New Unadorned Hadrosaurine Hadrosaurid (Dinosauria, Ornithopoda) from the Campanian of North America

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NEW UNADORNED HADROSAURINE HADROSAURID (DINOSAURIA, ORNITHOPODA) FROM THE CAMPAÑIAN OF NORTH AMERICA

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ABSTRACT—A new hadrosaurid dinosaur, Acristavus gogdarsarisoni, is here named on the basis of several autapomorphic characteristics of the frontal, postorbital, and dentary. Acristavus is a member of the newly erected clade Brachylophosaurini, which along with its other members, Brachylophosaurus and Maiasaura, constitutes the earliest hadrosaurine hadrosaurid clade. The new taxon occurred approximately 79 million years ago and has been recovered from the Two Medicine Formation of western Montana and nearly simultaneously in the Wahweap Formation of southern Utah. Corresponding with its age and relationship to the other members of the Brachylophosaurini, it is not surprising that Acristavus possesses traits seen in both Brachylophosaurus and Maiasaura, but not necessarily shared between them. One of the most interesting morphological features of Acristavus is the lack of cranial osteological ornamentation, which is in stark contrast to every other hadrosaurid dinosaur except Edmontosaurus. Combining stratigraphic and phylogenetic data from Acristavus yields support for the hypothesis that the hadrosaurid ancestor did not possess cranial ornamentation, and that the subfamilies Hadrosaurinae and Lambeosaurinae each independently developed display structures.

INTRODUCTION

Hadrosaurid dinosaurs represent a clade of ornithopod dinosaurs, which among the many derived characteristics diagnosing the group, a laterally expanded premaxilla (duck-like bill) is the most outwardly conspicuous. The evolution of this trait, along with many others such as the dental battery and the absence of an antorbital fenestra, are traceable through the evolution of more primitive iguanodontians into the Late Cretaceous hadrosaurs. Even though there is a general understanding of character evolution from primitive taxa to hadrosaurs, the fossil record of this transition currently contains a 10 million year gap (Turonian to Campanian) in North America, the continent with the earliest record of hadrosaurid dinosaurs. During the course of this temporal gap, hadrosaurs developed highly diagnostic cranial ornamentation not seen in the iguanodontian ancestors. More specifically, the nasals are unmodified in virtually all known iguanodontians outside of Hadrosauridae (see Norman, 2004), yet display a variety of pustulostegals, pustules, and scoops within Hadrosaurinae, and participate in the formation of hollow tubes and fans within the Lambeosaurinae. Only one hadrosaurid taxon, Edmontosaurus (we follow Prieto-Márquez [2010a] in considering Anatotitan as a junior synonym of Edmontosaurus), is known to maintain the plesiomorphic unornamented nasal morphology, yet this taxon occurs in the Maastrichtian approximately 15–20 million years after the latest possible origin of Hadrosauridae (as defined by Forster [1997]: Lambeosaurinae + Hadrosaurinae and their most recent common ancestor), meaning that the condition is likely a reversed apomorphic trait. Therefore, these taxa yield no insight into the advent of hadrosaurid cranial ornamentation.

Here we present a new early Campanian hadrosaurid dinosaur based on material recovered from the lower Two Medicine Formation of Montana and the Wahweap Formation of southern Utah (Fig. 1) that provides vital clues to the evolution of hadrosaurs in North America as well as macroevolutionary trends within the Hadrosaurinae. Definitions of Hadrosauridae and Hadrosaurinae throughout follow Forster (1997), which are equivalent to Saurolophidae and Saurolophinae in Prieto-Márquez (2010a), respectively. Given the drastic changes in hadrosaurid taxonomy presented in Prieto-Márquez (2010a), and the drastic changes to this nomenclature that may occur with a new phylogeny, we will comply with the simpler, more ubiquitous clade names and definitions of Hadrosauridae and Hadrosaurinae sensu Forster, 1997.


SYSTEMATIC PALEONTOLOGY

ORNITHOPODA Marsh, 1881
HADROSAURIDAE Cope, 1870
HADROSAURINAE Cope, 1870
BRACHYLOPHOSAURINI, taxon nov.

Definition—Hadrosaurine ornithopods more closely related to Brachylophosaurus, Maiasaura, or Acristavus than to Gryposaurus or Saurolophus.
Diagnosis—Hadrosaurine hadrosaurids that possess a diastema approximately one third the length of the tooth row; long anteromedial maxillary process seen through external nares and not associated with premaxillary downturning; anterior process of jugal dorsoventrally symmetrical; posteroventral jugal and not associated with premaxillary downturning; anterior pro-long anteromedial maxillary process seen through external nares; astema approximately one third the length of the tooth row; FIGURE 1. Map of North America showing locations of Acristavus discoveries. A, Two Medicine Formation, western Montana; B, Wahweap Formation, southern Utah.

Remarks—This specimen is still largely unprepared, although two well-exposed jugals clearly show the morphology characteristic of Brachylophosaurus (contra Lucas et al., 2006), and is here referred as Brachylophosaurus indet. The specimen collected from the Mancos Shale in western Colorado dates to just over 80 Ma, providing a minimum age boundary for this clade.

ACRISTAVUS GAGSLARSONI, gen. et sp. nov.
(Figs. 2A, 3A–D and G, 4, 7, 8, 10, 11)

Etymology—A (Latin)-non, crista (Latin)-crest, avus (Latin)-grandfather, in reference to the absence of an osteological nasal crest, its stratigraphic position relative to other hadrosaurid taxa in the Two Medicine Formation, and the primitive nature of the skull. gagslarsoni from Gags Larson, nickname of landowner Russell Ellsworth Larson, on whose property the specimen was discovered.

Holotype—MOR 1155, nearly complete partially articulated skull and associated articulated postcrania, including 11 cervical vertebrae, three fragmentary dorsal vertebrae, one anterior caudal vertebra, dorsal ribs, the left humerus, left ulna, right sternal, left pubis, left femur, left tibia, left fibula, left metatarsals II and III, left pedal phalanges II-1, II-3, IV-1, IV-3, and IV-4, and right pedal phalanx II-1.

