Journal of Vertebrate Paleontology 27(4):944–962, December 2007

ARTICLE

A REVISION OF THE LATE CAMPANIAN CENTROSAURINE CERATOPSID GENUS *STYRACOSAURUS* FROM THE WESTERN INTERIOR OF NORTH AMERICA

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ABSTRACT—The centrosaurine ceratopsid genus *Styracosaurus* is known from multiple specimens and a multigeneric bone bed in the upper 30 m of the Late Cretaceous Dinosaur Park Formation of southern Alberta, and a single specimen (*S. ovatus*) from approximately time equivalent sediments of the Two Medicine Formation of Montana. Key cranial elements (nasals and postorbitals) of *Styracosaurus* appear to undergo similar ontogenetic changes as documented in *Centrosaurus*. Although all adult-sized centrosaurines except *Centrosaurus apertus* are known to possess spike-like parietal ornamentation at the P3 position on the parietal, only *Styracosaurus* has the P4 ornamentation expressed as a well-developed spike. *Styracosaurus* shows intraspecific variation in the shape of the more anteriorly placed P5–P7 ornamentation that are either the typical unmodified crest-shaped epoccipitals of other centrosaurines or are developed as short spikes. *S ovatus* from Montana is retained as a valid species based on the autapomorphic convergence of the P3 spikes toward the midline.

INTRODUCTION

Although the late Campanian centrosaurine ceratopsid *Styracosaurus albertensis* Lambe, 1913 is one of the most familiar of the horned dinosaurs, it is actually known from only a few described specimens. Lambe (1913) originally described the taxon based on an almost complete skull (CMN 344; Figs. 1 and 2) collected by C.H. Sternberg from what is now southeastern Dinosaur Provincial Park, Alberta. The complete postcranium associated with this skull was collected in 1935 by his son Levi for the University of Toronto, and the complete skeleton now resides in the collections of the Canadian Museum of Nature in Gatineau, Quebec (Holmes, et al. 2006). This large bodied herbivore is unusual in having a pair of long spikes projecting from the caudal margin of the parietal frill.

A second species, *S. ovatus* Gilmore, 1930 (Fig. 3), was described on the basis of a partial frill, comprising most of the caudal and lateral parietal bar. This specimen was collected in 1928 by George Sternberg from the Two Medicine Formation, Glacier County, Montana. Dodson and Currie (1990:611) listed *S. ovatus* as a valid species, partially on the strength of the then recent (1986) discovery of putative new *Styracosaurus* material from the same formation and region. Although initially this new material was referred to in the press as *S. makeli* (Czerkas and Czerkas, 1990), this name is now a *nomen nudum*, and the material has been described as a new genus, *Einiosaurus procurvicornis* (Sampson, 1995).

A third species, *S. parksi* Brown and Schlaikjer 1937 (Brown and Schlaikjer 1937:Fig. 3) was described based on a partial skeleton and a fragmentary skull (AMNH 7372) collected by Barnum Brown for the American Museum of Natural History in 1915 from what is now Dinosaur Provincial Park. The skeleton was mounted and is now on display at the AMNH in New York City. Although the skull was reconstructed to resemble that of *S. albertensis*, it is unclear now how much of the skull is actually real bone or how many of the collected fragmentary parietal spikes were incorporated into the frill (several parietal spike fragments from the specimen are cataloged in the AMNH collections). *S. parksi* was distinguished from *S. albertensis* solely on the shape of its squamosal. Brown and Schlaikjer (1937:3–4) state that, "the squamosal, when compared with that of *S. albertensis*, is distinctly longer, and is sub-quadrangular in outline. In *S. albertensis* it is broader than long and is markedly pointed posteriorly. Likewise, the external border in the Ottawa specimen presents five convexities [marginal scallops] whereas in *S. parksi* there are three large, blunt, dorsoventrally compressed projections."

Excluding the parietal ornamentation, the similarities between *Centrosaurus apertus* and *Styracosaurus albertensis* (both confined to one formation [Fig. 4] and a limited geographical area [Fig. 5]) have long been noted (e.g. Ryan and Russell, 2005). Dodson (1987) suggested that the differences might be due to sexual dimorphism, with *S. albertensis* representing the male morph of *C. nasicornis*. In 1990 Dodson refined his earlier work on centrosaurine ceratopsid taxonomy and synonymized all the *Centrosaurus* species known at the time with *C. apertus*. As part of the same work he tentatively posited, ". . . that it [*C. nasicornis*] is actually a female *Styracosaurus albertensis* . . . , 1990:241," and suggested that . . . "a case could be made that *Centrosaurus* and *Styracosaurus albertensis* should be regarded as congeneric," although he did not formally advocate this. However, in the same year Dodson and Currie listed *C. nasicornis* as a junior synonym of *S. albertensis* Lambe, 1913 in their review of the Ceratopsia. This designation has also been retained in the recent review of the Ceratopsia (Dodson et al., 2004).

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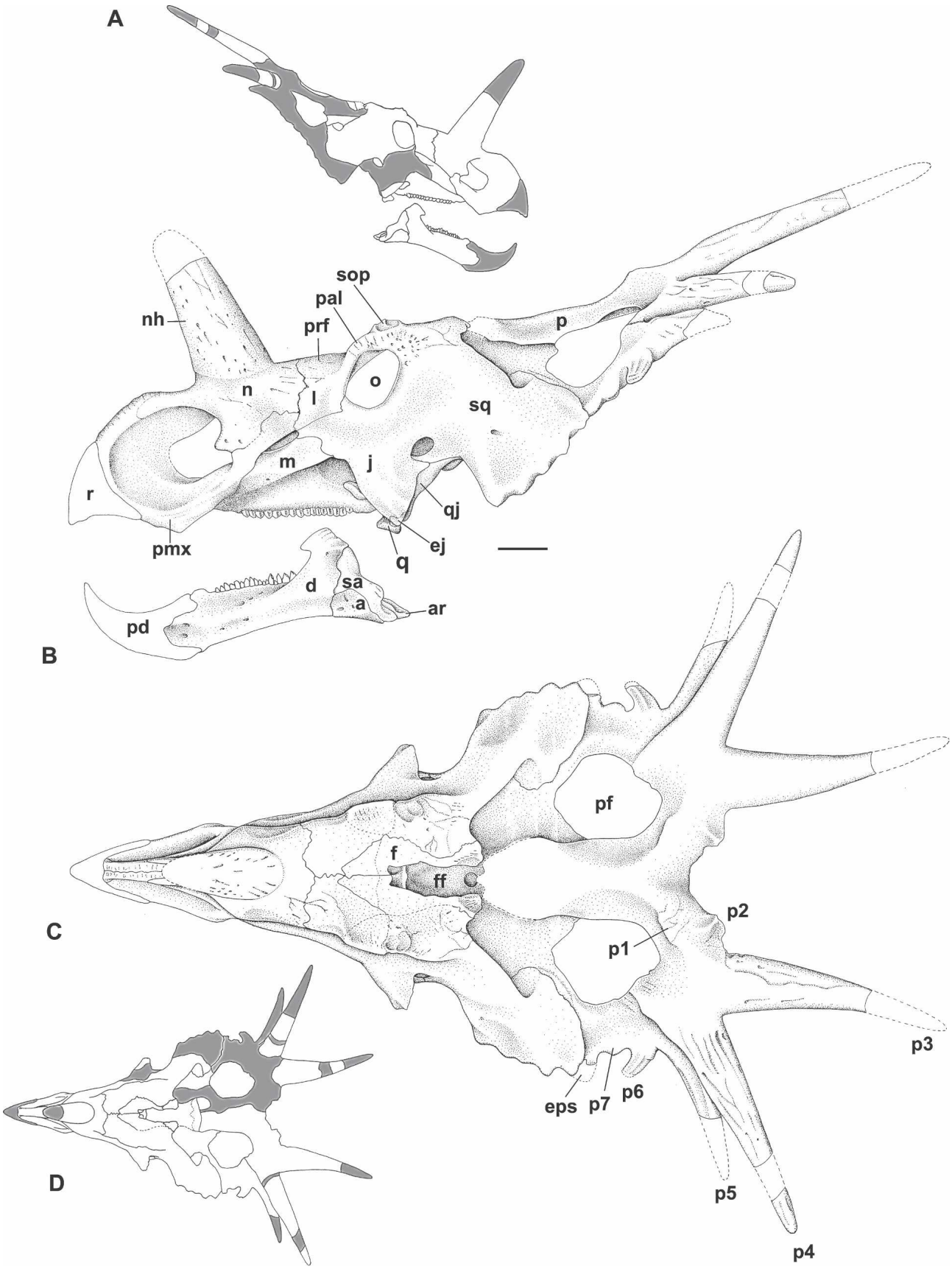
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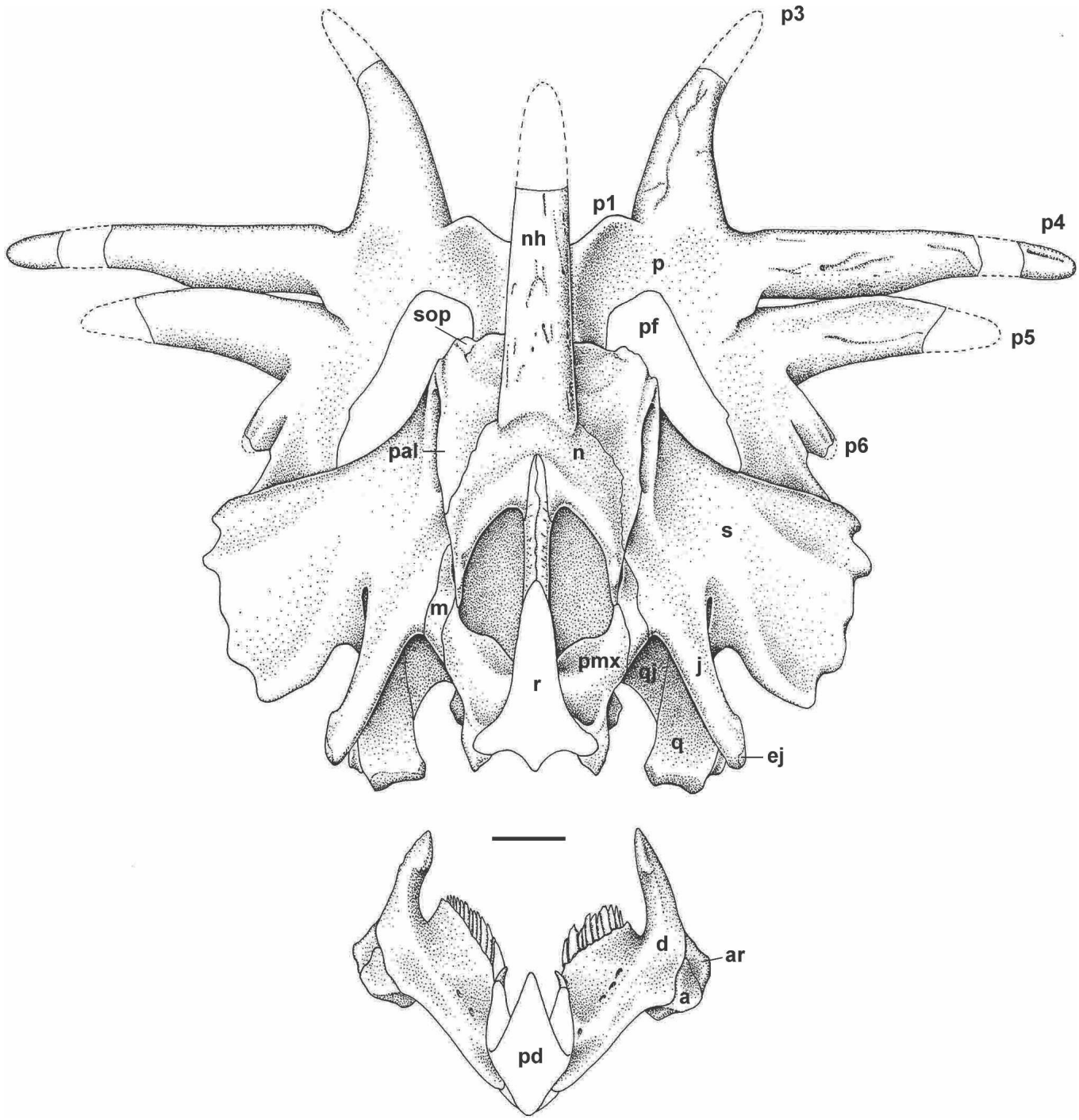

FIGURE 2. *Styracosaurus albertensis* Lambe 1913, CMN 344, holotype. reconstruction of the skull in anterior view. Missing portions of the skull are reconstructed assuming bilateral symmetry. Portions not preserved on either side or on the midline are drawn in outline. **Abbreviations** as in Figure 1. Scale bar equals 10 cm.

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FIGURE. 1. *Styracosaurus albertensis* Lambe 1913, CMN 344, holotype. Reconstruction of the skull. **A**, missing portions reconstructed in plaster are shaded. **B**, reconstruction in left lateral and **C**, dorsal views. Missing portions reconstructed assuming bilateral symmetry. **D**, missing portions reconstructed in plaster are shaded. No attempt has been made to correct for the apparent foreshortening of the damaged left lateral parietal bar. **Abbreviations** (restored bones drawn in outline only): **a**, angular; **ar**, articular; **d**, dentary; **ej**, epijugal; **eps**, epoccipital straddling the parietal-squamosal margin; **f**, frontal; **ff**, frontal fontanelle; **j**, jugal; **l**, lacrimal; **m**, maxilla, **n**, nasal; **nh**, nasal horncore; **o**, orbit; **p1–7**, parietal loci or processes; **p**, parietal; **pal**, palpebral; **pd**, predentary; **pmx**, premaxilla; **prf**, prefrontal; **q**, quadrate; **qj**, quadratojugal; **r**, rostral; **sa**, surangular; **sop**, supraorbital pitting; **sq**, squamosal. Scale bar equals 10 cm.

