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A COMPLETE SKULL OF *CHASMOSAURUS MARISCALENSIS*
(DINOSAURIA: CERATOPSIDAE) FROM THE AGUJA FORMATION
(LATE CAMPANIAN) OF WEST TEXAS

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ABSTRACT—The recent discovery of a nearly complete ceratopsid skull in the Aguja Formation of southwest Texas supports previous conclusions that the Aguja ceratopsid represents a distinct species, *Chasmosaurus mariscalensis*. The diagnostic features of *C. mariscalensis* include an extensive anteromedian projection of the nasal between the premaxillae, erect supraorbital horns, and laterally rounded squamosal. Nine cranial features that vary among *Chasmosaurus* species, *Pentaceratops sternbergii*, and other chasmosaurines are analyzed. *Chasmosaurus mariscalensis* appears to be most closely related to northern species of *Chasmosaurus* (*C. belli*, *C. russelli*), which also exhibit a transversely flattened nasal horn and modifications of the anterior margin of the external naris. The genus *Chasmosaurus*, in turn, appears to be most closely related to the other southern chasmosaurine, *Pentaceratops sternbergii*. The biogeographic history inferred from these relationships suggests that the biogeographic exchange between northern and southern chasmosaurines cannot be explained by a single dispersal event to the south.

INTRODUCTION

Fossil remains of horned dinosaurs become rare and more fragmentary toward the southern end of their range in North America. Only three ceratopsid species, *Pentaceratops sternbergii* (= *P. fenestratus*), *Chasmosaurus mariscalensis*, and *Torosaurus latus* (= *T. utahensis*) have been described from partial skeletons south of the Colorado Plateau (Rowe et al., 1981; Lawson, 1976; Lehman, 1981, 1989, 1990). We describe below a nearly complete skull of *Chasmosaurus mariscalensis* Lehman, 1989 from the Aguja Formation (late Campanian) of southwest Texas.

The skull was discovered during a field trip from the University of Chicago to Big Bend National Park in 1991. The locality, named Windy City (Fig. 1), also yielded hadrosaurid bones. When the skull was found, its left side was partially exposed, with the distal portion of the left supraorbital horncore and the left half of the frill and jugal weathered away. The remainder of the skull was intact except for mature maxillary teeth, which had loosened from their alveoli and washed away. Neither the mandible nor any of the postcranium was preserved. The skull was buried in a small sandstone lens in the “upper shale member” of the Aguja Formation (Fig. 2), which has been interpreted as a paralic and coastal floodplain deposit (Lehman, 1985). Small rounded clay rip-up clasts and carbonaceous plant debris were present under the skull within the sand lens.

Recent revision of Canadian *Chasmosaurus* (God-

frey and Holmes, in prep.) suggests that there are only two valid northern species, *C. belli* (including *C. brevisrostris*, *canadensis*, *kaiseni*) and *C. russelli*. The new skull of *C. mariscalensis* permits a more complete evaluation of its specific distinction as well as its relationship to northern species of *Chasmosaurus* and *Pentaceratops sternbergii*.

Institutional abbreviations include: AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh; MNA, Museum of Northern Arizona, Flagstaff; NMC, Canadian Museum of Nature, Ottawa; ROM, Royal Ontario Museum, Toronto; TMM, Vertebrate Paleontology and Radiocarbon Laboratory, University of Texas, Austin; RTMP, Royal Tyrrell Museum of Paleontology, Drumheller; UTEP, Centennial Museum of the University of Texas at El Paso; YPM, Yale University Peabody Museum of Natural History, New Haven.

SYSTEMATIC PALEONTOLOGY

Systematic Hierarchy

CERATOPSIA Marsh, 1888

NEOCERATOPSIA Sereno, 1986

CERATOPSIDAE Marsh, 1888

CHASMOSAURINAE Lambe, 1915

CHASMOSAURUS Lambe, 1914

CHASMOSAURUS MARISCALENSIS Lehman, 1989
Figs. 3, 4, 5A

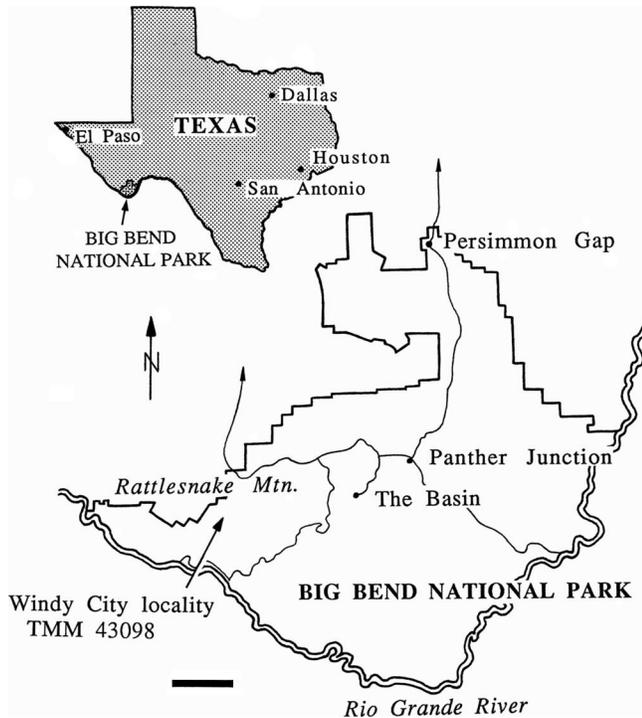


FIGURE 1. Windy City locality (TMM 43098) in Big Bend National Park, southwestern Texas. Scale bar equals 10 km.

Revised Diagnosis—Chasmosaurine with a strong anteromedian nasal process extending between the premaxillae on the internarial bar, erect supraorbital horncores that attain an angle of 85° to the maxillary tooth row in adults, and a squamosal with a convex lateral frill margin.

Referred Specimen—TMM 43098-1, well preserved skull lacking distal left supraorbital horncore, distal left jugal, left squamosal, and the distal parietal.

Locality—Windy City (TMM 43098), southwest of Rattlesnake Mountain in Big Bend National Park, Brewster County, Texas (Fig. 1). Lat. $29^\circ 13'$, Long. $103^\circ 33'$.