Referred Specimen—UMNHVP 16607 (Figs. 5, 6B, 9), a partial articulated skull roof including lacrimals and entire braincase, and a single cervical vertebra.

Horizon and Locality—MOR 1155 was collected from the base of a fluvial channel deposit (i.e., a tan-colored, moderately sorted, subangular to subrounded, calcareously cemented sublitharenite with a basal lag deposit containing macrovertebrate, microvertebrate, and plant remains) in the lower part of the Upper Cretaceous Two Medicine Formation, Museum of Rockies locality number TM-281, approximately 14 km southwest of Choteau, Teton County, Montana, U.S.A. The locality was discovered in 1999 by a group of ‘Junior Paleontologists’ from the University of Chicago while on a field expedition with the Old Trail Museum of Choteau. Based on its stratigraphic position, ~40 m above the 80 Ma dated crystal tuff of Rogers et al. (1993), its estimated age is ~79.43 Ma.

 Remarks—UMNHVP 16607 was collected from well-indurated tan-colored sandstone within the upper portion of the Middle Mudstone Member of the Wahweap Formation in Grand Staircase-Escalante National Monument, Utah. The specimen was located on the top of a tall butte by one of us (C.R.N.) in July of 2000 near the junction of Smokey Mountain Road and Right Hand Collet Canyon. It was found at a stratigraphic level approximately 170 m from the base of the Wahweap Formation. Using published sedimentation rates and radiometric ages (Jinnah et al., 2009), its estimated age range is 79.34–78.91 Ma.

Diagnosis—Acristavus is a hadrosaurine hadrosaurid diagnosed by the following unique features: enlarged postero-dorsal brow of postorbital and basioccipital extending posteriorly well beyond the dorsal border of the foramen magnum to a greater extent than in other hadrosaurine species (these two are preserved on the holotype MOR 1155), as well as the following best observed in the referred specimen UMNHVP 16607: deep laterally squared frontonasal suture; swelling of the interdigitate suture between the prefrontal and frontal; deep depression on the lateral surface of the postorbital jugal process. Acristavus also possesses a unique combination of the following features: widely expanded alar process; deeply developed basiptygoid ridge; deep, flattened supratemporal bar; absence of nasal ornamentation; lacrimal wide in posterior view; anterior nasal process terminating posteriorly to anterior margin of external nares; dentary with nearly flat ventral margin.

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FIGURE 1. Map of North America showing locations of Acristavus discoveries. A, Two Medicine Formation, western Montana; B, Wahweap Formation, southern Utah.
Acristavus also possesses the following differential diagnostic characters: alar processes positioned near vertically in a plane with the basipterygoid processes of the basisphenoid and expanded from near the dorsal surface of the basisphenoid to nearly contact the basisphenoid processes, a characteristic seen exclusively in this taxon, Brachylophosaurus, and Maiasaura; basipterygoid ridge descends to lower level of basipterygoid processes as seen in Brachylophosaurus and to a lesser extent in Maiasaura, but no other hadrosaurid taxa; supratemporal bar deep and flattened as seen in Maiasaura, Gryposaurus notabilis, and G. monumentensis, but not in Brachylophosaurus; absence of nasal ornamentation as seen in most (i.e., not Lophorhothon atopus) nonhadrosaurid iguanodontians as well as the hadrosaurine Edmontosaurus spp.; lacrimal wide in posterior view, as seen in Gryposaurus notabilis and G. monumentensis, but not in Brachylophosaurus or Maiasaura; anterior nasal process terminates prior to anterior margin of external nares as seen in nonhadrosaurid iguanodontians, some specimens of Brachylophosaurus, and Maiasaura, and all specimens of Gryposaurus spp., but no other hadrosaurid species; dentary with nearly flat ventral margin as seen in nonhadrosaurid iguanodontians such as Irontosaurus but not seen in any other hadrosaurid.

DESCRIPTION

The skull of Acristavus (Fig. 2) is long and low, mirroring the profile of Brachylophosaurus (Prieto-Márquez, 2005). Nearly every element from the skull is represented in the holotype except the vomer, splenial, and prefrontal. Postcranial elements in the holotype include 11 cervical vertebrae, three fragmentary dorsal vertebrae, one anterior caudal vertebra, dorsal ribs, left humerus, left ulna, right sternal, left pubis, left femur, left tibia, left fibula, left metatarsals II and III, left pes phalanges II-1, II-3, IV-1, IV-3, and IV-4, and right pes phalanx II-1. UMNHVP 16607 possesses the entire skull roof, including lacrimals and a well-preserved braincase.

Dermal Skull Roof

Premaxilla—Acristavus displays a laterally expanded premaxilla (Fig. 3A) as in other hadrosaurids, but lacks a prominent dorsally projecting premaxillary lip, as in other members of the Brachylophosaurini. However, there is a relatively large platform that divides the oral margin from the remainder of the element, such as that in Maiasaura (ROM 44770). The dorsal process is similar to that of Maiasaura (e.g., ROM 44770) and the lateral processes are typical for hadrosaurids. However, the size of the narial opening in Acristavus is larger than that of Maiasaura, being more similar to that of Brachylophosaurus (MOR 794).

Maxilla—Overall, the maxilla (Fig. 3B, C) is quite similar to that of Brachylophosaurus (Prieto-Márquez, 2005) and Maiasaura (Horner, 1983). The dorsomedial process of the maxilla is long and likely to have been visible laterally through the external nares as in the latter taxa (Fig. 2) and Gryposaurus monumentensis, a feature absent in other known hadrosaurids (Horner et al., 2004; Gates and Sampson, 2007). The length of the dorsomedial process is shorter than in Brachylophosaurus (MOR 794), however, and is more similar to the proportions seen in Maiasaura (ROM 44770). Interestingly, the dorsal process is set extremely close to the medial surface of the maxilla (Fig. 3D), instead of possessing a small shelf or cleft as in all other known iguanodontian taxa, including primitive iguanodontians such as Campitosaurus (e.g., UMNH VP 16455). Posteriorly, the ectopterygoid shelf is prominent, more so than in Brachylophosaurus. Several other differences between the Acristavus and Brachylophosaurus maxillae can be seen in Figure 3, including aspects of the anteroventral downturn, morphology and placement of the dorsal process, shape of the jugal articular facet, and pterygoid process.

