

# A new ceratopsid dinosaur (*Ornithischia*) from the uppermost Horseshoe Canyon Formation (upper Maastrichtian), Alberta, Canada

Xiao-chun Wu, Donald B. Brinkman, David A. Eberth, and Dennis R. Braman

**Abstract:** A skeleton of a new ceratopsid dinosaur, *Eotriceratops xerinsularis* gen. et sp. nov., is described in this paper. It is the first associated vertebrate skeleton found within the upper 20 m of the Horseshoe Canyon Formation. *Eotriceratops xerinsularis* is a large chasmosaurine that differs from other chasmosaurines in a unique set of features in the premaxilla, nasal horn core, squamosal frill, and epijugal. The most striking of those features includes an extremely tall, non-recessed narial process of the premaxilla; the presence of greatly elongate, spindle-shaped epoccipitals on the squamosal frill; a deep, well-demarcated fossa on the anteroventral surface of the squamosal frill; a sharply conical epijugal with a pronounced proximoposterior process and separate fossa-like facets for the jugal and quadratojugal; and the presence of an obliquely extending vascular trace meeting a transverse vascular trace ventrally on the anterior surface of the nasal horn core. Our phylogenetic analysis suggests that *E. xerinsularis* is nested within a clade including *Triceratops*, *Diceratops*, and *Torosaurus*, which are all from late Maastrichtian deposits. The upper 20 m of the Horseshoe Canyon Formation comprises a coal-rich interval (Carbon–Thompson coal zone, unit 5), which previously has been assigned to upper Maastrichtian magnetochrons 31n and 30r, and the *Manicorpus gibbus* miospore subzone. The ceratopsid specimen was collected from between the Carbon and Thompson coal seams, and thus, is inferred to (1) occur near the top of magnetochron 31n and (2) have an age of 67.6–68.0 Ma. Large chasmosaurine ceratopsids, such as *Triceratops* and *Torosaurus*, have not previously been described from the Horseshoe Canyon Formation or from magnetochron 31n or the *M. gibbus* miospore subzone. Thus, *Eotriceratops* is distinctly older than any other ceratopsid in the *Triceratops* group, and the discovery of *E. xerinsularis* helps fill a biostratigraphic gap between early and late Maastrichtian chasmosaurines.

**Résumé :** Le squelette d'un nouveau dinosaure cératopsidé, l'*Eotriceratops xerinsularis* gen. et sp. nov., est décrit dans cet article. Il s'agit du premier squelette vertébré associé observé dans les 20 derniers mètres de la Formation de Horseshoe Canyon. L'*Eotriceratops xerinsularis* est un grand chasmosauriné qu'un ensemble unique de caractères des prémaxillaires, du centre de la corne nasale, de la frange squamosale et de l'épijugal distinguent d'autres chasmosaurinés. Parmi les caractères les plus saillants figurent un processus narial des prémaxillaires non renforcé et extrêmement long, la présence d'époccipitaux en forme de fuseaux très allongés sur la frange squamosale, une fosse profonde et bien démarquée sur la surface antéroventrale de la frange squamosale, un épijugal fortement conique présentant un processus proximopostérieur prononcé et des facettes séparées en forme de fosse pour le jugal et le quadratojugal, et la présence d'une trace vasculaire oblique qui rejoint ventralement une trace vasculaire transversale sur la surface antérieure du centre de la corne nasale. L'analyse phylogénétique laisse croire que l'*E. xerinsularis* s'insère dans un clade qui comprend le *Triceratops*, le *Diceratops* et le *Torosaurus*, tous présents dans des dépôts du Maastrichtien tardif. Les 20 derniers mètres de la Formation de Horseshoe Canyon comprennent un intervalle riche en charbon (zone à charbon Carbon–Thompson; unité 5), précédemment affectée aux magnétochrons 31n et 30r du Maastrichtien supérieur, ainsi qu'à la sous-zone à miospores du *Manicorpus gibbus*. Le spécimen de cératopsidé a été prélevé entre les filons de charbon Carbon et Thompson et, par conséquent, il en est déduit (1) qu'il proviendrait de la partie supérieure du magnétochron 31n et (2) que son âge serait de 67,6–68,0 Ma. De grands cératopsidés chasmosaurinés tels que le *Triceratops* et le *Torosaurus* n'ont pas été décrits auparavant dans la Formation de Horseshoe Canyon, le magnétochron 31n ou la sous-zone à miospores du *M. gibbus*. Ainsi, l'*Eotriceratops* est nettement plus vieux que tout autre cératopsidé du groupe des *Triceratops* et la découverte d'*E. xerinsularis* contribue à combler une lacune biostratigraphique entre les chasmosaurinés du Maastrichtien précoce et du Maastrichtien tardif.

[Traduit par la Rédaction]

Received 13 November 2006. Accepted 20 March 2007. Published on the NRC Research Press Web site at <http://cjcs.nrc.ca> on 10 October 2007.

Paper handled by Associate Editor H.-D. Sues.

**X.-c. Wu.**<sup>1</sup> Canadian Museum of Nature, P.O. Box 3443, STN "D", Ottawa, ON K1P 6P4, Canada.

**D.B. Brinkman, D.A. Eberth, and D.R. Braman.** Royal Tyrrell Museum of Palaeontology, P.O. Box 7500, Drumheller, AB T0J 0Y0, Canada.

<sup>1</sup>Corresponding author (e-mail: [xcwu@mus-nature.ca](mailto:xcwu@mus-nature.ca)).

## Introduction

Southern Alberta is famous for its rich record of upper Cretaceous dinosaurian and other fossil vertebrates (Ryan and Russell 2001; Currie and Koppelhus 2005). Ceratopsids, or horned dinosaurs, are one of the best represented dinosaur groups in the region—and one of the last non-avian dinosaur groups to go extinct (Russell 1967; Weishampel et al. 2004). In western Canada, ceratopsid remains are abundant and well documented in the middle to upper Campanian Belly River Group and Wapiti Formation, the upper Campanian to lower Maastrichtian lower Horseshoe Canyon Formation, and the upper Maastrichtian Scollard and Frenchman formations (equivalent to the Hell Creek and Lance formations of the USA). However, until now, no ceratopsid remains have been documented in the upper one-quarter of the Horseshoe Canyon Formation and its equivalent deposits in neighboring areas, a peculiar pattern that contrasts greatly with the rich occurrence of other dinosaurs in this interval (Eberth et al. 2001). This gap in ceratopsid biostratigraphic data from western Canada is unfortunate in that it apparently coincides with a time of major faunal transition between the so-called “Edmontonian” and “Lancian” dinosaur assemblages (sensu Russell 1975; Sullivan and Lucas 2003, 2006).

In the 2001 field season, a team from the Royal Tyrrell Museum of Palaeontology and Canadian Museum of Nature began a systematic exploration for vertebrate fossils in the upper half of the Horseshoe Canyon Formation, with a particular focus on the vicinity of Dry Island Buffalo Jump Provincial Park, about 70 km northwest of Drumheller, Alberta (Fig. 1). During that first season, Mr. Glen Guthrie, the camp cook, found an incomplete skeleton of a very large ceratopsid near the western bank of the Red Deer River within the park.<sup>2</sup> Elements of the skeleton were not fully articulated, but were associated across an area of 3 m<sup>2</sup> (Fig. 2). Because no duplicate skeletal elements were found, we interpret these remains as pertaining to a single individual. This specimen represents the first discovery of associated-to-articulated and identifiable (to the species level) dinosaur skeletal remains from the top 20–25 m of the ~290 m thick Horseshoe Canyon Formation (Fig. 3); it is the first occurrence of identifiable ceratopsid remains in the top quarter of the formation. The large size and initial morphological assessment suggested that the specimen was a chasmosaurine that might be closely related to *Triceratops*, but its stratigraphic position, well below the *Triceratops*-producing beds of the Scollard Formation, indicated that the specimen was significantly older than any previously identified *Triceratops* remains from Alberta or from formations in Montana or Wyoming that are stratigraphically equivalent to the Scollard Formation. In this paper, we describe this specimen and discuss its systematic status, phylogenetic relationships, and stratigraphic significance.

## Geological setting, stratigraphy, and age

The Horseshoe Canyon Formation is the lowest formation of the Edmonton Group, and is overlain successively by the

Whitemud, Battle, and Scollard formations (Fig. 3). Five informal subdivisions (units) have been described within the Horseshoe Canyon Formation based on the presence or absence of coal and stratigraphic architecture (Eberth and O'Connell 1995; Eberth 2004). In the vicinity of Dry Island Buffalo Jump Provincial Park, outcrops of the Horseshoe Canyon Formation include, in ascending order, unit 3 (an interval of stacked sandstones), unit 4 (a mudstone dominated, non-coaly interval), and unit 5 (a coal-rich and organic shale-rich interval). Combined units 3 and 4, and unit 5, are broadly similar to Hamblin's (2004) Tolman and Carbon tongues of the Horseshoe Canyon Formation, respectively, but differ importantly in their contacts and inferred origins. Unit 5 is largely equivalent to the Carbon–Thompson coal zone of McCabe et al. (1989).

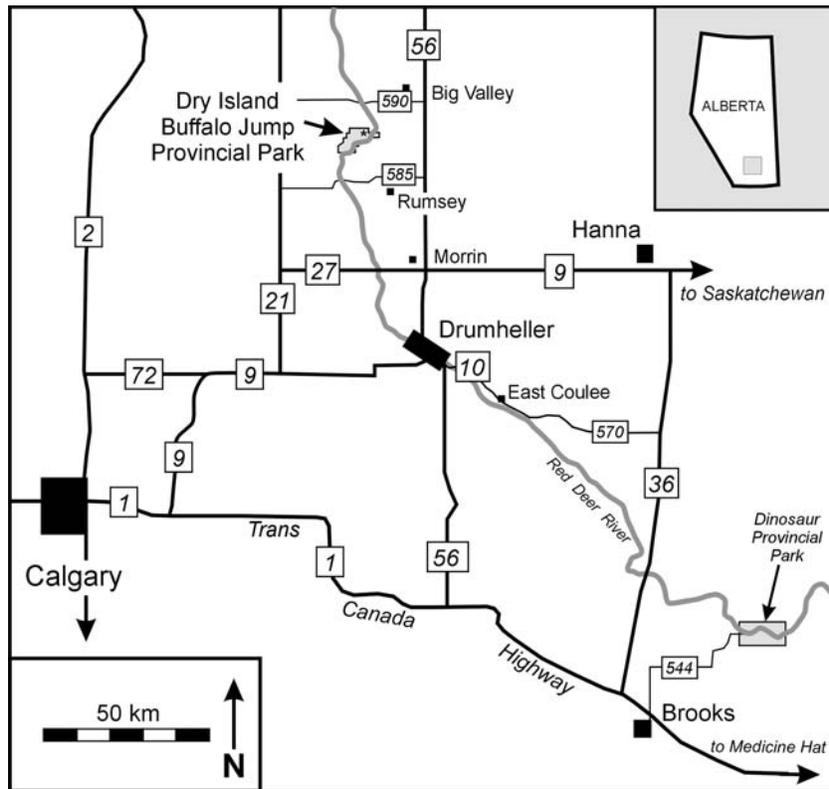
The new ceratopsid was collected from the middle of unit 5, 13.5 m above the base of the unit (Fig. 4). Unit 5 forms the uppermost 20–25 m of the formation and is characterized by the presence of coal seams that have been assigned to two thin, but laterally extensive, coal-producing intervals or zones: the lower, Carbon coal zone (seam 11 of Gibson (1977)) and the upper, Thompson coal zone (seam 12 of Gibson (1977)). The specimen occurs 9 m above the base of the Carbon coal zone and 6 m below the lowest coal in the Thompson zone (Fig. 4). Accordingly, the specimen occurs between both coal zones and is not assignable with any confidence to either.

Based on Srivastava (1970) and results from ongoing palynological study of the Horseshoe Canyon Formation (D.R. Braman, unpublished data, 2005), most of unit 5 (including the specimen locality) can be assigned to the *Mancicorpus gibbus* miospore subzone of the *Scollardia trapiformis* miospore Zone. This biozone is distinctive, can be traced across the Canadian portion of the Western Interior Basin (Braman and Sweet 1999), and correlates with magnetochrons 31n and 30r (Lerbekmo and Braman 2002). The lithostratigraphic interval, including and bounded by the Carbon and Thompson coal zones (including the specimen locality), has been assigned to the upper portion of magnetochron 31n by Lerbekmo (1985, fig. 4) and Lerbekmo and Coulter (1985, figs. 3, 17); we accept that chronostratigraphic assignment here. Ogg et al. (2004, fig. 19.1) place the 31n magnetochron within the upper Maastrichtian substage and assign it an age of 67.6–68.0 Ma. We tentatively accept these assignments until the lower and upper Maastrichtian substage boundary is formalized and more radioisotopic dates are available from unit 5.

Large chasmosaurine ceratopsids, such as *Triceratops* and *Torosaurus*, have not previously been described from the Horseshoe Canyon Formation or from magnetochron 31n or the *M. gibbus* miospore subzone, but are known from above these intervals. For example, the Frenchman Formation of southern Saskatchewan yields the late Maastrichtian ceratopsids *Triceratops* and *Torosaurus*, but is younger than unit 5 in having been deposited during magnetochron 29r (Lerbekmo 1985) and containing a palynological assemblage

<sup>2</sup>Barnum Brown, the famous fossil collector working for the American Museum of Natural History, apparently reported this specimen in his 1910 field notes as one of the team's first discoveries during their first field season in Alberta. However, he chose not to collect the specimen because it was considered low quality relative to other specimens in the area, including an assemblage of large theropod skeletal elements in what is now known as the *Albertosaurus* bonebed.

**Fig. 1.** Locality map for *Eotriceratops insularis*. The specimen locality is indicated by an asterisk in the northeast portion of Dry Island Buffalo Jump Provincial Park. More detailed locality information is available from the Royal Tyrrell Museum, Collections Section. Upper right inset shows field area in relation to the Province of Alberta.



that is assignable to the *Wodehouseia spinata* miospore Zone (Braman and Sweet 1999). Similarly, the Lance Formation of Wyoming, and the Hell Creek Formation of Montana and North Dakota also yield late Maastrichtian ceratopsids (*Triceratops*, *Torosaurus*, *Diceratops*) but are regarded as younger than the Horseshoe Canyon Formation because they yield *Aquilapollenites bertillonites* and *Wodehouseia spinata* (Norton and Hall 1969; Leffingwell 1971; Farabee and Canright 1986; Nichols 2002; D.R. Braman, unpublished data, 2005). Paleomagnetic data also support a younger age assignment for the Lance and Hell Creek formations, and suggest that their oldest non-marine portions are largely limited to magnetochron 30n (Hicks et al. 2002; Lund et al. 2002), but may be as old as 30r (Hicks et al. 1999).

In summary, all available stratigraphic data indicate that the new chasmosaurine ceratopsid is (1) younger than any ceratopsid previously collected from the Horseshoe Canyon Formation and (2) older than any previously known large chasmosaurine collected from the *Triceratops*-producing beds of the Scollard, Frenchman, Hell Creek, and Lance formations. Our review of magnetostratigraphic and palynological evidence indicates that this specimen fills a significant biostratigraphic gap between chasmosaurines of the so-called Edmontonian and Lancian dinosaur assemblages.

### Institutional abbreviations

AMNH, American Museum of Natural History, New York, N.Y.; ANSP, Academy of Natural Sciences, Philadel-

phia, Pa.; CM, Carnegie Museum of Natural History, Pittsburgh, Pa.; DMNH, Denver Museum of Natural History, Denver, Colo.; LACM, Natural History Museum of Los Angeles County, Los Angeles, Calif.; MOR, Museum of the Rockies, Bozeman, Mont.; NMC, Canadian Museum of Nature (formerly National Museum of Canada), Ottawa, Ont.; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alta.; SDSM, South Dakota State School of Mines, Rapid City, S.D.; USNM, National Museum of Natural History (Smithsonian Institution), Washington, D.C. (formerly the United States National Museum); YPM, Yale Peabody Museum of Natural History, New Haven, Conn.

