A New Species of Saurolophine Hadrosaurid Dinosaur from the Late Cretaceous of the Pacific Coast of North America

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A new species of saurolophine hadrosaurid dinosaur from the Late Cretaceous of the Pacific coast of North America

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We describe and re-evaluate the systematics of specimens from the Maastrichtian Moreno Formation of California (western USA) as a new species of *Saurolophus*, the only known genus of hadrosaurid dinosaur widespread in Asia and North America. Recognition of this new species adds substantially to the record of the taxonomic diversity of these animals west of the Rocky Mountains. The new species, *Saurolophus morrisi*, is diagnosed by the possession of a postorbital having ornamentation in form of wide oblique groove on jugal process. Placement of this new species in *Saurolophus* considerably expands the distribution of this genus, although this referral is arbitrary since phylogenetic analysis places the new species outside of the clade formed by *Saurolophus osborni* and *Saurolophus angustirostris*. However, recognition of a new, endemic Californian hadrosaurid, especially one so closely related to both Asian and North American species, may have implications for future studies of both the internal biogeography of Western North America, and the history of exchange with Asia.

Key words: Dinosauria, Hadrosauridae, Saurolophinae, evolution, phylogenetics, Cretaceous, North America.

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Introduction

Hadrosaurid ornithopods were among the most diverse and abundant dinosaurian clades during the Late Cretaceous of Eurasia, the Americas, and Antarctica (Horner et al. 2004). Two major clades of hadrosaurids are recognized, the hollow-crested Lambeosaurinae and the non-crested/solid-crested Saurolophinae (Prieto-Márquez 2010b). So far, the North American hadrosaurid fossil record has provided the greatest diversity of saurolophines (Lund and Gates 2006; Prieto-Márquez 2010a). The only saurolophine (and hadrosaurid) genera recorded in more than one continental landmass is *Saurolophus*, found in the Maastrichtian of North America and Asia. This hadrosaurid is notorious for possessing a rod-like median crest that projects posterodorsally over the skull (Brown 1912). The fossil bones of the type species, *S. osborni*, have been recovered from Early Maastrichtian strata of the Horseshoe Canyon of southern Canada (Brown 1912, 1913; Bell 2010). A second species, *S. angustirostris*, was erected by Rozhdestvensky in 1952 upon materials collected from the Early Maastrichtian Nemegt Formation of Mongolia.

Despite the widespread distribution of *Saurolophus*, the species *S. osborni* is among the rarest hadrosaurids, with only three large specimens known (AMNH 5220, the type skeleton; AMNH 5221, the paratype; and CMN 8796, referred partial skull; Bell 2010), and possibly a juvenile braincase (ROM WL-112; Prieto-Márquez, personal observations). In contrast, the Asian species, *S. angustirostris*, is known from abundant, well-preserved cranial and postcranial materials that include ontogenetic series ranging from juvenile to large adult exemplars (Rozhdestvensky 1957, 1965; Maryańska and Osmólska 1981, 1984; Bell 2011).

Morris (1973) referred three partial hadrosaurid skeletons from the Maastrichtian Moreno Formation of central California (western USA) to cf. *Saurolophus* sp. Recently, however, Bell and Evans (2010) provided a detailed description of the LACM/CIT 2852 skull. These authors rejected assignment

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of this specimen to *Saurolophus*, and argued that there was no clear basis to differentiate them from *Edmontosaurus*. They suggested that the greatest possible taxonomic resolution for the specimen was "Hadrosaurinae" (Saurolophinae) indeterminate.

Here, an alternative interpretation of LACM/CIT 2760 and 2852, supporting the original referral of Morris (1973), is presented. Specifically, we provide anatomical evidence for erecting a new species of *Saurolophus* for the Moreno Formation specimens. In doing so, we describe the cranial and appendicular anatomy of LACM/CIT 2760 and the appendicular skeleton of LACM/CIT 2852 (thus supplementing Bell and Evans' 2010 description), as well as present the results of cladistic analyses that integrate, for the first time, the character data available for those two specimens.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CIT, California Institute of Technology, Pasadena, USA (specimens currently housed at the LACM); CMN, Canadian Museum of Nature, Ottawa, Canada; FMNH, The Field Museum, Chicago, USA; LACM, Natural History Museum of Los Angeles County, Los Angeles, USA; MPC, Mongolian Paleontological Center, Ulaan Bataar, Mongolia; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ROM, Royal Ontario Museum, Toronto, Canada; TMP, Royal Tyrrell Museum of Paleontology, Drumheller, Canada; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Systematic paleontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Ornithopoda Marsh, 1881

Hadrosauridae Cope, 1870

Saurolophinae Brown, 1914 (sensu Prieto-Márquez, 2010b)

Genus *Saurolophus* Brown, 1912

Type species: *Saurolophus osborni* Brown, 1912. Unit 4 of the Horseshow Canyon Formation at Tolman Bridge, Alberta, Canada; lower Maastrichtian (Bell 2010).

Emended diagnosis.—Nasals elongated posterodorsally above skull roof (posterior to a point dorsal to squamosals in adults), forming solid, rod-like median crest with contributions from prefrontals and frontals; circumnarial structure extending posterodorsally over entire length of skull roof (in adults) on dorsal surface of nasals (convergent in *Brachylophosaurus canadensis*); tripartite frontal consisting of main body that roofs anterior braincase, an anteroventrally sloping shelf (convergent in some lambeosaurine hadrosaurids), and finger-shaped, posterodorsally-directed ramus that buttresses the underside of nasal crest; prefrontal with posterodorsally elongate process that supports and contributes laterally to the cranial crest; posterodorsal processes of frontal and prefrontal united to form dorsal promontorium that buttresses underside of cranial crest (convergent in some lambeosaurines); posterior deepening and steep down-warping of parietal crest in adults (convergent in Lambeosaurinae); two supraorbital elements present between prefrontal and postorbital; and parietal excluded from posterodorsal margin of occiput by intersquamosal articulation (convergent in *Maiasaura peeblesorum*, *Shantungosaurus giganteus*, and numerous lambeosaurines) (modified from Wagner 2001; Bell 2010, 2011).

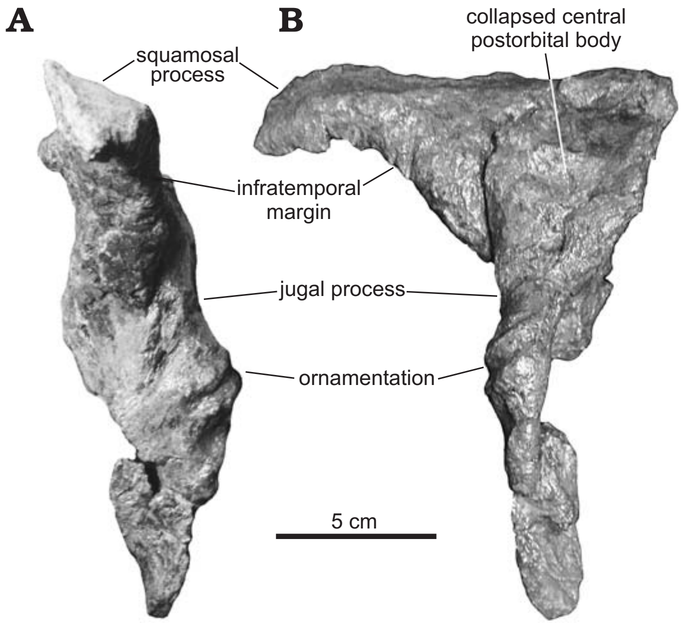

Fig. 1. Partial right postorbital of a hadrosaurid dinosaur *Saurolophus morrisi* sp. nov. (LACM/CIT 2852), lower Maastrichtian Moreno Formation of San Benito County, California, USA, showing the autapomorphic ornamentation of its jugal process. Posterior (**A**) and right lateral (**B**) views.

Remarks.—Bell (2011) considers the absence of frontal contribution to the orbital margin diagnostic for the genus *Saurolophus*. However, this condition is also present in *Prosaurolophus maximus*, where the prefrontal and postorbital show an extensive articulation that excludes the frontal from the orbital rim (e.g., AMNH 5386). This character is a synapomorphy (see below) for *Prosaurolophus* and *Saurolophus* within the context of Saurolophinae. This condition might also be present in *Anasazisaurus horneri* (Lucas et al. 2006), and, outside Saurolophinae, it is present in all lambeosaurines except *Aralosaurus tuberiferus* (Godefroit et al. 2004).