Horizon—"Upper shale member," Aguja Formation (Late Campanian) (Fig. 2).

DESCRIPTION

The skull appears to belong to a fully mature individual. Cranial sutures are coossified around the orbit, on the dorsal aspect of the skull, and between the skull bones and secondary dermal elements such as the epijugal. The epoccipitals are either partially or completely coossified with the squamosal. Ten epoccipitals are present on the squamosal (Fig. 3), the highest number ever recorded in ceratopsid skulls and presumably representing the full adult complement.

Snout (Figs. 3–4)

As in other chasmosaurines, the snout is proportionately elongate, with preorbital length equalling ap-

proximately twice snout depth (Table 1). The rostral bone is recurved, with concave ventral and posterior margins, and is tightly bound to the paired premaxillae. The premaxillae form the anterior and ventral margins of the large external naris, anterior to which there is a blind premaxillary fossa (Fig. 3, pmfo). The premaxillary fossa is excavated along its ventral margin, and although the central portion of its thin wall is fractured, there is no positive evidence that an interpremaxillary fenestra was present. A second fossa, much shallower than the first, occurs near the rostral. The anterior margin of the external naris is formed by a very thin lamina of bone, here termed the premaxillary flange

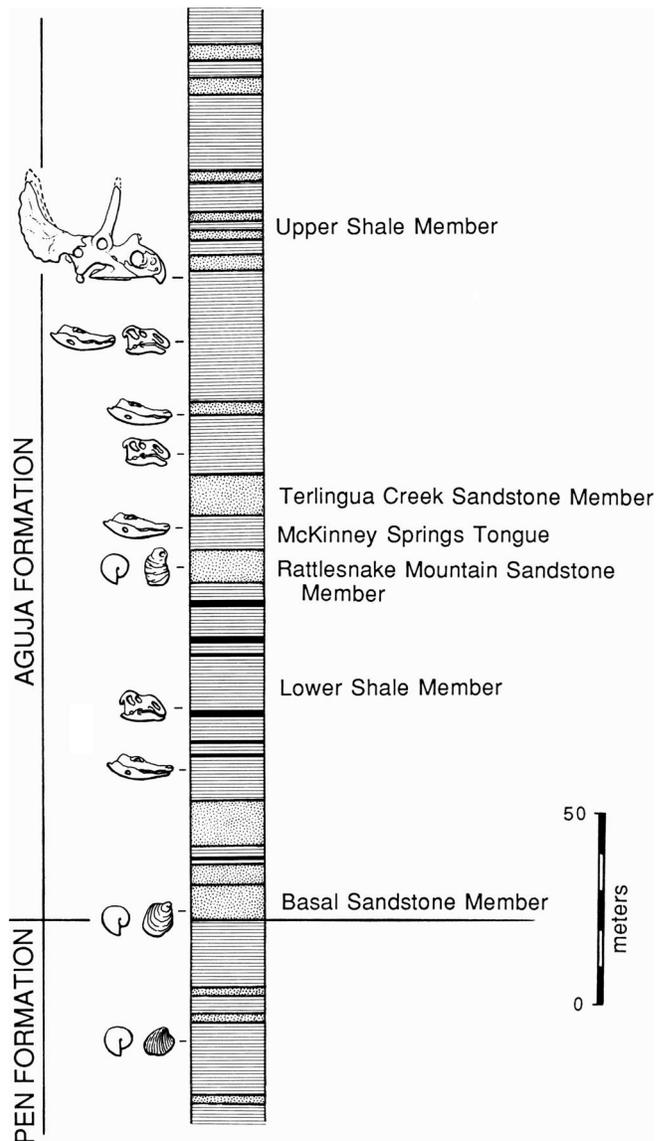


FIGURE 2. Stratigraphic section of the Aguja Formation, using informal nomenclature of Lehman (1985), showing the level of the skull of *Chasmosaurus mariscalensis* (TMM 43098-1). Other fossils indicated in section include a hadrosaurid (*Kritosaurus* sp.), crocodylian (*Deinosuchus riograndensis*), ammonites, and pelecypods (after Lehman, 1985).

