

Transitional evolutionary forms and stratigraphic trends in chasmosaurine ceratopsid dinosaurs: evidence from the Campanian of New Mexico (#43200)

1

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Transitional evolutionary forms and stratigraphic trends in chasmosaurine ceratopsid dinosaurs: evidence from the Campanian of New Mexico

Denver W Fowler^{Corresp., 1, 2}, Elizabeth A Freedman^{1, 2, 3}

¹ Badlands Dinosaur Museum, Dickinson Museum Center, Dickinson, North Dakota, United States

² Museum of the Rockies, Montana State University, Bozeman, Montana, United States

³ Department of Natural Sciences, Dickinson State University, Dickinson, North Dakota, United States of America

Corresponding Author: Denver W Fowler

Email address: df9465@yahoo.co.uk

Three new chasmosaurines from the Kirtland Formation (~75.0 - 73.4 Ma), New Mexico, form morphological and stratigraphic intermediates between *Pentaceratops* (~74.7 - 75Ma, Fruitland Formation, New Mexico) and *Anchiceratops* (~72 - 71Ma, Horseshoe Canyon Formation, Alberta). The new specimens exhibit gradual enclosure of the parietal embayment that characterizes *Pentaceratops*, providing support for the phylogenetic hypothesis that *Pentaceratops* and *Anchiceratops* are closely related. This stepwise change of morphologic characters observed in chasmosaurine taxa that do not overlap stratigraphically is supportive of evolution by anagenesis. Recently published hypotheses that place *Pentaceratops* and *Anchiceratops* into separate clades are not supported. This phylogenetic relationship demonstrates unrestricted movement of large-bodied taxa between hitherto purported northern and southern provinces in the Late Campanian, weakening support for the hypothesis of extreme faunal provincialism in the Late Cretaceous Western Interior.

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3 **chasmosaurine ceratopsid dinosaurs : evidence from the**
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5

6 Denver Warwick Fowler^{1,2} & Elizabeth Anne Freedman Fowler^{1,2,3}

7

8 ¹ Badlands Dinosaur Museum, Dickinson, North Dakota. 586019 ² Museum of the Rockies and Dept. Earth Sciences, Montana State University, Bozeman,

10 Montana, 59717, USA (where the majority of the research was conducted)

11 ³ Dept. Natural Sciences, Dickinson State University, Dickinson, North Dakota, 58602

12

13 Corresponding Author:

14 Denver Fowler

15 Badlands Dinosaur Museum, Dickinson Museum Center, 188 East Museum Drive, Dickinson,

16 ND 58601, USA

17 Email Address: df9465@yahoo.co.uk

18

19 **ABSTRACT**20 Three new chasmosaurines from the Kirtland Formation (~75.0 - 73.4 Ma), New Mexico, form
21 morphological and stratigraphic intermediates between *Pentaceratops* (~74.7 - 75Ma, Fruitland
22 Formation, New Mexico) and *Anchiceratops* (~72 - 71Ma, Horseshoe Canyon Formation,
23 Alberta). The new specimens exhibit gradual enclosure of the parietal embayment that
24 characterizes *Pentaceratops*, providing support for the phylogenetic hypothesis that
25 *Pentaceratops* and *Anchiceratops* are closely related. This stepwise change of morphologic
26 characters observed in chasmosaurine taxa that do not overlap stratigraphically is supportive of
27 evolution by anagenesis. Recently published hypotheses that place *Pentaceratops* and
28 *Anchiceratops* into separate clades are not supported. This phylogenetic relationship

29 demonstrates unrestricted movement of large-bodied taxa between hitherto purported northern
30 and southern provinces in the Late Campanian, weakening support for the hypothesis of extreme
31 faunal provincialism in the Late Cretaceous Western Interior.

32

33 INTRODUCTION

34 Intermediate or “transitional” fossils are an expected product of evolution, and are especially
35 celebrated when they occur within major evolutionary transitions (Anderson and Sues, 2007;
36 Wellnhofer, 2010; Daeschler et al., 2006). However, morphological intermediates also occur
37 within the 'normal' evolution that comprises the majority of the fossil record giving us key
38 insight into evolutionary mode, tempo, and trends, but also providing ancient examples of how
39 organisms respond to changes in their environment (Malmgren et al., 1984; Hull and Norris,
40 2009; Aze et al., 2011; Pearson and Ezard, 2014; Scannella et al., 2014; Tsai and Fordyce, 2015).

41

42 In dinosaurs, recognition of morphologic intermediates is confounded by a typically sparse fossil
43 record, characterized by taxa that may be widely separated in space and time, and often known
44 only from single specimens. Despite this, in the Upper Cretaceous rocks of North America a
45 combination of increasingly intensive sampling and newly refined stratigraphy is beginning to
46 fill in gaps in the dinosaur record. This is revealing hitherto unknown morphotaxa that link
47 previously disparate or misunderstood morphologies, and/or define new ‘end-members’ that
48 extend or emphasize stratigraphic morphological trends, challenging previously held
49 assumptions about the mode and tempo of dinosaur evolution (Horner et al., 1992; Sampson,
50 1995; Holmes et al., 2001; Ryan and Russell, 2005; Wu et al., 2007; Currie et al., 2008; Sullivan
51 and Lucas, 2010; Evans et al., 2011; Scannella and Fowler, 2014; Scannella et al., 2014).

52

53 Central to this emergent understanding are the Ceratopsidae: a North American (although see Xu
54 et al., 2010) clade of Late Cretaceous ornithischian dinosaurs that exhibit famously elaborate
55 cranial display structures (Hatcher et al., 1907). Differences in size or expression of these various
56 horns, bosses, and parietosquamosal frills are used to diagnose different taxa, with ~63 species
57 historically described within two families (the ‘short-frilled’ Centrosaurinae and ‘long-frilled’
58 Chasmosaurinae; Lambe, 1915), ~26 of which have been erected in the past 10 years. This

59 explosion of new taxa has led some researchers (Sampson and Loewen, 2010; Sampson et al.,
60 2010) to propose that ceratopsids radiated through the Campanian-Maastrichtian into numerous
61 contemporaneous geographically-restricted species. However, it is becoming clear that
62 differences in cranial morphology are not always representative of (contemporaneous) diversity.
63 Cranial morphology has been shown to change significantly through ontogeny (Horner and
64 Goodwin, 2006; Scannella and Horner, 2010), such that many historical taxa are now considered
65 growth stages of previously recognized forms. Furthermore, studies conducted within single
66 depositional basins have shown ceratopsid taxa forming stacked chronospecies that do not
67 overlap in time, demonstrating that cranial morphology evolves rapidly (in as little as a few
68 hundred thousand years), and supporting the hypothesis that much of what has been perceived as
69 diversity might instead represent intermediate morphospecies within evolving anagenetic
70 lineages (Horner et al., 1992; Holmes et al., 2001; Ryan and Russell, 2005; Mallon et al., 2012;
71 Scannella et al., 2014; Fowler, 2017).

72

73 Intermediate Campanian chasmosaurine ceratopsids were predicted by Lehman (1998; Fig. S1),
74 who showed successive morphospecies of the Canadian genus *Chasmosaurus* (Dinosaur Park
75 Formation, Alberta; Middle to Upper Campanian) with a progressively shallowing embayment of
76 the posterior margin of the parietosquamosal frill. This was contrasted with an opposite trend
77 seen in *Pentaceratops sternbergii* (Fruitland Formation, New Mexico; Upper Campanian) to
78 *Anchiceratops ornatus* (Horseshoe Canyon Formation, Alberta; Lower Maastrichtian),
79 whereupon the midline embayment deepens and eventually closes (Lehman, 1993; Lehman,
80 1998; Fowler, 2010; Fowler et al., 2011; Wick and Lehman, 2013). This hypothesis matched the
81 stratigraphic occurrence of taxa known at the time, and is supported by new taxa described since
82 1998 (*Vagaceratops* (*Chasmosaurus*) *irvinensis*; *Kosmoceratops richardsoni*; *Utahceratops*
83 *gettyi*; and *Bravoceratops polyphemus*; Holmes et al., 2001; Sampson et al., 2010; Fowler, 2010;
84 Fowler et al., 2011; Wick and Lehman, 2013; although see Supporting Information 1).

85

86 However, a recent phylogenetic analysis of chasmosaurines (Sampson et al., 2010) proposed a
87 starkly different relationship (Fig. S2) where a clade comprising *Vagaceratops* (*Chasmosaurus*)
88 *irvinensis* and *Kosmoceratops richardsoni* instead formed the sister group to a clade composed
89 of *Anchiceratops* and all other Maastrichtian chasmosaurines. This is significant as it implies that

90 the clade [*Vagaceratops* + *Kosmoceratops*] is more closely related to *Anchiceratops* than is
91 *Pentaceratops* (i.e. the opposite to the relationship suggested in Lehman, 1998). Indeed, the
92 poorly known chasmosaurine *Coahuilaceratops magnacuerna* formed a second successive sister
93 taxon to the [*Vagaceratops* + *Kosmoceratops*] + [*Anchiceratops*] clade, suggesting that
94 *Pentaceratops* is even more distantly related. Also, a *Chasmosaurus* clade [*C. russelli* + *C. belli*]
95 is recovered as separated from [*Vagaceratops* + *Kosmoceratops*] (Sampson et al., 2010), despite
96 *Vagaceratops* (*Chasmosaurus*) *irvinensis* being originally recovered as the most derived member
97 of a *Chasmosaurus* clade by Holmes et al. (2001), and the existence of morphological
98 intermediates between *C. belli* and *V. irvinensis* (e.g. cf. *C. belli* specimen YPM 2016; see later).
99 Subsequent analyses by Mallon et al. (2011; 2014; using an altered version of the data matrix
100 from Sampson et al., 2010) recovered cladograms (Fig. S2) that appear “upside down”, with the
101 Lower Maastrichtian taxa *Anchiceratops* and *Arrhinoceratops* occurring in a basal polytomy, and
102 some of the stratigraphically oldest taxa forming the most derived clade (Middle to Upper
103 Campanian [*Chasmosaurus belli* + *Chasmosaurus russelli*]); a configuration that would require
104 considerable ghost lineages for many clades. Mallon et al. (2014; p.63) acknowledged their
105 unlikely topology, stating that “while the monophyly of the Chasmosaurinae is secure, its basic
106 structure is currently in a state of flux and requires further attention”. This can only be resolved
107 by a combination of character reanalysis and the discovery of new specimens intermediate in
108 morphology between currently recognized taxa.

109

110 Here we describe new chasmosaurine material from the Kirtland Formation of New Mexico that
111 forms stratigraphic and morphologic intermediates between *Pentaceratops* and *Anchiceratops*.
112 This includes new taxa *Navajoceratops sullivan* and *Terminocavus seelyi* which, although based
113 on fragmentary specimens, both include the diagnostic posterior border of the parietal.
114 Geometric morphometric analysis supports the hypothesis that the posterior embayment of the
115 parietal deepens and closes in on itself over ~ 2 million years, and that *Vagaceratops* and
116 *Kosmoceratops* probably represent the most derived and successively youngest members of a
117 *Chasmosaurus* lineage. Phylogenetic analysis is less conclusive, but recovers *Navajoceratops*
118 and *Terminocavus* as successive stem taxa leading to *Anchiceratops* and more derived
119 chasmosaurines, and suggests a deep split within Chasmosaurinae that occurs before the Middle
120 Campanian. This is supportive of true speciation by vicariance occurring relatively basally

121 within Chasmosaurinae, followed by more prolonged periods of anagenetic (unbranching)
122 evolution. Recent hypotheses of basinal-scale faunal endemism are not supported; however, it
123 appears likely that continental-scale latitudinal faunal variation occurred in the Campanian. The
124 new specimens document incipient paedomorphic trends that come to characterize more derived
125 chasmosaurines in the Maastrichtian, such as *Triceratops*.

126

127 **Institutional abbreviations**

128 AMNH, American Museum of Natural History, New York; CMN (CMN), Canadian
129 Museum of Nature, Ottawa, Ontario; MNA, Museum of Northern Arizona, Flagstaff; NMMNH,
130 New Mexico Museum of Natural History and Science, Albuquerque; OMNH, Oklahoma
131 Museum of Natural History, Norman; PMU, Paleontologiska Museet, Uppsala University,
132 Sweden; SDNHM, San Diego Natural History Museum, California; SMP, State Museum of
133 Pennsylvania, Harrisburg; UTK/P, University of Kansas, Lawrence; UMNH, Utah Museum of
134 Natural History, Salt Lake City; UNM, University of New Mexico, Albuquerque; USNM, United
135 States National Museum, Smithsonian Institution, Washington D.C.; UTEP, University of Texas
136 at El Paso.

137

138 **Anatomical abbreviations**

139 Ep, epiparietal numbered from 1 to 3 (e.g. ep1) from medial to lateral; es, episquamosal.

140

141 **GEOLOGICAL SETTING, MATERIALS and METHODS**

142

143 ***Geological Setting***

144

145 All newly described material was collected from the Upper Campanian Fruitland and Kirtland
146 Formations of the San Juan Basin, New Mexico (Figs. 1, 2). Further information on Fruitland
147 and Kirtland Formations can be found in Supporting Information 1.

148

149 ***Fossil Materials and accepted taxonomy***

150 In order to make proper comparisons with the new specimens, it is necessary to review the
151 taxonomy, stratigraphy, and morphology of historical and type specimens of *Pentaceratops* and
152 related chasmosaurines. This is discussed in greater detail in Supporting Information 1, and only
153 the following summary is provided here.

154

155 One of the problems facing any new analysis which includes the taxon *Pentaceratops sternbergii*
156 is that although the holotype (AMNH 6325; Osborn, 1923) is a mostly complete skull, it
157 unfortunately lacks the diagnostic posterior end of the parietal, making it difficult to reliably
158 refer other specimens to the taxon. However, it should be noted that the taxonomic importance of
159 the posterior bar was not strongly emphasized until the current work, and so many specimens
160 have been historically referred to *P. sternbergii* by other researchers (see Supporting Information
161 1). Therefore, we have necessarily reviewed whether such taxonomic referrals are appropriate,
162 and consequently revised the referrals of many specimens, while simultaneously attempting to
163 preserve some semblance of taxonomic stability (especially regarding the original material). It is
164 also taken into account that some specimens are currently under study by other workers (J. Fry,
165 S. G. Lucas, H. N. Woodward, pers. comm.), and so new names are not yet erected for some
166 specimens. In summary, we follow Lull (1933) and all subsequent workers in considering
167 AMNH 1624 and AMNH 1625 as specimens of cf. *P. sternbergii*. However, referred specimens
168 MNA Pl.1747 and UKVP 16100 are moved into aff. *Pentaceratops* n. sp. along with the new
169 specimen NMMNH P-37880. Partial skull SDMNH 43470 is referred to aff. *Pentaceratops* sp.,
170 due to uncertainty concerning the relationship of its stratigraphic position and immature
171 ontogenetic condition to morphology. Many other fragmentary specimens previously referred to
172 *P. sternbergii* (e.g. AMNH 1622) are not considered diagnostic and so are here considered
173 Chasmosaurinae indet. We follow Lehman (1998, the original description) in considering the
174 large skull and skeleton OMNH 10165 as aff. *Pentaceratops* sp., and not the new taxon
175 *Titanoceratops ouranos* (Longrich, 2011). Autapomorphies used to diagnose the new taxon
176 *Pentaceratops aquilonius* (Longrich, 2014) are shown to be invalid and it should be considered
177 a nomen dubium.

178

179 Concerning chasmosaurines other than *Pentaceratops*, we follow Maidment and Barrett (2011)
180 and Mallon et al. (2012) in considering *Mojoceratops perifania* (Dinosaur Park Formation,
181 Alberta; Longrich, 2010) as a junior synonym of *Chasmosaurus russelli*. However, the taxonomy
182 of *C. russelli* has its own priority problems (see Supporting Information 1) and as such
183 specimens will be referred to as "*Chasmosaurus russelli*" and specimen numbers given. A
184 revision of the epiparietal numbering system is used for *Vagaceratops* (*Chasmosaurus*)
185 *irvinensis* (Dinosaur Park Formation, Alberta; Holmes et al., 2001; Sampson et al., 2010) and
186 *Kosmoceratops richardsoni* (Kaiparowits Formation, Utah; Sampson et al., 2010), based on
187 comparison to specimens of *Chasmosaurus*, especially *C. belli* YPM 2016 (Dinosaur Park
188 Formation, Alberta). *Bravoceratops polyphemus* (Javelina Formation, Texas; Wick and Lehman,
189 2013) is shown to be a *nomen dubium* as the element identified as the posterior end of the
190 parietal median bar is reidentified as the anterior end and is shown to be undiagnostic.

191

192 The electronic version of this article in Portable Document Format (PDF) will represent a
193 published work according to the International Commission on Zoological Nomenclature (ICZN),
194 and hence the new names contained in the electronic version are effectively published under that
195 Code from the electronic edition alone. This published work and the nomenclatural acts it
196 contains have been registered in ZooBank, the online registration system for the ICZN. The
197 ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed
198 through any standard web browser by appending the LSID to the prefix <http://zoobank.org/>. The
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200 57D4AEBFE2BF. The online version of this work is archived and available from the following
201 digital repositories: PeerJ, PubMed Central and CLOCKSS

202

203 ***Phylogenetic analysis***

204 Phylogenetic analysis was conducted using an adapted version of the character matrix from
205 Mallon et al. (2014). Edits were made to 22 characters; four new characters were added, making
206 a total of 156 characters (see Supporting Information 2 for further details).

207

208 **Morphometric analysis**

209 Landmark-based geometric morphometric analysis was used to compare parietal shape among 19
210 specimens (taxa) of chasmosaurine ceratopsids. The analysis was performed by the software
211 package “Geomorph” (version 2.1.1; Adams and Otárola-Castillo, 2013) within the R language
212 and environment for statistical computing, version 3.1.2 for Mac OSX ([http://www.R-](http://www.R-project.org/)
213 [project.org/](http://www.R-project.org/); R_Core_Team, 2014). Landmarks were plotted onto each image of a parietal in
214 dorsal view. Images used were a combination of photographs and specimen drawings, most of
215 which were taken directly from the literature. Landmarks were specifically selected to represent
216 morphological features that are observed to vary between specimens (Fig. 3). Only the left side
217 of the parietal was analyzed. Specimens with well preserved left and right sides were sampled for
218 both sides by plotting the coordinates from the left side, then mirroring the image of the right
219 side so that it appears as a left, and analyzing those as a separate dataset.

220

221 Although the parietal of *Agujaceratops mariscalensis* (UTEP P.37.7.065, 070, 071) is
222 fragmentary, the reconstruction of Lehman (1989) is included for comparison, although only the
223 left side was analysed since it is only this side that is based on fossil material. Only the right
224 sides of *Kosmoceratops richardsoni* holotype UMNH VP 17000 and "*Chasmosaurus russelli*"
225 referred specimen TMP 1983.25.1 were analysed as the left sides were damaged and missing
226 critical areas. Only the left side of *Chasmosaurus belli* specimen AMNH 402 was used as the
227 right side is unusually distorted.

228

229 Landmarks were digitized within the R program using “digitize2d” (version 2.1.1; Adams and
230 Otárola-Castillo, 2013). Parietals were rotated and scaled using Generalized Procrustes Analysis
231 (using the function “gpgen”) so that shape was the only difference among specimens.

232 Consequent Procrustes coordinates were analyzed in a Principal Components Analysis (function
233 “plotTangentSpace”).