### Systematic paleontology

Ornithischia Seeley, 1888

Ceratopsia Marsh, 1890

Ceratopsidae Marsh, 1888

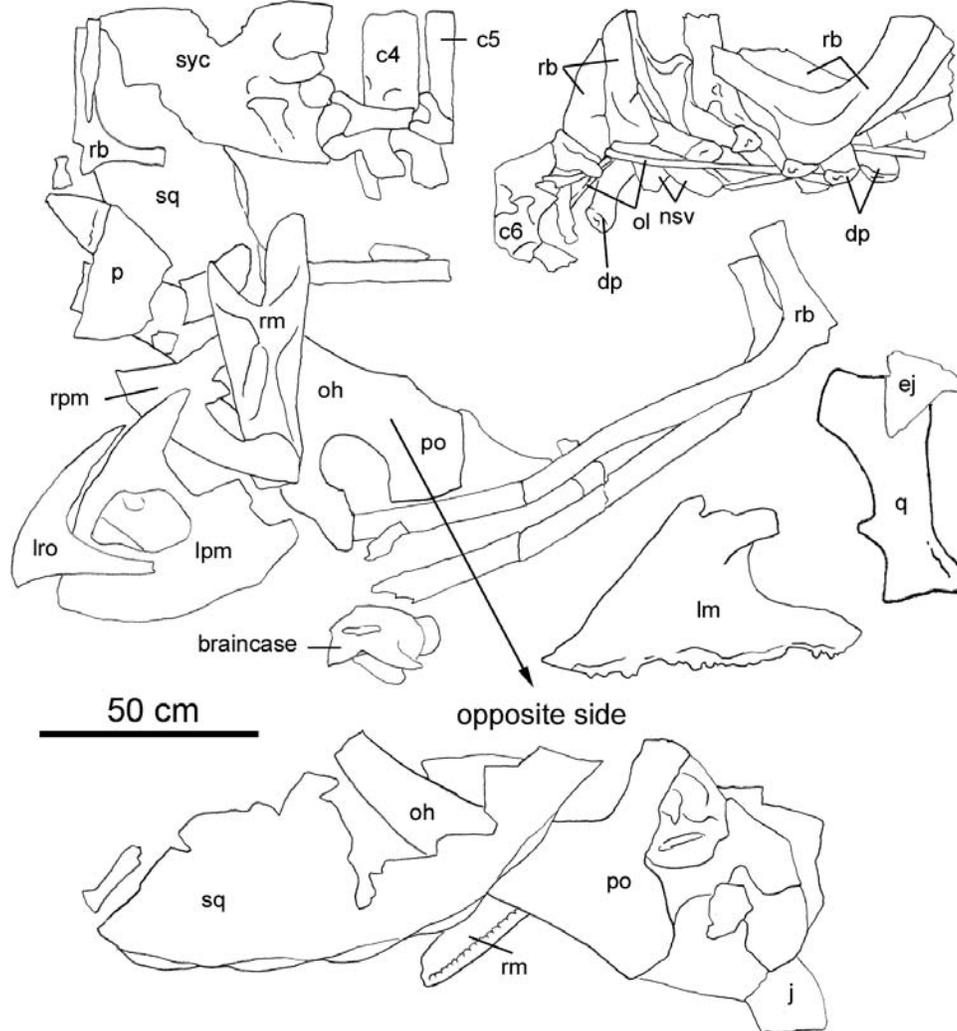
*Eotriceratops* gen. nov.

DIAGNOSIS: As for the type and only known species.

TYPE SPECIES: *Eotriceratops xerinsularis* gen. et sp. nov.

HOLOTYPE: RTMP 2002.57.7, an incomplete and disarticulated skeleton, including right rostral, both premaxillae, both maxillae, left supraorbital horn core with lacrimal, prefrontal, frontal, postorbital and jugal, left epijugal, right quadratojugal, left quadrate, partial parietal, left squamosal frill, braincase, syncervical, cervicals 4 and 5, a string of

**Fig. 2.** Spatial arrangement of preserved elements of *Eotriceratops xerinsularis* showing the distorted preservational state of the specimen. c4, c5, and c6, cervical vertebrae 4, 5, and 6, respectively; dp, diapophysis of vertebrae; ej, epijugal; j, jugal; lm, left maxilla; lpm, left premaxilla; lro, left rostrum; nsv, neural spine of vertebrae; oh, orbital horn core; ol, ossified ligament; p, parietal; po, postorbital; q, quadrate; rb, rib; rm, right maxilla; rpm, right premaxilla; sq, squamosal; syc, syncervical vertebrae.



vertebrae including posterior cervicals and anterior dorsals, some ribs and fragments of ossified ligaments.

**LOCALITY AND HORIZON:** Within Dry Island Buffalo Jump Provincial Park (northeastern quarter), southern Alberta; between coal seams 11 and 12, in the upper 20 m of the Horseshoe Canyon Formation; late Maastrichtian age.

**ETYMOLOGY:** Generic name *Eotriceratops* implies that it is an early member of the “*Triceratops*” group; specific name *xerinsularis* refers to Dry Island Buffalo Jump Provincial Park, where the specimen was collected.

**DIAGNOSIS:** A large chasmosaurine ceratopsid with a skull length of about 3 m, measured from the tip of the snout to the posterior edge of frill. It differs from other chasmosaurines in having the following combination of derived features: (1) tall lamina-like narial process of premaxilla lacking any fossa or recess and having its dorsal margin well above ventral border of interpremaxillary fenestra; (2) epoccipitals of squamosal frill extremely elongate, spindle-shaped, and contacting each other; (3) a well-demarcated elliptical depression or fossa on anteroventral surface of squamosal frill; (4) a deep, slightly oblique trace for blood vessels meeting a transverse trace ventrally on anterior surface of nasal horn; and (5) sharply conical epijugal with a pronounced proximoposterior process and separate fossa-like articular facets for jugal and quadratojugal.

gate, spindle-shaped, and contacting each other; (3) a well-demarcated elliptical depression or fossa on anteroventral surface of squamosal frill; (4) a deep, slightly oblique trace for blood vessels meeting a transverse trace ventrally on anterior surface of nasal horn; and (5) sharply conical epijugal with a pronounced proximoposterior process and separate fossa-like articular facets for jugal and quadratojugal.

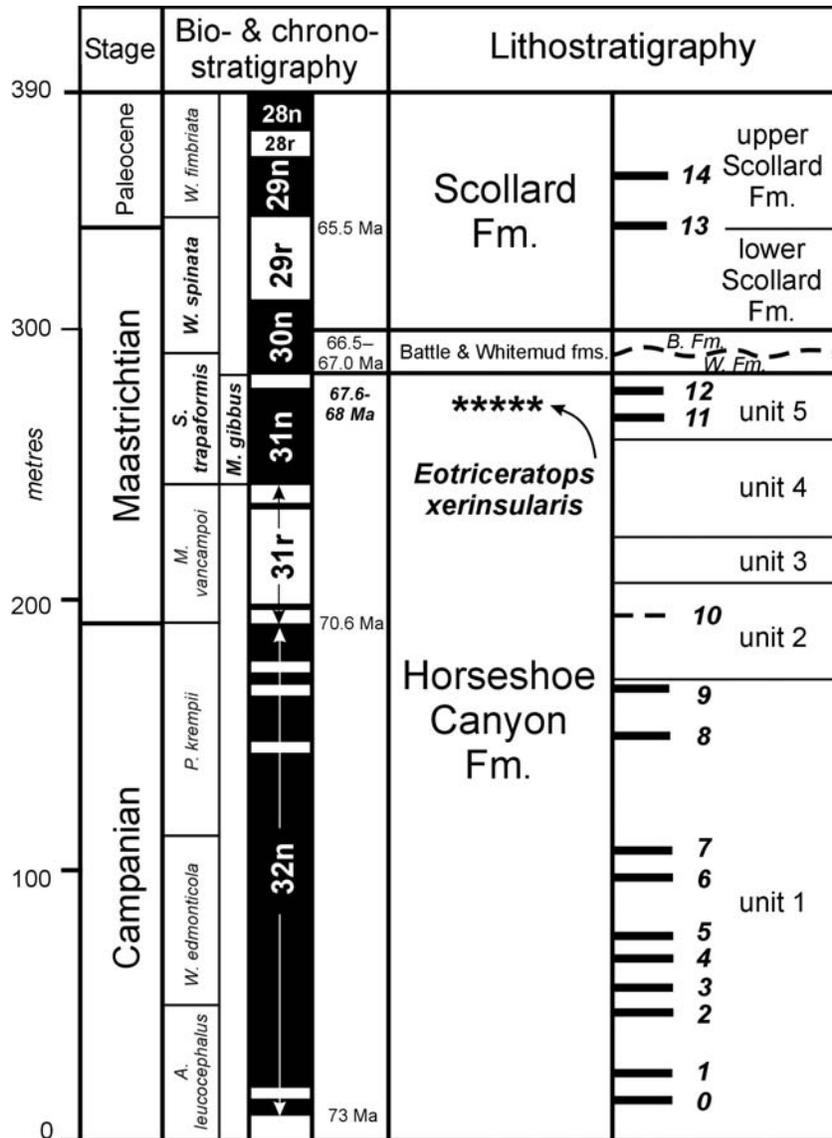
### Description

The specimen is preserved in carbonaceous shale. This structurally weak matrix allowed for crushing and distortion of bones during burial, resulting in a substantially flattened skeleton. The most striking evidence for distortion is visible in the occipital condyle and supraorbital horn core, which show a significant amount of compression.

### Rostral

The rostral is well preserved, although the posterior tip of the left ventral ramus and the posterior half of the right ventral ramus are missing (Fig. 5). Its left lateral surface is

**Fig. 3.** Stratigraphy of *Eotriceratops insularis*. Specimen occurs between the Carbon and Thompson coal zones (seams 11 and 12, Gibson 1977) in the middle of unit 5 (Eberth 2004), which occurs in the uppermost 20 m of the Horseshoe Canyon Formation. Biostratigraphic, magnetostratigraphic, and absolute age assignments are drawn from Srivistava (1970), Lerbekmo and Braman (2002), Lerbekmo (1985), Lerbekmo and Coulter (1985), and Ogg et al. (2004). Assignment to the upper Maastrichtian (see text) is compatible with Ogg et al. (2004); however, because the upper and lower Maastrichtian boundary is not formally fixed, we regard this assignment as tentative and not yet clearly defined for the Alberta Basin (cf. Braman and Sweet 1999). Numbered horizontal bars indicate the stratigraphic occurrence of coal seams recognized by Gibson (1977) and other authors. Fm., Formation; B. Fm., Battle Formation; W. Fm., Whitemud Formation.



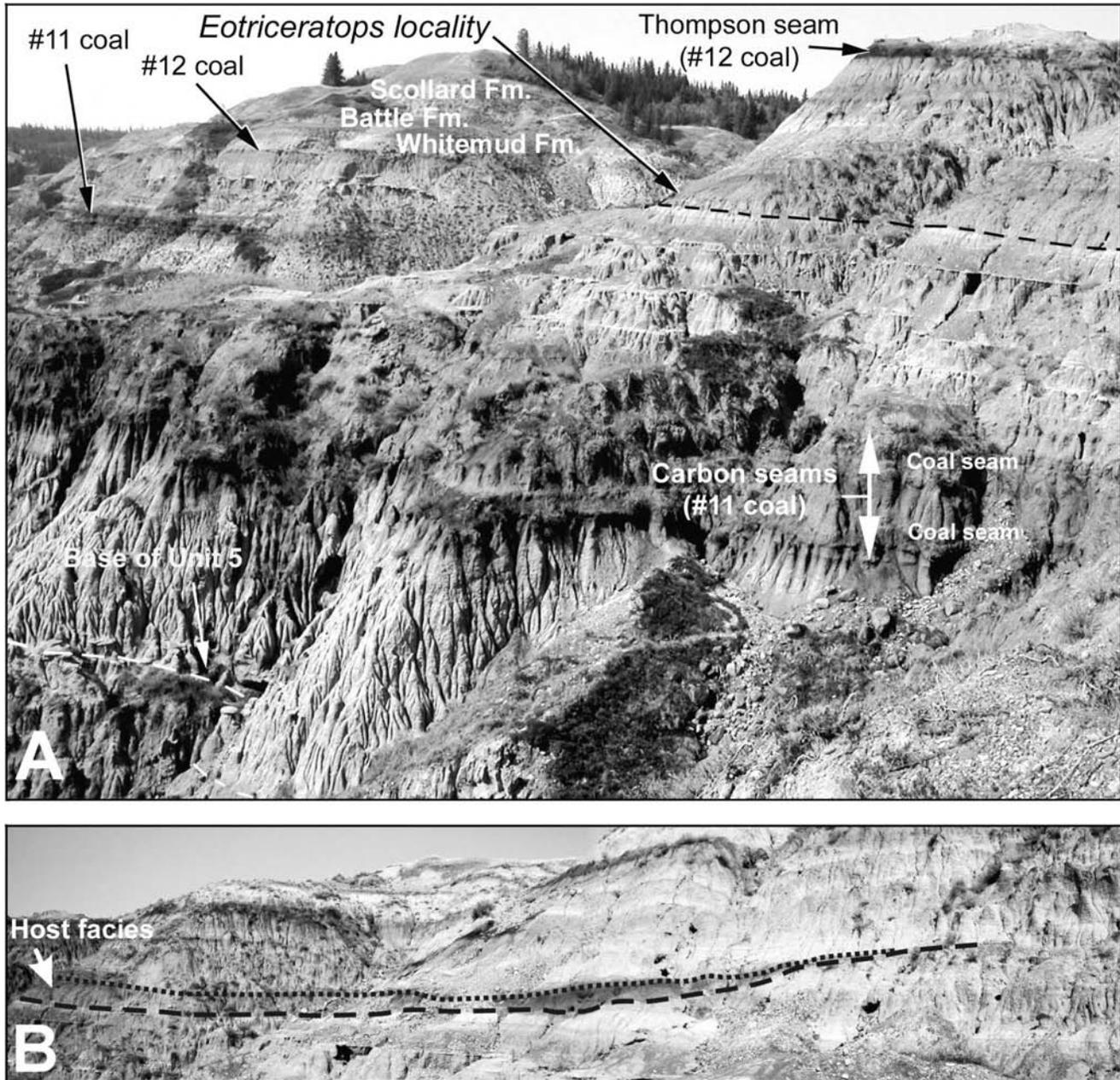
clearly convex, but its right lateral surface is much less so because of preservational distortion. Both lateral surfaces bear elongate pits or irregular grooves of different lengths. The rostral is large and roughly boomerang-shaped in lateral view, with elongate dorsal and ventral rami as in many chasmosaurines. The dorsal ramus is dorsally convex and tapers to a point posteriorly. It extends posteriorly along the dorsal edge of the premaxilla and sheathes the anterior three quarters of that bone, as suggested by an articular facet on the premaxilla (Figs. 6A–6D). The ventral ramus is shorter than the dorsal ramus and slightly concave ventrally. The ventral ramus may have tapered to a point in life. It differs from the dorsal ramus in that the articular facet for the

premaxilla is dorsoventrally much broader on the lateral side than on the medial side (Figs. 5C, 5D). The anterior tip of the rostral bends slightly downward to form a short pointed beak. The palatal surface of the rostral is not visible because its two rami were strongly compressed toward the midline.