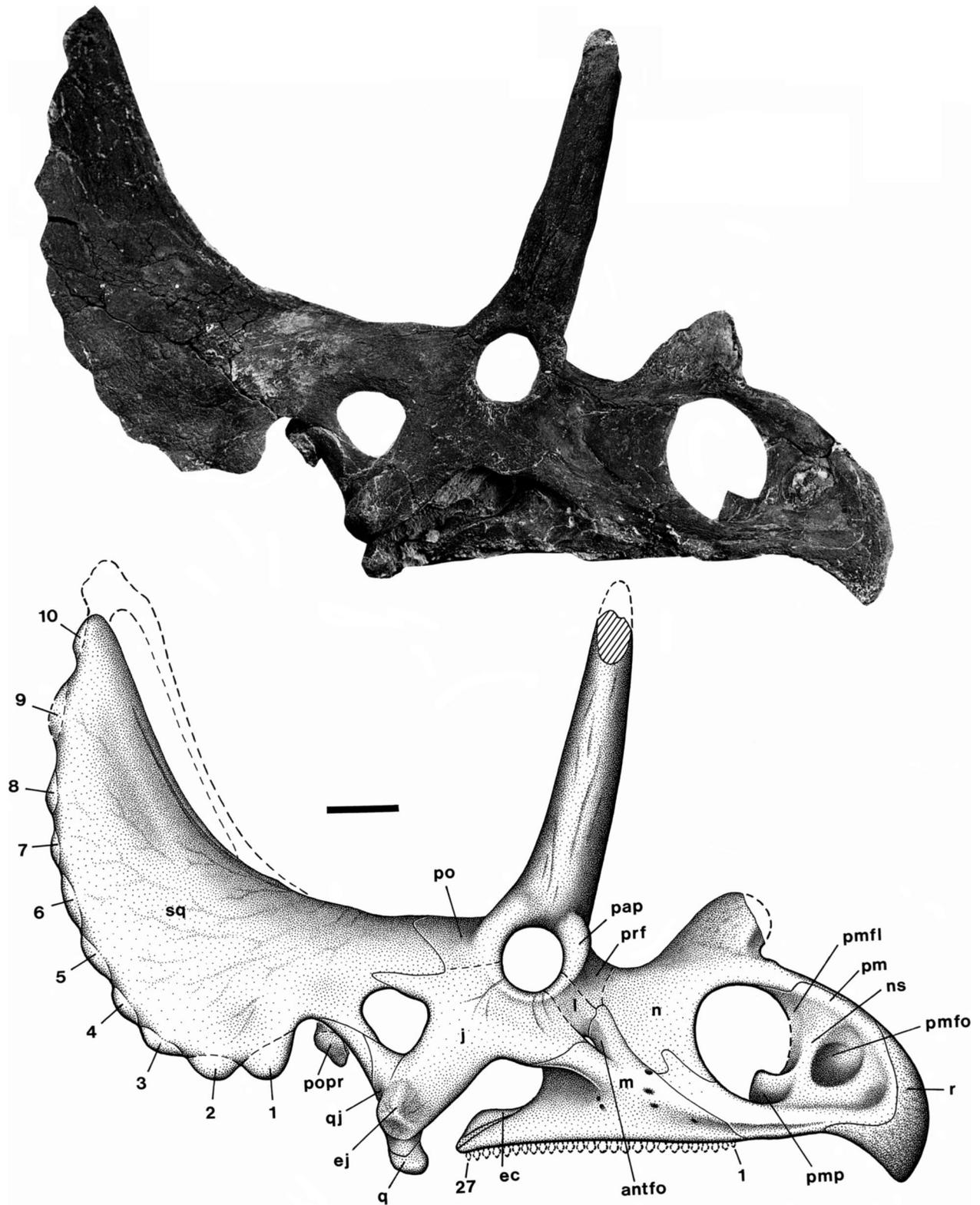


FIGURE 3. Skull of *Chasmosaurus mariscalensis* (TMM 43098-1) in right lateral view. Abbreviations used in figures: **antfo**, antorbital fossa; **ec**, ectopterygoid; **ej**, epijugal; **epo**, epoccipital; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **ns**, narial strut; **pap**, palpebral; **pm**, premaxilla; **pmfl**, premaxillary flange; **pmfo**, premaxillary process; **pmp**, premaxillary process; **po**, postorbital; **popr**, paroccipital process; **prf**, prefrontal; **q**, quadrate; **qj**, quadratojugal; **r**, rostral; **sq**, squamosal. Numbers indicate first and last tooth positions in maxillary tooth row (1, 27) and label the epoccipitals series (1–10). Scale bar equals 10 cm. Cross-hatching denotes broken surface.

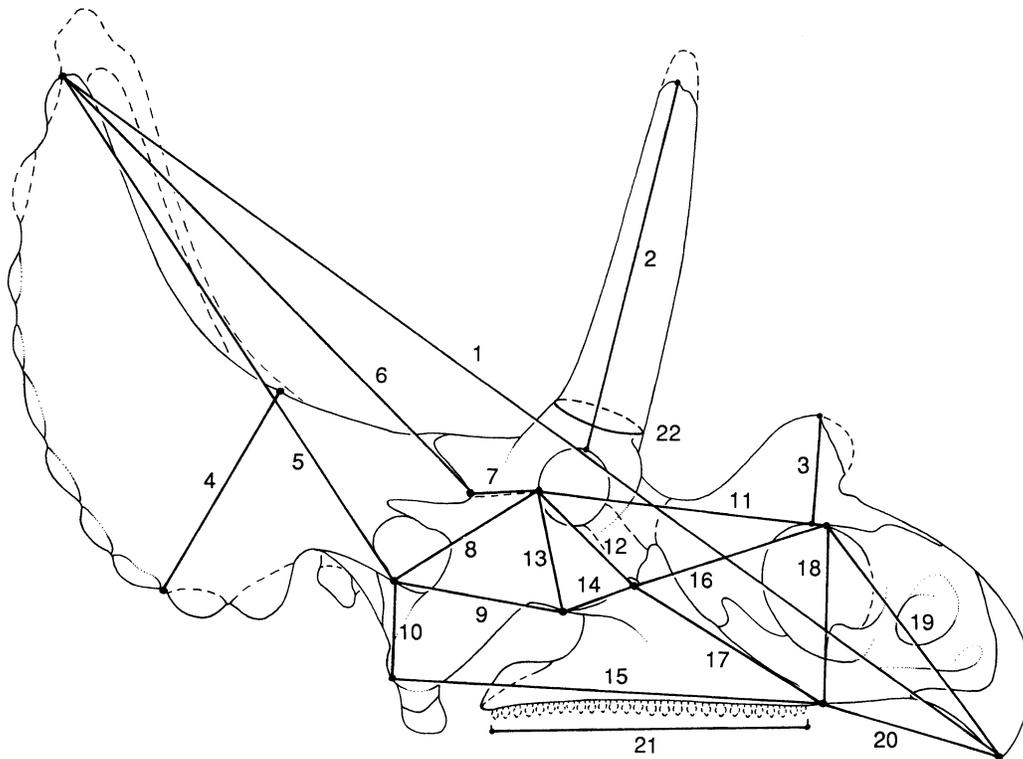


TABLE 1. Measurements (cm) of the skull of *Chasmosaurus mariscalensis* (TMM 43098-1). Bone abbreviations: j, jugal; m, maxilla; n, nasal; pm, premaxilla; po, postorbital; sq, squamosal.

