaborate epiparietal ornamentation in other centrosaurines, suggests that the simplified ornamentation condition present in Avaceratops and Nasutoceratops may also be derived. If additional finds support these contentions, Nasutoceratops may represent the first example of a previously unknown clade of late Campanian southern centrosaurines, with an evolutionary trajectory characterized by significant restructuring of the facial skeleton.

The discovery of Nasutoceratops elucidates several evolutionary trends within Centrosaurinae (e.g., reduction in post-orbital horncores; reduction of accessory antorbital fenestra; reorientation of dorsal ascending ramus of premaxilla; hypertrophy of ventral margin of premaxilla forming characteristic ventral angle; reduction in ventral displacement of maxillary tooth row; and reduction in epijugal size). In particular, long, robust supraorbital ornamentation, once thought to be diagnostic of Chasmosaurinae, can now be regarded confidently as plesiomorphic for Ceratopsidae. The recent discovery of the long-horned basal centrosaurines Albertaceratops and Diabloceratops, now augmented by the younger Nasutoceratops described here, highlight the evolutionary trajectory of at least one clade of centrosaurines from long-horned forms (e.g., Diabloceratops, Albertaceratops) to short-horned (e.g., Centrosaurus, Einiosaurus) and ultimately to bossed forms (e.g., Achelosaurus, Pachyrhinosaurs).

Similarly, the discovery of Diabloceratops—which possesses the plesiomorphic accessory antorbital fenestra otherwise only present in basal nonceratopsid neoceratopsians (e.g., *Magnirostris* [IVPP V 12513]; *Bagaceratops* [ZPAL MgD-I/126]; and Zuniceratops [MSM P2101])—and Nasutoceratops, which lacks an accessory antorbital fenestra, highlights the evolutionary loss of this feature in more derived centrosaurines (e.g., Centrosaurus, Pachyrhinosaurs). Likewise, the discoveries of Diabloceratops and Nasutoceratops elucidate several evolutionary changes associated with the craniofacial skeleton within Centrosaurinae, including hypertrophy of the premaxilla in general and the ventral margin in particular, forming the characteristic ventral angle; reorientation of the dorsal ascending ramus of the premaxilla to become more horizontal; and reduction in ventral displacement of the maxillary tooth row. The characteristic ventral angle of the premaxilla is present in Nasutoceratops and northern centrosaurines and absent in Diabloceratops. This distribution supports the notion that Nasutoceratops and the northern centrosaurines shared a more recent common ancestor than either did with Diabloceratops. Ventral displacement of the maxillary tooth row is present in several basal non-ceratopsid neoceratopsians (e.g., *Bagaceratops* [ZPAL MgD-I/126]; *Magnirostris* [IVPP V 12513]; and *Protoceratops* [AMNH 6425]), as well as the centrosaurines *Avaceratops* (ANSP 15800) and *Diabloceratops* (UMNH VP 16699), suggesting that the presence of this character state in Nasutoceratops (UMNH VP 16800) is symplesiomorphic. The discoveries of Diabloceratops and Nasutoceratops from the late Campanian of Utah demonstrate a reduction in the size and shape of the epijugal in centrosaurines, from a large, trihedral element to a small, tab-like ossification.

The phylogenetic analysis of Centrosaurinae presented here provides key support for the hypothesis of late Campanian dinosaur provinciality in the WIB, indicating the presence of a northern clade of short-horned forms and a southern clade of long-horned forms that were geographically separated for at least one million years. In particular, the temporal overlap of *Styracosaurus albertensis*, a typical short-horned, northern clade centrosaurine, and *Nasutoceratops titusi*, a long-horned, southern clade centrosaurine (Fig. 18), offers strong support for the dinosaur provincialism hypothesis and further suggests that the latitudinally arrayed provinces served as independent evolutionary centers of endemism (Sampson and Loewen, 2010; Sampson et al., 2013).

