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Hadrosaurian dinosaurs from the Maastrichtian Javelina Formation, Big Bend National Park, Texas

Thomas M. Lehman,[1] Steven L. Wick,[2] and Jonathan R. Wagner[3]

[1]Department of Geosciences, Texas Tech University, Lubbock, TX 79409, USA ⟨tom.lehman@ttu.edu⟩
[2]Division of Science and Resource Management, Big Bend National Park, TX 79834, USA ⟨steven_wick@nps.gov⟩
[3]Department of Geography, Texas State University-San Marcos, San Marcos, TX 78666, USA ⟨jonathan.r.wagner@txstate.edu⟩

Abstract.—Rare remains of hadrosaurian dinosaurs previously reported from the Maastrichtian Javelina Formation of West Texas had been attributed tentatively to either *Edmontosaurus* or *Kritosaurus*. Three recently recovered specimens include substantial skull parts and postcranial skeletal elements sufficient to recognize three distinct hadrosaurs. Two species are found in the lower part of the Javelina Formation; one of these is identified as *Kritosaurus* sp., confirming the earlier referral of specimens to this taxon. The most complete of these specimens combines features thought to be diagnostic of both *K. navajovius* Brown, 1910 and '*Naashoibitosaurus*' *ostromi* Hunt and Lucas, 1993 and exhibits some unique attributes such that its specific identity remains uncertain. A second species, documented by a single specimen found near the base of the Javelina Formation, is inadequate to confidently identify but appears to represent a 'solid-crested' saurolophine with frontals having upturned processes along the midline, similar to those that brace the posterior side of the narial crest in *Saurolophus*. A third hadrosaur is represented at a bonebed in the uppermost part of the Javelina Formation. Its remains are sufficient to justify designation as a new species *?Gryposaurus alsatei*. The skull roof elements are similar to those in species of *Gryposaurus*, and although no parts of the narial crest are preserved, the bordering elements indicate that *?G. alsatei* was a 'flat-headed' saurolophine. Referral of *?G. alsatei* to *Gryposaurus* would constitute a significant temporal range extension for the genus into late Maastrichtian time, and if correct, this long-lived lineage of hadrosaurs persisted nearly to the end of Cretaceous time in West Texas. *?G. alsatei* was a contemporary of *Edmontosaurus*, the sole terminal Cretaceous hadrosaur in the northern Great Plains region, and neither possessed the ornate narial crest that characterized many earlier hadrosaurs.

Introduction

Upper Cretaceous strata in the Big Bend region of Texas preserve one of the southernmost well-studied Maastrichtian terrestrial vertebrate faunas known in North America. Strata of Maastrichtian age in Big Bend include the Javelina Formation and lowermost part of the overlying Black Peaks Formation (Lehman and Coulson, 2002). A tuff bed in the middle of the Javelina Formation yields an age of 69.0 ± 0.9 Ma, and correlation with strata elsewhere in North America indicates that the Big Bend Maastrichtian vertebrate fauna spans the Edmontonian to Lancian NALMA ages (Lehman et al., 2006; Wick and Lehman, 2013).

Lehman (1987, 2001) contended that this 'southern' Maastrichtian vertebrate fauna (the '*Alamosaurus* fauna' of Texas, New Mexico, and Utah) differed substantially from better known faunas of comparable age recovered from 'northern' locales. Although some (e.g., Vavrek and Larsson, 2010) have indicated that there is no statistical evidence to support recognition of discrete Maastrichtian biogeographic provinces in western North America, we herein reiterate the contention that the faunal differences must indeed reflect strong provinciality. For example, the Javelina Formation of Texas and coeval strata of the Edmonton Group in Alberta appear to share no large terrestrial vertebrate species. This observation is buttressed by description herein of new specimens from the Javelina Formation representing three different taxa of hadrosaurian dinosaurs, including a new species, none of which are known from Maastrichtian strata of the northern Great Plains.

Remains of hadrosaurian dinosaurs are extremely rare in the Javelina Formation, where instead specimens of the sauropod *Alamosaurus* and pterosaur *Quetzalcoatlus* are the most common large vertebrate fossils (Lehman, 2001). Only a few hadrosaur specimens have previously been reported from these strata. Lawson (1972) and Davies (1983) described parts of a hadrosaur skeleton from the lower Javelina Formation; this specimen (TMM 41442-1) includes only a few cranial elements, a quadrate, and parts of the maxillae, which they referred to cf. *Edmontosaurus* sp. Wagner (2001) reexamined this specimen, as well as another isolated quadrate (LSUMG V-1183), and identified both instead as pertaining to *Kritosaurus* cf. *K. navajovius* Brown, 1910. Apart from a few isolated bones (e.g., TMM 45603-1, part of left dentary and surangular), these specimens were until recently the only hadrosaur remains recovered from the Javelina Formation that preserved any cranial material; even isolated postcranial bones are rare in these strata (only three cataloged in the TMM collection).

It is therefore of interest to describe several new hadrosaur specimens recently collected from the Javelina Formation in Big Bend National Park. The three specimens are the most informative thus far recovered from these strata. One of these (TMM 45603-2) is an isolated fragmentary skull referred herein to *Kritosaurus* sp. that supports Wagner's (2001) identification of material collected previously. Another specimen (TMM 46015-2) consists of a few skull parts associated with pelvic elements, which appear to represent an unknown saurolophine species. A third specimen (TMM 46033-1) includes significant parts of the skull and jaws, along with parts of the postcranial skeleton and skin impressions, described herein as *?Gryposaurus alsatei* n. sp.

Geologic setting

TMM 45603-2, referred herein to *Kritosaurus* sp., was recovered from the base of the Javelina Formation near Gano Spring (Fig. 1.2). It consists of a partial skull found in isolation within a mudstone bed with calcareous pedogenic concretions. The preserved elements of the skull had been disarticulated and broken prior to burial. A few meters away, on the same stratigraphic horizon, part of a dentary and surangular belonging to a much smaller individual were also collected (TMM 45603-1). The maxilla and quadrate in TMM 45603-2 compare favorably with TMM 41442-1, described previously by Davies (1983) and Wagner (2001), also from the basal sandstone of the Javelina Formation near 'Woodson's' on the River Road. These three specimens are believed to represent the same species.

TMM 46015-2 and -3 were also collected from near the base of the Javelina Formation but clearly represent a different taxon, described herein as an indeterminate saurolophine (Fig. 1.3). This specimen was found near Paint Gap Hills and consists of part of a skull roof and maxilla, as well as an ilium and fragmentary pubes collected on the same stratigraphic level several meters away. The skull parts almost certainly belong to a single individual; however, the pelvic elements might pertain to a different animal. Given the great rarity of hadrosaur material in the Javelina Formation generally, and the proximity of these elements to one another, they are attributed here to the same taxon.

TMM 46033-1, the holotype specimen of *?Gryposaurus alsatei* n. sp. was recovered from an area known informally as the 'Rough Run Amphitheater,' an erosional embayment on the south flank of Rough Run Creek in the western part of the Park (Fig. 1.1; Lehman and Busbey, 2007). The Rough Run Amphitheater exposes the uppermost part of the Javelina Formation and lower part of the Black Peaks Formation. A sandstone unit exposed in the Javelina Formation here is unusual in preserving a horizon with scattered remains of hadrosaurs, comprising essentially a low-density hadrosaur bonebed. Apart from two turtle shells, only hadrosaur bones occur in the bonebed, a very uncommon circumstance for these strata.

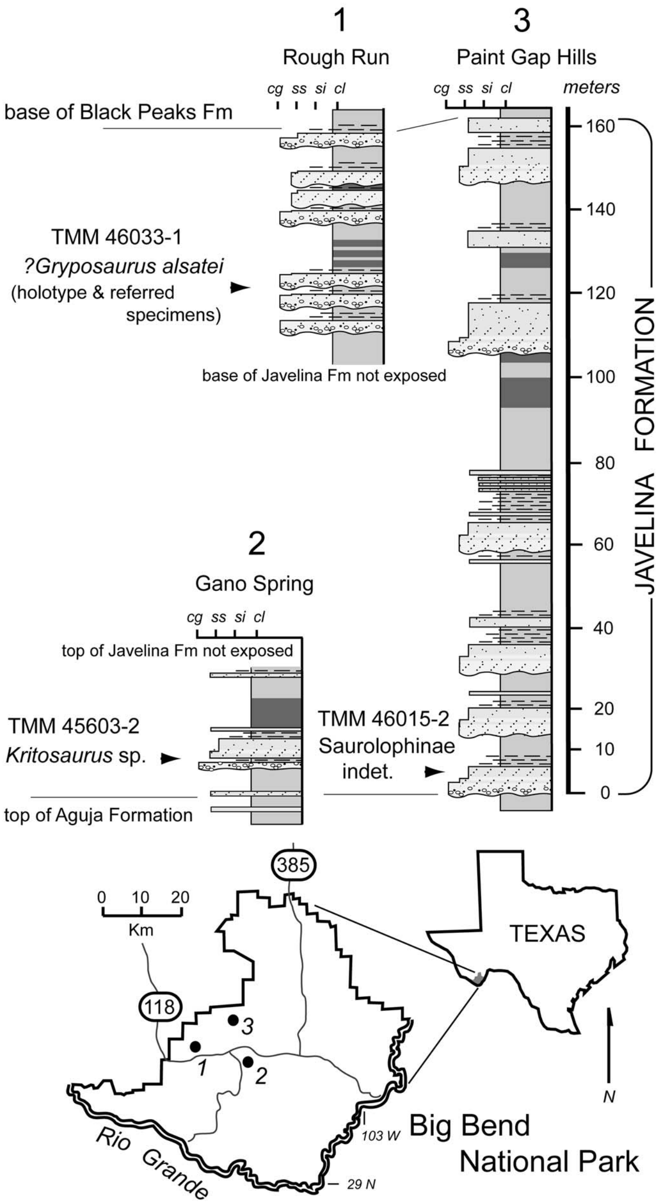

Figure 1. Stratigraphic sections of the Javelina Formation at Rough Run Amphitheater, Paint Gap Hills, and Gano Spring (above) showing positions of hadrosaur specimens discussed in text, and general location of sites (below) at Big Bend National Park in southwestern Texas.

Elements belonging to the *?Gryposaurus alsatei* holotype (TMM 46033-1) were recovered from a limited area of the bonebed, disarticulated but associated within several meters of each other, and almost certainly pertain to a single large individual (Fig. 2). However, a few bones (a humerus and caudal vertebra) belonging to a smaller hadrosaur were also found in the same area, as was a small fragmentary tibia (uncollected due to poor preservation). Therefore, it is clear that at least two individuals are preserved at this site. The smaller bones, as well as many other isolated hadrosaur skeletal elements (e.g., LSUMG V-1183) occurring in the same bonebed, preserved on the same stratigraphic level within several hundred meters of TMM 46033-1, appear to pertain to the same taxon. These isolated bones compare favorably with parts assigned to TMM 46033-1, and in light of their occurrence in a 'monodominant' assemblage (sensu Eberth et al., 2007) are used where noted to amplify description of some fragmentary elements.

Detailed coordinates and information pertaining to all the specimens and localities mentioned in the preceding are on file at the Vertebrate Paleontology Laboratory of the Jackson School of Geosciences (formerly Texas Memorial Museum) in Austin, Texas.

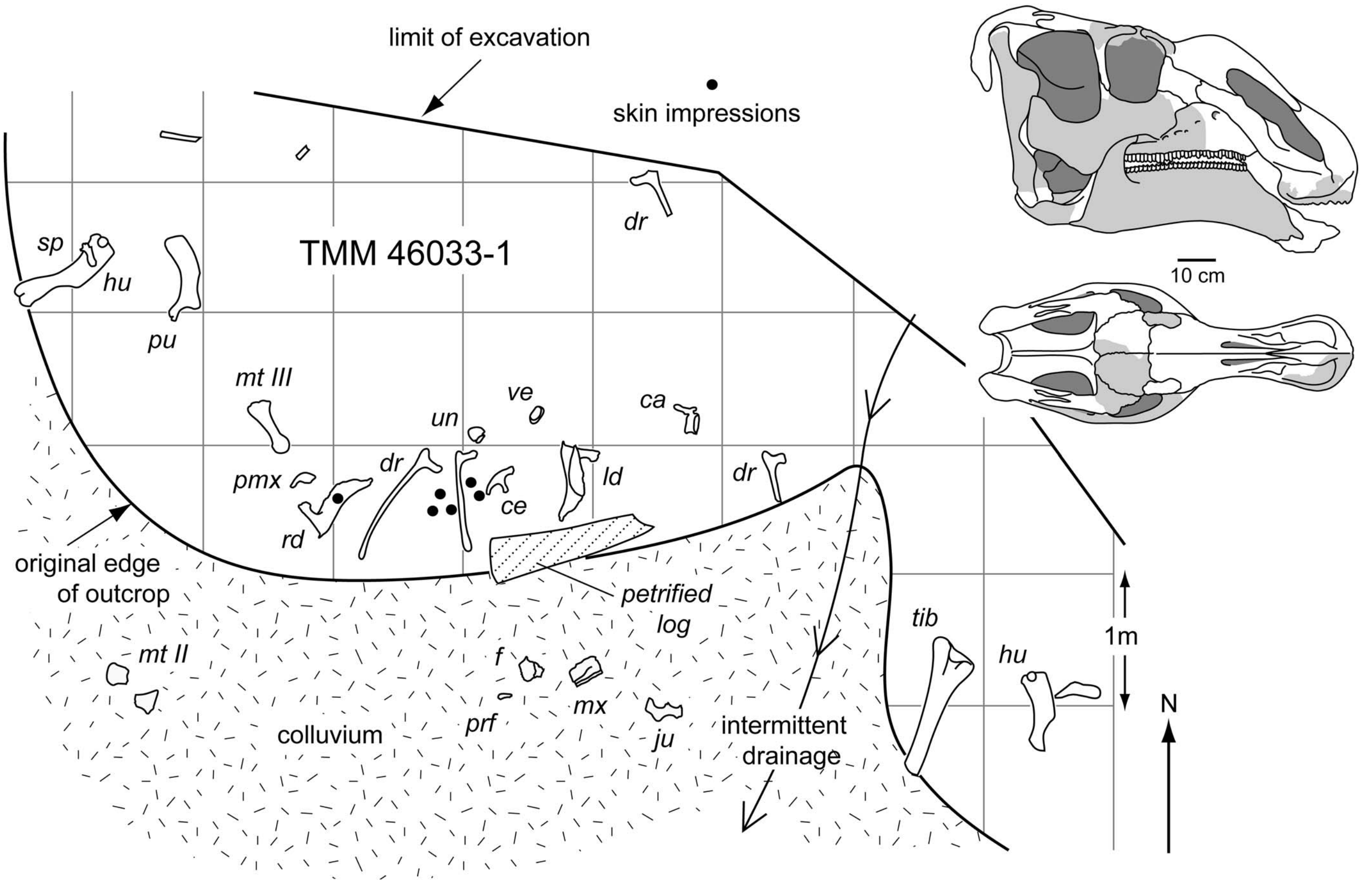

Figure 2. Quarry diagram showing preservational attitude of holotype specimen of *?Gryposaurus alsatei* n. sp. (TMM 46033-1) and composite reconstruction of the skull in *?G. alsatei* with preserved parts shaded (including LSUMG V-1183, with outlines of elements not preserved based on *Gryposaurus notabilis* ROM 873).

Systematic paleontology

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, NY, USA; IGM, Museo de Paleontologia, Instituto de Geologia, UNAM, Mexico D.F., Mexico; LSUMG, Lousiana State University Museum of Geology, Baton Rouge, LA, USA; MOR, Museum of the Rockies, Bozeman, MT, USA; PASAC, Paleontological Association of Sabinas, Coahuila, Sabinas, Mexico; ROM, Royal Ontario Museum, Toronto, Canada; TMM, Texas Memorial Museum collection now housed at the Vertebrate Paleontology Laboratory of the Jackson School of Geosciences, Austin, TX, USA; UMNHVP, Natural History Museum of Utah, Salt Lake City, UT, USA.

Order Ornithischia Seeley, 1887
Family Hadrosauridae Cope, 1870
Subfamily Saurolophinae Brown, 1914
(sensu Prieto-Márquez, 2010b)
Genus *Gryposaurus* Lambe, 1914

Type species.—*Gryposaurus notabilis* Lambe, 1914 from the Dinosaur Park Formation of Alberta, by original designation.

?*Gryposaurus alsatei* new species
Figures 3–12

Holotype.—TMM 46033-1 fragmentary skull including parts of basioccipital, left palatine, left and right frontals, left prefrontal, parts of right premaxilla, left maxilla, right jugal, fragment of left quadrate, left and right dentaries, left splenial, part of right surangular, and parts of postcranial skeleton including centrum of axis, neural arch of posterior cervical vertebra, sacral centrum, proximal and distal caudal vertebrae, right humerus, right tibia, right metatarsal II, right metatarsal III, right pedal ungual phalanx (digit II), right pubis, two dorsal ribs, skin impressions, and other bone fragments of uncertain identity.

Diagnosis.—Saurolophine hadrosaurid (sensu Prieto-Márquez, 2010b) having the following unique combination of character states: broad frontal with flat dorsal surface, lacking marked emargination for either the nasal or prefrontal, and forming small part of orbital rim; narrow prefrontal with dorsally convex nasal process; quadrate with expanded dorsal process; premaxilla with four large conical denticles along the oral margin and pronounced angular inflection along the ventrolateral border; pubis with long prepubic blade but only slightly constricted neck.

Etymology.—The specific name is an homage to Alsate, the legendary renegade last chief of the Chisos Apaches (Miles, 1976), and alludes to this hadrosaur being the last known to inhabit Texas prior to the terminal Cretaceous extinction event.