The postorbital in both specimens of *S. morrisi* is T-shaped in lateral view (Fig. 1), lacking the strong angulation between the squamosal and prefrontal processes seen in *Saurolophus osborni* and *S. angustirostris* (Bell 2011). The T-shaped postorbital is widespread among hadrosaurids and apparently plesiomorphic, with genera like *Gryposaurus*, *Edmontosaurus*, or *Brachylophosaurus* showing T-shaped or nearly T-shaped profiles with dorsal surfaces ranging from horizontal (e.g., *B. canadensis* TMP 90.104.1) to gently concave (e.g., *E. regalis* FMNH P15004). The postorbital of small *S. angustirostris* (e.g., ZPAL MgD-159) is similarly orthogonal, but larger (i.e., over 450–500 mm in skull length) specimens of *S. angustirostris* (e.g., MPC-D 100/706) and all known *S. osborni* (all presumably adult) display a Y-shaped postorbital with a deeply depressed dorsal margin (Bell 2011). Although LACM/CIT 2760 is relatively small, at approximately 1,000 mm in skull length LACM/CIT 2852 would be expected to display a Y-shaped postorbital if the contour of the dorsal margin of this element followed the ontogenetic trajectory documented in *S. angustirostris*. This morphology either developed at larger body size in *S. morrisi* or is absent; in either case it characterizes the more exclusive clade of *S. osborni* + *S. angustirostris*, and must be removed from the generic diagnosis.

The Y-shaped postorbital may be morphogenetically linked to the dorsal inflection of the orbital margin of the prefrontal, postorbital, and supraorbitals that partially conceals the base of the crest laterally in *Saurolophus osborni* and *S. angustirostris*. Practically, pronounced inflection of the orbital margin would seem to necessitate dorsal elevation of the prefrontal process of the postorbital. The degree to which this inflection is present is not clear in the holotype of *S. morrisi*, but the poorly preserved and incompletely prepared LACM/CIT 2760 shows minimal arching or flaring of the orbital margin. We therefore tentatively remove this character from the diagnosis of *Saurolophus* as well; it too diagnoses *S. osborni* + *S. angustirostris*.

Stratigraphic and geographic range.—The genus *Saurolophus* has been recorded in lower Maastrichtian strata of North America (Bell 2010; this paper) and ?upper Campanian–lower Maastrichtian strata of Asia (Bell 2011).

Saurolophus morrisi sp. nov.

Figs. 1–6, 9B.

Etymology: Named for paleontologist William J. Morris (1923–2000), in recognition of his substantial contributions to our understanding of the functional morphology and evolutionary history of the hadrosaurid dinosaurs of the Pacific coast and Western Interior of North America.

Holotype: LACM/CIT 2852, a skeleton including fragment of left and most of right premaxilla, both maxillae, right jugal, right quadratojugal, partial right quadrate, right postorbital, paroccipital process of right exoccipital, predentary, right- and posterior fragment of left dentary, partial surangular, angular, and splenial, various cervical, dorsal, and caudal vertebrae, partial right scapula, both ulnae, metatarsal III, and various manual and pedal elements.

Type locality: LACM locality CIT 357, Tumey Hills, San Benito County, California, USA (see Bell and Evans 2010 for further details).

Type horizon: Moreno Formation, lower Maastrichtian.

Referred material.—LACM/CIT 2760, LACM locality CIT 336, 36°40’21”N, 120°42’42”E, Panoche Hills, Fresno County, California, USA; Moreno Formation, lower Maastrichtian; fragmentary skull and postcrania consisting of posterior region of skull roof (including partial frontals, parietal, squamosals, prootics, supraoccipital, and fragmentary exoccipitals), possible conjoined distal nasals, both maxillae, nearly complete right quadrate, left- and posterior half of right dentary, partial surangular and angular, various isolated dentary teeth, left coracoid, left scapula missing distal end, left humerus, distal end of right humerus, proximal regions of both ulnae and radii, fragments of both femora, proximal end of the left tibia, left metatarsals III, and various fragmentary manual and pedal elements. These remains appear to represent a single individual approximately 30% smaller than the holotype.

Diagnosis.—Hadrosaurid conforming to diagnosis of *Saurolophus* (above)¸ with postorbital having ornamentation in form of wide oblique groove on jugal process (Fig. 1) (after Bell and Evans 2010).

Remarks.—In addition to the autapomorphy noted above, *Saurolophus morrisi* differs from *S. osborni* and *S. angustirostris* in two more ambiguous characters. The external narial foramen of *Prosaurolophus* and *Saurolophus* is elongate and slit-like, and forms a tightly constricted, almost V-shaped rostroventral terminus. While there is clear evidence that the acute anterior end of the foramen in *S. morrisi* also possesses a V-shaped rostral margin of the narial foramen, it is not clear that the aperture was in any way slit-like. Taken at face value, the premaxilla and maxilla of LACM/CIT 2852 as preserved suggest a much deeper opening. This may be partly due to diagenetic deformation of the specimen, but it is not clear how any deformation could geometrically account for all of the apparent expansion of the boney naris. We concur with Bell and Evans (2010) that this likely represents the original morphology to some extent. A broad narial foramen is likely ancestral for hadrosaurids, but its absence in *Prosaurolophus* and lack of information about *Kerberosaurus* renders interpretation of the polarity of this character in *S. morrisi* equivocal, and therefore, we have omitted it from the formal diagnosis.

Numerous characters in LACM/CIT 2760, discussed in more detail below, evidence its saurolophine affinities. In addition, when considered all together, these attributes form a combination of characters that support referral of this specimen to *Saurolophus*. Such character combination includes frontal doming (at least in subadults), long and extensive ectocranial surface of the frontal, substantial anteroventral downwarping of the parietal sagittal crest, intersquamosal joint that excludes the parietal from the occiput, long exoccipital roof above the foramen magnum, subrectangular and anteriorly oriented supratemporal fenestra, relatively high and extensive posterior surface of the squamosal, anteroposteriorly broad anterodorsal region of the maxilla, nearly straight posterior margin of the quadrate, quadratojugal notch of the quadrate being extremely wide and positioned ventral to the mid-length of the quadrate, broad proximal constriction of the scapula, relatively short and robust ulna, dentary with relatively low angle of ventral deflection, and dentition with very reduced or lack of marginal denticles.

Stratigraphic and geographic range.—*S. morrisi* occurs in lower Maastrichtian strata of central-western California, western North America.

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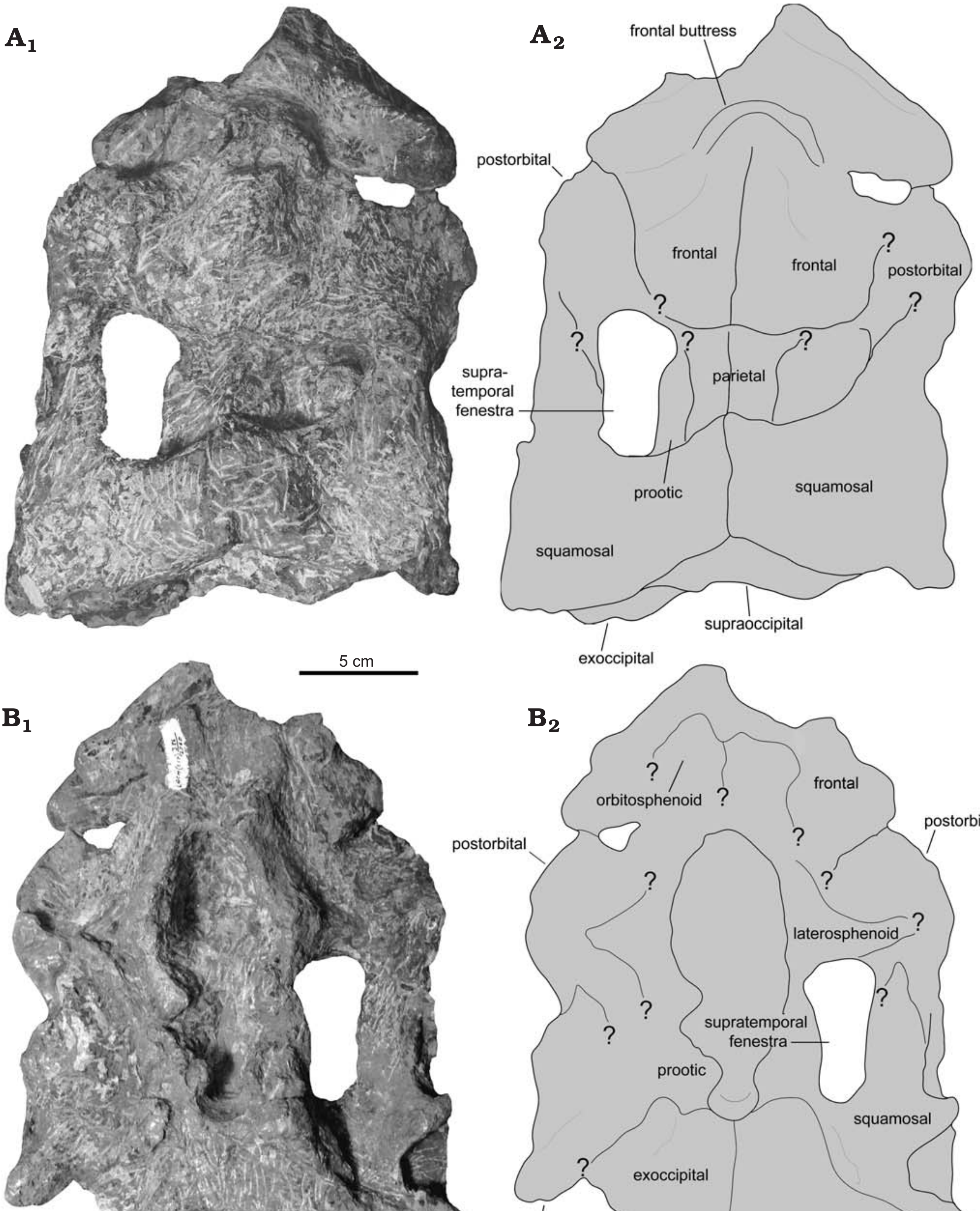

