A primitive hadrosaurid from southeastern North America and the origin and early evolution of ‘duck-billed’ dinosaurs

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INTRODUCTION

Hadrosaurids were large (7–14 m in length) herbivorous, facultatively bipedal ornithischian dinosaurs. They were keystone taxa in ecosystems of all major continental landmasses, with the exception of Africa and Australia, from the Santonian through the latest Maastrichtian (Late Cretaceous; Lund and Gates, 2006). Hadrosaurids evolved among the most derived skeletal anatomy of all ornithopod dinosaurs. The most notable apomorphies are the greatly hypertrophied narial passages and surrounding structures that in most taxa are associated with cranial crests, which vary substantially among taxa. Hadrosaurid crests are diagnostic at both higher and lower taxonomic levels (Prieto-Márquez, 2010b) and primarily functioned in communication (visual display and acoustic communication; Evans, 2006). It is uncertain, however, what the ancestral narial morphology was for hadrosaurids. Outgroup taxa to Hadrosauridae that preserve the entire skull; Carpenter et al., 1995; Prieto-Márquez, 2011a; Tsogtbaatar et al., 2014). This contrasts with the apparent sudden occurrence in the fossil record of derived circumnarial structures in the oldest and more basal hadrosaurids for which this region of the skull is preserved (Prieto-Márquez, 2010c; Gates et al., 2011; Prieto-Márquez and Wagner, 2013).

Although the hadrosaurid fossil record is widespread throughout most continental regions, it is also unevenly distributed (Prieto-Márquez, 2010a). One of the areas in which hadrosaurids remain poorly recorded and understood is the eastern half of North America. During the Late Cretaceous, an epeiric intercontinental seaway (the Cretaceous Western Interior Seaway) split North America into two continental landmasses: a strip of land known as Laramidia to the west and Appalachia to the east (Gates et al., 2012). Laramidia is renowned for its richness of hadrosaurid specimens (26 species recognized, about half of the known global diversity) and their high quality of preservation and skeletal completeness (Prieto-Márquez, 2010b; Gates et al., 2012). Conversely, Appalachia has hitherto provided just a few partial postcranial and fragmentary cranial remains, with only one recognized species, Hadrosaurus foulkii (late Coniacian of Kansas, missing almost the entire skull; Carpenter et al., 1995; Prieto-Márquez, 2011b) and Lophorhothon atopus (early Campanian of Alabama, partial skull and postcranium; Langston, 1960; Prieto-Márquez, 2008), were once believed to be members of Hadrosauridae but are now viewed as closely related outgroup hadrosauroids (Prieto-Márquez, 2010b; contra Xing et al. [2014], who positioned L. atopus within Saurolophinae).
Here we report a new hadrosaur from Alabama, south-eastern U.S.A. (Fig. 1). The new taxon is the most complete hadrosauroid collected so far from Appalachia, as well as one of the oldest hadrosaurids known. Notably, for this continental region, the described specimen is the only member of the clade for which the cranium has been recovered. A monographic detailed description of this animal is beyond the scope of the present study and is forthcoming elsewhere. Here, we focus on the osteological characters that allow erection of a new genus and species of hadrosaurid, considerably furthering our understanding of Appalachian hadrosaurid diversity and anatomy, inferring the ancestral morphology and timing of acquisition of the derived hadrosaurid circumnarial structure, and determining the geographic origin of Hadrosauridae.

**Institutional Abbreviations**—AUMP, Auburn University Museum of Paleontology, Auburn, Alabama, U.S.A.; MSC, McWane Science Center, Birmingham, Alabama, U.S.A.