The synonymy of *S. parksi* with *S. albertensis* by Dodson and Currie (1990) was also followed by Dodson et al. (2004). Although neither group of authors provided a justification of their synonymy it is now known that the differences in the squamosal that Brown and Schlaikjer (1937) used to support *S. parksi* fall within the normal range of variation seen in *S. albertensis*. Of note is that the quarry of AMNH 7372, long lost, was relocated by Darren Tanke of the Royal Tyrrell Museum in 2006 in the upper portion of the Dinosaur Park Formation (Tanke, pers. com., 2006).

Styracosaurus albertensis is known from one bone bed (BB 42; Fig. 5) from the upper Dinosaur Park Formation of Dinosaur Park, as well as from several isolated specimens from the upper Dinosaur Park Formation. Unlike the paucispecific *Centrosaurus apertus* bone beds from lower in formation, BB 42 is a mixed bone bed, dominated by indeterminate hadrosaur remains, and comprising approximately 40% ceratopsid material, with all diagnosable material being referred to *Styracosaurus albertensis* (Visser, 1984). Other reported *Styracosaurus* bone beds (e.g., BB 167) from the formation have, upon further investigation, proven to be mixed faunal bone beds containing non-diagnostic ceratopsid remains. Many museum collections contain elements (mostly cranial) that are labeled as, or have been referred to, *Styracosaurus*. These comprise mostly fragmentary probable frill spikes, or postorbitals, in which the horncore has been highly modified or lost due to remodeling by the development of supraorbital pitting. However, in the latter case, these elements cannot be distinguished from similarly remodeled elements of *Centrosaurus apertus* and *C. brinkmani*, (Ryan and Russell, 2005) and in almost all cases the locality and stratigraphic data are imprecise,

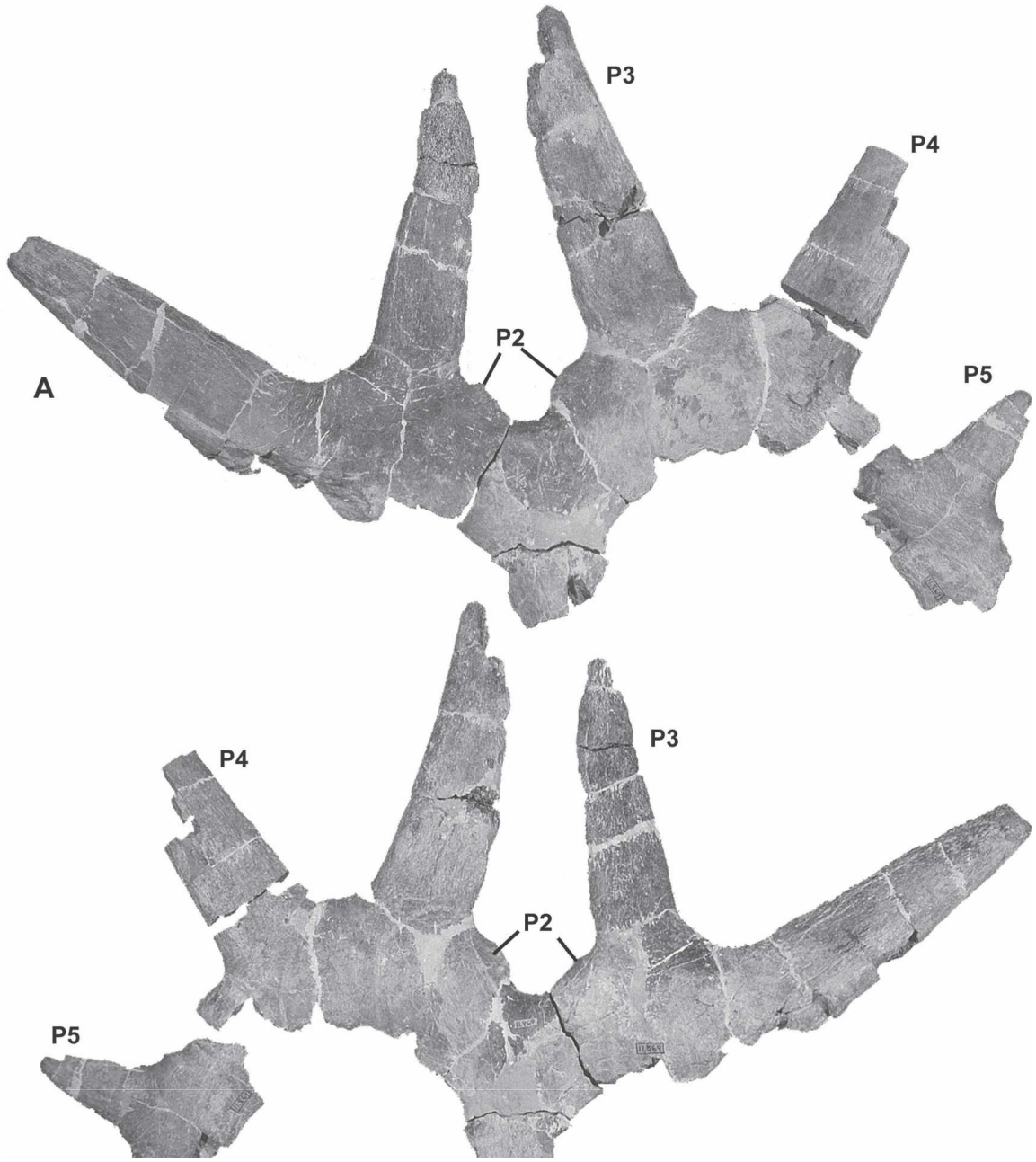

FIGURE 3. *Styracosaurus ovatus* Gilmore 1930, USNM 11869. Posterior parietal in **A**, dorsal view; **B**, ventral. **Abbreviations** as in Figure 1. Scale bar equals 10 cm.

although most are believed to have been collected from the region that now includes Dinosaur Provincial Park.

Today, other centrosaurines are also known to possess parietal spikes (e.g., *Achelousaurus*, *Centrosaurus brinkmani*, *Einiosaurus*, and *Pachyrhinosaurus*) and the original diagnosis for *Styracosaurus* is inadequate to differentiate it from other centrosaurines. In addressing the confusion, we present here a revised diagnosis of the genus *Styracosaurus* and of the two currently recognizable species of this taxon along with a more extensive description of the skull of the holotype specimen *Styracosaurus albertensis*, *S. ovatus*, other significant diagnostic specimens from Alberta, and selected elements from BB 42.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York; **CMN**, Canadian Museum of Nature, Ottawa, Canada; **ROM**, Royal Ontario Museum, Toronto, Canada; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; **USNM**, United States National Museum, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

ORNITHISCHIA Seeley, 1888
CERATOPSIA Marsh, 1890
NEOCERATOPSIA Sereno, 1986
CERATOPSIDAE Marsh, 1888
CENTROSAURINAE Lambe, 1915
Genus *Styracosaurus* Lambe, 1913

Diagnosis—(from Lambe, 1913): "skull massive, elongate, pointed in front, and greatly expanded behind to form a neck-frill with long, robust, tapering outgrowths projecting obliquely backward and outward from its posterior border. Fontanelles of moderate size within the coalesced parietals. Squamosals somewhat quadrangular and entering entirely into the formation of the front part of the frill. Postfrontal fontanelle large. Supratemporal fossae opening widely behind. Nasal horncore large, upright, straight, rising from the back of the nasals. Supraorbital horncore incipient."

"From *Monoclonius*, Cope, it differs in its greater size, the smaller fontanelles of the frill, the larger squamosals, and in having a straight, upright nasal horn instead of one which curves backward."

Emended Diagnosis—Centrosaurine ceratopsid possessing parietal

ornamentation with long, dorsoventrally compressed, tapering spikes at loci 3 and 4; spike 3 is longer than spike 4; loci 5–7 can be developed as short spikes.

Type Species—*Styracosaurus albertensis* Lambe 1913.

Emended Specific Diagnosis: Parietal ornamentation at locus 1 poorly developed as short, blunt, dorsally or rostrodorsally oriented processes; processes at locus 2 typically developed as small medially curled hooks; occasionally developed as small, dorsoventrally depressed tabs; tapering, dorsoventrally depressed, caudolaterally curled spikes at loci 3 and 4; locus 3 spikes divergent and longest on frill; locus 3 spikes greater in length to those of locus 4; loci 5–7 ornamentation variably developed as short, spike-like processes or are unmodified as preserved on other centrosaurines.

Differential Diagnosis—The erect, *Centrosaurus*-like adult-sized nasal horn differs from *Achelousaurus*, *Einiosaurus*, and

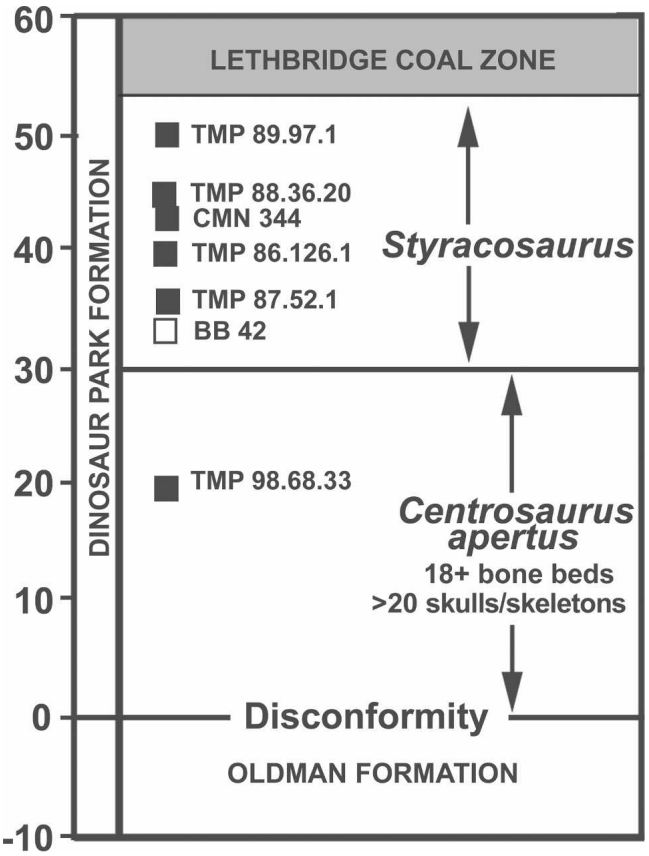

FIGURE 4. Stratigraphic distribution of *S. albertensis* (black boxes) from southern Alberta above the regional disconformity (0.0 m) separating the Dinosaur Park and Oldman formations. White box represents bone bed (BB) 42. TMP 98.68.33 has been catalogued as a *Styracosaurus* parietal spike but probably represents a *Centrosaurus apertus* P1 hook.

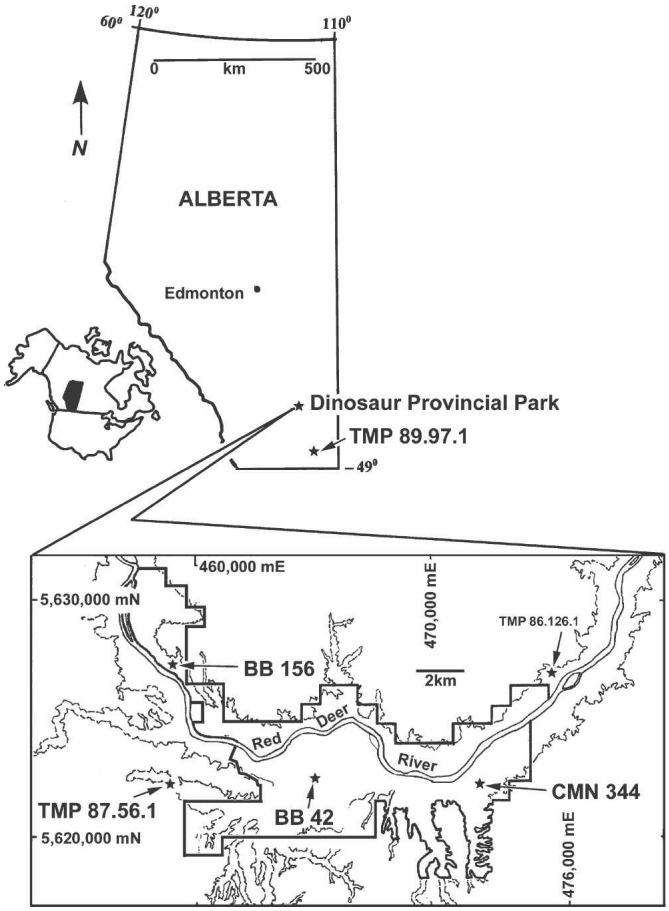

FIGURE 5. Location of selected *Styracosaurus* specimens from southern Alberta.

Pachyrhinosaurus that develop a prominent boss. Like *Achelousaurus*, *Einiosaurus*, and *Pachyrhinosaurus* the unmodified, adult-sized postorbital ornamentation is a low, rounded horn unlike the large pyramidal horn of *Centrosaurus apertus* or the laterally directed pyramidal horn of *C. brinkmani*. The adult-sized postorbital ornamentation differs from the massive bossing of *Achelousaurus*, *Einiosaurus*, and *Pachyrhinosaurus*, and can be modified as for *Centrosaurus apertus* by the development of supraorbital pitting that can eliminate the postorbital horn. The subadult postorbital horncore resembles the pyramidal horn of *C. apertus*. Unlike *Achelousaurus*, *Einiosaurus*, *Pachyrhinosaurus* (and possibly *Styracosaurus ovatus*), ornamentation is present at locus 1, but comprises only incipient 'hooks' on mature parietals. These do not develop into robust procurving hooks as they do in *Centrosaurus*. It shares with *Centrosaurus apertus* and *Pachyrhinosaurus* the development of medially curled processes at locus 2, although these can be variably developed and can, in some specimens, resemble the short, tab-like processes seen on *Achelousaurus*, *Einiosaurus* and *S. ovatus*. With *Achelousaurus*, *Einiosaurus*, and *Pachyrhinosaurus*, *Styracosaurus* shares the development of a long, robust spike at locus 3. As in *Achelousaurus*, this spike has a gentle caudolateral curve to the shaft and differs from that of *Einiosaurus* which is straight with a caudally directed tip; *Pachyrhinosaurus* in which it is directed laterally with rostrally curled tips, and *S. ovatus* in which the locus 3 spikes are straight and converge towards the midline.