**Premaxilla**

The left premaxilla is much more complete than the right, but the posterior end of its posteroventral process (prong) is missing. In lateral view (Figs. 6A, 6C), the premaxilla has a triangular anterior portion with dorsal and ventral margins that form an angle of about 75°. Both dorsal and ventral margins are convexo-concave, but much more so in the case of the ventral margin. The premaxillary septum anterior to

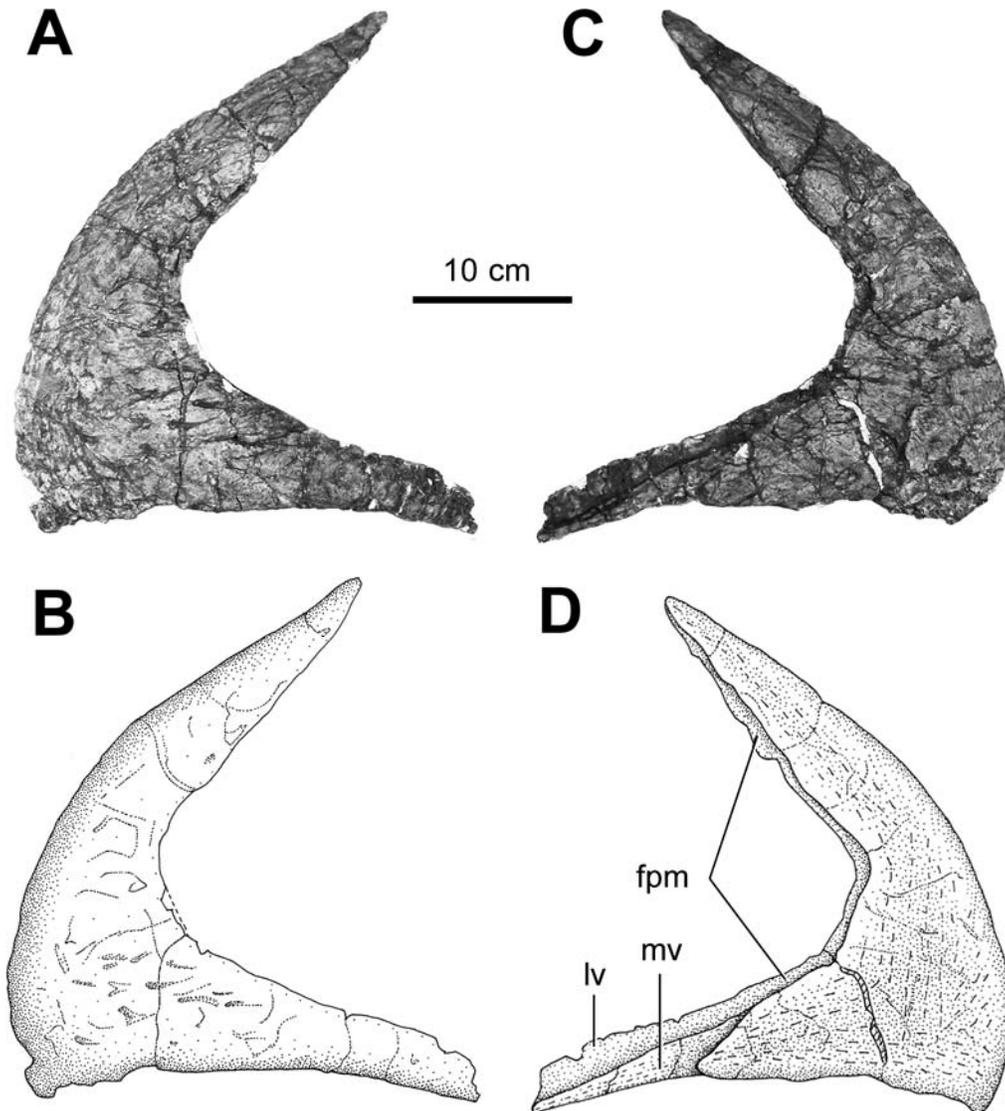
**Fig. 4.** Location, stratigraphic position, and facies association of *Eotriceratops xerinsularis*. (A) Specimen occurs between the Carbon and Thompson coal zones, 9 m above the base of the Carbon zone (a double seam) and 13.5 m above the base of unit 5 (here marked by the base of a fine-to-medium grained sandstone body). (B) Specimen occurs near the base of a broadly lenticular (tens of metres wide), dark red-brown, silty, carbonaceous shale that is up to 50 cm thick. Carbonaceous shale is sharp based to erosional, and exhibits patchy, irregular ironstone nodules, and local sulfur staining.



the external naris is moderately elongate, and bears a fossa (premaxillary fossa) that is perforated by a large and oval fenestra (interpremaxillary fenestra). The premaxillary fossa appears shallow, although this may have been a result of mediolateral compression during fossilization. A depression or fossa is present anteroventral to the interpremaxillary fenestra. This fossa is also shallow as a result of the flattening during fossilization. An opening within the fossa has an irregular shape but may be an artifact of preservation (its margins are broken). A semicircular process (interpremaxillary process) projects from the anteroventral border of the

premaxillary fossa into the interpremaxillary fenestra. In life, this process was flat and contacted its opposite. A comparable process is present in many specimens of *Triceratops* (USNM 4928, CM 1221, YPM 1822, YPM 1883, LACM 7207), *Diceratops* (USNM 2412), and *Pentaceratops* (AMNH 1624, AMNH 6325; Lehman 1998), although it is often triangular in shape, weakly developed, and sometimes more posteriorly positioned in *Pentaceratops*. The narial strut along the posterior margin of the premaxillary septum is thickened but narrow, with a straight posterior edge forming the anterior border of the external naris. A tall lamina-

**Fig. 5.** Left rostrum of *Eotriceratops xerinsularis* in lateral (A, B) and medial (C, D) views. fpm, facet for premaxilla; lv, lateral portion of ventral ramus; mv, medial portion of ventral ramus.

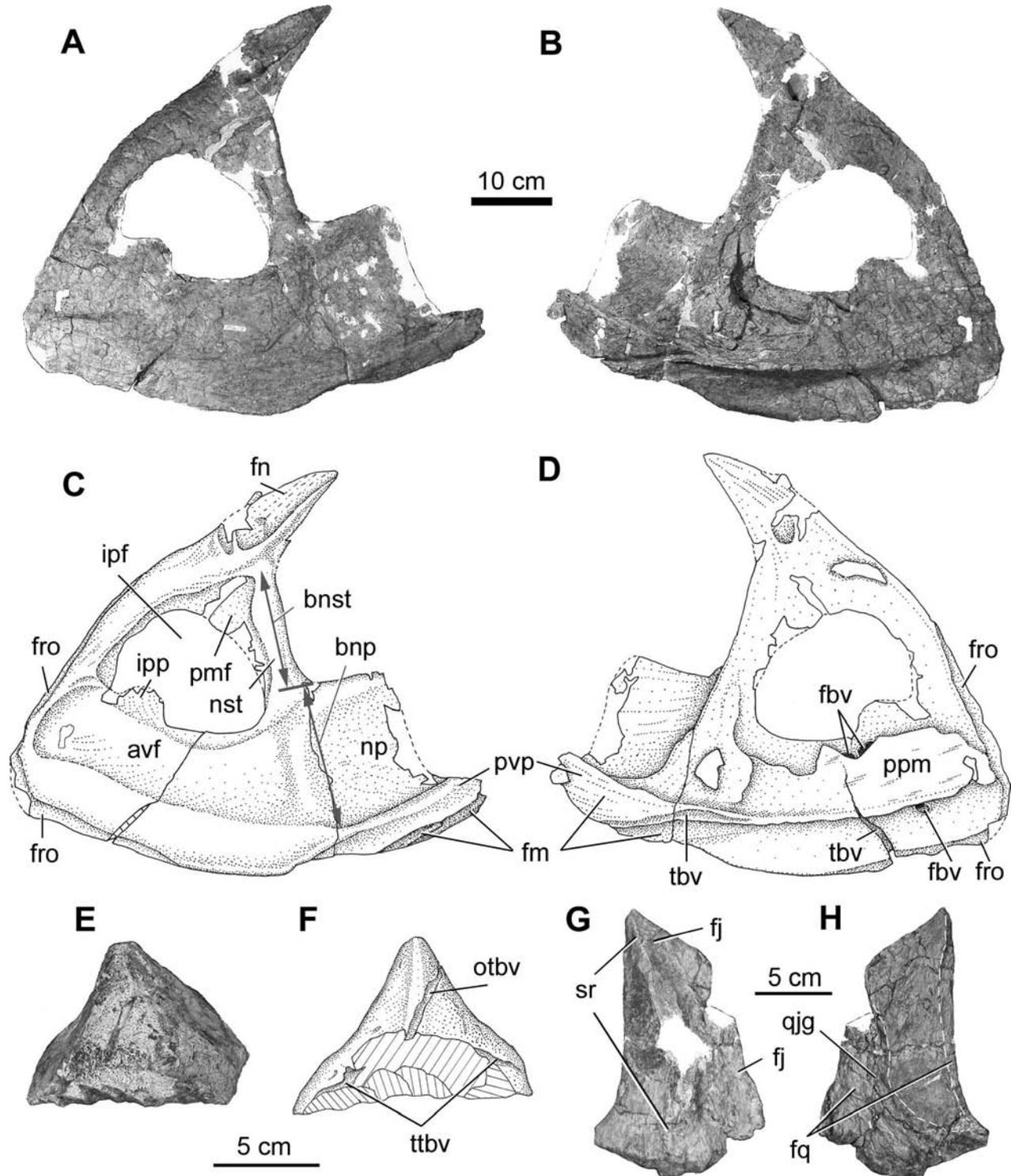


like narial process is present posteroventral to the strut. This process is nearly complete except for its posterior edge. Its lateral surface is slightly concave but does not have a deep invaginated fossa or recess as seen in *Triceratops* (Forster 1990), *Torosaurus* (MOR 1122), and *Diceratops* (USNM 2412). The narial process is 120% taller than the narial strut (measured along arrows in Fig. 6C). The dorsal margin of the narial process is positioned well above the ventral border of the interpremaxillary fenestra. The narial process is similarly tall in some specimens of *Triceratops* (USNM 4928, USNM 1201, LACM 7207, AMNH 5116, YPM 1821) but, as discussed later in the text, never reaches the proportions seen in *Eotriceratops*. Ventral to the narial process, the premaxilla is thickened laterally and bears an articular facet for the maxilla along its ventrolateral surface. Dorsal to the premaxillary fossa, the premaxilla is very narrow but thick. Posterodorsal to the narial strut, the premaxilla forms a short but sharp triangular nasal process. As indicated by a facet, the lateral surface of the nasal process was entirely over-

lapped by the nasal in life, except for a narrow area along the ventral margin. There is no evidence as to whether or not the nasal process extended up into the anterior base of the nasal horn core.

In medial view (Figs. 6B, 6D), the palatal portion of the premaxilla appears very narrow transversely because of mediolateral compression during preservation. As a whole, the medial surface is flat, with facets for the opposite premaxilla, the rostral, and the maxilla. The facet for the opposite premaxilla is extensive, occupying most of the medial surface including the narial strut. The facet for the ventral ramus of the rostral is narrow, running along the ventral edge, from the anterior tip to a midpoint along the preserved portion of the bone. The facet for the maxilla is restricted to the area ventromedial to the lamina-shaped narial process. A deep groove in the ventral portion of the maxillary facet may represent a trace for blood vessels and nerves. Relationships with other bones along the posterior border of the external naris are unknown because of the damage to the posterior

**Fig. 6.** Some skull elements of *Eotriceratops xerinsularis*. (A, C) Left premaxilla in lateral views. (B, D) Left premaxilla in medial views. (E, F) Nasal horn core in slightly different anterior views. (G, H) Right quadratojugal in lateral and medial views, respectively. avf, fossa or recess anteroventral to the interpremaxillary fenestra; bnp, dorsoventral breadth of narial process; bnst, dorsoventral breadth of narial strut; fbv, foramen for blood vessels and nerves; fj, facet for jugal; fn, facet for nasal; fm, facet for maxilla; fq, facet for quadrate; fro, facet for rostrum; ipf, interpremaxillary fenestra; ipp, interpremaxillary process; np, narial process; nst, narial strut; otbv, oblique trace for blood vessels; pmf, premaxillary fossa; ppm, palatal portion of maxilla; pvp, posteroventral process; qjg, quadratojugal groove; sr, swollen ridge; tbv, trace for blood vessels and nerves; ttbv, transverse trace for blood vessels.



portion of the posteroventral prong. Two foramina open into canals for blood vessels and nerves on the dorsolateral margin of the palatal portion. The foramina are close to each other and positioned just posteroventral to the inter-premaxillary process. The canals exit through foramina on the ventral surface of the palatal portion, but are farther apart from one another. The posteriormost foramen opens into a groove that continues ventrally and slightly anteriorly to the edge of the bone.

#### *Nasal horn core*

The nasal horn core is nearly complete (Figs. 6E, 6F). It is longer than wide, and broader anteriorly than posteriorly. Its upper portion is laterally compressed. An obliquely oriented groove and a slightly arched, transversely oriented groove are present on the anterior surface of the horn core and are probably vascular traces. Each groove is incompletely preserved. A transverse groove, which extends along the base of the horn core, is also present in *Triceratops* (Forster 1990). The oblique groove extends dorsally and laterally, and then turns onto the left lateral surface where it gradually fades away. It was probably connected ventrally to the transverse groove, although the area of inferred contact is not preserved. As described earlier in the text, the nasal process of the premaxilla is short, and its lateral surface is entirely overlapped by the nasal, except for the ventral margin of the process. This is comparable to the situation seen in *Triceratops* (CM 1221, YPM 1822, USNM 4928, DMNH 48617), *Torosaurus* (ANSP 15192), and *Diceratops* (sensu Forster 1990, 1996a (USNM 2412)), indicating that, as in those genera, the nasal horn core is anteriorly positioned just dorsal to the anterior edge of the external naris.

#### *Maxilla*

The left maxilla is almost complete with only its posteroventral tip missing (Fig. 7). It is a thick and roughly triangular bone, as in other chasmosaurines. It has a straight anterodorsal edge, a slightly incurved ventral (dental) edge, and a strongly convexo-concave posterodorsal edge. In lateral view (Figs. 7A, 7C), its surface is uneven. Articular facets suggest that its sloping anterodorsal edge overlaps the premaxilla but underlies the nasal. The suture between the maxilla and premaxilla is slightly longer than the maxillary–nasal suture. The convexo-concave posterodorsal edge of the maxilla can be divided into three portions: a greatly incurved dorsal portion, a vertical middle portion, and a strongly oblique ventral portion. Articular facets on the dorsal portion indicate that the maxilla overlaps the lacrimal and widely underlies the jugal. The deep notch between the lacrimal facet and the jugal facet is the part of the antorbital fenestra. This fenestra is interpreted to have been oval in shape, with an anteroventrally directed long axis. The articular facet for the jugal indicates that the latter may have been excluded from the fenestra. The dorsal portion of the posterior edge of the maxilla overhangs the top of the middle portion. The middle portion bears a thin free edge, forming a deep embayment between the dorsal and ventral portions. The ventral portion of the posterior edge of the maxilla runs along the posterodorsal margin of the alveolar process and bears an extensive facet for the ectopterygoid and a smaller facet for the pterygoid. The lateral surface of the maxilla,

anterior to the posterior embayment, is concave and contains a series of foramina. The concave area becomes narrow and shallow anteriorly. Ventral to the concave area, the surface of the maxilla is smooth.

In medial view (Figs 7B, 7D), the surface of the maxilla is concave, especially dorsal to the level of the secondary palate. A deep triangular fossa on the upper part extends anteriorly into the bone. This fossa is referred to here as the maxillary sinus, and may be equivalent to the vacuity between the temporal fossa and mouth (Hatcher et al. 1907). The maxilla is thicker anterior to the maxillary sinus. Sutural facets for the palatine are located dorsal and posteroventral to the maxillary sinus. The palatine facet extends posteroventrally onto the alveolar process, meeting the facet for the ectopterygoid laterally and the facet for the pterygoid posteriorly. Anteriorly, the articular facet for the posteroventral prong of the premaxilla is deep and groove-like. The facets for the palatal portion of the premaxilla and the vomer are not preserved because much of the palatal part of the maxilla anterior to the choana is missing. The lower part of the maxilla, ventral to the level of the secondary palate and dorsal to the tooth row, is divided into a dorsal and a ventral portion by a longitudinally elongate, step-like structure. The dorsal portion slightly overhangs the ventral and bears a series of foramina along the ventral side of the overhang.

The maxilla has 35 tooth rows preserved, and there may have been one or two more positioned posteriorly. The preserved dental margin of the maxilla is 60 cm long, and the anteriormost 5 cm of the margin are toothless.