Jugal—Acristavus possesses the characteristic jugal morphology seen in other brachylophoinines (Fig. 3G) with a near vertical postorbital process, narrow posterior process, and a large lobate posteroventral flange. Further, Acristavus shares a straight ventral margin of the anterior process with Maiasaura (Horner, 1983), differing from the sigmoidal ventral margin of all other hadrosaurines (see Gates and Farke, 2009).

Nasal—As in Maiasaura, most specimens of Brachylophosaurus (Prieto-Márquez, 2010), and all species of Gryposaurus, the anterior nasal process terminates posterior to
FIGURE 3. Various skull elements of MOR 1155, *Acristavus gagславсони* (A–G) and MOR 1071-8-13-92-559, *Brachylophosaurus* (E, F). A, premaxilla, right, in lateral view; B, maxilla, left, in lateral view; C, maxilla, right, in lateral view; D, maxilla, right, in dorsal view; E, right maxilla in dorsal view; F, right maxilla in lateral view; G, jugal, right in lateral view. Note the differing position of the maxillary dorsal process as well as the lack of a medial shelf near the same process between these two taxa. Abbreviations: eps, ectopterygoid shelf; jaf, jugal articular facet; jap, jugal anterior process; jpp, jugal posterior process; mdmp, maxilla dorsomedial process; mdp, maxilla dorsal process; mpp, maxilla pterygoid process; pmdp, premaxillary dorsal process; pml, premaxillary lip; pmlp, premaxillary lateral process; pop, postorbital process; pvf, posteroventral flange. Scale bar equals 10 cm.

the anterior margin of the external nares (Fig. 2). The nasal of *Acristavus* lacks ornamented outgrowths (Figs. 2 and 4) as seen in all hadrosaurines except *Edmontosaurus* (Lambe, 1920; Chapman and Brett-Surman, 1990). More primitive iguanodontian taxa, and presumably hadrosaurid ancestors, also largely lacked osteological nasal outgrowths (Norman, 2004), although the non-hadrosaurid hadrosauroid relative *Lophorothon atopus* (sensu Prieto-Márquez, 2010b) does possess a nasal outgrowth. Instead, the dorsal margin of the *Acristavus* nasal forms a smooth low profile arch from the premaxilla to the skull roof. Contact
FIGURE 4. MOR 1155, Acristavus gagslarsoni skull roof in A, lateral view and B, dorsolateral view. C, line drawing reconstruction of Acristavus based on MOR 1155 skull roof in A and B. Abbreviations: Dn, dentary; F, frontal; Ju, jugal; La, lacrimal; Mx, maxilla; Na, nasal; Pf, prefrontal; Po, postorbital; Qj, quadratojugal; Qu, quadrate; Sq, squamosal; Su, surangular. Scale bar equals 10 cm.

with the frontals is accomplished through a uniquely shaped frontonasal suture (Fig. 5). Firstly, the suture increases in depth posteriorly, with the posteroventral margin being one of the deepest sutures among hadrosaurids. Maiasaura (e.g., ROM 44770) shares with Acristavus the same characteristic of a deep posterior nasal suture that meets the floor of the contact at 90 degrees. Second, the posterolateral corners are square, with nearly 90 degree angles. A laterally squared-off contact such as in Acristavus is not seen in other taxa. Several large anteroposteriorly oriented ridges project from the frontal to secure the nasal. The midline of the frontonasal suture projects slightly anterior into the nasals, a feature observed in Prosaurolophus (Horner, 1992; Prieto-Márquez, 2008) and Kritosaurus (Prieto-Márquez, 2008). See Gates and Sampson (2007) and Prieto-Márquez (2005) for comparisons of Gryposaurus and Brachylophosaurus frontonasal sutures, respectively.

Lacrimal—In lateral view, the lacrimal has the characteristic triangular shape of hadrosaurids. Nonetheless, within Acristavus this element remains unique among brachylophosaurinines through several features of its posterior region. The relative height of the element is shorter than in both Brachylophosaurus and Maiasaura, whereas the thickness as measured on the posterior face is much larger. In addition to width, the posterior lacrimal is more robust, especially when compared to Brachylophosaurus (Fig. 6). The robust character of this region is more similar to that in the robust taxon Gryposaurus monumentensis (Gates and Sampson, 2007). As with all iguanodontians, the lacrimal foramen is large and perforates the posterior face, and is larger than in Brachylophosaurus.

Prefrontal—Overall, the prefrontal is not markedly different from that observed in other hadrosaurines. The prefrontal marks the anterolateral boundary of the orbital margin (Fig. 4), but bears little of the rugosity present on the postorbital (see below). Its medial margin rises to form a steep boundary contacting the posterolateral region of the nasal (Fig. 5). The interdigitate suture with the frontal forms a swelling that is not seen in other hadrosaurids.

Frontal—as described above, the frontonasal (Fig. 5) suture is the dominant feature of the anterior frontal. An upturned lip marks the dorsal boundary of the suture. The remaining portion of the anterior frontal is occupied by the prefrontal suture. A small section of frontal participates in the dorsal orbital rim, occupying a space between the prefrontal and postorbital. Participation by the frontal in the orbital margin is a characteristic of...
non-hadrosaurid iguanodontians (Norman, 2004), all members of the Brachylophosaurini, as well as the genera Gryposaurus (Gates and Sampson, 2007) and Edmontosaurus (Lambe, 1920; Prieto-Márquez, 2010), later hadrosaurid taxa exclude the frontal through unification of the postorbital and prefrontal. This margin of the frontal is slightly rugose, an ornamental pattern that is observed across most of the orbital rim. The broad central region of each frontal is slightly depressed, rising to a low ridge along the frontonasal suture.