1. Total skull length (preserved)	152
2. Supraorbital horn length (preserved)	43
3. Nasal horn length	15
4. Squamosal maximum width	32
5. Squamosal maximum length	89
6. Squamosal length to j-po-sq junction	85
7. Po-j suture length	9
8. Orbital po-j suture to sq anteroventral tip below lateral temporal fenestra	20
9. Anteroventral tip of sq to m-j suture	21
10. Anteroventral tip of sq to tip of jugal	13
11. Orbital po-j suture narial pm-n suture	37
12. Orbital po-j suture to antorbital fenestra	17
13. Orbital po-j suture to m-j suture	15
14. Antorbital fenestra to m-j suture	10
15. Tip of jugal to pm-m suture along tooth row	47
16. Antorbital fenestra to narial pm-n suture	26
17. Antorbital fenestra to pm-m suture along tooth row	25
18. Pm-m along tooth row to narial pm-n suture	24
19. Pm-n suture to tip of rostral	34
20. Pm-m suture along tooth row to tip of rostral	24
21. Maxillary tooth row length	32
22. Supraorbital horn base circumference	36

(Fig. 3, pmfl), which arises along the posterior side of the narial strut. It is slightly damaged in TMM 43098-1. A similar flange is present in *C. belli* and *C. russelli*. In other chasmosaurines, the flange is either restricted to the anterodorsal corner of the external naris (*P. sternbergii*, MNA Pl.1747) or absent. In the anteroventral corner of the external naris, a thin, quadrangular premaxillary process projects posteriorly from the narial septum (Fig. 3, pmp). Anterior to the nasal horncore, the dorsal process of the premaxilla is overlapped laterally by a tongue-shaped process of the nasal. The posterior process of the premaxilla curves posterodorsally onto the lateral side of the snout posterior to the external naris. The blunt distal end of the posterior process is finger-shaped, and fitted into a shallow fork on the side of the nasal, as in *P. sternbergii*, *C. belli*, and *C. russelli*.

The nasal horncore is positioned above the posterior portion of the external naris and is strongly compressed transversely, with a sharp posterior edge (Fig. 4A). The nasal horncores in other species of *Chasmosaurus* are flattened transversely, but none is as compressed as in TMM 43098-1. In lateral view, the nasal horncore curves anteriorly and narrows toward a broad (and possibly damaged) distal end, as observed in northern species of *Chasmosaurus* (e.g., *C. russelli*, NMC 2280). In *C. mariscalensis*, no external internasal suture is visible, and there is no sign of a separate epinasal ossification on the nasal horncore. An unusual antero-medial process of the conjoined nasals extends ante-

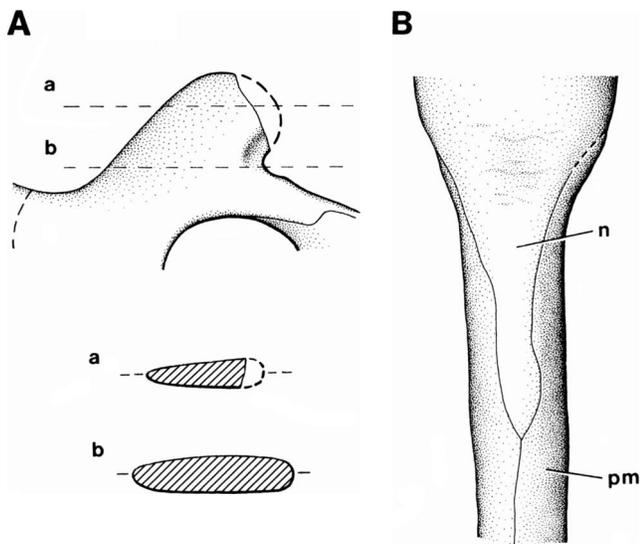


FIGURE 4. Narial region in *Chasmosaurus mariscalensis* (TMM 43098-1). **A**, nasal horn with cross-sections at two levels (a, b), $\times 0.31$; **B**, internarial bar in anterodorsal view, $\times 0.45$.

riorly between the premaxillae for approximately 8 cm (Fig. 4B). A similar nasal process does not occur in northern species of *Chasmosaurus* or found in any other ceratopsid.

The triangular maxilla contains 27 or 28 alveoli, as in the largest maxillae previously discovered in the Aguja Formation (Lehman, 1989). Canadian specimens of *Chasmosaurus* have a similar number of maxillary teeth. The teeth have a strong central keel, subtle fluting to each side of the keel, and low marginal denticles. The cheek is shallow anteriorly but deeply inset posteriorly, as in *P. sternbergii* (MNA Pl.1747) and other chasmosaurines. The depth and anteroposterior extent of the cheek emargination in specimens of *Chasmosaurus* appears to be correlated with the extent of dorsoventral crushing and may not constitute natural variation. Several vascular foramina open on the maxilla along the cheek emargination, with one large foramen opening above the cheek behind the sutural junction of the premaxilla, maxilla, and nasal (Fig. 3), as in other skulls of *Chasmosaurus* (e.g., *Chasmosaurus* sp., RTMP 81.19.17).

The maxillary processes dorsal and ventral to the small antorbital fossa in TMM 43098-1 are proportionately broad, as in other maxillae referred to *C. mariscalensis* (Lehman, 1989:fig. 11C). The large dorsal process contacts the prefrontal, narrowly separating the nasal and lacrimal; this sutural configuration also occurs in other specimens of *Chasmosaurus* (e.g., *C. belli*, ROM 839; *C. russelli*, NMC 2280). The smooth surface of the antorbital fossa, which borders the dorsal margin of the antorbital fenestra, is recessed into the dorsal process of the maxilla as in some other cera-