**Anatomical Abbreviations**—arf, accessory rostral fossa (autapomorphy); bn, external bony naris; bnmg, margin of bony naris; cdf, caudal circumnarial fossa; cvfg, caudoventral flange; cmm, circumnarial depression; cpr, caudal process; djt, dorsal jugal tubercle; dp, dorsal process; dsf, dorsal circumnarial fossa (autapomorphy); dssf, oblique dorsal shelf of medial articular surface; dt, dentary; erg, ectopterygoid ridge; esf, ectopterygoid shelf; f, frontal; itf, infratemporal fenestra; itfm, infratemporal margin; j, jugal; jar, articular surface for jugal; lc, lacrimal; lcar, articular surface for lacrimal; mxar, articular surface for maxilla; mlf, large maxillary foramen; mx, maxilla; ns, nasal; obm, orbital margin; par, parietal; pdt,
predentary; pf, prefrontal; pfar, articular surface for prefrontal; plp, palatal process; plr, palatine ridge; pmx, premaxilla; pmxs, premaxillary shelf; po, postorbital; pop, postorbital process; q, quadrate; qjig, quadratojugal flap; sa, surangular; sq, squamosal; stf, supratemporal fenestra; th, teeth; vpr, ventral process; vtf, ventral circummaxillary fossa (autapomorphy).

SYSTEMATIC PALAEOONTOLOGY

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1887
ORNITHOPODA Marsh, 1881
IGUANODONTIA Dollo, 1888
HADROSAURIDAE Cope, 1870

(Eosens Prieto-Márquez, 2010a)

EOTRACHODON ORIENTALIS, gen. et sp. nov. (Figs. 1, 2)

Holotype—The only known specimen, MSC 7949, consists of a well-preserved, nearly complete, partially articulated cranium and a fragmentary postcranium. Cranial elements include both premaxillae, maxillae, jugals, partial right nasal, left lacrimal, left prefrontal, frontals, postorbitals, squamosals, left quadrate, partial braincase (parietal, supraoccipital, left opisthocoel–exoccipital complex, prootics, basisphenoid, laterosphenoids, and paraphyseoid), prefrontary, dentaries, surangulars, angular, hyoïd, and various maxillary and dentary teeth. The postcranium is represented by the axis and several cervical, dorsal, sacral, and caudal vertebrae; partial left pubis; partial left ischium; partial right ilium; partial left ilium; partial right femur; partial left femur; partial right tibia; and two manual phalanges. A transverse petrographic histological section of the tibia (Fig. S1 of Supplementary Data 1) shows cortices composed exclusively of highly vascularized plexiform bone (one of the faster growing bone types; Castanet et al., 2000; de Margerie et al., 2002) and no evidence of Haversian remodeling or growth lines (e.g., lines of arrested growth, annuli). These observations, in conjunction with the lack of complete fusion of the neurocranium (e.g., disarticulated prootics and open neurocentral sutures in cervical and cranial dorsal vertebrae, indicate that MSC 7949 had not yet reached skeletal maturity and was destined to become a larger animal in adulthood.

Locality and Horizon—Outcrops of uppermost Santonian (Late Cretaceous) strata of the Mooreville Chalk near Montgomery, Montgomery County, Alabama, southeastern U.S.A.

Etymology—From eōs (Greek, dawn), Trachodon (Greek, rough tooth; a homonym to the first hadrosaurid genus described [Leidy, 1856], long considered a nomen dubium [Lambe, 1881]), and orientalis (Latin, eastern), in reference to the southeastern occurrence in North America of this hadrosaurid.

Diagnosis—Hadrosaurid dinosaur characterized by the following autapomorphies: tripartite circummaxillary depression divided longitudinally into dorsal and ventral fossae, the latter being subdivided into caudoventral and lightly incised rostroventral fossae; dorsal fossa of circummaxillary depression above bony naris extending further caudally than caudal extent of caudoventral fossa; caudodorsal region of circummaxillary depression above bony naris excavating lateral nasal surface, deeply rostrally but gradually fading caudally; premaxillary lateral process abruptly deflected ventrally, forming a 165° angle with long axis of circummaxillary depression; maxilla with subtriangular joint surface for jugal that is more laterally than dorsally facing and prominent dorsal jugal tubercle projected caudally; and steeply down-warped sagittal crest of parietal substantially elevated above temporal bar. In addition, Eotrhachodon differs from other hadrosaurids in possessing the following unique combination of characters: thin, reflected oral margin of premaxilla (convergent in Gryposaurus, Prosauropolophus, and Saurolophus); maxilla combining deep rostral region; steeply angled rostroventral margin of rostroventral apex that forms a 45° angle with rostral alveolar margin; dorsal process positioned entirely caudal to mid-length of maxilla; extensive rostroventral margin with wide lateral exposure under lacrimal; and short (25% of maxillary length) and steeply sloping ectopterygoid shelf.