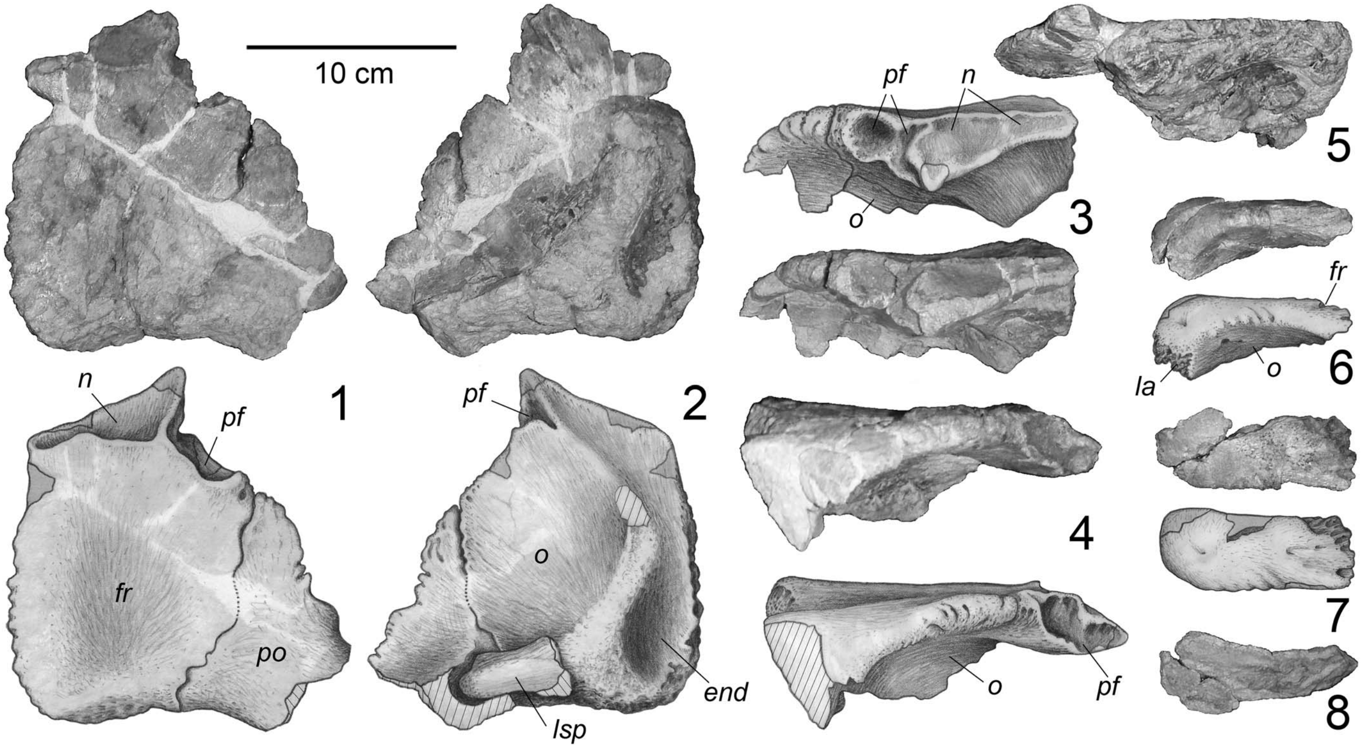

Figure 3. *?Gryposaurus alsatei* n. sp. (TMM 46033-1) photographs and companion drawings of right frontal with adjoining parts of postorbital and laterosphenoid in (**1**) dorsal, (**2**) ventral, (**3**) anterior, (**4**) lateral, and (**5**) medial views; left prefrontal in (**6**) lateral, (**7**) dorsal, and (**8**) ventral views. *end* = endocranial cavity; *fr* = frontal; *la* = suture for lacrimal; *lsp* = laterosphenoid; *n* = suture for nasal; *o* = orbit; *pf* = suture for prefrontal.

Occurrence.—Upper part of Javelina Formation, late Maastrichtian, Big Bend National Park, Brewster County, Texas.

Materials.—TMM 46033-2 maxillary tooth, TMM 46033-3 dentary tooth, and LSUMG V-1183 right quadrate were recovered from the same bonebed as the holotype and are referred herein to *?Gryposaurus alsatei* n. sp.

The holotype and referred specimens of *?Gryposaurus alsatei* n. sp. are parts of very large individuals, comparable in size to the holotype of *Kritosaurus navajovius* (~9 m estimated body length), and so their characteristics are presumed to represent those manifested in adults. In the following description, all linear and angular measurements were taken in the manner shown by Prieto-Márquez (2010b) unless otherwise indicated.

Frontal.—The right frontal in TMM 46033-1 is preserved completely, although it was necessary to assemble it from broken fragments (Fig. 3.1). It remains firmly sutured to part of the postorbital. Part of the antorbital buttress of the laterosphenoid also remains in articulation. Only the medial part of the left frontal is preserved; the suture with the right frontal is not closed, and the two meet firmly along a deeply serrated interdigitating joint.

The dorsal surface of the frontal is broad and nearly flat. It is mildly concave anteroposteriorly but rises only slightly anteriorly, indicating that if a narial crest was present, the frontal did not participate in its base. There is no raised welt along the frontal-nasal contact as there is in some hadrosaurs (e.g., *Acristavus*; Gates et al., 2011). The nasal overlapped the frontal posteriorly resulting in a shallow sutural shelf on the frontal that is broad mediolaterally, weakly W-shaped in dorsal view, and divided into two facets—one directed anteromedially, the other anterolaterally (Fig. 3.3). The suture for the nasal does not result in a marked emargination in the frontal. The suture for the prefrontal is a deep socket also divided into two facets; the most medial of the two extends as a cleft in the ventral surface of the frontal between the inner wall of the orbit and olfactory expansion of the endocranial cavity (Fig. 3.2, 3.3). The frontal participates in a small part of the rugose rim of the orbit inset between the prefrontal and postorbital sutures. The suture with the postorbital is oriented parasagitally, only slightly inclined anterolaterally in dorsal view, and is open anteriorly but closed posteriorly. The suture for the parietal is oriented transversely and extends slightly forward to divide the frontals along the midline (Fig. 4).

Prefrontal.—The left prefrontal in TMM 46033-1 is preserved almost completely. Part of the anteromedial edge is broken, but little else appears to be missing (Fig. 3.6). It is relatively small compared to the frontal. The posterior end of the prefrontal is expanded mediolaterally and was overlapped on its dorsal surface by the frontal along a digitate joint. The anterior end of the prefrontal is expanded dorsoventrally and forms a thick rugose buttress for the lacrimal below and a thin smooth overlapping flange for the nasal medially. The medial edge is, however, not dorsally deflected and does not appear to participate in the flank of a narial crest. The orbital rim is rugose, exhibits faint oblique fluting, and is pierced by several small foramina (Fig. 3.7).

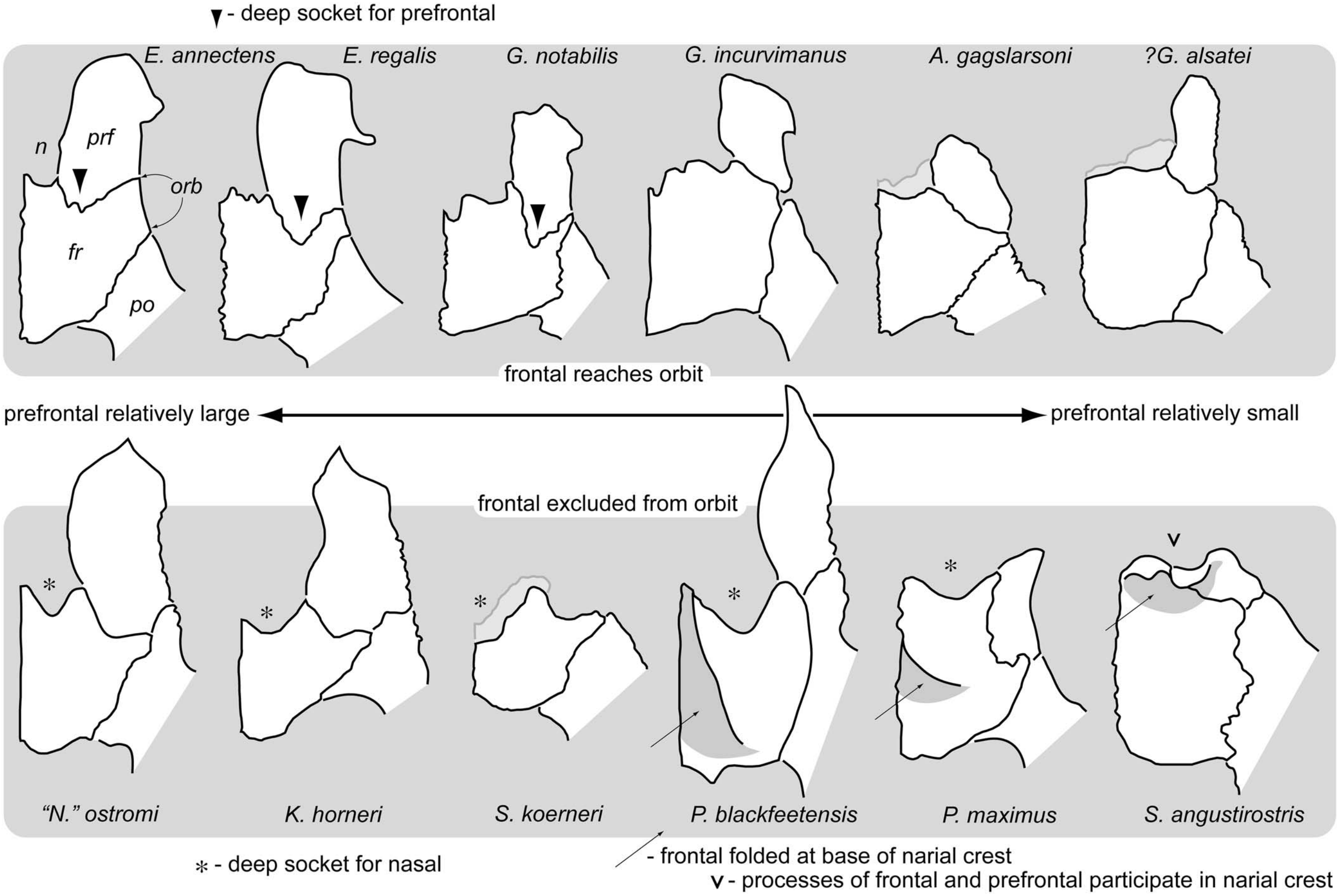

Figure 4. Comparison of saurolophine right frontals (*fr*) with adjoining postorbital (*po*) and prefrontal (*prf*), showing variation in suture with nasal (*n*) and rim of orbit (*orb*), all reduced to common width; drawings based on Lull and Wright (1942), Horner (1988, 1992), Gates and Sampson (2007), Prieto-Márquez and Salinas (2010), Gates et al. (2011).

Postorbital.—Only the main body and prefrontal process of the right postorbital is preserved in TMM 46033-1; it remains sutured to the frontal along its medial surface and with part of the laterosphenoid in a socket on its ventral surface (Fig. 3.2). The entire part of the orbital rim formed by the postorbital is obliquely corrugated and pitted.

Premaxilla.—Part of the right premaxilla is preserved in TMM 46033-1; most of the oral surface and lateral margin is complete, but the dorsal ascending process ('narial bar') is broken or missing, as is most of the posterior articular process for the maxilla (Fig. 5). The margins of the narial fenestra are not preserved, and the remaining intact portions of the medial wall of the premaxilla are very thin (<2 mm). In dorsal and ventral views, the form of the lateral margin is narrow and arcuate, not broad or spatulate. Part of the midline articulation for the adjacent premaxilla is preserved at the anterior end of the bone and can be used as a guide to estimate the mediolateral expansion of the premaxillary oral margin (ratio of mediolateral width of the premaxilla to narrowest post-oral constriction = 1.4). If this estimate is correct, the oral margin was very narrow (Fig. 5).

The border of the circumnarial depression is set back from the oral margin at the anterior end of the premaxilla but runs very close to its lateral margin, where it forms a thin upturned ridge. There is a sharply upturned inflection in the lateral margin of the premaxilla at its posterior preserved limit. The oral surface has an elevated inset 'extra denticulate' margin (sensu Prieto-Márquez, 2010b) that parallels the outermost edge of the bone and is separated from the outer denticulate margin by a pronounced sulcus (Fig. 5.4). There are four large conical denticles on the outer oral margin that diminish in height posteriorly from the midline. Posterior to the large denticles, both outer and inner margins have irregular oblique corrugations. The inset inner oral margin has low longitudinal ridges that extend posteriorly from the large denticles. There do not appear to be any anterior premaxillary foramina, although this may be due to crushing and poor preservation in that part of the specimen.

Maxilla.—Only the central part of the left maxilla, including parts of the jugal and lacrimal articulation surfaces, is preserved in TMM 46033-1. The dorsal process is broken at the base. The dentition is preserved in place but partly disintegrated. Two conjoined neurovascular foramina emerge below the ventral jugal articulation, and two others emerge separately just anterior to the articulation. The lateral surface of the maxilla is relatively short and outwardly convex, more as in TMM 46015-2 (referred herein to Saurolophinae indet.), rather than tall and flat as in TMM 45603-2 (referred to *Kritosaurus* sp.).

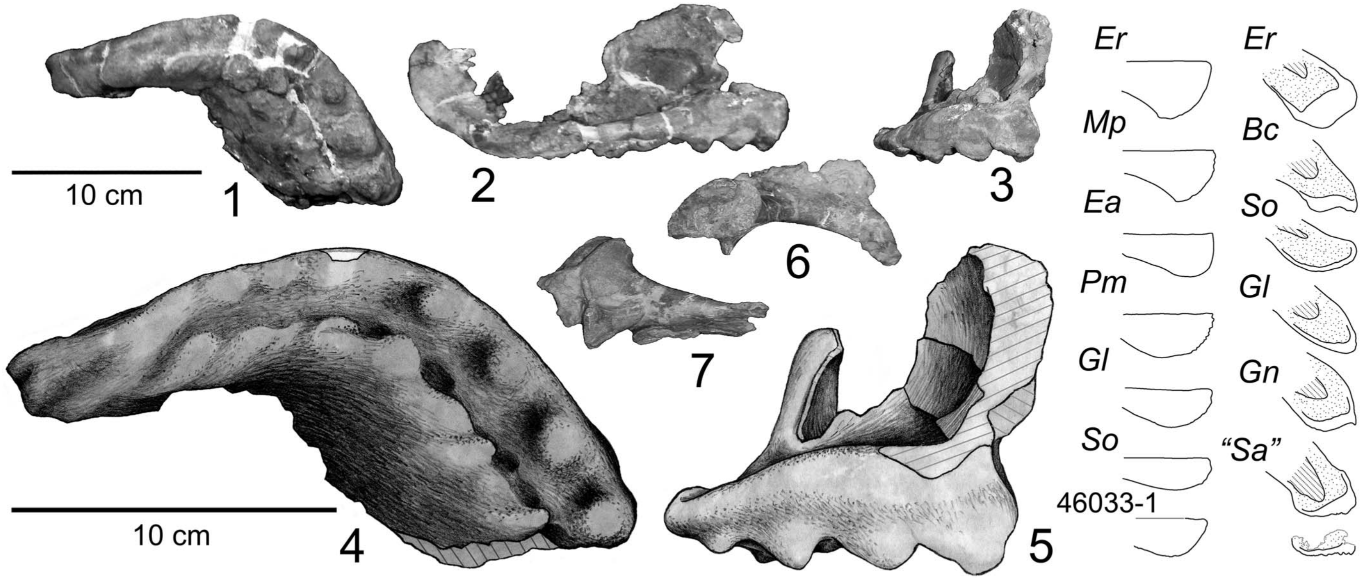

Figure 5. *?Gryposaurus alsatei* n. sp. (TMM 46033-1) part of right premaxilla in (**1**) oral, (**2**) lateral, (**3**) anterior views, with companion drawings in (**4**) oral and (**5**) anterior views; part of left palatine in (**6**) ventral and (**7**) anterior views; line drawings compare premaxillae in other saurolophine hadrosaurs (reduced to common length). *Bc* = *Brachylophosaurus canadensis*; *Ea* = *Edmontosaurus annectens*; *Er* = *Edmontosaurus regalis*; *Gl* = *Gryposaurus latidens*; *Gn* = *Gryposaurus notabilis*; *Mp* = *Maisaura peeblesorum*; *Pm* = *Prosaurolophus maximus*; "*Sa*" = Presa de San Antonio saurolophine; *So* = *Saurolophus osborni*.

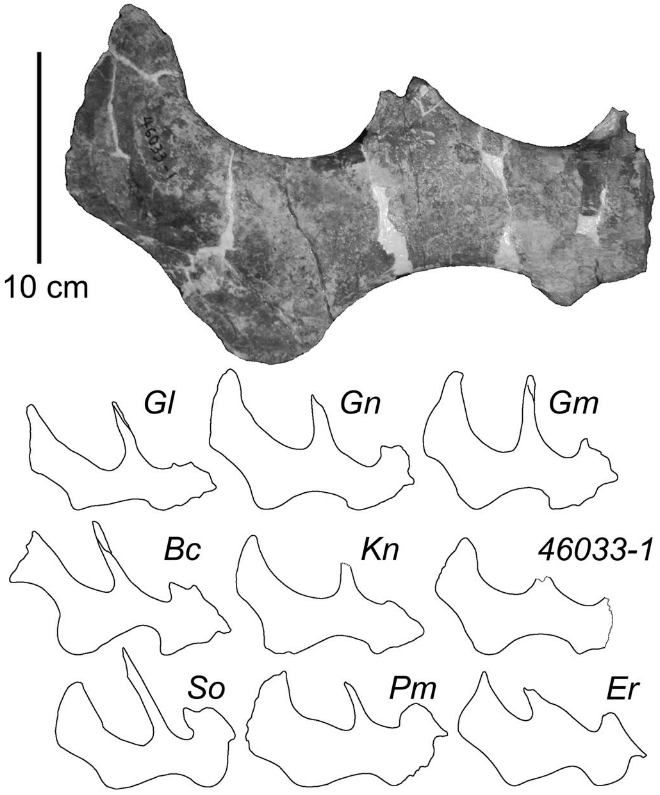

Figure 6. *?Gryposaurus alsatei* n. sp. (TMM 46033-1) right jugal in lateral view; line drawings compare jugals in other saurolophine hadrosaurs (reduced to common length). *Bc* = *Brachylophosaurus canadensis*; *Er* = *Edmontosaurus regalis*; *Gl* = *Gryposaurus latidens*; *Gm* = *Gryposaurus monumentensis*; *Gn* = *Gryposaurus notabilis*; *Kn* = *Kritosaurus navajovius*; *Pm* = *Prosaurolophus maximus*; *So* = *Saurolophus osborni*.