Comments—This species may exhibit sexual dimorphism in the development of the locus 2 and loci 5–7 ornamentation.

Distribution—Stratigraphically confined to the upper 30 m of the Dinosaur Park Formation, Alberta. All specimens from the area of Dinosaur Provincial Park, Alberta except for one specimen from Sage Creek near Onefour, Alberta. **Synonym**—*S. parksi* Brown and Schlaikjer, 1937.

Type Specimen—CMN 344.

Assigned Specimens—AMNH 5372, AMNH 5361, ROM 1436, TMP 86.126.1, TMP 89.91.1, all ceratopsid material from bone bed 42, Dinosaur Provincial Park, Alberta.

Styracosaurus ovatus Gilmore, 1930

Diagnosis–(from Gilmore, 1930:36): "The two processes forming the hindermost pair lack the tips but it is quite evident that they are not as long as in the Canadian specimen [*S. albertensis*]." "Furthermore, these two horns are convergent as opposed to the divergent processes in *S. albertensis*."

Emended Diagnosis—locus 3 and 4 spikes straight, dorsoventrally depressed; locus 3 spikes convergent towards midline; locus 4 spikes caudolaterally directed.

Type specimen USNM 11869

Distribution—known from a single specimen collected from T.37 N., R.8 W., Milk River, Blackfoot Indian Reservation, Glacier County, Montana, upper Two Medicine Formation.

REDESCRIPTION OF THE HOLOTYPE OF *STYRACOSAURUS ALBERTENSIS* LAMBE 1913 (CMN 344)

The skull of CMN 344 (Figs. 1, 2) is currently configured as a mounted specimen supported from below by a steel armature that partially covers the ventral side of the palate and frill, rendering these regions inaccessible for study. The type skull (NMC 344) was originally described in a short paper by Lambe as a "magnificent specimen . . . . almost perfect on the left side and is in a splendid state of preservation" (Lambe 1913, p. 109). Although he goes on to note that the nasal horncore and some of the frill spikes on the left side are incomplete, the rostral and lower jaws were absent, and the jugal and frill margin on the right side had suffered damage, the impression given is one of a virtually compete skull. Subsequently published illustrations (e.g., Dodson and Currie, 1990; Dodson et al., 2004) have reinforced this impression. A detailed examination of NMC 344 was undertaken to verify this. It was determined that, although the left side is indeed largely complete, a surprising amount of the skull has been reconstructed in plaster (Fig. 1A and D).

Lambe reported that "On the right side, the jugal had fallen to pieces and the lateral border of the frill had suffered some damage from exposure. The posterior processes had been broken off and fractured, but, with the exception of a few fragments, they were recovered and have been restored and replaced in position." Examination of the specimen revealed that the right jugal, as well as the posterior portion of the right squamosal, and the entire right side of the frill have been reconstructed in plaster. At best, there are a few islands of surficial bone set in plaster outside of the main preserved parts of the skull. Only portions of two of the three larger right frill spikes are preserved (Fig. 1A).

The complete absence of the right side of the frill is unfortunate, because this information has the potential to shed light on an apparent anomaly on the preserved left side of the frill. Lateral to the parietal fenestra, the left lateral parietal bar is abnormally thickened at the base of the middle major spike (P4, Fig. 1B). Close examination of the region indicates that this is a consequence of a transverse fracture and subsequent telescoping of the bar, with the portion posterior to the fracture having been displaced anteriorly, overriding the anterior portion of the bar for a distance of approximately six cm. Although the break was largely healed at the time of death, the anterior end of the fracture is still visible on the ventral surface of the bar. As a consequence of this dislocation, the base of the P4 spike overlies the base of the P5 spike, and the frill has been abnormally foreshortened. How this affected the contralateral side of the frill is unknown, because it is not preserved. Although it is impossible to be sure how such an injury would affect growth of the frill, we have attempted to compensate for the injury by retracting the posterior portion of the frill six cm. An outline of the hypothesized undamaged frill is rendered in Figure 6B (right side). Measurements of significant parameters (Fig. 7) are listed at http://www.vertpaleo.org/publications/jvp/contents-27-4.cfm.

The skull has also undergone some dorsoventral crushing resulting in the displacement of the maxilla dorsally and the slight compaction of the nasal into the underlying bones. Additionally the parietal has been pulled back from the skull such that the anterior margin of the parietal midline bar, which forms the posterior wall of the frontal fontanelle, has been separated from it by approximately 100 mm. This has also caused the frill to take on a curved appearance, somewhat exaggerated by the natural ventral bowing of the parietal spikes. Despite these postmortem alterations, the significant features of the skull have not been appreciably distorted, and it can be reconstructed with confidence (Fig. 1).

Styracosaurus has been recognized (Dodson, 1990) as being similar to the well described *Centrosaurus apertus* (Lull, 1933), differing only in details of the ornamentation of the nasal, postorbital and parietal. Only these elements are discussed in detail in this paper. The now prepared postcrania will be described elsewhere.

Nasal—The straight, robust nasal horncore of NMC 344 (Fig. 1) is incomplete distally. According to Lambe (1913: 107), "at the time of discovery of the skull the nasal horncore had been broken off a little below its midheight . . . ." The missing portion was subsequently reconstructed, presumably by extending the straight anterior and posterior margins of the horncore from their base to their dorsal intersection, producing a horn of 570 mm (Lambe, 1913, Plates X–XII). However, if the horncore tapered to a blunt point, as it does in most specimens of *Centrosaurus* and the disarticulated *Styracosaurus* nasals found at bone bed 42 (Fig. 8), the total horncore length in NMC 344 would have

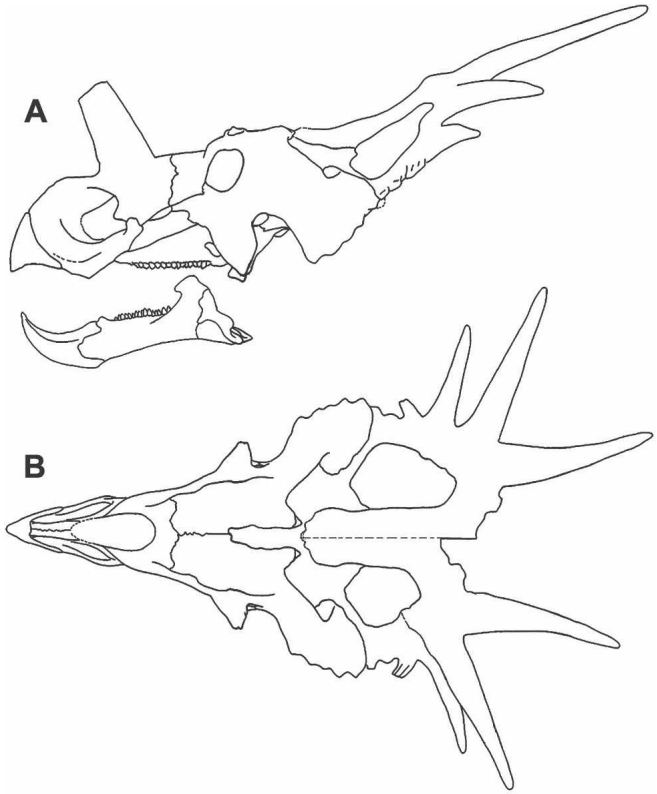

FIGURE 6. *Styracosaurus albertensis* Lambe 1913, CMN 344, holotype. **A**, reconstruction of the skull in left lateral view, foreshortening of the lateral parietal bar corrected. **B**, reconstruction of the skull in dorsal view, the right side of the parietal has been adjusted to correct for the foreshortening of the lateral parietal bar. The left parietal is illustrated as preserved.

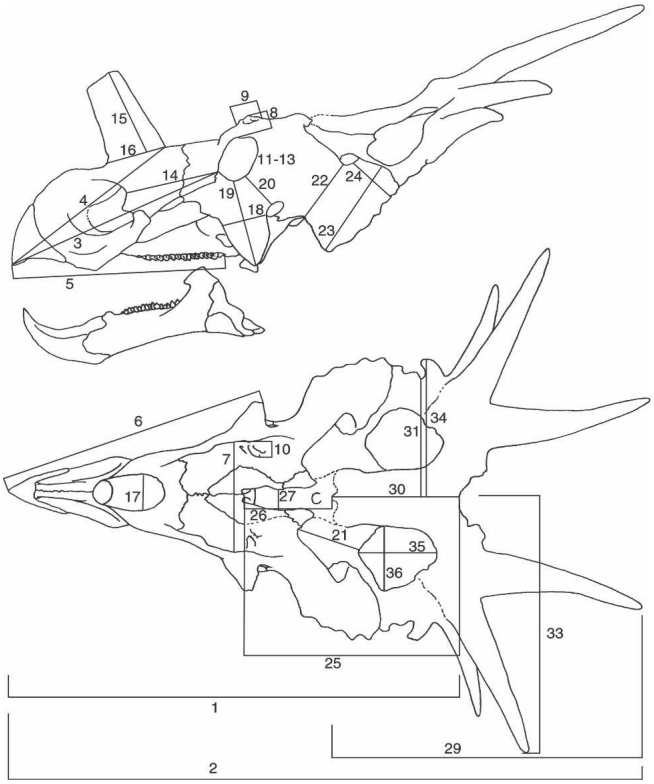

FIGURE 7. *Styracosaurus albertensis* Lambe 1913, CMN 344, holotype. Selected measurements of the skull recorded in Table 1. Note that measurements 31 and 34 were taken on the left side of the skull but are here indicated on the right side only for clarity of presentation.

been considerably shorter (Fig. 1) and would lie within the range noted for other specimens of *Centrosaurus* (i.e., 280 mm; TMP 82.18.44, *C. apertus*).

Of note is the slight constriction at the anterior base of the nasal horncore in the form of a low arch of surficial bone that is similar in shape to the 'nasal overgrowth' present on adult-sized nasal horncores on *C. brinkmani* and some specimens of *C. apertus* (Ryan and Russell, 2005).

Postorbital Ornamentation—The fused supraorbital elements of *Styracosaurus* (Fig. 1B and C; 2) have the same compliment as those of other centrosaurines (frontal, lacrimal, palpebral, parietal, postorbital, and prefrontal—the jugal can also be fused to this unit but typically it is not). On CMN 344 not all of the sutures between these elements are visible, possibly due to the maturity of the individual at the time of its death. The sutures, where present, are indicated on Fig. 1C and appear to correspond to those described for *Centrosaurus apertus* by Sampson et al. (1997).

The nature of the ornamentation of the postorbital has been the subject of much debate over the years. Lambe (1913:113) first described this as, "... a small, smooth depression, irregularly oval in outline, which indicates the position of an extremely small, or incipient, supraorbital horncore, which appears to have been present as a separate ossification and to have become detached." This explanation was accepted by Dodson and Currie (1990). Subsequently, Sampson and colleauges (1997:Fig. 7C), Ryan and colleagues (2001:Fig. 10 and 11), Ryan and Russell (2005: Fig. 5A) recognized such depressions as being supraorbital pits that appear to develop on most mature centrosaurine and some chasmosaurine postorbital horncores late in ontogeny. They also conclusively documented that these pits did not represent a point of attachment for a separate dermal element.

As the supraorbital pits developed, they modified and reduced the postorbital horncores present earlier in ontogeny, and, in some cases, completely eliminated any trace of the horncores presence in mature specimens. CMN 344 has supraorbital pitting on the dorsal surface of both orbits (Fig. 1C), the largest of which are 53 × 37 mm (right) and 53 × 52 mm (left). Isolated, fragmentary, subadult-sized postorbitals from bone bed 42 indicate that *Styracosaurus* had pyramidal horncores similar in size and shape to those of *Centrosaurus apertus* at equivalent stages of development. On CMN 344 the postorbital horncores have undergone significant remodeling leaving just the supraorbital pits behind (Fig. 1B).

In all ceratopsids the supraorbitals contact at the midline. During ontogeny the sagittally positioned supracranial sinus developed within the dorsoventrally expanded frontals. The sinus opens dorsally via the elongate frontal fontanelle (occasionally closed over in large, mature specimens), and communicates with the brain via a large (typically >25 mm) oval foramen in the posterior sinus floor in centrosaurines. In CMN 344 the supracranial sinus is almost completely accessible due to the slight telescoping of the skull that has pulled the parietal back from the skull roof. This deformation has also displaced the portion of the sinus floor enclosing the foramen posteriorly.