Description—The skull of Eotrhachodon orientalis combines characters of hadrosaurids and derived attributes that are exclusive to saurolophid hadrosaurids. Among the former is the moderate ventral offset of the premaxillary oral margin relative to the occlusal plane of the maxilla (Fig. 1A), so that the distance between these premaxillary and maxillary areas is half of the mean depth of the dentary ramus (Prieto-Márquez, 2010b). However, the oral margin of the premaxilla is relatively derived in E. orientalis, being thin and reflected (Fig. 1A) as in saurolophids (Bell, 2011) and kritosaurin (Prieto-Márquez, 2010c) saurolophines. Ventrally, the premaxillary denticles are arranged in two rows. As in hadrosaurids (Wagner, 2004; Prieto-Márquez, 2010b), the circummaxillary depression entirely surrounds the bony naris and, like in saurolophines (Prieto-Márquez and Wagner, 2014), it is compartmented. The circummaxillary depression of E. orientalis consists of three fossae, as in species of Edmontosaurus (Campione and Evans, 2011). In E. orientalis, two faint ridges that converge rostroventrally divide the depression into dorsal, caudoventral, and rostroventral fossae (Fig. 1A, B). Premaxillary foramina are absent within the circummaxillary depression.

The maxilla exhibits a deep palatine process (Fig. 1C). This bone shares two characters with the kritosaurin saurolophines Gryposaurus spp. (Gates and Sampson, 2007) and Kritosaurus horneri (Prieto-Márquez, 2014): a steep premaxillary shelf that forms a 45° angle with the rostral segment of the tooth row and a subtrapezoidal lateral surface of the rostroventral margin of the maxilla that is extensively exposed under the lacrimal (Fig. 1C). The triangular dorsal process rises caudal to the mid-length of the maxilla. It is twice as wide as it is tall, and its apex is caudally skewed. The articular surface for the jugal is subtriangular and faces laterally, as is common in hadrosaurids (Prieto-Márquez and Wagner, 2009). In E. orientalis, this articular surface displays a prominent, caudally projected dorsal tubercle (Fig. 1C). The large rostral maxillary foramen is partially exposed laterally and lies about mid-depth to the rostral region of the maxilla. This is below the position typically seen in hadrosaurids, where the foramen is located closer to the rostroventral margin of the maxilla (Prieto-Márquez, 2010b). The ectopterygoid shelf is morphologically plesiomorphic in that it accounts for only one fourth of the total length of the alveolar margin of the maxilla (as in Eolambia caroljonesae; see McDonald et al., 2012) and in being steeply inclined caudoventrally, forming a 20° angle with the caudal segment of the alveolar margin (as in Levnesovia transoxiana; see Sues and Averianov, 2009; Fig. 1C). The maxillary dental battery also presents a mixture of derived and plesiomorphic characters in the context of Hadrosauridae. It bears 32 tooth characters in the context of Hadrosauridae. It bears 32 tooth battery also presents a mixture of derived and plesiomorphic characters in the context of Hadrosauridae. It bears 32 tooth characters in the context of Hadrosauridae. It bears 32 tooth characters in the context of Hadrosauridae. It bears 32 tooth characters in the context of Hadrosauridae. It bears 32 tooth characters in the context of Hadrosauridae. It bears 32 tooth characters in the context of Hadrosauridae.
FIGURE 2. Strict consensus tree of the four most parsimonious trees resulting from the phylogenetic analysis of hadrosauroid relationships, showing
the position of *Eotrachodon orientalis*. Numbers above branches are bootstrap proportions, whereas those below indicate decay indices (Bremer
support).
The lacrimal is triangular and rostrally elongate, with a ventral margin that is convex rostral to the jugal notch (Fig. 1A), as in *Gryposaurus* spp. (Gates and Sampson, 2007), *Kritosaurus horneri* (Prieto-Márquez, 2014), *Saurolophus* spp. (Bell, 2011), and *Prosaurolophus maximus* (McGarry et al., 2013). The prefrontal has a broad rostroventral flange and a subquadrangular orbital margin. The apex of the rostral process of the jugal is elongate and positioned within the dorsal half of the rostral process (Fig. 1E) as in non-brachylophosaurus saurolophines (Prieto-Márquez, 2010b). As in basal hadrosaurids (for example, *Bactrosaurus johnsoni*; Godfrey et al., 1998; Prieto-Márquez, 2011a), the medial articular surface of the jugal rostral process is roofed by a narrow shelf that extends medially from the orbital margin (Fig. 1E). However, unlike in basal hadrosaurids (e.g., *Tanisaurus sinensis*; Wiman, 1929), with the exception of *Lophorhothon atopus* (Langston, 1960), the shelf of *Eotrachodon orientalis* is autapomorphically oblungety (rostrodorsally) rather than horizontally oriented (Fig. 1E). The articular facet is deeper than wide.