Postorbital — The lateral edge of the postorbital, which participates in the orbital rim, is more rugose than that of other hadrosaurid taxa (Fig. 7). It is most comparable to a more basal iguanodontian described by McDonald et al. (2006) from the upper Turonian Moreno Hill Formation of New Mexico. The rugose bone texture follows the orbital rim for a short distance ventrally along the jugal process before disappearing. However, raised bumps continue onto the main body of the postorbital, where a straight line of this ornamentation is present, which is nearly identical to that seen in the Moreno Hill Formation iguanodontian (McDonald et al., 2010). Among hadrosaurids, Brachylophosaurus (e.g., MOR 794) also possesses a very rugose postorbital lateral margin, although in this taxon the rugosity is in the form of an upraised lip rather than distinct rugosities.

The jugal process is much broader than that seen in most other hadrosaurids. Of particular interest is an anteriorly directed sheet of bone that covers the posterooral corner of the orbit that is larger in UMNHVP 16607 than in MOR 1155 (Fig. 7). It is unclear if this expansion served a functional purpose. Immediately posterior to the expanded corner, a depression is present on the jugal process (Fig. 7). This depression is not seen on any other hadrosaurid and is a unique feature of this taxon.

Proceeding posteriorly, the squamosal process lies in line with the rest of the postorbital body, a condition that differs drastically from all hadrosaurid taxa except Brachylophosaurus (MOR 794). Even the brachylophosaurine Maiasaura (e.g., ROM 44770) demonstrates the more typical condition of dorsally projecting squamosal processes, the result of such a configuration being a more dorsally positioned posterior skull region. Brachylophosaurus and Acristavus both have relatively horizontal skull roofs (Fig. 2).

Squamosal — The squamosal does not vary substantially from that observed in other hadrosaurid taxa. However, as mentioned above, the posterior region of the element does not rise drastically above the anterior region of the skull roof, a characteristic shared only with Brachylophosaurus (MOR 794). The brachylophosaurine Maiasaura (e.g., ROM 44770) shows the more typical hadrosaurine morphology of the squamosal, parietal, and supraoccipital rising well above the frontals (Horner et al., 2004). Coalescence of the squamosal and postorbital is accomplished via the supratemporal bar, which is unusually broad for a taxon from this clade, and more comparable to that in other robust taxa, such as Gryposaurus monumentensis (ROM 6797).

Palatoquadrate Complex

Among the palatoquadrate elements present (Fig. 8), the quadrate and palatine are well-enough preserved for description
and comparisons. Because the pterygoid is lacking such information and the vomer is completely missing, they will not be described here.

**Quadratex**—The quadratex (Fig. 8A) is slender and gracile, lacking the large quadratex buttress that is seen on the dorsal quadratex head in *Brachylophosaurus* (Prieto-Márquez, 2005). Further down the shaft, the quadratojugal notch is quite shallow, differing from the deeper notch on more basal iguanodontians and even some hadrosaurids (e.g., *Gryposaurus* and *Hypacrosaurus*). The pterygoid wing is incompletely preserved hampering comparison with other taxa.

**Palatine**—The palatine (Fig. 8B) appears to shift drastically in morphology between hadrosaurine taxa. In gross morphology, the palatine of *Acristavus* is broader than that of *Brachylophosaurus* (e.g., MOR 1071 7-16-98-248-S) with the anterior blade longer and the angle between this feature and the articular facet being more acute in the latter taxon. The *Brachylophosaurus* element is clearly more elongate than in *Acristavus*. Comparing *Acristavus gagslarsoni* to *Prosaurolophus blackfeetensis*, the anterodorsal blade is broader in *A. gagslarsoni*, but the anterior vomer articular process is distinctly hooked and longer in *P. blackfeetensis* (Horner, 1992). Nevertheless, both specimens are incomplete so more extensive comparisons of the postero medial surfaces cannot be made. Given the disparate morphology observed thus far in hadrosaurine palatines, this element may prove an important diagnostic tool at the generic-level and would benefit from more extensive comparisons among hadrosaurid taxa.

**Braincase**

Both the type specimen (MOR 1155) and referred specimen UMNH VP 16607 have a complete braincase. The sutures on UMNH VP 16607 are more easily discernible and will therefore be the focus of the braincase description.

**Parietal**—Composing the dorsal surface of the braincase, the parietal is a hourglass-shaped element with a strong sagittal crest that extends along the dorsal midline (Figs. 5 and 9A). The parietal inserts a small interdigitate suture between the paired frontals, a configuration common among hadrosaurids (e.g., Gates and Sampson, 2007). Two anterior ‘arms’ extend laterally to overlap the posterior region of the frontals and contact the postero medial side of the postorbital. In UMNH VP 16607, the contact between the postorbital and parietal is not extensive. This element has numerous contacts with other cranial elements, including the squamosals posterolaterally, the supraoccipital posteriorly, and the laterosphenoid and prootic ventrally. Anteriorly, the contact with the laterosphenoid is unremarkable except for a raised ridge along the curved margin of the ‘arms.’ This feature is not discussed in the literature and a broader survey of hadrosaurine parietals is needed to affirm or refute the uniqueness of the parietal-laterosphenoid ridge. More posteriorly, an ovoid foramen perforates the parietal at the contact between the laterosphenoid and prootic. The remainder of the element corresponds to the morphology seen in other hadrosaurines.

**Supraoccipital**—In dorsal view, the supraoccipital (Fig. 5) is a triangular element observed to occupy the posterior aspect of the skull. It is wedged between the parietal anteriorly, the exoccipital ventrally, and the squamosals laterally. The supraoccipital possesses no distinguishing features in *Acristavus* except for a series of finely compressed ridges that extend transversely along the posterior-most margin.