Fig. 2. Partial skull roof of a hadrosaurid dinosaur *Saurolophus morrisi* sp. nov. (LACM/CIT 2760, a subadult), lower Maastrichtian Moreno Formation of Panoche Hills, Fresno County, California, USA. Dorsal (**A**) and ventral (**B**) views. Photographs (A_1, B_1) and interpretative drawings (A_2, B_2).

Description

Cranial morphology

Neurocranium: The frontal forms the central region of the skull roof, anterior to the supratemporal fenestrae (Fig. 2A). The ectocranial surface is extensive, being at least more than 80% longer than it is wide, as it occurs in other saurolophines (Prieto-Márquez 2010b). The frontals of LACM/CIT 2760 exhibit an anterior, crescentic, and elevated sagittal structure that extends dorsal to the plane of the skull roof (Figs. $2A_1$, 3). The morphology of this structure is consistent with the abraded base of the posterodorsal process of the frontals that underlies the nasal in the crest of *Saurolophus osborni* and *S. angustirostris* (Bell 2010, 2011). We can find no other explanation for this structure. The base of the crest seems somewhat less robust that that in the latter species; a more robust posterodorsal process, and possibly a larger crest, may be an apomorphy of *Saurolophus osborni* and *S. angustirostris*. However, given the poor preservation of the specimen, we are reluctant to include this in the diagnosis. Notably, posterior to the buttress the ectocranial surface of the frontals forms a dome-like convexity centered around the sagittal plane of the skull. Although this upward doming of the frontals is characteristic of Lambeosaurinae (Horner et al. 2004), it is also present in juveniles of *Saurolophus angustirostris* (Bell 2011).

The hourglass-shaped parietal contributes to the medial and anterior margins of the supratemporal fenestra. As in all non-lambeosaurine hadrosauroids (Prieto-Márquez 2008: fig. F.30), the supratemporal fenstra of LACM/CIT 2760 (deformed on the right side, but well preserved on the left half of the skull roof) is subrectangular and its long axis is anteroposteriorly oriented (Fig. 2A). Ventrally, the parietal articulates with the laterosphenoid, prootic, opisthotic-exoccipital, and supraoccipital. Its anterior region is mediolaterally expanded into two anterolateral processes, which meet the frontals anteriorly and likely the postorbitals laterally. Although minimized by dorsoventral crashing of the specimen, in lateral view the sagittal crest displays a concave profile and slopes anteroventrally forming an obtuse angle with the frontals, as in lambeosaurines (Horner et al. 2004) and species of *Saurolophus* (Bell 2010; Prieto-Márquez 2010b).

At the anteroventral, median region of the braincase lays the orbitosphenoid (Fig. 2B). This bone is slightly convex ventrally and its external surface faces ventrolaterally. The median, posteroventral margin of the orbitosphenoid forms the dorsal border of the foramen for the optic nerve.

The laterosphenoid contributes to the laterodorsal wall of the braincase, between the orbitosphenoid and the prootic (Fig. 2B). The posterodorsal region is concave anterodorsally and extends posteriorly to meet the prootic. The dorsal margin of the posterodorsal region of the laterosphenoid probably contacts the parietal. The concave surface of this region of the latersophenoid is continuous anterolaterally with the postorbital process. This process projects perpendicularly from the long axis of the skull, becoming anteroposteriorly narrower laterally.

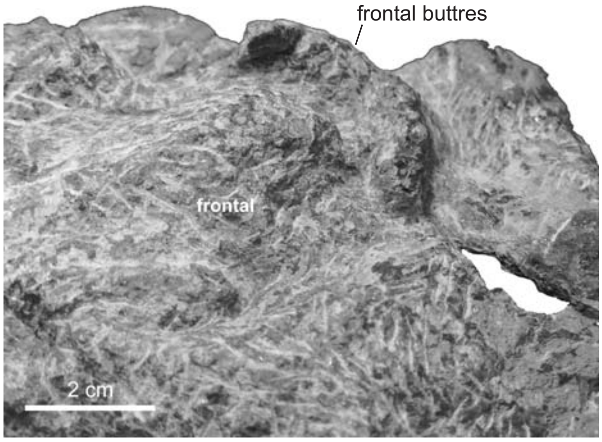

Fig. 3. Right posterolateral view of the frontal of a hadrosaurid dinosaur *Saurolophus morrisi* sp. nov. (LACM/CIT 2760, a subadult), lower Maastrichtian Moreno Formation of Panoche Hills, Fresno County, California, USA, showing the eroded remnant of the buttressing base of the posterodorsal frontal ramus.

The prootic occupies a median position in the lateral wall of the braincase below the parietal (Fig. 2). It probably joins the laterosphenoid anteriorly, the opistothic-exoccipital posteriorly, and the parietal dorsally.

The opisthotic-exoccipital complex contributes to the posterolateral wall of the braincase, lateral and dorsal to the foramen magnum. The posteromedial region of the opistothic-exoccipal that would give raise to the proximal portion of the paroccipital process is only partially preserved, attaching to the posterior surface of the squamosal. The dorsomedian region of the opistothic-exoccipital underlies the supraoccipital. Notably, the exoccipital roof above the foramen magnum is anteroposteriorly long (Fig. 2B), a derived condition shared with *Kritosaurus navajovius*, *Edmontosaurus* spp., *Saurolophus* spp., *Prosaurolophus maximus*, the Sabinas hadrosaurine described by Kirkland et al. (2006), and *Shantungosaurus giganteus* (Prieto-Marquez 2008).

The supraoccipital occupies a median position in the braincase (Fig. 1A, B), inset on the posterodorsal region of the occiput between the squamosals and the opistothic-exoccipitals. Little details of its morphology may be appreciated in LACM/CIT 2760, aside from the fact that the ventral surface of the posterior region of the supraoccipital is resting on the dorsal surface of the opisthotic-exoccipital shelf.

Facial skeleton.—The maxilla displays a triangular lateral profile (Fig. 4A, B). The anterodorsal region of the maxilla is anteroposteriorly very broad, unlike the narrower and triangular morphology typically present in lambeosaurines (e.g., *Hypacrosaurus altispinus* ROM 702). The articular surface for the jugal is anteroposteriorly extensive and the geometry of its ventral margin appears to have accommodated a similarly long and asymmetrical rostral process of the jugal; such jugal morphology is found in saurolophines except Brachylophosaurini (sensu Gates et al. 2011). The summit of the antero-

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dorsal region of the maxilla is positioned slightly anterior to the mid-length of the bone. Given the latter condition, the base of the dorsal process (not preserved) was probably located approximately above the level of the mid-length of the maxilla. The ectopterygoid shelf is horizontally oriented and comprises about 40% of the total length of the maxilla. The lateral emargination of the shelf is dorsoventrally thick and gradually becomes slightly shallower anteriorly. Its ventral margin is very prominent. Medial and dorsal to the ectopterygoid shelf is a relatively large palatine ridge, which extends over the dorsal margin of the medial surface of the posterior third of the maxilla. Posterior to the palatine ridge, near the posterodorsal end of the maxilla, lays the finger-like pterygoid process. This process is mediolaterally compressed and relatively deep, missing the distal end in LACM/CIT 2760.

Only the dorsal region of the main body of the postorbital is preserved, articulated in the skull roof of LACM/CIT 2760 (Fig. 2). The main postorbital body is mediolaterally compressed and triangular. The abraded orbital and infratemporal margins of the postorbital converge ventrally forming an angle of 120° to give rise to the jugal ramus.