The dorsal segment of the quadrate is slightly curved caudally. The distal articular surface of this bone is subtriangular due to the rostrocaudal expansion of the lateral condyle. The distal end of the squamosal ramus of the postorbital is bifid and extends caudally to overlap as much as one fourth of the quadratotocus. The prectyloid process of the squamosal is relatively short, being only 60% as long as the breadth of the quadratotocus. The infratemporal fenestra is deeper and broader than the orbit, as in kritosaurus saurolophines (Prieto-Márquez, 2014) but unlike that of the basal hadrosaurid *Lophorhothon atopus* (Langston, 1960; Fig. 1A). The frontal contributes extensively to the orbit and its cribriform surface is about 30% longer than wide (Fig. 1B). Extreme thinning and lack of articular facets of the rostromedial margin of the frontal, in the area surrounding the sagittal plane of the skull, suggests the presence of a fontanelle in MSC 7949. The parietal is nearly twice as long as wide at its minimum width (Fig. 1D). In the braincase, the rostral constriction of the basisphenoid, caudal to the basipterygoid processes, is moderately developed: the maximum width of the basisphenoid across the sphenoc-occipital tubera is one and a half times that of the constriction.

As in most basal hadrosaurids, the dentaries of the prede- tary are not limited to the rostral margin but rather extend caudolaterally onto the dorsal surface of each lateral ramus. The lingual surface of the sagittal keel lacks a median ridge. The dentary displays a short proximal exdentulous margin, a characteristic of basal iguanodontians. In *Eotrachodon orientalis* this margin is only 8% of the distance between the rostralmost tooth position and the caudal edge of the coronoid process. The sylphysial process is ventrally deflected 15° relative to the long axis of the dental battery. The coronoid process displays a plesiomorphic morphology: it is vertically oriented, and its apex is only moderately expanded so that it is taller than it is wide. The caudal end of the dental battery is flush with the caudal margin of the coronoid process. There are 26 tooth positions in the dentary. The labio-lingually narrow alveolar space suggests that there were one or at most two functional teeth exposed on the occlusal plane at each tooth position. This contrasts with the derived count of three functional teeth present in hadrosaurids. The surangular displays the derived hadrosaurid morphology: it lacks foramina and has a strap-like rostral ascending process that wedges dorsally into a thin sliver, and the convex side of the lateral and lateroventral surface of the surangular face more ventrally than laterally (Fig. 1A). The angular is positioned mediadly and is not exposed in lateral view.

Dentary tooth crowns have a mean height : width ratio of 2.3. There is a median primary ridge and one or two fainter accessory ridges. The marginal denticles are small papillae that are similar in size on both margins. The mesial margin of each tooth crown overlaps the distal one of the adjacent crown. The maxillary teeth show height/width ratios ranging from 2.5 to 3.1. The enamelled lingual surfaces of these teeth show a prominent single median ridge.

Of the preserved postcranial bones, the only informative ele- ments are in the pelvic girdle. The pubis is relatively short, with a total length that is slightly more than twice the maximum width of the acetabular margin. The distal blade of the prepubic process is expanded more ventrally than dorsally, as in all saurolo- phine hadrosaurids and *Lophorhothon atopus* (e.g., AUMP 2295; Prieto-Márquez, 2008). The prepubic process is also deeper than the acetabular margin. The ischium has a short and straight distal iliac process margin, as in saurolophines but unlike the recurved process characteristic of most basal hadrosauroids and all lambeosaurine hadrosaurids.