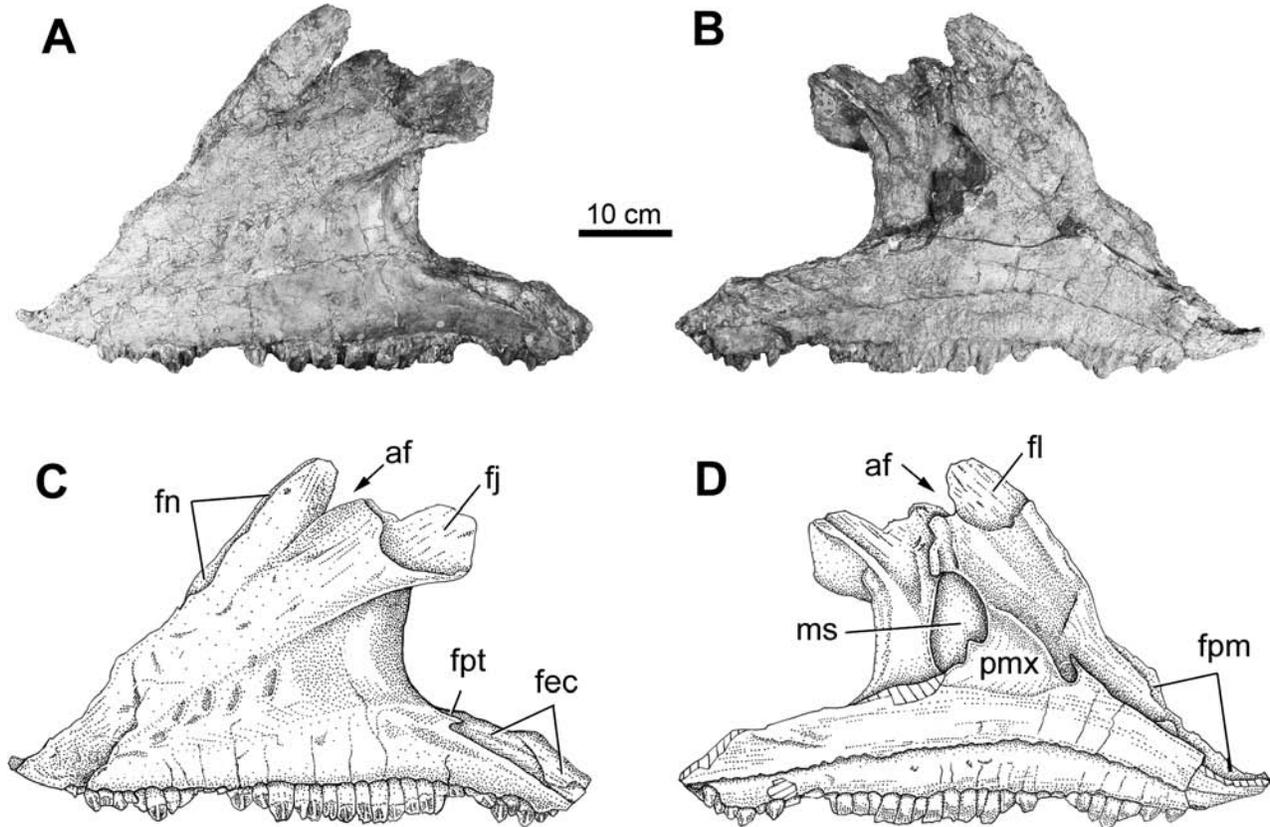
#### *Supraorbital horn core and circumorbital elements*

The left **supraorbital horn core** is nearly complete, missing only its distal tip. Adjacent bones, especially those around the orbit, are present, although not all are in articulation. The lacrimal is indistinguishably fused with the prefrontal. It is rough and thickened where it forms the rim of the orbit (Figs. 8A, 8B). The lacrimal–nasal suture and the articular facet for the maxilla are not preserved. An articular facet on the jugal indicates that the jugal was overlapped by the lacrimal.

The **prefrontal** is fused with the postorbital posterodorsally and the frontal anterodorsally. It is strongly thickened and very rough, forming a rugose swollen rim around the anterodorsal border of the orbit (Fig. 8B). The prefrontal rim of the orbit is much broader than the lacrimal rim.

Much of the left **jugal** is preserved, and is slightly displaced beneath the postorbital (Fig. 8). The jugal is T-shaped as in other chasmosaurines. In lateral view, the jugal–postorbital suture is probably V-shaped as in some specimens of *Triceratops* (e.g., YPM 1821). Anteriorly, the jugal overlaps the postorbital, but much of the posterior portion of the jugal may have been overlapped by the postorbital. The jugal forms the ventral rim of the orbit, which is rough but not very swollen. The anteroventral portion of the jugal, which typically overlaps the maxilla, and the posterodorsal portion, which typically meets the squamosal, are incomplete. The anterior margin of the jugal flange is complete although cracked. The posterior edge of the jugal flange ventral to the jugal–squamosal suture and dorsal to the jugal–quadratojugal facet is well-preserved. This edge forms

**Fig. 7.** Left maxilla of *Eotriceratops xerinsularis* in lateral (A, C) and medial (B, D) views. af, antorbital fenestra; fec, facet for ectopterygoid; fj, facet for jugal; fl, facet for lacrimal; fn, facet for nasal; fpm, facet for premaxilla; fpt; facet for pterygoid; ms, maxillary sinus; pmx, palatal portion of maxilla.



the anterior border of the infratemporal fenestra. The distal end of the jugal become narrow but does not taper to a point. In medial view, the surface of the jugal is smooth. Its articular surface for the postorbital is obscured, but the facet for the quadratojugal is clear along the posteroventral margin of the flared flange (Fig. 8B).

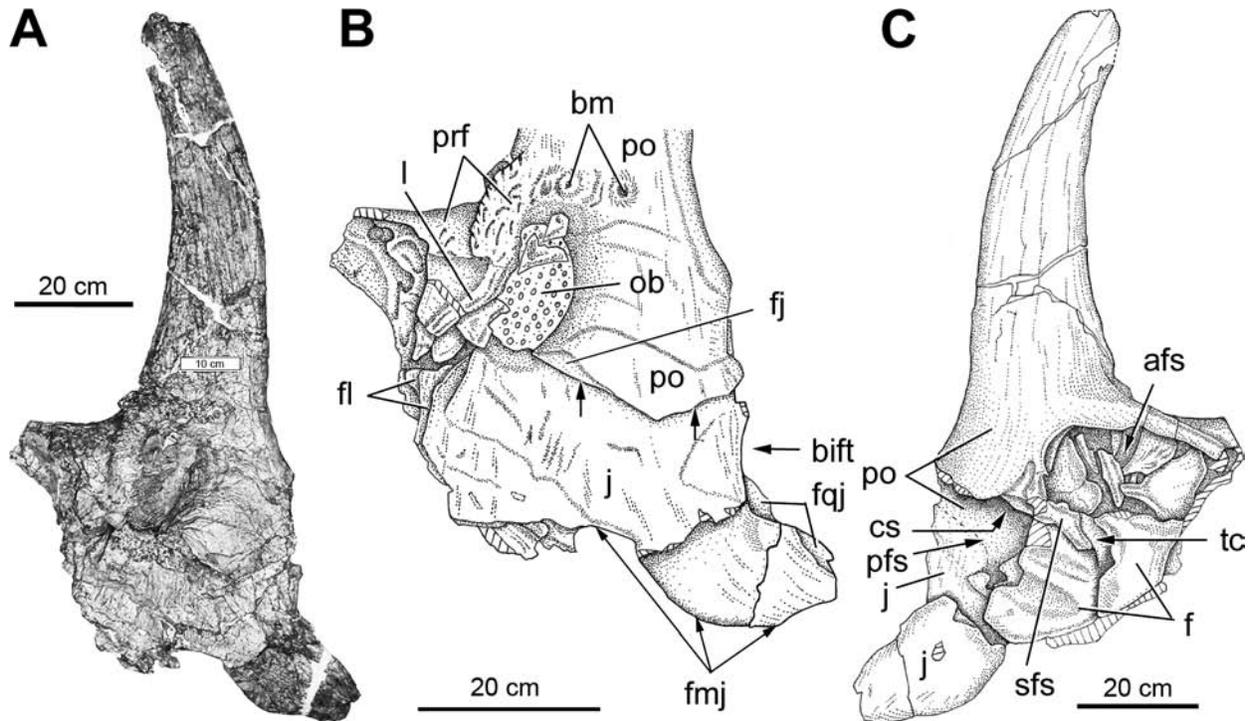
The left **epijugal**, which is preserved together with the left quadrate, is almost complete. In lateral outline it is triangular and taller than wide, with a straight proximal margin that extends posteriorly onto a proximoposterior process that overhangs the main body of the triangle (Figs. 9A–9C). In life, it may have been roughly cone shaped and oval in cross-section. The lateral surface of the epijugal is ornamented by vertically oriented grooves and ridges. In medial view, the lower half of the epijugal is flat, but its upper half is occupied by a triangular, cup-like fossa that extends inwards and downwards into the bone (Fig. 9B). In proximal view, the surface of the epijugal is entirely occupied by a trough-like fossa that expands onto the proximoposterior process (Fig. 9C). These two fossae are well separated. It is likely that the fossa on the proximal surface capped the distal end of the jugal flange, whereas the fossa on the proximomedial surface received the anterodistal end of the quadratojugal. These two fossa-like articular facets are not present in other chasmosaurines.

Much of the **postorbital** is preserved, although the areas where it meets the squamosal and parietal are missing (Fig. 8). As described earlier, its suture with the jugal is

clear but its suture with the prefrontal is obscured by fusion of the two bones. The supraorbital horn core was laterally compressed during preservation. The preserved portion is about 77 cm long from the dorsal edge of the orbit to its tip, and originally may have been 80 cm long. The body of the horn core curves anteriorly. The external surface of the horn core exhibits many vertically oriented, fine grooves and ridges. Posterior to the orbit, the grooves—some of which are deep and broad—extend anteroposteriorly. The postorbital forms the smooth posterior border of the orbit. Three shallow pits dorsal to the orbit are interpreted as bite marks.

In medial view, breakage near the base of the supraorbital horn core has exposed internal sinuses (Fig. 8C). The frontal sinus is surrounded by the postorbital and internal portion of the frontal. As in *Triceratops* (Lull 1933; Forster 1996b), the sinus is divided into the anterior and posterior portions by a septum (transverse buttress). The anterior portion is more complete than the posterior portion. It is longer than high, and is enclosed dorsally by the postorbital and ventrally by the frontal. Bony struts or lamina from the postorbital partially subdivided the anterior portion of the frontal sinus. A canal just anterior to the base of the transverse buttress appears to perforate the floor of the anterior portion of the frontal sinus to enter the brain cavity. The shape and size of the posterior portion of the frontal sinus are unknown because only the lateral wall and part of the floor are preserved. No struts or lamina are present. The cornual sinus is

**Fig. 8.** Supraorbital horn core and bones around orbit of *Eotriceratops xerinsularis* in lateral (A, B) and medial views. asf, anterior frontal sinus; bift, border of infratemporal fenestra; bm, bite marks; cs, conual sinus; f, frontal; fj, facet for jugal; fl, facet for lacrimal; fmj, free margin of jugal flange; fqj, facet for quadratojugal; j, jugal; l, lacrimal; ob, orbit; pfs, posterior frontal sinus; po, postorbital; prf, prefrontal; sfs, septum of frontal sinus; tc, trace of canal. Two arrows below the postorbital–jugal suture indicate that the jugal was pushed upward underneath the postorbital during preservation.



visible within the posterior half of the frontal sinus. It is small but enters deeply into the supraorbital horn core anterodorsally, as in *Triceratops* (Forster 1996b). The ventral surface of the preserved part of the frontal, which roofs the brain cavity and olfactory tube, is smooth but concave.

#### Quadratojugal

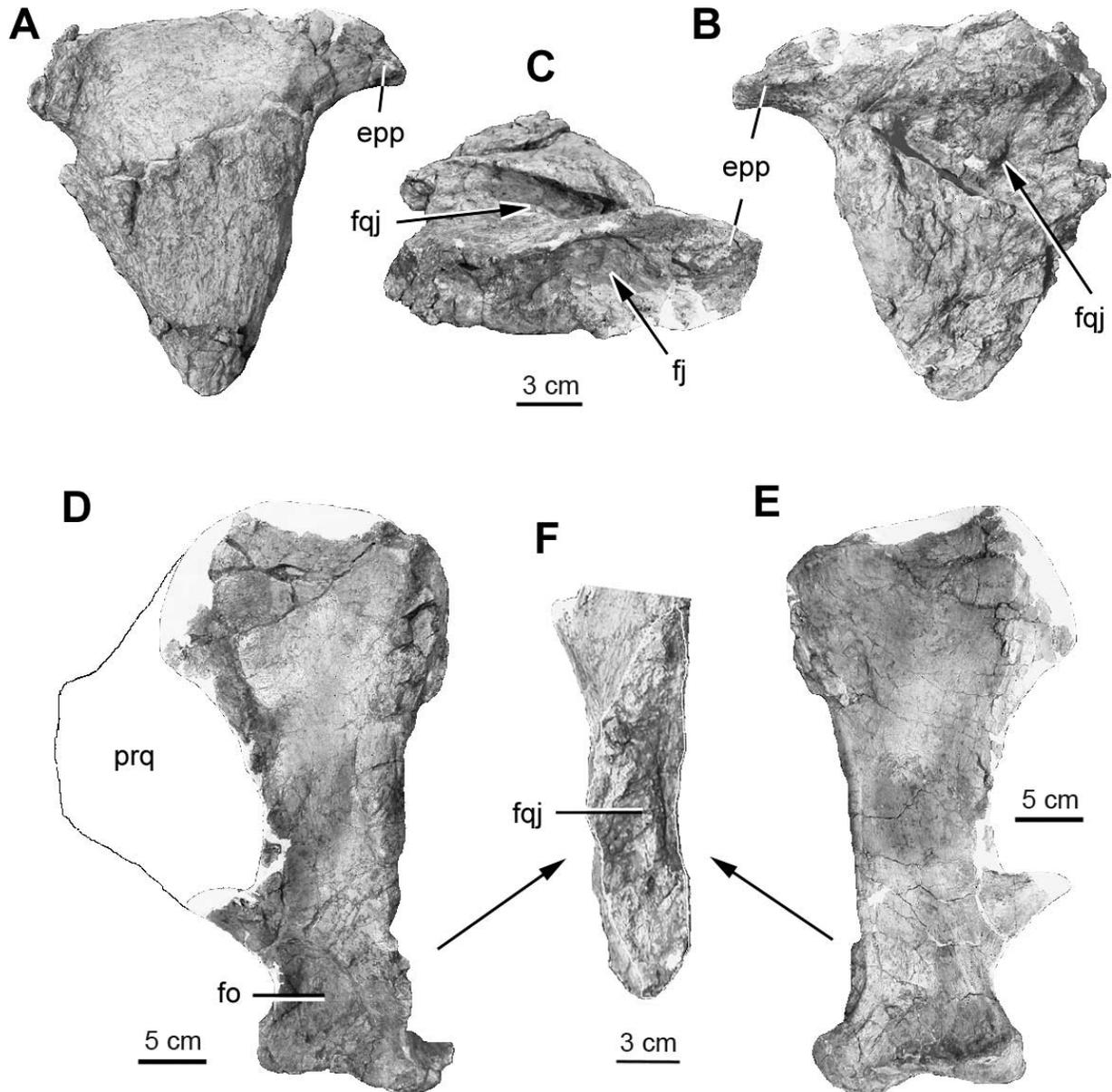
Much of the right quadratojugal is preserved. It is broader ventrally than dorsally, and it has a thickened and strongly convex ventral edge and a dorsal edge that slopes anteriorly (Figs. 6G, 6H). The lateral surface of the bone is arched along a swollen ridge (here termed the lateral quadratojugal ridge) that runs from a midpoint on the ventral margin of the bone to its posterodorsal tip. The lateral quadratojugal ridge forms the posterior edge of the facet that receives the overlapping jugal as in other ceratopsids. In *Eotriceratops*, the dorsal most part of the quadratojugal is very narrowly exposed and may have not bordered the infratemporal fenestra dorsally, a situation opposite that of *Triceratops*. Posterior to the ridge, the bone surface is smooth and concave. Ventrally, the thickened edge of the quadratojugal overlaps the lateral side of the quadrate. A convex ventral prominence of the quadratojugal inserts into the fossa on the proximomedial surface of the epijugal. The medial surface of the quadratojugal is flat. The full extent of the articular facet for the quadrate is not clear. An area marked by many fine ridges on the anteroventral portion of the inner surface is interpreted as one portion of this facet, and a narrow rough surface along the posterior edge of the bone may represent

another portion. These two surfaces meet ventrally. A groove or trough, presumably for blood vessels and nerves, is present within the quadrate facet.

#### Quadrate

The left quadrate is well preserved although its pterygoid ramus and dorsal edge are missing (Figs. 9D–9F). This bone is similar in shape to that of *Triceratops*. The preserved part of the bone is 42 cm tall and 15 cm wide (measured along the long axis of the mandibular condyle). It is broad but very thin dorsally and narrow but thickened ventrally, where it forms the jaw joint. This joint is subdivided into medial and lateral condyles by a shallow trough. The lateral condyle is slightly larger than the medial, and because the quadratojugal also contributes to the lateral condyle, the lateral portion of the jaw joint would have been more massive than the medial. In anterior view, the surface of the quadrate is smooth and concave (Fig. 9D). A depression or fossa that may be exaggerated by preservation is present on the ventral quarter, close to the mandibular condyles. Although the pterygoid ramus is not preserved, the base of the ramus, as seen medially, suggests a fan shape, as in other ceratopsids. In posterior view, the surface of the quadrate is smooth and convex. A depressed area on the ventral part of the posterior surface (Fig. 9E) is an artifact of preservation. The lateral margin of the quadrate is thickened to form a ridge, and a low round process is present midway along this margin. The articular facet for the quadratojugal, seen in lateral view, is very rough. The quadrate thins dorsal to this facet (Fig. 9F).