234

235 **RESULTS**236 **SYSTEMATIC PALAEOLOGY**

237

238 DINOSAURIA Owen, 1842, *sensu* Padian and May 1993.239 ORNITHISCHIA Seeley, 1887, *sensu* Sereno 1998.240 CERATOPSIA Marsh, 1890, *sensu* Dodson, 1997. 241 CERATOPSIDAE Marsh, 1888, *sensu* Sereno 1998.242 CHASMOSAURINAE Lambe, 1915, *sensu* Dodson et al., 2004.

243

244 ***Pentaceratops sternbergii* (Osborn, 1923)**

245

246 **Type specimen** - AMNH 6325 (Osborn, 1923), nearly complete skull, missing the mandible and
247 the posterior half of the parietal and squamosals.

248

249 **Referred specimens** - AMNH 1624, nearly complete skull, missing mandible and the medial
250 part of the parietal; AMNH 1625, nearly complete frill, missing anterior end of the parietal and
251 right squamosal, and most of the left squamosal. Referred to as *cf. Pentaceratops sternbergii*.

252

253 **Locality and Stratigraphy** - AMNH 6325, 1624, and 1625 were all collected by C. H.254 Sternberg in 1922 and 1923 from the Fruitland Formation, San Juan Basin, New Mexico (Figs. 1
255 and 2; see Supporting Information 1 for discussion).

256

257 **Diagnosis** - Chasmosaurine ceratopsid characterized by the following combination of characters
258 (modified from Lehman, 1998; and Longrich, 2014): Posterior bar of the parietal M-shaped, with
259 well-developed median embayment. Arches of the M-shape angular, with apex of arch occurring
260 at locus ep2. Anteroposterior thickness of the parietal posterior bar uniform (or nearly so) from
261 medial to lateral. Three large subtriangular epiparietals. Ep1 curved dorsally or anterodorsally
262 and sometimes twisted such that the epiparietal contacts the posterior margin of the frill laterally,
263 and lies atop the frill medially. Parietal median bar with slender ovoid cross section. Frill long

264 and narrow, broader anteriorly than posteriorly. Temporal episquamosal enlarged relative to
265 penultimate episquamosal. Parietal fenestrae subangular in shape. Postorbital horns present and
266 relatively slender, curving anteriorly (at least in adults). Epijugal spikelike, more elongate than in
267 other chasmosaurines, curving ventrally. Nasal horn positioned over the naris.

268

269 Can be distinguished from *Chasmosaurus* by the following characters: Lateral rami of the
270 parietal posterior bar meet medially at $<90^\circ$, rather than $>90^\circ$. Ep1 occurs within the embayment
271 of the parietal posterior bar, rather than at the lateral edges of the embayment. Ep1 typically
272 curved anteriorly and oriented anterolaterally, rather than pointing posteriorly. Ep2 oriented to
273 point posteriorly rather than posterolaterally. Ep2 triangular and symmetrical (or nearly so)
274 rather than asymmetrical. Posteriormost point of the parietal posterior bar (apex of the curved
275 lateral ramus) occurs at locus ep2 rather than ep1. Maximum point of constriction for the parietal
276 median bar occurs approximately halfway along its length, rather than within the posterior third.
277 Frill broader anteriorly than posteriorly. Nasal horn positioned over the naris rather than 50% or
278 more positioned posterior to the naris. Premaxillary flange restricted to dorsal margin of
279 premaxilla, rather than along entire anterior margin of external naris. Postorbital horns elongate
280 and anteriorly curved (in large individuals assumed to represent adults), rather than abbreviated,
281 resorbed, and/or curved posteriorly (adapted from Forster et al., 1993; Maidment and Barrett,
282 2011; Longrich, 2014).

283

284 Can be distinguished from *Utahceratops gettyi* by the following characters: nasal horn more
285 anterior than *U. gettyi*, being positioned over the naris rather than posterior to the naris.
286 Postorbital horns elongate and anteriorly oriented (in large individuals assumed to represent
287 adults), rather than abbreviated or resorbed and oriented anterolaterally.

288

289 **Comment** - The virtually complete parietosquamosal frill, AMNH 1625 is the most diagnostic of
290 the original referred materials. As AMNH 1624 is missing the central part of the parietal it can
291 only be tentatively referred to the same taxon as AMNH 1625 based on the following shared
292 diagnostic characters (which are not seen in *Pentaceratops* n. sp. specimens; MNA Pl. 1747,
293 UKVP 16100, and NMMNH P-37880; see later): the posteriormost point of the parietal posterior
294 bar is positioned at locus ep2. Ep2 is not positioned within the parietal median embayment. Ep2

295 is oriented posteriorly. The lateralmost edge of the lateral rami of the parietal posterior bar is
296 slightly expanded in AMNH 1624, more so than in AMNH 1625, but less so than seen in MNA
297 Pl.1747 and UKVP 16100. The M-shape of the posterior bar is slightly angular in AMNH 1624,
298 more similar to AMNH 1625 than the rounded M-shape in MNA Pl.1747 and UKVP 16100.

299

300 Both AMNH 1624 and 1625 were referred to *Pentaceratops sternbergii* without comment by
301 Lull (1933; see Supporting Information 1). From 1933 to 1981, the defined morphology of *P.*
302 *sternbergii* was based on the combination of these specimens along with the holotype AMNH
303 6325, thus forming a hypodigm (Simpson, 1940). In 1981 Rowe et al. referred the then newly
304 discovered MNA Pl.1747 and UKVP 16100 to *P. sternbergii*, but implicitly recognized that
305 these new specimens were distinct from the *P. sternbergii* hypodigm. They state (p. 40) that the
306 reconstructed frills of AMNH 6325 and 1624 were "on the basis of [MNA Pl.1747], seen to be
307 incorrect". The frills of AMNH 6325 and 1624 were presumably reconstructed based on the
308 complete frill of AMNH 1625 (which Rowe et al. 1981 acknowledge the existence of, but had not
309 been able to locate, nor observe a photograph). Following this, based on the morphology of the
310 posterior end of the parietal, here we show that MNA Pl.1747 and UKVP 16100 should be
311 referred to a different taxon from AMNH 1624 and 1625.

312

313 As the *P. sternbergii* holotype specimen AMNH 6325 lacks the diagnostic posterior bar of the
314 parietal, then we cannot currently know whether the holotype would have been more similar to
315 AMNH 1624 and 1625; MNA Pl.1747 and UKVP 16100; or a different morphology entirely. A
316 possible exception is that the preserved portion of the parietal median bar of AMNH 6325 is
317 narrow and particularly elongate, more so than the median bars of chasmosaurines recovered
318 from the Kirtland Formation (*Navajoceratops*, *Terminocavus*, new taxon C, and "*Pentaceratops*
319 *fenestratus*"). AMNH 6325, 1625, and 1624, MNA Pl.1747, and UKVP 16100 are all recorded
320 as having been collected in the Fruitland Formation (with no better stratigraphic resolution
321 available for the AMNH specimens; see Supporting Information 1), so that stratigraphy is mostly
322 uninformative regarding their potential separation.

323

324 Despite the inadequacy of the holotype AMNH 6325, it is desirable to conserve the name
325 *Pentaceratops*, and *P. sternbergii*. In order to do so the original hypodigm of Lull (1933) is

326 maintained here, and we thus refer  specimens AMNH 1624 and 1625 as cf. *P. sternbergii*. For
327 this to be formalized, it would be best to petition the ICZN to transfer the holotype to another
328 specimen, preferably AMNH 1625. Without transfer of the holotype, *Pentaceratops* and *P.*
329 *sternbergii* should be considered nomen dubia, and a new taxon erected for diagnostic specimen
330 AMNH 1625 and (possibly) 1624.

331

332 **aff. *Pentaceratops* n. sp.**

333

334 **Referred specimens** - MNA Pl.1747, complete skull and partial postcranium; UKVP 16100,
335 complete skull; NMMNH P-37880, partial right lateral ramus of parietal posterior bar.

336

337 **Locality and Stratigraphy** - All specimens were collected from the upper part of the Fruitland
338 Formation, San Juan Basin, New Mexico (Figs. 1 and 2; see Supporting Information 1).

339

340 **Diagnosis** - Differs from cf. *Pentaceratops sternbergii* (principally, AMNH 1625) by possession
341 of the following characters. Arches of the M-shaped parietal posterior bar rounded rather than
342 angular. Apices of M-shaped arch more laterally positioned, occurring either between loci ep2
343 and ep3, or at locus ep3, rather than at locus ep2. Lateral rami of the parietal posterior bar
344 become more anteroposteriorly broad from medial to lateral, rather than being "strap-like" with
345 near-uniform thickness. Locus ep2 positioned on the lateralmost edge within the embayment,
346 oriented medioposteriorly. Lateral bars more strongly developed.

347

348 **Comment** - UKVP 16100 and MNA Pl.1747 have historically been referred to *Pentaceratops*
349 *sternbergii* (e.g. Rowe et al., 1981; Lehman, 1993, 1998; Longrich, 201  014), but are here
350 shown to differ from the historical hypodigm (Lull, 1933; see above). NMMNH P-37880 is
351 described for the first time in Supporting Information 1.

352

353 Morphological features known to indicate relative maturity in chasmosaurines (Horner and
354 Goodwin, 2006, 2008) suggest that referred specimens of aff. *Pentaceratops* n. sp. are not fully
355 mature (MNA Pl.1747, subadult or adult; UKVP 16100, subadult; and NMMNH P-37880,

356 subadult; see Supporting Information 1). Since AMNH 1625 exhibits features supportive of full
357 adult status (see Supporting Information 1), then this raises the possibility that any
358 morphological differences between cf. *P. sternbergii* and aff. *Pentaceratops* n. sp. are
359 ontogenetic rather than taxonomic. This is possibly supported by stratigraphic data as AMNH
360 1625 is thought to have been collected from below the Bisti Bed sandstone, as were MNA Pl.
361 1747, UKVP 16100, and NMMNH P-37880. However, given the close similarity in size and
362 ontogenetic status of AMNH 1625 and MNA Pl.1747, we prefer to consider their morphological
363 differences as taxonomic, although remain open to the ontogenetic hypothesis. Further discovery
364 of mature material with stratigraphic data would help resolve this question.
365

366 ***Navajoceratops sullivanii* gen. et sp. nov.**

367 urn:lsid:zoobank.org:act:765215F5-81E4-4DC9-9900-49BC9B07B3A2
368

369 **Etymology** - *Navajoceratops*, 'Navajo horned face', after the Navajo people indigenous to the
370 San Juan Basin; *sullivanii*, after Dr. Robert M. Sullivan, leader of the SMP expeditions to the San
371 Juan Basin that recovered the holotype.

372

373 **Holotype** - SMP VP-1500; parietal, squamosal fragments, fused jugal-epijugal, other
374 unidentified cranial fragments. Collected in 2002 by Robert M. Sullivan, Denver W. Fowler,
375 Justin A. Spielmann, and Arjan Boere.

376

377 **Locality and Stratigraphy** - SMP VP-1500 was collected from a medium brown-grey mudstone
378 at SMP locality 281 ("Denver's Blowout"), Ahshislepah Wash, San Juan Basin, New Mexico
379 (Sullivan, 2006; detailed locality data available on request from NMMNH). The locality occurs
380 in the lower part of the Hunter Wash Member of the Kirtland Formation (Fig. 2), ~ 43 m
381 stratigraphically above the uppermost local coal, and ~ 6 m stratigraphically above the top of a
382 prominent sandstone thought to represent the Bisti Bed (SMP locality 396; "Bob's Bloody
383 Bluff"; Sullivan, 2006). Hence SMP VP-1500 occurs stratigraphically higher than specimens
384 referred to cf. *Pentaceratops sternbergii* and aff. *Pentaceratops* n. sp. which all occur below the
385 Bisti Bed sandstone.

386

387 Most elements of SMP VP-1500 were collected as weathered surface material, with the
388 exception of the parietal, which was only partly exposed and required excavation. The parietal
389 was preserved dorsal-side up with the median bar broken and displaced ~ 10 cm anteriorly (see
390 Fig. S4), and the distal part of the right ramus of the posterior bar broken and displaced ~ 20 cm
391 posterolaterally.

392

393 **Diagnosis** - Can be distinguished from aff. *Pentaceratops* n. sp. by the following characters:
394 Lateral rami of the parietal posterior bar meet medially at a more acute angle (~60°, rather than
395 87 or ). Median embayment of the parietal posterior bar especially deep, extending anterior to
396 the posteriormost extent of the parietal fenestrae (which consequently overlap anteroposteriorly
397 slightly with ep2).

398 **Description**

399

400 **Parietal** - The parietal (Fig. 4) is missing the lateral bars and most of the anterior end, but is
401 otherwise relatively complete. Deep vascular canals are visible across the dorsal and ventral
402 surfaces, and are especially well developed on the ventral surface. The posterior and medial
403 borders of both parietal fenestrae are well preserved; enclosing the parietal fenestrae that are
404 large and subangular. Six epiparietal loci are interpreted to occur on the posterior bar, numbered
405 ep1-3 on each side.

406

407 The preserved portion (~60%) of the median bar measures 37.4 cm in length, and tapers
408 anteriorly, measuring 4.1 cm wide at the anteriormost end. The dorsal and ventral surfaces of the
409 median bar are convex, with lateral margins of the median bar tapering to give a lenticular cross
410 section. These tapering lateral edges broaden posteriorly. The dorsal surface bears no prominent
411 medial crest, ridge, or bumps (such features are restricted to the anteriormost third of the median
412 longitudinal bar in other chasmosaurines; e.g. *Anchiceratops*, Brown, 1914, Mallon et al., 2011;
413 "*Torosaurus*" *utahensis*, Gilmore, 1946; "*Torosaurus*" sp., Lawson, 1976; "*Titanoceratops*",
414 Longrich, 2011; *Triceratops*, Hatcher et al., 1907; see discussion in Supporting Information 1 on
415 "*Bravoceratops*", Wick and Lehman, 2013). Two fragments found during excavation may
416 represent parts of the anterior end of the median bar. The largest fragment bears parallel vascular

417 traces along its length, suggesting it is indeed part of the midline of the anterior end of the
418 parietal.

419

420 The median bar and lateral rami of the posterior bar form a Y-shape, with the rami of the
421 posterior bar meeting at an angle of 60° , forming a deep U-shaped median embayment that
422 incises 13.2 cm anterior to the posteriormost extent of the parietal fenestrae. The lateral rami are
423 slightly wavy rather than straight, and form an M-shape with the curved apices of the M
424 occurring between epiparietal loci ep2 and ep3. The lateral rami of the posterior bar vary in
425 anteroposterior thickness, being relatively thick at the contact with the median bar (R: 11.5 cm;
426 L: 12.8 cm), reaching their narrowest point slightly medial of the apex (R: 9.37 cm; L: 9.17 cm),
427 broadening at the apex (R: 20.2 cm; L: 20.0 cm), then narrowing again laterally towards the
428 contact with the squamosal.

429

430 There are two raised areas on either side of the anterior central margin of the posteromedial
431 embayment. During excavation, the lateral rami bore an especially thick concretion in this area,
432 suggesting bone underneath the surface (see Fig. S4); however, if present, all of this bone was
433 lost during preparation. A very similar raised area is considered as representing ep1 in
434 *Utahceratops* referred specimen UMNH VP 16671 (Sampson et al., 2010). This raised area is
435 also considered as an attachment point of ep1 in aff. *Pentaceratops* n. sp. specimen UKVP 16100
436 and aff. *P. sternbergii* specimen SDNHM 43470, and is the attachment site for a fused outwardly
437 turned ep1 in specimens MNA Pl.1747, and the left side of AMNH 1625. Therefore it is
438 tentatively suggested that these raised areas are the attachment sites for ep1. Both the left and
439 right ep2 are preserved imperceptibly fused to the posterior bar and project posteromedially into
440 the embayment, almost touching medially. Ep2 on both sides is a rounded D-shape, rather than
441 triangular. There is no evidence of ep3, which might be expected to occur at the lateralmost
442 edges of the lateral rami. However, although ep3 is typically reconstructed as occurring in this
443 position in *Pentaceratops sternbergii* (e.g. Lehman, 1998), only AMNH 1624 and 1625 actually
444 preserve an ep3, and in these specimens it abuts or straddles the squamosal-parietal margin
445 (although see notes on MNA Pl.1747 in Supporting Information 1). An isolated D-shaped frill
446 epioossification (Fig. S5) was recovered adjacent to the parietal during excavation of SMP VP-

447 1500. It is unlike the spindle-shaped or triangular episquamosals, and so may be an unfused
448 ep1 or ep3.

449

450 **Squamosal** - SMP VP-1500 includes pieces of at least one squamosal (probably a left), but most
451 of these are too small and fragmentary to impart much morphological knowledge. The two
452 largest fragments are shown in Figure S6. The first fragment (Fig. S6A, B) is roughly triangular
453 in shape and preserves part of the lateral margin, which is thicker than the more medial area.
454 Two episquamosals are preserved fused to the lateral margin. Both episquamosals are trapezoidal
455 or D-shaped. The second large fragment (Fig. S6C, D) is also triangular, but is narrower than the
456 first fragment and as such might be part of the distal blade of the squamosal. Few features are
457 diagnostic on the second fragment, although a relatively complete straight edge may represent
458 the medial margin where the squamosal articulates with the parietal. Both of the large fragments
459 exhibit the woven, vascularized surface texture typical of ceratopsid skull ornamentation.

460

461 **Jugal / Epijugal or Episquamosal** - A ~10 cm fragment (SMP VP-1813) bearing a pointed
462 epioffification possibly represents the ventral margin of a fully fused right jugal, quadratojugal,
463 and epijugal (Fig. S7). It was collected as float from the same locality as SMP VP-1500 and
464 possibly pertains to the same individual. The epijugal is relatively stout, but not unusually so, nor
465 is it especially long or pointed ("long" and "hyperlong" were character states of the epijugal for
466 character 50 of Sampson et al., 2010). An alternative identification of this element is a large
467 episquamosal. Regardless, the specimen is not especially diagnostic.

468

469 ***Terminocavus sealeyi* gen. et sp. nov.**

470 urn:lsid:zoobank.org:act:1B71F56A-B196-4BFA-B75B-C6680F1255CA

471

472 **Etymology** - *Terminocavus*, 'closing cavity' after the nearly-closed parietal embayment; *sealeyi*
473 after Paul Sealey who discovered the holotype specimen.

474

475 **Holotype** - NMMNH P-27468; parietal, jugal, epijugal, partial quadratojugal, partial sacrum,
476 vertebral fragments. Collected in 1997 by Paul Sealey.

477

478 **Locality and Stratigraphy** -. NMMNH P-27468 was collected from a grey siltstone beneath a
479 white channel sandstone (locality NMMNH L-3503; precise locality data available from
480 NMMNH upon request) in the middle of the Hunter Wash Member, stratigraphically
481 intermediate between ash 3 (75.02 ± 0.13 Ma) and ash 4 (74.57 ± 0.62) (Fowler, 2017). Although
482 in Fig. 1 NMMNH L-3503 appears to be approximately halfway between these radiometrically
483 dated horizons, it occurs in a topographic high between Hunter Wash and Alamo Wash, placing
484 it stratigraphically closer to ash 4. Trigonometric calculations place the locality at ~83 m
485 stratigraphically above ash 2, and ~48 m stratigraphically below ash 4 (based on a northeast dip
486 of 1°). This agrees quite well with Bauer (1916) who published a thickness of 1031 feet (314 m)
487 for the Hunter Wash Member (then called the Lower Shale Member) at Hunter Wash itself.
488 However, in their description of the ashes, Fassett and Steiner (1997) suggest that the ashes are
489 separated stratigraphically by only ~45 m. This would appear to be an underestimate, based on
490 both Bauer (1916) and on the fact that ash 4 is ~130 ft (40 m) topographically higher than ash 2,
491 and ~5 km NE (basinwards, parallel to 1-3° dip).