Frill Ornamentation—As demonstrated by Sampson and colleagues (1997) and Ryan and colleagues (2001), the distinctive centrosaurine parietal ornamentation develops at specific loci on the scalloped margins of the parietal and squamosal by the fusion and subsequent modification of an epoccipital to the adjacent element. For centrosaurines with elaborate parietal ornamenta-

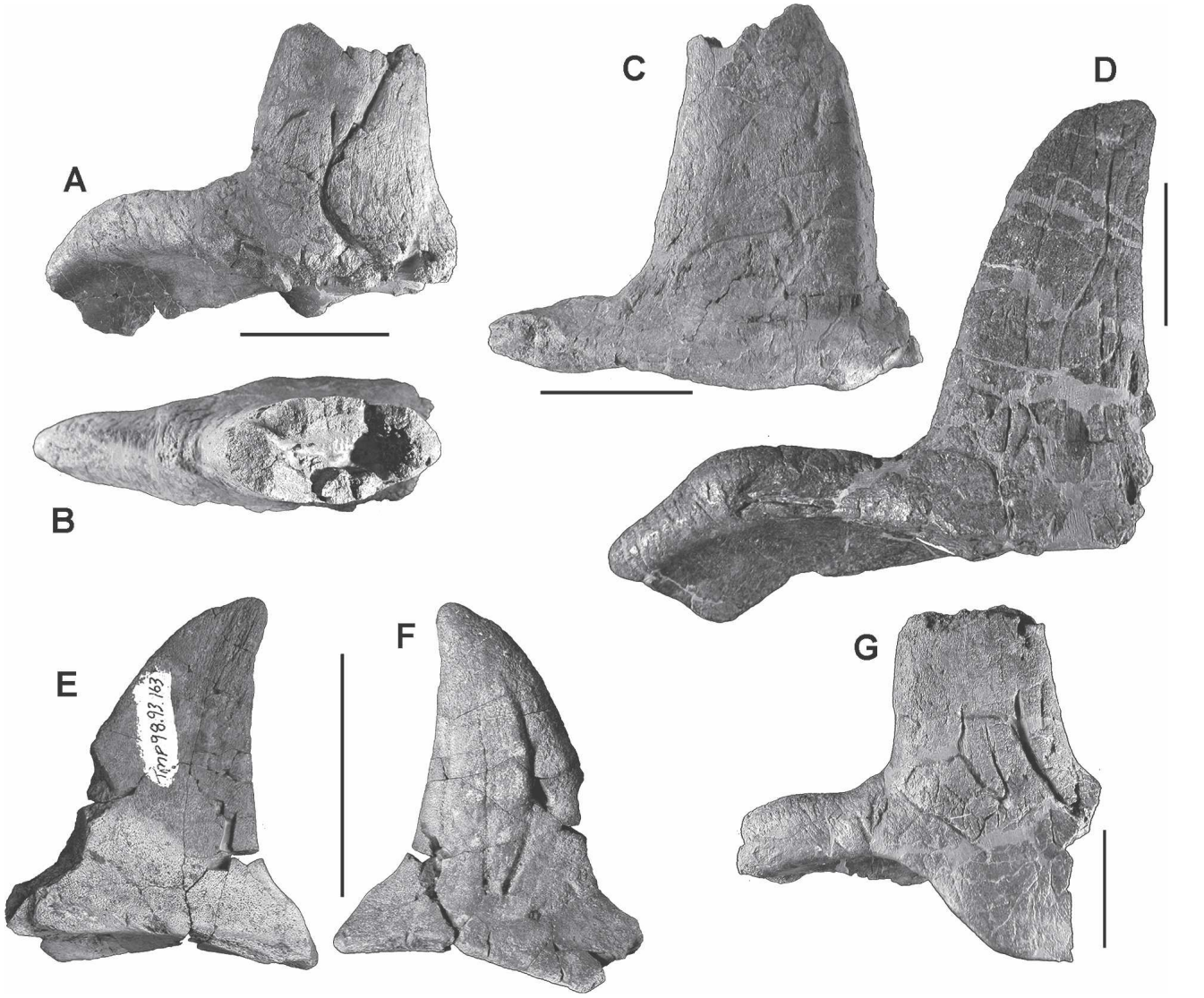

FIGURE 8. *Styracosaurus albertensis* nasal horncores. All material from Dinosaur Provincial Park. TMP 66.10.20 in **A**, lateral, and **B**, dorsal view; TMP 66.10.22 in **C**, lateral view; **D**, TMP 66.10.19, lateral view; TMP 94.14.866, c.f. *Styracosaurus* juvenile nasal in **E**, medial, and **F**, lateral view; **G**, TMP 66.10.21 in lateral view. **Abbreviations** as in Figure 1. Scale bars equal 10.

tion (hooks or spikes), the body of the structure appears to be comprised primarily of a highly modified epoccipital that has overgrown an excrescence of the parietal into its base (Ryan et al., 2001; Ryan and Russell, 2005). On the centrosaurine parietal there are typically seven distinct loci present numbered 1–7 (P1–P7, Fig. 1C) corresponding to the order of fusion and development of the modified epoccipitals.

The most distinctive feature of CMN 344 is the development of long robust spikes at loci 3 and 4 (Fig. 1), with shorter spikes at loci 5 and 6. Additionally, the suture for a small diamond-shaped epoccipital that straddles the scalloped margin of the frill at the parietal-squamosal border in most centrosaurines and *Triceratops* is present, although the epoccipital is absent.

The P1 and 2 processes are only preserved on the left side of the frill; the corresponding right side has been reconstructed. The P1 process is a raised, rostrodorsally oriented thickening of the parietal. This is distinct from the condition in *Achelousaurus*, *Einiosaurus*, and *Pachyrhinosaurus*, in which P1 did not develop, and from *S. ovatus*, which, if present, P1 is only very poorly developed.

P2 is a short, dorsoventrally compressed, tab-like process that projects caudomedially from the parietal. It closely resembles that of *Achelousaurus*, *Einiosaurus* and *S. ovatus*, but differs from that of *Centrosaurus apertus* and *Pachyrhinosaurus* in which it is a robust, medially curved process, and other specimens of *Styracosaurus* collected from BB 42 (e.g., Fig. 9) that generally display more modestly developed curved processes. The P2 loci of *C. brinkmani* display an autapomorphic cluster of 'extra ossifications' modified as short spines.

CMN 344 shares long, robust spikes at locus 3 with all specimens of *Achelousaurus*, *Einiosaurus*, *Pachyrhinosaurus*, and *Styracosaurus ovatus*; however, the orientation of these spikes varies between taxa. In *S. albertensis*, the spikes diverge from the midline, pointing caudolaterally, with a modest lateral inflection of the shaft. *S. ovatus* has straight P3 spikes that converge toward the middle, but, because the taxon is only known from a single specimen, its range of variation is unknown. Similarly to *S. ovatus*, the P3 spikes of *Einiosaurus* are straight but they extend subparallel to the midline. The P3 spikes of *Achelousaurus* are shorter and more dorsoventrally depressed than those of *S. al-*

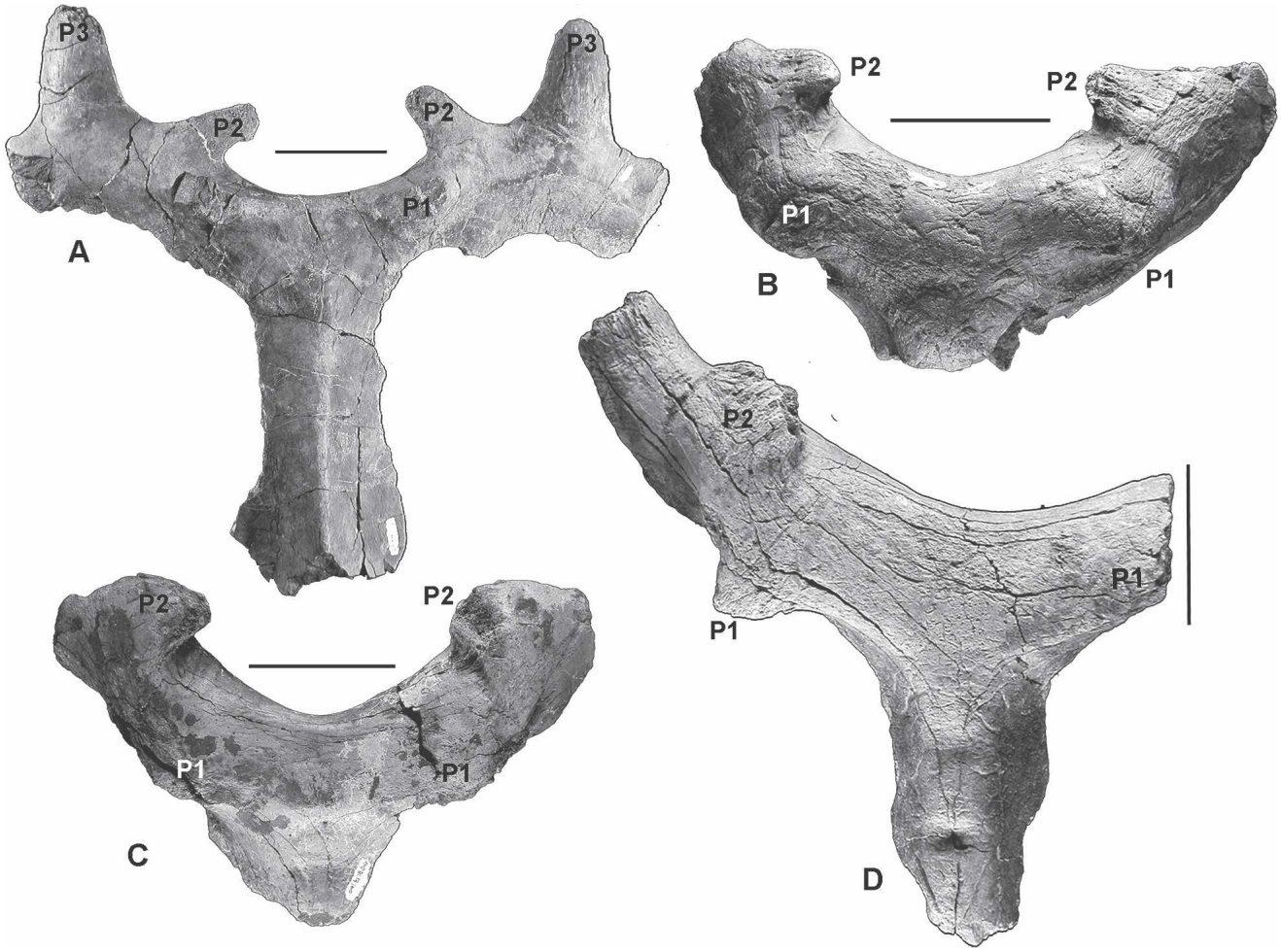

FIGURE 9. *Styracosaurus albertensis* parietals in dorsal view All material from Bone bed 42, Dinosaur Provincial Park, Alberta. **A**, TMP 99.55.2; **B**, TMP 66.10.4; **C**, TMP 81.19.160; **D**, TMP 99.5 2**. Abbreviations** as in Figure 1. Scale bar equals 10 cm.

bertensis, but also project caudolaterally and have substantial lateral curvature of the shaft. In CMN 344, the incomplete P3 spike is 385 mm long, but judging from the converging lateral and medial margins, was close to the reconstructed length of 560 mm. It is oval in cross-section and slightly flattened on its ventral surface. Lightly inscribed grooves ornament the length of the spike. A portion of the right P3 spike is incorporated into the restoration.

Styracosaurus is unique amongst ceratopsids in having P4 (Fig. 1) developed as a spike, although it is consistently shorter than P3.

In CMN 344, P5 and 6 are also developed as spikes (Fig. 1). However, in material of *Styracosaurus albertensis* from BB 42, the processes at loci 5–7 can be developed variably as either short spikes or as unmodified *Centrosaurus*-like epoccipitals.

On CMN 344, the P5 process (Fig. 1) is fused at its base and along its proximolateral margin with the P4 spike. P5 is 350 mm in length with the distal 140 mm being reconstructed. A few isolated parietal fragments from BB 42 also exhibit some degree of spike fusion or the development of a smaller secondary spike from loci 3 or 4.

The short, anterolaterally-directed spike at locus 6 (Fig. 1) has been broken distally. Unlike the other spikes it has several distinct, shallow, longitudinal grooves on its surface. CMN 344 is the only specimen of *Styracosaurus* in which any of the P5–P7 processes are oriented in this direction, but it may be pathological in this regard. P7 is a short, unmodified centrosaurine epoccipital. There is no evidence of basal fusion of these elements and it is possible that there is some reconstruction in this region.

Of longstanding interest with respect to this specimen is the thin, gracile appearance of the lateral parietal ramus adjacent to the contact with the squamosal when compared to its more robust posterior lateral ramus and the posterior parietal bar (Fig. 1). Two points are of significance with regard to this. First, both the width and thickness of the gracile portion fall within the range of variation exhibited by the homologous structure in *Centrosaurus*, which has relatively unmodified epoccipitals in this region. The difference between this region and the more posterior portion of the parietal can be explained simply by noting the large, thick bases of the spikes that require support by more robust bone. Secondly, there is a significant amount of plaster reconstruction on the skull (Fig. 1A, D).

DESCRIPTION OF BONE BED 42 MATERIAL

Bone Bed 42 is located in the upper Dinosaur Park Formation 27 m above the regional disconformity at the base of the formation in Dinosaur Provincial Park, Alberta (Figs. 4, 5) (12, 465,220 E; 5,620,750 N [WGS 84]; 698.9 m ASL). Excavations have been carried out sporadically over the past 40 years, including significant collections made in 1966 and 1983 and now cataloged in the collections of the Royal Tyrrell Museum of Palaeontology. The

1983 excavation was supervised by John Visser, who completed a M.Sc. thesis in 1984 on the sedimentology and stratigraphy of BB 42. However, he gave only a cursory description of the fossil material collected from it.