Jugal.—Most of the right jugal is preserved in TMM 46033-1; parts of the postorbital process and the rostral process of the maxillary articulation are broken (Fig. 6). The posterior ramus is relatively short and broad, with a blunt quadratojugal flange. The posteroventral flange is pronounced. The ratio of maximum depth of the posterior ramus across the posteroventral flange to its minimum depth across the constriction at the base of the infratemporal fenestra is 1.55 (see Prieto-Márquez, 2010b). The ventral margin is smoothly concave. The base of the postorbital process is narrow and not posteriorly inclined; it is not parallel to the quadratojugal process as in some other hadrosaurs (e.g., *Saurolophus osborni* Brown, 1912). The anterior ramus is deflected ventrally, not straight (see Gates et al., 2011), and is only slightly constricted below the orbit and posterior to the maxillary articulation. The lacrimal process is broken, but the preserved base indicates that it was sharply upturned and not smoothly confluent with the apex of the rostral process.

Quadrate.—Only the left ventral part of the quadratojugal process is preserved in TMM 46033-1. However, a nearly complete isolated right quadrate (Fig. 7.1–7.4; LSUMG V-1183) was recovered from the same bonebed about 100 m northwest of TMM 46033-1. It is compatible in size but may be from a different individual; it is here assumed also to represent *?G. alsatei* and the basis for the present description. The dorsal end is missing most of the squamosal articulation, but there appears to be a slight 'caudal buttress' along its posterior margin. The shaft of the quadrate is nearly straight in lateral view but markedly bowed outward in posterior view. The ventral end is missing most of the mandibular articulation condyles, but it is very broad mediolaterally and much more robust than the dorsal end. The quadratojugal (or 'paraquadrate') notch is positioned below the midpoint in dorsoventral length of the quadrate. The notch is wide and arcuate in lateral view; the lower border of the notch is inclined ventrally, and the upper border is inclined dorsally at a similar angle (~25°) relative to the axis of the quadrate. The dorsal margin of the quadratojugal notch is markedly expanded anteriorly and forms a distinct process that would have projected

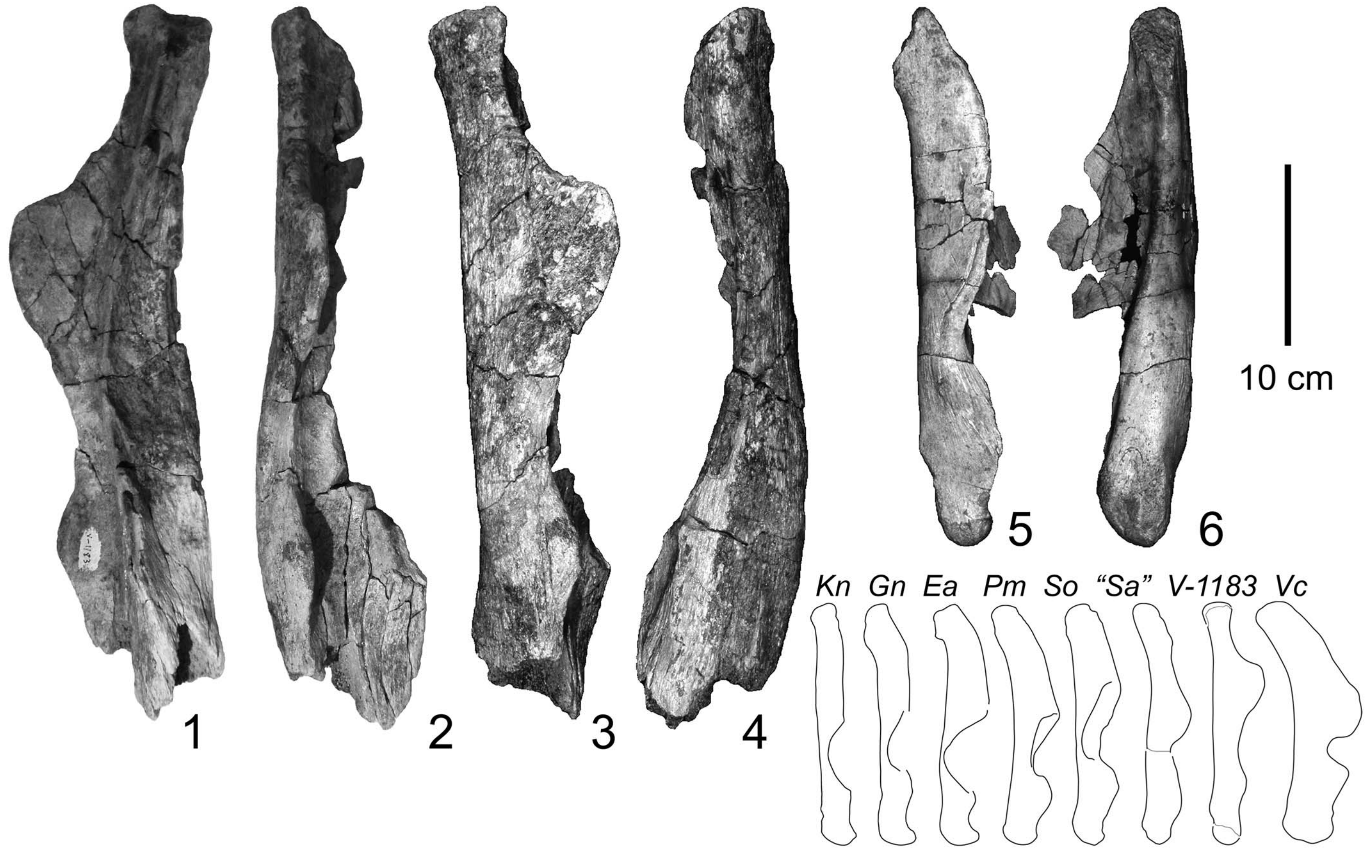

Figure 7. *?Gryposaurus alsatei* n. sp., right quadrate (LSUMG V-1183) in (**1**) medial, (**2**) anterior, (**3**) lateral, and (**4**) posterior views; compared with right quadrate in *Kritosaurus* sp. (TMM 41442-1) in (**5**) lateral and (**6**) posterior views; line drawings compare quadrates in other saurolophine hadrosaurs (reduced to common length). *Ea* = *Edmontosaurus annectens*; *Gn* = *Gryposaurus notabilis*; *Kn* = *Kritosaurus navajovius*; *Pm* = *Prosaurolophus maximus*; "*Sa*" = Sabinas saurolophine; *So* = *Saurolophus osborni*; *Vc* = *Velafrons coahuilensis*.

into the infratemporal fenestra (Fig. 7.3; an autapomorphy of *?G. alsatei*). A deep groove passes along the lateral surface of the quadrate below the quadratojugal notch, extending toward the mandibular articulation. The pterygoid 'wing' is broken, but its preserved base indicates that it spanned most of the length of the quadrate. A short, shallow, rugose depression near the base of the pterygoid wing along its posteroventral margin marks the articulation for the head of the ventral process of the pterygoid.

Palatine.—The left palatine is preserved in TMM 46033-1; part of the pterygoid process is broken. It is a slender, thin, triradiate element (Fig. 5.6, 5.7). The maxillary and jugal articulation surfaces are robust, nearly at a right angle to one another, and together partly surround an oval foramen. The maxillary articulation is not as elongate posteriorly, but otherwise the form of the palatine is comparable to that shown in *Brachylophosaurus canadensis* Sternberg, 1953 (Prieto-Márquez, 2005) and in cf. *Kritosaurus* (Horner, 1992, plate 22). It is much more slender than the same element in *Acristavus gagslarsoni* (Gates et al., 2011).

Dentary.—The left and right dentaries are well preserved in TMM 46033-1 (Fig. 8.1–8.3). In the left, the thin lingual plate is entirely broken away, and most of the teeth are missing. In the right, parts of the lingual plate are preserved intact, and some of the teeth are preserved in place; other teeth are displaced and fragmentary. The alveolar grooves are narrow and parallel-sided; there are at least 43 tooth positions in the left, and more than 40 in the right, but the anterior part of the right dental battery is slightly crushed and incomplete. The longitudinal axis of the tooth row is relatively straight in dorsal view, inclined medially 15° relative to the lateral surface of the dentary, and extends posterior to the coronoid process.

The predentary articulation surface extends as a narrow groove along the anterior edge of the dentary and ends as a forwardly projecting flange with a deep socket on the ventral surface. The mandibular symphysis is relatively short, projects only slightly lingually, and at a shallow angle relative to the long axis of the dentary (ratio of lingual projection to width of dentary is 1.3; angle of symphysis is 15°, measured as shown by Prieto-Márquez, 2010b, character 30).

The edentulous margin, between the predentary articulation and the first tooth position, is short, convex, and downturned at an angle of 135° relative to the tooth row or 120° relative to the long axis of the dentary (ratio of length of edentulous margin to tooth-bearing margin is 0.27). The ventral margin of the dentary is also downturned anteriorly (25°) with an inflection point anterior to midlength (0.62 ratio of length posterior to inflection point to length of tooth-bearing margin). The lateral surface of the dentary has several small oval foramina in series beneath the tooth row and is expanded lateral to the coronoid process. There is a distinct bulge along the

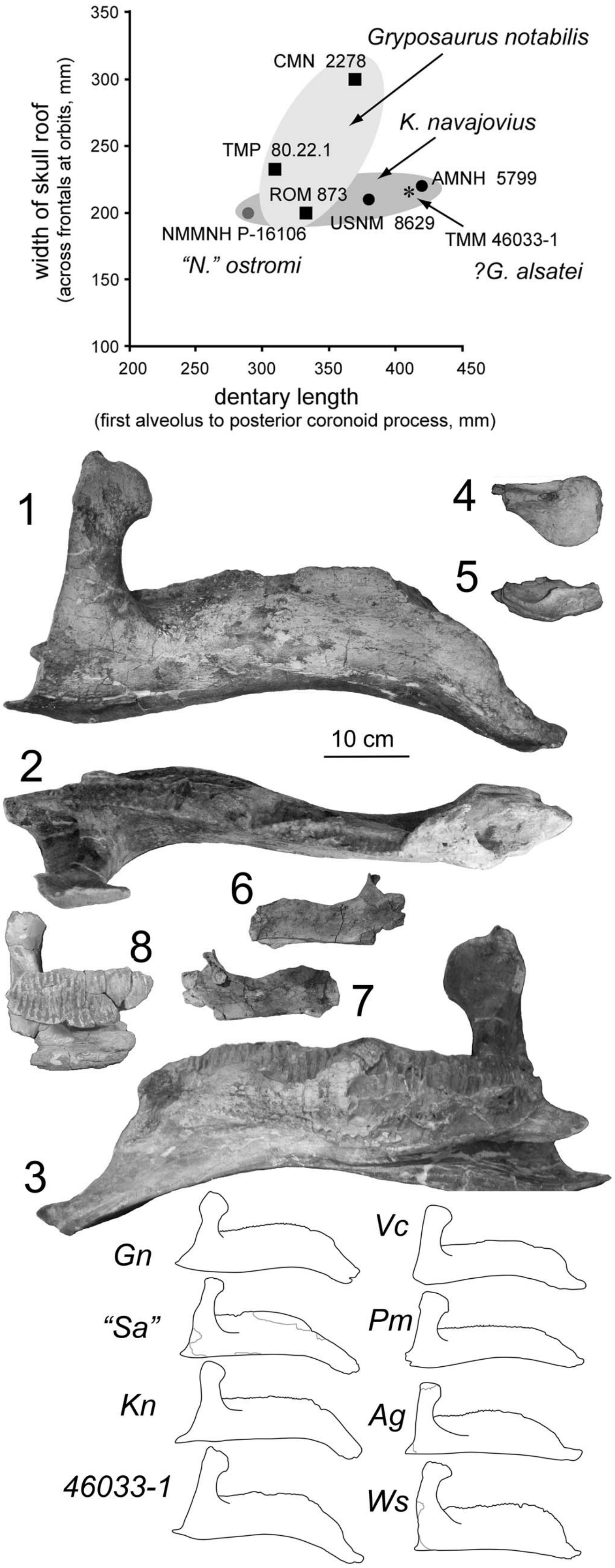

Figure 8. *?Gryposaurus alsatei* n. sp. (TMM 46033-1) right dentary in (**1**) lateral, (**2**) dorsal, and (**3**) medial views; part of right surangular in (**4**) dorsal and (**5**) lateral views; left splenial in (**6**) medial and (**7**) lateral views; (**8**) TMM 45603-1 part of left dentary in medial view; line drawings below compare dentaries in other saurolophine hadrosaurs (reduced to common length); bivariate plot above compares dentary length with skull width in species of *Gryposaurus*, *Kritosaurus*, and '*Naashoibitosaurus*' (some measurements from Prieto-Márquez, 2014). *Ag* = *Acristavus gagslarsoni*; *Gn* = *Gryposaurus notabilis*; *Kn* = *Kritosaurus navajovius*; *Pm* = *Prosaurolophus maximus*; "*Sa*" = Sabinas saurolophine; *Vc* = *Velafrons coahuilensis*; *Ws* = *Willinakaque salitralensis*.

lateroventral margin beneath the coronoid process. The coronoid process is tilted anteriorly (74° relative to tooth row) and well offset laterally from the tooth row; its apex is extended anteriorly, slightly posteriorly also, and has a pointed dorsal projection. A thick ridge extends along the medial side of the coronoid process and defines the anterior edge of a deep socket for articulation with the surangular posteriorly. The flange for articulation with the splenial is broad, triangular, and extended posteriorly; the angular facet is also broad but only slightly extended posteriorly, and the Meckelian canal is closed anterior to midlength.

Surangular.—Only part of the quadrate articulation surface of the right surangular is preserved in TMM 46033-1 (Fig. 8.4, 8.5). It is indistinguishable from the same part in the more complete surangular of TMM 45603-2 (referred here to *Kritosaurus* sp.).

Splenial.—The left splenial is well preserved in TMM 46033-1 (Fig. 8.6, 8.7). The proximal end is expanded dorsoventrally and has a V-shaped notch for articulation with the dentary on its lateral surface. There is a marked inset shelf that extends along the entire length of the ventral surface for articulation with the angular and surangular. The articular would rest in a concavity along the posterior end of the medial surface. The splenial has not been illustrated for comparison in many hadrosaurs, but the present specimen is essentially identical to that in *Prosaurolophus blackfeetensis* (Horner, 1992, plate 31), and significantly taller than in *Brachylophosaurus canadensis* (Prieto-Márquez, 2005).

Dentition.—The maxillary teeth in TMM 46033-1 are intact but poorly preserved; none of the crowns are completely visible. A loose maxillary tooth crown was collected on the same stratigraphic level nearby but may not pertain to the same individual (TMM 46033-2, Fig. 9.1). Several similar teeth (TMM 43678-1) described by Wagner (2001) were also found at the same level 100 m south of the main quarry. These loose teeth are comparable in size and morphology, here assumed to represent the same taxon, and provide an opportunity to observe the crown apices and denticulation more clearly. The apex of the crown has short crenulations that parallel the midline carina. There are large bulbous papillae of varied sizes along the crown margins, grouped in botryoidal clusters that become increasingly pronounced and extend onto the labial surface of the crown toward the apex (Fig. 9.1).

Most of the dentary teeth were lost prior to preservation in TMM 46033-1. Only fragments are preserved in the left

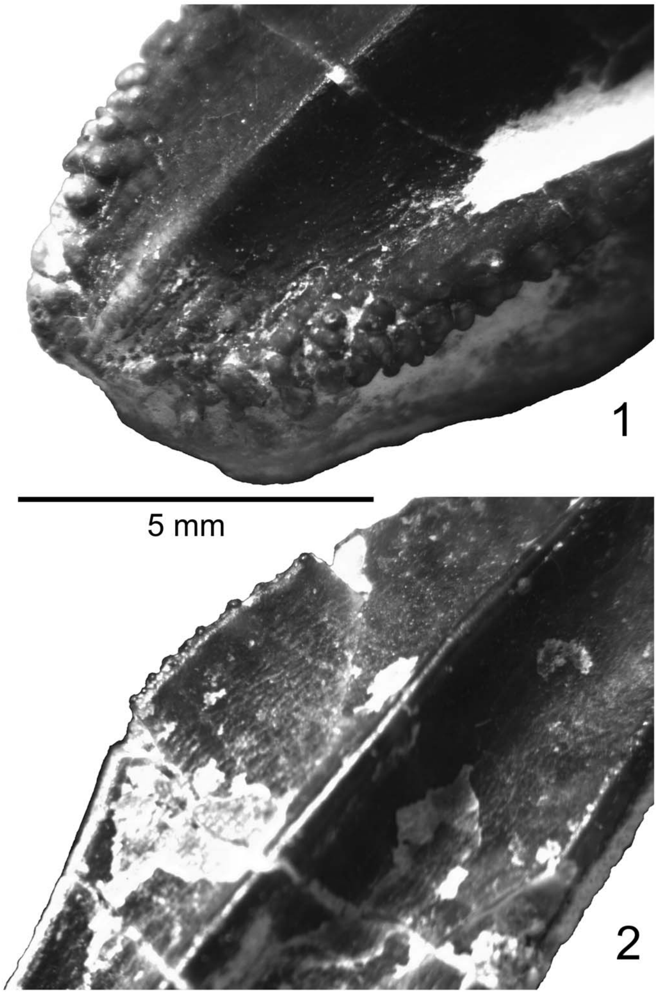

Figure 9. *?Gryposaurus alsatei* n. sp., referred isolated tooth crowns: (**1**) crown of maxillary tooth (TMM 46033-2) in oblique view showing apical crenulations and coarse papillae; (**2**) crown of dentary tooth (TMM 46033-3) in oblique view showing restricted fine papillae along mesial and distal base of crown margin.