492

493 It is worth mentioning that the locality is only ~0.6 km SE of another ash (JKR-54) that was
494 dated by Brookins and Rigby (1987). The large margin of error for their K / Ar date of 74.4 ±
495 2.6 Ma (sanidine) places it within the expected range based on the more precise Ar / Ar
496 recalibrated dates of Fassett and Steiner (1997; recalibrations by Fowler, 2017). Although the K /
497 Ar date of Brookins and Rigby (1987) is imprecise and not really usable, the JKR-54 horizon
498 would be useful to resample in future San Juan Basin research.

499

500 **Comment** - NMMNH P-27468 has only previously been mentioned in an abstract by Sealey et
501 al. (2005) where it was identified as an aberrant specimen of *Pentaceratops sternbergii*.
502 NMMNH P-27468 is the only diagnostic chasmosaurine specimen from the middle or upper part
503 of the Hunter Wash Member of the Kirtland Formation; other Kirtland Formation chasmosaurine
504 specimens collected by C.H. Sternberg in the 1920s (described by Wiman, 1930; including the
505 holotype of "*Pentaceratops fenestratus*"; see Supporting Information 1) are mostly undiagnostic
506 or fragmentary, and lack detailed locality and stratigraphic data.

507

508 **Diagnosis** - Differs from *Navajoceratops* holotype SMP VP-1500 by the following characters:
509 Posterior bar flattened and plate-like (i.e. not bar-like). Lateral rami of the parietal posterior bar
510 strongly expanded anteroposteriorly both medially and laterally. Maximum anteroposterior
511 thickness of the posterior bar ~35% of the parietal maximum width (compared with <3% in
512 *Navajoceratops* and ~19-30% in aff. *Pentaceratops* n. sp.). Median embayment of the posterior
513 bar narrower and more notch-like. Parietal fenestrae subrounded rather than subangular.

514 **Description**

515

516 **Parietal** - The parietal of NMMNH P-27468 (Fig. 5) is missing ~50% of the anterior end, but is
517 otherwise relatively complete forming a rounded-M or heart-shape reminiscent of later occurring
518 chasmosaurines such as the holotype of "*Torosaurus gladius*" YPM 1831. The parietal is not
519 formed of obvious narrow bars as seen in stratigraphically older chasmosaurines, rather, it is
520 expansive, flat, and more plate-like. The parietal is comparatively thin (typically ~1-2 cm in
521 thickness), although this may reflect postburial compression. Bone surfaces have a thin
522 concretion of sediment that obscures most fine surface detail, although shallow vascular canals
523 are visible on some areas of the dorsal surface. The ventral surface is mostly either obscured by
524 concreted sediment or damaged, but in some places longitudinal vascular canals can be observed,
525 similar to those in *Navajoceratops* and other chasmosaurines. The posterior and medial borders
526 of both parietal fenestrae are well preserved. However, the posterior, median, and lateral bars are
527 expanded at the expense of the parietal fenestrae, which are thus slightly reduced in size relative
528 to stratigraphically preceding chasmosaurines. The fenestrae are subrounded in shape,
529 comparable to derived chasmosaurines such as *Anchiceratops* and triceratopsins, but unlike the
530 subangular- or angular-shaped fenestrae of stratigraphically older chasmosaurines.

531

532 The preserved portion of the median bar measures 31.1 cm in length and tapers anteriorly. The
533 dorsal surface of the midline bar is convex, lacking a medial crest, ridge, or bump. The ventral
534 surface of the median bar is flat to weakly convex. The lateral margins of the median bar taper to
535 give a lenticular cross section. The median bar bears small flanges that run along both the lateral
536 edges, and are directed laterally into the fenestrae. Although broken anteriorly, the flanges are

537 more laterally extensive than in *Navajoceratops* and other stratigraphically preceding
538 chasmosaurines.

539

540 The left and right lateral bars are incomplete and probably represent only ~50% of their original
541 length. The preserved portions are of nearly equal antero-posterior length, and are almost
542 parallel, suggesting the anterior end of the parietal was slightly narrower than the posterior, or at
543 least narrowed in its midline (as in *Pentaceratops sternbergii* MNA Pl. 1747; Rowe et al.,
544 1981). Both lateral bars are convex dorsally, and flat to weakly convex ventrally. Dorsoventral
545 thickness decreases laterally such that they are moderately lenticular in cross section. The lateral
546 edges which articulate with the squamosal are thin and plate-like. Each lateral bar bears a
547 relatively large (diameter ~1 mm) blood vessel groove that runs anteroposteriorly to the lateral
548 rami of the posterior bar. However, like other blood vessel traces on this specimen, the grooves
549 are shallow and difficult to trace onto the lateral rami.

550

551 The lateral rami of the posterior bar meet medially at an angle of 73° , which is steeper than in
552 stratigraphically preceding chasmosaurines, however, it is awkward to measure as the lateral
553 rami are curved rather than being straight lines (see Supporting Information Fig. S1 for details of
554 measurement). The lateral rami are anteroposteriorly thicker than those of *Utahceratops*,
555 *Pentaceratops*, and *Navajoceratops*, but less so than in *Anchiceratops*. They vary in
556 anteroposterior thickness from medial to lateral, being at their narrowest medially, at the contact
557 with the median bar (R: 13.2 cm; L: 12.2 cm), reaching their broadest point at the apex (R: 23.4
558 cm; L: 23.6 cm), then narrowing again laterally towards the contact with the squamosal.

559

560 The median embayment is narrower than in preceding chasmosaurines, forming a notch that is
561 almost enclosed by the first pair of epiparietals. The embayment does not extend anterior to the
562 posteriormost border of the parietal fenestrae. The anterior edge of the embayment is notably
563 thickened, similar to that seen in *Utahceratops gettyi* specimen UMNH VP-16671 (Sampson
564 et al., 2010). On the left lateral ramus, the thickened border of the embayment is extended
565 continuously in a posterior direction helping form the anteromedial edge of the left ep1 (see
566 below). However, on the right side, the thickened border is discontinuous, forming a small
567 prominent bump below the main part of the ep1. A similar double bump at the ep1 locus is seen

568 on the left side of  *U. gettyi* specimen UMNH VP-16671 where it is labeled as a "dorsal
569 parietal process", with the right side continuous (Sampson et al., 2010).

570

571 Five epiparietals are preserved fused to the parietal, with at least one missing, which is therefore
572 probably representative of three pairs of epiparietals (ep1-3) as is typical for chasmosaurines.

573 The medialmost pair of epiparietals is considered to represent locus  ep1, and is positioned on the
574 medial margin of the median embayment, as it is in specimens referred to cf. *Pentaceratops*

575 *sternbergii*, aff. *Pentaceratops* n. sp., and cf. *Utahceratops gettyi*. The left ep1 is triangular,

576 whereas the right ep1 was probably also triangular but is missing the distal tip, instead exhibiting
577 a shallow, possibly pathological trough. This is of interest because if the right ep1 tip was present

578 then the epiparietals are close enough (separated by only ~5 mm) that they would probably have
579 touched (especially if they bore keratinous sheaths). Ep1 is the only epiparietal that does not lie

580 flat within the plane of the parietal. Both left and right ep1 are deflected slightly dorsally, similar
581 to the ep1 on the right side of cf. *Pentaceratops sternbergii* specimen AMNH 1625 and parietal

582 fragments referred to "*Pentaceratops aquilonius*" (CMN 9814; Longrich, 2014; see Supporting
583 Information  1). Ep2 is preserved on both sides, although it is broken slightly on the right side.

584 Ep2 is triangular and projects posteromedially from the posterior bar, laying flat within the plane
585 of the rest of the parietal. Ep3 is only preserved on the left side where it is fused to the posterior

586 bar. There is an empty space at locus ep3 on the right side. Ep3 is more D-shaped than triangular
587 and projects posteriorly laying flat within the plane of the rest of the parietal. There is no

588 indication of an epiparietal more lateral than the ep3 locus, despite there probably being enough
589 space for an additional epiossification (as seen in some specimens of *Anchiceratops*; Mallon et

590 al., 2011).

591

592 **Right Squamosal** - The preserved right squamosal (Fig. S8) comprises a nearly complete
593 anterior end (including the narrow processes that articulate with the quadrate and exoccipital),
594 the anteriormost episquamosal, and most of the medial margin of the squamosal blade. Almost
595 the entire lateral margin and the posterior end are not preserved. The medial margin is robust and
596 forms what is termed the squamosal bar. Although incomplete, the squamosal bar is long enough
597 to suggest that the squamosal itself was elongate, as seen in most adult chasmosaurines, rather
598 than short and broad, as seen in young chasmosaurines (Lehman, 1990; Scannella and Horner,

599 2010); the preserved portion measures 83 cm in length, and the conservative reconstruction (Fig.
600 S8) is 94 cm. Lateral to the squamosal bar, the squamosal dorsoventrally thins and is broken. The
601 single preserved episquamosal is fused to the anterolateral border and represents the anteriormost
602 episquamosal. It is common in chasmosaurine specimens for the anteriormost episquamosal to be
603 fused to the anterolateral border of the squamosal, suggesting that it is one of the first
604 episquamosals to fuse through ontogeny (Godfrey and Holmes, 1999). The episquamosal is very
605 rugose and not obviously triangular in shape.

606

607 **Jugal / Epijugal** - NMMNH P-27468 also has a fused left jugal, epijugal, and quadratojugal
608 (Fig. S9). The orbital margin of the jugal is not preserved, and only a little remains of the
609 anterior process. The ventral part of the jugal is tongue shaped, terminating in the
610 indistinguishably fused epijugal. The epijugal is large and robust, but not notably long. Only the
611 ventralmost part of the quadratojugal is preserved, fused to the epijugal. Similar to the parietal,
612 surface texture is partly obscured by sediment, but some shallow vascular grooves are visible.

613

614 **Chasmosaurinae sp. "taxon C"**

615

616 **Material** - NMMNH P-33906; parietal median bar, epijugal, indeterminate skull fragments,
617 vertebral fragments.

618

619 **Locality and Stratigraphy** - NMMNH P-33906 was collected in 2001 by Thomas E.
620 Williamson at NMMNH locality L-4715, from the De-na-zin Member of the Kirtland Formation
621 at South Mesa, San Juan Basin, New Mexico (Figure 1, 2; precise locality coordinates are
622 available from NMMNH). Two radiometrically dated ashes (at Hunter Wash, ~10 km to the
623 northwest) bracket the age of the De-na-zin Member of the Kirtland Formation. Ash H (73.83 +/-
624 0.18 Ma) occurs less than 5 m above the basal contact of the De-na-zin Member with the
625 underlying Farmington Member (Fassett and Steiner, 1997; Sullivan et al., 2005). Ash J (73.49
626 +/- 0.25 Ma) occurs 4.9 m below the upper contact of the De-na-zin Member with the overlying
627 Ojo Alamo Sandstone (Fassett and Steiner, 1997; both radiometric dates recalibrated by Fowler,

628 2017, from Fassett and Steiner, 1997). NMMNH P-33906 therefore occurs between 73.83 Ma
629 and 73.49 Ma.

630

631 **Comment** - Although fragmentary, the previously undescribed specimen NMMNH P-33906
632 represents one of the few records of chasmosaurines from the De-na-zin Member of the Kirtland
633 Formation, and preserves the median bar of the parietal, which is diagnostic enough to permit
634 comparison to other chasmosaurines.

635

636 **Diagnosis** - Differs from *Utahceratops*, cf. *Pentaceratops sternbergii*, aff. *Pentaceratops* n. sp.,
637 *Navajoceratops*, and *Terminocavus* by the following characters: Median bar bears extensive
638 lateral flanges extending into the parietal fenestrae. Flanges are extensive such that the cross
639 section of the median bar is a broad flat lenticular shape, rather than being narrow and strap-like.

640 **Description**

641 **Parietal** - The preserved portion measures 31 cm in length and represents most of the parietal
642 median bar (Fig. 6). As with many vertebrate fossils from the De-na-zin Member, NMMNH P-
643 33906 has a thin covering of pale-colored concretion, and many adhered patches of hematite.
644 This obscures fine surface details, although most morphological features can be discerned. The
645 dorsal side is gently curved laterally, but otherwise has no obvious surface features (i.e. it lacks a
646 prominent medial crest, ridge, or bumps). In contrast, the ventral side bears a raised central bar
647 with lateral flanges which extend laterally into the fenestrae. The lateral flanges are much more
648 strongly developed than in *Pentaceratops*, *Navajoceratops*, and *Terminocavus*, but overall the
649 median bar is less broad than in *Anchiceratops* (with the possible exception of referred specimen
650 CMN 8535; Sternberg, 1929; Mallon et al., 2011). The cross section is different at either end of
651 the median bar, which is used to infer orientation. At the inferred anterior end, the cross section
652 is concave-convex, with a shallowly concave ventral side. At the inferred posterior end, the cross
653 section is biconvex and lenticular in shape. In other chasmosaurines the anterior end of the
654 parietal median bar can be slightly concave ventrally (e.g. aff. *Pentaceratops* n. sp., MNA Pl.
655 1747; Rowe et al., 1981; *Chasmosaurus belli* holotype CMN 491; Hatcher et al., 1907), so we
656 have identified the ventrally concave end as anterior in NMMNH P-33906. The median bar is
657 expanded laterally at both ends; this is typical of chasmosaurine median bars, but is important as

658 it helps constrain the size that the fenestrae would have been. Lateral expansion is more notable
659 at the posterior end, although this is probably due to the anterior end being less complete. At its
660 narrowest point, the median bar is 9 cm wide.

661

662 **Epijugal** - NMMNH P-33906 includes an epijugal which is fused to the jugal (and probably the
663 quadratojugal). However, the jugal and quadratojugal are almost entirely missing, with the only
664 remaining parts being small pieces that are fused to the base of the epijugal. The epijugal
665 measures ~10 cm g, and is moderately pointed in shape.

666

667 ***Ontogenetic assessment***

668 Significant morphologic change through ontogeny can strongly affect the phylogenetic
669 placement of a specimen (Campione et al., 2013). It is therefore important to determine the
670 ontogenetic status of new specimens so that appropriate comparisons can be made. No limb
671 bones are preserved with the new specimens described here, so the age in years of individuals
672 cannot be determined. Ontogenetic change in cranial morphology is not well studied in non-
673 triceratopsin chasmosaurines (although see Lehman, 1997  although it has been intensively
674 studied in the derived chasmosaurine *Triceratops* (Horner and Goodwin, 2006; 2008; Scannella
675 and Horner, 2010; 2011; Farke, 2011; Horner and Lamm, 2011; Longrich and Field, 2012;
676 Maiorino et al., 2013). Base  is prior work, a combination of ontogenetically variable cranial
677 features (size, sutural fusion, shape and fusion of epiossifications, frill surface texture, squamosal
678 elongation) are here hypothesized to also be indicative of subadult or adult status in SMP VP-
679 1500, NMMNH P-27468, and NMMNH P-33906.

680

681 **Size** - Size is an unreliable measure of maturity, as individual body size variation has been
682 shown to be considerable in some dinosaurs (Sander and Klein, 2005; Woodward et al., in press).
683 Nevertheless, large size is often used as a rough gauge of maturity (and conversely, small size of
684 immaturity), and this is a reasonable approach when used in combination with other
685 morphological features that are ontogenetically informative. The holotype parietal of
686 *Navajoceratops*, SMP VP-1500, is of comparable size to other specimens of *Pentaceratops* and
687 related chasmosaurines (Fig. 7). The holotype parietal of *Terminocavus*, NMMNH P-27468, was

688 described as small in the abstract by Sealey et al. (2005), but it is only slightly smaller than
689 specimens of *Pentaceratops* (Fig. 7). The squamosal of NMMNH P-27468 has a reconstructed
690 length of 94 cm, which is slightly smaller than MNA Pl.1747 (127 cm, J., Fry pers. comm.), but
691 larger than the juvenile aff. *Pentaceratops* SDMNH 43470 (77 cm; Diem and Archibald, 2005);
692 the only other complete *Pentaceratops* squamosal is AMNH 1624, which is undescribed. The
693 jugal of NMMNH P-27468 is only slightly smaller than *Utahceratops* referred specimen UMNH
694 VP-12198 (Fig. 7), which is a large and aged individual (fused frill epiossifications that are
695 mediolaterally elongate, spindle-shaped, and blunt; resorbed postorbital horns; fused epijugal;
696 Sampson et al., 2010; pers. obs.). The median bar of NMMNH P-33906 (Taxon C) is much
697 broader than the median bar of any specimen of *Pentaceratops*, *Navajoceratops*, or *Utahceratops*
698 (Fig. 7). At 10 cm long, the epijugal of NMMNH P-33906 is also of similar size to the epijugal
699 of UMNH VP-12198.

700

701 **Cranial fusion** - Fusion of cranial sutures is often used as an indicator of maturity, but this is
702 fraught with problems as the timing of suture closure may not be consistent between taxa (for
703 example, the nasals and epinasal fuse relatively early in young subadult specimens of
704 *Triceratops horridus*, whereas the congeneric *T. prorsus* these elements fuse in late
705 subadulthood, to adulthood; Horner and Goodwin, 2006; 2008; Scannella et al., 2014). However,
706 similar to size, degree of cranial fusion can be informative when used in conjunction with other
707 data. Fusion of the epijugal to the jugal and quadratojugal is observed in all three of the new
708 specimens (albeit based only a tentative identification in SMP VP-1500). In *Triceratops*, fusion
709 of the epijugal to the jugal and quadratojugal occurs relatively late in ontogeny, as a subadult or
710 adult (Horner and Goodwin, 2008). A similar survey has not been conducted for more basal
711 chasmosaurids, although the small-sized purportedly immature aff. *Pentaceratops* specimen
712 SDMNH 43470 (Diem and Archibald, 2005) includes an unfused jugal and quadratojugal, but no
713 epijugal as it was unfused and not recovered with the rest of the skull. Larger specimens of
714 *Pentaceratops* and related taxa exhibit fusion of the epijugal to the jugal (holotype AMNH 6325,
715 AMNH 1625, UKVP 16100; J. Fry, pers. comm.). From this, fusion of the epijugal in NMMNH
716 P-27468 and P-33906 (also, tentatively SMP VP-1500; Figs. S7, S9) is considered supportive of
717 subadult or adult status.

718

719 **Frill epioossifications** - Shape and fusion of frill epioossifications varies through ontogeny in
720 chasmosaurines. In *Triceratops*, the episquamosals fuse first, followed by the epiparietals
721 (Horner and Goodwin, 2008).

722

723 Godfrey and Holmes (1995) suggest that in *Chasmosaurus*, fusion of the episquamosals begins at
724 the anterior end of the squamosal, and proceeds posteriorly through ontogeny. This pattern is
725 similarly observed in *Pentaceratops* and related taxa, notably in aff. *Pentaceratops* n. sp. MNA
726 Pl. 1747 (Rowe et al., 1981) and aff. *P. sternbergii* SDMNH 43470 (Diem and Archibald, 2005)
727 in which only the anterior episquamosals are fused. Fusion of episquamosals in SMP VP-1500
728 (probably from the middle of the squamosal; Fig. S6) supports the identification of this specimen
729 as a subadult or adult. NMMNH P-27468 only preserves the anteriormost fused episquamosal
730 (the rest of the squamosal lateral border is damaged; Fig. S8), so it is consistent with subadult or
731 adult status, but this cannot be confirmed without additional material or data on the timing of the
732 fusion of the first episquamosal.