**Fused Exoccipital and Opisthotic**—The paroccipital processes of the exoccipitals are only viewable on the type specimen MOR 1155 because they are broken on UMNH VP 16607. These lateral-most extensions of the exoccipital descend anteromedially, tapering to a rounded point approximately on the same level as the middle of the orbit. The anterior bending seen in the processes is more severe than in other hadrosaurines, including *Brachylophosaurus* (CMN 8893), *Gryposaurus* spp. (e.g., RAM 6797, CMN 2278, ROM 873), *Maiasaura* (ROM 44770), *Prosaurolophus maximus* (TMP 84-1-1), and *Saurolophus osborni* (AMNH 5220). It is currently unclear how significant and variable paroccipital anterior bending is between individual hadrosaurids; however, it seems that this characteristic may prove to be another autapomorphy of *Acristavus* if further specimens confirm that the morphology seen in MOR 1155 is not the result of postdepositional plastic deformation. Medially, the exoccipital condyloid descends to articulate with the basioccipital, and do not coalesce to form the ventral margin of the foramen magnum. Articulation with the prootic anteriorly is along an angular contact, and it appears that the two elements combine to form the opening for cranial nerve (CN) VIII. Otherwise, CNs X, XI, and XII are visible in the base of the exoccipital.
FIGURE 9. Braincase of UMNH VP 16607, Acristavus sp., in A, right lateral view, photograph; B, right lateral view, line drawing; C, ventral view, photograph; D, ventral view, line drawing. Abbreviations: ap, alar process; Bo, basioccipital; bpp, basipterygoid process; Bs, basisphenoid; CN, cranial nerve foramen; Ex, exoccipital; F, frontal; ibpp, interbasipterygoid ridge median process; ibpr, interbasipterygoid ridge; Ls, laterosphenoid; Os, orbitosphenoid; Pa, parietal; Pf, prefrontal; Po, postorbital; Pr, prootic; prsp, parasphenoid process; Ps, presphenoid. Note that the right postorbital and frontal are broken; therefore, the dimensions shown in A and B do not represent the true proportions. The interbasipterygoid ridge is postdepositionally broken and shifted dorsally a few millimeters, and the left basipterygoid process is slightly misshapen. Scale bars equal 5 cm.

Prootic—Long and relatively narrow, the prootic (Fig. 9A) is located on the dorsolateral aspect of the braincase. The anterior contact with the laterosphenoid is unremarkable except that the suture is sigmoidal. Similarly, the contact with the parietal bears no features of note aside from a small foramen that marks the triple-contact of the prootic, parietal, and laterosphenoid. The prootic creates the dorsal-most and posterior margins of the nearly triangular CN V opening, and contacts the basisphenoid at the base of CN V. This contact continues posteriorly until the prootic contacts the basisphenoid for a short distance, producing the opening for CN VII, and maybe CN VIII, which differs from the condition in Gryposaurus monumentensis where the prootic definitely encompasses CN VIII (Gates and Sampson, 2007).

If Gates and Sampson (2007) are correct in the position of CN VII on G. monumentensis, then the placement of cranial nerves within Acristavus differs from the latter taxon. For instance, in Acristavus the opening for CN VII is directly posterior to CN V, whereas in G. monumentensis the CN VII opening is positioned posteroventral to CN V. Brachylophosaurus (Prieto-Márquez, 2005) shows less divergent placement of these foramina, nonetheless, the configuration differs still from Acristavus. The prootic ascends at an angle to its narrow terminus contacting the exoccipital-opisthotic complex.

Basioccipital—As in other hadrosaurids, the basioccipital (Fig. 9) is a rounded, lightly rugose element that composes the posteroventral portion of the braincase. In Acristavus, this
element makes up most of the floor of the foramen magnum. A similar condition, albeit a narrower contribution, is seen in *Gryposaurus* (Gates and Sampson, 2007), which contrasts with *Prosaurolophus* (Horner, 1992). It appears that there is some phylogenetic significance to the occurrence of this character through ontogeny and phylogeny. Both UMNH VP 16607 and MOR 1155 possess small basal tubera on the anterior end of the basioccipital. All other hadrosaurines have larger, more developed basal tubera. There is also a small excavation accompanying each basal tuber in UMNH VP 16607 that may be artifacts of preservation or preparation, but their uniform depth and position suggests that they are original features. The articulations between this element and others are obscured due to preservation and crushing, and it is difficult to discern which cranial nerve openings the basioccipital contributes to. Compared to other taxa and the visible sutures on UMNH VP 16607, the ventral borders of CNs VII and VIII are likely to consist of the basioccipital.

**Basisphenoid**—This element is one of the most phylogenetically important elements distinguishing the *Brachylophosaurus* from the remainder of Hadrosaurinae. The parasphenoid process extends anteriorly as in other hadrosaurines, but may possess a network of supporting bone, as in the hadrosaurine AMNH 5850, or a tract for CN II, as in *Brachylophosaurus* (see also Presphenoid below; Prieto-Márquez, 2005), although both regions on MOR 1155 and UMNH VP 16607 are broken. More posteriorly on the basisphenoid, the alar processes project laterally from the main body of the element (Fig 5 and 9B). These processes are larger—both in lateral extent and in dorsoventral breadth—than other hadrosaurines outside of *Brachylophosaurus*. In addition, they are positioned at a higher angle relative to the horizontal than in other hadrosaurine clades. Prieto-Márquez (2005) mentioned the large size of the alar processes in *Brachylophosaurus* and *Maiasaura*, and Gates and Sampson (2007) further characterized the difference between the brachylophosaurinian condition and that found in *Gryposaurus* spp. The basipterygoid processes extend lateroventrally at a low angle relative to the horizontal, similar to the condition in other hadrosaurines (e.g., Gates and Sampson, 2007). However, the area between the basipterygoid processes is, again, unique in brachylophosaurus taxa relative to other hadrosaurines. As noted by Prieto-Márquez (2005) for *Brachylophosaurus*, the interprocess region in brachylophosaurine taxa consists of a raised bony wall that extends almost to the ventral-most position of the basipterygoid processes. This differs from other hadrosaurines in that the same interprocess region has a ‘V’-shaped embayment that can be described as a converging angle for the basipterygoid processes. The midline between the processes displays a short ventrally descending process in many hadrosaurines, although the condition differs between brachylophosaurine taxa and other hadrosaurines such as *Gryposaurus*. Gates and Sampson (2007) described the process in *Gryposaurus* spp. as wider than *Brachylophosaurus*. This study verifies that conclusion and further adds this characteristic size disparity as a synapomorphy of the new clade. Gates and Sampson (2007) also mentioned that the process did not appear in *Prosaurolophus blackfeetensis* based on published illustrations of this taxon, but further examination of this genus is necessary. Directly posterior to the alar processes and basipterygoid processes is a large exit for the carotid artery. The size and position of this foramen does not differ among other hadrosaurines. Dorsally, the basisphenoid forms the ventral border of the CN V opening. This cranial nerve foramen has an overall shape that is perfectly triangular with the anterior corner terminating in a tapering point. The entire outline is demarcated by a sharp raised ridge. Overall the shape differs significantly from that seen in *Gryposaurus monumentensis* and *Prosaurolophus* (in which it is subcircular in outline; Gates and Sampson, 2007), but is more similar to that in *Brachylophosaurus* (Prieto-Márquez, 2005), although much more angular than in the latter. Posterior to the slightly constricted body of the basisphenoid, the basioccipital contacts this element along a broad suture that is typical for hadrosaurines.