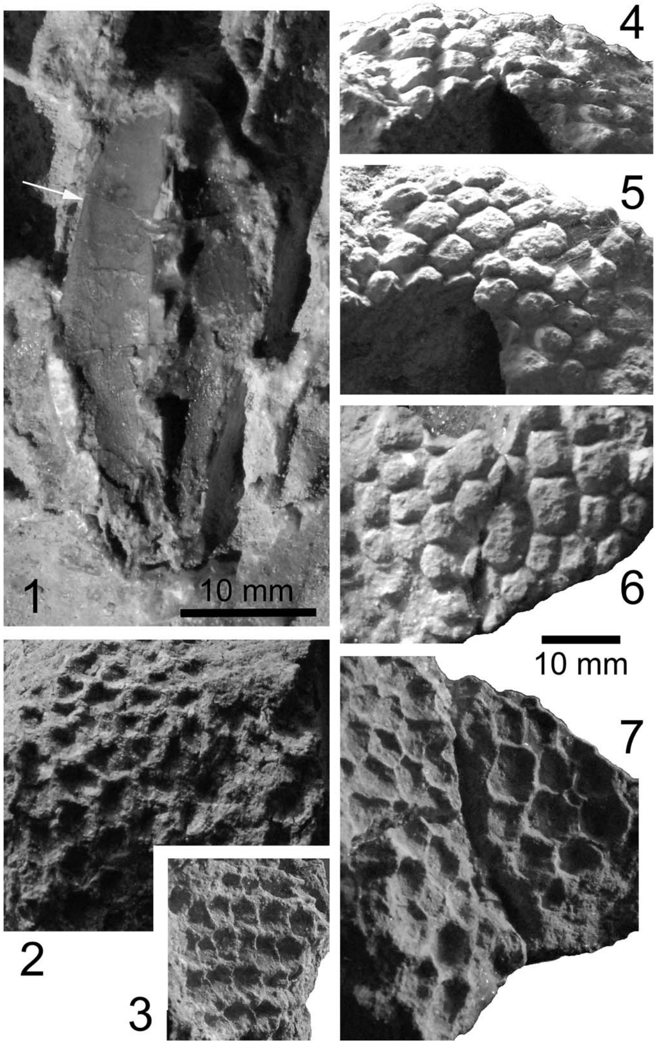

Figure 10. *?Gryposaurus alsatei* n. sp. (TMM 46033-1): (**1**) crown of mid-dentary tooth preserved in place within dentary showing single median carina and smooth upper part of crown border (arrow); varied natural molds and casts of integument in oblique lighting showing (**2**,**3**) small rhombic scales and (**4–7**) larger polygonal scales.

dentary; however, a few whole teeth remain within the alveolar grooves on the right dentary. It is not possible to determine the number of teeth within each alveolus or the functional number within the occlusal plane. The few remaining whole teeth have enamel only on their lingual surface, a crown height-to-width ratio of 2.7, and a single, straight, midline carina (Fig. 10.1). The crown/root angle cannot be determined on any of the remaining teeth. Most of the exposed crown margins appear to be nearly smooth; however, on the flanks of a few crowns there are faint, small irregular marginal papillae visible in oblique lighting. A loose dentary tooth (TMM 46033-3) collected from the same bonebed, but perhaps not pertaining to the holotype individual, preserves the margins of a crown more clearly; the papillae are bulbous, irregularly spaced, and better developed on the labial rather than lingual edge of the crown margin (Fig. 9.2).

Vertebrae and ribs.—In TMM 46033-1, the only parts of the axial skeleton preserved are the centrum of the axis vertebra, the neural arch of a posterior cervical vertebra, a sacral vertebral centrum, a proximal caudal vertebra, a distal caudal vertebral centrum, an anterior thoracic rib, and posterior thoracic rib. These elements are not distinctive and exhibit morphology typical of other hadrosaurs.

Humerus.—The right humerus in TMM 46033-1 is complete and well preserved (Fig. 11.1–11.3). Although quite large (815 mm in length), it is proportionally slender and gently curved anteriorly. The head is well defined, elevated, and extends onto the posterior surface of the bone. The ulnar and radial condyles are well defined, extend onto the anterior surface of the bone, and are separated by a marked trochlear notch. The deltopectoral crest is relatively long (ratio of deltopectoral crest length to total humerus length = 0.52), expanded lateroventrally (ratio of mediolateral width to minimum shaft width = 1.8), and extends abruptly from the humeral shaft at its ventral margin.

Pubis.—The right pubis in TMM 46033-1 is well preserved (Fig. 12.1). It is missing most of the postpubic process, and a fracture passes through the acetabulum between the ischial and

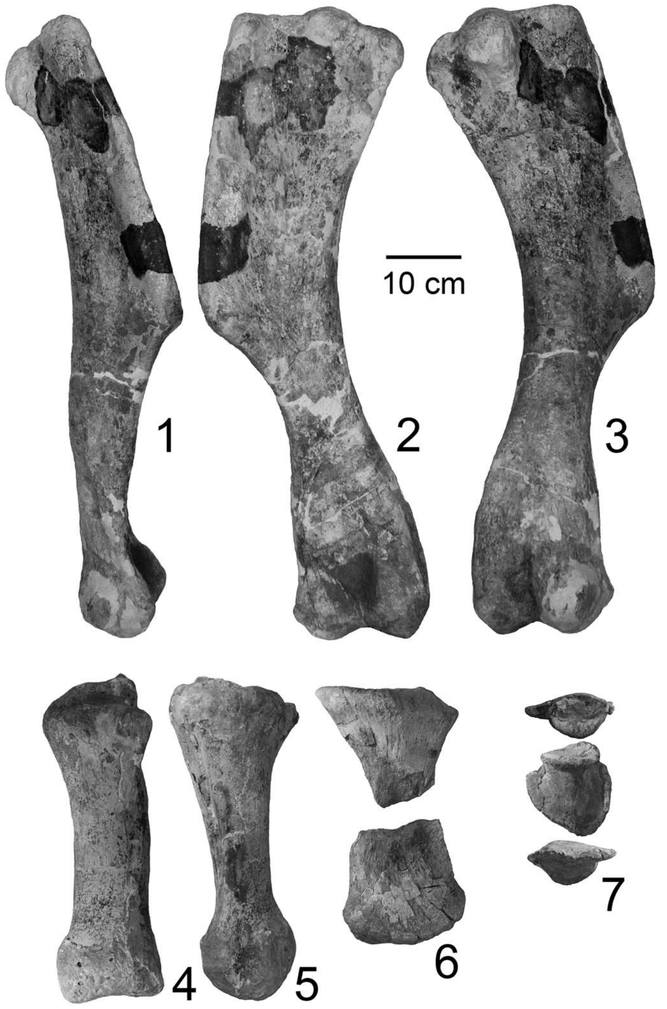

Figure 11. *?Gryposaurus alsatei* n. sp. (TMM 46033-1) left humerus in (**1**) lateral, (**2**) posterior, and (**3**) anterior views; right metatarsal III in (**4**) anterior and (**5**) lateral views; proximal and distal ends of right metatarsal II in (**6**) lateral view; (**7**) right pedal ungual digit II in proximal, ventral, and distal views.

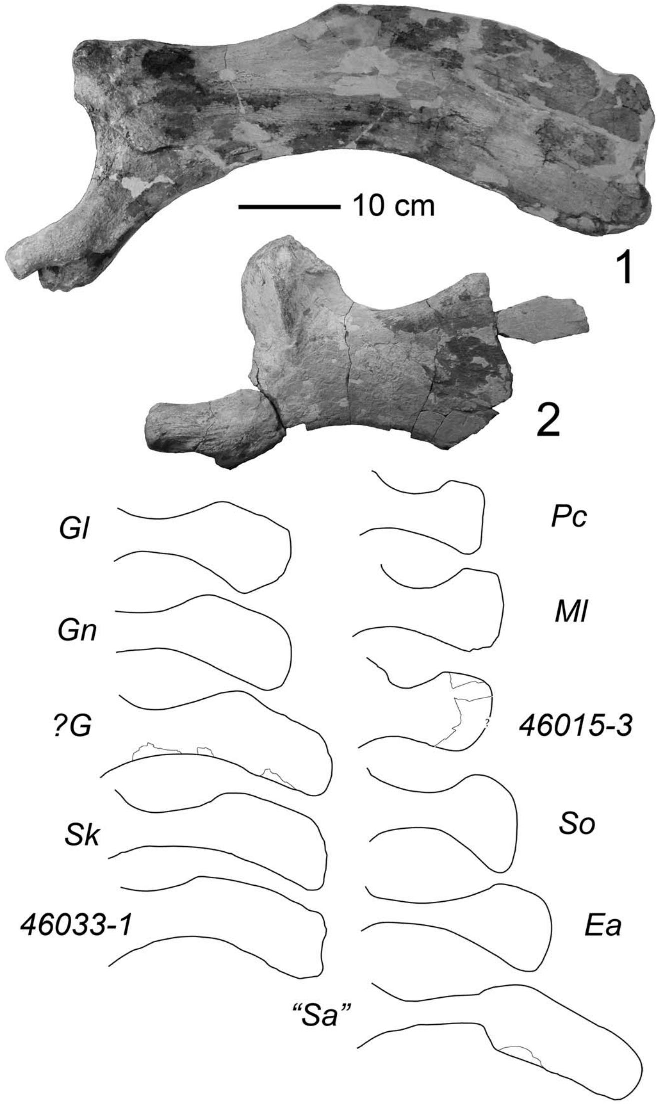

Figure 12. Right pubis in lateral view of (**1**) *?Gryposaurus alsatei* n. sp. (TMM 46033-1) and (**2**) Saurolophinae indet. (TMM 46015-3). Line drawings compare prepubes in these and other hadrosaurs (reduced to common height). *Ea* = *Edmontosaurus annectens*; *?G* = *Gryposaurus* sp. (YPM-PU 19670); *Gl* = *Gryposaurus latidens*; *Gn* = *Gryposaurus notabilis*; *Ml* = *Magnapaulia laticaudus*; *Pc* = *Parasaurolophus cyrtocristatus*; "*Sa*" = Sabinas saurolophine; *Sk* = *Secernosaurus koerneri*; *So* = *Saurolophus osborni*.

iliac peduncles. Both peduncles are short, but missing parts of their cortical surfaces, and the acetabular margin is only weakly defined below the iliac peduncle. Although the pubis is quite large (525 mm in length), it is proportionally short (ratio of length from acetabular margin to end of prepubic process to height from postpubic shaft to iliac peduncle = 2.4). The prepubic blade is broad, thin (<10 mm in thickness), slightly convex on its medial surface, flat to mildly convex on its lateral surface, downturned anteriorly, and rectangular with subparallel dorsal and ventral margins (Fig. 12). In contrast to most hadrosaurs, the shaft of the prepubis is not strongly constricted; it is nearly as tall dorsoventrally as the blade. The ratio of the minimum height of the prepubic proximal constriction to the maximum height of the distal blade is 0.82 (Fig. 13; measured in the manner shown by Prieto-Márquez et al., 2006). Its maximum ventral concavity is slightly anterior to its maximum dorsal concavity. The length of the proximal neck of the prepubis, from the iliac peduncle to the highest point on the dorsal surface of the blade, is only half the total length of the pubis (ratio = 0.51; measured in the manner shown by Prieto-Márquez et al., 2006, fig. 7). There is a rugose protuberance on the lateroventral surface of the ischial peduncle.

Tibia, metatarsals, and phalanges.—The proximal end and shaft of the right tibia is preserved in TMM 46033-1 but lacks any distinctive features. Metatarsal III is preserved completely (Fig. 11.4), as is most of metatarsal II, which is missing part of the shaft; both are from the right foot (Fig. 11.6). Metatarsal III is relatively short and broad; the ratio of its length to midshaft width is 3.95. A single pedal ungual phalanx, probably from digit II on the right foot, is preserved (Fig. 11.7). It is highly asymmetric. The hoof-like expansion on the presumed medial side is markedly reduced compared to the lateral side, much more so than in other hadrosaurs for which the pedal unguals have been described (e.g., *Edmontosaurus*, Zheng et al., 2011).

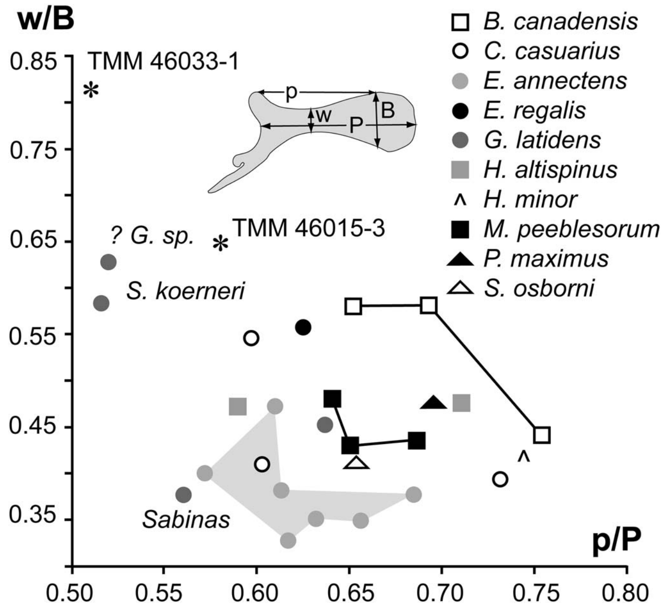

Figure 13. Bivariate plot (modified from Prieto-Márquez et al., 2006) comparing proportions of prepubic shaft and blade in selected hadrosaurs, showing method of measurement. *G. sp* = *Gryposaurus* sp. (YPM-PU 19670); *Sabinas* = Sabinas saurolophine.

Integument.—Several isolated patches of sediment matrix with skin impressions were recovered during excavation of TMM 46033-1.These small fragments preserve as many as seven separate segments of skin impressions, each up to a maximum area of about 4 by 8 cm, and were not parts of a single larger contiguous section of integument. The impressions were found adjacent to the lower jaws, two dorsal ribs, and neural arch of a cervical vertebra (Fig. 2). Hence, it is uncertain which parts of the integument may be represented, but their association suggests that they pertain to the anterior part of the body.

The sediment matrix is heterogeneous fine muddy sandstone with scattered fragments of carbonized plant tissues, and so the fidelity of the skin impressions is not high (Fig. 10.2–10.7). Most of the impressions are preserved as molds, but a few are casts. All of the impressions exhibit comparable morphology but vary in the size of the scales. The scales are closely spaced, small, pentagonal, hexagonal, or rhombic tubercles ranging from 3 to 8 mm in diameter (Fig. 10). There is little variation in size among scales in a given impression; in some, they are all at the small end of the size range, in others, most or all are at the relatively large end of the range. Individual scales are 1 to 3 mm in height and separated by narrow, deep, grooves; they do not show any preferred alignment or pattern. The pentagonal to hexagonal scales are slightly asymmetric, with their apices offset from the midpoint, but do not overlap one another ('polygonal basement scales' of Bell, 2012). However, the diamond-shaped scales appear to be more markedly asymmetric and overlap one another ('imbricated shell basement scales' of Bell, 2012). No large 'shield feature scales' (sensu Bell, 2012) are preserved.

Several sections of the large pentagonal to hexagonal scales are preserved well enough to show fine surface details, and these have faint ridges that radiate from the apices, particularly on the more gently inclined side of the asymmetric scales ('radially ornamented scales' of Bell, 2012). It is possible that most or all of the scales are ornamented, but preservation is insufficient to reveal it in most cases. Similar radial scale ornamentation has been reported in some specimens of *Edmontosaurus annectens* Marsh, 1982 (Bell, 2012), an indeterminate hadrosaur from the Lance Formation (Wegweiser et al., 2006), and an indeterminate hadrosaur from the Fruitland Formation (Anderson et al., 1998).

There have been several recent reviews of the occurrence of hadrosaur skin impressions (e.g., Bell, 2012, 2014; Davis, 2014). Similar impressions are remarkably common in Upper Cretaceous strata and found in association with either articulated skeletons or with disarticulated parts of skeletons, as is the present case. The impressions found with TMM 46033-1 indicate that desiccated fragments of the 'hide' were relatively tough and could be dispersed by running water, a taphonomic process much like that described by Herrero and Farke (2010).

Remarks.—The broad flat frontal in *?Gryposaurus alsatei* n. sp. is not incorporated into a narial crest or embayed along the midline by posterior retraction of the nasals (Fig. 4). The prefrontal is relatively small; its dorsal surface is convex and not elevated along the medial border in a way as to suggest the presence of a narial crest, nor was it included within the circumnarial fossa. Together, these features indicate that *?G. alsatei* was among the relatively 'flat-headed' saurolophines, had only a subdued narial crest, if it had one at all, and is not a member of either the *Brachylophosaurus-Maiasaura* clade (Brachylophosaurini of Gates et al., 2011) or the *Prosaurolophus-Saurolophus* clade (Saurolophini of Prieto-Márquez et al., 2014). In both of these groups of 'solid-crested' saurolophines, the frontals, and in some cases prefrontals, are modified by posterior retraction of the narial crest over the skull roof between the orbits. Apart from their narial crest, the *Prosaurolophus-Saurolophus* clade also shares a feature of the jugal (marked dorsal inclination of the rostral process; Prieto-Márquez, 2010b) that is lacking in *?G. alsatei* and a significantly greater number of dentary tooth positions (~50). Similarly, in the analysis of Prieto-Márquez (2010b), the Brachylophosaurini share features of the prefrontal (everted dorsolateral rim), dentary (more gently inclined edentulous margin that articulates with the predentary), maxilla (lower angle between the rostroventral shelf and tooth row), and jugal (greater expansion of the ventral flange) that differ from *?G. alsatei*. It seems clear that *?G. alsatei* is not closely related to either of these saurolophine groups.