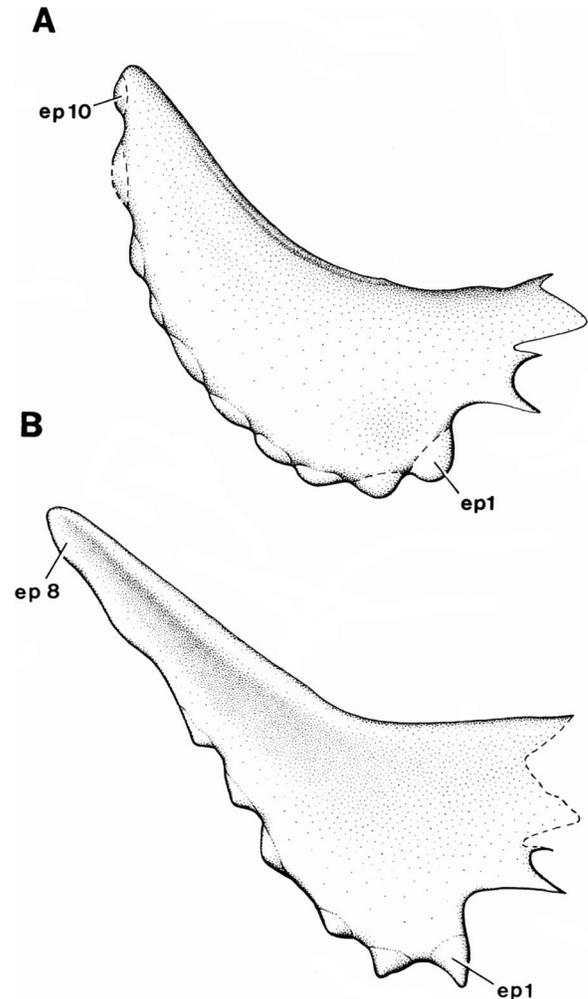


FIGURE 5. Right squamosal of *Chasmosaurus* in lateral view. **A**, *Chasmosaurus mariscalensis* (TMM 43098-1) $\times 0.8$. **B**, *Chasmosaurus belli* (AMNH 5401), $\times 0.10$.

topsids (e.g., *Triceratops*, Hatcher et al., 1907:fig. 22). Its smooth surface contrasts with surrounding areas, suggesting that the skin overlying the fossa was not tightly bound to the bony surface.

Circumorbital Region (Fig. 3)

The circumorbital sutures between the postorbital, jugal, lacrimal, prefrontal, and palpebral are partially, or completely, coossified. The palpebral is fused to the lateral margin of the prefrontal as a rugose prominence, on the anterodorsal margin of the orbit. The long erect supraorbital horncore is solid to its base (43 cm preserved, with 49 cm estimated to tip, as measured along the curve of the horn; Table 1). Several referred adult specimens (Lehman, 1989) have an erect orientation for the supraorbital horncores as well. Judging from a growth series of isolated horncores (Lehman, 1989:fig.

TABLE 2. Measurements (cm) of the squamosal in *Chasmosaurus* and *Pentaceratops*.

Taxon	Maximum length	Maximum width	Length/width ratio
<i>Chasmosaurus mariscalensis</i>			
TMM 43098-1	89	32	2.8
<i>Chasmosaurus russelli</i>			
NMC 2280	78	26	3.0
<i>Chasmosaurus belli</i>			
AMNH 5402	70	27	2.6
AMNH 5401	79	28	2.8
YPM 2016	81	23	3.5
<i>Pentaceratops sternbergii</i>			
MNA Pl.1747	132	35	3.8
AMNH 1624	125	49	2.6

4), the supraorbital horncores straighten and become more erect during growth.

Laterotemporal Region (Fig. 3)

The subtriangular laterotemporal fenestra has a maximum diameter approximately 75 percent that of the orbit, which is relatively large for a ceratopsid. As is typical among ceratopsids, the jugal is T-shaped with the main axis inclined somewhat posteroventrally. On the ventral side of the laterotemporal fenestra, the jugal and squamosal are separated by the quadratojugal, which forms a significant portion of the ventral margin of the opening. In *C. belli* (e.g., ROM 843) and *C. russelli* (e.g., NMC 2280), in contrast, the jugal has a distinct posterior process that contacts the squamosal and excludes the quadratojugal from the margin of the fenestra.

The quadratojugal overlaps the quadrate shaft laterally and extends ventrally to the quadrate condyle. The quadrate and squamosal, as usual in ceratopsids, are not coossified, and the right quadrate is slightly displaced. The large pyramidal epijugal, which is completely fused to the jugal and quadratojugal, projects laterally. The anterior surface of the epijugal is flat and tilted slightly dorsally, with the dorsal margin developed as a rounded crest.

Frill (Figs. 3, 5)

Central and posterior sections of the parietal frill are lacking, and severe transverse compression of the posterior frill has rotated the lateral margin of the right squamosal slightly ventrally from its natural position (Fig. 3). The squamosal is longer in adult *C. mariscalensis* than previously reconstructed on the basis of less complete material (Lehman, 1989:fig. 9A). The maximum width of the squamosal (relative to its length) is similar to that in other chasmosaurines (Table 2), and this measure, therefore, is not diagnostic for *C. mariscalensis*. The squamosal, nevertheless, appears distinctly broader in *C. mariscalensis* because the distal

two-thirds of its lateral margin are convex, rather than straight or gently concave as in most other chasmosaurines (Fig. 5). Thus, the distal two-thirds of the squamosal are proportionately broader in *C. mariscalensis* than in other chasmosaurines.

Ten epoccipitals are present along the margin of the right squamosal, more than have been recorded in any other ceratopsid and one more than in adult specimens of *C. belli*, *C. russelli*, and *P. sternbergii*. Juvenile squamosals of *C. mariscalensis* (Lehman, 1989:fig. 8) and *C. belli* (NMC 1254) have fewer epoccipitals than do those of adults. In TMM 43098-1, only the two anterior epoccipitals are fully coossified with the squamosal; progressive coossification of epoccipitals from anterior to posterior during growth has also been observed in other ceratopsids (Lehman, 1989; Forster, in prep.) and probably also occurred in *C. mariscalensis*.

DISCUSSION

Chasmosaurus mariscalensis

The diagnosis of *Chasmosaurus mariscalensis* was originally based on five characters: broad squamosal; six large epoccipitals; maxillary horizontal shelf absent; premaxillary "posterodorsal extension" absent; long supraorbital horncores (Lehman, 1989:139). The new skull has allowed a revision of these original characters.