The dorsal surface of the squamosal, at the posterodorsal region of the skull roof, is relatively extensive (Fig. 2A). The medial rami are anteroposteriorly broad and meet medially to exclude the parietal from the sagittal plane of the skull; this condition is typically found in lambeosaurines, as well as in saurolophines *Maiasaura peeblesorum*, *Saurolophus angustirostris* (Bell 2011), and *Shantungosaurus giganteus* (Prieto-Márquez 2010b). The posterior surfaces of the squamosals of LACM/CIT 2760 substantially increase in depth toward the sagittal plane of the skull, showing steep dorsal margins that converge mediodorsally. Notwithstanding the dorsoventral postdepositional compression experienced by the specimen, the posterior surface of the squamosal is relatively high. This condition is typically found in lambeosaurinaes (Horner et al. 2004) and is also present in *Saurolophus* spp. (Prieto-Márquez 2010b). On the lateral side of the squamosal, the quadrate cotylus is shallow and anteroposteriorly wide. Only the wedge-shaped proximal extent of the precotyloid process is preserved.

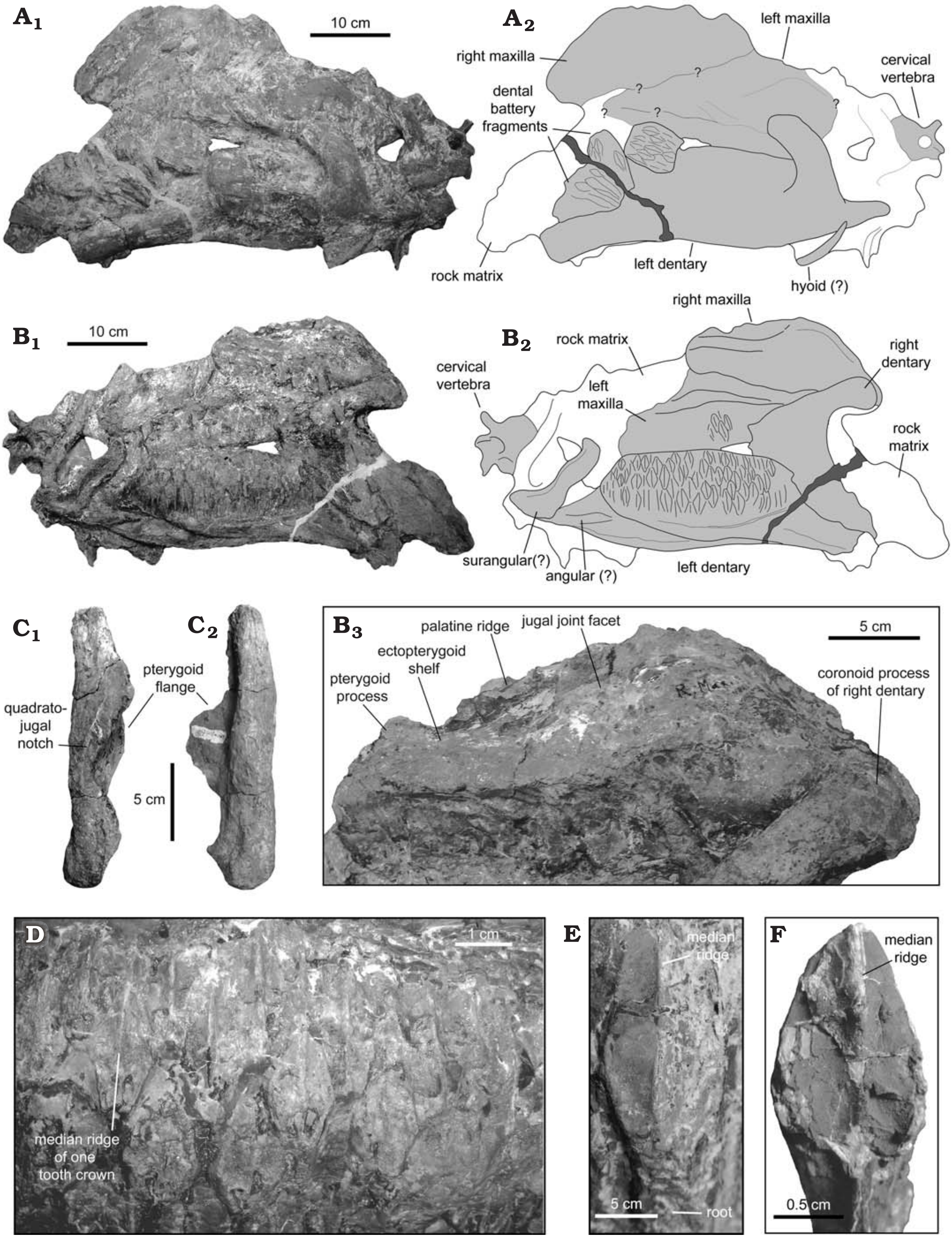
The quadrate is missing the proximal end and most of the pterygoid flange (Fig. 4C). The posterior margin of the bone is relatively straight, displaying only a very gently curvature proximally. Straight to slightly curved quadrates are typically present in saurolophines, in contrast to the strongly curved lambeosaurine quadrates (Prieto-Márquez 2008: fig. D.76). The quadratojugal notch is very wide; its dorsal margin is slightly longer than the ventral margin, and forms a 23° angle with the posterior margin of the quadrate. In saurolophines this angle is always less than 45° (in most cases even less than 30°), whereas in lambeosaurines it is greater than 45° (Prieto-Márquez 2008: fig. D.78). The mid-length of the notch is located well below the mid-length of the quadrate; this condition is also commonly seen in saurolophines, whereas lambeosaurines typically display a quadratojugal notch centered around the mid-length of the quadrate (Prieto-Márquez 2008: fig. D.77).

Mandible: The left dentary is 350 mm in length. The dorsal margin of the edentulous region and the medial surface of the coronoid process are concealed by rock matrix (Fig. 4A, B_1, B_2). The anterior region of the ventral margin of the dentary is ventrally deflected forming a 12° angle (in medial view) with the tooth row (this angle increases to 19° when measured in lateral view). In species of *Saurolophus* the angle of deflection ranges from 10° to 15° in adults (measured in medial view; see Prieto-Márquez 2008: fig. C.17). However, in subadults this angle can be as hight as 19°, as it occurs in the *S. angustirostris* specimen ZPAL MgD I-159 (measured laterally). In LACM/CIT 2760 the ventral deflection originates near the rostral end of the dentary. Specifically, the ratio between the distance from the posterior margin of the coronoid process to the origin of the deflection and the distance between the posterior margin of the coronoid and the rostral-most tooth position (Prieto-Márquez 2008: fig. C.20) is 0.82. The lingual projection of the symphyseal process is moderate, as in most hadrosaurids except *Tsintaosaurus* and *Pararhabdodon* (Prieto-Márquez and Wagner 2009). The bulging of the ventral margin of the dentary is very well developed in LACM/CIT 2760 and it is located rostral to the base of the coronoid process, a condition shared by species of *Edmontosaurus* and *Saurolophus* (Prieto-Márquez 2010b). The coronoid process is large in comparison with the dentary ramus and its long axis is strongly tilted rostrally, forming a 69° angle with the tooth row. A minimum of 32 tooth families are preserved. There are at least four tooth crowns arranged dorsoventrally within a single alveolus at the middle of the dental battery. The occlusal plane is not exposed.

An elongate strap of bone, oriented anterodorsally and found adjacent to the posterior end of the dentary, may represent part of the anterior ascending flange of the surangular (Fig. 4B_1, B_2). Likewise, a small finger-like bony fragment lies above the ventral margin of the posterior region of the medial side of the dentary. This element is probably part of the left angular (Fig. 4B_1, B_2).

Dentition: The apicobasal height/mediodistal width ratio of the diamond-shaped crowns (Fig. 4D–F) is relatively low, ranging from 2.3 to slightly over 2.4. These values are only slightly higher than the height/width ratios found in *Gryposaurus latidens* (Horner 1992; Prieto-Márquez 2010c) and a large dentary referable to *Saurolophus* cf. *angustirostris* (ZPAL MgD-I 162). The enameled lingual sides of tooth

Fig. 4. Facial and mandibular elements of a hadrosaurid dinosaur *Saurolophus morrisi* sp. nov. (LACM/CIT 2760, a subadult), lower Maastrichtian Moreno Formation of Panoche Hills, Fresno County, California, USA. **A**. Partially articulated maxillae and dentaries in lateral view. Photograph (A_1), interpretative drawing (A_2). **B**. Partially articulated maxillae and dentaries in medial view. Photograph (B_1), interpretative drawing (B_2), photograph of the right maxilla in lateral view (B_3). **C**. Right quadrate in lateral (C_1) and medial (C_2) views. **D**. Dentary teeth of the posterior region of the dental battery in lingual view. **E**. Lingual view of a dentary teeth. **F**. Isolated dentary tooth crown in lingual view. →