Nasals—Although only one of the large mature nasal horns from BB 42 is complete to its tip (TMP 66.10.19, Fig. 8D), all have a similar overall morphology. Each preserves at least the proximal half of an erect, laterally compressed horn that is completely fused across its medial surfaces with moderate to heavy rugose texture that includes longitudinal grooving. As for *Centrosaurus*, the degree of lateral compression varies considerably, with the cross-sectional shape immediately above the base ranging from a broad oval (TMP 66.10.20 [Fig. 8A, B] and TMP 66.10.21 [Fig. 8G]) to a compressed blade (TMP 66.10.22 [Fig. 8C] and TMP 66.10.19 [Fig. 8D]). The most complete nasal, TMP 66.10.19 (Fig. 8D), lacks only the portions caudal and lateroventral to the horncore. The horn is abraded at the tip, but there is little doubt as to its height and shape. The longitudinal height measured from the base through the center of the horncore is 250 mm (length of anterior margin 280 mm; length of caudal margin 190 mm, length of base 150 mm, maximum thickness of base 75 mm). The horn is laterally compressed with a rounded anterior margin and a distinct caudal edge, and is oriented vertically. It curves slightly anteriorly near its tip.

The remaining horns are approximately perpendicular to their base. The only other nasal for which nasal horncore height can be estimated is TMP 66.10.22 (Fig. 8C) at 300 mm. All these horns appear to lie within the range of variation displayed by the largest *Centrosaurus apertus* specimens. The length of the horncore of the holotype also falls within the known range of those of *Centrosaurus apertus*, and, thus, is not a diagnostic character of the taxon.

Only a single juvenile-sized c.f. *Styracosaurus* nasal (TMP 94.14.866, Fig. 8 E and F) is known. This was collected from a multigeneric bone bed (BB 55), from the upper 30 m of the Dinosaur Park Formation and is referred to *Styracosaurus* based on its stratigraphic position. The horn is 71 mm tall, with a length along its anterior face of 85 mm (estimated, a portion of its anterior base is broken away) with a relatively short base (58 mm estimated); basal thickness 14 mm. It is a typical short-based centrosaurine (e.g., *Centrosaurus*) unfused juvenile nasal horncore, slightly curved at its tip and laterally compressed. Long grain bone texture radiates over the medial surface from the base of the nasal horncore indicative of its juvenile age. A slight beveling is present at the median apex. Laterally there are several deep grooves that extend along the length of the nasal horncore.

Postorbitals—The postorbital ornamentation of *Styracosaurus albertensis* has only been described previously for CMN 344, the holotype, and is here referred to a mature, highly modified form. Unfused and unmodified postorbitals were heretofore unknown for the taxon. The mostly fragmentary supraorbital elements recovered from BB 42 do not fall outside of the range of variation for these elements seen in *Centrosaurus apertus* and CMN 344. However, TMP 98.93.64 (Fig. 10A–C), an isolated, nearly complete supraorbital was recovered 100 m from, and at the same elevation as, the quarry of CMN 344. In this part of the Dinosaur Park Formation the only centrosaurines present are *Styracosaurus* and a new, undescribed 'pachyrhinosaur' represented by a single specimen, TMP 2002.56.1. TMP 98.93.64 does not resemble any known subadult-sized *Pachyrhinosaurus* post- or supraorbital and is tentatively assigned here to *S. albertensis*.

TMP 98.93.64 is somewhat crushed dorsoventrally, and the ventral surface is broken and cracked, but the overall shape and size are identical to those of *Centrosaurus* of the same size. Its gracile form, lack of deeply rugose dorsal surface texture, and the long grain texture on the dorsal and ventral surfaces of the postorbital and prefrontal regions of this element, indicate that it is from a young, subadult-sized *Styracosaurus* in which the supraorbital elements had recently coossified (with the exception of the palpebral that forms a completely open suture with the lacrimal). As in most centrosaurines, the suture between the postorbital and frontal is visible dorsally but not ventrally.

Of particular interest is the size and shape of the postorbital horncore of this subadult-sized specimen. The horncore takes the form of a low, long-based pyramid with roughly equal sides (the lateral surface is flattened, and the medial surface has slightly flattened anteromedial and caudomedial surfaces). The horncore height measured from the dorsal orbital surface is 53 mm. Its height above the rim is 30 mm. Basal horncore length is 60 mm and its width from the orbital margin to the frontal suture is 43 mm. The orbital horncore is untextured but has fine pitting indicative of subadult bone, as well as two deep foramina on the medial surface above the frontal suture where the transverse groove is variably developed in other mature centrosaurines.

The palpebral, the visible sutural surface of which is restricted to the rostral face of the postorbital, is a large element (70 × 41 mm). It forms a distinctive raised brow when the orbit is viewed in profile. Posterior to the orbital horncore is the small raised 'bump' seen on most centrosaurine postorbitals.

The preserved margin of the frontal fontanelle lying on the dorsal skull roof between the orbital horncores is a straight-margined U-shape. This fontanelle opens into the supracranial cavity comprising the space within the medially adjacent, vaulted frontals. The supracranial cavity is characteristically subdivided into a larger anterior and a smaller posterior section, and the lateral borders formed by the frontals are preserved on this specimen. The anterior portion of the frontal suture with the lacrimal is preserved dorsally and confirms that the frontal forms the anterior margin of the frontal fontanelle.

The putative development and remodeling of the postorbital horncore seen on the series of TMP 98.93.64 (Fig. 10A–C), TMP 66.10.41 (Fig. 10D, E), and CMN 344 (Figs. 1B, 10F) indicates that the postorbital ornamentation of *Styracosaurus* underwent an ontogenetic growth series that began with a small pyramidal horn indistinguishable from that of *Centrosaurus apertus* of the same size, and that during growth, developed supraorbital pitting that obliterated the horn. Given the lack of mature *Styracosaurus* postorbitals with well-developed horns, it is probable that this taxon did not develop the inflated postorbital horns seen in most mature *Centrosaurus*, but, like *Einiosaurus*, remodeled and obliterated its subadult-sized horns through the development of supraorbital pitting at maturity.

Frill

Squamosals—In overall morphology, *Styracosaurus* squamosals (Fig. 11) closely resemble those of all other centrosaurines (apart from *Avaceratops*) and appear to have only limited diagnostic utility. As for *Centrosaurus*, the caudal portion has a 1:1 height-to-length ratio, with length being measured from the 'stepped-up' medial margin above the quadrate groove to the caudal margin. This ratio varies due to the presence or absence of fused epoccipitals, and the natural intraspecific variation seen amongst specimens. The caudal margin scallops number from 4 (e.g., TMP 66.10.34, Fig. 11) to 5 (rarely numbering 6, as seen in some *Centrosaurus* specimens). The scallop nearest the jugal process is occasionally modified into a less distinct, low, long, thickened process that, if misidentified, gives a total scallop count of three. As seen in some *Centrosaurus* specimens, the scallops tend to be dorsally upturned and frequently imbricated, as they are on the parietals, even in smaller specimens. On large mature specimens the caudal scallops nearest the parietal contact may have small lozenge-shaped epoccipitals fused to their tips, similar to those seen on other centrosaurine specimens. As in other centrosaurines, the caudomedial contact with the lateral parietal bar is wide, concave and deeply grooved.

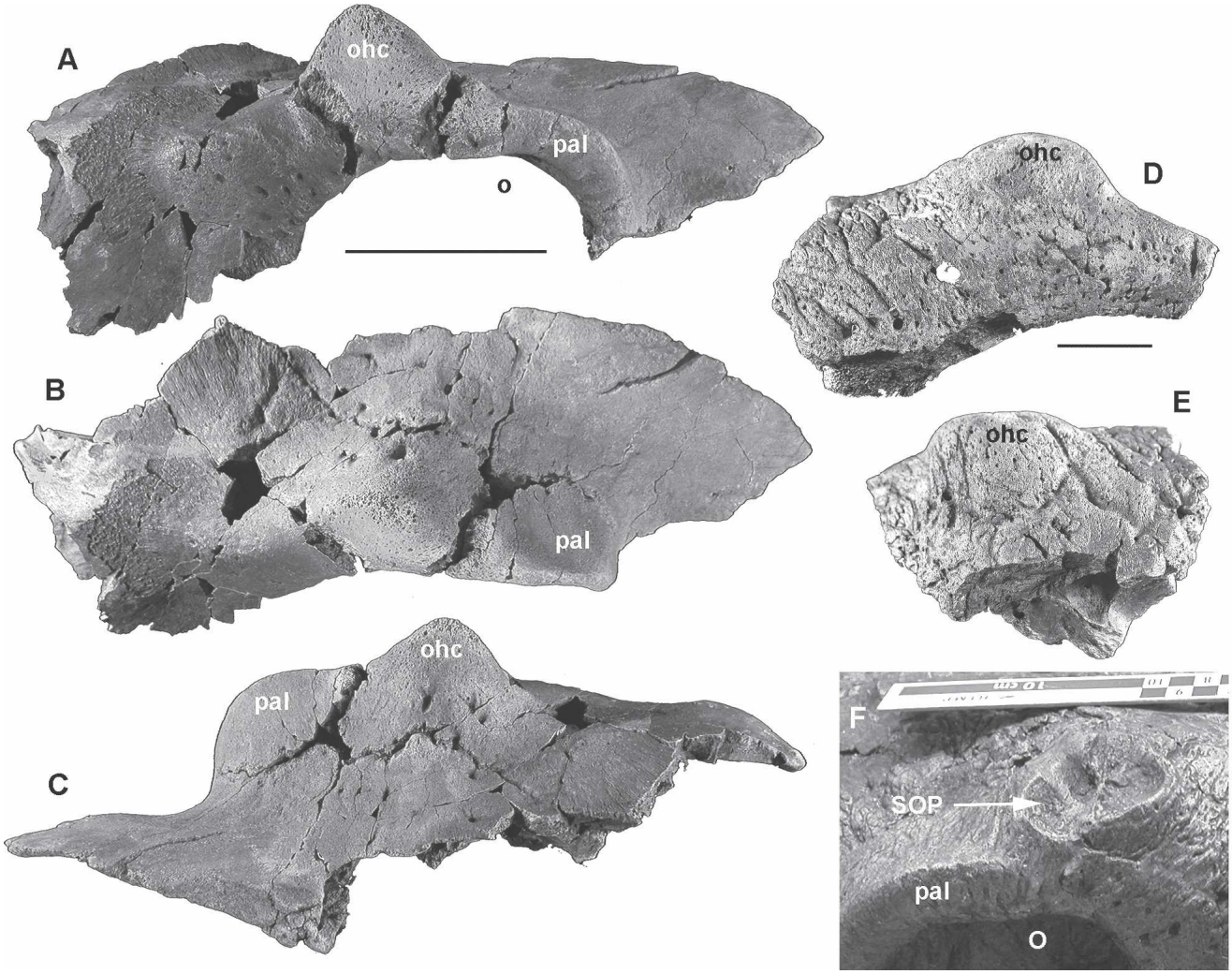

FIGURE 10. *Styracosaurus albertensis* postorbitals. TMP 98.93.64 in **A**, lateral, **B**, dorsal, and **C**, medial views; TMP 90.58.4 in **D**, lateral, and **E**, medial views. CMN 344, **F**, close-up of supraorbital pitting over left orbit. **Abbreviations** as in Figure 1. Scale bars **A**–**G** equal 10 cm. Scale bar for **H** and **I** equals 5 cm.

Although several features listed here tend to be consistently different from most *Centrosaurus* specimens (i.e., number of caudal margin scallops and shape of the rostralmost margin scallop), at least some *Centrosaurus* specimens share one or both of these characters. *Styracosaurus* squamosals cannot be reliably distinguished from those of other centrosaurines as isolated elements collected in the field.

Parietals—More than 50 partial parietals or fragments thereof, (Figs. 9, 12) have been collected from BB 42. As reconstructed from the BB 42 material, the parietal has the typical centrosaurine morphology, and its ornamentation closely resembles that of the type of *S. albertensis*.

The P1 ornamentation is variably developed as an abbreviated *Centrosaurus apertus*–like P1 hook ranging in shape from a small, raised bump to a wide based, short, rostrally inclined process. None of the known P1 processes could be mistaken for the 'typical' large *Centrosaurus apertus* (e.g., CMN 348) P1 hook. P2 is a typically medially-curved process that can resemble that of *Centrosaurus apertus*, but tends to be shorter, more gracile and more lightly textured (e.g., TMP 66.10.28). On some parietals (e.g. TMP 99.5.2, Fig. 9A), these processes are developed only as small, dorsoventrally depressed, medially oriented, tab-shaped processes similar to those seen in *Achelousaurus* and *Einiosaurus*. The abbreviated form of the P1 and 2 processes is best seen on TMP 66.10.4 (Fig. 9B), 81.19.157 (L [left] P1 base only + LP2), 81.19.160 (Fig. 9C), 81.19.209, 90.58.7 (R [right] P1 only), 90.58.5 (RP1 only), and TMP 99.5 2 (Fig. 9D).

The P3 and 4 processes are developed as long spikes. (e.g., TMP 66.10.3 [Fig. 12A], TMP 66.10.2 [Fig. 12K]) that, where it can be determined, had both the same shaft curvature and orientation as those of CMN 344 (Fig. 1). All P3 spikes are consistently longer and more robust than P4. Each spike is slightly dorsoventrally compressed with wide grooves that are variably developed on both dorsal and ventral surfaces. These spikes tend to have a slight ventral bow in their shafts, and a slight lateral inflection distally. The bases of the spikes do not preserve any well developed point of fusion for the epoccipital, but are slightly inflated where they separate from the underlying parietal. Typically the lower halves of the P3 and 4 shafts diverge from each other.

Processes P5–P7 are known from both short, thick, spike-like processes (Fig. 12D, F–H, J) or from typical centrosaurine P5–P7 processes (rounded epoccipitals) (Fig. 12I), either of which may be sharply imbricated (e.g., Fig. 12G). Processes 5–7 decrease in size towards the parietal-squamosal contact. TMP 81.19.223 (Fig. 12J) is noteworthy for being from a large, subadult-sized animal.