**Laterosphenoid**—The laterosphenoid (Fig. 9) contacts the postorbital laterally, the frontal dorsally, the orbitosphenoid anteriorly, the basisphenoid ventrally, and the prootic posteriorly. Contact with the postorbital is made through a socket on the dorsomedial side of the latter element, where the ball-shaped lateral end of the laterosphenoid inserts. This configuration is common among hadrosaurids (e.g., *Prosaurolophus* [Horner, 1992], *Gryposaurus* [Gates and Sampson, 2007], and *Edmontosaurus* [Lambe, 1920]). A sharp ventrally oriented ridge extends mediolaterally from the postorbital contact to the basisphenoid. The laterosphenoid in UMNH VP 16607 extends posteriorly to contact the prootic near the midpoint of the parietal. In doing so, the laterosphenoid constructs the majority of the anterodorsal border of CN V. It is difficult to ascertain the remaining sutural contacts of this element.

**Orbitosphenoid**—This element does not differ markedly from that seen in other hadrosaurine hadrosaurids, consisting of a broad anteriorly projecting sheet of bone that slightly bulges ventrally to allow for the presence of neurovascular material and CN II. There is a lateral lobe that overlaps the laterosphenoid and the frontal (Fig. 9B; as also occurs in other hadrosaurines such as *Prosaurolophus* and *Gryposaurus* [Horner, 1992; Gates and Sampson, 2007]).

**Presphenoid**—A small, but well-defined, anterior lobe demarcates the anterior border of the presphenoid. The left and right anterior lobes (i.e., the anterior portions of the left and right presphenoids) are separated by a deep ‘V’-shaped cleft, which is deeper in *Acristavus* (UMNH VP 16607) than *Brachylophosaurus* (MOR 1071 7-7-98-86). At the posterior apex of the cleft, a small anteroposteriorly oriented ovoid process descends. The process is missing on UMNH VP 16607 and not observable in MOR 1155. A similar structure can be seen in *Brachylophosaurus* (Prieto-Márquez, 2005) as forming the tract for CN II. Although this structure was not mentioned in Gates and Sampson (2007) for species of *Gryposaurus*, similar morphology is present in an unidentified hadrosaurine (AMNH 5850), which is more like a strut that contacts the base of the orbitosphenoid with the parasphenoid process.

**Lower Jaw**

The only elements of the lower jaw presently known for *Acristavus* consist of the dentary and surangular. The surangular is virtually identical to that of *Brachylophosaurus* (Prieto-Márquez, 2005), therefore no further description of this element is provided here.

**Dentary**—The dentary (Fig. 10) has the plesiomorphic condition of a virtually straight ventral margin, differing from the downturned anterior region of all other hadrosaurids and some iguanodontians (Norman, 1998). Anteriorly, the dentary expands dorsoventrally so that it is taller anteriorly than posteriorly, whereas other hadrosaurids tend to decrease dentary depth concordant with ventral deflection. A similar expansion of the anterior dentary is seen in *Protobadros* (Head, 1998), although the latter taxon possesses an extremely downturned dentary as well. In other characteristics, the *Acristavus* dentary does not differ drastically from those of other hadrosaurids, including the extension of the tooth row posterior to the coronoid process. More clade-specifically, it lacks the unique spur on the posteroventral margin of the coronoid process that is present in *Brachylophosaurus* (e.g., MOR 10.71.9-8.98-W) and *Maiasaura* (e.g., ROM 44770).
The dentary teeth of *Acristavus* (MOR 1155) are either covered by the dental plate, or in very poor condition. The length of the tooth row is approximately 24.5 cm, although there is some distortion from crushing. There are 32 or 33 tooth positions. Only one dentary tooth (left dentary, mid-row) is well preserved enough for a measurement. The enameled crown is 25 mm long and 11.5 mm wide. The tooth has a single, slender carina and the entire crown appears to be smooth with little or no evidence of papillae. In dimensions and shape, the dentary teeth of *Acristavus* are similar to those of *Maiasaura* and *Brachylophosaurus*, and considerably different from those of *Gryposaurus*, and in particular those of *Gryposaurus latidens* (Horner, 1992). The right maxilla is well preserved and reveals 36 tooth positions. None of the dentition is preserved in good enough condition to warrant illustration.

### Postcranial Elements

In addition to skull elements, numerous postcranial elements were recovered from the site (Fig. 11). Of these, the most phylogenetically important element is the pubis. Not surprisingly, the general shape of the element demonstrates a more primitive, but distinctly hadrosaurine, morphology of a long neck uniting the pubic blade with the ischiadic and iliac peduncles. The anterior blade is incomplete so it is currently unclear if the blade was deflected ventrally as in some basal iguanodontians (Norman, 2004). The long pubic blade seems to be a feature that shortens in lambeosaurine taxa (Prieto-Marquez, 2010). Despite ambiguity in the interpretation of anterior blade morphology, it is clear that the postpubic process is short as in other hadrosaurids.