733

734 The order of epiparietal fusion is not studied in basal chasmosaurines and a specific pattern has
735 not yet been identified for *Triceratops*. However, a survey of specimens referred to
736 *Pentaceratops* (and related taxa) reveals a general pattern where ep1 fuses first, followed by ep2,
737 then ep3. Ep1 is fused in the four largest specimens (cf. *P. sternbergii* AMNH 1625, aff.
738 *Pentaceratops* n. sp. MNA Pl. 1747, UKVP 16100, and cf. *Utahceratops* UMNH VP-16671 and
739 16784; Fig. 7), but is unfused in the aff. *P. sternbergii* small specimen SDMNH 43470, and in
740 newly described parietal fragment NMMNH P-37890 (see Supporting Information 1). Ep2 is
741 fused in AMNH 1625, MNA Pl. 1747, UMNH VP-16671 and 16784, but not in UKVP 16100.
742 Ep3 is fused in AMNH 1625, UMNH VP VP-16671 and 16784, and possibly MNA Pl. 1747 (see
743 Supporting Information 1), but is unfused in UKVP 16100. The *Navajoceratops* holotype SMP
744 VP-1500 has fused ep1 (probable) and ep2, but ep3 is unfused hence it exhibits a state of fusion
745 between UKVP 16100 and MNA Pl.1747 (or AMNH 1625), and on this basis could be
746 considered subadult. The holotype of *Terminocavus* (NMMNH P-27468) has fused ep1 and ep2
747 on both sides; ep3 is fused only on the left side, with an open space on the right side at the ep3
748 locus. On this basis, NMMNH P-27468 should be considered subadult or adult.

749

750 Regarding shape, all *Triceratops* frill epiossifications develop from being triangular-shaped with
751 pointed apices and short bases in juveniles, to spindle shaped with blunt apices and elongate
752 bases in adults (Horner and Goodwin, 2006, 2008). Similar patterns exist in the episquamosals of
753 more basal chasmosaurines with probable juvenile and immature specimens of *Chasmosauri*
754 *Agujaceratops* (Lehman, 1989) and aff. *Pentaceratops* (SDMNH 43470; Diem and Archibald,
755 2005), exhibiting more short-based, pointed episquamosals. The episquamosals of
756 *Navajoceratops* holotype SMP VP-1500 (Fig. 11) are spindle shaped, and blunt with elongate
757 bases, consistent with a subadult or adult condition. The *Terminocavus* holotype, NMMNH P-
758 27468, only has the anteriormost episquamosal preserved, which tends to remain triangular and
759 slightly pointed in subadult and adult chasmosaurines, even when more posterior episquamosals
760 develop into spindle shapes. Thus, the triangular shape of the episquamosal of NMMNH P-
761 27468 is not ontogenetically informative. Note that triceratopsins are slightly unusual among
762 chasmosaurines in that their epiparietals and episquamosals are of similar morphology to each
763 other; whereas in *Anchiceratops* and more basal chasmosaurines, the epiparietals take a greater
764 variety of forms. Most notable is that the epiparietals remain large and triangular through to
765 adulthood in *Utahceratops*, cf. and aff. *Pentaceratops*, *Navajoceratops*, and particularly
766 *Terminocavus* and *Anchiceratops*.

767

768 **Frill surface texture** - The texture of the parietosquamosal frill (and many of the facial bones)
769 has been shown to change ontogenetically in both centrosaurine and chasmosaurine ceratopsids
770 (Sampson et al., 1997; Brown et al., 2009; Scannella and Horner, 2010). Adult ceratopsids are
771 characterized by a distinctive frill texture where indented vascular channels form complex
772 dendritic patterns. This texture gradually develops through ontogeny, with juveniles exhibiting a
773 smooth or "long-grain" bone texture (Sampson et al., 1997; Brown et al., 2009; Scannella and
774 Horner, 2010), which is replaced by a pebbled or pitted texture with shallowly developed
775 vascular traces in young subadults. This is complicated somewhat by recognition that this long-
776 grain texture is associated with rapid growth (Francillon-Vieillot et al., 1990; Sampson et al.,
777 1997) and/or expansion of the frill, as expected in juveniles, but is also seen in some specimens
778 of *Torosaurus* which are reshaping their frills relatively late in ontogeny (Scannella and Horner,
779 2010). The *Navajoceratops* holotype SMP VP-1500 has well developed adult frill texture on
780 both the parietal (Fig. 4) and the squamosal (Fig. S6). In the *Terminocavus* holotype, NMMNH

781 P-27468, the frill texture on the parietal is partially obscured by a thin layer of sediment covering
782 the surface, but can be seen to be pitted with shallow vascular canals. The same texture is visible
783 on the dorsal surface of the squamosal. This suggests that NMMNH P-27468 is not yet fully
784 mature and may be considered a young subadult. Surface texture is not discernible on Taxon C
785 specimen NMMNH P-33906.

786

787 **Squamosal elongation** - In juvenile chasmosaurines, the squamosal is anteroposteriorly short,
788 similar to the condition in adult centrosaurine ceratopsids and more basal neoceratopsians
789 (Lehman, 1990; Goodwin et al., 2006; Horner and Goodwin, 2006; Scannella and Horner, 2010) 
790 In chasmosaurines, the squamosal elongates through ontogeny, although the timing of the
791 elongation varies phylogenetically (Lehman, 1990; Scannella and Horner, 2010). The derived
792 taxon *Triceratops* has been shown to retain an anteroposteriorly short squamosal until relatively
793 late in ontogeny (Scannella and Horner, 2010), whereas in *Chasmosaurus* and *Pentaceratops*
794 (albeit based on more limited data) it would appear that elongation occurs at smaller body sizes
795 (inferred to be younger; Lehman, 1990). Although the squamosal of SMP VP-1500 comprises
796 only fragments, one fragment (Fig. S6 C, D) might represent the more bladed posterior end,
797 which would be supportive of a subadult or adult status. The squamosal of NMMNH P-24768 is
798 incomplete, but enough remains to show that it was relatively elongate, supporting a subadult or
799 adult status.

800

801 **Geometric morphometric analysis**

802 Results of the geometric morphometric Principal Components Analysis (PCA) on chasmosaurine
803 parietals are presented in Fig. 8. PC 1 (x-axis) accounts for 50.5% of variation, and assesses
804 depth of the median embayment from shallow (negative) to deep (positive), and orientation of 
805 ep1 from mediolateral (negative) to anteroposterior (positive); PC 2 (y-axis) accounts for 19.0%
806 of variation and assesses lateral expansion of the ep1 locus, shape of the posterolateral corner of
807 the parietal, and overall anteroposterior length.

808

809 Specimens previously assigned to the same taxon largely cluster into groups, with
810 "*Chasmosaurus russelli*", *C. belli*, and *Anchiceratops* specimens all clustering together.

811 Specimens referred to cf. *Pentaceratops* n. sp (MNA Pl.1747 and UKVP 16100) are separated
812 from cf. *P. sternbergii* specimen AMNH 1625, justifying their consideration as different taxa.

813 The new taxa, *Navajoceratops* and *Terminocavus*, plot as intermediate between these
814 stratigraphically preceding chasmosaurines and the stratigraphically higher *Anchiceratops*.

815

816 Two perpendicular morphological trends correlate with the stratigraphic occurrence of taxa and
817 match the lineages proposed by Lehman (1998). From stratigraphically oldest to youngest,

818 "*Chasmosaurus russelli*", *C. belli*, and *Vagaceratops irvinensis* occupy the negative end of the
819 PC 1 axis, and are spread down the PC 2 axis in stratigraphic order, showing little variation

820 along the PC 1 axis. This demonstrates progressive expansion of the ep1 locus, concentrating ep2

821 and ep3 to the lateralmost corner of the parietal. The trend in *Chasmosaurus* is contrasted by a

822 second group (comprising *Utahceratops*, *Pentaceratops*, *Navajoceratops*, *Terminocavus*, and

823 *Anchiceratops*) which is mostly distributed along the PC 1 axis in stratigraphic order, and shows

824 relatively little variation on PC 2. This group exhibit progressive deepening and eventual closure

825 of the median embayment, an increasingly steep angle of the ep1 locus, and anteroposterior

826 expansion of the posterior bar.

827

828 There are some inconsistencies in that *Kosmoceratops* does not plot close to *Vagaceratops* on the
829 PC 1 axis (although it is very close on the PC 2 axis), despite being recovered as sister taxa in

830 most phylogenetic analyses (Sampson et al., 2010; Mallon et al., 2014; and this analysis, see

831 be ). Similarly, aff. *Pentaceratops* n. sp. specimen MNA Pl.1747 plots more negatively on the

832 PC 2 axis than other specimens within the *Pentaceratops* grouping (although it is very similarly

833 placed along the PC 1 axis). These issues might be a reflection of potential problems with the

834 input data concerning these two specimens. First, for *Kosmoceratops*, points were plotted on to

835 the dorsal view provided by Sampson et al. (2010). However, this is not completely

836 perpendicular to the parietal surface. Consultation of photographs of skull casts shows that the

837 parietal posterior bar of *Kosmoceratops* is not as medially embayed as it appears in the image

838 used (this being an artifact of slight arching of the parietal). Hence it is predicted that upon

839 reanalysis of a perpendicular photograph, *Kosmoceratops* might plot more negative along PC 1

840 (x axis), closer to other members of the *Chasmosaurus* clade. Second, aff. *Pentaceratops* n. sp.

841 MNA Pl.1747 may require revision if the redescription of J. Fry indeed identifies that ep3 is

842 fused to the posterolateral corners of the parietal. This would reduce the anteroposterior offset of
843 the lateralmost margin of the parietal, bringing the morphology of MNA Pl.1747 more similar to
844 UKVP 16100.

845

846 **Phylogenetic analysis**

847 Phylogenetic analysis recovers *Navajoceratops sullivanii* and *Terminocavus sealyi* as close
848 relatives of both *Pentaceratops* and *Anchiceratops*. The initial analysis was run using the
849 amended matrix of Mallon et al. 2014 (see Supporting Information 2), with only *Mojoceratops*
850 *perifania* excluded because this is considered a junior synonym of *Chasmosaurus russelli*
851 (Maidment and Barrett, 2011; Mallon et al., 2014). This resulted in 6 most parsimonious trees (L
852 = 319 steps; CI = 0.72; RI = 0.79). The strict consensus tree (Fig. 9A) supports a monophyletic
853 Chasmosaurinae, and recovered *Navajoceratops* and *Terminocavus* as successive sister taxa to
854 *Anchiceratops*, *Arrhinoceratops*, and Triceratopsini. However, [*Pentaceratops* + *Utahceratops*]
855 + [*Coahuilaceratops* + *Bravoceratops*] is recovered as sister group to this clade, rather than a
856 direct relationship between *Pentaceratops* and *Navajoceratops*, as would have been predicted
857 based on parietal morphology. A basal *Chasmosaurus* clade was separated from a [*Vagaceratops*
858 + *Kosmoceratops*] clade by *Agujaceratops*.

859

860 Reanalysis 1 additionally excluded nomen dubium *Bravoceratops*, and *Agujaceratops* because it
861 is coded partly from juvenile material and specimens that may not be referred to the taxon (see
862 Supporting Information 1). This yielded 6 most parsimonious trees (L = 310 steps; CI = 0.72; RI
863 = 0.79). The strict consensus tree (Fig. 9B) maintains the relationship of [*Utahceratops* +
864 *Pentaceratops* + *Coahuilaceratops*] as sister group to [*Navajoceratops* + *Terminocavus* +
865 *Anchiceratops* + *Arrhinoceratops* + Triceratopsini]. The most significant result of reanalysis 1 is
866 the unification of a *Chasmosaurus* clade with [*Vagaceratops* + *Kosmoceratops*]. This is similar
867 to the original description of *Vagaceratops* (*Chasmosaurus*) *irvinensis* (Holmes et al., 2001),
868 where the taxon was considered the most derived (and stratigraphically youngest) form of
869 *Chasmosaurus*, a relationship also recovered in the phylogenetic analysis of Longrich (2014).

870

871 Reanalysis 2 investigated the effect of excluding *Coahuilaceratops* from the dataset because
872 *Coahuilaceratops* is known from very fragmentary material. This yielded 28 most parsimonious
873 trees ($L = 308$; $CI = 0.72$; $RI = 0.79$). The strict consensus tree (Fig. 9C) maintained the basal
874 *Chasmosaurus* clade, but *Utahceratops*, *Pentaceratops*, *Navajoceratops*, *Terminocavus*, and
875 *Anchiceratops* collapsed into a polytomy.

876

877 These analyses support the finding of the morphometric analysis in that the new taxa
878 *Navajoceratops* and *Terminocavus* are morphological intermediates between *Pentaceratops* and
879 *Anchiceratops*, although the absence of a sister group relationship between *Navajoceratops* and
880 *Pentaceratops* is not supportive of evolution by anagenesis. However, this may be due to the
881 way that *P. sternbergii* is coded in this dataset (see below). The topology  reanalysis 1 and 2
882 also supports the proposal of Lehman (1998) that a deep split divides the Chasmosaurinae into
883 two lineages.

884

885 These results match the evolutionary hypotheses based on the stratigraphic positions of taxa, but
886 represent only a first step in the many revisions required of the phylogenetic matrix. Most
887 significant to this study is that in the current matrix, the composite coding of *P. sternbergii*
888 includes specimens that are probably not all referable to the same taxon, e.g. AMNH 6325, 1624,
889 1625, NMMNH P-50000, and those considered here as aff. *Pentaceratops* n. sp. (MNA Pl.1747
890 and UKVP 16100). It is therefore required for these specimens to be coded and analysed as at
891 least three separate taxa, but this action awaits the description of the anterior skull elements of
892 these specimens currently being completed by Joshua Fry. A similar recoding is required for
893 *Agujaceratops*; the immature holotype material should not be used for coding the taxon, as its
894 immature status may affect its phylogenetic positioning (e.g. Campione et al., 2013). Instead,
895 referred specimens UTEP P.37.7.065 (isolated parietal) and TMM 43098-1 (near-complete skull,
896 missing the parietal) should be coded separately. The holotype of *Chasmosaurus russelli* (CMN
897 8800) is in the process of being redescribed (see Campbell  et al., 2013), and will likely need to
898 be moved out of *Chasmosaurus* and coded separately from other referred specimens.
899 *Chasmosaurus belli* referred specimen YPM 2016 is also in the process of being redescribed
900 (Campbell et al., 2015), and will need to be  coded separately as a morphologic intermediate
901 between more typical *C. belli* specimens and *Vagaceratops*. Finally, some recently described

902 chasmosaurine taxa (e.g. *Judiceratops*; *Mercuriceratops*; *Regaliceratops*, and *Spiclypeus*;
903 Longrich, 2013; Ryan et al., 2014; Brown and Henderson, 2015; Mallon et al., 2016) have yet to
904 be coded into the revised matrix, although new taxa known from fragmentary remains may
905 require some reassessment which is beyond the scope of this current work.

906

907 **DISCUSSION**

908 ***Comparisons and discussion of morphological characters***

909 As the holotype specimens are probable subadults or adults, *Navajoceratops* and *Terminocavus*
910 can be appropriately compared with other taxa which are based on putative adults.

911

912 *Navajoceratops* and *Terminocavus* form progressive morphological intermediates between the
913 stratigraphically preceding *Pentaceratops* and succeeding *Anchiceratops*. Although limited in
914 available material, *Chasmosaurinae* sp. "Taxon C" (NMMNH P-33906) exhibits morphology
915 intermediate between the stratigraphically preceding *Terminocavus*, and succeeding
916 *Anchiceratops*. A number of characters of the parietal provide the best means to compare among
917 chasmosaurine taxa.

918

919 **Median embayment of the posterior bar**

920 The median embayment of the posterior bar is one of the most important morphological features
921 in distinguishing chasmosaurine taxa. It is defined by the angle at which the lateral rami meet
922 medially, and the proportion of the posterior bar occupied by the embayment.

923

924 The angle at which the lateral rami of the posterior bar meet medially (see Supporting
925 Information for figures) is comparable in more basal chasmosaurines, but becomes disparate in
926 more derived forms. Within chasmosaurines allied to *Chasmosaurus*, the lateral rami meet at a
927 relatively shallow angle, measuring 87-131° in specimens referred to "*C.  elli*", and 
928 shallowing in stratigraphically successive taxa *C. belli* (149-167°) and *Vagaceratops* (177°). In
929 contrast, the lateral rami meet at a relatively steep angle in *Utahceratops* (75°), cf. *Pentaceratops*
930 *sternbergii* (83°), and aff. *Pentaceratops* n. sp. (87-88°). *Navajoceratops* (60°) and

931 *Terminocavus* (~73°) exhibit angles that are more acute than stratigraphically preceding
932 chasmosaurines, indicating the deepening and enclosing of the median embayment. However, in
933 *Terminocavus* and especially *Anchiceratops*, measurement of the angle of the lateral rami is not
934 straightforward as the lateral rami have become curved and anteroposteriorly expanded.

935

936 The median embayment is restricted to the central 30-50% of the posterior bar in
937 stratigraphically older chasmosaurines such as "*Chasmosaurus russelli*", *Agujaceratops*,
938 *Utahceratops*, and cf. *Pentaceratops sternbergii*. In more derived forms, the apex of the arch
939 formed by each lateral bar migrates towards the lateral margin, broadening the median
940 embayment. In *C. belli*, *Vagaceratops* and (to an extent) *Kosmoceratops*, this occurs
941 concomitantly with an increase in the angle of the lateral bars such that the embayment appears
942 weakened or lost. In contrast, in aff. *Pentaceratops* sp., the angle increases, and the embayment
943 appears deeper. In *Navajoceratops* and *Terminocavus* the embayment is again restricted to the
944 central 30-50% of the posterior bar, mainly because anteroposterior expansion of the posterior
945 bar at the ep3 locus gives the lateral bars a more rounded shape. In *Anchiceratops*, the median
946 embayment is effectively completely closed, with only a shallow depression remaining between
947 left and right ep2.

948

949 In both *Navajoceratops* and *Terminocavus*, the depth of the embayment and close position of ep1
950 and ep2 suggest that in life the embayed area might have been completely enclosed by keratin
951 such that an embayment would not be externally visible. This remains speculative, but might be
952 important when formulating hypotheses as to the display function of the frill ornamentation.

953

954 **Epiparietal Number, shape, size, and orientation**

955 Chasmosaurines typically exhibit three epiparietal loci on each side. Important morphological
956 differences among taxa include shape and size of all epiparietals; position and consequent
957 orientation of ep1 and ep2 relative to the median embayment of the parietal posterior bar;
958 position and orientation of ep3 relative to the posteriormost point of the posterior bar and the
959 articulation with the squamosal.