**PHYLOGENETIC POSITION OF EOTRACHODON**

The phylogenetic position of *Eotrachodon orientalis* among hadrosauroid iguanodontians was inferred via maximum parsimony analysis. The taxonomic sample consisted of 61 hadrosauroid species (including 16 outgroups to Hadrosauridae, 22 saurolophines, and 21 lambeosaurines). The data set consisted of 273 equally weighted morphological characters (189 cranial and 84 postcranial; see Supplementary Data 2 and 3). Multistate characters containing states that are not mutually exclusive, following a natural morphocline, were ordered. This criterion allows for 'crediting' shared intermediate states. An example of such a character is the position of the large maxillary foramen (character 85) that includes three states: exposed laterally and opening ventral to the mid-depth of the premaxillary shelf (0); exposed laterally and opening near the dorsal margin of the premaxillary shelf (1); not exposed laterally and opening on the dorsal surface of the premaxillary shelf (2). The optimal tree(s) search was conducted in TNT version 1.1 (Goloboff et al., 2008).

A heuristic search of 10,000 replicates using random addition sequences was performed, followed by branch swapping by tree bisection-reconnection holding ten trees per replicate. Decay indices (Bremer support) and bootstrap proportions were computed using TNT. The bootstrap analysis was set for 5,000 replicates using heuristic searches, in which each search was conducted using random addition sequences with branch-swapping by subtree pruning and regrafting and 25 replicates.

The analysis resulted in four most parsimonious trees of 990 steps each (Consistency Index = 0.40, Retention Index = 0.78); the best score was found in 8,573 of the 10,000 replicates. Such a relatively low consistency index indicates that there is substantial homoplasny in these data, a fact already noticed in previous phylogenetic studies of hadrosaurids (e.g., Horner et al., 2004; Prieto-Márquez, 2010a). The strict consensus tree shows *Eotrachodon orientalis* within Hadrosauridae as sister to Saurolophidae (Saurolophinae + Lambeosaurinae) (Fig. 2). Our specimen shares various synapomorphies with saurolophids, including: pre- dentary with subsquared rostrolateral corner and subrectangular denticles; dentary occlusal plane parallel to the lateral surface of the mandibular ramus; strap-like rostral ascending process of the surangular that wedges dorsally into a thin sliver; circummarial depression containing a subsidiary rostral fossa; maxilla with broad rostral dorsal region extensively exposed laterally and with its horizontal dorsal margin under the lacrimal; subtriangular maxillary joint surface for the jugal that is more laterally than dorsally oriented: apex of the rostral process of the jugal set within the dorsal half of the process; orbital and infratemporal margins of the jugal subequally wide; circummarial depression surrounding, at least, the caudal margin of the bony naris (convergent in *Lophorhothon atopus*); orbit deeper than wide; and pubic process of the ischium proximodistally shorter than the width of the distal articular surface of the bone. Except for the
latter ischiadic character, all of the above synapomorphies are ambiguous due to lack of preservation of virtually all cranial bones, except for a handful of maxillary fragments in Hadrosaurus foulkii (Prieto-Márquez et al., 2006), which is the most basal hadrosaurid and outgroup to the Eotrichodon–Saurolophidae clade.

_Eotrichodon orientalis_ is excluded from Saurolophidae because it unambiguously lacks the following saurolophid synapomorphies: length : width ratio of dentary tooth crowns of 2.8 or greater; absent or very reduced marginal denticles on dentary teeth; predentary denticles restricted to the rostral oral margin; presence of a ridge on the lingual surface of the median keel-shaped process of the predentary; symphyseal process of the dentary ventrally deflected forming a 17°–25° angle with the tooth row; greatly expanded apex of the coronoid process of the dentary; premaxillary margin well offset ventrally from the maxillary occlusal plane (the distance between the occlusal plane of the maxilla and the premaxillary oral margin is greater than the mean depth of the dentary); large maxillary foramen positioned near the rostrodorsal margin of the maxilla; caudoventral margin of the rostral process of the jugal being as deep as or slightly deeper than wide; maxillary articular surface of the rostral process of the jugal facing medially, lacking dorsal shelf; and presence of cranial crest (convergent in _Lophorhothon_).