**Fig. 9.** Left epijugal and left quadrate of *Eotriceratops xerinsularis*. Left epijugal in lateral (A), medial (B), and dorsomedial (C) views. Left quadrate in posterior (D), anterolateral (F, lower half), and anterior (E) views. epp, proximoposterior process of epijugal; fj, facet for jugal; fo, fossa; fqj, facet for quadratojugal; prq, pterygoid ramus of quadrate.



#### **Parietal**

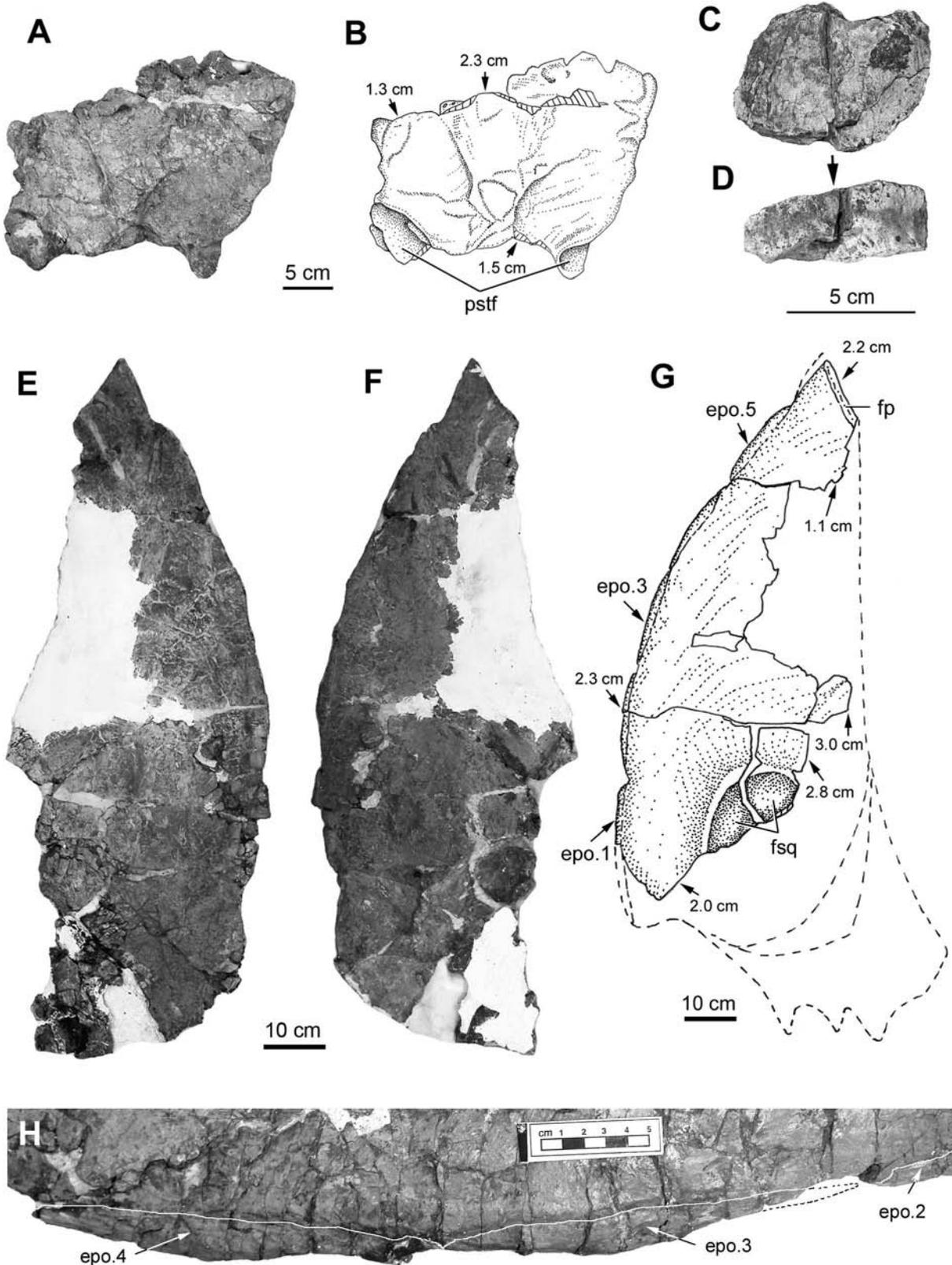
Only the anterior part of the parietal is preserved (Figs. 10A, 10B). It is convex dorsally and shows no midline suture. Its dorsal surface is rough, with fine traces for blood vessels. A portion of the edge of the supratemporal fossa is preserved on the anterolateral corner of the bone. The remaining edges of the bone are broken. The ventral surface is not exposed. The preserved portion of the parietal is thickest (2.3 cm) at the posterior midline. Laterally, it thins to about 1.3–1.5 cm, and is much thinner than in *Triceratops*. A fragmentary bone preserved close the parietal is identified as a fragment of the parietal frill (Figs. 10C, 10D) and is 3.1 cm thick.

#### **Squamosal**

The left squamosal is represented by the portion of the bone that contributed to the frill. Much of the anteromedial

part and anterolateral corner of the squamosal is missing (Figs. 10E–10G). The preserved portion of the squamosal is 113.8 cm long and 43.3 cm wide. Although no trace of a fenestra is present, the element is incomplete, and the possibility of fenestration in its more anterior portion cannot be excluded. Except for the anterior portion, the lateral margin of the squamosal is nearly complete. This edge is convex and not obviously scalloped as in most specimens of *Triceratops* (e.g., YPM 1822). Four and one-half epoccipitals are present, with the partial epoccipital being the anteriormost. The posteriormost epoccipital is missing. The sutural pattern, seen most clearly on the ventral surface, indicates that the more posteriorly positioned epoccipitals are more loosely attached to the frill and would have fused to the frill later in life (Lehman 1990). The lengths of the

**Fig. 10.** Frill fragments of *Eotriceratops xerinsularis*. (A, B) Anterior part of parietal frill in dorsal views. (C, D) A piece of parietal frill in dorsal and cross-section view, respectively. (E–G) Partial squamosal frill in dorsal (E) and ventral (F, G (a reconstruction)) views. (H) lateral edge of squamosal. epo.1–epo.5, epoccipitals 1–5, respectively; fp, sutural facet for parietal frill; fsq, fossa on ventral surface of squamosal frill; pstf, parietal portion of supratemporal fenestra; 1.1 cm, 1.3 cm, 1.5 cm... indicate, respectively, number of centimetre thicknesses of bone in areas shown by arrows.



epoccipitals suggest that the posteriormost epoccipital would have extended across the suture between the squamosal and parietal. Thus, if the reconstruction of the anterior portion of the squamosal is correct, the squamosal would have had five and one-half epoccipitals (Fig. 10G). All epoccipitals are slender and differ little in length. The fourth epoccipital, which is the most complete, is 18.5 cm long. This is an extremely elongated, crescent- or spindle-like element, with a length to width ratio of about 10:1 when viewed ventrally. As shown by the third and fourth epoccipitals, these elements contacted one another in life, a feature that differs from the arrangement of the epoccipitals in most chasmosaurines. The squamosal epoccipitals most resemble those of *Torosaurus utahensis* in shape (Sullivan et al. 2005) but, as discussed later in the text, differ in shape and proportions. In dorsal view, the surface of the squamosal is relatively smooth, with some fine traces for blood vessels. In ventral view, the surface is smooth and characterized by an elliptical fossa that is incomplete anteriorly and located in the anterior half of the bone. With its well-defined margin, this fossa differs from the depression or concave area seen in other chasmosaurines. Posterior to the fossa, the surface of the squamosal is concave. The squamosal–parietal suture is preserved along the posteromedial side of the squamosal. The suture is not thickened to form a distinct ridge like that of *Torosaurus* (ANSP 15192). As preserved, the frill differs from the evenly thickened frill of *Triceratops* in being relatively thin, having a thickness of 1.1 cm along the posteromedial edge, 2.2 cm at the posterior tip, 2.3 cm along anterolateral edge, 2.0 cm along the anteromedial edge, and about 3 cm along the medial edge at the midpoint. However, we cannot exclude the possibility that this variable thickness was accentuated during preservation.

### Braincase

The braincase is badly crushed and the foramen magnum has collapsed (Fig. 11). Some elements are missing, and the preserved bones are difficult to distinguish from one another. In dorsal view, much of the left side and the anterior portion of the braincase are damaged. The right wall of the braincase is displaced towards the left side and has shifted posteriorly to cover most of the occipital condyle (Fig. 11A). The preserved part of the left wall may include the **prootic** (anterior portion), the **supraoccipital** (mid-portion), and large **exoccipital** (posterior portion). No foramen or fenestra can be identified in dorsal view. Anteriorly, the keel-like ventral ridge of the **basisphenoid** is visible because of the missing anterior portion of the braincase. This ridge is incomplete anteriorly and dorsally. On the left side, a bone fragment is also visible in ventral view, where it is separated from the braincase by the matrix. It is likely that this fragment is not part of the braincase.

The occipital condyle was strongly compressed during preservation and is preserved as a round plate-like structure in lateral view (Figs. 11C, 11D). It is not known how much of the exoccipital would have contributed to the formation of the occipital condyle. The fan-like ventral process of the **basioccipital** is partially visible in lateral view, and it has a thickened and rough ventral edge. A foramen anterolateral to the neck region of the basioccipital may be an exit for cranial nerve XII. Anterodorsally, the lateral surface of the

exoccipital–prootic part of the braincase bears a series of depressions. Posteroventrally, a pair of large processes (basal tubera of the basisphenoid) are directed posteroventrally as in other ceratopsids. These tuberosities, which are thickened posteroventrally and become flattened anteriorly, extend further posteriorly than the fan-shaped ventral process of the basioccipital. As seen in ventral view (Figs. 11E, 11F), the basal tuberosities of the basisphenoid, together with the fan-shaped ventral process of the basioccipital, were displaced toward the left side. The posterior end of the right basal tuberosity is missing. The two basal tuberosities converge anteriorly toward the midline and merge with the keel-like ventral ridge.

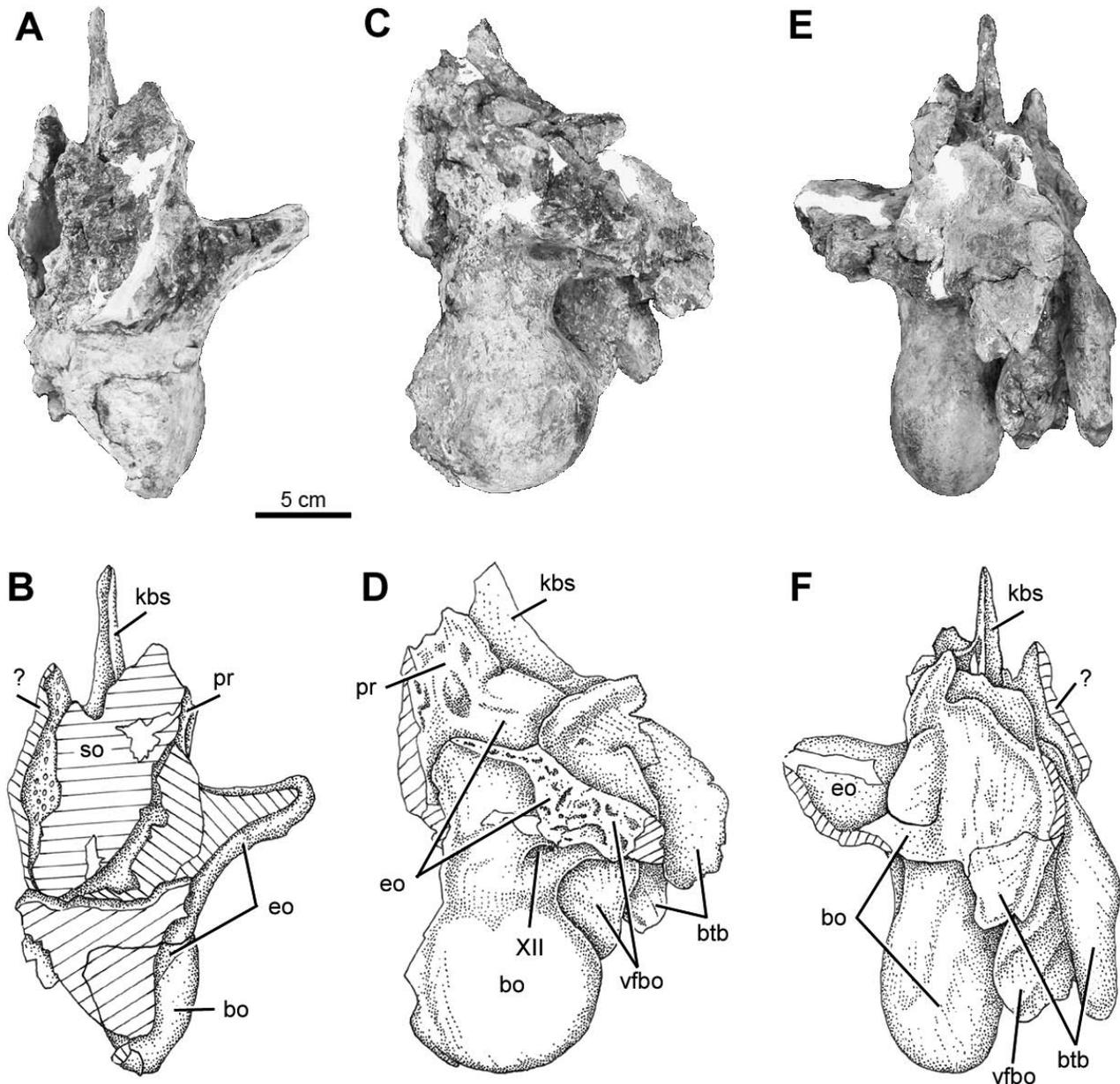
### Syncervical

The syncervical is incomplete and distorted, with much of its centrum damaged and the dorsal edge of its neural spine missing (Figs. 12A, 12B). Although none of the sutures between the individual vertebrae can be recognized, as a whole, the syncervical resembles that of *Triceratops*. Two intervertebral foramina are present, although they are filled with matrix and were laterally flattened during preservation. We identify the two foramina as those that occur between the atlas and axis, and between the axis and cervical 3. Thus, the syncervical would have been formed by the first three cervical vertebrae plus a ring-like hypocentrum, as is typically the case in ceratopsians (Lull 1933). The anterior surface of the centrum is deeply concave. Anterodorsal to the anterior intervertebral foramen, the neural arch of the atlas is broad and posterodorsally merges into the neural spine of the syncervical. The neural spine is low anteriorly and becomes tall posteriorly. A thickened ridge posterodorsal to the posterior intervertebral foramen extends dorsally and posteriorly. It is bordered ventrally by a shallow groove that most probably represents the suture between the axis and the third cervical. A slightly swollen area just anteroventral to the intervertebral foramen on the right side may represent the transverse process of the axis. The postzygapophyses face ventrolaterally and extend only a little posterior to the centrum. The posterior surface of the centrum is slightly concave.

### Cervical vertebrae 4 and 5

Cervical vertebrae 4 and 5 are preserved in articulation and are closely associated with the syncervical (Fig. 2). Cervical 4 is almost complete, and both cervical vertebrae 4 and 5 are better preserved on the right side. Each cervical bears the proximal portion of the corresponding rib on the right side, although these are displaced anteriorly. The centra are shallowly amphicoelous, laterally concave, and short, with the length to height ratio of the fourth being about 1:2 (Figs. 12C, 12D). The parapophysis is located at the anterodorsal edge of the centrum in cervical 4, but slightly posterior and dorsal to the edge in cervical 5. The diapophysis is well developed and is longer in cervical 5 than in cervical 4. This is also the case with the neural spine. The complete prezygapophysis of cervical 4 faces medially and dorsally, and extends anteriorly well beyond the centrum. The ventral surfaces of both cervicals are incomplete.

**Fig. 11.** Braincase of *Eotriceratops xerinsularis* in dorsal (A, B), right lateral (C, D) and ventral (E, F) views. As the occipital condyle shows, the braincase was laterally compressed. bo, basioccipital; eo, exoccipital; btb, basal tuber of basisphenoid; kbs, ventral keel of basisphenoid; pr, prootic; so, supraoccipital; vfbo, ventral fan of basioccipital; ?, a bone fragment not related to braincase; XII, cranial nerve XII.