960

961 Of the new specimens, ep1 is only preserved in *Terminocavus* holotype NMMNH P-27468,
962 where its triangular shape is comparable to cf. *Pentaceratops sternbergii*, aff. *Pentaceratops* n.
963 sp., *Anchiceratops*, and some specimens referred to "*Chasmosaurus russelli*", and unlike the
964 laterally expanded ep1 locus in *C. belli*, *Vagaceratops*, and *Kosmoceratops*. In *Terminocavus*
965 ep1 is only slightly deflected dorsally, comparable to the right side of cf. *P. sternbergii* AMNH
966 1625, and "*P. aquilonius*" referred specimen CMN 9814 (Longrich, 2014), rather than folded
967 over the posterior bar to point anterolaterally (as in the left side of cf. *P. sternbergii* AMNH
968 1625, and aff. *Pentaceratops* n. sp.) or laterally (*Anchiceratops*). Given its phylogenetic position,
969 it might be expected for *Terminocavus* to exhibit an anterolaterally oriented ep1 rather than being
970 only slightly deflected dorsally. It is possible that ep1 folds over anteriorly through ontogeny,
971 and that the condition in NMMNH P-27468 is indicative that it is not fully mature; ontogenetic
972 indicators (see above) suggest a status between young subadult to adult for NMMNH P-27468,
973 which leaves open the possibility that the epiparietals might have folded anteriorly if the
974 individual had survived to later greater maturity. However, different ep1 orientations between
975 left and right sides of the putative adult cf. *P. sternbergii*, AMNH 1625, demonstrates that this
976 character is variable, even in an adult.

977

978 In *Navajoceratops* and *Terminocavus* locus ep1 occurs within the median embayment, as in
979 *Utahceratops*, cf. *Pentaceratops sternbergii* and aff. *Pentaceratops* n. sp.. This is unlike cf.
980 *Agujaceratops* (UTEP P.37.7.065) and specimens referred to "*Chasmosaurus russelli*" where ep1
981 occurs at the edge of the embayment. In *C. belli*, *Vagaceratops*, and *Kosmoceratops*, the ep1
982 locus is expanded laterally and occupies most of the posterior bar (see reinterpretation of
983 *Vagaceratops* and *Kosmoceratops* in Supporting Information 1). In contrast, in *Anchiceratops*,
984 the median embayment is closed such that ep1 effectively occurs at the midline on the dorsal
985 surface of the posterior bar. Orientation of the long axis of ep1 follows the angle of the lateral
986 rami upon which it is mounted. In *Chasmosaurus* it is therefore oriented mostly mediolaterally.
987 In contrast, ep1 is oriented slightly anteroposteriorly in cf. *Pentaceratops sternbergii*, and at an
988 increasingly steep angle from cf. *P. sternbergii* through *Navajoceratops*, *Terminocavus*, and
989 finally *Anchiceratops* in which it is oriented anteroposteriorly such that the tips point laterally.
990

991 In both *Navajoceratops* and *Terminocavus* holotypes ep2 is large and triangular; in
992 *Navajoceratops* the apices are broadly rounded apices rather than being pointed, whereas in the
993 *Terminocavus* holotype, both ep2 have damaged apices. Large triangular ep2 are seen in most
994 chasmosaurines, although these reach especially large size in *Anchiceratops*. Ep2 is small in
995 some specimens of *C. belli*, and anteriorly inclined in *Vagaceratops*, and *Kosmoceratops*. In the
996 derived *Triceratops* all frill epiossifications are triangular in juveniles, and become broad and
997 flattened in adults (Horner and Goodwin, 2006).

998

999 In *Navajoceratops*, ep2 occurs within the median embayment and the pointed tip is
1000 medioposteriorly oriented, as in aff. *Pentaceratops* n. sp., and unlike the stratigraphically
1001 preceding cf. *P. sternbergii* and *Utahceratops*, where ep2 points posteriorly. In *Terminocavus*,
1002 the position and orientation of ep2 is intermediate between *Navajoceratops* and *Anchiceratops*;
1003 anteroposterior expansion and increased curvature of the lateral rami causes the constriction of
1004 the median embayment such that ep2 is less medially oriented than in *Navajoceratops*, and closer
1005 to a posterior orientation.

1006

1007 Locus ep2 is the posteriormost locus in basal chasmosaurines "*Chasmosaurus russelli*", most
1008 specimens of *C. belli*, *Kosmoceratops*, *Utahceratops*, and cf. *Pentaceratops sternbergii*. The
1009 posteriormost epiparietal locus switches to ep3 in chasmosaurines more derived than cf. *P.*
1010 *sternbergii* (aff. *Pentaceratops* n. sp, *Navajoceratops*, *Terminocavus*, and *Anchiceratops*).

1011

1012 In chasmosaurines, the apex of locus ep3 points laterally in "*Chasmosaurus russelli*",
1013 posterolaterally in *C. belli*; *Vagaceratops*, *Kosmoceratops*, *Utahceratops*, and cf. *Pentaceratops*
1014 *sternbergii*; and posteriorly in aff. *Pentaceratops* n. sp. (inferred from locus), *Navajoceratops*
1015 (inferred from locus), *Terminocavus*, and *Anchiceratops*.

1016

1017 **Anteroposterior thickness of the posterior bar lateral rami**

1018 The anteroposterior thickness of the posterior bar is narrow and strap-like in more basal
1019 chasmosaurines (*Chasmosaurus*, *Vagaceratops*, *Kosmoceratops*, *Utahceratops*, cf.
1020 *Pentaceratops sternbergii*), broadening to become flat and plate-like in the most derived forms

1021 (*Anchiceratops*, *Arrhinoceratops*, and *Triceratopsini*). In *Navajoceratops* the posterior bar is
1022 anteroposteriorly expanded laterally, being broadest at locus ep3. This is also exhibited by the
1023 stratigraphically preceding aff. *Pentaceratops* n. sp., but is unlike cf. *Pentaceratops sternbergii*,
1024 *Utahceratops*, *Chasmosaurus*, and *Vagaceratops*, where the posterior bar is strap-like and
1025 subequal in anteroposterior thickness along its length. In *Terminocavus* the lateral rami are much
1026 more similar to *Anchiceratops* in being strongly anteroposteriorly expanded such that they are
1027 plate-like rather than bar-like.

1028

1029 **Characters of the median bar and parietal fenestrae**

1030 The parietal median bar exhibits two characters that differ among taxa; the anteroposterior
1031 position of the point of maximum constriction, and the development of lateral flanges which
1032 invade the parietal fenestrae (with consequent effect on the shape of the median bar cross
1033 section).

1034

1035 In referred specimens of "*Chasmosaurus russelli*", *C. belli*, and *Kosmoceratops*, the point of
1036 maximum constriction occurs in the posteriormost third of the median bar. In most specimens of
1037 *C. belli*, this is immediately at the point of contact with the posterior bar. In *Vagaceratops*
1038 *irvinensis*, the median bar is slightly damaged, but the preserved portion also seems to have the
1039 point of maximum constriction in the distal third. In contrast, in cf. *Pentaceratops sternbergii*,
1040 aff. *Pentaceratops* n. sp., *Anchiceratops*, *Arrhinoceratops*, and fenestrated specimens of
1041 *Triceratopsini*, the point of maximum constriction occurs approximately at the anteroposterior
1042 midpoint of the median bar. The median bar is incomplete in parietals of cf. *Agujaceratops*,
1043 *Utahceratops*, *Navajoceratops*, *Terminocavus*, and *Chasmosaurinae* sp. "taxon C" (NMMNH P-
1044 33906), but in these taxa the maximum constriction does not occur adjacent to the posterior bar
1045 (as in *Chasmosaurus*), and probably occurs approximately half way along its length.

1046

1047 In basal chasmosaurines *Chasmosaurus*, *Agujaceratops*, *Utahceratops*, cf. *Pentaceratops*
1048 *sternbergii*, aff. *Pentaceratops* n. sp., and *Navajoceratops* the median bar is narrow and strap-
1049 like, but develops into a broader structure in *Vagaceratops* (slightly), *Kosmoceratops*, and
1050 especially from *Terminocavus* through *Chasmosaurinae* sp. "taxon C", *Anchiceratops*,

1051 *Arrhinoceratops*, and Triceratopsini. Broadening of the median bar is therefore possibly
1052 convergent between *Chasmosaurus* and *Anchiceratops* clades. In the taxa basal to
1053 *Anchiceratops*, broadening occurs by development of thin lateral flanges which project from the
1054 lateral edges of the median bar, generally only easily observable on the ventral side. These are
1055 very weakly developed in *Utahceratops* referred specimen UMNH VP-16671, and remain weak
1056 to absent in cf. *P. sternbergii* and aff. *Pentaceratops* n. sp.. In *Navajoceratops* they are slightly
1057 more prominent than in stratigraphically preceding taxa, and are similarly further developed in
1058 *Terminocavus*. Lateral flanges are much more developed in the stratigraphically younger
1059 Chasmosaurinae sp. "taxon C" (NMMNH P-33906; Figure 6), where they are conspicuous and
1060 approach the level of development seen in some specimens of *Anchiceratops* (e.g. CMN 8535;
1061 TMP 1983.001.0001; Mallon et al., 2011). Development of lateral flanges is associated with the
1062 reduction in size, and change in shape of the parietal fenestrae.

1063

1064 An obvious character that differentiates basal and derived chasmosaurines is the size and shape
1065 of the parietal fenestrae. The fenestrae of derived chasmosaurines (*Kosmoceratops*,
1066 *Anchiceratops*, *Arrhinoceratops*, and Triceratopsini) are subrounded to subcircular (although
1067 only subangular to subrounded in *Kosmoceratops*), relatively small, and enclosed within the
1068 parietal by a broad median bar and wide parietal lateral bars. This is contrasted with the large
1069 angular to subangular fenestrae of basal chasmosaurines ("*Chasmosaurus russelli*", *C. belli*,
1070 *Vagaceratops irvinensis*, *Utahceratops*, cf. *Pentaceratops sternbergii*, and aff. *Pentaceratops* n.
1071 s and *Navajoceratops*) which are typically enclosed only by a narrow median bar and thin
1072 lateral bars which may not be anteroposteriorly continuous (hence part of the squamosal may
1073 form the lateral border of the fenestra). *Terminocavus* is morphologically and stratigraphically
1074 intermediate between the two morphotypes, and has subrounded parietal fenestrae. Because
1075 Chasmosaurinae sp. "taxon C" is incomplete it is not possible to know the shape of the fenestrae.

1076

1077 The parietal fenestrae of ceratopsian dinosaurs open and expand in size through ontogeny
1078 (Dodson and Currie, 1988; Brown et al., 2009; Scannella and Horner, 2010; Fastovsky et al.,
1079 2011). As such, it is possible that smaller and more rounded parietal fenestrae in *Terminocavus*
1080 holotype NMMNH P-27468 may indicate that the individual was not fully mature, and that the
1081 fenestrae would have been larger and perhaps more angular in the final growth stage. Although

1082 this is possible, the purportedly juvenile aff. *Pentaceratops* sp. SDMNH 43470 has fenestrae that
1083 are relatively larger and more angular (inferrable from the strap-like and straight posterior bar)
1084 than in the *Terminocavus* holotype which ontogenetic indicators suggest is a subadult or adult.
1085 As such, it is hypothesized that the final size and shape of the fenestrae might not be significantly
1086 different from that observed.

1087

1088 ***Implications of findings***

1089 Although this study demonstrates that most chasmosaurine taxa are still in need of detailed
1090 revision, the description of the new taxa provides a good basis from which to investigate the
1091 paleobiology of Chasmosaurinae as a group, and the influence of these findings on our
1092 understanding of dinosaur evolution in the Late Cretaceous of North America.

1093

1094 **Phylogeny: anagenetic stacks of stratigraphically segregated "species"**

1095 In his discussion on the validity of the badly distorted "*Pentaceratops fenestratus*", Mateer
1096 (1981; p. 52) suggested that "the presence of two species [of *Pentaceratops*] in the San Juan
1097 Basin separated stratigraphically may be real". The new taxa *Navajoceratops* and *Terminocavus*,
1098 along with taxon C (NMMNH P-33906), effectively corroborate this view with better preserved
1099 material, expanding it beyond only two taxa, and providing critical morphological links between
1100 the stratigraphically preceding form *Pentaceratops* and succeeding *Anchiceratops*.

1101

1102 It is important to recognize that there is little evidence that the naming of these new taxa
1103 represents increased diversity in Chasmosaurinae; rather, the new taxa support identification of
1104 an unbranching lineage linking *Pentaceratops* and *Anchiceratops*, consistent with the hypothesis
1105 of Lehman (1998). The term "diversity" is used broadly in paleontology, typically when referring
1106 to multiple named species within a given clade as evidence of diversity. This is often
1107 inappropriate; "diversity" should properly only be used to denote two or more contemporaneous
1108 species or lineages. In this usage, diversity is therefore evidence of lineage splitting or
1109 multiplication, also termed cladogenesis (*sensu* Rensch, 1959) or "speciation" (*sensu* Cook,
1110 1906; Vrba, 1985). The new taxa provide little evidence of lineage splitting, being instead more

1111 supportive of an unbranching lineage of stratigraphically separated taxa ("anagenesis"; Rensch,
1112 1959, used here *sensu* Wiley, 1981; syn. "phyletic evolution"; Simpson, 1961) from
1113 *Utahceratops* through *Pentaceratops*, *Navajoceratops*, *Terminocavus*, and *Anchiceratops*. The
1114 morphometric analysis strongly supports this anagenetic lineage, with each taxon recovered
1115 progressively more positive along the PC1 axis (Figure 8). The phylogenetic analysis is less
1116 supportive of such a long lineage, with [*Utahceratops* + *Pentaceratops*] forming a separate clade
1117 to [*Navajoceratops* + *Terminocavus* + *Anchiceratops*]. However, it is expected that this might
1118 not be a problem when specimens of cf. *Pentaceratops sternbergii* (e.g. AMNH 1625  which
1119 show strong similarity with *Utahceratops*, are coded separately from aff. *P. n. sp.* (MNA
1120 Pl.1747; UKVP 16100). However, this awaits full description of the aff. *P. n. sp.* materials. Since
1121 each of the new taxa is stratigraphically separated from preceding and succeeding forms, and
1122 stratigraphically preceding forms are recovered as less derived, then we fail to reject the
1123 hypothesis that they are transitional forms within a single unbranching lineage (note that if
1124 *Navajoceratops* and *Terminocavus* represent intermediate forms within an anagenetic lineage
1125 then it is arguable that they should be considered as a single species, rather than new species or
1126 genera; see Supporting Information 1).
1127

1128 **Phylogeny: a deep split Chasmosaurinae**

1129 A deep split within a monophyletic Chasmosaurinae is suggested by the morphometric and
1130 phylogenetic analyses, supported by stratigraphic data, and consistent with the proposed lineages
1131 of Lehman (1998). The split divides Chasmosaurinae into two clades: a *Chasmosaurus* clade
1132 [*C. russelli*" + *C. belli* + *Vagaceratops* + *Kosmoceratops*] and a *Pentaceratops* clade
1133 [*Utahceratops* + *Pentaceratops* + *Navajoceratops* + *Terminocavus* + *Anchiceratops* +
1134 *Arrhinoceratops* + *Triceratopsini*]. With the exclusion of [*Arrhinoceratops* + *Triceratopsini*] (see
1135 later discussion) both clades comprise stratigraphically separated taxa which do  overlap (Fig.
1136 10), with the oldest forms more basal, and younger forms more derived. This is supportive of an
1137 initial cladogenesis (speciation) event which created two resultant lineages that subsequently
1138 evolved by anagenesis.
1139

1140 The two clades are characterized by a number of divergent, often opposite, morphological trends
1141 (expanded from those proposed by Lehman, 1998) observed in stratigraphically successive taxa
1142 within their respective clades. Basal members of both clades exhibit an anteroposteriorly narrow
1143 parietal posterior bar bearing a median embayment, and three discrete epiparietals. In the
1144 *Chasmosaurus* clade the median embayment shallows as ep1 expands laterally, ep2 and ep3 loci
1145 migrate to the posterolateral corners of the parietal, the posterior bar remains anteroposteriorly
1146 narrow, and the apices of the curved lateral rami of the posterior bar migrate laterally but remain
1147 at ep1 or ep2. This is contrasted with the *Pentaceratops* clade where the median embayment
1148 deepens and closes in on itself, ep1 remains medial but rotates its long axis such that it becomes
1149 anteroposteriorly oriented, ep2 and ep3 become large and triangular (maintained in adults), and
1150 the posterior bar becomes anteroposteriorly broad and plate-like with rounded lateral ramus at the
1151 apex of which occurs at locus ep3. Some morphologic trends are parallel between the clades. The
1152 parietal fenestrae of both clades exhibit a trend towards reduction in size, and increase in
1153 roundedness, concomitant with laterally expanded median and lateral bars.

1154

1155 The phylogenetic pattern, morphological trends, and stratigraphic occurrence imply divergence
1156 from a common ancestral population. The oldest known representative of either clade are
1157 specimens referred to "*Chasmosaurus russelli*" (not including the holotype; see Supporting
1158 Information 1) from the lower part of the Dinosaur Park Formation (Holmes et al., 2001; Mallon
1159 et al., 2012; see Supporting Information 1). This horizon is radiometrically dated as between 77
1160 and 76.3 Ma, corresponding to the uppermost part of the Middle Campanian (Eberth, 2005;
1161 2011; Fowler, 2017). The oldest member of the *Pentaceratops* clade, *Utahceratops*, is slightly
1162 younger than this at between ~75.97 Ma to ~75.6 Ma (Roberts et al., 2013; Fowler, 2017). The
1163 cladogenetic split between *Chasmosaurus* and *Pentaceratops* clades must therefore have
1164 occurred before 77 Ma.

1165

1166 Collection of new chasmosaurine material from before 77 Ma is thus essential to further our
1167 understanding of the timing, rate, and cause of the divergence. Appropriately-aged dinosaur-
1168 bearing formations in the Western Interior include the Foremost (~80.2 - 79.4 Ma) and Oldman
1169 Formations, Alberta (~79.4 - 77Ma); lower parts of the Judith River (~80 - 77 Ma) and Two
1170 Medicine (~81 - 75 Ma) Formations, Montana; Wahweap Formation, Utah (~80 - ~79 Ma), and

1171 possibly the Aguja Formation, Texas (Lower to Middle Campanian; Goodwin and Deino, 1989;
1172 Rogers et al., 1993; Rogers and Swisher, 1996; Jinnah et al., 2013; Roberts et al., 2013; Fowler,
1173 2017; see Supporting Information 1). Although a good amount of material has been collected
1174 from the Aguja Formation (Lehman, 1989; Forster et al., 1993), most is fragmentary, immature,
1175 or is missing the critical parietal, making comparisons difficult. However, an isolated middle
1176 portion of the parietal posterior bar (UTEP P.37.7.065) is tantalizingly similar to basal members
1177 of both *Chasmosaurus* and *Pentaceratops* clades in exhibiting a median embayment restricted to
1178 the middle third, however, more complete parietal material is required for further comparisons
1179 (also see Supporting Information 1). A range of material has also recently been collected from
1180 the Judith River Formation of Montana and lower Oldman of southern Alberta (some published,
1181 e.g. the highly fragmentary remains named *Judiceratops tigris*; Longrich, 2013; Campbell, 2015)
1182 which has great potential to increase our knowledge of early, and presumably basal, members of
1183 these clades.

1184

1185 **Latitudinal biogeography and vicariance**

1186 The deep split within Chasmosaurinae provides support for the hypothesis of latitudinal
1187 differences (but critically, not endemism) of North American Campanian dinosaur faunas,
1188 implying vicariance in the middle or (more likely) early Campanian which split chasmosaurines
1189 into a northern *Chasmosaurus* clade, and a southern *Pentaceratops* clade. Geological and
1190 biological evidence demonstrate that geographic isolation of northern and southern populations
1191 was not of continuous duration, with northern and southern biomes overlapping or mixing again
1192 by the middle Campanian.