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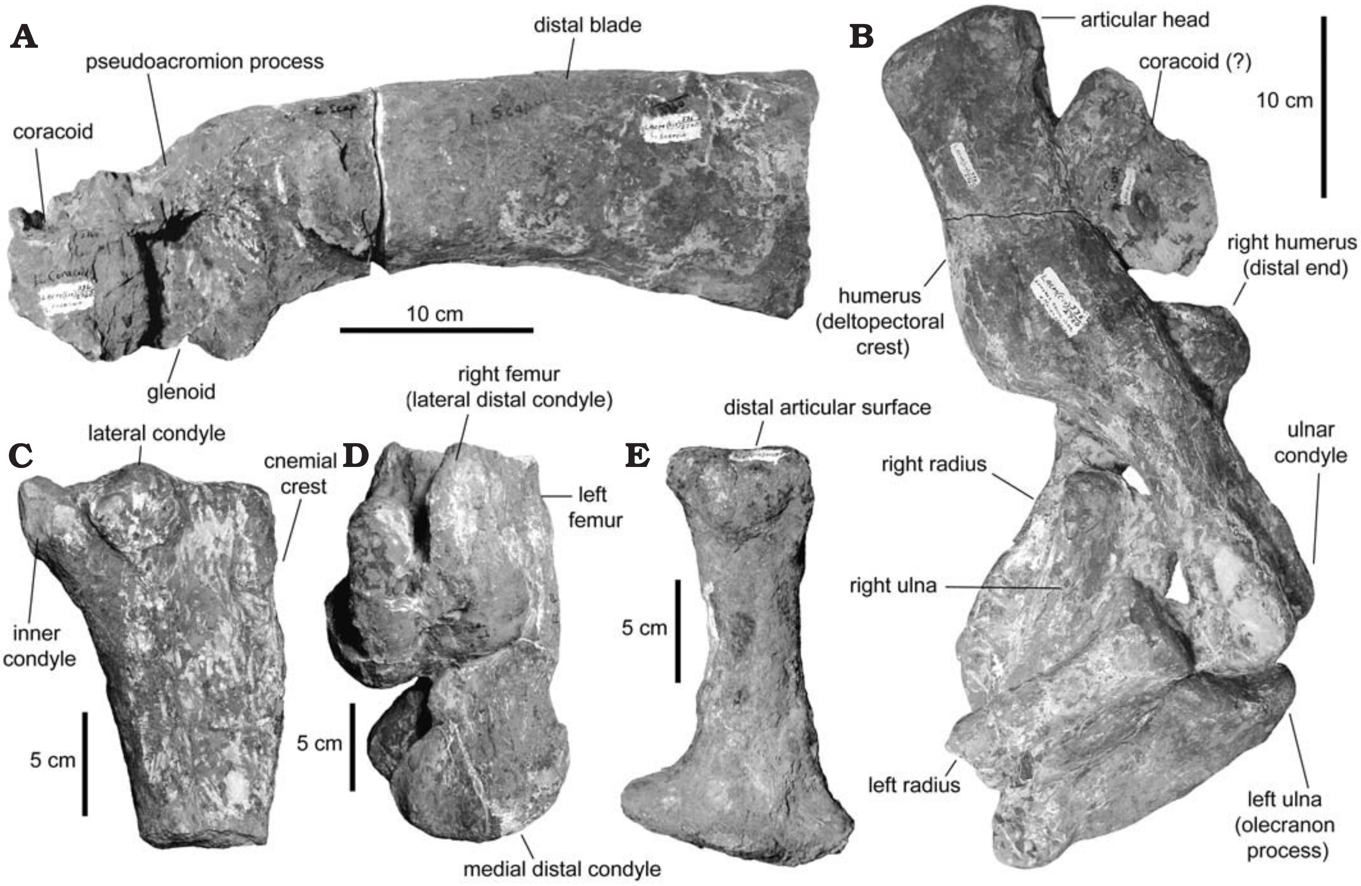

Fig. 5. Appendicular elements of a hadrosaurid dinosaur *Saurolophus morrisi* sp. nov. (LACM/CIT 2760, a subadult), lower Maastrichtian Moreno Formation of Panoche Hills, Fresno County, California, USA. **A**. Partial left scapula and coracoid in lateral view. **B**. Partially articulated forelimb elements. **C**. Proximal segment of right tibia in lateral view. **D**. Distal fragments of femora. **E**. Right metatarsal III in dorsal view.

crowns have a single large and prominent median ridge. This ridge is straight in most teeth and sinuous in a few tooth crowns. Marginal denticles are either very reduced or absent; poor preservation of the specimen does not allow to discriminate between these two possibilities. Notably, all these dental attributes are also present in the dentary teeth of LACM/CIT 2852 (Bell and Evans 2010). In addition, the reduced or absent denticulation is a condition shared with *Saurolophus* spp. (e.g., AMNH 5221 and ZPAL MgD-I 162) and *Edmontosaurus* spp. (e.g., CMN 2289).

Maxillary tooth crowns are almost entirely concealed by matrix. They appear to have a single straight and median ridge, and height/width proportions similar to those of the taller dentary crowns.

Appendicular anatomy

Pectoral girdle: The available coracoids are so poorly preserved and severely eroded that no anatomical details can be discerned (Fig. 5A, B), except for its medially concave plate-like morphology that is expanded posteriorly to form the glenoid and scapular articular facets, and the subtriangular ventral process.

The scapula shows a wide proximal constriction in proportion to the dorsoventral breadth of the distal blade (Figs. 5A, 6A). Scapulae with relatively wide proximal constrictions are characteristic of saurolophine hadrosaurids, unlike the proportionately narrower constrictions present in lambeosaurines (Prieto-Márquez 2008: fig. H.11). The deltoid ridge is prominent and bounds dorsally a moderately deep deltoid fossa. The pseudoacromion process forms a narrow ledge at the proximodorsal region of the scapula and it is nearly horizontally oriented, a synapomorphy of saurolophines (Prieto-Márquez 2010b). The dorsal margin displays a gentle convex lateral profile and diverges gradually from the ventral margin toward the distal end of the blade.

Forelimb: The humerus (Fig. 5B) is moderately elongate in overall proportions, with a length/width (across the proximolateral margin) ratio of 4.8. The deltopectoral crest comprises slightly more than half of the total length of the humerus. Its laterodistal corner is prominent and its maximum breadth is 1.91 times the minimum diameter of the humeral shaft. Such expansion of the deltopectoral crest is comparable to the greater breadth ratios recorded in saurolophine hadrosaurids and lower than those observed in the more expanded crests of lambeosaurines (Prieto-Márquez 2008: fig. H.16).

The ulna is robust and moderately elongate (Figs. 5B, 6B). Its length/width (dorsoventrally at mid-length) ratio is 8.9. Among hadrosaurids, that value is relatively low and compa-

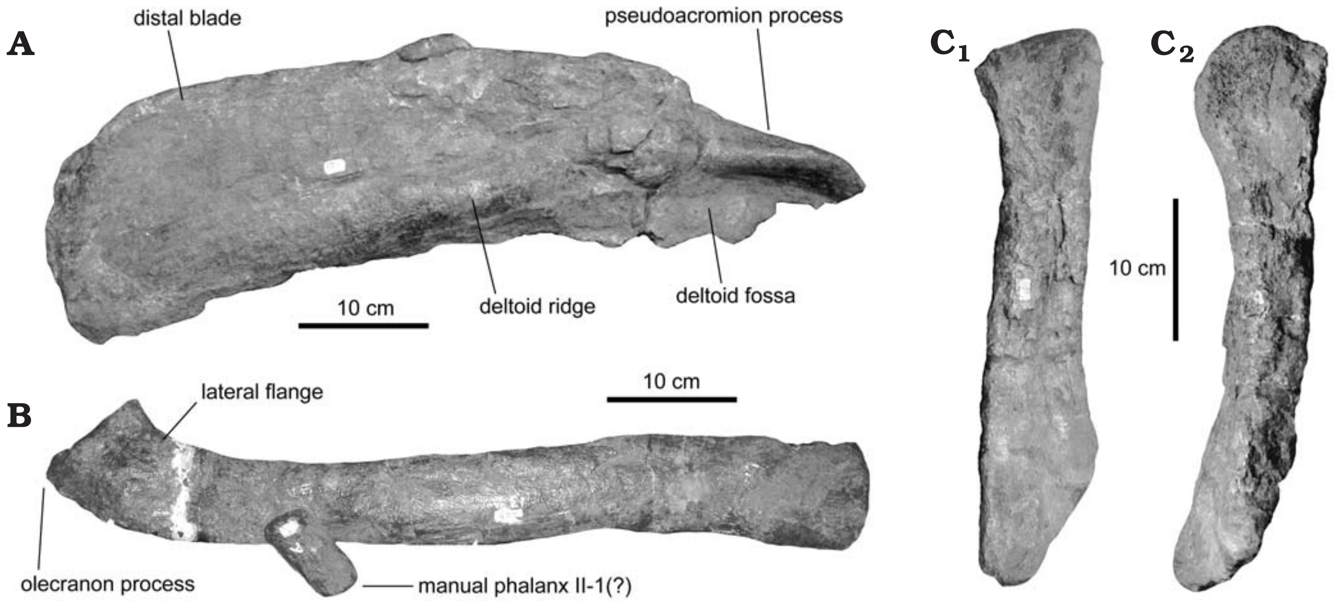

Fig. 6. Appendicular elements of a hadrosaurid dinosaur *Saurolophus morrisi* sp. nov. (LACM/CIT 2852), lower Maastrichtian Moreno Formation of San Benito County, California, USA. **A**. Partial right scapula in lateral view. **B**. Right ulna in lateral view and possible manual phalanx II-1 in dorsal view. **C**. Right metatarsal III in dorsal (C_1) and lateral (C_2) views.

rable to the low ratios recorded in *Saurolophus osborni* (e.g., 8.7 in AMNH 5220) and *S. angustirostris* (e.g., 7.8 in MPC-D 100/706); in all other hadrosaurids, except *Gryposaurus latidens* (e.g., AMNH 478) and *Parasaurolophus walkeri* (e.g., ROM 768) the ulna is more than 9 times long than it is deep at mid-length (Prieto-Márquez 2008: fig. H.19). The olecranon process is massively constructed and dorsoventrally compressed. The lateral and medial flanges are relatively thick.