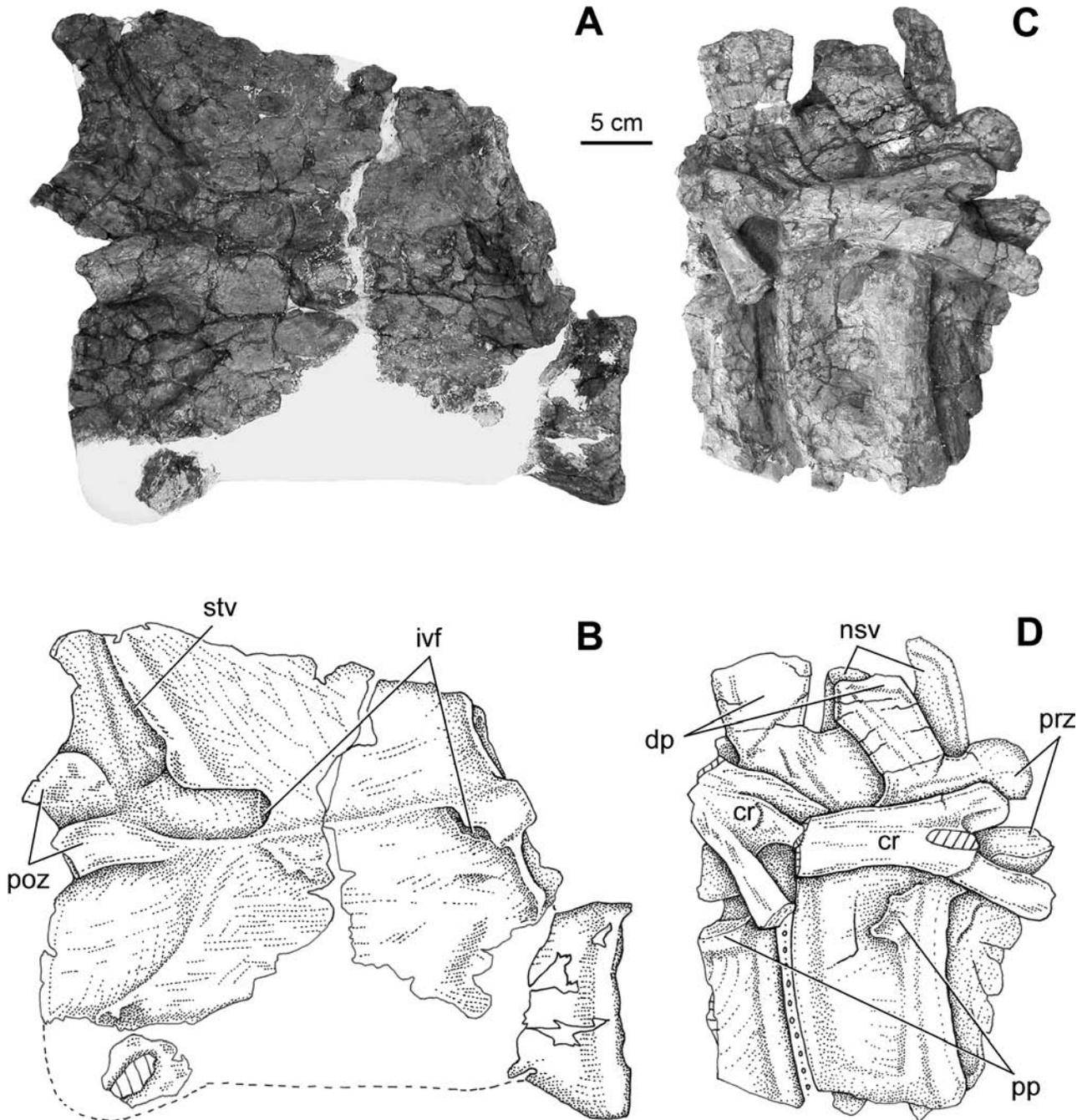


#### *Posterior cervical and anterior dorsal vertebrae*

An articulated series of vertebrae including posterior cervicals and anterior dorsals is preserved close to cervicals 4 and 5 (Fig. 2). Based on the number of the diapophyses and attached ribs, seven vertebrae, identified as the eighth to fourteenth, are present in the series. Thus, if the cervical series consists of nine vertebrae, these likely represent cervical 8 to dorsal 5 (Figs. 13A, 13B). Both the first and last vertebrae in this series are missing their centra and, except for the third dorsal, they are largely covered by the attached ribs. The centrum of the third dorsal is laterally concave. Its parapophysis is located on the neural arch at the level of the prezygapophysis, and its diapophyses is very pronounced

and widely separated from the parapophysis, corresponding to the relative positions of the two heads of the attached rib. Parapophyses of the first and second dorsals are hidden by the attached ribs but, as indicated by the tall position and massiveness of the diapophyses, are probably on the neural arch as well. The relative position of the parapophyses and diapophyses on the eighth and ninth cervical vertebrae is unclear because of poor preservation, and those on the fourth and fifth dorsal vertebrae are covered by ribs. The rib facet of the diapophyses becomes anteroposteriorly elongate and dorsoventrally narrow in the posterior vertebrae in this series. The neural spine is anteroposteriorly broader in the dorsal vertebrae than in the cervicals.

**Fig. 12.** Anterior cervical vertebrae of *Eotriceratops xerinsularis* in right lateral views. (A, B) Syncervical. (C, D) cervical vertebrae 4 and 5. cr, cervical rib; dp, diapophysis of vertebrae; ivf, intervertebral foramen; nsv, neural spine of vertebrae; poz, postzygapophysis; pp, parapophysis; prg, prezygapophysis; stv, sutural trace between vertebrae.

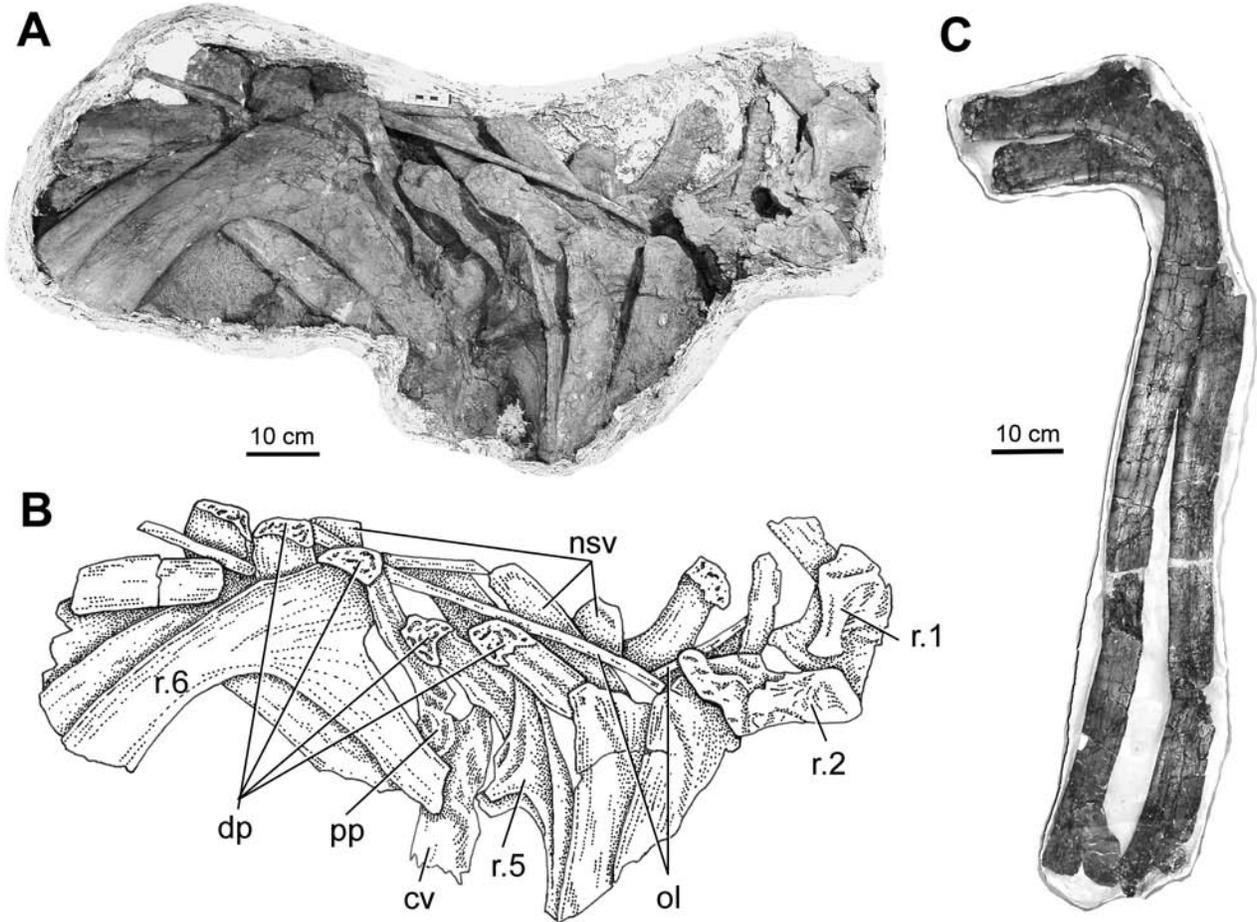


### **Ribs and ossified ligaments**

Except for two isolated and nearly complete ribs, all of the preserved ribs are represented only by their proximal ends and are preserved in articulation with the vertebrae. Two rib heads on the right side of cervicals 4 and 5 are typical for archosaurs in bearing three heads: a central one that is free and extends anteriorly, a short but stout dorsal process that articulates with the diapophysis, and an elongate ventral process that articulates with the parapophysis of the vertebra (Figs. 12C, 12D). The central head of the rib associated with cervical 4 and the anterior tip of the central head

of the rib associated with cervical 5 are missing. When complete, it is likely that these were as long as the dorsal process. The series, including vertebrae 8 to 14 (cervicals 8 and 9, and dorsals 1 to 5), has at least eight rib heads attached on the right side (Figs. 13A, 13B). The rib heads associated with cervicals 8 and 9 are fragmentary. Of the other six rib heads, only that associated with dorsal 3 is nearly complete. It has only two processes: a very short but broad dorsal process, and a long and slender ventral process. The two more posterior rib heads are similar in outline. The three more anterior ribs have a similar dorsal process but their

**Fig. 13.** Some vertebrae and ribs of *Eotriceratops xerinsularis*. cv, centrum of vertebra; dp, diapophysis of vertebrae; nsv, neural spine of vertebrae; ol, ossified ligament; pp, parapophysis; r.1, r.2, r.5, and r.6, ribs 1, 2, 5, and 6, respectively, reserved in the vertebral series.



ventral processes are missing. A bar-like bone fragment overlapping the rib heads 13 and 14 may represent the slender ventral process of rib 15. The two isolated ribs are nearly complete although their distal ends and the posterior margins of their proximal heads are damaged (Fig. 13C). The better preserved of the two is 118.5 cm long, measured from the knob-like dorsal process to the distal end. The other is 116.5 cm long. The knob-like dorsal process for the diapophysis is preserved in the longer rib, and the length of the ventral process, which articulated with the parapophysis of the vertebra, is similar to that of the third dorsal rib. On the basis of the morphology of their heads and relatively straight shafts, these two ribs are likely from a relatively anterior position along the dorsal series. Mediolaterally compressed ossified ligaments run between the transverse processes and neural spines in the articulated string of cervical and dorsal vertebrae (Fig. 13A, 13B).

### Comparison and discussion

*Eotriceratops* is a chasmosaurine because it shares with other members of the group the synapomorphies of a large rostral with deeply concave posterior margin and hypertrophied dorsal and ventral rami, an anteriorly elongate premaxillary septum, the presence of the thickened narial strut along the posterior margin of the premaxillary septum,

the perforation of the premaxillary septum, the presence of a narial process projecting into the external naris from the posteroventral margin of the premaxillary septum, and the presence of an anteriorly curved supraorbital horn core (Dodson et al. 2004; also see later in the text). Among the chasmosaurines, *Eotriceratops* has a closer relationship with more crownward members than *Chasmosaurus* and *Pentaceratops* on the basis of two synapomorphies: the supraorbital ornamentation centered posterodorsally or posterior to the orbit; and the broad supracranial cavity (sinus), underlying the supraorbital ornamentation and confluent with the cornual sinus (Dodson et al. 2004; also see later in the text). Therefore, in the following comparison, those crown chasmosaurines that occur in horizons either lower (*Anchiceratops*, *Arrhinoceratops*) or higher (*Triceratops*, *Diceratops*, *Torosaurus*) than *Eotriceratops*, are emphasized.

Although *Eotriceratops* is represented by an incomplete specimen, it can be defined by a combination of derived features. Among these, the large, non-recessed narial process of the premaxilla (Figs. 6A–6D) is unique for *Eotriceratops*. As indicated by the arrows in Fig. 6C, its dorsoventral height is greater than the height of the narial strut. Also, its dorsal margin is much higher than the ventral border of the interpremaxillary fenestra. In most other chasmosaurines, the narial process is anteroposteriorly short and dorsoventrally

narrow, and in more derived taxa, such as *Triceratops* (CM 1221, YPM 1822, YPM 1823, DMNH 48617), *Torosaurus* (ANSP 15192), and *Diceratops* (USNM 2412), it bears a deep recess laterally. In some specimens of *Triceratops* (e.g., USNM 4928, USNM1201, LACM 7207, AMNH 5116, YPM 1821), the laterally recessed narial process also appears to be dorsoventrally broad. However, the process is still relatively dorsoventrally narrower than in *Eotriceratops* when measured in the same way (Fig. 6C), and the dorsal margin of the process is lower than the ventral border of the interpremaxillary fenestra because of the small size of the fenestra (e.g., YPM 1821; Hatcher et al. 1907, fig. 18). The condition of this feature is unknown in *Arrhinoceratops* (ROM 5135) because of poor preservation. In *Anchiceratops* (TMP 83.01.01), the narial process is short compared with the narial strut and the dorsal margin of the narial process is at the level of the ventral margin of the interpremaxillary fenestra.

*Eotriceratops* also differs from other chasmosaurines in having extremely elongate, crescent- or spindle-shaped epoccipitals on the squamosal (Fig. 10H). As mentioned earlier in the text, the epoccipitals are most similar to those of *Torosaurus utahensis* (this taxon may represent a new chasmosaurine (R.M. Sullivan, personal communication, 2005)). However, they are still distinguishable in shape, size, and relationship with the squamosal from the epoccipitals in that taxon. In *Eotriceratops*, the squamosal epoccipitals have a similar shape and size, and contact one another along the margin of the frill. The slenderness of the epoccipitals is indicated by the length/width ratio, which is approximately 10. In *Torosaurus utahensis* (USNM 15583 = USNM 494473 of Sullivan et al. (2005)), 13 disarticulated epoccipitals are preserved. Nine of the 13 are more triangular than elongate crescent- or spindle-shaped, have a pronounced medial apex (sensu Sullivan et al. 2005), and are relatively larger. The remaining four are small, narrow, and rod-like. Based on comparisons with other specimens, we believe that the nine elongate triangular epoccipitals belong to the squamosal and the four rod-like epoccipitals belong to the parietal. The most elongate of the squamosal epoccipitals is 14.5 cm long and is estimated to have been ~15.2 cm long. This element has a length to width ratio of 4:2, and the ratio reaches about 4:4 in the most slender epoccipital of the series, although it is relatively short. In a recently collected torosaur skull, MOR 1122, the epoccipitals, which are in place, have a length/width ratio of about 5 and do not contact one another. In *Torosaurus latus*, no squamosal epoccipitals have been described for the type specimen (YPM 1830) or referred skull (ANSP 15192; Colbert and Bump 1947). Our examination of ANSP 15192 reveals that the squamosal epoccipitals are obscured because of fusion with the frill. The epoccipitals of *Anchiceratops* differ in being strongly triangular and the epoccipitals of *Arrhinoceratops* differ in being small. Further, the lateral margin of the squamosal in those taxa is straight rather than convex as in *Eotriceratops*. Variation is present in the shape of the squamosal epoccipitals in chasmosaurines, and the shape of these bones is often obscured because of fusion with the frill in late stages of life. However, we consider the elongate crescent or spindle shape of epoccipitals on the squamosal to be one of the diagnostic features of *Eotriceratops* because epoccipitals of this shape

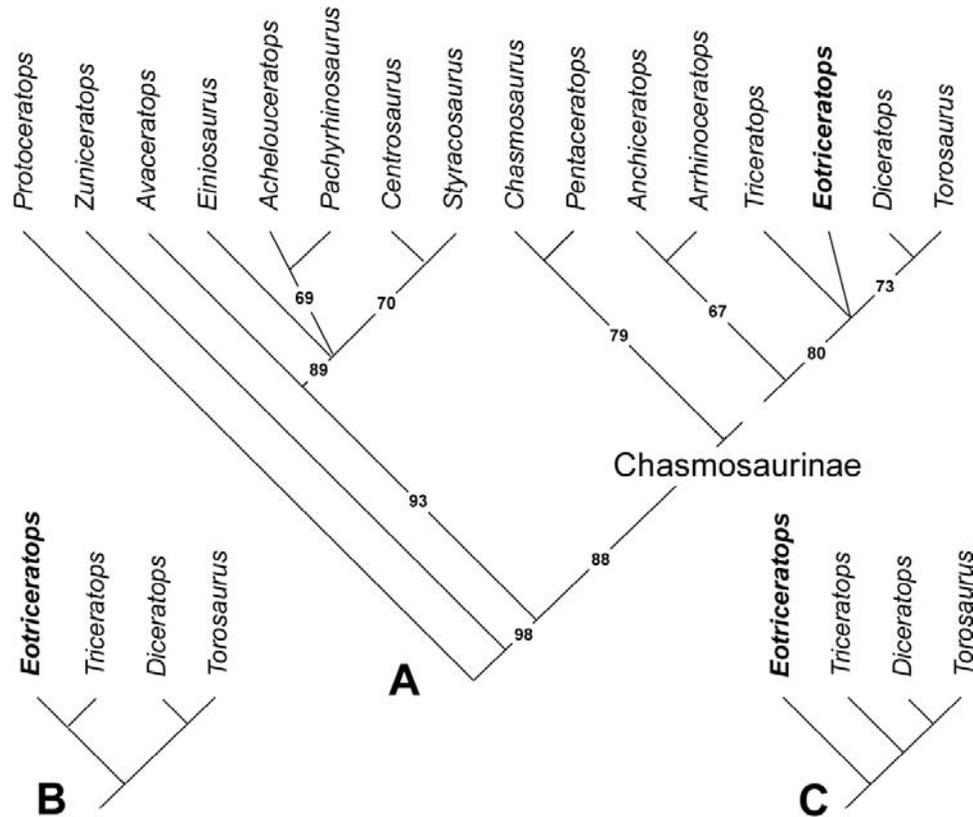
are not seen in other ceratopsids we examined. Furthermore, the presence of a contact between the epoccipitals in *Eotriceratops* is also a rare phenomenon because, based on a growth series of the squamosal frills of the chasmosaurine *Pentaceratops sternbergii* (Lehman 1990, fig. 16.10), the epoccipitals do not change in mutual relationships, remaining separate from one another through ontogeny among the chasmosaurines we examined.