1193

1194 In a series of papers, Lehman (1987; 1997, 2001; Lehman et al., 2006) proposed that in the
1195 Campanian and Maastrichtian of the North American Western Interior, dinosaur faunas were
1196 segregated into northern and southern biogeographic provinces, with the dividing line positioned
1197 roughly in central Utah. This hypothesis was criticized and partly falsified as many of the
1198 purportedly coeval northern and southern taxa were not contemporaneous and were therefore
1199 indicative of stratigraphic rather than geographic segregation (Fowler, 2006; Sullivan and Lucas,
1200 2006; Fowler, 2017). Despite this, an expansion of Lehman's hypothesis was proposed (Sampson

1201 et al., 2010), based partly on the description of new chasmosaurine taxa *Kosmoceratops*
1202 *richardsoni* and *Utahceratops gettyi* from the Kaiparowits Formation, Utah. Later (Sampson et
1203 al., 2013), previous stratigraphic criticism of the biogeographic hypothesis was rejected,
1204 suggesting that recalibrated radiometric dates (Roberts et al., 2013) showed that chasmosaurines
1205 from the Dinosaur Park Formation, Alberta and Kaiparowits Formation, Utah were indeed
1206 contemporaneous, and indicative therefore of intracontinental endemism. However, many of
1207 these radiometric recalibrations of (Roberts et al., 2013) are in error, some by as much as a
1208 million years (Fowler, 2017). Correctly recalibrated dates (Fowler, 2017), show the Kaiparowits
1209 taxa are stratigraphically slightly younger than the more basal chasmosaurines from Alberta,
1210 with *K. richardsoni* the youngest and most derived member of the *Chasmosaurus* lineage, and *U.*
1211 *gettyi* the oldest and most basal member of the *Pentaceratops* lineage. Thus the contemporaneity
1212 required for basinal-scale faunal endemism collapses.

1213

1214 Nevertheless, amidst this criticism, the emphasis on 'lineage-thinking' in the current analysis
1215 provides evidence for a subtle form of gradational latitudinal provincialism, but not endemism.
1216 Although the *Chasmosaurus* and *Pentaceratops* lineages are not exclusive (e endemic) to either
1217 north or south (a similar point is raised by both Wick and Lehman, 2013; and Longrich, 2014), it
1218 is apparent that the relative abundance of the lineages varies latitudinally in Campanian-aged
1219 units (albeit based on a small sample size). Specimens of the *Chasmosaurus* clade are much
1220 more abundant in the northern United States and Canada, with the southernmost representative
1221 (*Kosmoceratops richardsoni*), represented by two specimens from the Kaiparowits Formation of
1222 southern Utah. Specimens of the *Pentaceratops* clade are more common in the southern states of
1223 New Mexico and Utah, with only one or two possible representative specimens from southern
1224 Alberta (see discussion on *Chasmosaurus russelli* in Supporting Information 1). This
1225 biogeographic pattern does not represent endemism as the two lineages overlap geographically
1226 during the uppermost part of the middle Campanian in Alberta and Utah. However it is
1227 suggestive that latitudinally aligned vicariance might have been the cause of the speciation event
1228 that created the two chasmosaurine lineages. As the oldest member of the *Chasmosaurus* lineage
1229 occurs at ~77Ma (see above) then vicariance must have occurred before this time. Similarly, as
1230 both lineages are seen to coexist in the uppermost part of the Dinosaur Park Formation (~76 Ma)
1231 then any physical barrier must have been passable by this time. The location of the barrier is

1232 suggested by the fact that the dividing line between northern and southern provinces appears to
1233 lie somewhere between southern Utah and northern Montana.

1234

1235 It has been stated (Sampson et al., 2010; 2013) that there is currently no evidence for a physical
1236 barrier separating northern and southern provinces, but this is not the case. In 1990, Lillegraven
1237 and Ostresh (not referenced by Sampson et al., 2010; 2013) produced 33 maps illustrating Late
1238 Cretaceous transgression and regression of the western shoreline of the Western Interior Seaway
1239 (WIS). The maps were at a very high stratigraphic resolution, documenting almost every
1240 ammonite zone from the middle Santonian (*Clioscapites choteauensis*; 85.23 Ma; Ogg et al.,
1241 2012) through to the K-Pg boundary (66 Ma). Most importantly, the maps contrast the
1242 paleoshoreline with the modern position of the eastern Sevier thrust front of the Rocky
1243 Mountains. Although the position of the thrust front was slightly more western in the Late
1244 Cretaceous (and the mountains were not as elevated; DeCelles, 2004), it is a good approximation
1245 for the position of the upland or mountainous area which flanked the coastal plain. From these
1246 maps it can be readily observed that during the middle Santonian (85 Ma) through to the earliest part
1247 of the middle Campanian (81 Ma), the shoreline of the WIS intermittently abutted the thrust front
1248 of the incipient Rockies from central Utah to southern Alberta. For hundreds of miles the coastal
1249 plain would have been extremely narrow, in some places perhaps as little as 5-10 kilometers,
1250 providing very limited habitat. This would be similar to, for example, the modern day Zagros
1251 Mountains of Iran which are abutted by the eastern shoreline of the Persian / Arabian Gulf. This
1252 bottleneaking of the available coastal plain effectively cut off the north-south dispersal route,
1253 latitudinally bisecting the coastal plain habitat of North America into southern and northern areas
1254 separated by hundreds of miles. The latitudinal climate gradient might have exacerbated
1255 difference in climate between northern and southern regions, although the latitudinal climate
1256 gradient was not as strong in the Late Cretaceous as it is today. Lillegraven and Ostresh (1990)
1257 show that from the early part of the middle Campanian (~80 Ma) regression of the WIS results in
1258 a broader coastal plain, and it is hypothesized here that this may no longer have presented a
1259 physiographic boundary, thereby permitting interspersal of chasmosaurine lineages, as evidenced
1260 by the presence of *Pentaceratops* lineage taxa in the uppermost Dinosaur Park Formation, ~76
1261 Ma (Longrich, 2014), and later *Anchiceratops* in the Horseshoe Canyon Formation, ~71 Ma
1262 (Mallon et al., 2011).

1263

1264 **The role of heterochrony in evolution of the frill and effects on**
1265 **phylogenetic analysis**

1266

1267 The process of heterochrony describes changes in the rate and timing of development between
1268 stratigraphically successive populations. Most morphological trends recognized in this study are
1269 potentially controlled or affected by heterochrony, but inference of this requires knowledge of
1270 change through both ontogeny and stratigraphy. Although stratigraphic position is at least
1271 roughly known for most species in the current study, few especially young or old individuals of
1272 relatively basal chasmosaurines have been published, such that their ontogenetic change is not
1273 well understood. Nevertheless, some possible heterochronic trends can be identified or
1274 hypothesized based on the limited available material and comparison to the well documented
1275 growth series of the Late Maastrichtian derived chasmosaurine *Triceratops* (Horner and
1276 Goodwin 2006; 2008; Scannella and Horner, 2010). This may have important practical
1277 implications for taxonomy and the way specimens are coded for phylogenetic analysis, but also
1278 in a broader sense may be informative about some of the unusual features of basal and derived
1279 chasmosaurines.

1280

1281 **Development of the median embayment**

1282 The median embayment of the parietal posterior bar successively shallows and broadens through
1283 time in the *Chasmosaurus* lineage, and deepens then closes in the *Pentaceratops* lineage. There
1284 is some evidence to suggest that similar patterns are observed ontogenetically. In "*Chasmosaurus*
1285 *russelli*", referred adult specimen CMN 2280 has a shallow central embayment with lateral rami
1286 at an angle of 131°. The immature referred specimen, AMNH 5656, has an embayment that is
1287 less shallow (99°) and is more restricted to the central third of the posterior bar. Adult specimens
1288 of the stratigraphically successive *C. belli*, and *Vagaceratops irvini* have an even shallower
1289 embayment than adult "*C. russelli*" suggesting peramorphosis in the *Chasmosaurus* lineage.

1290

1291 Concerning basal members of the *Pentaceratops* lineage, there are no published juvenile
1292 specimens which preserve the median embayment, that have been recovered from the same strata

1293 as the various holotypes (and as such, could be more reliably assigned to a given taxon).
1294 Consequently the progressive deepening of the median embayment (observed stratigraphically
1295 and phylogenetically) cannot currently be assessed for an ontogenetic component.

1296

1297 **Development of parietal fenestrae**

1298 In Ceratopsia, the parietal fenestrae open during ontogeny by resorption of central regions of the
1299 previously solid parietal. Although this is still controversial (e.g. Farke, 2011), opening of
1300 fenestrae through ontogeny has been proposed in both basal neoceratopsians (*Protoceratops*;
1301 Fastovsky et al., 2011) and the highly derived Late Maastrichtian ceratopsid *Triceratops*
1302 (Scannella and Horner, 2010). As such, it is probable that ontogeny influences the size and shape
1303 of parietal fenestrae in both the *Chasmosaurus* and *Pentaceratops* lineages, reflected in the width
1304 of the median, posterior and lateral bars.

1305

1306 In adult specimens of basal chasmosaurines, the median bar of the parietal either lacks lateral
1307 flanges that invade the fenestrae, or they are only weakly developed. Flanges are more strongly
1308 developed and conspicuous in Chasmosaurinae sp. taxon C (NMMNH P-33906) and more
1309 derived chasmosaurines like *Anchiceratops*. It is likely that development of the flanges occurs by
1310 pedomorphosis; ie. that flanges form as a result of the fenestrae opening less extensively during
1311 ontogeny (in more derived forms), rather than the flanges growing laterally from the median bar.
1312 It is expected therefore that juveniles of some of the more derived *Pentaceratops* lineage taxa
1313 (e.g. *Terminocavus* or taxon C) would exhibit relatively wider median bars with more developed
1314 lateral flanges, and smaller parietal fenestrae. In this respect, they might appear more similar to
1315 adults of derived chasmosaurines. This is seen in the *Chasmosaurus* lineage, where juvenile "*C.*
1316 *russelli*" referred specimen AMNH 5656 has very weak lateral flanges on the median bar,
1317 whereas in more mature specimens (e.g. CMN 2280) lateral flanges are absent. 

1318

1319 The development of the broad plate-like posterior bar (in *Pentaceratops* lineage) and lateral bars
1320 of the parietal is similarly expected to be a result of pedomorphosis. The posterior bar of
1321 immature aff. *Pentaceratops* sp. SDMNH 43470 comprises a bar-like posterior portion (typical
1322 of more basal members of the *Pentaceratops* lineage) which has small thin flanges extending
1323 anteriorly into the parietal fenestrae. These could be interpreted as remnants of a previously more

1324 extensive plate-like part of the posterior bar that is resorbed by adulthood in more basal
1325 chasmosaurines (thereby increasing the size of the fenestrae). Hypothesized paedomorphosis in
1326 more derived members of the *Pentaceratops* lineage might lead to retention of this flange.

1327

1328 In derived chasmosaurines (e.g. "*Torosaurus*", *Anchiceratops*, and *Kosmoceratops*), the lateral
1329 bars of the parietal are laterally broad and completely enclose the fenestrae within the parietal. In
1330 basal chasmosaurines the lateral bars are much narrower and might not fully enclose the fenestra
1331 (such that the squamosal forms part of the lateral margin). Within the *Chasmosaurus* lineage,
1332 "*Chasmosaurus russelli*" referred adult specimen CMN 2280 is illustrated by Godfrey and
1333 Holmes (1995) as exhibiting incomplete lateral rami (the squamosal contributes to the
1334 fenestra), whereas in immature referred specimen AMNH 5656, the lateral bars are continuous,
1335 fully enclosing the fenestrae. This limited sample suggests that ontogenetic expansion of the
1336 parietal fenestrae may cause resorption of the central parts of the lateral bars, causing them to
1337 become discontinuous in adults. If so, this would be a paedomorphic trend as in specimens of the
1338 slightly more derived *C. belli*, the fenestra is enclosed entirely within the parietal (Godfrey and
1339 Holmes, 1995). A similar paedomorphic trend is probably present in the *Pentaceratops* lineage
1340 where basal members have continuous but thin lateral bars, which are broad in *Anchiceratops*
1341 and more derived forms. This is only hypothetical as lateral bars are not preserved in
1342 *Navajoceratops*, *Terminocavus*, and "taxon C".

1343 **Origin of *Arrhinoceratops* and the Triceratopsini: a second speciation?**

1344

1345 The description of intermediate morphotaxa between *Pentaceratops* and *Anchiceratops* has
1346 implications for the origin of *Arrhinoceratops* and the Triceratopsini [*Ojoceratops* +
1347 *Eotriceratops* + "*Torosaurus*" + *Triceratops*]. In most phylogenetic analyses, *Arrhinoceratops*
1348 and the Triceratopsini are recovered as very closely related to *Anchiceratops* (e.g. Dodson et al.,
1349 2004; Sampson et al., 2010; Longrich, 2014; and the current analysis). Since *Anchiceratops* and
1350 *Arrhinoceratops* were contemporaneous (co-occurring in the Horsethief and Morrin members of
1351 the Horseshoe Canyon Formation, Alberta; ~72.4 - 71.6 Ma; Eberth et al., 2013; Mallon et al.,
1352 2014) then the phylogenetic relationship illustrated in Figs 19-21 require that a second
1353 speciation event splitting the two must have occurred prior to this time, but after the occurrence

1354 of the immediately basal *Terminocavus* (~74.7 Ma). However, taxa immediately basal to
1355 *Anchiceratops* do not resemble *Arrhinoceratops*, being generally characterized by a deep notch-
1356 like median embayment and large triangular epiparietals, neither of which are observed in
1357 *Arrhinoceratops* at any ontogenetic stage (Mallon et al., 2014). It is possible that character states
1358 shared between *Arrhinoceratops* and *Anchiceratops* (for example, small circular parietal
1359 fenestrae) may be homoplastic rather than synapomorphic, and could instead reflect shared long
1360 term trends observed across Chasmosaurinae (see above). Although this is speculative,
1361 candidates for a different origin of *Arrhinoceratops* and the Triceratopsini are present in the
1362 poorly known *Coahuilaceratops* (Loewen et al., 2010) and "*Bravoceratops*" (Vick and Lehman,
1363 2013; see Supporting Information 1), from the lower Maastrichtian of Mexico and Texas,
1364 respectively. Although both taxa are known from only very scant remains, both exhibit anteriorly
1365 positioned nasal horns and retain bumps on the anterior end of the parietal relatively late in
1366 ontogeny, with features characteristic of Triceratopsini. Recovery of more complete specimens
1367 of *Coahuilaceratops* and "*Bravoceratops*" may be enlightening.

1368

1369 Regardless of their precise phylogenetic origin, the slightly embayed, cardioid shape of the frill
1370 in some specimens referred to "*Torosaurus*" (YPM 1831; TMM 41480-1) and *Triceratops* (e.g.
1371 AMNH 5116) may be a remnant feature of their ancestry; a plesiomorphy or atavism exhibited
1372 by a few members of the population, which is gradually being lost. This is supported by the fact
1373 that very few specimens of *Triceratops prorsus* exhibit any parietal midline embayment, despite
1374 many specimens having been collected.

1375

1376 CONCLUSIONS

1377

1378 Description of the new taxa *Navajoceratops sullivanii* and *Terminocavus sealyi*, and the
1379 fragmentary Taxon C, provides critical stratigraphic and morphologic links between the
1380 Campanian *Pentaceratops*, and the Maastrichtian *Anchiceratops*, reinstating the phylogenetic
1381 hypothesis originally postulated by Lehman (1993, 1998). Combined with significant revision of
1382 other chasmosaurine taxa, this reveals a deep split of the Chasmosaurinae into *Chasmosaurus*
1383 and *Pentaceratops* clades, which are mostly arranged into stacks of stratigraphically successive

1384 taxa. Morphological divergence from similar basal forms suggests the clades evolved from a
1385 common ancestor which was subject to a true speciation or cladogenetic event, probably in the
1386 early Campanian. After this initial speciation, stratigraphically successive taxa suggest that
1387 evolution proceeded mostly by unbranching anagenesis, with evidence for only one additional
1388 speciation event, that of *Arrhinoceratops* (and the Triceratopsini).

1389

1390 Analysis of paleogeographic maps suggest that high sea level in the Santonian through to middle
1391 Campanian may have acted as an agent of vicariance, separating an ancestral chasmosaurine
1392 population into northern and southern subpopulations which over time led to divergence and
1393 speciation. This lends support to recent hypotheses of latitudinally arrayed differences in
1394 terrestrial faunal composition (e.g. Lehman, 1987; 1997, 2001), but stops short of supporting
1395 basinal-level endemism in the middle to late Campanian (e.g. Sampson et al., 2010).

1396

1397 Description of the new material places San Juan Basin chasmosaurines as among the best
1398 documented of their clade, second only to *Triceratops* in number of specimens and quality of
1399 accompanying data.

1400

1401 Although this work presents significant revision of many chasmosaurine taxa, much reanalysis
1402 and redescription remains. Inclusion of more recently described taxa and separation of
1403 problematic taxa and specimens (see Supporting Information 1) will be attempted in forthcoming
1404 manuscripts based on Fry (2015) and Fowler and Freedman Fowler (2017).

1405

1406 **ACKNOWLEDGEMENTS**

1407 Special thanks to John R. Horner and Robert M. Sullivan for immeasurable support and
1408 opportunity. Thanks for specimen access or assistance, discussion, or general help to Arjan
1409 Boere, David Eberth, David Evans, Joshua Fry, David Gillette, Andrew Heckert, Steven Jasinski,
1410 Benjamin Kear, Matt Lavin, Spencer Lucas, John Scannella, Paul Sealey, Justin Spielmann,
1411 Steven Wick, Tim Williams, John Wilson, and Oliver Wings. Thanks to the Bureau of Land
1412 Management for collection permits issued to Robert M. Sullivan and Thomas Williamson.

1413

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Figure 1

Geological map of the southeast San Juan Basin showing localities of radiometric dates and important fossil specimens mentioned in the text

Collection localities; **A**, SMP VP-1500, *Navajoceratops sullivani*, holotype; **B**, NMMNH P-27486, *Terminocavus sealeyi*, holotype; **C**, NMMNH P-33906, Denazin chasmosaurine; **D**, NMMNH P-37880, c.f. *Pentaceratops sternbergii*, parietal fragment; **E**, UKVP 16100, c.f. *P. sternbergii*, complete skull; **F**, MNA Pl.1747, c.f. *P. sternbergii*, complete skull; **G**, USNM 8604, Chasmosaurinae sp. anterior end of a parietal median bar; **H**, purported collection area of AMNH 6325, *P. sternbergii*, holotype. **I**, NMMNH P-50000, Chasmosaurinae sp., skull missing frill. Radiometric dates recalibrated from Fassett and Steiner (1997) by Fowler (2017). Bedrock geology altered from O'Sullivan and Beikman (1963). 