The radius (Fig. 5B) is subcylindrical and displays an expanded cup-shaped proximal end. The proximal surface is slightly more expanded mediolaterally than dorsoventrally. The shaft of the radius gently becomes deeper towards its distal end, but less so than the proximal end.

The manus is represented by a possible phalanx II-1 (Fig. 6B). This element is dorsoventrally compressed and it is slightly wider proximally than distally, with lateral and medial dorsal margins that are nearly parallel to each other. The phalanx is 2.2 times longer than it is mediolaterally wide at mid-length.

Hindlimb: Only the distal segments of both femora are preserved (Fig. 5D). Their morphology does not differ from that in other hadrosaurids: the shaft is straight and ends in two large, mediolaterally compressed and anteroposteriorly expanded condyles. Anteriorly, these distal condyles are fused in the better-preserved right femur, whereas a wide intercondylar groove separates the condyles posteriorly.

The tibia is known from a proximal fragment (Fig. 5C). This region of the tibia is anteroposteriorly expanded and mediolaterally compressed, with a convex lateral surface. The cnemial crest extends along the anterior margin of the proximal tibia; however, most of the crest is abraded. Posteriorly, the lateral condyle is massive and more prominent than the posterior condyle, protruding from the proximolateral margin of the tibia. A narrow and deep groove separates the two posterolateral proximal condyles.

In the pes, metatarsal II is solely represented by a proximal fragment. This fragment is mediolaterally compressed and greatly expanded dorsoventrally at the proximal end, having a long and elliptical articular surface. Metatarsal III is composed of a relatively long but robust shaft that expands proximally and distally (Figs. 5E, 6C). The proximal articular surface is mediolaterally compressed, with the dorsomedial corner further projected medially than the ventral margin. The metatarsal III of LACM/CIT 2760 is dorsoventrally crashed; consequently, the proximal dorsomedial corner is deformed and unnaturally prominent (Fig. 5E). The proximal half of the medial surface of the metatarsal shows a large depression for articulation with metatarsal II. The distal region is dorsoventrally compressed and the distal surface is dorsoventrally convex and mediolaterally concave.

Phylogenetic position of *Saurolophus morrisi*

Two maximum parsimony analyses (one with LACM 2760 and 2852 as separate taxonomic units and the other including these two specimens merged as *Saurolophus morrisi*) were undertaken in order to infer the position of the new species within Hadrosauridae, as well as testing its referral to the genus *Saurolophus*. For the first time all the available cranial and postcranial material of LACM/CIT 2852 and 2760 was included in a cladistic study. We used the character matrix of Prieto-Márquez (2010b), which consists of 196 cranial and 90 postcranial morphological characters, all equally weighted, to

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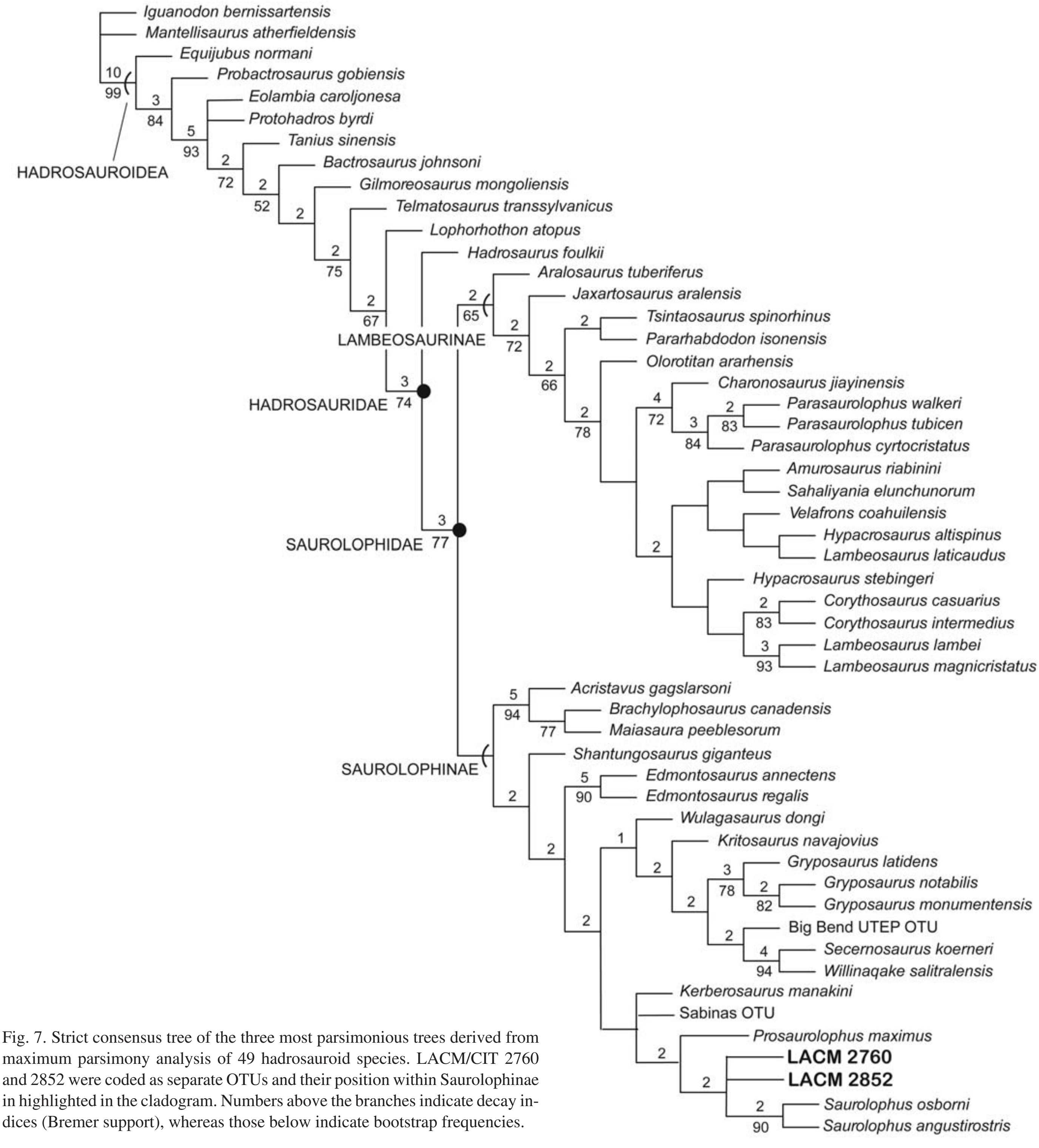

Fig. 7. Strict consensus tree of the three most parsimonious trees derived from maximum parsimony analysis of 49 hadrosauroid species. LACM/CIT 2760 and 2852 were coded as separate OTUs and their position within Saurolophinae in highlighted in the cladogram. Numbers above the branches indicate decay indices (Bremer support), whereas those below indicate bootstrap frequencies.

which three new cranial characters were added (see SOM_1 at http://app.pan.pl/SOM/app58-PrietoMarquez_Wagner_SOM.pdf). Counting *S. morrisi* (see SOM_2), the hadrosauroid taxonomic sample consisted of 49 species (including 20 Saurolophinae, 19 Lambeosaurinae, and 9 non-hadrosaurid Hadrosauroidea; see SOM_3). A heuristic search of 10,000 replicates, using random addition sequences followed by branch swapping using tree-bisection-reconnection holding 10 trees per replicate, was performed in TNT version 1.1 (Goloboff et al. 2008). Bremer support was assessed by computing decay indices using the TNT software. Bootstrap proportions were calculated with PAUP version 4.0b10 (Swofford 2002), setting the analysis to 5,000 replicates using heuristic searches, where each search was conducted using random additional sequences with branch-swapping by subtree pruning and regrafting and 25 replicates.