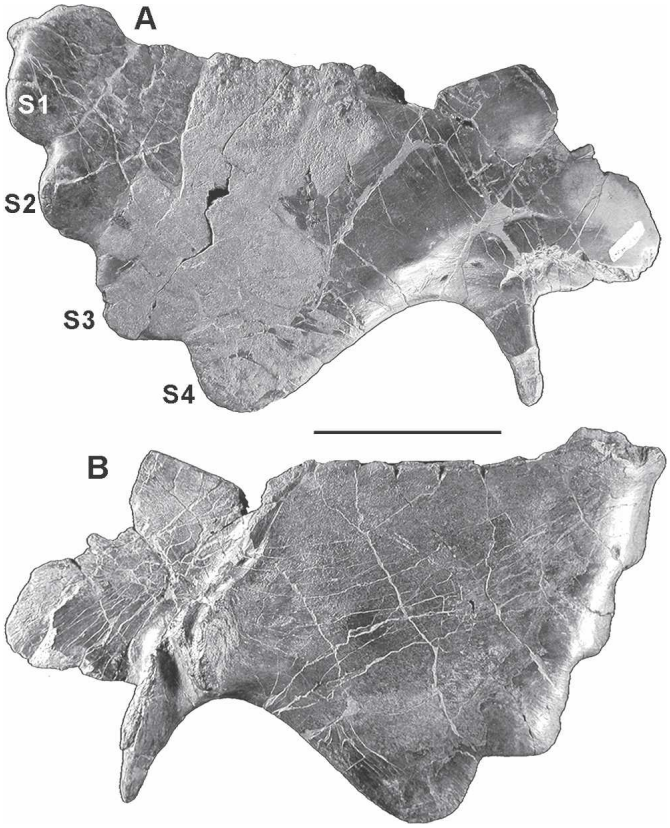

FIGURE 11. *Styracosaurus albertensis* squamosal TMP 66.10.34 from Bone bed 42, Dinosaur Provincial Park, Alberta. **A**, dorsal view; **B**, ventral view. **Abbreviations**: **S1–4**, squamosal scallops. Scale bar equals 10 cm.

One process is preserved as a short, dorsoventrally compressed, imbricated spike, and lateral to this process is an open suture for an epoccipital.

OTHER SPECIMENS REFERRED TO *STYRACOSAURUS ALBERTENSIS*

There are a number of diagnostic *Styracosaurus albertensis* specimens (mostly incomplete frills) known from the uppermost Dinosaur Park Formation of southern Alberta. Significant measurements are listed in Table 1.

Description of TMP 89.97.1

TMP 89.97.1 (Table 1, Fig. 13A) is an almost complete, large, subadult skeleton and skull collected from Sage Creek, southeastern Alberta (12, 545,414 E; 451,340 N [WGS 84]), from near the top of the Dinosaur Park Formation, less than 10 m below the Lethbridge Coal Zone near Onefour, Alberta (Fig. 4). It was found approximately 130 km SE of the holotype locality of *S. albertensis*. The specimen was preserved in a fine-grained, friable shale with the bones coated in a thin, but extremely hard, ironstone. The bone is poorly permineralized and extremely soft, making preparation difficult. All the long bones have undergone significant compression.

During the current study the postcranial skeleton was prepared enough to reveal that, other than the smaller size of the bones and the less pronounced development of the articular heads on the long bones, all of which would be expected in an immature animal, there are no significant differences from the postcranial material described by Lull (1933) for a mature *Centrosaurus apertus*.

The skull includes an almost complete parietal and a partial face (supraorbital, jugal and squamosal) from the left side of the skull. Unfortunately the face can no longer be located in the RTMP collections. However, based on data from field notes and field photographs, the elements making up this specimen are of typical centrosaurine shape and do not differ markedly from those of *Centrosaurus*. Of note in the photographs is the presence of the same small, pyramidal orbital horncore described for the subadult supraorbital TMP 98.93.64.

Based on the size and gracile nature of the parietal and its processes, TMP 89.97.1 (Table 1, Fig. 13A) was a smaller, less mature animal than TMP 86.126.1 (Fig. 14A). Although both specimens have parietals with a greater diameter than the holotype this can be attributed to the probable pathological nature of the left ramus of CMN 344 which gives the specimen a seemingly anomalous narrow frill diameter. Both TMP 89.97.1 and TMP 86.126.1 have parietal ornamentation of the size and shape predicted for almost full adult-sized *Styracosaurus* that had not fully developed the parietal ornamentation at the time of death.

Although slightly abraded, the dorsal surface of the frill is well preserved. The compaction of the specimen seems to have exaggerated the compression of the P2–P7 processes. Maximum length across the frill is 810 mm at the P7 processes (including their length). There are seven processes on each side of the frill, although P6 and 7 are poorly defined. The P1 process is preserved on the right but the corresponding area on the left has been broken away. Indicative of its immature status, RP1 is a small, poorly defined process resembling the small, lozenge-shaped epoccipitals seen on the margins of some older squamosals. The P2 processes resemble the small, depressed tabs of the holotype CMN 344.

The left and right P3 and P4 are the best defined processes on the parietal, being short spikes with elongated triangular profiles. The P3 processes diverge from the midline, are longer than the P4 processes, and both processes have a slight ventral bowing. The P5–P7 processes are progressively more poorly defined along the lateral margin, but are better preserved on the right side (Fig. 13A). Each is a low, long-based process that is dorsoventrally depressed, with sharp, bladelike margins, all of which lack epoccipitals. The squamosal contacts each have a minimum thickness of 20 mm. The contacts have the typical convex and deep longitudinal grooves that meet their beveled counterparts on the squamosal.

The bone bordering the parietal fenestrae is broken along its margins, but the fenestrae are ovoid in shape, with their long axes subparallel to the axis of the midline bar.

Despite its immature status TMP 89.97.1 can be confidently assigned to *S. albertensis* based on the spike-like ornamentation at loci 3 and 4, and their orientation.

Description of TMP 88.36.20

TMP 88.36.20 (Table 1, Fig. 13B) is a large posterior parietal that preserves the posterior portion of the midline bar, portions of three massive spikes, and at least one P5 process. It was collected from the uppermost Dinosaur Park Formation in the northeast part of Dinosaur Provincial Park, Alberta (12, 477,238 E; 5629954 N [WGS 84]) approximately 500 m north of TMP 86.126.1.

The specimen is prepared in ventral view so the P1 processes, if present, are not visible. The P2 processes are short, thickened, medially oriented tab-like protrusions on the caudal margin of the parietal. Processes 3–5 are preserved on the left side. LP3 is represented by a broad base indicating that it supported a thick, long spike. LP4 is missing only its tip, judging by the degree of tapering of this more gracile spike. The specimen does not ap-

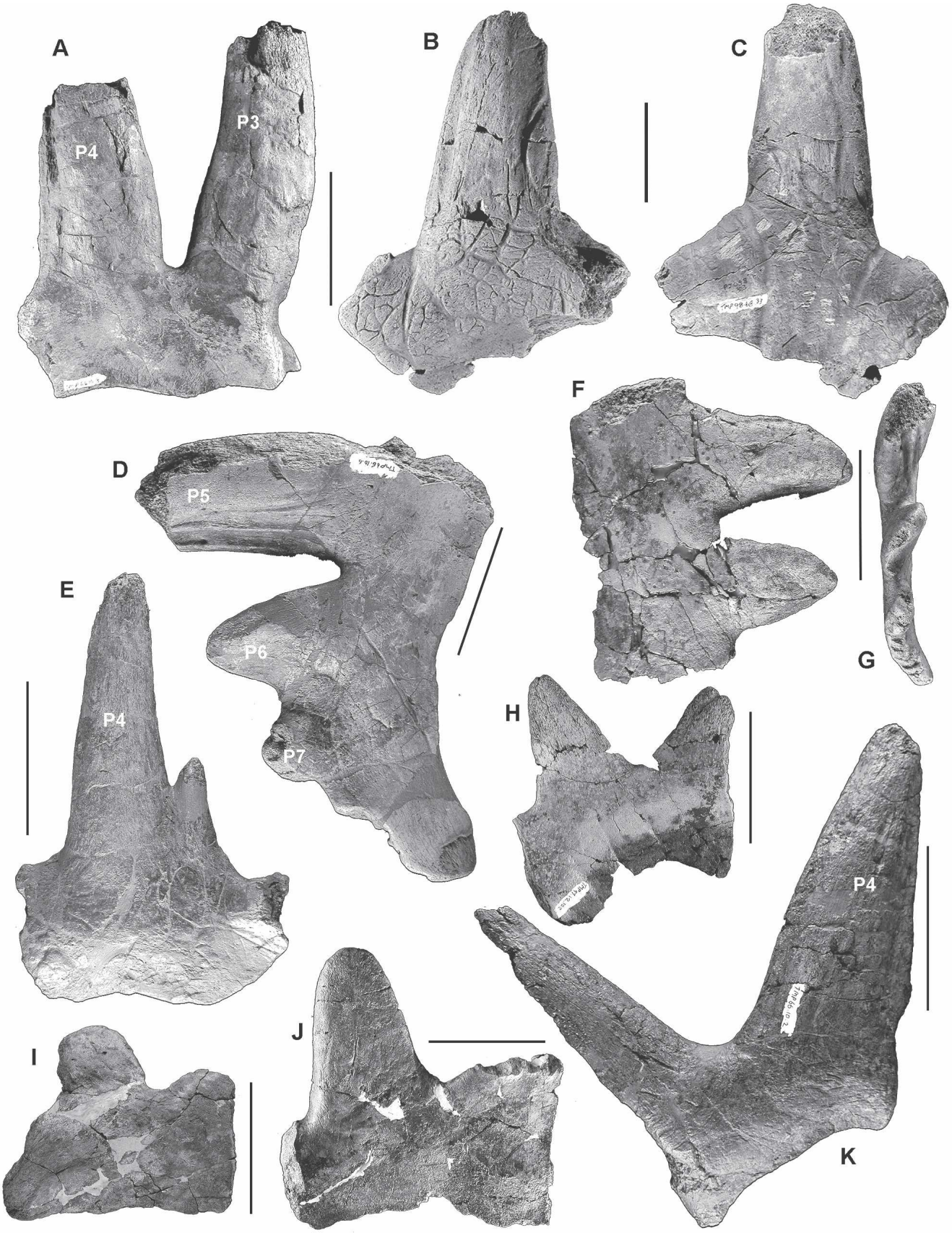

FIGURE 12. *Styracosaurus albertensis* parietal ornamentation. **A**, TMP 66.10.3, dorsal view; TMP 98.68.33, ?P3 spike, in **B**, dorsal, and **C** ventral view; **D**, TMP 66.10.6, dorsal view; **E**, TMP 66.10.5, dorsal view; TMP 81.19.141, ?P5 and ?P6 spikes in, **F**, dorsal, and **G**, lateral **view**. **H**, TMP 97.12.122, ?P5 and ?P6 spikes, dorsal view; ; **I**, DHT-DPP-157, ?P7; **J**, TMP 81.19.223; **K**, TMP 66.10.2, dorsal view . **Abbreviations** as in Figure 1. Scale bars equal 10 cm.

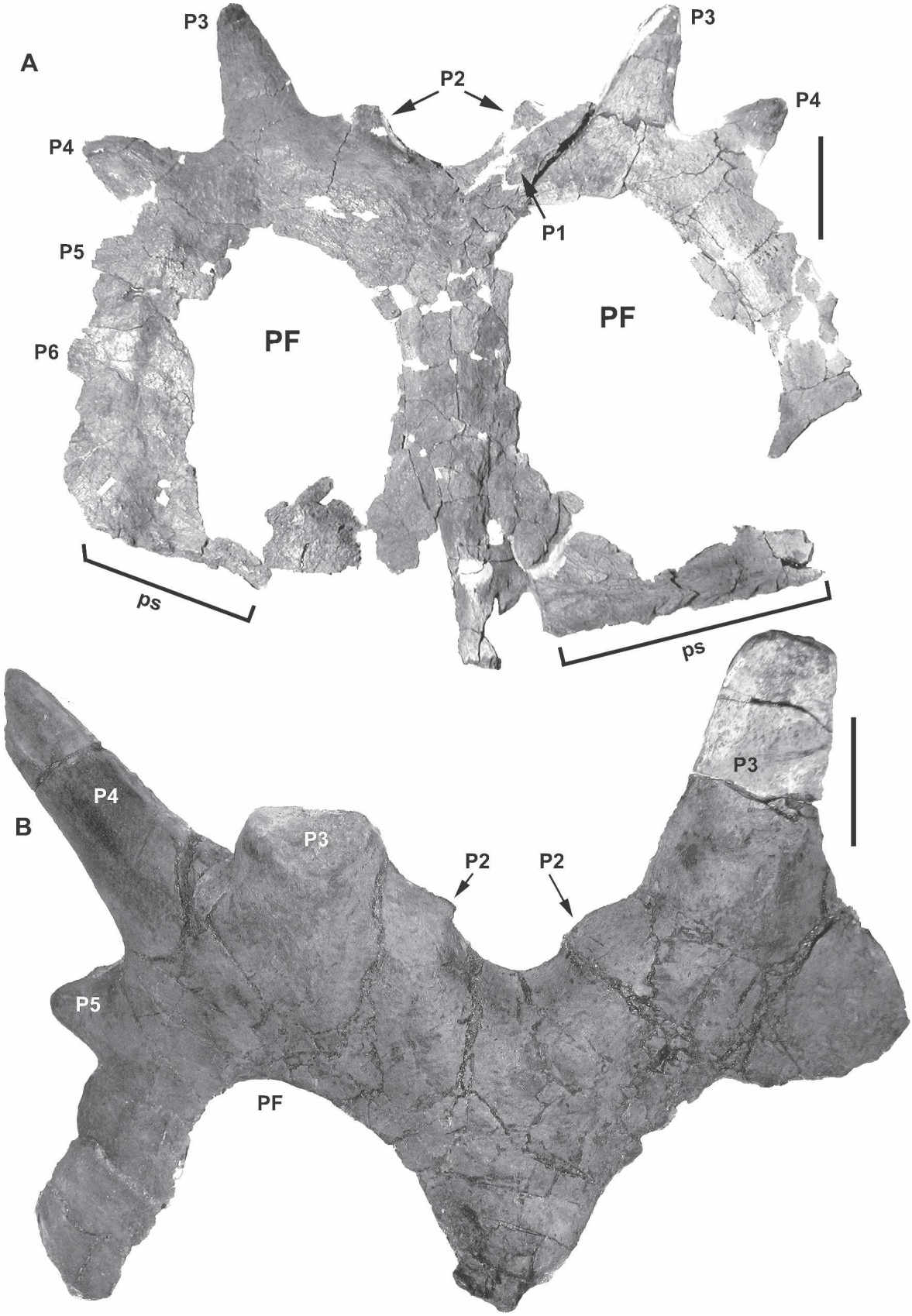

FIGURE 13. *Styracosaurus albertensis* parietals. **A**, TMP 89.97.1, partial subadult skull in dorsal view; **B**, TMP 88.36.20, large adult partial parietal. In ventral view. **Abbreviations** as in Figure 1 and 12. Scale bars equal 10 cm.