Among the less ornate flat-headed saurolophines, *?Gryposaurus alsatei* n. sp. also differs from *Edmontosaurus*, which has a wider prefrontal, an appreciably greater number of dentary tooth positions (~50), a jugal with rostral constriction that is significantly narrower than the caudal one, and a postorbital process of the jugal that is markedly inclined caudally. The premaxilla in *Edmontosaurus* is laterally expanded and spatulate, with a broad lip-like oral margin; the dentary has a longer edentulous section and a greater angular deflection of the edentulous margin. The pubis in *Edmontosaurus* also differs notably; the prepubic process has an oval blade, taller than it is long, with a well-developed proximal constriction (Prieto-Márquez, 2010b).

In *Kritosaurus* and '*Naashoibitosaurus*' (= *Kritosaurus* sensu Horner, 1992; Williamson, 2000; see discussion to follow), the frontal is deeply embayed along its anterior margin as a result of posterior retraction of the narial crest, and in '*Naashoibitosaurus*,' the frontal is excluded from the margin of the orbit by the postorbital and prefrontal (Prieto-Márquez, 2014; Fig. 4). In both, the prefrontal is relatively much larger than in *?G. alsatei*, participates in the flank of the narial crest, and is included within the posterior border of the circumnarial depression (Fig. 4). Although the jugal is similar in all three taxa, the differences in the frontal and prefrontal are sufficient to demonstrate that *?G. alsatei* cannot be referred to either *Kritosaurus* or '*Naashoibitosaurus*.'

The frontal and prefrontal in *?G. alsatei* closely resemble those in species of *Gryposaurus* (Fig. 12). There are differences in the dentary and quadrate, as well as minor differences in the jugal and pubis; otherwise, the elements preserved are all similar to those in *Gryposaurus*. The characters shown by Prieto-Márquez (2010b, clade 27, fig. 9) to unite the species of *Gryposaurus* are the long edentulous part of the dentary (ratio between length of the proximal edentulous slope of dentary to length of the tooth row anterior to coronoid process is between 0.32 and 0.45; in *?G. alsatei* this is 0.27), and features of the ilium and narial crest not preserved in *?G. alsatei*. As a result, the preserved material of *?G. alsatei* cannot be shown to possess the synapomorphies thought to characterize *Gryposaurus*.

An unnamed Mexican saurolophine (PASAC-1) included in some phylogenetic analyses ("Sabinas OTU" allied with the *Prosaurolophus*-*Saurolophus* clade by Prieto-Márquez, 2010b; referred to *Kritosaurus* sp. by Kirkland et al., 2006) has few preserved elements that can be adequately compared with parts preserved in *?Gryposaurus alsatei* n. sp. The preserved part of the quadrate in the Sabinas specimen exhibits an expansion that extends into the infratemporal fenestra, similar to that in *?G. alsatei* (Fig. 7). The tooth battery in the dentary, however, extends farther posteriorly and has a significantly greater number of tooth rows (53); the coronoid process is not inclined anteriorly and lacks a dorsal projection; and the ventral deflection of the edentulous portion of the dentary is not as prominent. The pubis in the Sabinas saurolophine has an extremely narrow neck and differs markedly from that in *?G. alsatei* (Fig. 12). The premaxilla in a second specimen, from the Cerro del Pueblo Formation near Presa de San Antonio (IGM 6685), referred by Kirkland et al. (2006) to the Sabinas saurolophine (to *Kritosaurus* sp. instead by Prieto-Márquez, 2014) is, however, very similar to that in *?G. alsatei*. It has the same narrow arcuate oral margin and narrow border for the circumnarial depression, steep inflection in the lateral process, and large raised conical denticles (Kirkland et al., 2006, fig. 11). It is possible that the Presa de San Antonio specimen may not pertain to the same taxon as the Sabinas specimen (e.g., Prieto-Márquez, 2014), and if so, it might well represent *?G. alsatei*.

An unnamed Big Bend saurolophine included in some phylogenetic analyses ("UTEP Big Bend OTU" of Prieto-Márquez, 2010b) is known from the upper shale member of the Aguja Formation, which underlies the Javelina Formation in Big Bend National Park (Wagner, 2001). These specimens were tentatively referred to *Kritosaurus* cf. *navajovius* by Davies (1983) and by Wagner (2001), but on the basis of postcranial features (coracoid and ilium) allied instead with the South American hadrosaurs (*Secernosaurus* and *Willinakaqe*) by Prieto-Márquez (2010b). There are few elements preserved in specimens referred to the Aguja saurolophine that can be compared with *?G. alsatei*; the pubis in one specimen (TMM 42309-3, see Davies, 1983) differs substantially from that in *?G. alsatei*. Neither the coracoid nor ilium is preserved in material currently known of *?G. alsatei*, and so it is uncertain whether *?G. alsatei* shares features of those elements that are believed to ally the Aguja saurolophine with the Argentinian species.

?Gryposaurus alsatei n. sp. differs from both of the Argentinian hadrosaurs. The premaxilla in *Willinakaqe* lacks the sharp border of the circumnarial fossa, the marked inflection in its lateral border, the large conical denticles, and the pronounced sulcus that define the inner denticulate margin in *?G. alsatei*; the body of the dentary is also much deeper in *Willinakaqe*, and it has fewer, longer alveolar grooves (Juarez Valieri et al., 2010). The frontal in *Secernosaurus* is markedly shorter, and it has a deeply embayed nasal contact compared to *?G. alsatei* (Prieto-Márquez and Salinas, 2010); the pubes are similar, but the ischial peduncle is longer, and the prepubic neck is longer and more constricted in *Secernosaurus* (Fig. 12).

?Gryposaurus alsatei n. sp. also differs from both of the Asian saurolophines, *Kerberosaurus* and *Wulagasaurus*. In *Wulagasaurus*, the dentary is much more slender than in other saurolophines, including *?G. alsatei* (Godefroit et al., 2008). The jugal lacks a ventral flange and has a posteriorly inclined postorbital process. The frontal in *Kerberosaurus* differs markedly from that in *?G. alsatei*. It is very narrow, not included in the orbit margin, dorsally concave on the parietal suture, and with the nasal suture embayed along the midline (Bolotsky and Godefroit, 2004).

Comparison with Kritosaurini.—Together *Gryposaurus*, *Kritosaurus*, and '*Naashoibitosaurus*,' along with the unnamed Aguja and Presa de San Antonio saurolophines, which may be referable to one of these three genera, and if Prieto-Márquez (2010b, 2014) is correct, the Argentinian saurolophines comprise a clade referred to as Kritosaurini (Prieto-Márquez, 2014; Fig. 14). *Latirhinus* (Prieto-Márquez & Serrano Brañas, 2012) is probably also a member of this clade, and closely related to *Gryposaurus*, but the only part of the skull preserved in *Latirhinus* is the nasal, and so it cannot be adequately compared with other members of the group. All of the taxa included within this group are so similar to *Kritosaurus* that all, including the Argentinian forms, have been at one time or another referred to *Kritosaurus*. Those members of Kritosaurini known from cranial material each have a characteristic conformation of the skull roof that reflects relative development of the narial crest, and even in those taxa where the nasals themselves are not preserved, the frontals are distinctive (e.g., *Secernosaurus*).

?Gryposaurus alsatei n. sp. seems likely a member of Kritosaurini but appears to possess few unique apomorphies, instead exhibiting a combination of character states closest to those found in species of *Gryposaurus*. Although the narial crest is not preserved in *?G. alsatei*, the form of the bordering parts of the frontal and prefrontal indicate that, if it had one at all, the narial crest in *?G. alsatei* may have been much like that in *Gryposaurus* spp. In *?G. alsatei* the frontal is large in

comparison to the prefrontal. This is the condition in species of *Gryposaurus*, and unlike that in *Kritosaurus* for example, where the prefrontal is relatively much larger (Fig. 4). In *G. notabilis*, the prefrontal/frontal suture is posteriorly extended to form a deep embayment in the frontal, and leaving a narrow extension of the frontal that reaches the rim of the orbit. *?G. alsatei* lacks this deep embayment, but the frontal also participates in the rim of the orbit, unlike in '*Naashoibitosaurus*,' for example, where it is excluded. In *?G. alsatei*, the dorsal surface of the frontal is flat as in species of *Gryposaurus*, not upwardly curved, and the nasal-frontal suture is not extended posteriorly to form a deep embayment in the frontal as in *Kritosaurus*. By contrast, the nasal-frontal suture is extended anteriorly in *?G. alsatei* and interdigitates, resulting in a W-shaped contact, as in *G. notabilis* and *G.* '*incurvimanus*.' As in species of *Gryposaurus*, the prefrontal in *?G. alsatei* is relatively small, and the nasal process is outwardly convex, not elevated medially, or included in the circumnarial fossa. There is not a sharp angle in the orbital border of the prefrontal, as there is in *G. notabilis* and *G. monumentensis* Gates and Sampson, 2007. Hence, the preserved skull roof elements in *?G. alsatei* differ slightly but are most similar to those in species of *Gryposaurus*.

The jugal in *?Gryposaurus alsatei* n. sp. also differs slightly from species of *Gryposaurus*. The ventral edge of the jugal in *G. latidens* Horner, 1992 is nearly straight; the posteroventral flange in *G.* '*incurvimanus*' has a short spur that is lacking in other species; and the quadratojugal articulation in both *G. notabilis* and *G. monumentensis* narrows dorsally to form an extended part of the border of the infratemporal fenestra (Fig. 6). In *?G. alsatei*, the posterior jugal process is instead blunt and hatchet shaped, as in *Kritosaurus* and '*Naashoibitosaurus*.' The part of the quadrate in *?G. alsatei* that borders the infratemporal fenestra is broad and anteriorly convex, such that it would have exaggerated that part of the border of the fenestra more markedly than in any species of *Gryposaurus*, *Kritosaurus*, or '*Naashoibitosaurus*.'

The premaxilla in *?Gryposaurus alsatei* n. sp. is relatively narrow, with an arcuate lateral margin, as in *Gryposaurus*, and the edge of the circumnarial depression is close to the labial margin. The muzzle is exceptionally narrow in *?G. alsatei* (ratio of mediolateral width to narrowest post-oral constriction = 1.4). No specimen of *Kritosaurus* has the premaxilla preserved well enough for comparison; however, in the holotype of *K. navajovius*, the lateral border of the premaxilla is smoothly curved (e.g., Kirkland et al., 2006, fig. 17). Instead, along the lateral edge of the premaxilla in *?G. alsatei* there is a sharply upturned inflection in the labial margin, more marked than in any species of *Gryposaurus*. The Presa de San Antonio 'muzzle' (IGM 6685) exhibits a very similar sharp inflection; and a less-pronounced inflection is also present in *G. notabilis* and in *G. monumentus* (Fig. 5). The four pronounced conical denticles along the outer oral margin may be a unique feature in *?G. alsatei*. Although most saurolophines, including *Gryposaurus*, have a rugose irregularly corrugated oral surface on the premaxilla, in most cases they lack these distinct large smooth conical protruberances. The Presa de San Antonio specimen (IGM 6685) appears to have very similar large conical denticles, but its oral surface has not been illustrated or described in detail. A similar, but more subdued, series of four conical premaxillary denticles is also present in the Baja lambeosaurine *Magnapaulia* (Prieto-Márquez et al., 2012). These large conical denticles were probably exaggerated in the horny rhamphotheca that encased the beak in life and would have meshed with similar denticles or corresponding pits on the oral surface of the predentary when the jaws were in occlusion (see Brown, 1910; fig. 4, oral surface of the predentary in *Kritosaurus navajovius*). Presumably, the resulting interdigitating triturating surface reflects a feeding specialization in *?G. alsatei* and other hadrosaurs that possessed similar coarsely denticulate beaks.

The pubis is, among bones of the postcranial skeleton, peculiarly variable among hadrosaurs and to some extent diagnostic taxonomically (Brett-Surman and Wagner, 2007; Prieto-Márquez, 2010b). The proportions of the pubis in *?Gryposaurus alsatei* n. sp. are unusual and distinctive compared to those in other hadrosaurs for which data are available (Fig. 13). The neck is short relative to the entire length of the prepubis, 51% its length (~55% to 75% in other hadrosaurs), and tall dorsoventrally, 82% the breadth of the blade, (~35% to 55% in other hadrosaurs; Fig. 13). In species of *Gryposaurus* for which the pubis is known (e.g., *G. latidens*; Fig. 13), the prepubis is similar in form, but the blade is proportionally shorter, and the neck more constricted. The pubis in YPM-PU 19670 (referred to *Gryposaurus* sp. by Prieto-Márquez, 2014; to *Kritosaurus* sp. by Horner, 1992) is closer to that in *?G. alsatei* than to any other hadrosaur (Fig. 12). No pubis is preserved, however, in any specimen confidently referred to either *Kritosaurus* or '*Naashoibitosaurus*.'

In summary, from the specimens currently available, there is no compelling morphological basis to exclude *?G. alsatei* n. sp. from referral to *Gryposaurus*. Such a referral intuitively seems unlikely; *Gryposaurus latidens* is among the oldest saurolophines known in North America (ca. 79 Ma, early Campanian; Prieto-Márquez, 2012). *G. notabilis* and *G. monumentensis* are found in slightly younger strata (ca. 75 Ma, late Campanian; Gates and Sampson, 2007). Referral of *?G. alsatei* to *Gryposaurus*, if correct, would require survival of the genus into middle to late Maastrichtian time (69 to 66 Ma), a range over 10 to 13 million years in duration (Fig. 14). Although such a long-lived hadrosaur genus seems unlikely, the preserved parts of *?G. alsatei* provide no contrary indication. This circumstance could alternatively reflect reversal in *?G. alsatei* to plesiomorphic morphology shared with *Gryposaurus* spp. and might not be an indication of close relationship.

Phylogenetic analysis.—To evaluate the phylogenetic position of *?G. alsatei*, we conducted a phylogenetic analysis of Saurolophinae. TMM 46033-1 was coded into the morphological character data set of Prieto-Márquez (2014), with no new characters added. Preserved parts allowed for 77 of the 265 characters to be coded (see Appendix). The resulting matrix consists of 265 characters and 35 taxa (including three lambeosaurine and 9 nonsaurolophid, nonlambeosaurine outgroup taxa). The data were analyzed under the maximum parsimony criterion using PAUP* 4.0a142 (Swofford, 2015), with heuristic search using starting trees found by 10 random addition replicates and with tree search accomplished using tree bisection reconnection. Nonparametric bootstrap analysis was

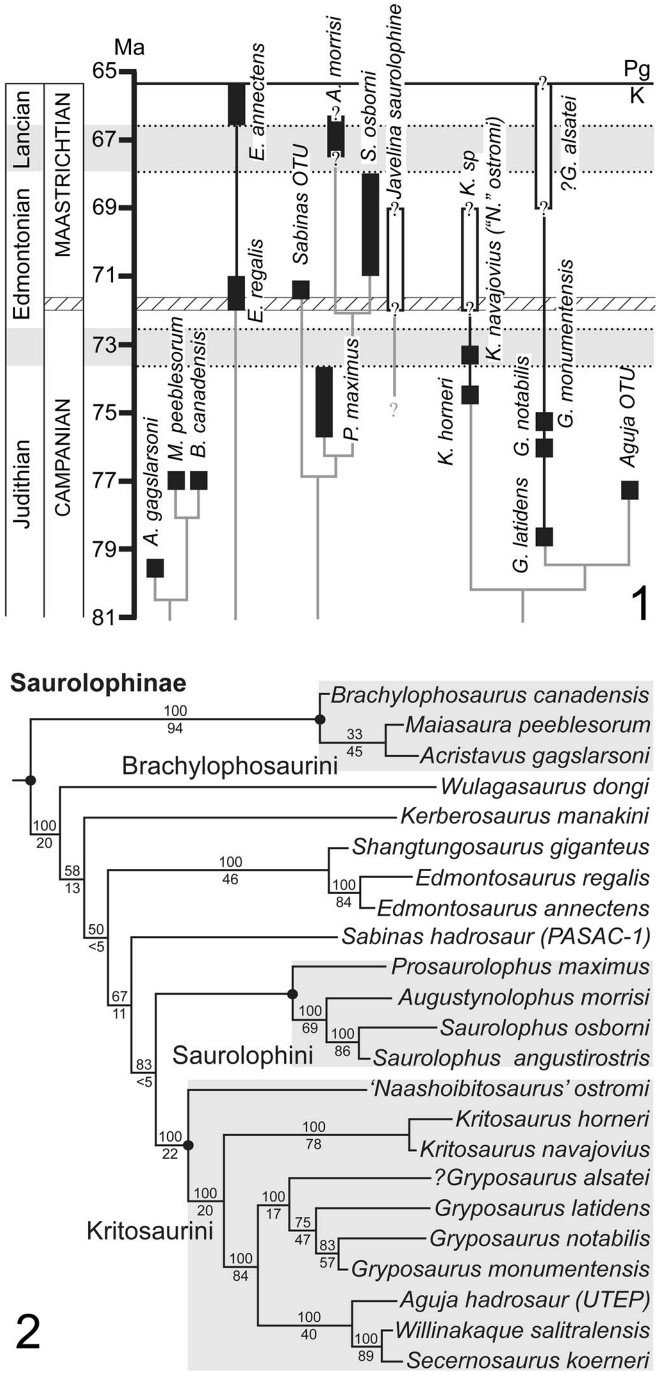

Figure 14. Stratigraphic distribution of Campanian-Maastrichtian saurolophine hadrosaurs in western North America (**1**) based on Gates et al. (2012) and Eberth et al. (2013) showing likely position of Javelina hadrosaurs. (**2**) Saurolophine relationships found in majority-rule consensus tree of 36 most-parsimonious trees resulting from phylogenetic analysis of data set described in text. Numbers above branches reflect percentage representation of the clade among most-parsimonious trees; numbers below represent bootstrap support values.

conducted to evaluate support for the resulting tree topology, with 1,000 bootstrap replicates generated under the same conditions as the initial analysis, except that starting trees were limited to one random addition replicate for each bootstrap run.