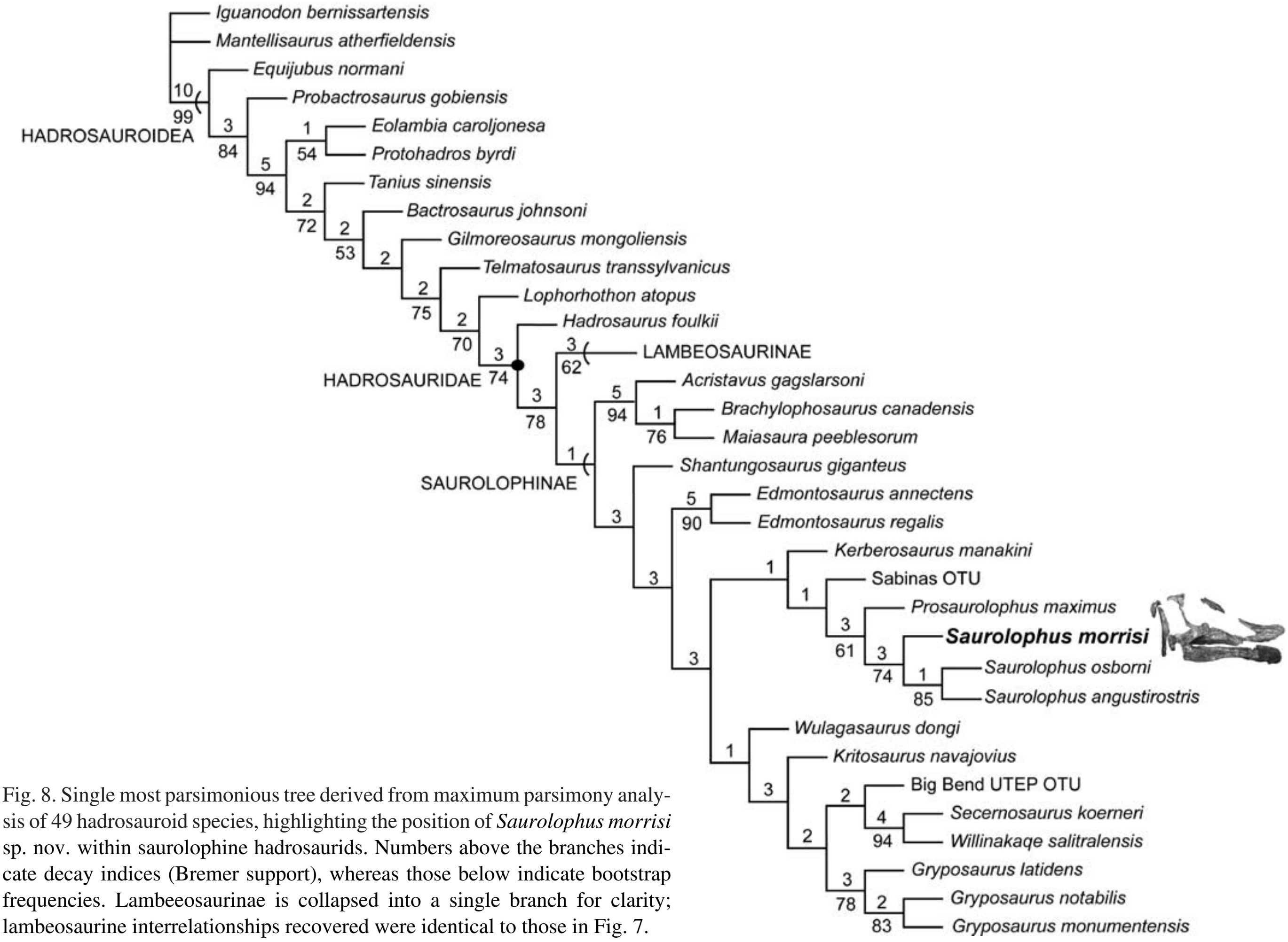

Fig. 8. Single most parsimonious tree derived from maximum parsimony analysis of 49 hadrosauroid species, highlighting the position of *Saurolophus morrisi* sp. nov. within saurolophine hadrosaurids. Numbers above the branches indicate decay indices (Bremer support), whereas those below indicate bootstrap frequencies. Lambeeosaurinae is collapsed into a single branch for clarity; lambeosaurine interrelationships recovered were identical to those in Fig. 7.

Referral of LACM/CIT 2760 to *Saurolophus* was congruent with the results of the maximum parsimony analysis in which this specimen and LACM/CIT 2852 were scored as separate taxonomic units. The analysis returned three most parsimonious trees of 903 steps each (C.I. = 0.51; R.I. = 0.79). The strict consensus tree positioned LACM 2760 and 2852 within the *Prosaurolophus–Saurolophus* clade, forming a polytomic relationship with the clade *S. angustirostris* + *S. osborni* (Fig. 7).

Scoring of LACM 2760 and 2852 together as *Saurolophus morrisi* resulted in a single most parsimonious tree of 902 steps (C.I. = 0.51; R.I. = 0.79) (Fig. 8). Two synapomorphies supported the position of *S. morrisi* within the *Kerberosaurus–Prosaurolophus–Saurolophus* clade (Fig. 8): angle between the dorsal margin of the anteroventral process of the maxilla and the anterior segment of the tooth row between 26° and 39° (convergent in the *Brachylophosaurus* clade, and *Parasaurolophus walkeri* and *P. tubicen*; missing in *Wulagasaurus dongi*) and robust jugal, with a ratio between the minimum depth of the posterior constriction and the distance between the point of maximum curvature of the infratemporal margin and the posterior margin of the lacrimal process of 0.6 or greater (convergent in *Edmontosaurus* spp., *Gryposaurus monumentensis*, and all lambeosaurines except *Aralosaurus tuberiferus* and *Jaxartosaurus aralensis*; missing in most of the *Gryposaurus* clade).

Within this group, inclusion of *Saurolophus morrisi* within the *Prosaurolophus–Saurolophus* clade is unambiguously supported by the presence in the dentary of a well-developed ventral bulge rostral to the coronoid process (convergent in *Edmontosaurus* spp.) and quadrate with a wide, arcuate, asymmetrical quadratojugal notch (convergent in the non-hadrosaurid hadrosauroids *Lophrorhothon atopus*, *Bactrosaurus johnsoni*, and *Gilmoreosaurus mongoliensis*). In addition, *S. morrisi* shares three ambiguous synapomorphies with *Prosaurolophus maximus*, *S. osborni*, and *S. angustirostris*: jugal with orbital constriction being equal or greater in depth than the infratemporal constriction (convergent in *Tsintaosaurus spinorhinus*); concave dorsal margin of the rostrum present in at least one or more specimens (unknown in the Sabinas saurolophine and *Kerberosaurus manakini*); and broadly arcuate anterolateral contour of the thin everted oral margin of the premaxilla in subadult and/or adult individuals (ambiguous due to widespread missing data).

The node here identified as *Saurolophus*, including *S. morrisi*, *S. osborni*, and *S. angustirostris*, is supported unambiguously by several characters, most significantly including the presence of a posterodorsal process of the frontals that pre-