### Comparative Anatomy Summary

*Brachylophosaurus* and *Maiasaura* differ significantly in external skull morphology, such as in the lateral profile, size of external nares, and most obviously in nasal ornamentation (Fig. 2). Whereas *Acristavus* completely lacks nasal ornamentation, it does possess a long low lateral profile and narial opening similar to *Brachylophosaurus*, along with numerous features that compare favorably to *Maiasaura*, such as shape of the jugal (anterior process), similarities in the premaxillary dorsal process, and features of the frontonasal suture. Therefore, this new taxon provides a morphological connection between *Maiasaura* and *Brachylophosaurus*. Further, when one considers the plesiomorphic conditions of a straight, anteriorly expanded dentary and no nasal outgrowths, coupled with its low stratigraphic position, *Acristavus* may be one of the most basal hadrosaurine dinosaurs yet discovered in spite of inclusion within an established hadrosaurine clade.
FIGURE 12. Time-calibrated phylogeny demonstrating relationships among hadrosaurine hadrosaurids. Character support for Brachylophosaurini (Node A, grey box) includes unambiguous characters 10, 22, 37, 40, 52, 59, 72, 75, 84, and 96, and ambiguous characters 23, 55, and 74. Tree statistics: tree length = 202, Consistency Index = 0.64, Retention Index = 0.65, Rescaled Consistency Index = 0.42. *Iguanodon bernissartensis* was used as the outgroup, but does not appear in the tree because its age, ∼120 Ma, is beyond the focus of the paper. *Corythosaurus* was also included within the analysis but excluded because it plotted as the sister taxon to Hadrosaurinae and had no bearing on the study taxa. Numbers on stems represent bootstrap values (1000 replicates /decay indices; note that branches with no values indicate bootstraps below 50% and decay indices of 1. Decay indices were produced in PAUP 4.0b10 using the method described by Forey (2007). Phylogenetic characters and codings are listed in Supplementary Data.

PHYLOGENY

*Acristavus* nests within a well-supported clade—here named Brachylophosaurini—containing its sister taxon *Maiasaura* and *Brachylophosaurus* (Fig. 12, node A; see figure caption for tree statistics). One most parsimonious tree was derived from an analysis of 15 taxa and 116 characters (see Supplementary Data; available online at www.vertpaleo.org/jvp/JVPcontents.html) using ACCTRAN optimization within a Branch and Bound search in PAUP 4.0b10 (Swofford, 2002) and subsequent character tracing and tree manipulation in MacClade 4.06 (Maddison and Maddison, 2000). When calibrated for time, the cladogram in Figure 12 firmly establishes that Brachylophosaurini extended back to at least 80 Ma, making it the oldest hadrosaurid clade (following the strict node-based definition by Forster [1997; see above]) known from North America.

*Acristavus* is positioned as the sister taxon to *Maiasaura* (Fig. 12), sharing the derived trait 48(1), which is a broad postorbital with a squared anteromedial corner. The taxa also share the primitive condition for two characteristics in which *Brachylophosaurus* scores derived conditions including character 31 (0: nasal anterior process terminates prior to anterior margin of external nares) and character 53 (0: jugal, ventral margin of anterior process straight to slightly curved).

Brachylophosaurini has been an established part of hadrosaurid phylogenies since Horner (1983) placed *Maiasaura peeblesorum* into a phylogenetic context as the sister taxon to *Brachylophosaurus*. Although Weishampel and Horner (1990) included *Gryposaurus* and *Aralosaurus* in a clade with *Maiasaura* and *Brachylophosaurus*, the close relationship between the latter two taxa was retained. Other notable phylogenies
that include a sister-taxon relationship between Maiasaura and Brachylophosaurus include Weishampel et al. (1993), Horner et al. (2004), Prieto-Márquez et al. (2006), Gates and Sampson (2007), Godefroit et al. (2008), and most recently Prieto-Márquez (2010a). This final phylogenetic analysis is the most comprehensive to date (containing 286 characters and 41 ingroup taxa) and follows the general topology presented here of a clade consisting of Brachylophosaurus, Maiasaura, and Acristavus (referred to as “Two Medicine OTU” in Prieto-Márquez [2010a]), although the interclade relationships are different. Most specifically, Acristavus does not occupy a sister-taxon relationship with Maiasaura, but is instead placed as the basal-most member of the clade. Despite utilizing more morphologic characters, as well as incorporating a morphometric approach that had never been utilized in hadrosaurid phylogenetics, the phylogeny presented by Prieto-Marquez (2010a) unites Maiasaura and Brachylophosaurus in a clade on the basis of one character, whereas the analysis presented here posits three characters supporting a clade consisting of Maiasaura and Acristavus. We suggest that the Prieto-Márquez (2010a) result is not substantial enough to discount the phylogenetic hypothesis presented in our analysis and, therefore, a more critical examination of the characteristics presented in both phylogenies will be required before the exact placement of Acristavus can achieve consensus.

**DISCUSSION**

Despite the confluence of Brachylophosaurus characteristics present in Acristavus, the new hadrosaurid falls out as the sister taxon to Maiasaura, not as the most basal member of the Brachylophosaurus as might be expected. Nonetheless, the stratigraphic position and many seemingly primitive features may prove to be decisive in the phylogenetic placement of this taxon in future studies. Another interesting observation of the phylogenetic analysis presented here is that the closest hadrosaurid taxon to Acristavus is Maiasaura, both of which are found in the Two Medicine Formation less than three million years apart. These data bear only rudimentary significance, however, until more information on stratigraphic distributions and hadrosaurid faunal turnover is obtained.