**ANCESTRAL AREA OF HADROSAURIDAE**

Asia has been traditionally regarded as the most likely area of origin for hadrosaurids because morphologically plesiomorphic taxa preceding the hadrosaurid radiation were first recognized from this continent (e.g., Wiman, 1929; Gilmore, 1933; Rozhdestvensky, 1966; Milner and Norman, 1984; You et al., 2003; Godefroit et al., 2008). However, the subsequent discovery of additional outgroup taxa to hadrosaurids in other continents opened the door to alternative hypotheses that include Europe (Company et al., 1998; Casanovas et al., 1999), North America (Head, 1998, 2001; Kirkland, 1998; Horner et al., 2004; Prieto-Márquez, 2010a), and South America (Brett-Surman, 1979; Powell, 1987) as ancestral areas. Biogeographic reconstructions have involved dispersal and vicariance as the primary processes shaping the diversification and distribution of hadrosaurids (Head, 1998; Brett-Surman, 1979; Weishampel and Weishampel, 1983; Russell, 1993; Casanovas et al., 1999; Godefroit et al., 2003; Godefroit, Bolotsky, and Van Itterbeeck et al., 2004; Prieto-Márquez, 2010a; Prieto-Márquez et al., 2013).

The recognition of _Eotrichodon orientalis_ as one of the oldest and most basal hadrosaurids preceding the major diversification of the clade led us to reevaluate the ancestral ranges for Hadrosauridae and its principal constituent subclades. Ancestral areas for the internal nodes of the hadrosaurid phylogenies resulting from the maximum parsimony analysis were quantitatively inferred via Statistical Dispersal-Vicariance Analysis (S-DIVA; Yu et al., 2010; Figs. S1–S4 of Supplementary Data 4). Because this technique requires fully bifurcating phylogenies, we applied S-DIVA to each of the four most parsimonious trees resulting from the parsimony analysis. This option was preferred instead of other alternatives for obtaining an entirely resolved phylogeny, such as pruning taxa from the consensus tree or using a maximum agreement subtree. This is because the latter options allow for obtaining a fully bifurcating phylogeny at the expense of deleting taxa and their associated recorded geographical areas, i.e., the omission of taxa may seriously affect the biogeographical results by creating spurious ancestral range reconstructions. The program uses a model in which vicariance, sympatric speciation, dispersal, and extinction events are given different costs that are inversely related to the likelihood of occurrence of these events. Specifically, vicariance (speciation due to emergence of a dispersal barrier) and duplication (speciation within the same area) have a cost of zero, whereas dispersal and extinction events have a cost of one per each area unit added or deleted, respectively, from the distribution (Ronquist, 1997). The method uses parsimony as optimality criterion and searches for the reconstruction that minimizes the number of dispersal–extinction events (or cost) required to explain the geographical distribution of terminal taxa (Ronquist, 1997). A modification of DIVA, S-DIVA incorporates the methods of Nylander et al. (2008) and Harris and Xiang (2009) in order to calculate statistical support for the reconstruction of each ancestral area (Yu et al., 2010). In S-DIVA, the frequencies of each ancestral range for a given node of the phylogeny are averaged over all trees, so that each alternative ancestral range at a node is weighted by the frequency of occurrence of the node (Yu et al., 2011). The method was implemented in the program RASP 2.0b (Yu et al., 2010). Five general areas where hadrosaurid species have been recorded were considered: the European Archipelago (present-day Europe), Asia, Laramidia (present-day western North America), Appalachia (present-day eastern North America), and South America. The geographical distribution of terminal taxa is shown in Supplementary Data 4.

The analysis unambiguously inferred Appalachia as the most likely ancestral area for hadrosaurids (Fig. 3). The most recent common ancestor of Saurolophidae (the major hadrosaurid radiation) was reconstructed as widespread in Laramidia and Asia (Fig. 3). This reconstruction implies the dispersal of early Appalachian hadrosaurids to Laramidia and subsequently from this continent to Asia. According to Blakey (2009), Laramidia and Appalachia remained connected in southern North America approximately 100 million years ago (early Cenomanian); it should be noted that, except for _Eotrichodon orientalis_, all known Laramidian pre-Campanian hadrosaurids fall outside Hadrosauridae; these include _Eolambia caroljonesa_ [Kirkland, 1998; Head, 2001; McDonald et al., 2012], _Protohadros byrdi_ [Head, 1998], _Jeyawati rugoculus_ [McDonald et al., 2010], and _Huehuecanauhtlis tiquichensis_ [Ramirez-Velasco et al., 2012]. This may have been a feasible dispersal route for early hadrosaurids and predicts the presence of these animals in Appalachia in Cenomanian times. This assumes a ghost lineage of about 16 million years until the late Santonian occurrence of _Eotrichodon orientalis_. The dispersal from Laramidia to Asia may have occurred through Beringia. This likely occurred no later than the late Santonian, with the oldest saurolophids being Santonian in age (Averianov and Nesov, 1995; Godefroit, Alifanov, and Bolotsky, 2004).