Importantly, all centrosaurines other than Nasutoceratops with elongate postorbital horncores (e.g., *Diabloceratops*, *Avaceratops*, and *Albertaceratops*) come from significantly older sediments (Fig. 18), making Nasutoceratops by far the latest occurring long-horned centrosaurine in the WIB (Sampson et al., 2013). Given that derived northern centrosaurines (e.g., *Centrosaurus*, *Einiosaurus*, *Pachyrhinosaurs*) are likely descended from long-horned forms closely related to Albertaceratops (Ryan, 2007), the results presented here suggest that the centrosaurines in the southern and northern regions of the WIB may prove to be descended from independent branches arising from within the basal, long-horned radiation of centrosaurines. Furthermore, the biogeographic hypothesis presented here relies on Centrosaurinae having originated in the southern WIB and subsequently dispersing to the north. A hypothesized sequence of origination and dispersal may be as follows: (1) by ~80 Ma the
basal-most centrosaurine (e.g., *Diabloceratops*) is present in the southern WIB; (2) by ~79 Ma, long-horned centrosaurines have dispersed throughout the WIB, as evidenced by the occurrence of *Xenoceratops*; (3) the previously unrecognized clade containing *Avaceratops* and *Nasutoceratops* that originated from *Diabloceratops* or a relative thereof in the south WIB is found throughout the WIB by ~78.5–78 Ma; (4) speciation occurs (sympatric or allopatric) through which northern and southern centrosaurines become biogeographically or reproductively isolated; and (5) northern centrosaurines, suggested here to be derived from *Xenoceratops*, evolve enlarged parietal ornamentation, while reducing their supraorbital ornamentation. Meanwhile, *Avaceratops* goes extinct in the northern WIB, whereas the clade of long-horned, short-faced centrosaurines persists in the southern WIB (i.e., *Nasutoceratops*).

CONCLUSION

*Nasutoceratops titusi*, recovered from the middle unit of the late Campanian Kaiparowits Formation of southern Utah, represents a basal centrosaurine. This species is distinguished from other centrosaurines by the following features: an anteroposteriorly abbreviated and dorsoventrally deep preorbital region (e.g., short length to height ratio); highly pneumatized nasals; anteroposteriorly narrow maxillae; hypertrophied premaxilla–maxilla contact; a medially directed double-faceted maxillary process contributing to a short hard palate; and extremely elongate and robust horncores. In contrast to virtually all other centrosaurines, the key diagnostic characters of *N. titusi* appear to be related not to skull roof structures linked to mate competition (i.e., horns and frills) but rather to the extreme shortening of the facial skeleton.

A phylogenetic analysis recovers *Nasutoceratops titusi* as the sister taxon to *Avaceratops lammersi* from the late Campanian of Montana. A Bayesian phylogenetic analysis, a first for ceratopsians, similarly recovers *Nasutoceratops* as the sister taxon to *Avaceratops lammersi*, and this union is well supported with a posterior probability of 94%. The Bayesian analysis reveals some ambiguity in the placement of *Xenoceratops* and *Sinoceratops* with respect to the parsimony-based analysis. The resulting Bayesian topology, when evaluated under a parsimony framework, produces a tree of 150 steps—10 additional steps when compared to the unconstrained parsimony tree.

*Nasutoceratops* elucidates multiple overall evolutionary patterns within greater Centrosaurinae, including: reduction in postorbital horncores; reduction of accessory antorbital fenestra; reorientation of the dorsal ascending ramus of the premaxilla; hypertrophy of the ventral premaxillary margin, forming a characteristic ventral angle and associated anteroventral trough; reduction in ventral displacement of the maxillary tooth row; and reduction in epiglial size. Long, robust supraorbital ornamentation, once thought to be diagnostic of Chasmosaurinae, can now be shown as plesiomorphic for Ceratopsia. The discoveries of *Diabloceratops* and *Nasutoceratops* from GSENM also underscore the evolutionary loss of the accessory antorbital fenestra, a feature once thought to be restricted to basal non-ceratopsid neoceratopsians. Additionally, *Nasutoceratops* highlights a reorientation of the craniofacial skeleton (e.g., dorsal ascending ramus of the premaxilla and maxilla) within centrosaurines, as well as a reduction in epiglial size characterized by one subclade of derived forms.

Ceratopsids represent one of the best documented dinosaurian clades, with high taxonomic diversity known from a relatively narrow temporal distribution. Recent discoveries (e.g., Ryan, 2007; Ryan et al., 2012; Sampson et al., 2013) are providing key insights into the mosaic evolution of ceratopsids generally and centrosaurines in particular. Given the pace of discovery of new ceratopsid taxa, together with persistent temporal gaps in the existing fossil record of ceratopsids, it is probable that the diversity of North American horned dinosaurs will continue to rise.

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