*Eotriceratops* has an elliptical fossa on the anterior portion of the ventral surface of the squamosal frill, a feature that may be unique within chasmosaurines. This fossa is bordered with thickened margins, so it cannot be an artifact of preservation (Figs. 10F, 10G). The ventral surface of the squamosal frill in other chasmosaurines we examined, as in ceratopsids generally, is usually very smooth or has a broad, shallow depression with no consistent shape and no clearly demarcated borders. Such an ill-defined, shallow depression is present in some specimens of *Triceratops* (YPM 1821, 1824) and *Torosaurus* (YPM 1831), and an oval depression along the longitudinal axis is present in *Arrhinoceratops* (Parks 1925, pl. I). Our examination of a specimen of *Arrhinoceratops* (ROM 5135) reveals that this depression is smoothly transitional with the concave ventral surface of the frill and lacks the well-distinguished border seen in *Eotriceratops*. Based primarily on the skulls of *Torosaurus*, Lull (1908) interpreted these depressions as the site of the insertion of the *M. latissimus dorsi*. We believe that different shapes and different marginal conditions of the depression or fossa reflect different bone-muscle relationships and biomechanical differences associated with features such as the size and weight of the skull; therefore, we consider the structure of this fossa to be a diagnostic feature of *Eotriceratops*.

The presence of an obliquely dorsoventrally extending vascular trace meeting a transversely arched vascular trace ventrally on the anterior surface of the nasal horn core of *Eotriceratops* is an unusual feature within chasmosaurines. A transversely arched vascular trace on the anterior surface of the nasal horn core is consistently present in *Triceratops* (Forster 1990, 1996b); among the chasmosaurine specimens we examined, a pattern of vascular traces similar to that of *Eotriceratops* is seen only in USNM 1201, a specimen of *Triceratops*.

The epijugal differs from that of other chasmosaurines in the combination of the following two structures: (1) a sharply cone-shaped or dorsoventrally elongated, triangular configuration with a pronounced proximoposterior process in lateral view; and (2) separate fossa- or cup-like articular facets on its proximal surface and its proximomedial surface that cap the jugal and quadratojugal, respectively. A cone-shaped epijugal with a triangular outline in lateral view is present in *Arrhinoceratops* (Parks 1925) and *Torosaurus utahensis* (Sullivan et al. 2005), but it is proximally broader than deep in those taxa. *Anchiceratops*, as documented by specimen TMP 83.1.1, is like *Eotriceratops* in having a cone-shaped epijugal that is dorsoventrally elongate, but differs in lacking a pronounced proximoposterior process. In most other chasmosaurines, the epijugal shows an irregular shape in lateral view, or a trihedral shape (see CM 1221, YPM 1822, YPM 1821 for *Triceratops*; see TMP 81.19.175, TMP 87.45.1, AMNH 5401, ROM 843 for *Chasmosaurus*;

**Fig. 14.** Cladograms showing phylogenetic relationships of *Eotriceratops*. (A) Strict consensus tree computed from the six most parsimonious trees (MPTs) recovered by PAUP\* analysis of a modified version of the character–taxon matrix by Dodson et al. (2004). (B, C) Alternative relationships of *Eotriceratops* with crown taxa among the six most parsimonious trees. Nodal numbers indicate bootstrap proportions based on 1 000 replicates using the branch and brand algorithm in PAUP\*.



see Lehman (1996, fig. 9) for *Pentaceratops* and *Torosaurus*; see USNM 2412 for *Diceratops*). In other chasmosaurines, it is typical for the epijugal to have a bipartite medial surface for articular contact with the jugal and quadratojugal (e.g., *Torosaurus utahensis* (Sullivan et al. 2005, fig. 6.4)). However, none of the specimens of those taxa we examined shows a facet for the quadratojugal in the form of a cup-like fossa. Thus we interpret the presence of this feature as diagnostic for *Eotriceratops*.

### Phylogenetic relationships

Phylogenetic relationships of *Eotriceratops* are established on the basis of a cladistic analysis that employs the data matrix recently used by Dodson et al. (2004). Three additional characters of *Eotriceratops* were included (Appendix A) so that the complete data matrix consists of 76 characters and 16 taxa. Character 45 is slightly modified by the addition of a state 2 (elongate spindle-shaped squamosal epoccipitals). The data matrix is subjected to maximum parsimony analyses using PAUP\* (Swofford 2002). These apply 100 branch and bound searches with input order of terminal taxa randomized in each search. Characters are given uniform weight and multistate characters are unordered. Nodal support is assessed through calculation of bootstrap proportions based on 1 000 replicates using branch and bound algorithm in PAUP\*.

The parsimony analysis produces six shortest trees, with a tree length of 92, a CI of 0.880, a RI of 0.925, and a RC of 0.815. In all of the six trees, *Eotriceratops* is hypothesized to be a chasmosaurine (Fig. 14). The monophyly of the Chasmosaurinae is supported by 12 synapomorphies including five unequivocal characters. Among the 12 synapomorphies (based on tree 1), seven can be scored for *Eotriceratops*. They include the large rostral with deeply concave posterior margin, and hypertrophied dorsal and ventral rami (1); the anteriorly elongate premaxillary septum (4); the presence of the thickened narial strut along the posterior margin of the premaxillary septum (5); the perforation of the premaxillary septum (8); the presence of a narial process projecting into the external naris from the posteroventral margin of the premaxillary septum (11); the supraorbital horn core anteriorly curved (25); and the shape of epoccipitals (45). Among these seven synapomorphies, characters (1), (5), and (11) are unequivocal.

*Eotriceratops* is located successively more crownward in phylogenetic position than the clade including *Chasmosaurus* and *Pentaceratops* and the clade consisting of *Anchiceratops* and *Arrhinoceratops*; it forms, together with *Triceratops*, *Diceratops*, and *Torosaurus*, a monophyletic group in all the six trees. This is supported by five synapomorphies including two that are unequivocal (character 9, the presence of a recess in ventral portion of the premaxillary septum, and character 74, the nasal horn core anteriorly positioned), and three that are equivocal

(character 43, the epoccipital crossing squamosal-parietal contact; character 75, the presence of transversely arched vascular trace across the anterior surface of the nasal horn core; and character 76, the presence of interpremaxillary process). Within the group, *Eotriceratops* either forms a sister-group relationship with *Triceratops* (Fig. 14B), which is primarily supported by two unequivocal synapomorphies (character 43, an epoccipital crossing the squamosal-parietal contact, and character 75, the presence of a transversely arched vascular trace on the anterior surface of the nasal horn core), or is hypothesized to be the most basal taxon of the group because of the small size of the recess along the ventral aspect of the premaxillary septum (character 10) and the lack of a recess on the lateral surface of the nasal process of the premaxilla (character 12, Fig. 14C). Thus the phylogenetic relationships among *Eotriceratops*, *Triceratops*, and a subgroup consisting of *Diceratops* and *Torosaurus* are uncertain. However, because *Triceratops*, *Diceratops*, and *Torosaurus* are all from the strata younger than those that yielding *Eotriceratops*, the hypothesis that *Eotriceratops* occupies a basal position within the group appears likely.

## Acknowledgments

We thank G. Guthrie for rediscovering the specimen and a team of technicians and volunteers of the Royal Tyrrell Museum of Palaeontology (RTMP), led by K. Kruger and G. Harding, for collecting the specimen. M. Mitchell skillfully prepared this difficult specimen and graciously took extra time to provide the original sketch of Fig. 2, which was instrumental in describing the specimen. P. Currie kindly provided information on the original discovery of the specimen 91 years ago by B. Brown and provided field support for this project with the help of British Petroleum Canada. P. Dodson provided very helpful reference materials, and R. Sullivan provided beautiful photos of a new torosaur skull (MOR 1122) for comparison. This study benefitted from discussions with S. Sampson, M. Ryan, R. Sullivan, and R. Holmes. T. Sato helped with the initial computer analysis of the data matrix, and D. Tanke and A. Farke kindly provided references and information. X.-c. Wu is very grateful to J. Gardner and the collection personnel of the RTMP for assistance during his visits, and thanks W. Joyce, M. Norell, C. Mehling, R. Purdy, N. Gilmore, T. Daeschler, Z.-x. Lou, J. Eberle, and B. Small for opportunities to examine specimens in their care. C.A. Forster, T.M. Lehman, and H.-D. Sues carefully reviewed the manuscript and made helpful comments and suggestions, which improved it significantly. This project was supported by grants from the RTMP and CMN, and the RTMP Cooperating Society.

## References

- Braman, D.R., and Sweet, A.R. 1999. Terrestrial palynomorph biostratigraphy of the Cypress Hills, Wood Mountain, and Turtle Mountain areas (Upper Cretaceous–Paleocene) of western Canada. *Canadian Journal of Earth Sciences*, **36**: 725–741.
- Colbert, E.H., and Bump, J.D. 1947. A skull of *Torosaurus* from south Dakota and a revision of the genus. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **XCIX**(49): 93–106.
- Currie, P.J., and Koppelhus, E.B. 2005. *Dinosaur Provincial Park*. Indiana University Press, Bloomington and Indianapolis, Ind.
- Dodson, P., Forster, C.A., and Sampson, S.D. 2004. *Ceratopsidae*. In *The Dinosauria*. 2nd ed. Edited by D.B. Weishampel, P. Dodson, and H. Osmólska. University of California Press, Berkeley, Los Angeles, and London, pp. 494–513.
- Eberth, D.A. 2004. A revised stratigraphy for the Edmonton Group (Upper Cretaceous) and its potential sandstone reservoirs. Pre-conference field trip #7. Canadian Society of Petroleum Geologists – Canadian Heavy Oil Association Joint Conference, Calgary, Alta. 31 May – 4 June 2004. Canadian Society of Petroleum Geology, Calgary, Alta., 44 pp.
- Eberth, D.A., and O'Connell, S.C. 1995. Notes on changing paleoenvironments across the Cretaceous–Tertiary boundary (Scollard Formation) in the Red Deer River valley of southern Alberta. *Bulletin of Canadian Petroleum Geology*, **43**: 44–53.
- Eberth, D.A., Currie, P.J., Brinkman, D.B., Ryan, M.J., Braman, D.R., Gardner, J.D., et al. 2001. Alberta dinosaurs and other fossil vertebrates: Judith River and Edmonton Groups (Campanian–Maastrichtian). In *Guidebook for the Field Trips. Mesozoic and Cenozoic Paleontology in the Western Plains and Rocky Mountains*. Society of Vertebrate Paleontology 61st Annual Meeting, Bozeman, Mont. 3–6 October 2001. Edited by C.L. Hill. Museum of the Rockies, Bozeman, Montana, Occasional Paper 3, pp. 49–75.
- Farabee, M.J., and Canright, J.E. 1986. Stratigraphy, palynology of the lower part of the Lance Formation (Maastrichtian) of Wyoming. *Palaeontographica, Abteilung B*, 199, pp. 1–89.
- Forster, C.A. 1990. The cranial morphology and systematics of *Triceratops* with a preliminary analysis of ceratopsid phylogeny. Ph.D. dissertation, University of Pennsylvania, Philadelphia, Pa.
- Forster, C.A. 1996a. A species resolution in *Triceratops*: cladistic and morphometric approaches. *Journal of Vertebrate Paleontology*, **16**: 259–270.
- Forster, C.A. 1996b. New information on the skull of *Triceratops*. *Journal of Vertebrate Paleontology*, **16**: 246–258.
- Gibson, D.W. 1977. Upper Cretaceous and Tertiary coal-bearing strata in the Drumheller-Ardley region, Red Deer River Valley, Alberta. In *Geological Survey of Canada, Paper 76-35*, 41 pp.
- Hamblin, A.P. 2004. The Horseshoe Canyon Formation in southern Alberta: Surface and subsurface stratigraphic architecture, sedimentology, and resource potential. *Geological Survey of Canada, Bulletin 578*.
- Hatcher, J.B., Marsh, O.C., and Lull, R.S. 1907. *The Ceratopsia*. US. Geological Survey, Monograph 49, pp. 1–300.
- Hicks, J.F., Obradovich, J.D., and Tauxe, L. 1999. Magnetostratigraphy, isotopic age calibration and intercontinental correlation of the Red Bird section of the Pierre Shale, Niobrara County, Wyoming, USA. *Cretaceous Research*, **20**: 1–27.
- Hicks, J.F., Johnson, K.R., Obradovich, J.D., Tauxe, L., and Clark, D. 2002. Magnetostratigraphy and geochronology of the Hell Creek and basal Fort Union formations of southwestern North Dakota and a recalibration of the age of the Cretaceous–Tertiary boundary. In *The Hell Creek Formation and the Cretaceous–Tertiary boundary in the northern Great Plains: an integrated continental record of the end of the Cretaceous*. Edited by J.H. Hartman, K.R. Johnson, and D.J. Nichols. Geological Society of America, Special Paper 361, pp. 35–55.
- Leffingwell, H.A. 1971. Palynology of the Lance (Late Cretaceous) and Fort Union (Paleocene) formations of the type Lance area, Wyoming. In *Symposium on Palynology of the Late Cretaceous and Early Tertiary*. Edited by R.M. Kossanke. Geological Society of America, Special Paper, **127**: 1–64.