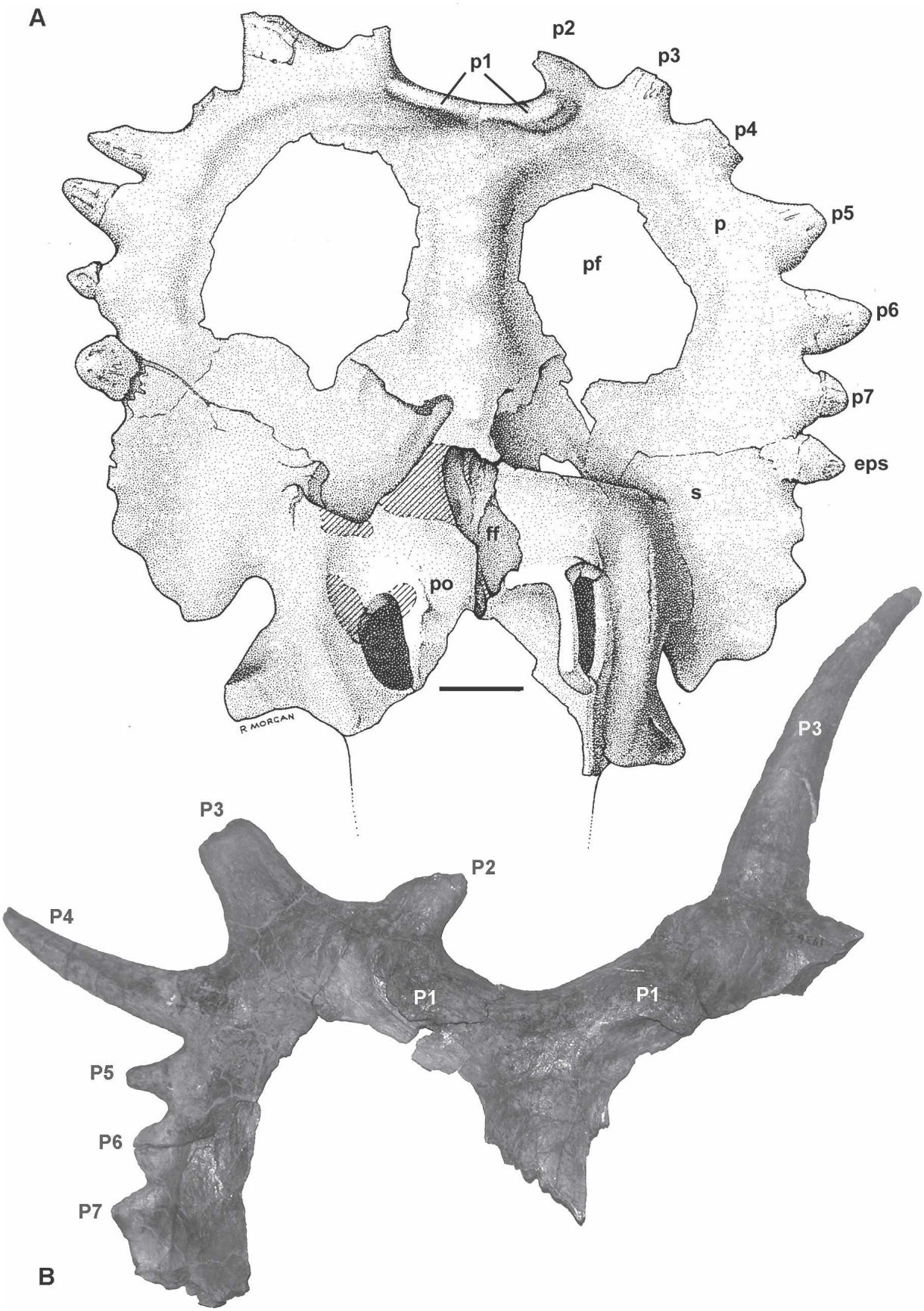

FIGURE 14. *Styracosaurus albertensis* partial skulls. **A**, TMP 86.126.1, partial subadult skull in dorsal view. **B**, ROM 1436. **Abbreviations** as in Figure 1. Scale bar equals 10 cm.

pear to have undergone much distortion, so the oval cross-sectional shape of each spike is probably natural. LP5 is a relatively small, dorsoventrally compressed epoccipital with a triangular profile. A large, thick P3 spike is present on the right side but it is broken approximately 150 mm above its base.

This specimen closely resembles the morphology of CMN 344 and the reconstructed morphology of the BB 42 material. Notably, both the P3 spikes diverge from the midline, and the RP3 and RP4 spikes diverge from each other as seen on other *Styracosaurus albertensis* parietals.

Description of TMP 86.126.1

TMP 86.126.1 (Table 1, Fig. 14A) is a partial skull, collected in 1986 from high in section (700.3 m ASL) (Figs. 4, 5) in the badlands of Dinosaur Park Formation along the north side of the Red Deer River, just outside of the eastern boundary of Dinosaur Provincial Park (12, 477,300 E; 5,629, 500 N [WGS 84]). It was subsequently prepared and mounted in the Royal Tyrrell Museum Field Station in the park in 1988, where it remains on display. The specimen consists of a dorsoventrally crushed skull including both postorbitals, portions of both jugals, both squamosals and the complete parietal, but is missing the face anterior to the postorbitals. The left maxilla has been crushed onto the ventral side of the skull roof and is barely visible. The rostral and left dentary were preserved but they have not been mounted with the specimen. Numerous broken and badly weathered fragments representing at least some of the missing parts of the skull were collected. The missing portions of the face have been replaced by sculpted material or, in the case of the nasal horncore, a cast of a juvenile *Centrosaurus* nasal.

Originally referred to *Centrosaurus apertus*, it was subsequently recognized as a subadult *Styracosaurus* (Ryan et al., 1998). The referral to subadult age is based, in part, on the size of the elements (typically smaller than adult-sized centrosaurine ceratopsids), the presence of long grain and mottled bone texture on the ventral and portions of the dorsal surface of the parietal, squamosal and postorbitals, the lack of development of heavy, rugose texturing on the postorbitals and the posterior parietal, the lack of fused epoccipitals at all preserved parietal loci other than P3, and the overall gracility of the specimen. Referral to *Styracosaurus* is based on the development of the spike-like, lateral parietal processes at loci 3–6 on the left and 3, 5 and 6 on the right side of the frill. Additionally, the stratigraphic position of the specimen also supports its referral (Ryan and Evans, 2005).

The rostral has the typical triangular centrosaurine shape, with a maximum length of 208 mm. Length of the anterior margin is 90 mm (although some of the contact with the nasal has been lost).

The jugals are of typical centrosaurine size and shape but, indicative of the specimens' subadult nature, neither has attached epijugals.

Both postorbitals are missing their anterior portions and are crushed laterally and posteriorly. The orbital horncore, best preserved on the left side, most closely resembles the unmodified horncore of TMP 66.10.41 from BB 42 in size and shape. The low, indistinctly formed horncore rises approximately 17 mm above the orbital rim. It has a rounded dorsal surface and a flat lateral surface. The presence of supraorbital pitting cannot be confirmed due to the condition of the bone.

The frontal fontanelle is partially broken and distorted, but retains an elongated 'U'-shape with typical straight lateral margins.

Frill—The parietals and squamosals are of typical centrosaurine morphology. The squamosals on both sides are crushed but exhibit the typical 1:1 ratio of length to width for the caudal portion of this element. Indicative of its subadult status, no epoccipitals are preserved on either squamosal. Rather, the scalloped margins closest to the parietal contact both have open sutures where the epoccipitals contacted the parietal but had not fused at the time of death.

The dorsal surface of left parietal process 1 was lost prior to collection and has been reconstructed as a low, rounded tip, but probably more closely resembled the RP1 process. These abbreviated P1 processes are typical in morphology and dimensions of *Styracosaurus* posterior parietal bars from BB 42.

Both the left and right P2 processes are short and recurve towards the midline. LP2 is completely preserved and has the rugose dorsal and ventral texture suggestive of a fused epoccipital. The RP2 process is broken at its tip but was much thinner and lacks any rugose texturing, suggesting that it represents the parietal surface to which the modifying epoccipital had not yet fused at the time of death.

The RP3 process is a short, thickened spike that closely resembles those of some subadult-sized *Styracosaurus* P3 processes from BB 42 (e.g., TMP 99.55). It tapers along its length to a blunt and somewhat abraded tip, and has a rugose texture on its dorsal surface. The LP3 process is a flattened, long based epoccipital missing the apex. This process resembles the inflated epoccipitals seen at locus 3 on other *Styracosaurus* parietals from BB 42. The partially preserved left and right P4 parietal loci lack fused epoccipitals but illustrate the modification that occurs to the parietal at these points prior to the fusion of the capping epoccipitals.

On the right side of the skull, the P5–P7 processes are short, laterally compressed, spikes that progressively decrease in length towards the rostral margin. The RP5 process is the most spikelike and its distal portion is comprised of an elongated epoccipital that was in the process of fusing to the underlying parietal at the time of death.

On the left side, the P5–P7 processes are less spikelike, resembling larger, elongated triangular epoccipitals. The difference between LP5 and RP5 is particularly striking, with LP5 being a large triangular process in profile and RP5 being a much narrower distinct spike. However, this is not unusual considering the amount of variation in the development of the spike-like processes seen on isolated fragments from BB 42.

The triangular LP6 and LP7 more closely resemble their right-hand counterparts but are both longer and wider. Like their counterparts, they had not completely fused to their underlying bases at the time of death. On both sides of the frill the P5–P7 processes are imbricated, with the medial edge being angled dorsally. Both sides of the frill have large, inflated epoccipitals inserted wedge-like into the margins between the parietals and squamosals.

The parietal fontanelles are roughly oval in shape, with preserved mediolateral and rostrocaudal lengths of 245 mm and 230 mm, respectively, on both sides. In life, each fontanelle would have been somewhat smaller, as the complete margins are not preserved.

Evaluation of TMP 86.126.1

Where preserved, processes P3–P7 can each be argued to have been developing into elongated *Styracosaurus*-like spikes at the time of death. The P3 spikes diverge from the midline and are longer than the P4 spikes. Even at this sub-adult stage of development, the right processes 5 and 6 already have a ratio of length to base width of greater than 1, and are attenuated towards the tip. No other centrosaurine has parietal processes 4–7 of this shape. Typically, these processes have ratios of length to base width of usually 1: ≥1, and have ovoid outlines when viewed in profile. CMN 344 is noted for having the shortest midline parietal bar length (379 mm, estimated) of any centrosaurine for which this element is completely preserved. However, the range of variation for this and other elements of *Styracosaurus* have

not been reported before. TMP 86.126.1 has one of the shortest parietal bar lengths (434 mm) when compared to other known centrosaurines (Ryan, 1992; Sampson, 1995), exceeding only CMN 971 (*Centrosaurus apertus*; 421 mm) and CMN 344. The most parsimonious argument to be made regarding the identity of TMP 86.126.1 is that it is a sub-adult *Styracosaurus*, and that its parietal ornamentation was developing into spikes at the time of death. This specimen is the second most complete skull referable to *S. albertensis*.

Description of ROM 1436

ROM 1436 (Field number 1935 #8) (Table 1, Fig. 14B) is a partial parietal that was collected by Levi Sternberg in 1935 on the west branch of Sand Creek, Red Deer River Valley, about 2 miles south west of the mouth of the creek and about 200 feet above the river. This would put it in the upper Dinosaur Park Formation of the region that is now Dinosaur Provincial Park.

This specimen is incomplete but preserves LP1–3 and RP1–7, and in general closely resembles the material collected from BB 42 except that RP2 is an incomplete, but robust, medially curled hook (LP2 is either poorly developed or broken). Both P1s are abbreviated procurved hooks and the complete LP3 is a tapering, caudolaterally curved spike. RP 4 spike is unusual for *Styracosaurus* material from DPP in that it is caudomedially curved. RP5 is a short, spike-like process, and RP6 and 7 are rounded, unmodified *Centrosaurus*-like processes that are imbricated.

Description of *Styracosaurus ovatus* USNM 11869

This taxon is based on a single specimen (Table 1, Fig. 3) from the upper Two Medicine Formation of northwestern Montana. Its exact geographic and stratigraphic locations are unknown although it is believed to have found approximately coincident with the juvenile centrosaurine "*Brachyceratops*" (nomen dubium; Sampson et al., 1997) occurring approximately 60 m below the Bearpaw Formation and 15 m below the *Einiosaurus* specimens (locality data for these sites are given by Sampson, 1995) placing it approximately equivalent to the uppermost Dinosaur Park Formation of Alberta (Ryan, 2003).