The new skull shows that the squamosal is proportionately more elongate in more mature individuals, and that, although the squamosal is distinctly broader in its distal two-thirds, the maximum width of the squamosal is not relatively greater than in other species of *Chasmosaurus* or most other chasmosaurines. There are ten, rather than six, epoccipitals in TMM 43098-1, due to its larger size relative to previously described material. These tab-shaped or elliptical epoccipitals do not appear to differ in size from those in other adult chasmosaurines. The anterior portion of the maxillary cheek emargination is indeed shallow in TMM 43098-1, in contrast to the deeply emarginated cheeks found in specimens of other species of *Chasmosaurus*. The appearance of a more marked cheek emargination in other skulls of *Chasmosaurus*, however, may be the result of dorsoventral crushing of the skull (e.g., in skulls of *C. belli*: deep cheek in NMC 2280 and AMNH 5402 versus shallow cheek in ROM 839). Furthermore, a shallow anterior cheek emargination may characterize other chasmosaurines (e.g., *P. sternbergii*, MNA Pl.1747). The new skull also shows that a complete premaxillary "posterodorsal process" extends as far posteriorly in *C. mariscalensis* as in other species of *Chasmosaurus*. The absence of the premaxillary "posterodorsal process" in previously described specimens was due to damage and poor preservation. Finally, when viewed within a cladistic framework, the long supraorbital horncores in *C. mariscalensis* may constitute a retained primitive condition—a condition that was present in the common chasmosaurine ancestor. The short supraorbital horncores in other species of

Chasmosaurus, in other words, may represent the evolutionary novelty, as a reversal from a primitive, long-horned chasmosaurine condition (see Discussion, Character 5).

Three other cranial characters, however, confirm that *C. mariscalensis* represents a distinct species. First, the erect orientation of the supraorbital horncores in *C. mariscalensis* is unique among ceratopsids. The horncore rises dorsally at approximately 85° from the maxillary tooth row in adults (Fig. 3), as measured along the straight axis of the proximal half of the horncore. Although more difficult to estimate in fragmentary materials, the holotype horncore and adult referred horncores in *C. mariscalensis* all seem to show the nearly vertical orientation of the supraorbital horncore (Lehman, 1989). The orientation of the supraorbital horncore in other ceratopsids, in contrast, varies between 45° and 60° from the maxillary tooth row (Dodson and Currie, 1990:fig. 29.3). Second, the long median process of the nasal, which projects anteriorly between the premaxillae (Fig. 4B), is unique among ceratopsids. And third, as discussed briefly above, the distal two-thirds of the squamosal have a convex lateral margin, resulting in a broader distal squamosal than is present in other chasmosaurines (Fig. 5). In addition, the keel-shaped nasal horn is more strongly compressed transversely than in other chasmosaurines and may eventually prove to be diagnostic for *C. mariscalensis*. In other species of *Chasmosaurus*, the cross-sectional shape of the nasal horn varies from subcircular (e.g., *C. belli*, ROM 839) to elliptical (e.g., *C. belli*, AMNH 5402). As with TMM 43098-1, the discovery of additional specimens may further clarify the structure of *C. mariscalensis* and provide answers to these questions.

Chasmosaurus

Chasmosaurus mariscalensis shares several derived features with *C. belli* and *C. russelli*, suggesting that the genus *Chasmosaurus* is monophyletic. These characters are described below (see Appendix for a tabulation of character-states among chasmosaurines).

1. Thin premaxillary flange along the anterior margin of the external naris (Fig. 3, pmfl). In *Chasmosaurus*, the entire anterior margin of the external naris is bordered by a thin flange of the premaxilla along the posterior side of the narial strut. The flange articulates with its opposite in the midline to form a thin nasal septum. In other chasmosaurines, this lamina of bone is either limited to the anterodorsal corner of the external naris (e.g., *P. sternbergii*, MNA Pl.1747) or is absent (e.g., *Triceratops*, CM 1221). The condition in centrosaurines is difficult to compare, given the less complex configuration of the premaxilla, but a distinct marginal lamina of bone is not developed.

2. Supraorbital horncores curved posteriorly (Fig. 3). In *Chasmosaurus*, the axis of the supraorbital horncore curves posteriorly. In *C. mariscalensis* the curvature decreases with growth but is still apparent in the adult.

In *C. belli* and *C. russelli*, the horncore is shorter but the posterior curvature is usually discernible. The horncore in juvenile *C. mariscalensis* (e.g., UTEP P.37.7.083) is identical to that in juvenile *C. belli* (e.g., NMC 1254). In all other chasmosaurines, the supraorbital horncores curve anteriorly (Dodson and Currie, 1990:fig. 29.3). In centrosaurines, supraorbital horncores are not well enough developed to evaluate their curvature.

3. Straplike posterior border of parietal fenestra (Fig. 6A). In *Chasmosaurus*, the straplike posterior border of the parietal fenestra is more than twice as broad transversely as deep proximodistally (*C. mariscalensis*, Lehman, 1989:fig. 7A; *C. belli*, Lull, 1933). The narrow posterior margin is not necessarily correlated with the large size of the fenestra in *Chasmosaurus*. *P. sternbergii* also has very large parietal fenestrae, but the posterior parietal margin is proportionately deeper than in *Chasmosaurus* (Fig. 6B). In other chasmosaurines and centrosaurines, the posterior margin of the parietal fenestra is also proportionately much deeper (Dodson and Currie, 1990:fig. 29.3). Although some basal neoceratopsians (e.g., *Protoceratops*) also have a straplike posterior border, a posterior border of deeper proportions is present in *Montanoceratops* and thus would be primitive within Ceratopsidae.

4. Posterior frill very broad (Fig. 6A). In *C. belli* and *C. russelli*, the frill expands distally as a broad, triangular shield, with a maximum transverse width more than twice the width across the orbital skull roof. In other ceratopsids, the maximum width of the frill is less than twice the width of the interorbital skull roof. *Torosaurus* is the only exception and appears to have evolved its broad frill independently. The dimensions of the posterior frill in *C. mariscalensis* cannot be determined.

Two characters shared by the northern species, *C. belli* and *C. russelli*, are absent in *C. mariscalensis*.

5. Short supraorbital horncores (Fig. 6A). The supraorbital horncores in *C. belli* and *C. russelli* are shorter than in any other chasmosaurines and usually consist of low, hooked prominences (e.g., *C. belli*, AMNH 5402, ROM 839, ROM 843; *C. russelli*, NMC 2280, NMC 8800). In one specimen of *C. belli* (AMNH 5401; Lull, 1933), however, the horncores reach a length and diameter somewhat more than half that seen in other adult chasmosaurines. The supraorbital horncore dimensions in *C. belli* and *C. russelli* are clearly very small, and this appears to represent a partial reversal within the genus *Chasmosaurus* to the primitive ceratopsian condition, which is retained in centrosaurines.