- Lehman, T.M. 1990. The ceratopsian subfamily chasmosaurinae: sexual dimorphism and systematics. *In* Dinosaur systematics: approach and perspectives. *Edited by* K. Carpenter and P. J. Currie. Cambridge University Press, Cambridge, UK., pp. 211–230.
- Lehman, T.M. 1996. A horned dinosaur from the El Picachu Formation of west Texas and review of ceratopsid dinosaurs from the American Southwest. *Journal of Paleontology*, **70**: 494–508.
- Lehman, T.M. 1998. A gigantic skull and skeleton of the horned dinosaur *Pentaceratops sternbergi* from New Mexico. *Journal of Paleontology*, **72**: 894–906.
- Lerbekmo, J.F. 1985. Magnetostratigraphic and biostratigraphic correlations of Maastrichtian to early Paleocene strata between south-central Alberta and southwestern Saskatchewan. *Bulletin of Canadian Petroleum Geology*, **33**: 213–226.
- Lerbekmo, J.F., and Braman, D.R. 2002. Magnetostratigraphic and biostratigraphic correlation of late Campanian and Maastrichtian marine and continental strata from the Red Deer Valley to the Cypress Hills, Alberta, Canada. *Canadian Journal of Earth Sciences*, **39**: 539–557.
- Lerbekmo, J.F., and Coulter, K.C. 1985. Late Cretaceous to early Tertiary magnetostratigraphy of a continental sequence: Red Deer Valley, Alberta, Canada. *Canadian Journal of Earth Sciences*, **22**: 567–583.
- Lull, R.S. 1908. The cranial musculature and the origin of the frill in the ceratopsian dinosaurs. *The American Journal of Sciences*, **25**: 387–399.
- Lull, R.S. 1933. A review of the Ceratopsia or horned dinosaurs. *Memoirs of the Peabody Museum of Natural History*, **3**, pp. 1–175.
- Lund, S.P., Hartman, J.H., and Banerjee, S.K. 2002. Magnetostratigraphy of interfingering upper Cretaceous–Paleocene marine and continental strata of the Williston Basin, North Dakota and Montana. *In* The Hell Creek Formation and the Cretaceous–Tertiary Boundary in the northern Great Plains: an integrated continental record of the end of the Cretaceous. *Edited by* J.H. Hartman, K.R. Johnson, and D.J. Nichols. Geological Society of America, Special Paper 361, pp. 57–74.
- 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 Ceratopsia, with notice of new Cretaceous dinosaurs. *American Journal of Science*, **39**: 419–426.
- McCabe, P.J., Strobl, R.S., Macdonald, D.E., Nurkowski, J.R., and Bosman, A. 1989. An evaluation of the coal resources of the Horseshoe Canyon Formation and laterally equivalent strata, to a depth of 400 m, in the Alberta Plains area. Alberta Research Council, Open File Report 1989-07.
- Nichols, D.J. 2002. Palynology and palynostratigraphy of the Hell Creek Formation in North Dakota: a microfossil record of plants at the end of Cretaceous time. *In* The Hell Creek Formation and the Cretaceous–Tertiary boundary in the northern Great Plains: an integrated continental record of the end of the Cretaceous. *Edited by* J.H. Hartman, K.R. Johnson, and D.J. Nichols. Geological Society of America, Special Paper 361, pp. 393–456.
- Norton, N.J., and Hall, J.W. 1969. Palynology of the Upper Cretaceous and Lower Tertiary in the type locality of the Hell Creek Formation, Montana, USA. *Palaeontographica, Abteilung B*, **125**, pp. 1–64.
- Ogg, J.G., Agterberg, F.P., and Gradstein, F.M. 2004. The Cretaceous period. *In* A geologic timescale 2004. *Edited by* F.M. Gradstein, J.G. Ogg, A. Smith, A.G., Bleeker, W., and Lourens, L.J. Cambridge University Press, Cambridge, UK., pp. 344–383.
- Parks, W.A. 1925. *Arrhinoceratops brachyops*, a new genus and species of Ceratopsia from the Edmonton Formation of Alberta. University of Toronto Studies, Geological Series, **19**: 1–15.
- Russell, D.A. 1967. A census of dinosaur specimens collected in Western Canada. National Museum of Canada, Natural History Papers, **36**: 1–13.
- Russell, L.S. 1975. Mammalian faunal succession in the Cretaceous system of western North America. *In* The Cretaceous system in the western interior of North America. *Edited by* W.G.E. Caldwell. The Geological Association of Canada, Special Paper 13, pp. 137–160.
- Ryan, M.G., and Russell, A.P. 2001. Dinosaurs of Alberta (exclusive of Aves). *In* Mesozoic vertebrate life. *Edited by* D.H. Tanke and K. Carpenter. Indiana University Press, Bloomington, Ind., pp. 279–297.
- Seeley, H.G. 1888. The classification of the Dinosauria. Report of the British Association for the Advancement of Science, **57**: 31–68.
- Srivastava, S.K. 1970. Pollen biostratigraphy and paleoecology of the Edmonton Formation (Maastrichtian), Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **7**: 221–276.
- Sternberg, C.M. 1929. A new species of horned dinosaur from the Upper Cretaceous of Alberta. *Bulletin of National Museum of Canada*, **54**: 34–37.
- Sullivan, R.M., and Lucas, S.G. 2003. The Kirtlandian, a new land-vertebrate “age” for the Late Cretaceous of Western North America. *In* New Mexico Geological Society Guidebook: Geology of the Zuni Plateau 2003, 54th Field Conference. pp. 369–377.
- Sullivan, R.M., and Lucas, S.G. 2006. The Kirtlandian Land-Vertebrate “Age” faunal composition, temporal position and biostratigraphic correlation in the nonmarine Upper Cretaceous of western North America. *New Mexico Museum of Natural History and Science Bulletin*, **35**: 7–30.
- Sullivan, R.M., Boere, A.C., and Lucas, S.G. 2005. Redescription of the ceratopsid dinosaur *Torosaurus utahensis* (Gilmore 1946) and a revision of the genus. *Journal of Paleontology*, **79**: 564–582.
- Swofford, D.L. 2002. PAUP\*. Phylogenetic analysis using parsimony (\*and other methods), version 4.0b10. Sinauer associates, Sunderland, Mass.
- Weishampel, D.B., Dodson, P., and Osmólska, H. (Editors). 2004. *The Dinosauria*. 2nd ed. University of California Press, Berkeley, Los Angeles, and London.

## Appendix A. Characters and character state descriptions

The first 73 characters are from Dodson et al. (2004), character 74 is from Forster (1990), and the last two are newly added.

1. Rostral, size and shape: triangular in lateral view with short dorsal and ventral processes (0); enlarged with deeply concave caudal margin and hypertrophied dorsal and ventral processes (1).
2. External naris, size and position: small, restricted to dorsal one-third of snout (0); large, expanded to occupy most of the depth of the snout (1).
3. Premaxillary septum: absent (0); present, rostral premaxillae lie directly on one another (1).
4. Premaxillary septum, shape: subcircular (0); rostrally elongate (1).

5. Premaxilla, thickened narial strut along posterior margin of the premaxillary septum: absent (0); present (1).
6. Premaxilla, narial strut orientation: rostrally inclined (0); caudally inclined (1).
7. Premaxilla, bony flange on caudal margin of narial strut: absent (0); present (1).
8. Premaxilla, interpremaxillary fossa perforating premaxillary septum: absent (0); present (1).
9. Premaxilla, recess in ventral portion of septum: absent (0); present (1).
10. Premaxilla, size of recess in septum: small, slight in-pocketing along ventral aspect of septal fossa (0); large, deeply recessed into premaxilla (1).
11. Premaxilla, premaxillary (narial) process extending into the external naris from the caudoventral margin of the premaxillary septum: absent (0); present (1).
12. Premaxilla, recess on lateral surface of the premaxillary (narial) process: absent (0); present (1).
13. Premaxilla, ventral expansion of the caudoventral oral margin: absent, caudoventral oral margin of premaxilla level with alveolar margin of the maxilla (0); present, expanded ventrally to extend well below alveolar margin of the maxilla (1).
14. Premaxilla, caudal tip of caudoventral process inserts into an embayment in the nasal and is surrounded by the nasal: present (0); absent (1).
15. Premaxilla, forked distal end of caudoventral process: absent (0); present (1).
16. External antorbital fenestra, size: large, 20% or more length of body of maxilla (0); greatly reduced to less than 10% length of body of maxilla, or absent (1).
17. Nasal, ornamentation: absent (0); horncore (1); pachyostotic boss (2).
18. Nasal, ornamentation position: centered caudal or caudodorsal to internal naris (0); shifted forward, centered dorsal or rostradorsal to endonaris (1).
19. Nasal, horncore length: small, length of horncore less than 15% basal skull length (0); moderate to large, length of horncore 20% or more of basal skull length (1).
20. Lacrimal, size: large, forms 50% or more of the rostral orbital margin (0); small, forms 40% or less of the rostral orbital margin (1).
21. Postorbital, supraorbital ornamentation: absent (0); present (1).
22. Postorbital, supraorbital ornamentation: horncore (0); rugose boss (1).
23. Postorbital, position of supraorbital ornamentation: centered rostradorsal or dorsal to orbit (0); centered caudodorsal or caudal to orbit (1).
24. Postorbital, length of supraorbital horncore: elongate, greater than 35% basal skull length (0); short, less than 15% basal skull length (1).
25. Postorbital, curvature of supraorbital horncore in adults: caudally recurved (0); straight or rostrally curved (1).
26. Prefrontal–prefrontal contact: absent (0); present (1).
27. Jugal infratemporal flange: absent (0); present, contacts jugal process of squamosal below the infratemporal fenestra (1).
28. Quadratojugal, position of contact with jugal and quadrate: jugal, quadratojugal, quadrate contact in a rostral to caudal order (0); jugal, quadratojugal, quadrate contact in a lateral to medial order (1).
29. Supracranial cavity complex: absent (0); present, supracranial cavities narrow and shallow, do not underlie supraorbital ornamentation (1); present, supracranial cavities broad, underlie supraorbital ornamentation and may be confluent with extensive cornual sinuses (2).
30. Frontal, contribution to orbital margin: present (0); absent (1).
31. Frontal fontanelle, shape: rostrocaudally long and uniformly narrow transversely (0); key-hole shaped with a broad rostral half (1); broadly oval to circular (2).
32. Parietosquamosal frill, length relative to basal skull length: elongate, 0.80 or more (0); shortened, 0.70 or less (1).
33. Parietosquamosal frill, marginal undulations: absent (0); present (1).
34. Parietal, imbrication effect on lateral margin of frill in adults: absent (0); present (1).
35. Squamosal, length relative to parietal: equal or subequal in length (0); squamosal much shorter than parietal (1).
36. Squamosal, rostromedial lamina forming the caudolateral floor of dorsotemporal fossa: absent (0); present (1).
37. Squamosal–quadrate contact: socketlike cotylus on squamosal for ball-like quadrate head (0); elongate groove on squamosal to receive lamina of quadrate (1).
38. Parietal fenestra, orientation: long axis directed transversely (0); long axis directed axially (1).
39. Parietal fenestra, maximum proximodistal diameter: 40% or less total parietal length (0); 45% or more total parietal length (1).
40. Parietal, accessory fenestra medial to the rostral end of the infratemporal fenestra: absent (0); present (1).
41. Parietal, median bar: narrow and straplike, width less than 0.05 total parietal length (0); wide, 0.15 or more total parietal length (1).
42. Epoccipitals on parietal and squamosal: absent (0); present (1).
43. Epoccipital crossing squamosal–parietal contact: absent (0); present (1).
44. Epoccipitals, pattern of fusion to frill margin: occurs from rostral to caudal (0); occurs from caudal to rostral (1).
45. Squamosal epoccipital, shape: crescentic or ellipsoidal (0); triangular (1); elongate spindle-like (2).
46. Parietal epoccipitals, number per side: one to three (0); six to eight (1).
47. Parietal epoccipital, most median epoccipital (locus 1) developed into a curved process with pronounced external sulci and ridges: absent (0); present (1).
48. Parietal epoccipital, orientation at locus 1 relative to parietal: dorsal to rostrally directed (0); caudally directed (1).
49. Parietal epoccipital, locus 2 developed into a curved process, with pronounced external sulci and ridges: absent (0); present (1).
50. Parietal epoccipital, orientation at locus 2: caudally directed from and perpendicular to parietal margin (0); medially directed, comes off the parietal at an angle (1).
51. Parietal epoccipital, locus 3 modified into a large horn-like process: absent (0); present (1).

52. Basioccipital, contribution to occipital condyle: large, forms more than one-third of condyle (0); reduced, forms ventral one-third of condyle only (1).
53. Frontal, contribution to exit for cranial nerve I: present (0); absent, enclosed entirely by ossifications of the interorbital septum (1).
54. Supraoccipital, contribution to foramen magnum: present (0); absent, eliminated from margin by exoccipital-exoccipital contact on midline (1).
55. Exoccipital, number of exits for cranial nerves X, XI, XII: three (0); two (1).
56. Lower jaw, level of articulation with quadrate: same as occlusal surface of tooth row (0); substantially ventral to tooth row (1).
57. Prementary, orientation of triturating surface: nearly horizontal (0); inclined steeply laterally (1).
58. Dentary, caudal extent of tooth row: terminates medial to the coronoid process (0); terminates caudal to the coronoid process (1).
59. Dentary, shape of the coronoid process: low, with gently convex apex and no neck (0); high, expanded into a rostrally projecting hook at apex, constricted neck present (1).
60. Tooth, number of roots: one (0); two (1).
61. Tooth vertical replacement series: one or two replacement teeth (0); more than two replacement teeth (1).
62. Tooth ornamentation: subsidiary ridges present, extend from margin to base of tooth (0); subsidiary ridges reduced, present only at margin of teeth (1).
63. Atlas, neural arch orientation: nearly vertical (0); steeply inclined caudally (1).
64. Sacrum, number of fused vertebrae: eight or less (0); ten or more (1).
65. Sacrum, deep longitudinal channel on ventral surface: present (0); absent (1).
66. Sternum, shape: elongate and narrow (0); short and broad (1).
67. Manual and pedal unguals, shape: clawlike (0); hooflike (1).
68. Ilium, laterally everted shelf on dorsal margin: absent (0); present (1).
69. Ilium, supracetabular process on dorsal margin over caudal part of acetabulum: absent (0); present (1).
70. Ischium, cross-sectional shape of shaft: ovoid (0); laterally compressed and bladelike, narrow along dorsal margin (1).
71. Ischium, orientation of shaft: nearly straight (0); slightly decurved (1); broadly and continuously curved (2).
72. Femur, coalescence of greater and cranial trochanters: absent (0); present (1).
73. Femur-tibia proportion: tibia longer than femur (0); femur longer than tibia (1).
74. Position of nasal horn core: posterior (0); over front of nares (1) (Forster 1990).
75. Transversely arched vascular trace across the anterior surface of the nasal horn core: absent (0); present (1).
76. A process projecting into the interpremaxillary fenestra: absent (0); present (1).

**Table A1.** Character state data matrix.

<i>Protoceratops</i>	000?0 ??0? 0?000 00000 0???? 00000 ?0000 00000 00?? ???? ?0000 00000 00000 00000 00NN ?
<i>Zuniceratops</i>	???? ???? ???? ???? 10000 ????? ????? ????? ????? ????? ?010 00?? ????? ???? ?
<i>Achelousaurus</i>	01100 ?00? 0?110 120?1 1101? ?1111 01111 11100 11110 10001 11111 11111 11110 11110 1110? N
<i>Anchiceratops</i>	11111 101?0 10010 11101 10101 ?0121 20100 01100 11001 00000 01111 10111 111?? 11111 21100 ?
<i>Arrhinoceratops</i>	11111 1010? 10010 11101 10101 ?01?1 ?0100 01100 1???? 00000 01?11 1???1 ????? ???? ?000 ?
<i>Avaceratops</i>	?1100 ?00? 0?11? ????? ????? ?1?? ?101 01??? ????? ????? ?1?11 1?111 111?? ?1??? ?1?? N
<i>Centrosaurus</i>	01100 ?00? 0?110 11011 10010 11111 01111 11100 11110 11111 01111 11111 11110 11110 11100 N
<i>Chasmosaurus</i>	11111 011?0 10001 11?01 100?0 0?111 10100 01110 01001 00100 01111 10111 11111 11111 21100 0
<i>Diceratops</i>	11111 00111 11010 11101 10101 ?0121 20100 01101 110?1 00000 01?11 1???1 11??? ????? ?010 1
<i>Einiosaurus</i>	01100 ?00? 0?110 11011 1001? ?1111 01111 11100 11110 10001 11111 11111 11110 11110 11100 N
<i>Pachyrhinosaurus</i>	01100 ?00? 0?110 120?1 1101? ?1111 01111 11100 11110 10011 11111 11111 11110 11110 11100 N
<i>Pentaceratops</i>	11111 011?0 10001 11?01 10001 ?01?1 10100 01110 01001 00100 01111 10111 11111 ?1111 21100 1
<i>Styracosaurus</i>	01100 ?00? 0?110 11011 1001? 11111 01111 11100 11110 11111 11111 11111 11110 11110 11100 N
<i>Torosaurus</i>	11111 00111 ?010 11101 10101 00121 20100 01101 11001 00000 01111 10111 11??? ????? ?010 ?
<i>Triceratops</i>	11111 00111 11010 11101 10101 00121 21100 01100 11101 00000 01111 10111 11111 11111 21111 1
<i>Eotriceratops</i>	11111 00110 100?? 1??0? 10101 ??121 ?1?? ?1??? ?1102 ????? ?1??? ????? 111?? ????? ?011 1