Finally, Saurolophinae and Lambeosaurinae were unambiguously inferred to have originated after vicariance in Laramidia (no later than the early Campanian, given the age of the oldest known saurolophines: _Gryposaurus latidens_ [Prieto-Márquez, 2010c] and _Acristavus gagslarsoni_ [Gates et al., 2011]), and Asia (no later than the late Santonian, given the age of the oldest known lambeosaurines, _Aralosaurus tuberiferus_ [Godefroit, Alifanov, and Bolotsky, 2004], _Jaxartosaurus aralenis_ [Averianov and Nesov, 1995], and _Kazaklambia convincex_ [Bell and Brink, 2013]), respectively. The latter inferences support previous hypotheses that posited a North American ancestral area for saurolophines (Horner et al., 2004; Sues and Averianov, 2009; Prieto-Márquez, 2010a) and an Asian ancestral area for lambeosaurines (Sues and Averianov, 2009; Prieto-Márquez, 2010a; Godefroit, Bolotsky, and Van Itterbeeck, 2004b; Godefroit et al., 2008, Prieto-Márquez et al., 2013).

**DISCUSSION**

Soon after their origin in the Santonian (Sues and Averianov, 2009; Prieto-Márquez, 2010a), hadrosaurids diversified into two major clades: the solid-crested or crestless Saurolophinae
(Prieto-Márquez, 2010b) and the hollow-crested Lambeosaurinae (Evans, 2006). Among other attributes, these clades greatly differ in their narial anatomy. In saurolophines, the nasal passage remains rostral to the orbits as in ancestral iguanodontians (Weishampel, 1981; Wagner, 2004). In addition, the external bony naris and nasal vestibulum lie within the circumnarial depression and an extensive excavation surrounds the bony naris and is exposed on the lateral surface of primarily the premaxilla and nasal (Prieto-Márquez and Wagner, 2014). Variation in the depth of the circumnarial depression and length, proportions, and number and placement of various foramina, ridges, and subordinate fossae characterize saurolophine species (Hopson, 1975; Prieto-Márquez, 2010a, 2010b; Bell, 2011; Gates and Sampson, 2007; Campione and Evans, 2011). In contrast, the lambeosaurine bony naris, like those of basal iguanodontians and non-hadrosaurid hadrosauroids, is smooth and lacks
foramina, ridges, and accessory fossae (Wagner, 2004). The nasal passage of lambeosaurs is apomorphically enclosed by thin sheets of bone (hollow cranial crests), extending caudodorsally and arcing in a broad loop to enter the skull rostrodorsally to the orbits (Weishampel, 1981; Evans, 2006).