6. Jugal-squamosal contact below the laterotemporal fenestra. In *C. belli* and *C. russelli*, a posterior process of the jugal passes under the laterotemporal fenestra, contacting the squamosal and excluding the quadratojugal from the border of the fenestra. This posterior jugal process is absent in *C. mariscalensis* (Fig. 3), *Pentaceratops*, and other chasmosaurines, and as a re-

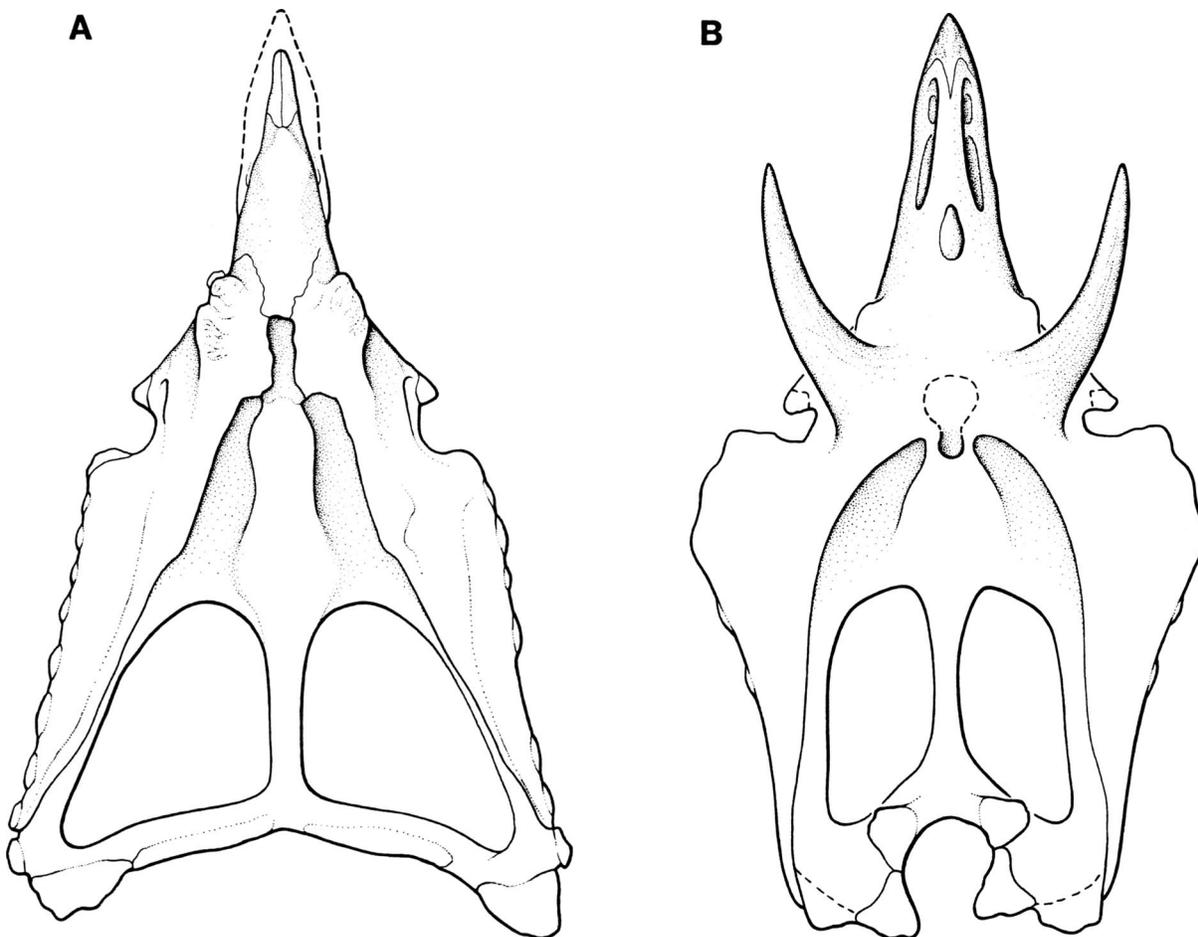
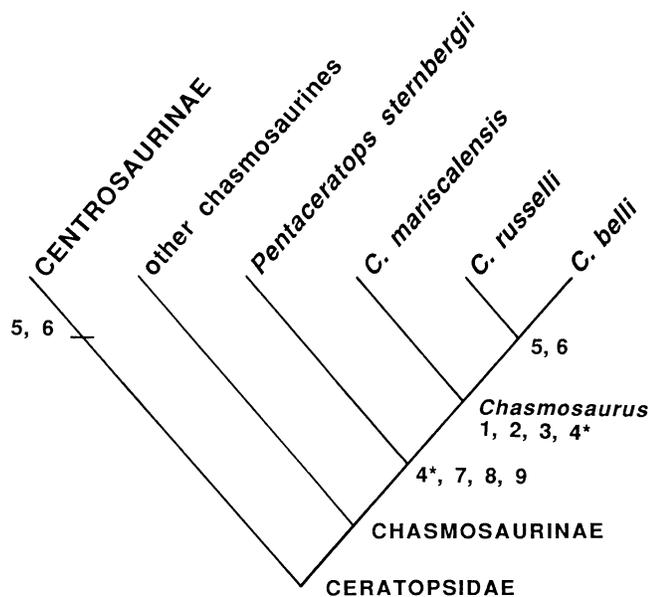


FIGURE 6. Chasmosaurine skulls in dorsal view. **A**, *Chasmosaurus russelli* (based on ROM 843). **B**, *Pentaceratops sternbergii* (based on AMNH 6325 and MNA Pl.1747).



sult, the quadratojugal borders the laterotemporal fenestra. A very similar posterior jugal process, however, is developed in all centrosaurines (e.g., *Centrosaurus*). But given the absence of jugal-squamosal contact below the fenestra in basal ceratopsians (e.g., *Psittacosaurus*, *Protoceratops*), it is more parsimonious to suppose that the posterior jugal process evolved independently in centrosaurines and in the common ancestor of *C. belli* and *C. russelli*.