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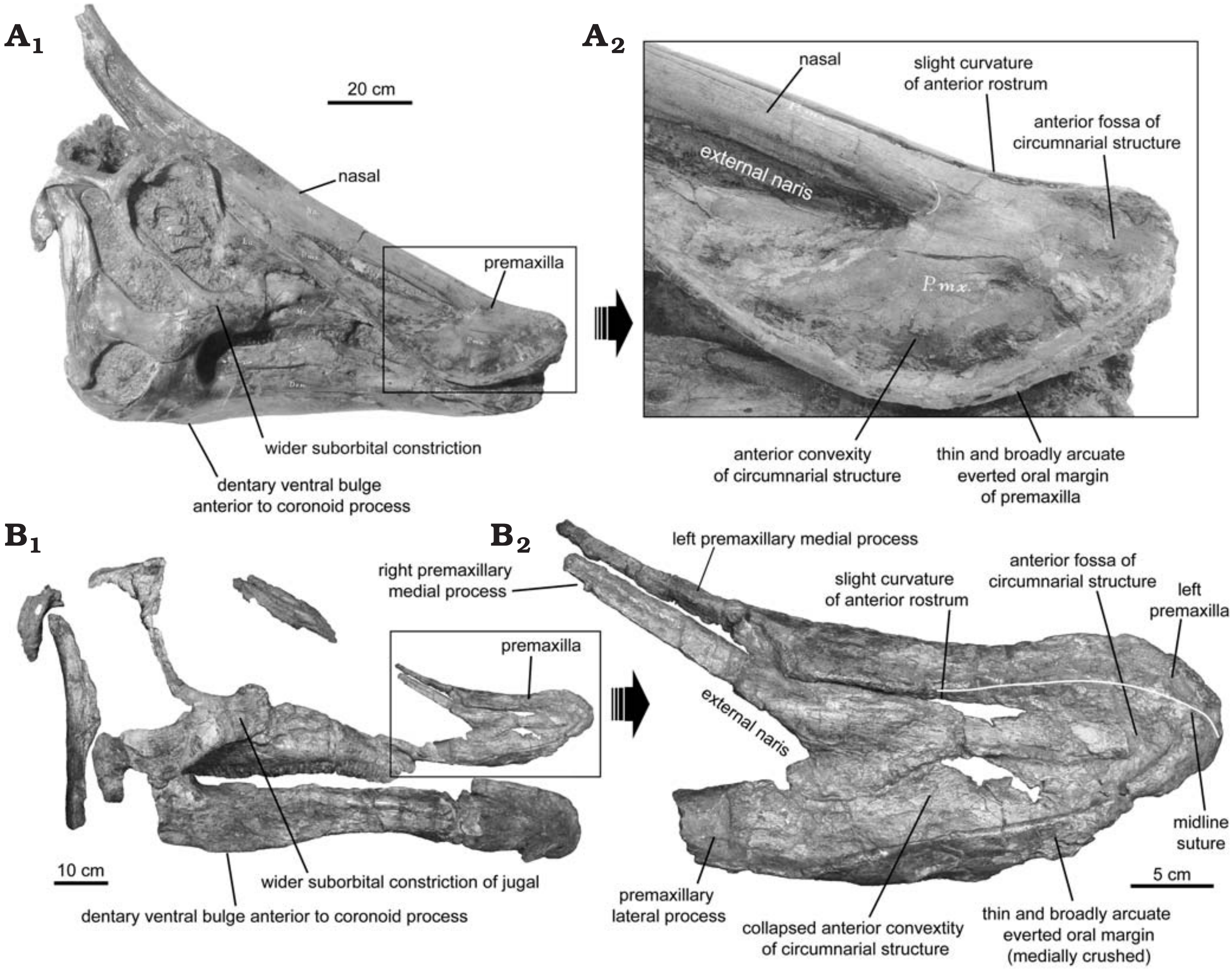

Fig. 9. Comparison of the general skull and premaxillary morphology of two hadrosaurid dinosaurs *Saurolophus osborni* Brown, 1912, holotype AMNH 5220 (**A**) and *Saurolophus morrisi* sp. nov., holotype LACM/CIT 2852 (**B**), highlighting characters shared by these two taxa. Skull in right lateral view (A_1, B_1), right premaxilla in lateral view (A_2, B_2).The white inscription on the premaxilla denote the abbreviation for that bone, painted by the curatorial staff back in the early twentieth century.

sumably buttressed the underside of the nasal crest. In LACM/CIT 2760, the frontals are domed, being dorsally convex anterior to the frontoparietal suture, a condition present in immature *S. angustirostris* (e.g., PIN 551/8) and possibly in *S. osborni* (e.g., AMNH 5221). This character is reminiscent of the heterochronic retention of juvenile frontal doming in adult lambeosaurine hadrosaurids (Horner et al. 2004), but this is found here to be convergent. The condition in adult lambeosaurines is associated with a general axial compaction of the braincase involving a shortened exoccipital roof above the foramen magnum and, with the exception of *Tsintaosaurus spinorhinus* (e.g., IVPP V725), oval and anterolaterally elongated supratemporal fenestrae (e.g., *Hypacrosaurus altispinus* ROM 702). LACM/CIT 2760 shares with *S. osborni*, *S. angustirostris*, and other saurolophines like *Prosaurolophus maximus*, *Edmontosaurus* spp., *Gryposaurus* spp., and *Kritosaurus navajovius* an anteroposteriorly extensive exoccipital roof and parasagittally elongate, subrectangular supratemporal fenestrae (Prieto-Márquez 2010b). All three *Saurolophus* species also share an extensive intersquamosal joint that completely excludes the parietal from the posterodorsal margin of the occiput (convergent in *Maiasaura peeblesorum*, *Shantungosaurus giganteus*, and several lambeosaurines), and a very expanded deltopectoral crest, with a maximum lateral crest expansion to minimum humeral shaft diameter ratio greater than 1.90 (convergent in *Wulagasaurus dongi* and all known Lambeosaurinae). As noted previously, *S. osborni* and *S. angustirostris* are united to the exclusion of *S. morrisi* by the presence of a deeply everted orbital margin and a Y-shaped postorbital.

Discussion and conclusions

Bell and Evans (2010) contended that LACM/CIT 2852 is not referable to *Saurolophus* due to the possession of a reduced dorsal process of the maxilla, and the presence of dentary teeth that lack marginal papillae and show low height/width ratios. The dorsal process is not sufficiently complete in either maxilla of LACM/CIT 2852 to permit assessment of its proportions. In the left maxilla, only the base of the process remains, consisting of a shallow margin that extends above the dental battery. In the right maxilla, at least the dorsal half of the dorsal process is missing. This is readily evidenced as the dorsal half of the rostral process of the right jugal (preserved in articulation with the right maxilla) rises above the dorsal margin of the preserved portion of the corresponding articular surface in the maxilla. The apparent lack or extreme reduction of marginal papillae in the dentary teeth, as well as the low aspect ratio (i.e., twice or slightly over twice taller than wide) of tooth crowns, are in fact observed in specimens of *Saurolophus* (Bell 2011) as well as *Edmontosaurus* (e.g., *E. annectens* MOR 003; Prieto-Márquez 2008), and are therefore equivocal.

It does appear to be the case that the narial foramen is broader in LACM/CIT 2852 than it is in other *Saurolophus*, more like that of *Edmontosaurus*, as noted by Bell and Evans (2010). However, unlike the broadly rounded rostral end of the narial foramen seen in *Edmontosaurus*, this specimen exhibits the tightly acute, V-shaped terminus of *Saurolophus*. Further, the everted oral margin of LACM/CIT 2852 is thin (Fig. 9B_1) as in *Prosaurolophus* and species of *Saurolophus* (as noted by Bell and Evans 2010; also present to some extent in *Gryposaurus*). In fact, the lateral segment of the oral margin in LACM/CIT 2852 has been medially crushed diagenetically, causing the margin to appear slightly deeper than it was in life. In other saurolophine taxa where the premaxilla is known (*Brachylophosaurus canadensis*, *Maiasaura peeblesorum*, *Edmontosaurus* spp.) the oral margin is at least three times deeper dorsoventrally, forming an extensive, lip-like flat to convex surface oriented dorsolaterally and anterodorsally. Additionally, despite substantial diagenetic deformation, the oral margin of LACM/CIT 2852 shows a broadly arcuate contour as in *Prosaurolophus* and *Saurolophus*, quite unlike the narrower and more subrectangular proportions present in the premaxilla of *Gryposaurus* and other saurolophines. Similarly, the dorsal profile of the rostrum (seen in lateral view) is gently concave, as in some *Prosaurolophus* and *Saurolophus* specimens. When this is added to the presence of the frontal buttress, the Moreno Hills specimens clearly exhibit a much greater affinity for *Saurolophus* than *Edmontosaurus*.

In summary, there is very little ambiguity about the referral of this specimen, nor about its phylogenetic affinities. The only ambiguity stems from amending the diagnosis of *Saurolophus* by referring a specimen that falls outside of the previously established clade. We feel that the alternative, erecting a new monospecific genus, would misrepresent the importance of this specimen. Generic referral is often arbitrary, but among hadrosaurids is typically made based on crest morphology. Although identification of possible crest fragments themselves is problematic, there is every indication from the morphology of the preserved base of the crest that most likely the crest morphology of *S. morrisi* was essentially similar to that of other species of *Saurolophus*.

As an act of nomenclatural fiat, referral of this species to *Saurolophus* does not substantively change our understanding of the biogeographic importance of the genus (e.g., Bell 2011) beyond the (arbitrary) increase in its range. However, the fact that one of the best-known dinosaurian specimens from the west coast of western North America is shown here to be distinct from those found elsewhere has implications for latest Cretaceous faunal dynamics, and will likely serve to bolster claims of endemism and provinciality (Lehman 1987, 1997, 2001). Equally significantly, the close phylogenetic interdigitation of species of Asian *Kerberosaurus*, North American *Prosaurolophus*, and the Asiamerican *Saurolophus* cannot but have a profound impact on the interpretation of the complex pattern of interchange between the two continents in the terminal Cretaceous. That such "marginal" specimens, previously dismissed as taxonomically indeterminate, might prove so important argues for close and careful consideration of the many other incomplete, poorly preserved, or otherwise unappealing specimens languishing in "peripheral" collections.

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