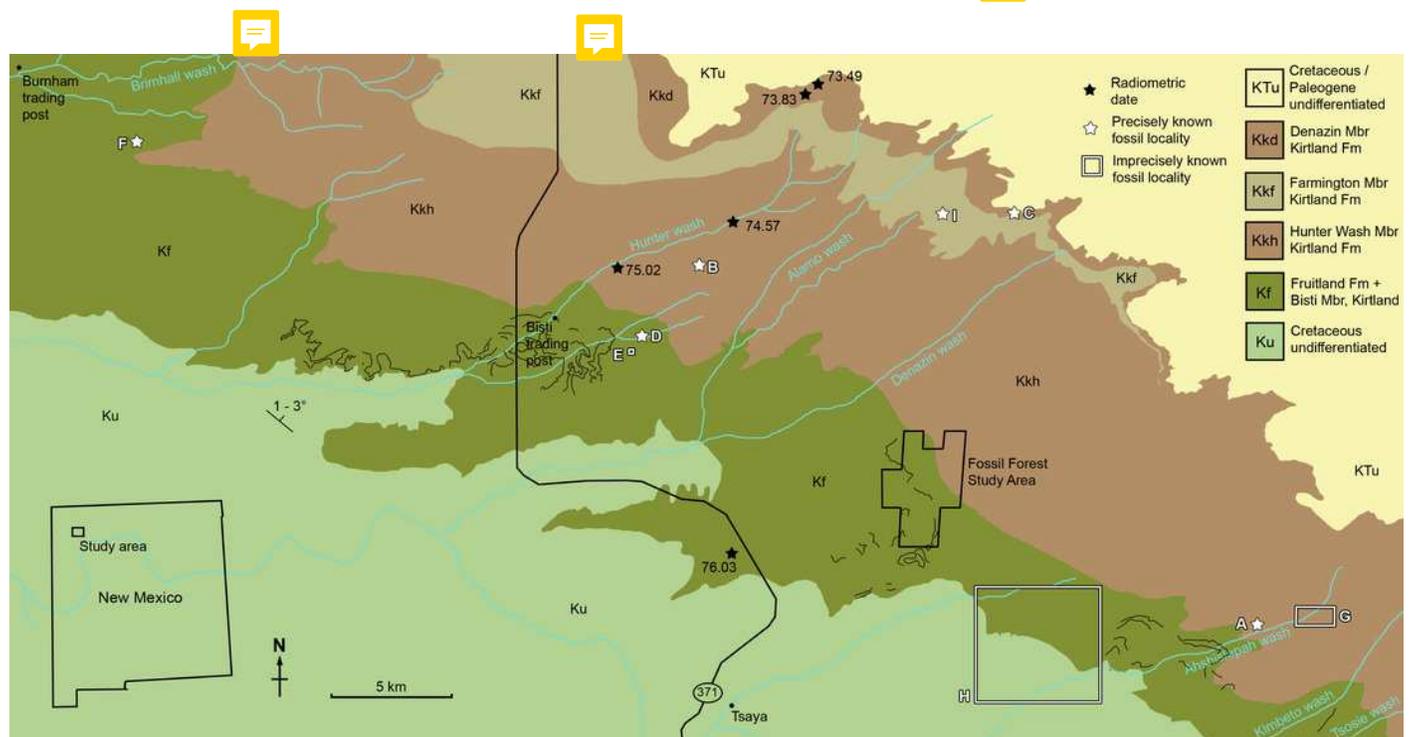


Figure 2

Generalized stratigraphic column of Fruitland and Kirtland Formation with radiometric dates and fossil occurrences

Specimens mentioned in the main text or supporting information: *Pentaceratops sternbergii* holotype, AMNH 6325; cf. *P. sternbergii*, AMNH 1624, 1625; aff. *Pentaceratops* n. sp., MNA PI.1747, UKVP 16100, NMMNH P-37880; *Navajoceratops sullivanii* holotype SMP VP-1500; *Terminocavus sealeyi* holotype, NMMNH P-27468; Chasmosaurinae sp., NMMNH P-50000; "Taxon C", NMMNH P-33906. Radiometric dates (*) recalibrated from Fassett and Steiner (1997) by Fowler (2017).



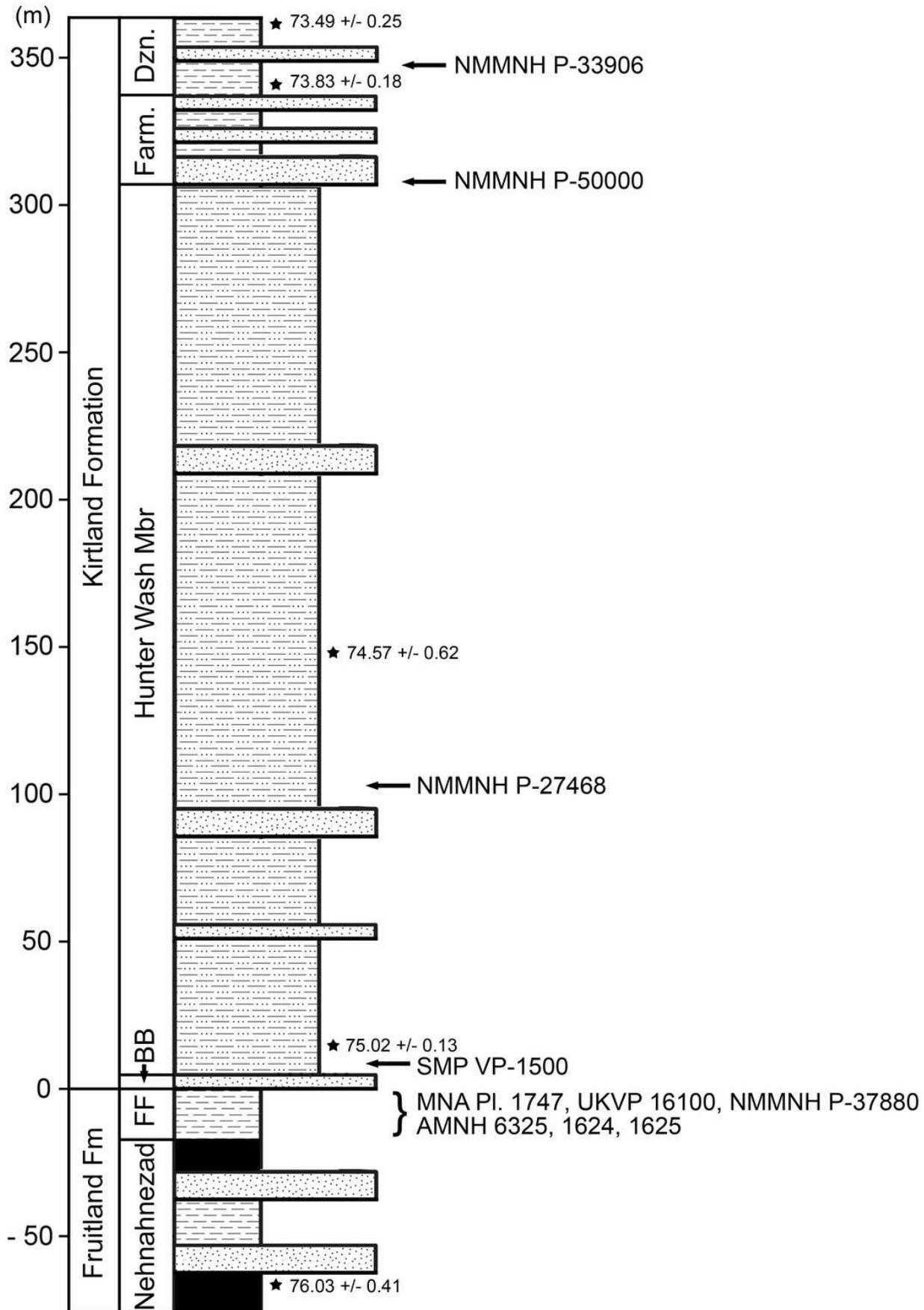


Figure 3

Morphological landmarks used in morphometric analysis of chasmosaurine parietals

All landmarks were measured on the parietal only. Points 1 and 2 are the same for both left and right sides, but all other points were mirrored for the right side and analysed along with the non-mirrored left side. Points are defined as follows: (1-4; green): **1**, maximum constriction of the median bar, positioned on the midline; **2**, posteriormost point of the parietal at the midline; **3**, posteriormost point of the parietal anywhere along the posterior margin; **4**, lateralmost point of the parietal; (5, yellow): **5**, point at which the lateral ramus of the posterior bar meets the median bar as expressed on the posteriomedial border of the parietal fenestra, may be marked by a change in angle of the fenestra border; (6, 7; magenta): **6**, posteriormost point of parietal fenestra; **7**, lateralmost point of parietal fenestra; (8-13; blue): **8**, contact point of the medial margin of epiparietal 1 with the parietal itself; **9**, contact point of the lateral margin of epiparietal 1 with the parietal itself; **10**, contact point of the medial margin of epiparietal 2 with the parietal itself; **11**, contact point of the lateral margin of epiparietal 2 with the parietal itself; **12**, contact point of the medial margin of epiparietal 3 with the parietal itself; **13**, contact point of the lateral margin of epiparietal 3 with the parietal itself; (14-16; red): **14**, The contact point of the midpoint of epiparietal 1 with the parietal itself; **15**, The contact point of the midpoint of epiparietal 2 with the parietal itself; **16**, The contact point of the midpoint of epiparietal 3 with the parietal itself. Colors are intended to aid in visual distinction only. Points illustrated on *Chasmosaurus russelli* referred specimen CMN 2280, adapted from Godfrey and Holmes (1996).

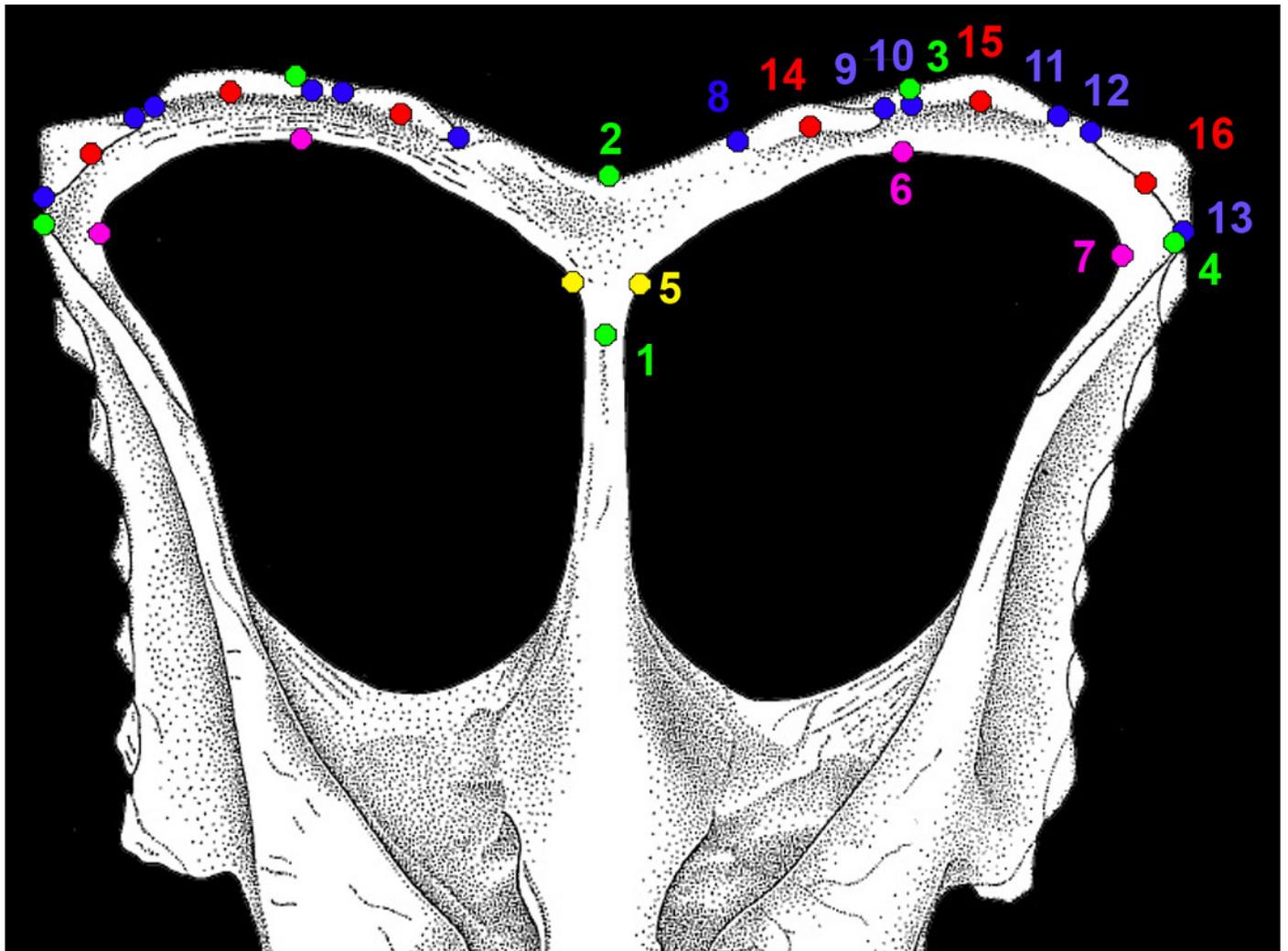


Figure 4

Navajoceratops sullivanii holotype SMP VP-1500 parietal

Dorsal (left) and ventral (right) views.  s section of median bar (**mb**) illustrated on dorsal view. Ep1 mostly removed during extraction or preparation (see Fig. 7 for original extent). **em**, median embayment of the posterior bar; **ep**, epiparietal loci numbered by hypothesized position (no epioassifications are fused to this specimen). **f**, parietal fenestra. **L-Ir / R-Ir**, Left / Right lateral rami of the posterior bar. **te**, tapering lateral edges of the median bar. Scalebar = 10 cm. Reconstruction adapted from Lehman (1.

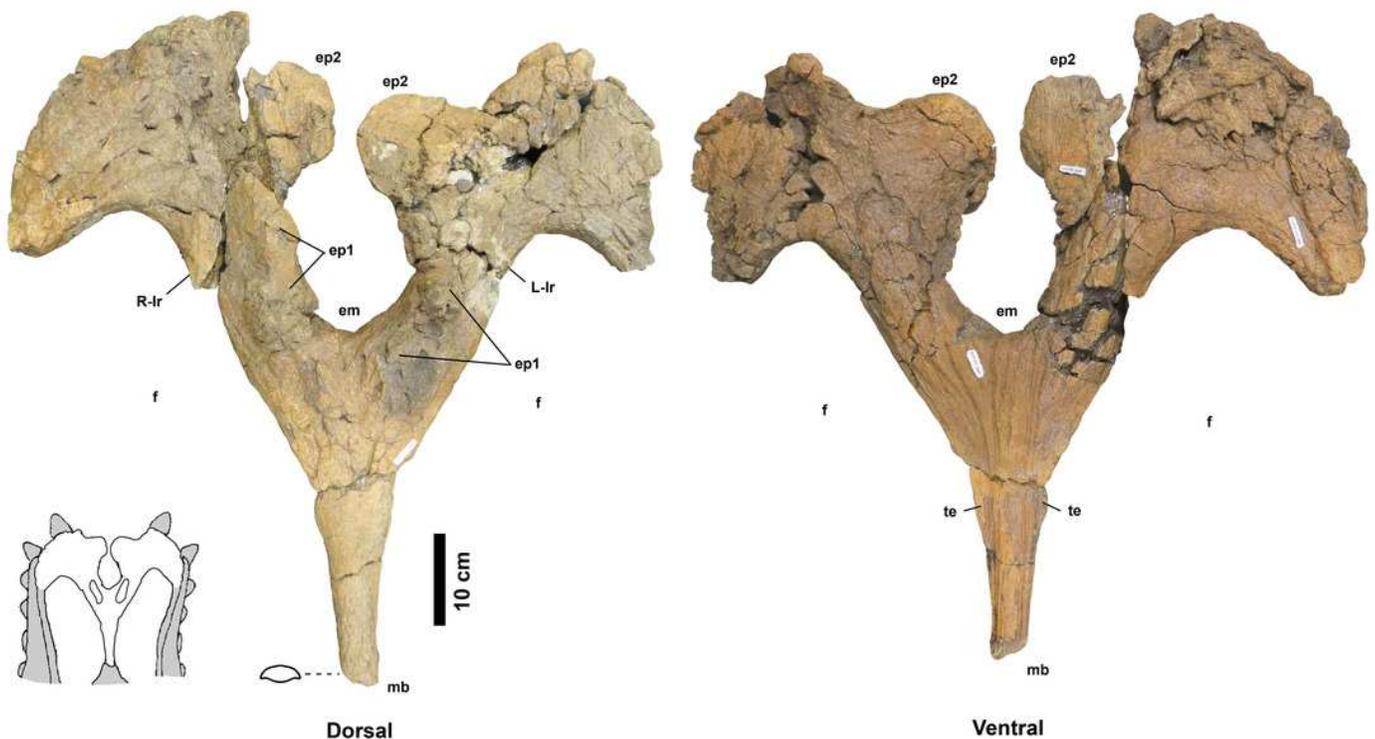


Figure 5

Terminocavus sealeyi holotype NMMNH P-27468 parietal

Dorsal (left) and ventral (right) views. Paired ep1 are deflected dorsally. **em**, median embayment of the posterior bar. **ep**, epiparietal loci numbered by hypothesized position (no epioassifications are fused to this specimen). **f**, parietal fenestra. **lb**, lateral bar. **L-lr / R-lr**, Left / Right lateral rami of the posterior bar. **mb**, median bar. **te**, tapering lateral edges of the median bar. Scalebar = 10 cm. Reconstruction adapted from Lehman (1998).

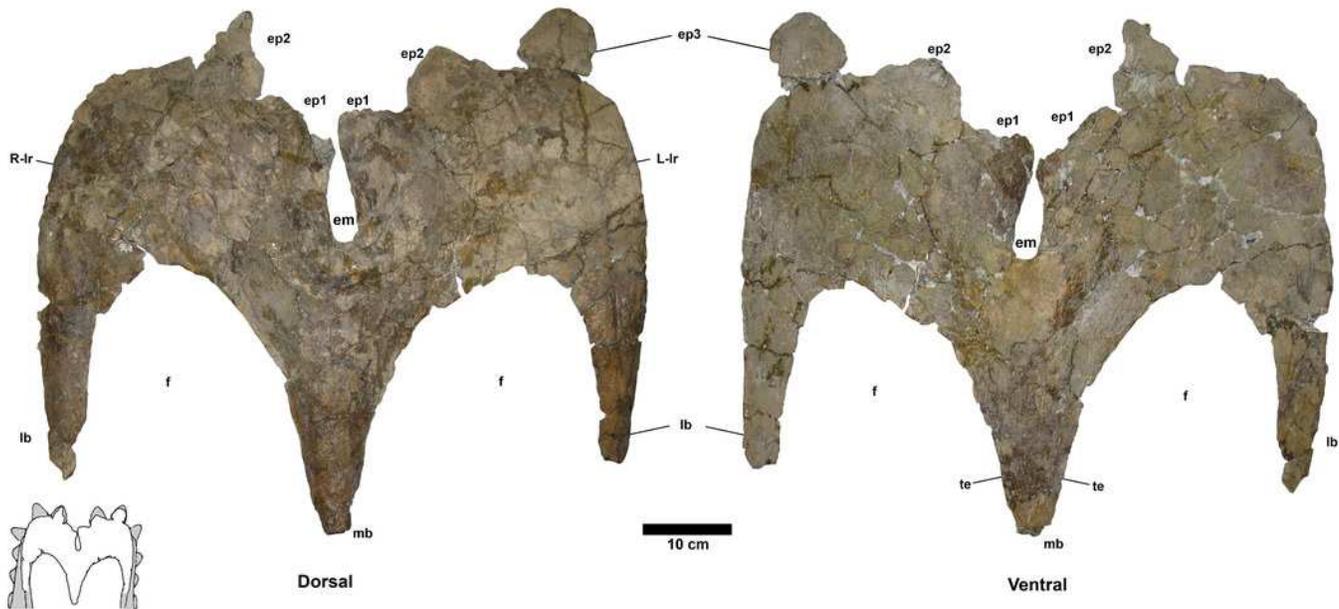


Figure 6

Chasmosaurinae sp. "Taxon C" NMMNH P-33906 parietal median bar

Near-complete parietal median bar in right lateral (**A**), dorsal (**B**), left lateral (**C**), ventral (**D**), and ventral outline (**E**) views. Cross sections in posterior (**F**) and anterior (**G**) inferred views. Subtle lateral expansion at both anterior and posterior ends suggests that the length of the median bar is complete, and as such is much wider than in stratigraphically preceding forms *Utahceratops*, *Pentaceratops*, *Navajoceratops*, and *Terminocavus*. The extra width is due to more extensive tapering lateral edges (**te**) of the median bar which extend out into the parietal fenestrae. Scalebar = 10 cm.