Chasmosaurus and *Pentaceratops*

After comparisons between *Chasmosaurus* and other ceratopsids, we have identified three characters that

FIGURE 7. Cladogram showing relationships of three species of *Chasmosaurus* and *Pentaceratops sternbergii*, based on analysis of nine characters. This tree has a length of 11 steps and a consistency index of 0.82. Character numbers show position of apomorphic states on the most-parsimonious tree (* = equivocal; see Appendix for character list and character-state distributions).

support a sister-group relationship between *Chasmosaurus* and *Pentaceratops*.

7. Posterior process of the premaxilla with blunt, finger-shaped distal end inset on the nasal (Fig. 3). The unusual shape and position of the distal end of the posterior process of the premaxilla has been recognized previously as a derived similarity uniting *Chasmosaurus* and *Pentaceratops* (Lehman, 1990; Forster, 1990). In other chasmosaurines, the process is evenly tapered distally and is situated on the maxilla-nasal suture. In centrosaurines, the posterior process of the premaxilla is broad and spatulate and is also situated on the maxilla-nasal suture.

8. Large parietal fenestrae (Fig. 6). The parietal fenestrae are very large in *Chasmosaurus* and *Pentaceratops*, with a proximodistal diameter that exceeds the preorbital length of the skull. The preserved portions of the parietal and squamosal in *C. mariscalensis* strongly suggest that this species had parietal fenestrae comparable in size to that in other species of *Chasmosaurus*. In all other ceratopsids, the diameter of the parietal fenestrae is less than preorbital length.

9. Marked median embayment in posterior parietal margin (Fig. 6). In *Chasmosaurus* and *Pentaceratops*, the posterior margin of the frill has a V-shaped median embayment. In *C. russelli* (Fig. 6A), *C. mariscalensis* (Lehman, 1989), and *P. sternbergii* (Fig. 6B), the embayment is marked and is not merely a notch between the innermost pair of epoccipitals. In *C. belli*, the depth of the embayment varies from shallow (YPM 2016) to deep (ROM 843). A similar embayment of the posterior frill margin is not present in other chasmosaurines. Centrosaurines also lack a comparatively deep median embayment of the parietal, although the anteriorly curled innermost pair of epoccipitals in adults gives the impression of a deep parietal embayment.

CONCLUSIONS

The discovery of a nearly complete skull of *Chasmosaurus mariscalensis* in the Aguja Formation of Texas permits a more detailed comparison of this southern chasmosaurine to northern species of *Chasmosaurus*, to *Pentaceratops sternbergii*, and other northern chasmosaurines. *C. mariscalensis* exhibits several unique cranial features, confirming an earlier study (Lehman, 1989) that described the Texas ceratopsid as a distinct species.

Comparisons to other chasmosaurines suggests that *C. mariscalensis* is most closely related to the Canadian species, *C. belli* and *C. russelli* (Fig. 7, characters 1–4), rather than a transitional form between these species of *Chasmosaurus* and *Pentaceratops sternbergii*, as previously hypothesized (Lehman, 1989). The genus *Chasmosaurus*, in turn, appears to be most closely related to *Pentaceratops* based on several cranial characters (Fig. 7, characters 7–9).

Analysis of the new skull of *C. mariscalensis* confirms the endemism of southern chasmosaurines during the Campanian. If the phylogenetic conclusions of

this study are sustained, the roughly contemporaneous southern chasmosaurines, *C. mariscalensis* and *P. sternbergii*, are not each other's closest relatives. Rather, *C. mariscalensis* is closer to the northern species of *Chasmosaurus*, *C. belli* and *C. russelli*. This phylogenetic interplay between southern and northern chasmosaurines necessarily involves a more complex biogeographic history than a single vicariant event separating once continuous southern and northern ceratopsid populations or a single dispersal event to the south from the more diverse northern ceratopsid faunas. Undoubtedly, the biogeographical relations of chasmosaurines during the Late Cretaceous were more complex, with movement of chasmosaurines both north and south along the western North American cordillera. Phylogenetic hypotheses that include all ceratopsids and careful description of rare ceratopsid remains from Maastrichtian deposits in the south will improve our understanding of the biogeographic history of ceratopsids.

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APPENDIX

Character-state distributions are listed below for the nine binary characters discussed in the text that vary among *Pentaceratops sternbergii* and three species of *Chasmosaurus* (Fig. 7). "Other chasmosaurines" and centrosaurines were chosen as successive outgroups to *Pentaceratops* and *Chasmosaurus*, and the monophyly of each of these outgroups is supported

by numerous synapomorphies (e.g., Lehman, 1990; Forster, 1990). The data matrix was analyzed using the exhaustive search algorithm in PAUP (Swofford, 1985), and one most-parsimonious tree was determined. This tree had a length of 11 steps with a consistency index of 0.82.

Characters and Character-States:

1. Flange along anterior margin of external naris: partial (0), complete (1).
2. Supraorbital horncore curvature: anterior (0), posterior (1).
3. Dimensions of the posterior margin of parietal fenestra: transverse width less (0), or more (1), than twice anteroposterior depth.
4. Posterior frill transverse width: less (0), or more (1), than twice skull width across the orbits.
5. Supraorbital horncore length: long (0), short (1).
6. Jugal-squamosal contact below the laterotemporal fenestra: absent (0), present (1).
7. Premaxillary posterolateral process: evenly tapered with tip on maxilla-nasal suture (0), abruptly narrowed with tip isolated on nasal (1).
8. Parietal fenestra diameter: less (0), or more (1), than preorbital length.
9. Parietal posteromedian embayment: weak or absent (0), marked (1).

Character-State Distributions.

Taxa	Characters	
	5	9
<i>Chasmosaurus mariscalensis</i>	111?0	0111
<i>Chasmosaurus belli</i>	11111	1111
<i>Chasmosaurus russelli</i>	11111	1111
<i>Pentaceratops sternbergii</i>	00000	0111
Other chasmosaurines	00000	0000
Centrosaurinae	0N001	1000

0 = primitive state; 1 = derived state; N = not available due to transformation; 0 = primitive state for taxon with some ingroup variation; ? = not available due to lack of preservation.

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