The narial region of *Eotrachodon orientalis* shares various characters with saurolophine hadrosaurids. In addition to being exposed on the lateral surface of the rostrum, the circumnarial depression is divided into subordinate fossae as in all saurolophine taxa (Fig. 3). Specifically, in Brachylophosaurus (Hong and Miyata, 1999; Prieto-Márquez, 2005), Kritosaurus (Prieto-Márquez, 2010c, 2014), and Saurolophini (Bell, 2011; McGarrity et al., 2013) the circumnarial depression consists of two fossae: a longer and extensive caudal fossa and an abbreviated rostral fossa lying adjacent to the oral margin of the premaxilla; these fossae are separated by a low transverse ridge. *Edmontosaurus* also displays a larger caudal fossa but, unlike in the aforementioned tribes, the rostral fossa is further subdivided into rostrodorsal and rostroventral fossae; a triradiate promontory separates all three fossae (Prieto-Márquez and Wagner, 2014). *Eotrachodon orientalis* exhibits a tripartite circumnarial depression, but the subordinate fossae are arranged differently than those of *Edmontosaurus* and all other saurolophines. Whereas in saurolophines the fossae are arranged rostrocaudally (i.e., the main division of the fossae is transverse to the long axis of the premaxilla), in *E. orientalis* they are arranged dorsoventrally (i.e., the main division bisects the premaxilla longitudinally; Figs. 1A, 3). Furthermore, the entire circumnarial depression of *E. orientalis* is shallower than that of saurolophines and the ridges dividing the various subordinate fossae of the rostral half of the premaxilla of *E. orientalis* are thinner and substantially less prominent than in saurolophines (Figs. 1A, 3). Unlike saurolophines, however, there is no premaxillary foramen in *E. orientalis*, basal hadrosaurids, and lambeosaurs (Prieto-Márquez, 2010b). The premaxilla of saurolophines shows a large foramen located between the rostromedial margin of the caudal fossa of the circumnarial depression and the rostroventral margin of the bony naris (Prieto-Márquez and Wagner, 2014).

As in saurolophines, the circumnarial depression of *Eotrachodon orientalis* extends caudal to the bony naris (Fig. 3). The depth of the caudal region of the circumnarial depression varies among saurolophine species. It is gently incised in *Gryposaurus* (Prieto-Márquez, 2010c) and *Brachylophosaurus* (Prieto-Márquez, 2005), whereas it is deeply excavated in *Prenocephalus* (M. G. Bell, 2011), and *Edmontosaurus* (Prieto-Márquez and Wagner, 2014). In *E. orientalis*, the post-narial region of the circumnarial depression is gently incised to a degree comparable to that of species of *Gryposaurus* (Gates and Sampson, 2007).

The premaxillary oral margin is everted in *Eotrachodon orientalis* and saurolophines (however, with notable variation in the depth and eversion of the margin; Fig. 3). This condition stands in contrast to the convex and rostrolaterally ventrally deflected oral margin of the premaxilla in non-hadrosaurid hadrosauroids and lambeosaurs (Prieto-Márquez, 2010b).

Consideration of *Eotrachodon orientalis* as the sister taxon to Saurolophidae and optimization of the above characters in the inferred phylogeny indicate that a saurolophine-like narial structure (i.e., a laterally exposed circumnarial depression with sub-sidialy fossae that extends caudal to the bony naris) likely evolved before the split between Saurolophinae and Lambeosaurinae, no later than the late Santonian (Fig. 3). This narial structure might have also been ancestral for hadrosaurids, but at this juncture this possibility remains untestable because of the near absence of preserved cranial elements in the most basal hadrosaurid, *Hadrosaurus foulkii* (Prieto-Márquez et al., 2006).

As an ancillary conclusion, the acquisition of a saurolophine-like circumnarial structure during the earlier stages of hadrosaurid evolution has implications for the evolution of the simplified rostral narial morphology observed in lambeosaurs. It confirms that the lambeosaurine condition evolved independently from the similar configuration observed in basal hadrosaurids. In doing so, our results provide additional support to previous hypotheses that posited a caudodorsal migration of the ancestral circumnarial structure inside a hollow supracranial crest via rotation of the facial skeleton and transposition of the dorsal rostrum to the skull roof. This resulted in the simplified morphology of the rostrum and external bony naris present in lambeosaurs (Hopson, 1975; Wagner, 2004; Evans, 2006). This hypothesis is congruent with the presence of a laterally exposed and subdivided circumnarial depression in *Tsintaosaurus spinorhinus*, which is reminiscent of that seen in *Eotrachodon orientalis* and saurolophines (Prieto-Márquez and Wagner, 2013). *Tsintaosaurus spinorhinus* occurs in lower Campanian strata of the Jingangkou Formation in Shandong Province, China (Young, 1958; Hong and Miyata, 1999), and is the most basal lambeosaurine for which the premaxilla is preserved. Notably, it suggests the possibility that the caudodorsal migration of the circumnarial structure and subsequent reconfiguration of the facial skeleton and the nasal passage in lambeosaurs occurred relatively late in hadrosaurid evolution during Campanian times.

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