The analysis resulted in 36 most parsimonious trees with a length of 623 steps (C.I. = 0.57; R.I. = 0.74, Fig. 14).

The analysis found a close relationship between *?Gryposaurus alsatei* and the three included species of *Gryposaurus* in all most-parsimonious trees, but with limited (17%) bootstrap support. We acknowledge that this is tenuous grounds for including the former with the genus, but we consider this preferable to coining a new genus for a species that might be easily accommodated within *Gryposaurus*. The resulting range extension (into the Maastrichtian) is notable, but does not strike us as sufficient to warrant a new generic epithet for *alsatei*.

Genus *Kritosaurus* Brown, 1910

Type species.—*Kritosaurus navajovius* Brown, 1910 from the Kirtland Formation of New Mexico, by original designation.

Kritosaurus sp.
Figures 15–17

Materials.—TMM 45603-2 fragmentary skull including parts of neurocranium, frontals, postorbitals, parietal, right maxilla, right palatine, fragment of left quadrate, part of the right dentary, and right surangular; TMM 45603-1 fragmentary dentary and surangular; TMM 41442-1 fragmentary skull including parts of both maxillae, right quadrate, part of left dentary, neural arch, and rib fragments.

Frontal and parietal.—Parts of both frontals are preserved and coossified with the parietal in TMM 45603-2; articulation surfaces for adjoining skull roof elements are broken away (Fig. 15.1–15.5). The sutures between frontals and parietal are completely fused and obscured; there is only a low ridge along their transverse contact, forming the anterior border of the supratemporal fenestrae. The dorsal surface of the conjoined frontals is nearly flat, slightly raised along the midline suture between the two, and only faintly depressed on either side. Although incomplete anteriorly, the preserved parts of the frontals extend well forward over the olfactory tract and show no indication that they were raised to participate in the base of a narial crest or overlapped by the nasals along their preserved anterior edges.

The dorsal surface of the parietal is steeply inclined posteoventrally relative to the skull roof, as defined by the plane of the conjoined frontals. Most of the parietal sagittal crest is broken away, although the part preserved indicates that the crest was broad based and probably tall posteriorly. The sagittal crest diminishes anteriorly and does not bifurcate or bound a prominent triangular fossa at the junction of the parietal with frontals (e.g., as in some specimens of *Gryposaurus* and *Prosaurolophus*; Horner, 1992; Prieto-Márquez, 2010a). The sutures between the parietal and subjacent prootic and laterosphenoid are obscured by coossification; however, a low ridge along the lateral wall of the braincase probably marks this contact. This ridge flares outward near the preserved end of the braincase, which is broken just posterior to the fenestra vestibuli (VIII; Fig. 15.3). Together, these features indicate that the parietal was relatively short and is broken in this specimen near its contact with the supraoccipital.

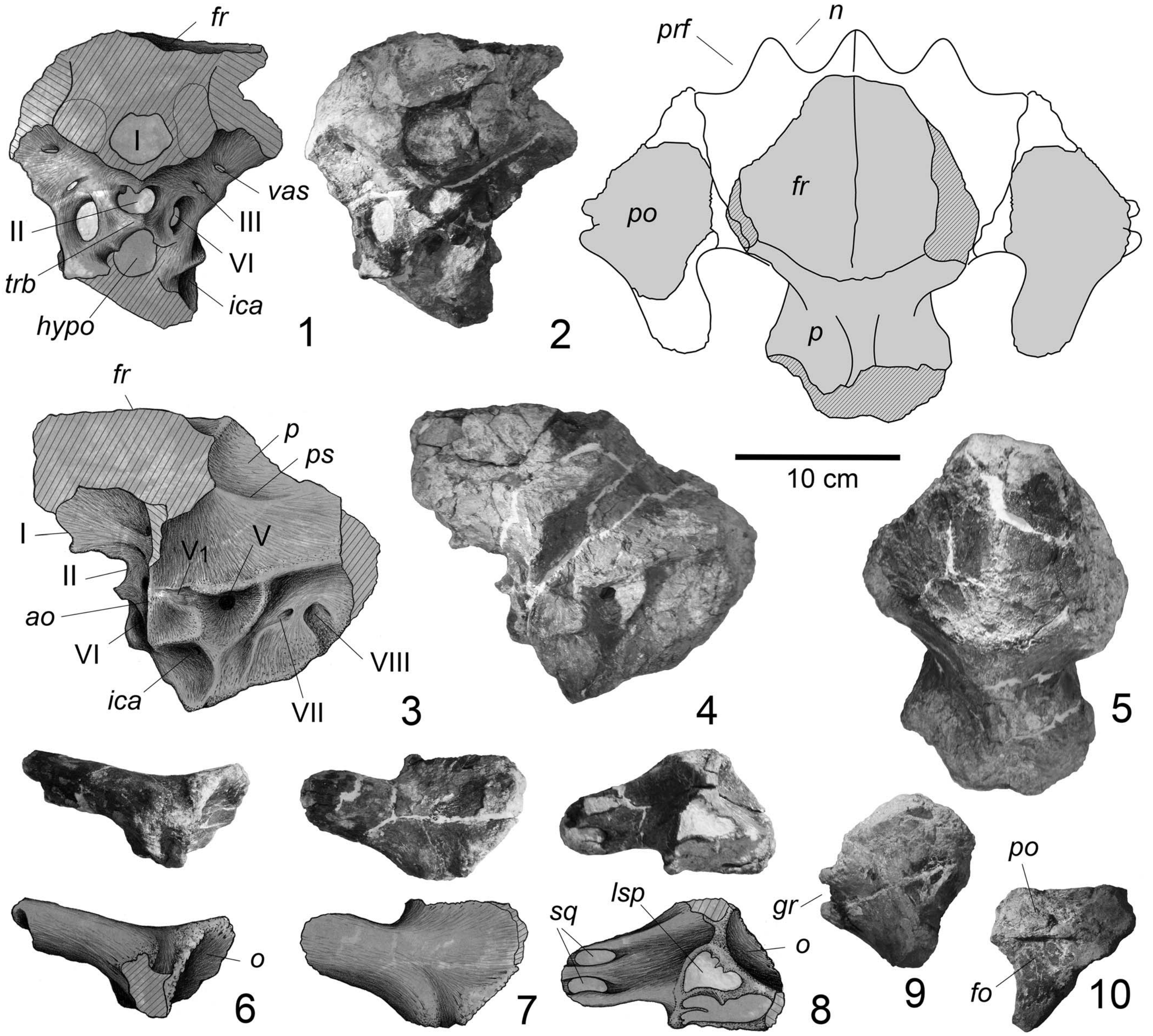

Figure 15. *Kritosaurus* sp. (TMM 45603-2) photographs and companion drawings of skull roof and neurocranium in (**1**,**2**) anterior, (**3**,**4**) left lateral, and (**5**) dorsal views; right postorbital in (**6**) lateral, (**7**) dorsal, and (**8**) ventral views; (**9**) left postorbital in dorsal view; (**10**) fragment of precotyloid process of left squamosal in lateral view; reconstruction of skull roof (above right). I–VIII = exits for cranial nerves; *ao* = crista antotica; *fo* = precotyloid fossa; *fr* = frontal; *gr* = groove on jugal process of postorbital; *hypo* = hypophyseal cavity; *ica* = foramen for internal carotid artery; *lsp* = suture for antorbital buttress of laterosphenoid; *n* = suture for nasal; *o* = orbit; *p* = parietal; *po* = postorbital; *prf* = suture for prefrontal; *sq* = suture for squamosal; *trb* = transverse bridge; *vas* = vascular foramen.

Postorbital.—Parts of both postorbitals are preserved in TMM 45603-2. In dorsal view, the main body of the postorbital is stout and triangular, with the frontal articulation approximately in the parasagittal plane, but the rim of the orbit inclined anteromedially. The orbital rim is arcuate in lateral view. The squamosal process is elongate, cylindrical, and dorsally elevated such that the entire postorbital is broadly Y-shaped in lateral view (Fig. 15.6). There are two deep grooves along the ventral surface of the squamosal process to receive rostral prongs of the squamosal; these indicate that the postorbital-squamosal suture was deeply interdigitating and that the suture extended rostrally along the dorsal border of the infratemporal fenestra nearly to the jugal process of the postorbital. The lateral surface of the jugal process has a deep groove along its axis, and the lateral borders of both the orbit and infratemporal fenestra are rugose and curled back over the groove, increasing its depth (Fig. 15.9). The distal end of the jugal process is broken away on both left and right postorbitals.

Squamosal.—Only the left postorbital ramus with the precotyloid process and part of the quadrate cotylus are preserved in TMM 45603-2 (Fig. 15.10). The precotyloid process is curved rostrally, mediolaterally compressed, and although it is missing its tip, would have been comparatively short. The lateral surface of the precotyloid process is recessed relative to the postorbital ramus and relative to a low ridge that defines the rostral border of the quadrate cotylus. This ridge and the cotylus itself extend distally only about half the length of the precotyloid process. The lateral surface of the postorbital ramus has the distal end of one of the articular prongs of the postorbital preserved in place, indicating that the postorbital suture extended only as far caudally as the precotyloid process.

Maxilla.—A complete right maxilla was recovered with TMM 45603-2 (Fig. 16.1–16.3). The dorsal process is tall, and the rostrolateral surface is broadly exposed beneath a long, horizontal lacrimal articulation. There is a prominent triangular spur on the dorsal surface at the junction between the lacrimal and premaxillary articulation surfaces. The rostrodorsal process is very short, downturned, and parallel with the rostroventral process; neither projects far anteriorly beyond the tooth-bearing margin (Fig. 16.1). The portion of the maxilla anterior to the jugal joint is about equal in length to that portion posterior to the joint. The ectopterygoid shelf is broad, directed as much laterally as it is dorsally, and bears a short but well-defined pterygoid process. The ectopterygoid ridge parallels the toothed margin posteriorly and merges with the jugal articulation, which is divided into dorsal and ventral facets, anterior to which there is a pronounced dorsal deflection in the exposed lateral face of the maxilla. A cluster of small foramina emerges below the ventral jugal articular facet. The large oval primary maxillary foramen emerges from the lateral surface near the posterior end of the premaxillary articulation. The medial surface of the maxilla is nearly flat and bears a high arcuate row of alveolar (‘special dental’) foramina. There are 43 visible tooth rows.

Quadrate.—Only the central part of the dorsal shaft of the left quadrate is preserved in TMM 45603-2. This part can be compared directly with both TMM 41442-1 (Fig. 7.5, 7.6; referred here also to *Kritosaurus* sp.) and LSUMG V-1183 (referred here to ?*Gryposaurus alsatei* n. sp.). The morphology of the dorsal half of the shaft, above the quadratojugal articulation, differs markedly from that in ?*G. alsatei* and provides a means for discrimination of the two taxa (see discussion to follow). The right quadrate in TMM 41442-1 is nearly complete and was the basis for a detailed description given by Wagner (2001). Although the posterior surface of the squamosal articular head is abraded, a faint ‘caudal buttress’ is clearly present and, together with the dorsal end of the shaft, slightly curved posteriorly (Fig. 7.5). The shaft is otherwise nearly straight, gently bowed laterally in posterior view. The quadratojugal notch is positioned below midlength, broadly arcuate in lateral view, with the dorsal part of the articulation surface recessed to form a narrow shelf. Dorsal and ventral margins of the articulation surface are inclined at a similar angle (~20°) relative to the longitudinal axis of the quadrate. The pterygoid ‘wing’ is broken but extends from just below the head nearly the complete length of the bone.

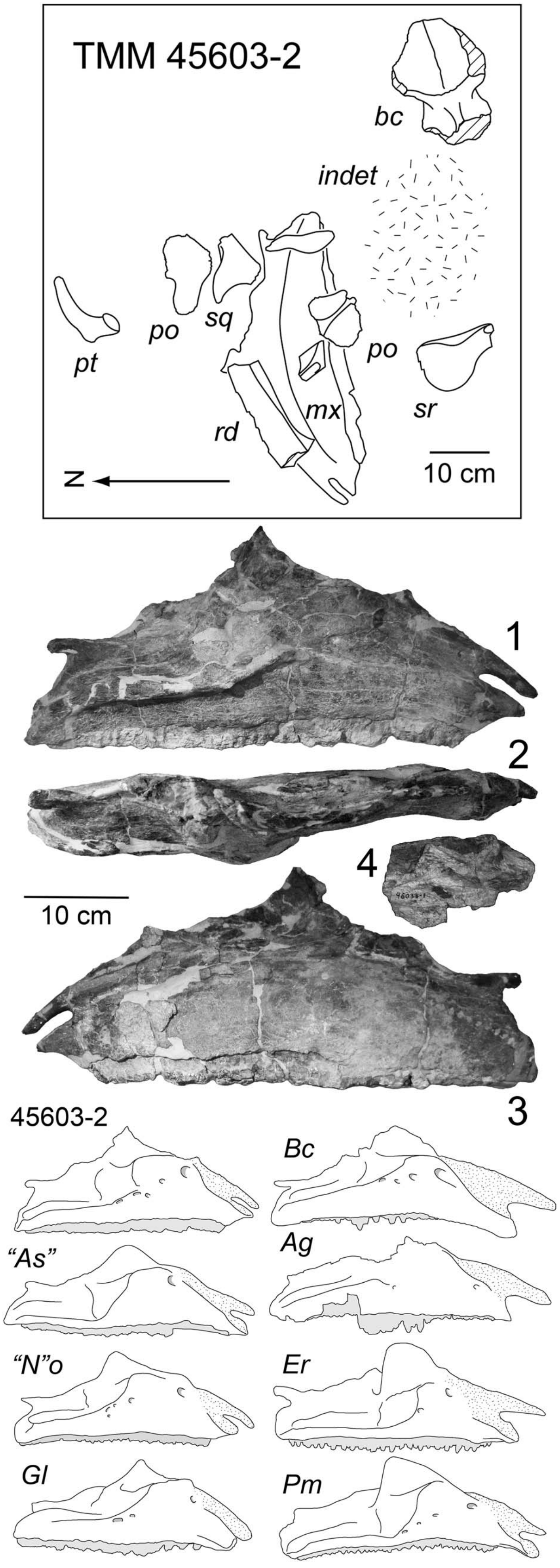

Figure 16. *Kritosaurus* sp. (TMM 45603-2) quarry diagram showing position of preserved elements (above) with right maxilla in (**1**) lateral, (**2**) dorsal, and (**3**) medial views; (**4**) fragment of left maxilla TMM 46033-1 in lateral view; line drawings compare maxillae in other saurolophine hadrosaurs (reduced to common length). *Ag* = *Acristavus gagslarsoni*; “*As*” = Aguja saurolophine (AMNH 3079); *Bc* = *Brachylophosaurus canadensis*; *Er* = *Edmontosaurus regalis*; *Gl* = *Gryposaurus latidens*; “*N*”*o* = “*Naashoibitosaurus*” *ostromi*; *Pm* = *Prosaurolophus maximus*.

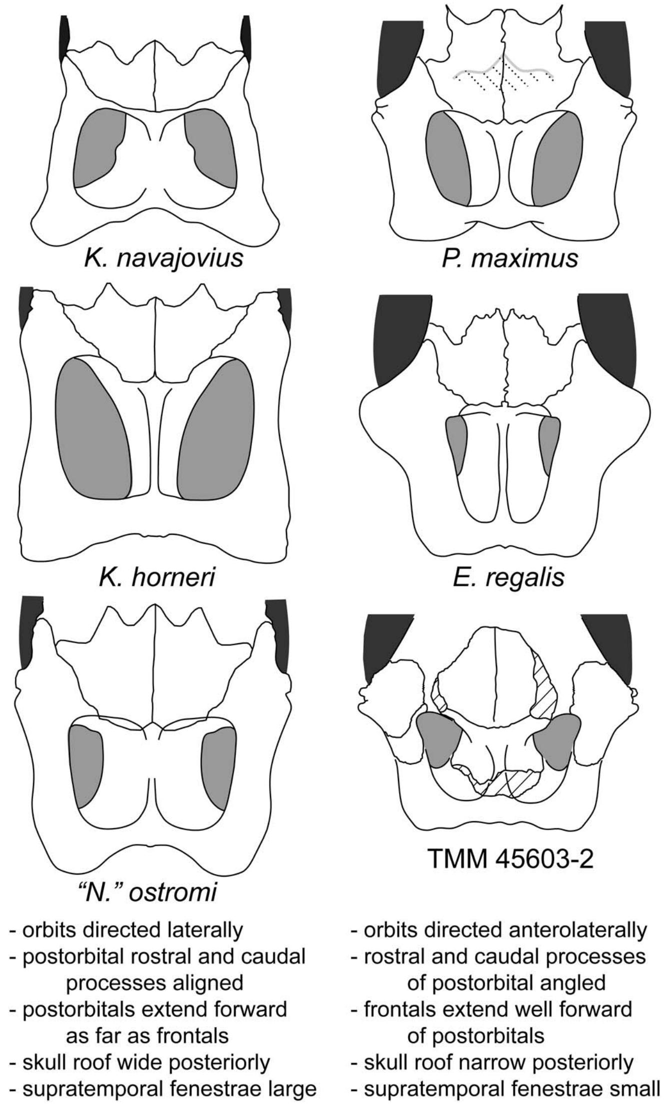

Figure 17. Reconstructed skull roof in Javelina *Kritosaurus* sp. (TMM 45603-2) compared to other saurolophine hadrosaurs, highlighting proportional differences among them.

The mandibular articulation is relatively narrow transversely. The medial (articular) condyle is elevated relative to the lateral (surangular) condyle of the mandibular articulation, but only a weak intercondylar depression divides the two posteriorly.

Palatine.—Part of the right palatine is preserved in TMM 45603-2; the thin pterygoid process is broken. The maxillary and jugal articulation surfaces are robust, nearly at a right angle to one another, and separated by the narrow border of a fenestra that would pass between the three elements in articulation. The maxillary articulation is not as elongate posteriorly, but otherwise the form of this element is comparable to that shown in YPM-PU 16970 (referred to cf. *Kritosaurus* by Horner, 1992; plate 22).