Broader interpretation of the time-calibrated phylogeny shows that the Brachylophosaurus goes extinct around 76.5 Ma (Horner, 1984), superseded by the contemporaneous Gyratosaurus (Weishampel et al., 1993), Protohadros (Head, 1998), and Bactrosaurus (Godefroit et al., 1998). Given that the closest relatives of hadrosaurs do not have cranial crests and most members of the Hadrosauridae do have prominent crests, two hypotheses for the development of such structures may be derived: (1) the hadrosaur ancestor possessed cranial ornamentation and the two clades independently modified the ancestral version into their typical style; or (2) the hadrosaurid ancestor did not have ornamentation and both hadrosaurines and lambeosaurines evolved genus-specific crest morphology of their own, with no ancestral ratcheting. The discovery of Acristavus as the oldest hadrosaurid unfortunately does not shed much light on these hypotheses, if one considers the possibility of ornamentation loss within this taxon. However, the flat head of Acristavus demonstrates that at least one stratigraphically and phylogenetically basal hadrosaurid lacked ornamentation, whereas later forms within its clade developed them (i.e., Maiasaura and Brachylophosaurus). This isolated datum shifts the balance toward the second hypothesis, that hadrosaurines and lambeosaurines independently evolved cranial display structures from unadorned ancestors. Much more information on the hadrosaurid fossil record is needed before further headway may be gained on this problem.

**Biogeography**

Remains of this new hadrosaurid taxon have been recovered from penecontemporaneous sediments of the Two Medicine Formation of western Montana and the Wahweap Formation of southern Utah, which are separated by a distance of over 1100 km (Fig. 1). The Two Medicine specimen is calculated to be ~79.43 Ma old based on estimated sedimentation rate and radiometric ages reported by Rogers et al. (1993), and correlation of a measured stratigraphic section through locality TM-281 (on file at MOR) to stratigraphic sections measured by Roberts (1999). The Utah specimen occurs at the top of the Middle Mudstone Member of the Wahweap Formation and is estimated minimally to occur around 78.91 Ma based on minimum average sedimentation rate and radiometric ages published by Jinnah et al. (2009). Note that if maximum sedimentation rate is used for calculation, the age occurrence drops to 79.34 Ma, nearly identical to that calculated for the A. gagslarsoni type specimen. McDonald et al. (2006, 2010) reported a late Turonian (~90 Ma) NHI from the Moreno Hill Formation of New Mexico, which is currently the latest NHI known in North America. Therefore, it seems plausible that the earliest North American hadrosaurid iguanodontian will be found in sediments that date between 90 and 80 Ma, using the Moreno Hill Formation iguanodontian and the Mancos Shale brachylophosaurus iguanosaurid (MWC 129; see Systematic Paleontology) as brackets. This estimate agrees with the large biogeographic study of Prieto-Márquez (2010b) in which the split between NHI and Hadrosauridae (sported Sauropoda) occurs in the Santonian of North America, based on the age of Brachylophosaurus. Although, it is likely that hadrosaurs coexisted with NHI, and only after species sorting ending prior to 80 Ma did hadrosaurs become the only iguanodontian clade in North America. This temporal gap is beginning to be filled by large ornithopod fossils recovered from the Straight Cliffs Formation of southern Utah (Gates et al., 2009), and with additional specimens will come a clearer picture of the transition between and possible coexistence of nonhadrosaurid and hadrosaurid iguanodontians.

**Crest Development**

Hadrosaurid dinosaurs are divided into two clades, the Hadrosaurinae and Lambeosaurinae, based most easily on the ostensibly varying morphology of their cranial ornamentation (Horner et al., 2004), which is described as solid nasal crests in the former and hollow crests incorporating the nasal and premaxilla in the latter. To date, only the hadrosaurine genus Edmontosaurus spp. is known to lack ornamentation on or near the dorsal surface of the skull. Yet, the vast majority of nonhadrosaurid iguanodontians (NHIs) do not possess cranial ornamentation, including those taxa most closely related to hadrosaurs, such as Telmatosaurus (Weishampel et al., 1993), Protohadros (Head, 1998), and Bactrosaurus (Godefroit et al., 1998). Given that the closest relatives of hadrosaurs do not have cranial crests and most members of the Hadrosauridae do have prominent crests, two hypotheses for the development of such structures may be derived: (1) the hadrosaurid ancestor possessed cranial ornamentation and the two clades independently modified the ancestral version into their typical style; or (2) the hadrosaurid ancestor did not have ornamentation and both hadrosaurines and lambeosaurines evolved genus-specific crest morphology of their own, with no ancestral ratcheting. The discovery of Acristavus as the oldest hadrosaurid unfortunately does not shed much light on these hypotheses, if one considers the possibility of ornamentation loss within this taxon. However, the flat head of Acristavus demonstrates that at least one stratigraphically and phylogenetically basal hadrosaurid lacked ornamentation, whereas later forms within its clade developed them (i.e., Maiasaura and Brachylophosaurus). This isolated datum shifts the balance toward the second hypothesis, that hadrosaurines and lambeosaurines independently evolved cranial display structures from unadorned ancestors. Much more information on the hadrosaurid fossil record is needed before further headway may be gained on this problem.

**CONCLUSIONS**

Acristavus gagslarsoni is a new taxon of hadrosaurid iguanodontian from the Late Cretaceous of North America. Specimens of this new genus have been identified from both the Two Medicine Formation of Montana as well as the Wahweap Formation of southern Utah. The holotype consists of a mostly complete, partially articulated skull with associated to articulated postcrania, whereas the referred material from southern Utah is composed of a complete skull roof and a single cervical vertebra. All known material of Acristavus shares important autapomorphic features including but not limited to rugose orbital rims and squared frontonasal suture.

The clade Brachylophosaurus is established based on phylogenetic data that robustly support a close relationship between Brachylophosaurus, Maiasaura, and Acristavus, with the latter
two as sister taxa. This group of hadrosaurids is united by several characteristics of the braincase not observed in other hadrosaurid taxa. Interestingly, Brachylophosaurusini is the earliest clade of hadrosaurids known from North America and narrows the gap between the first hadrosaurid (Campanian) and the last non-hadrosaurid iguanodontian (Turonian) to only 10 million years in North America. Therefore, it seems likely that the origin of North American hadrosaurids occurred sometime in the Coniacian stage, but maybe as late as the Santonian.

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LITERATURE CITED


Lambe, L. M. 1920. The hadrosaur Edmontosaurus from the Upper Cretaceous of Alberta. Canada Department of Mines Memoir 120:1–79.


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