Chasmosaurinae sp. "taxon C"
NMMNH P-33906

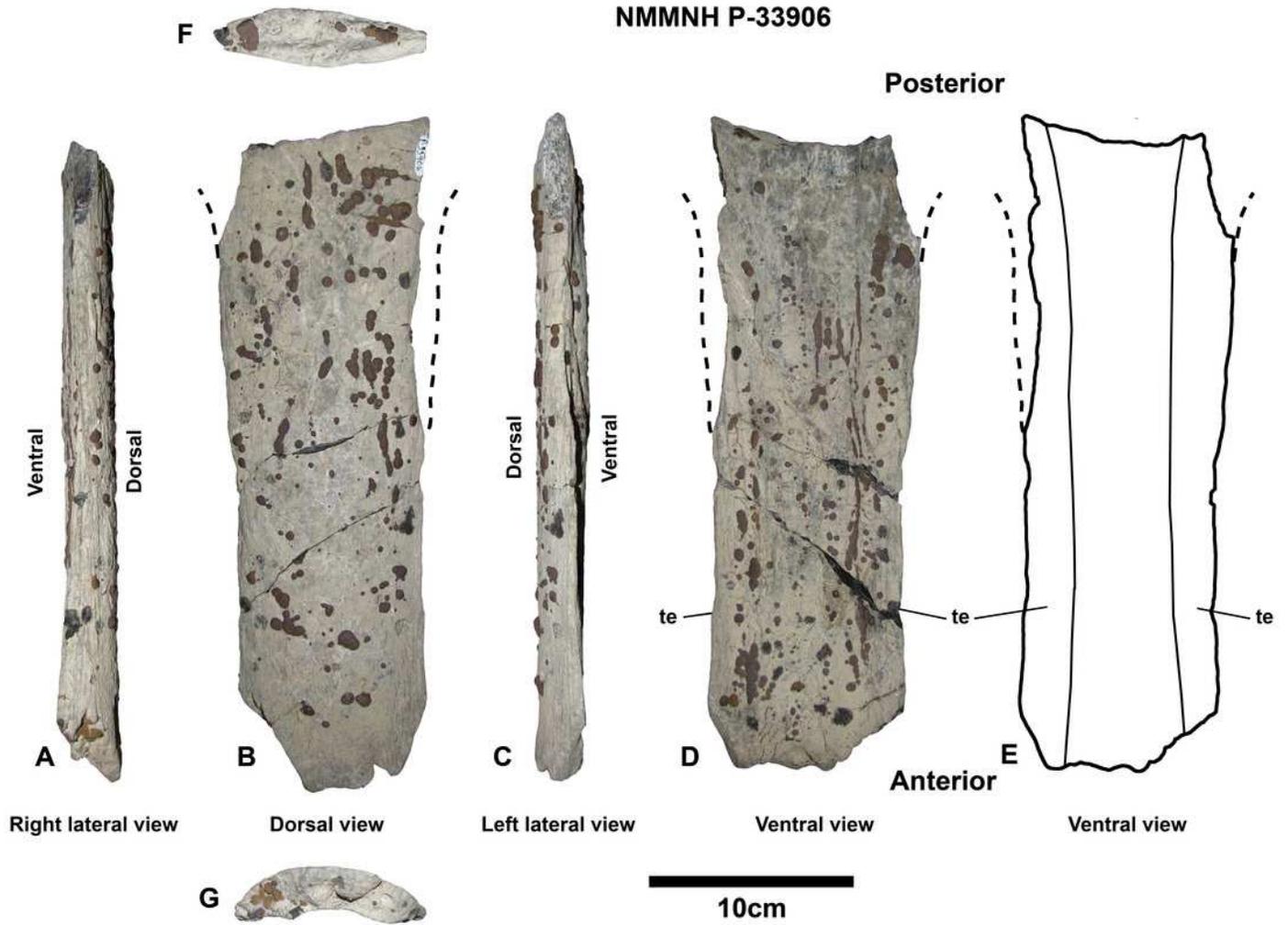


Figure 7

Parietal relative sizes among specimens of *Pentaceratops*, and related chasmosaurines

Parietals of chasmosaurine taxa mentioned in the main text, all in dorsal view and to scale with each other to show relative size. Taxa shown in stratigraphic order (with the exception of **E**, SDMNH 43470). **A**, *Utahceratops gettyi* referred specimen UMNH VP-16671. **B**, cf. *Pentaceratops sternbergii* referred specimen AMNH 1625. Aff. *Pentaceratops* sp. referred specimens **C**, UKVP 16100; **D**, NMMNH P-37880, and **F**, MNA Pl. 1747. **E**, aff. *Pentaceratops sternbergii* referred specimen SDMNH 43470. **G**, *Navajoceratops sullivanii* holotype SMP VP-1500. **H**, *Terminocavus sealeyi* holotype NMMNH P-27468. **I**, Chasmosaurinae sp. "Taxon C" specimen NMMNH P-33906. **ep**, epiparietal loci numbered by hypothesized position (no epiossifications are fused to this specimen). **mb**, median bar. Line drawings adapted from Longrich (2014), and Sampson et al. (2010). Scalebar = 10 cm.

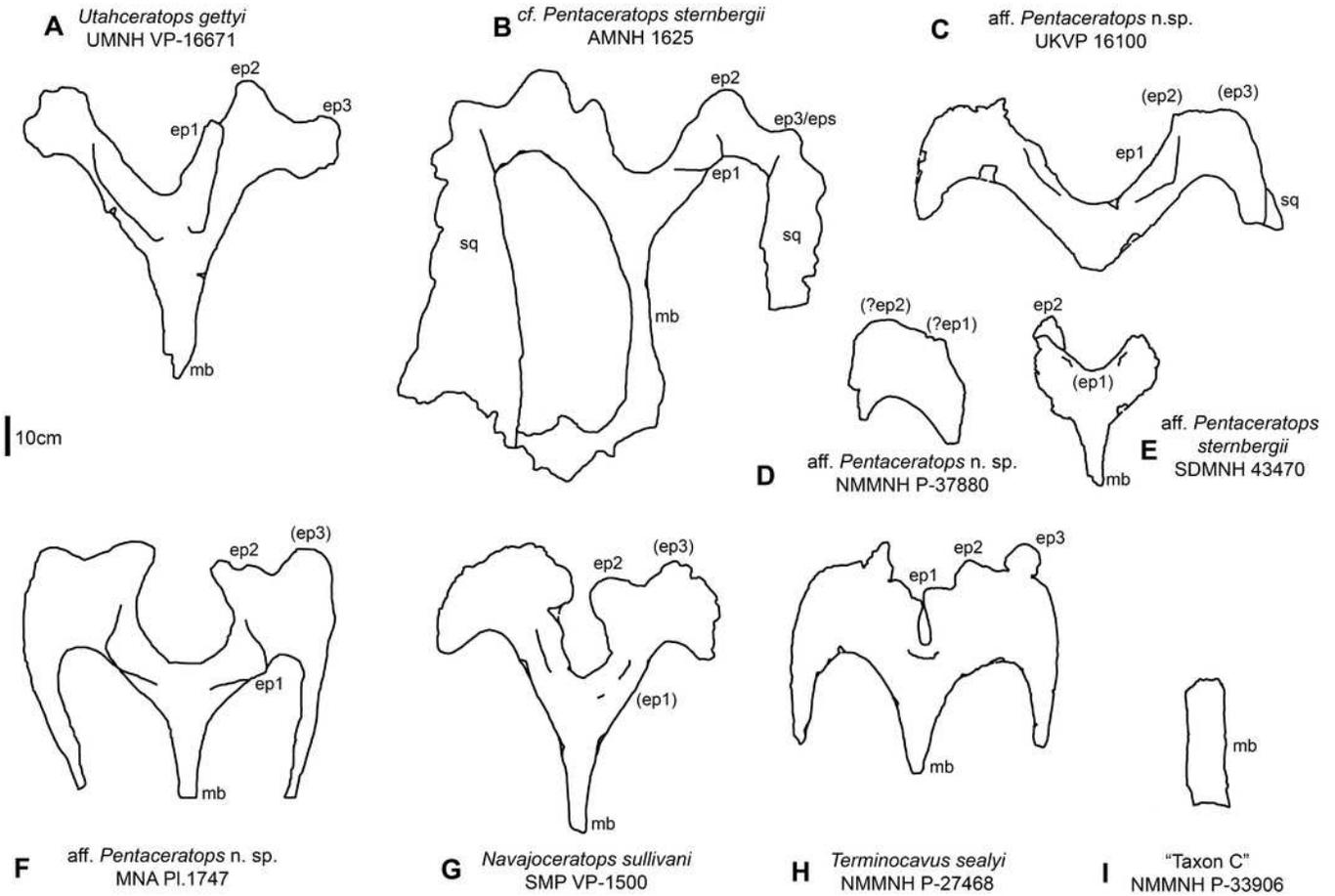


Figure 8

Morphometric analysis of chasmosaurine posterior parietals

Deformation grids illustrate shape of left lateral ramus of each specimen at the end of each principal component axis (**PC**). PC 1 (x axis) accounts for 50.5% of variation and assesses depth of the median embayment from shallow (negative) to deep (positive), and orientation of ep1 from mediolateral (negative) to anteroposterior (positive). PC 2 (y axis) accounts for 19.0% of variation. Points connected by a bar represent left and right sides of the same specimen (where adequately preserved). *Pentaceratops* through *Anchiceratops* plot along PC 1, demonstrating progressively deeper median embayment, and an increase in the angle of ep1. *Chasmosaurus* through to *Vagaceratops* are concentrated on the negative side of PC 1, following a trend from positive to negative along PC 2. Key: "**Ag**", *Agujaceratops*; **An**, *Anchiceratops*; **Ch.b**, *Chasmosaurus belli*; **Ch.r**, cf. *Chasmosaurus russelli*; **Ko**, *Kosmoceratops*; **Na**, *Navajoceratops*; **aff. Pe n.sp.**, aff. *Pentaceratops* n. sp.; **cf. Pe**, cf. *Pentaceratops sternbergii*; **Te**, *Terminocavus*; **Ut**, *Utahceratops*; **Va**, *Vagaceratops*. Color to aid in distinction only.

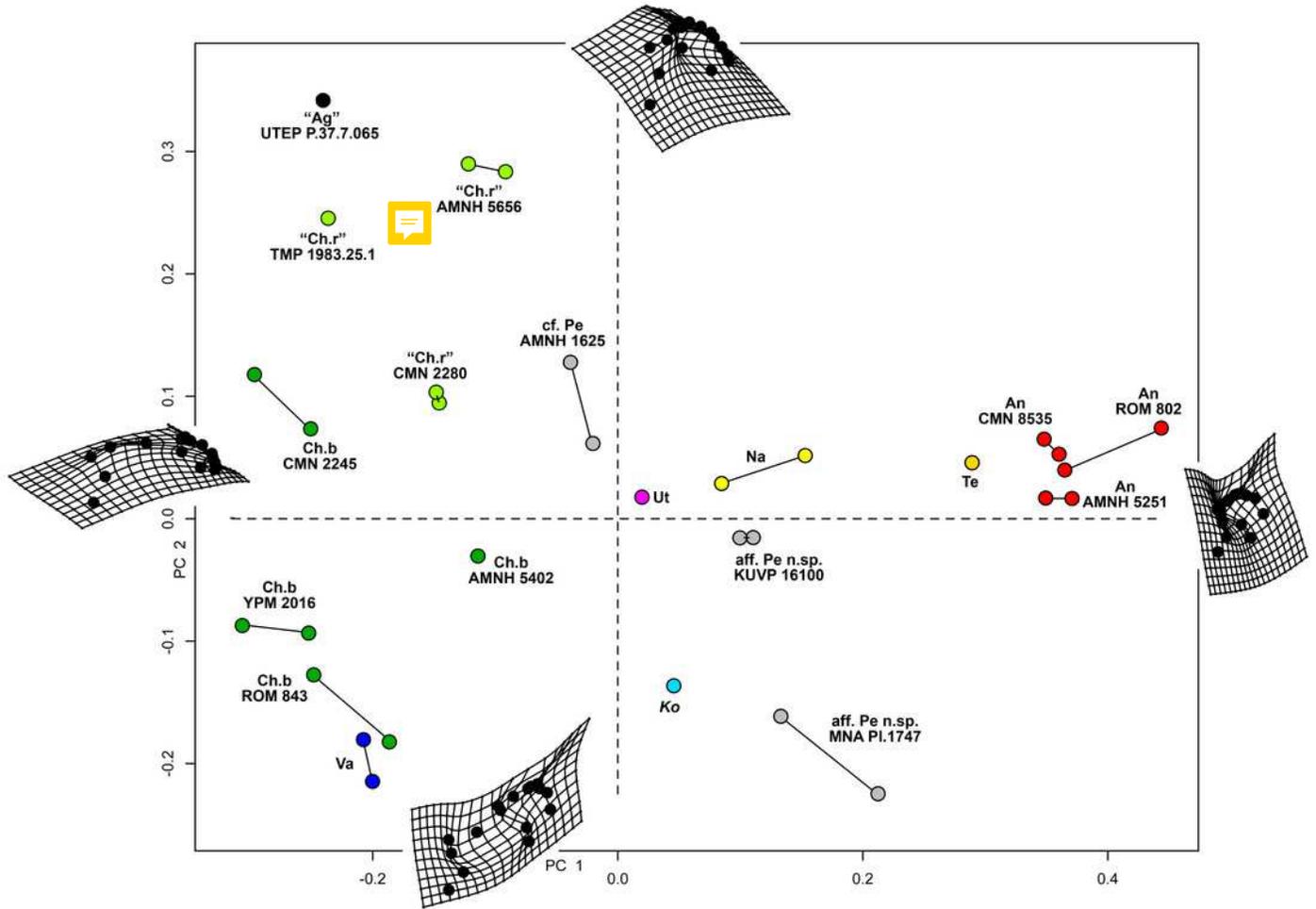


Figure 9

Phylogenetic analysis

(A) Strict consensus tree showing all taxa (MPT = 6; L = 319; CI = 0.72; RI = 0.79). (B) Reanalysis 1, strict consensus tree (MPT = 6; L = 310; CI = 0.72; RI = 0.79). *Bravoceratops*, *Agujaceratops* removed from the character matrix. (C) Strict consensus tree showing all taxa (MPT = 28; L = 308; CI = 0.72; RI = 0.79). *Bravoceratops*, *Agujaceratops*, *Coahuilaceratops* removed from the character matrix. Numbers on nodes indicate bootstrap values >50%; nodes without values had <50% support. Character matrix altered from Sampson et al. (2010) and Mallon et al. (2014).

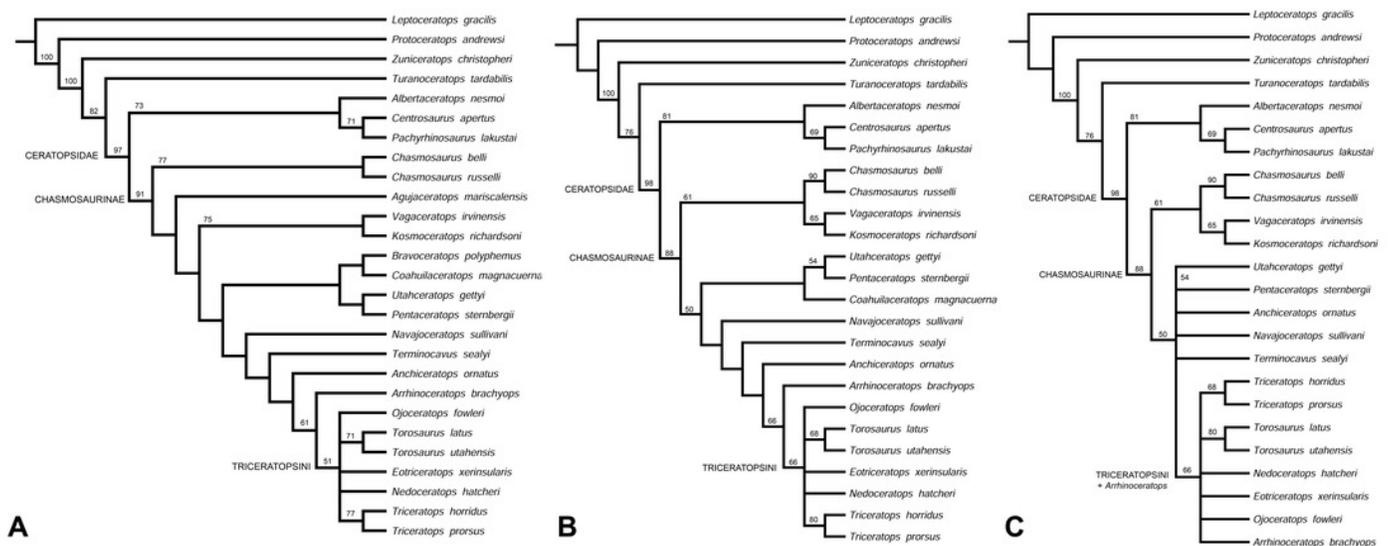


Figure 10

Stratigraphic positions of chasmosaurine taxa

Morphospecies of *Chasmosaurus* (**A-D**) and *Pentaceratops* (**E-J**) clades which do not overlap stratigraphically. These are hypothesized to form two anagenetic lineages which resulted from a cladogenetic branching event prior to the middle Campanian. **A**, "*Chasmosaurus russelli*", lower Dinosaur Park Fm, ~76.8 Ma. **B**, *Chasmosaurus belli*, middle Dinosaur Park Fm, ~76.5 - 76.3 Ma. **C**, *Vagaceratops irvinensis*, upper Dinosaur Park Fm, ~76.1 Ma. **D**, *Kosmoceratops richardsoni*, middle Kaiparowits Fm, ~76.0 - 75.9 Ma. **E**, *Utahceratops gettyi*, middle Kaiparowits Fm, ~76.0 - 75.6 Ma. **F**, c.f. *Pentaceratops sternbergii*, unknown occurrence within "Fruitland Formation" ~76.0 - 75.1 Ma. **G**, aff. *Pentaceratops* n. sp., uppermost Fossil Forest Mbr, Fruitland Fm, ~75.1 Ma. **H**, *Navajoceratops sullivanii*, lowermost Hunter Wash Mbr, Kirtland Fm, ~75.0 Ma. **I**, *Terminocavus sealyi*, middle Hunter Wash Mbr, Kirtland Fm, ~74.7 Ma. **F**, *Anchiceratops ornatus*, Drumheller to Morrin Mbr, Horseshoe Canyon Fm, ~71.7 - 70.7 Ma. Stratigraphic positions and recalibrated radiometric dates from Supporting Information 1 and Fowler (Chapter 2). Timescale from Gradstein et al. (2012). Specimens not to scale. Images adapted from Lehman (1998); Holmes et al., 2001; Sampson et al. (2010); Maidment and Barrett (2011); and Longrich (2014).