Neurocranium.—In TMM 45603-2, the occipital condyle, basioccipital, and exoccipitals are broken and missing, but a substantial part of the neurocranium is well preserved and thoroughly coossified with the surrounding skull roof elements (Fig. 15.3, 15.4). Contacts between adjacent bones are obscured by sutural fusion; however, the prominent postorbital buttress of the laterosphenoid (crista antotica) divides the braincase into a distinct laterally facing temporal region and a rostrally directed orbital cavity.

On the temporal face of the braincase, the trigeminal foramen (V) is large and conspicuous. It is set within a deep, funnel-shaped fossa immediately posterior to the postorbital buttress. A distinct shallow canal for the opthalmic branch (V_1) extends forward from the trigeminal fossa, but the path of the mandibular branch is not marked; there is only a broad depression below the fossa. Most of the basisphenoid is broken away, but there is a hemispherical cavity ventral to the trigeminal fossa, with a foramen in its roof that probably transmitted the internal carotid artery (Fig. 15.3). Immediately behind the trigeminal fossa is the facialis foramen (VII); a shallow groove descending from the foramen probably marks the path of the palatine ramus. The auditory canal (VIII) forms a large opening, flush with the lateral wall of the braincase and posterior to the facialis foramen, but the posterior part of the braincase is poorly preserved.

On the rostral face of the braincase, the large, circular, olfactory (I) opening is conspicuous (Fig. 15.1). The forward ends of the frontals are broken off, and although the presphenoids and parasphenoid are not preserved, sutural surfaces for these elements are not apparent. There is a single midline cavity below the olfactory opening that probably housed the optic chiasma just behind the point of divergence for separate tracts of the optic (II) nerves. The common opening for the optic nerves is separated from the hypophyseal fossa below by a stout transverse bony bridge. This is the anterior ramus of the unique "bifid bridge-like structure" described by Prieto-Márquez (2010a, p. 846) in neurocrania of *Gryposaurus notabilis* and *Kritosaurus navajovius*, although in both cases Prieto-Márquez indicated that this feature is partly or entirely reconstructed in plaster and of uncertain significance. It is well preserved in the present example. The bridge-like structure separates the optic foramen above from an opening into the hypophyseal fossa below and the large foramen for the abducens nerve (VI). The part of this structure that borders the opening into the hypophyseal fossa is more completely preserved on the right side, where it is slightly embayed for the passage of a vascular feature (?palatine artery). Above the opening for the abducens nerve on the wall of the orbital cavity are two small foramina. In *Gryposaurus notabilis* (Prieto-Márquez, 2010a, fig. 6) there are two identically placed openings; the lower of these is identified as the exit for the oculomotor nerve (III), but the upper opening is unmarked and presumably neurovascular in origin.

Dentary.—Part of the left dentary is preserved in TMM 45603-1. A larger part of a left dentary is also preserved in TMM 45603-2 (Fig. 8.8). Neither specimen is sufficiently complete to reveal any informative features.

Surangular.—Part of the right surangular is preserved in TMM 45603-2. A smaller part of the same element is preserved in TMM 45603-1. There is no foramen in the main body of the surangular, and the lateral flange of the quadrate articulation surface faces ventrally rather than laterally. Although most of the rostrodorsal process is broken, its base is slender and strap-like.

Dentition.—All of the maxillary teeth are intact in TMM 45603-2, but it has not been possible to completely remove the sediment matrix that surrounds them. There appear to have been two functional teeth within most of the alveoli in the occlusal plane except for the posteriormost ten or so tooth files. A few tooth crowns are free of matrix, and these have a single, straight, midline ridge. The margins of the crowns appear to be smooth. No dentary teeth are preserved in any of the specimens.

Remarks.—The maxilla in TMM 45603-2, with its distinctive short, downturned rostrodorsal process, is essentially identical to that in *Kritosaurus navajovius* and in '*Naashoibitosaurus*' *ostromi* Hunt and Lucas, 1993 (Fig. 16). These two taxa are thought to be synonymous by some authors (e.g., Williamson, 2000), although Prieto-Márquez (2014, supplementary data table 2) suggested several criteria that may distinguish them. Two such features evident in the maxilla of TMM 45603-2 are shared with *K. navajovius*; the base of the dorsal process is anterior to midlength, and the angle between dorsal process and alveolar margin exceeds 40°. The upwardly angled caudal process of the postorbital in TMM 45603-2 indicates that the dorsal margin of the infratemporal fenestra was elevated, another feature thought to distinguish *K. navajovius* (Prieto-Márquez, 2014). Two other aspects of TMM 45603-2 are instead among those thought to characterize '*N.*' *ostromi*: the posterior margin of the quadrate is curved, and the laterosphenoid ophthalmic sulcus is open (although the latter feature may be of dubious significance). In contrast to both *K. navajovius* and '*N.*' *ostromi*, the rostral and caudal processes of the postorbital in TMM 45603-2, rather than aligned parasagittally are inclined medially in dorsal view and join each other at a marked angle (~110°; Fig. 17). This condition requires that the orbit be directed slightly forward or that the rear part of the skull be relatively narrow compared to the width of the skull across the postorbitals, or in all likelihood both (Fig. 17). This general morphology is unlike that in either *K. navajovius* or '*N.*' *ostromi*, where the orbits are directed laterally, but is instead similar to that for example in *Edmontosaurus regalis* Lambe, 1917 or *Prosaurolophus maximus* Brown, 1916 (Fig. 17). The geometry of the preserved posterior end of the neurocranium and postorbitals in TMM 45603-2 also indicate that the rear part of the skull was relatively short and that the supratemporal fenestrae were small. This condition is more like that in '*N.*' *ostromi*.

The jugal process of the postorbital in TMM 45603-2 has rugose swollen edges that bound a deep groove intervening between the orbit and infratemporal fenestra. A similar but less pronounced groove is found in '*Naashoibitosaurus*' but is also present in some other saurolophines (e.g., *Acristavus* sp. UMNHVP 16607, *Brachylophosaurus canadensis* MOR 794, *Prosaurolophus blackfeetensis* MOR 454).

In summary, it seems likely that TMM 45603-2 represents a species closely related to *K. navajovius* or '*N.*' *ostromi*, given the marked similarity of their maxillae, although the orbital orientation is unlike either. TMM 45603-2 and other specimens attributed here to the same taxon (e.g., TMM 41442-1) share characteristics of both *K. navajovius* and '*N.*' *ostromi*, although key apomorphic features are not preserved. In addition, there remains considerable uncertainty as to whether these two species, along with *K. horneri* Hunt and Lucas, 1993, truly represent three distinct species belonging to two different genera (e.g., Horner, 1992; Williamson, 2000). The slight morphological differences pointed out in the preceding, as well as geographic and stratigraphic separations, suggest that TMM 45603-2 might reasonably represent an unknown species. On the other hand, its combination of features may provide support for the argument that *K. navajovius* and '*N.*' *ostromi* represent adult and younger individuals of the same species (e.g., Williamson, 2000). Consequently, identification of the Javelina specimens to species level is unwarranted, and the material is herein assigned to *Kritosaurus* sp.

Subfamily Saurolophinae Brown, 1914
(sensu Prieto-Márquez, 2010b)
Genus and species indeterminate
Figures 18–20

Materials.—TMM 46015-2 conjoined frontals and a left maxilla; 46015-3 a right ilium, parts of both left and right pubes,

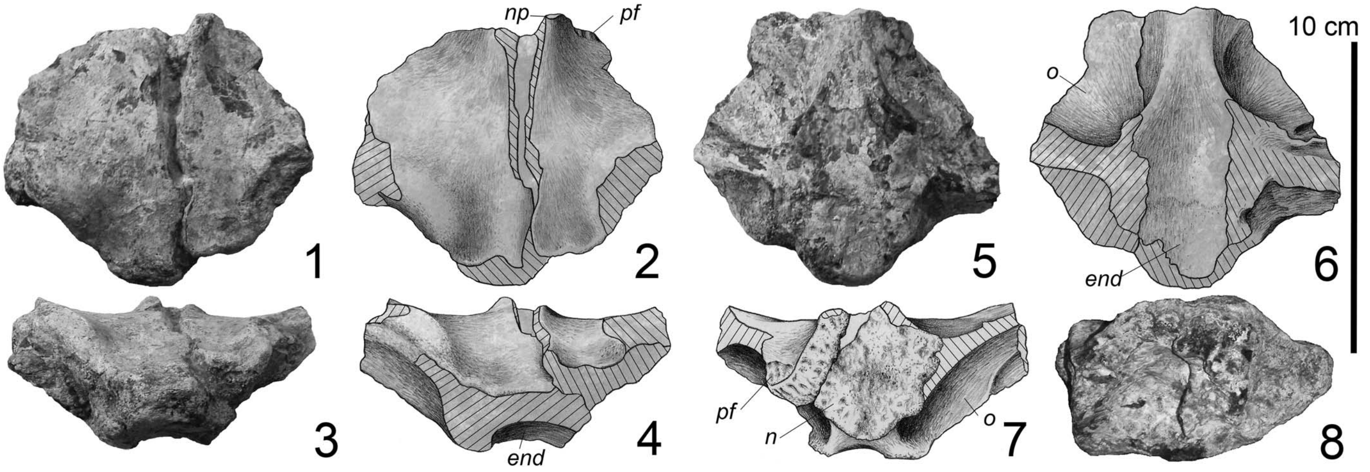

Figure 18. Saurolophinae indet. (TMM 46015-2) fragmentary skull roof with companion drawings in (**1**,**2**) dorsal, (**3**,**4**) posterior, (**5**,**6**) ventral, (**7**) anterior, and (**8**) left lateral views. *end* = endocranial cavity; *n* = suture for nasals; *np* = narial process; *o* = inner wall of orbit; *pf* = suture for prefrontal.

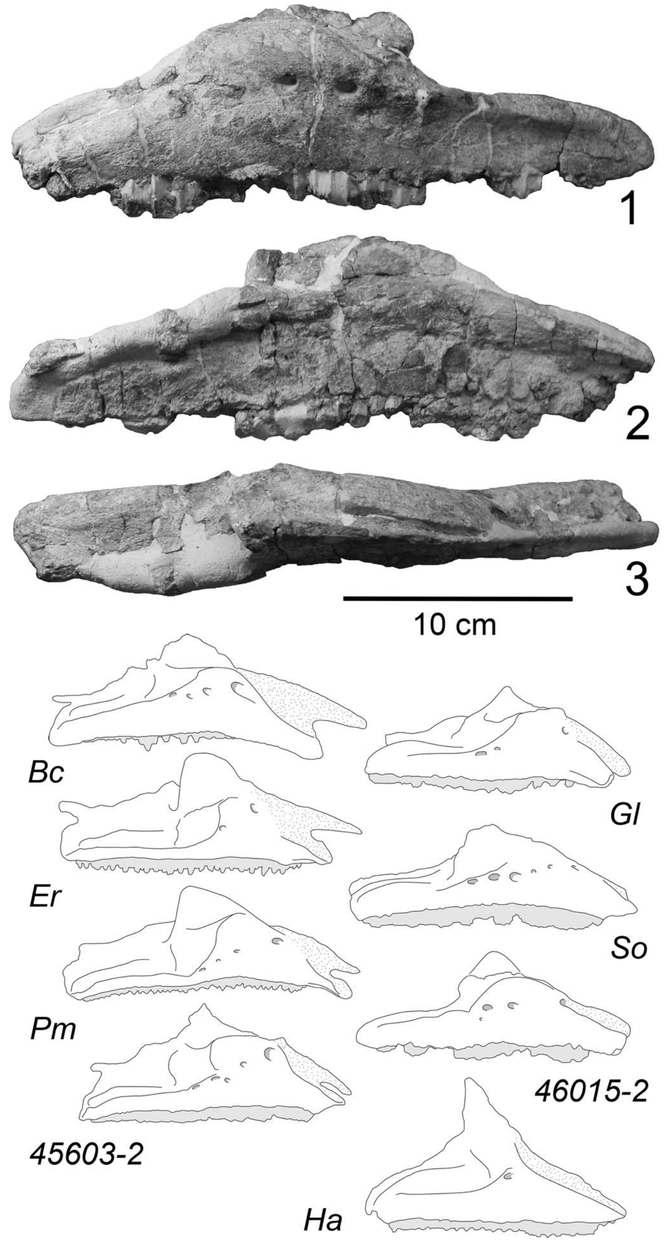

Figure 19. Saurolophinae indet. (TMM 46015-2) left maxilla in (**1**) lateral, (**2**) medial, and (**3**) dorsal views; line drawings compare maxillae in other hadrosaurs (reduced to common length). *Bc* = *Brachylophosaurus canadensis*; *Er* = *Edmontosaurus regalis*; *Gl* = *Gryposaurus latidens*; *Ha* = *Hypacrosaurus altispinus*; *Pm* = *Prosaurolophus maximus*; *So* = *Saurolophus osborni*.

and fragments of uncertain identity. These elements were found on the same stratigraphic horizon within about 20 m of each other; it is assumed here that they pertain to the same taxon, though not necessarily the same individual.

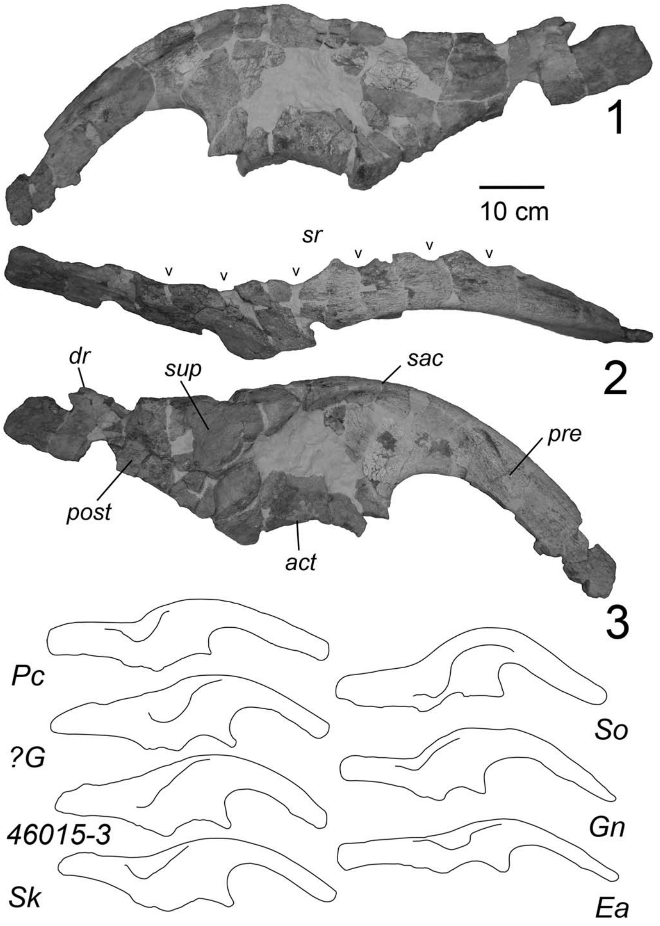

Figure 20. Saurolophinae indet. (TMM 46015-3) right ilium in (**1**) medial, (**2**) dorsal, and (**3**) lateral views; showing *act* = acetabulum; *dr* = short dorsal ridge; *post* = postacetabular process; *pre* = preacetabular process; *sac* = supracetabular crest; *sr* = sacral rib facets (shown with "v"); *sup* = supracetabular process; line drawings compare ilia in other hadrosaurs (reduced to common length). *Ea* = *Edmontosaurus annectens*; *?G* = *Gryposaurus* sp. (YPM-PU 19670); *Gn* = *Gryposaurus notabilis*; *Pc* = *Parasaurolophus cyrtocristatus*; *Sk* = *Secernosaurus koerneri*; *So* = *Saurolophus osborni*.

Frontal.—The conjoined frontals in TMM 46015-2 are broken and slightly separated near their mutual contact along the midline, but otherwise nearly complete (Fig. 18). The anterior end of the parietal is firmly coossified to the frontals, but sutures are obscure. In contrast to many hadrosaurs, where the dorsal surface of the skull roof is either flat or slightly domed, here the dorsal surface is concave, although slightly raised along the midline. Together the frontals curve upward markedly on the midline along the nasal contact, indicating that they participated in the posterior base of the narial crest. Among saurolophines, a similar condition is observed in *Maisaura* (Horner, 1988), *Saurolophus* (Bell, 2011), and *Augustynolophus* (Prieto-Márquez et al., 2014). In lambeosaurines, the frontals also form part of the base of the narial crest, but here the nasofrontal articulation forms a broad, shallowly inclined shelf such that the nasals significantly overlap the frontals dorsally (Evans et al., 2007); an extensive overlapping articulation is also found in *Brachylophosaurus* (Prieto-Márquez, 2005).

In TMM 46015-2, the frontals were not overlapped dorsally by the nasals along their preserved edges. Instead, the anterior ends of the frontals together form a stout, anteriorly directed buttress above the olfactory tract of the endocranial cavity. The frontals also curve upward posterolaterally and form raised welts along their contact with the postorbitals, indicating that the postorbitals were elevated above the skull roof (Fig. 18.3). The lateral edges are not preserved; however, the posterior end of the prefrontal suture appears to be preserved on the right side. It is unclear whether the frontal participated in the rim of the orbit, although the broken edge at the prefrontal suture suggests that it did not.

On the ventral surface of the frontals, the laterosphenoid articulations are directed anterolaterally, rather than strictly laterally, and bound deeply concave posterior walls of the orbits (Fig. 18.6). The cerebral cavity is shallow, not deep and hemispherical as in some other hadrosaurs, and at the anterior end there is little expression of olfactory tract due to dorsoventral expansion of the frontal buttress.