USNM 11869 consists of the posterior portion of the parietal, including the posterior midline bar, and the loci for left P?1, 2–5 and right P2–P4 (see Table 3.1 for dimensions). At locus 1 on the left side is an indistinct 'bump' best viewed using low-angle lighting that might represent an incipient P1 process. The bone surface at locus 1 on the right side is broken but, if present, RP1 would have been extremely small. It is possible that, as for *Achelousaurus* and *Einiosaurus*, P1 is absent on this specimen. The processes at P2 are short, laterally compressed tabs. The ornamentation at loci 1 and 2 of *S. ovatus* more closely resemble those on the parietals of *Achelousaurus* and *Einiosaurus* (both lack P1 processes and have small, tablike P2 processes), also from the Two Medicine Formation of Montana, than they do those of *S. albertensis* (except for the holotype, CMN 344).

As for *S. albertensis*, the processes at loci 3 and 4 are large, robust spikes. Due to their incomplete nature it is difficult to determine if P3 was longer than P4, as is the case for all known *S. albertensis* specimens. The only other process preserved is LP5, which is a short but robust spike. Based on the presence of the P4 and 5 spikes this parietal can be assigned to *Styracosaurus*. In addition to its greatly diminished P1 and P2 processes, *S. ovatus* differs from *S. albertensis* and has one autapomorphy—the convergence of its P3 spikes towards the midline—and can therefore be supported as a valid species. Reiterating the comments of Gilmore (1930:37), we believe that, "... establishing this species on the available material, fragmentary though it may be, it is the hope that more complete specimens will disclose other and perhaps more stable characters.." It is possible that the specimen may be referable to the adult form of '*Brachyceratops*,' or another genus.

BIOGEOGRAPHICAL DISTRIBUTION OF *STYRACOSAURUS*

Within Dinosaur Provincial Park the various ceratopsid taxa appear to be stratigraphically segregated (Ryan et al., 1998; Ryan, 2003; Ryan and Evans, 2005; Fig. 4). Based on a survey of 45 localities, including 23 paucispecific bone beds (including some outside of DPP), *Centrosaurus apertus* is confined to the lower 30 m of the Dinosaur Park Formation. The last occurrence of *C. apertus* overlaps the first occurrence of *Styracosaurus albertensis* which is otherwise confined to the upper 20+ m of the formation (Fig. 4). The anomalous *Styracosaurus* specimen, an isolated cf. *Styracosaurus* parietal spike (TMP 98.68.33, Fig. 12B, C), was recovered from BB 156, approximately 20 meters above the disconformity that separates the Dinosaur Park Formation from the underlying Oldman Formation. Reexamination of TMP 98.68.33 shows that it has a very similar morphology to the P2 hook of the holotype of *C. apertus* (CMN 348) and should more probably be referred to that taxon. If this assignment is accepted then there is no known stratigraphic overlap between *Centrosaurus* and *Styracosaurus*.

Given the extensive sampling that has taken place within Dinosaur Provincial Park over the past 100 years, the abundance of correctly identified material from each taxon in museum collections is probably an accurate reflection of their relative abundances throughout the time of the deposition of the Dinosaur Park Formation. The apparent temporal replacement of *C. apertus* by *S. albertensis* is consistent with a pattern interpretable as a faunal turnover.

Geographically, *Styracosaurus albertensis* is primarily confined to Dinosaur Provincial Park and its immediate environs, except for the skeleton of TMP 89.97.1 from the Sage Creek badlands (Fig. 5). In this region the Dinosaur Park Formation is approximately 10 m thick, and the specimen was found within the upper 5 m, making it stratigraphically equivalent to the uppermost portion of the Dinosaur Park Formation in Dinosaur Provincial Park (see Eberth and Hamlin (1993) for a discussion of the correlation of Belly River Group sediments across southern Alberta). Together these occurrences record a known north-south range of approximately 170 km for *Styracosaurus albertensis*.

The presence of *Styracosaurus ovatus* in Montana indicates that *Styracosaurus* ranged at least 300 km. The rare southerly occurrence of *Styracosaurus albertensis* in southern Alberta, and *S. ovatus* in Montana implies that the genus preferred the more mesic, more proximal Dinosaur Park Formation (relative to the Western Interior Seaway) and that *S. ovatus* might represent a species adapted to the more distal and relatively xeric Two Medicine Formation.

CONCLUSION

Styracosaurus is a monophyletic taxon within the subfamily Centrosaurinae (Ryan and Russell, 2005) with two valid species, *S. albertensis* and *S. ovatus*. This genus shares a number of synapomorphies with other centrosaurines, including the expanded ventral margin of the premaxilla and the rostral projection of the nasal from the caudal margin of the nares. It differs from all other centrosaurines in expressing a robust spike at locus 4 on the lateral parietal ramus of adult-sized specimens.

The development of the diagnostic centrosaurine cranial ornamentation of the nasals, parietals and postorbitals of *Styracosaurus albertensis* share a similar ontogenetic development to that previously documented for *Centrosaurus* (Sampson et al. 1997, Ryan et al., 2001). The nasal horns of each grow from a pair of appressed, short based, laterally compressed triangular blades into tall, erect conical horns that are typically oval in cross-

section. With *C. apertus*, *Styracosaurus* shares a pyramidal subadult postorbital horncore that in the adult was usually resorbed and modified to form postorbital ornamentation that came to most closely resemble the low, rounded postorbital surface of *Einiosaurus*. The development of supraorbital pitting on the dorsal postorbital surfaces of adult-sized specimens completely eliminated the horns on some specimens such as CMN 344. Neither the nasal or postorbital ornamentation is useful for distinguishing between *Styracosaurus* and *C. apertus*; however, the unmodified postorbitals horns of each can be distinguished from those of *C. brinkmani* which are longer and have a markedly dorsolateral orientation (Ryan and Russell, 2005).

The diagnostic characters of *Styracosaurus* are within the parietal ornamentation. As for other centrosaurines, epoccipitals fused to the scalloped margins of the subadult-sized parietal margin and then elaborated into their characteristic morphology as the animal grew to maturity. On adult-sized *S. albertensis* the abbreviated process at locus 1 is intermediate between the large hook expressed on most specimens of *Centrosaurus apertus* and the absence of this feature in *Achelousaurus*, *Einiosaurus* and *Pachyrhinosaurus* and *S. ovatus(?)*. Ornamentation at locus 2 is dimorphic in *Styracosaurus*, appearing either as the small, compressed tabs seen on the holotype CMN 344, *Achelousaurus*, *Einiosaurus* and *Pachyrhinosaurus*, or the more robust, medially-directed hooks similar to those of *Centrosaurus apertus*. It is possible that this feature may represent sexual dimorphism but the hypothesis cannot be tested at this time. With *Achelousaurus*, *Einiosaurus* and *Pachyrhinosaurus*, *Styracosaurus* shares a large spike at parietal locus 3 although the shape and orientation vary between these taxa. *Styracosaurus* is the only centrosaurine with a P4 parietal spike. The P5–P7 processes of *Styracosaurus* show intraspecific variability in their morphology (spike-like or unmodified centrosaurine epoccipitals).

Styracosaurus ovatus, from the Two Medicine Formation of Montana, is known from only one partial posterior frill margin. This material can be distinguished from *S. albertensis* based on the orientation of the P3 spikes (convergent in *S. ovatus* and divergent in *S. albertensis*), the extremely reduced (absent?) P1 process, and the tab-like P2 processes that closely resemble those of *Achelousaurus* and *Einiosaurus*, also from the Two Medicine Formation. The relatively large sample of parietals available for *S. albertensis* suggest that the P3 spikes never converge towards the midline in this taxon. The potential variability of this feature is unknown for *S. ovatus* but, based on the single specimen available, USNM 11869, this taxon can continue to be recognized. The veracity of this will be tested against future finds.

Monoclonius nasicornis Brown, 1917, based on AMNH 5351, is currently regarded as a junior synonym of *Styracosaurus albertensis* Lambe, 1913 (Dodson et al., 2004). However, this specimen exhibits all of the diagnostic characters of *Centrosaurus apertus* Lambe 1904 and none of those of *Styracosaurus* Lambe, 1913. *M. nasicornis* should therefore be referred to as junior synonym of *C. apertus* Lambe, 1904.

ACKNOWLEDGMENTS

We thank J. Gardner and the Collections staff of the RTMP, K. Sheperd and M. Feuerstack of the CMN, M. Brett-Surman of the USNM, K. Seymour of the ROM, and the Collections staff of the AMNH for access to material. Participants in the 2001–2 RTMP Field Experience Volunteer Preparation Program finished the preparation of material collected under the direction of John Visser in 1982 and 1983. The Phaeton Group (San Francisco) provided logistical support. P. Currie, D. Brinkman, G. Danis, D. Eberth, D. Tanke, and A. Murray provided helpful discussion and comments. R. Morgan (Calgary) drew figure 14A. Editor David Weishampel and reviewers Andy Farke and Thomas Lehman made constructive suggestions for improvement of the manuscript. This project was supported, in part, by a National Science and Engineering Research Council operating grant to APR.

REFERENCES

Brown, B. 1917. A complete skeleton of the horned dinosaur *Monoclonius*, and description of a second skeleton showing skin impressions. Bulletin of the American Museum of Natural History 37:281–306.

Brown, B., and E. M. Schlaikjer. 1937. The skeleton of *Styracosaurus* with the description of a new species. American Museum Novitates 955:1–12.

Czerkas. S, and S. Czerkas. 1990. Dinosaurs—A Global View. BDD Promotional Books Company, New York, 247 pp.

Dodson, P. 1987. Microfaunal studies of dinosaur paleoecology, Judith River Formation of southern Alberta; pp.71–75 in P. J. Currie and E. H. Koster, (eds.), Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers. Occasional Papers of the Tyrrell Museum of Palaeontology, No. 3.

Dodson, P. 1990. On the status of the ceratopsids *Monoclonius* and *Centrosaurus*; pp. 231–243 in K. Carpenter and P. J. Currie (eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press.

Dodson, P., and P. J. Currie. 1990. Neoceratopsia; pp. 593–618 in D. B. Weishampel, P. Dodson, P., and H. Osmolska, (eds.), The Dinosauria. University of California Press, Berkeley, California.

Dodson, P., C. A. Forster, and S. D. Sampson. 2004. Ceratopsidae; pp. 494–513 in D. B. Weishampel, P. Dodson, and H. A. Osmólska (eds.), The Dinosauria. University of California Press, Berkeley, California.

Eberth, D. A., and A. P. Hamblin. 1993. Tectonic, stratigraphic, and sedimentological significance of a regional disconformity in the upper Judith River Formation (Belly River Wedge) of southern Alberta, Saskatchewan and northern Montana. Canadian Journal of Earth Sciences 30:174–200.

Gilmore, C. W. 1930. On dinosaur reptiles from the Two Medicine Formation of Montana. Proceedings of the United States National Museum 77:1–50.

Holmes, R., M. J. Ryan, and A. Murray. 2006. Photographic atlas of the postcranial skeleton of the type specimen of *Styracosaurus albertensis* with additional isolated cranial elements from Alberta. Syllogeus 75:1–75.

Lambe, L. M. 1904. On the squamoto-parietal crest of two species of horned dinosaurs from the Cretaceous of Alberta. Ottawa Naturalist 18:81–84.

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

Lambe, L. M. 1915. On *Eoceratops canadensis*, gen. nov., with remarks on other genera of Cretaceous horned dinosaurs. Geological Survey of Canada, Geological Series 24:1–49.

Lull, R. S. 1933. Revision of the Ceratopsia. Memoirs of the Peabody Museum of Natural History 3:1–175.

Marsh, O. C. 1888. A new family of horned dinosaurs from the Cretaceous. American Journal of Science, Series 3. 36:477–478.

Marsh, O. C. 1890. Additional characters of the Ceratopsidae, with notice of new Cretaceous dinosaurs. American Journal of Science, Series 3, 39:418–426.

Ryan, M. J. 1992. The taphonomy of a *Centrosaurus* (Reptilia: Ornithischia) bone bed (Campanian), Dinosaur Provincial Park, Alberta, Canada. M.Sc. thesis, University of Calgary, Calgary, Alberta, 526 pp.

Ryan, M. J. 2003. Taxonomy, systematics and evolution of centrosaurine ceratopsids of the Campanian Western Interior Basin of North America. Ph.D. dissertation, University of Calgary, Calgary, Alberta, Canada, 578 pp.

Ryan, M. J., and D. Evans. 2005. A review of the Ornithischia of Dinosaur Provincial Park; pp. 313–348 in P. J. Currie and E. Koppelhus (eds.), Dinosaur Provincial Park. Indiana University Press, Bloomington, Indiana.

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

Ryan, M. J., D. A. Eberth, D. A. Brinkman, and A. P. Russell. 1998. A sub-adult *Styracosaurus* (Ornithischia) from the Dinosaur Park For-

mation (Late Campanian), Alberta, Canada. Journal of Vertebrate Paleontology 18 (3, Supplement):72A.

Ryan, M. J., A. P. Russell, P. J. Currie, and D. A. Eberth. 2001. Taphonomy of a *Centrosaurus* (Dinosauria: Ornithischia) bone bed from the Dinosaur Park Formation (Campanian) of Alberta, Canada with comments on cranial ontogeny. Palaios 16:482–506.

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

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

Seeley, H. G. 1888. On the classification of the fossil animals commonly named Dinosauria. Proceedings of the Royal Society of London 43:165–171.

Sereno, P. C. 1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). National Geographic Research 2:234–256.

Visser, J. 1984. Sedimentology and taphonomy of a *Styracosaurus* bonebed in the Late Cretaceous Judith River Formation, Dinosaur Provincial Park, Alberta. M.Sc. thesis, University of Calgary, Calgary, Alberta, Canada, 150 pp.

Submitted June 20, 2006; accepted May 9, 2007.