Maxilla.—The left maxilla is preserved in TMM 46015-2; it has a low lateral profile, and ~28 tooth positions (Fig. 19). Although most of the dorsal process is missing, the preserved base indicates that it was relatively short (Fig. 19). The rostrolateral surface is outwardly convex and broadly exposed beneath an arcuate articulation slot for the jugal and lacrimal. The premaxillary articulation forms a distinct medially inset shelf, and the anterior maxillary foramen exits the surface of the maxilla within the dorsal summit of this shelf. The rostrodorsal process is a blunt rounded nib, barely differentiated from the rostroventral process; there is no slot in the rostral margin separating the two, and neither extends forward of the anteriormost tooth file. The dorsal margin of the rostrodorsal process forms an angle of 24° with the alveolar margin. The portions of the maxilla anterior and posterior to the jugal joint are about equal in length. The ectopterygoid shelf faces dorsally, rather than laterally, and bears a very weak pterygoid process on its posteromedial corner, not visible in lateral view. The ectopterygoid ridge rises anteriorly and merges with a relatively short jugal articulation. Dorsal and ventral tubercles for the jugal articulation are weakly defined. A cluster of three peribuccal maxillary foramina exit below and anterior to the jugal joint. The medial surface of the maxilla is spanned by a continuous gently arcuate ridge below the palatine process and extending from the rostrodorsal process to the end of the ectopterygoid shelf; the series of alveolar foramina emerge below this ridge.

Ilium.—The right ilium is preserved in TMM 46015-3 (Fig. 20). The interior of the central iliac plate is missing, but it is otherwise nearly complete. In dorsal aspect the ilium is weakly sinuous; the preacetabular process is directed slightly laterally, and the postacetabular process is directed medially relative to the iliac plate. The dorsal surface is broad mediolaterally and bears six marked facets for sacral rib articulations along its medial border. In lateral view, the preacetabular process is deflected ventrally at an angle of 136° relative to a plane connecting ventral ends of the pubic and ischial peduncles. The depth of the proximal end of the preacetabular process is about half that of the iliac plate. The supracetabular crest extends well forward of the pubic peduncle. The supracetabular process (‘antitrochanter’) is abraded, but asymmetric, with the apex deflected posteriorly and its ventral extension about half the depth of the central iliac plate. The articulation surfaces of the pubic and ischial peduncles are beveled medially, triangular and rectangular in distal outline, respectively. The postacetabular process is broad based, longer than the central iliac plate, not set off by a marked angulation in its dorsal border, and narrowing posteriorly rather than having a squared-off distal termination. It is dorsoventrally erect, not dorsomedially rotated as in some other hadrosaurs (*Secernosaurus* and the Aguja saurolophine, UTEP P.37.7.222; Prieto-Márquez and Salinas, 2010). There is a short ridge along the medial side of its dorsal edge, projecting slightly above the dorsal border, just posterior to the posteriormost sacrocaudal rib articulation facet (Fig. 20). In most attributes, the ilium is nearly indistinguishable from that in *Gryposaurus* sp. (YPM-PU 19670, referred to cf. *Kritosaurus* by Horner, 1992).

Pubis.—Parts of both pubes are preserved in TMM 46015-3; the right element is nearly complete, missing the postpubic process and distal parts of the prepubic blade (Fig. 12.2). Only the acetabular border and prepubic neck are preseserved in the left element. The iliac process is triangular in section and mediolaterally expanded, forming a sharp ridge separating the acetabular wall from the prepubic neck. The ischial process is cylindrical, with a triangular articulation surface, not expanded distally, and bearing a rugose lateral protruberance at its junction with the base of the postpubic process. The acetabular wall is coarsely striated circumferentially. Although much of the prepubic blade is missing, part of its anterior distal edge is preserved, sufficient to indicate that the blade is very short and deep. The prepubic neck is only slightly constricted; its maximum ventral concavity is slightly posterior to its maximum dorsal concavity. As preserved, the ratio of the minimum height of the prepubic proximal constriction to the maximum height of the distal blade is 0.65; the ratio of the length of the proximal neck of the prepubis to the total length of the pubis is 0.58 (Fig. 13; both measured in the manner shown by Prieto-Márquez et al., 2006, fig. 7). The very short prepubic blade is unlike that typical of saurolophines, although *Saurolophus* is closest in this regard (Fig. 20; Brown, 1913). Instead, the pubis is most like that in the lambeosaurines, *Parasaurolophus* (Ostrom, 1963) and *Magnapaulia* (Prieto-Márquez et al., 2012), although the prepubic neck is not as constricted as in either.

Remarks.—The morphology of the frontal and maxilla are sufficient to indicate that TMM 46015-2 cannot be assigned to either of the two Javelina hadrosaurs described in the preceding, ?*Gryposaurus alsatei* n. sp. or *Kritosaurus* sp. Some features of the maxilla (weak rostrodorsal process and recessed maxillary foramen) are not typical of saurolophines, although approached to some extent in *Gryposaurus latidens* and *Saurolophus osborni* (Fig. 19). The rostral end of the maxilla in TMM 46015-2 is relatively tall; however, it does not narrow to point anteriorly, and although part of the dorsal process is missing, it would not have been as tall as is typical of lambeosaurines (Fig. 19). The pubis in TMM 46015-2 differs markedly from that in *?G. alsatei*.

Although TMM 46015-2 is somewhat smaller than specimens attributed herein to *?G. alsatei* and *Kritosaurus* sp., these significant differences are not likely a result of ontogenetic variation. For example, participation of the frontals in the base of the narial crest observed in TMM 46015-2 is a condition typical of more mature rather than less mature hadrosaur individuals. Hence, it appears certain that these specimens represent a third hadrosaur taxon in the Javelina Formation. None of the elements preserved in TMM 46015-2 are sufficiently similar to those in other taxa to allow for confident attribution of the specimen.

The separate elements assigned to TMM 46015-2 and 46015-3 exhibit an unusual combination of character states. The form of the ilium is nearly identical to that in *Gryposaurus* sp. (YPM-PU 19670; assigned to cf. *Kritosaurus* by Horner, 1992) and similar to that in *Secernosaurus*. By contrast, the short prepubic process of the pubis bears no resemblance to either, and instead is most like that in lambeosaurines. The maxilla exhibits features atypical of other saurolophines. Hence, it is likely that TMM 46015-2 and -3 represent an unknown taxon. Because the separate elements were not found in articulation, an alternative explanation for this unusual combination of character states is that one or another of the elements included in TMM 46015-2 and -3 may actually pertain to different taxa. This possibility was considered, but is herein regarded as an unlikely one for several reasons: the separate elements were found within a few meters of one another, and on the same stratigraphic level; the remains of hadrosaurs are otherwise very rare in these strata; and the spatial association of an ilium from one taxon for example with the pubes of a different taxon seems highly improbable.

On the basis of its upwardly curved frontals, TMM 46015-2 likely represents a 'solid-crested' saurolophine, perhaps related to *Saurolophus*. The maxilla in TMM 46015-2 is also similar to that in *S. osborni* (Fig. 19; Bell, 2011) although this may be due in part to incomplete preservation of the rostrodorsal process in the latter; the process is substantially larger in *S. angustirostris* Rozhdestvenskii, 1952 (Maryanska and Osmolska, 1981). The short prepubis in TMM 46015-3 is among saurolophines, also closest to that in *Saurolophus*, although much more like that in lambeosaurines (Fig. 12).

Biostratigraphic significance

Although the few fragmentary hadrosaur specimens previously reported from the Javelina Formation had initially been attributed with uncertainty to cf. *Edmontosaurus* sp. (Lawson, 1972; Davies, 1983), the new specimens from Rough Run Amphitheater, Gano Spring, and Paint Gap Hills indicate that *Edmontosaurus* does not occur here. Instead, there are three different hadrosaurs in the Javelina Formation, and their disjunct stratigraphic distribution supports other evidence that these strata span two distinct biostratigraphic intervals (Wick and Lehman, 2013).

Two hadrosaurs are found in the base of the Javelina Formation; one is referable to *Kritosaurus* sp., the other is an indeterminate saurolophine, possibly related to *Saurolophus*. This interval overlies pyroclastic deposits in the uppermost Aguja Formation dated at ca. 72 Ma (Breyer et al., 2005), is below a tuff bed in the middle of the Javelina Formation dated at ca. 69 Ma (Lehman et al., 2006), and is therefore early Maastrichtian ('Edmontonian') in age (Fig. 14).

A different hadrosaur is present in the upper Javelina Formation, described herein as a new species, *?Gryposaurus alsatei*, doubtfully assigned to the genus. These strata lie above the ca. 69 Ma tuff bed and below the Cretaceous–Paleogene boundary (ca. 66 Ma); although poor constraints on the boundary interval here leave uncertain whether this entire time span is represented, it is at least in part late Maastrichtian ('Lancian') in age.

Very few hadrosaurs of Maastrichtian age are known from North America (Fig. 14). In Alberta, the saurolophine *Saurolophus* and the lambeosaurine *Hypacrosaurus* occur in early Maastrichtian strata (Horseshoe Canyon Formation; Eberth et al., 2013). *Edmontosaurus regalis* is found in latest Campanian strata, and the genus must extend through early Maastrichtian time because *Edmontosaurus annectens* is the sole hadrosaur known to have survived into late Maastrichtian ('Lancian') time in Saskatchewan, Montana, Wyoming, and Colorado (Campione and Evans, 2011). *Augustynolophus* is found in late Maastrichtian strata of California (Prieto-Márquez et al., 2014), but only indeterminate hadrosaurs are known from correlative strata in Utah (Difley and Ekdale, 2002) and New Mexico (Williamson, 2000). Although meager, the Javelina specimens are therefore significant in further documenting the biogeography of Maastrichtian hadrosaurs in North America.

Identification of *Kritosaurus* sp. in the lower Javelina Formation supports Wagner's (2001) earlier assessment that *Kritosaurus* cf. *navajovius* is present in these strata and extends the range of *Kritosaurus* into the early Maastrichtian (ca. 72 to 69 Ma). There has long been debate, however, regarding the taxonomic validity of *Kritosaurus*, the stratigraphic provenance of the holotype, and the identity of comparable specimens recovered from the same stratigraphic interval but attributed instead to '*Naashoibitosaurus*.' The holotype and only known specimens of both *Kritosaurus navajovius* and '*Naashoibitosaurus*' *ostromi* were collected in the same area and from the same stratigraphic level in the De-na-zin Member of the Kirtland Formation in New Mexico (late Campanian, ca. 74–73 Ma; Williamson, 2000). Although the holotype of '*N.*' *ostromi* was originally attributed to the overlying Naashoibito Member of the Kirtland Formation (Maastrichtian), this was later shown to be incorrect, and none of the hadrosaur material presently known from that unit is generically determinate (Williamson, 2000). The holotype specimens of *K. navajovius* and '*N.*' *ostromi* are so similar to one another that it seems unlikely they could represent sympatric genera. Indeed, contemporary authorities continue to disagree as to whether they may even belong to the same species (Horner, 1992; Williamson, 2000; Prieto-Márquez, 2014). The Javelina specimens may lend credence to supposition that the two species are synonymous and that the indeterminate hadrosaur found in the Naashoibito Member could well be *Kritosaurus* or a close relative.

The indeterminate saurolophine that also occurs in the lower Javelina Formation is clearly not *Kritosaurus* and exhibits a puzzling combination of character states reminiscent of those in lambeosaurines as well as in *Saurolophus*. It is regarded as likely here that the Javelina saurolophine represents an unknown species related to *Saurolophus*, a possibility that would not be unforeseen given the occurrence of *Saurolophus* and *Augustynolophus* also in Maastrichtian strata. If the Javelina species is a member of the Saurolophini lineage, it would represent an extension into western Texas of the solid-crested saurolophines—a group that is otherwise very widespread from Asia to Alberta (Bell, 2011), as well as California (Prieto-Márquez et al., 2014).

By contrast, the presence of *?Gryposaurus alsatei* n. sp. in the upper part of the Javelina Formation is extraordinary. The new species is clearly a member of Kritosaurini, and if correctly referred to *Gryposaurus*, its occurrence results in a significant range extension for the genus from late Campanian into late Maastrichtian time and persistence of the seemingly primitive *Gryposaurus* lineage throughout most or all of latest Cretaceous time. Regardless of its correct generic affiliation, the species indicates that Kritosaurini survived into Lancian time in western Texas. *?Gryposaurus alsatei* was therefore a contemporary of Edmontosaurus, the typical hadrosaur found in Maastrichtian strata of Alberta, Saskatchewan, Montana, Wyoming, and Colorado. It is significant that none of the three hadrosaurs found in the Javelina Formation is *Edmontosaurus*, the only hadrosaur known to have survived to the end of Cretaceous time in the northern Great Plains.

Conclusions

Rare specimens of hadrosaurian dinosaurs previously reported from the Maastrichtian Javelina Formation of West Texas were attributed tentatively to either *Edmontosaurus* or *Kritosaurus*. Several new specimens recently recovered indicate that three distinct hadrosaurs are present in these strata. Although the new specimens are also fragmentary, they include substantial skull parts and postcranial skeletal elements sufficient to distinguish them.

Two hadrosaurs are found in the lower part of the Javelina Formation. One of these is identified as *Kritosaurus* sp., supporting Wagner's (2001) earlier referral of specimens to this taxon. A new specimen from Gano Spring preserves significant parts of the skull that allow for more confident attribution to the genus; however, some of its features are unique, and some are thought to be diagnostic for either *K. navajovius* or '*Naashoibitosaurus*' *ostromi*. These species occur together in the upper Kirtland Formation in New Mexico, and some authors believe that the two are synonymous. The combination of features in the Gano Spring specimen lends credence to this hypothesis, and so the specific identity of the Javelina *Kritosaurus* remains uncertain. Most of the material previously reported from the lower part of the Javelina Formation appears referable to this species.

A second new specimen from Paint Gap Hills preserves parts sufficient to indicate that it does not pertain to *Kritosaurus* but inadequate to confidently identify or to designate as a new taxon. This specimen is also from the base of the Javelina Formation and suggests that a 'solid-crested' saurolophine also occurs in the lower part of the stratigraphic section. The frontals have upturned processes along the midline similar to those that brace the posterior side of the narial crest in *Saurolophus*. The rostrodorsal process of the maxilla is little developed, and the maxillary foramen opens into a broad trough along the premaxillary suture; these are features more typical of lambeosaurine maxillae. Although the ilium in the Paint Gap specimen is comparable to those in several other saurolophines, the prepubic blade of the pubis is very short and deep, as in lambeosaurines. This perplexing combination of features is difficult to interpret; it is herein surmised that the Paint Gap specimen pertains to an unknown 'solid-crested' saurolophine related to *Saurolophus*.

A third hadrosaur is represented at a bonebed in the uppermost part of the Javelina Formation on Rough Run Creek. Its remains are sufficient to justify recognition as a new taxon, here designated *?Gryposaurus alsatei* n. sp. The form of the dentary, large number of tooth positions, single primary ridge on the tooth crowns, and 'double denticulate' ventrally deflected premaxillary oral margin are among the significant features that indicate *?G. alsatei* is a saurolophine hadrosaurid. The skull roof elements are similar to those in species of *Gryposaurus*, and although no parts of the narial crest are preserved, the bordering elements indicate that *?G. alsatei* was a 'flat-headed' saurolophine and had a subdued narial crest, or may have lacked one entirely. The dorsal process of the quadrate expands above the quadratojugal articulation and would have embayed the infratemporal fenestra. Although the basic shape of the pubis is comparable to that in species of *Gryposaurus*, its proportions are unique. The neck of the prepubis is only slightly constricted, short relative to its entire length, and tall dorsoventrally, while the prepubic blade is proportionally much longer.

Some of the features of the Presa de San Antonio 'muzzle' specimen (IGM 6685) from the Cerro del Pueblo Formation in Mexico, referred to *Kritosaurus* sp. (Kirkland et al., 2006; Prieto-Márquez and Serrano Brañas, 2012; Prieto-Márquez, 2014) are much like those in *?Gryposaurus alsatei* n. sp. The only elements preserved in that specimen (anterior ends of premaxillae, predentary, and dentaries) are compatible with those in *?G. alsatei*, and in particular the marked deflection in the lateral border of the premaxilla, and its large conical denticles, are shared distinctive features in *?G. alsatei*. The Cerro del Pueblo Formation in Coahuila was deposited contemporaneously with the upper Aguja Formation in Texas, and it would not be surprising if the hadrosaurs in these areas were similar.

The doubtful referral of *?G. alsatei* n. sp. to *Gryposaurus* constitutes a significant, and perhaps unlikely, temporal range extension for the genus into late Maastrichtian time. It is surprising that *?G. alsatei*, a Maastrichtian hadrosaur, should bear such strong similarity to species of *Gryposaurus*, otherwise known from Campanian strata. Although future recovery of other parts of the skull or skeleton not preserved in the present specimens may reveal that *?G. alsatei* differs more considerably from *Gryposaurus*, it appears that this long-lived lineage of hadrosaurs persisted nearly, if not entirely, to the end of Cretaceous time in West Texas. It is significant that none of the hadrosaurs thus far recovered from Maastrichtian strata in Texas are referable to the well-known taxa found in correlative Edmontonian and Lancian strata of the northern Great Plains. This strangely disjunct distribution has also been recognized in other contemporaneous large herbivorous dinosaurs and reinforces conjecture that many of these animals were much more provincial than large mammalian herbivores (Lehman, 2001).

Because the narial crest is such a hallmark of hadrosaurs, it is also puzzling that the members of the group that survived to the end of Cretaceous time in North America represent lineages that either lost the narial crest or never possessed one. *Edmontosaurus* was the sole hadrosaur to survive into late

Maastrichtian time in the northern Great Plains (e.g., Campione and Evans, 2011), and *?Gryposaurus alsatei* n. sp. was the latest Cretaceous hadrosaur in Texas. Neither possessed the ornate narial crest that characterized many Campanian hadrosaurs. The same regression to less elaborate skull morphology characterized ceratopsids, the other large terrestrial herbivores that survived to the end of Cretaceous time. Collectively, the late Maastrichtian representatives of dinosaur herbivore lineages may have been less specialized 'generalists' than their more ornate predecessors (Lehman, 2001).

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Appendix

Character state scores for ?*Gryposaurus alsatei* n. sp. using 265 characters given by Prieto-Márquez (2014).

1???1312?0	1??112????	?????11201	1111011121	?111?????2
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