



## ***Glishades ericksoni*, a new hadrosauroid (Dinosauria: Ornithopoda) from the Late Cretaceous of North America**

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### **Abstract**

A new genus and species of hadrosauroid dinosaur, *Glishades ericksoni*, is described based on paired partial premaxillae collected from the Upper Cretaceous Two Medicine Formation of Montana, in the Western Interior of the United States of America. This taxon is diagnosed on the basis of a unique combination of characters: absence of everted oral margin, arcuate oral margin with wide and straight, obliquely oriented, and undeflected anterolateral corner, grooved transversal thickening on ventral surface of premaxilla posterior to denticulate oral margin, and foramina on anteromedial surface above oral edge and adjacent to proximal end of narial bar. Maximum parsimony analysis positioned *G. ericksoni* as a derived hadrosauroid. Exclusion of *G. ericksoni* from Hadrosauridae was unambiguously supported by the lack in AMNH 27414 of a dorsomedially reflected premaxillary oral margin. Furthermore, the maximum agreement subtree positioned *G. ericksoni* as the sister taxon to *Bactrosaurus johnsoni*. This position was unambiguously supported by posteroventral thickening on the ventral surface of the premaxilla (independently derived in saurolophid hadrosaurids and *Ouranosaurus nigeriensis*) and having foramina on each premaxilla on the anterior surface, adjacent to the parasagittal plane of the rostrum (reconstructed as independently derived in *Brachylophosaurus canadensis*, *Maiasaura peeblesorum*, and *Edmontosaurus annectens*).

**Key words:** Hadrosauroidea, Hadrosauridae, cladistics, ontogeny, Cretaceous, dinosaur

### **Introduction**

Hadrosauroidea is a diverse clade of herbivorous dinosaurs whose remains have been found in Late Cretaceous (Barremian/Aptian through Maastrichtian) strata of Europe, Asia, the Americas, and Antarctica (Horner *et al.* 2004; Prieto-Márquez in press). Over the last century and the beginning of the present one, numerous discoveries of basal hadrosauroids have filled a gap in our understanding of the early evolution of the clade, particularly regarding the skeletal modifications that took place from basal iguanodontoideans to the Hadrosauridae, one of the most derived and abundant clades of large herbivores during the Campanian and Maastrichtian (Horner *et al.* 2004). The majority of these discoveries came from Aptian through Maastrichtian strata of Eurasia (Gilmore 1933; Rozhdestvensky 1966; Weishampel *et al.* 1993; Godefroit *et al.* 1998; Wang & Xu 2001; You *et al.* 2003; Dalla Vecchia 2009; Sues & Averianov 2009) and, with at least 13 known species, constitute most of the known diversity of basal hadrosauroids. In contrast, the fossil record of these animals in North America is relatively small, being currently restricted to a few species. According to Prieto-Márquez (in press), these include the following taxa: *Claosaurus agilis*, from the Coniacian of Kansas (Carpenter *et al.* 1995); *Lophorhothon atopus*, from the Late Santonian–Early Campanian of Alabama (Langston 1960); *Protohadros byrdi*, from the Cenomanian of Texas (Head 1998); *Eolambia caroljonesa*, from the Cenomanian of Utah (Kirkland 1998; Garrison *et al.* 2007; Gradstein *et al.* 2008); possibly *Cedrorestes crichtoni*, from the Barremian of Utah (Gilpin *et al.* 2007); and a new taxon from the Turonian of New Mexico (McDonald *et al.* in press).

Here, a new genus and species of basal hadrosauroid is described based on a fragmentary specimen collected from the Two Medicine Formation of Montana (United States of America). The new taxon is

founded upon a unique combination of derived and plesiomorphic characters and adds to the knowledge of the distribution and diversity of North American basal hadrosauroids. It substantially extends stratigraphically and biogeographically the fossil record of relatively derived non-hadrosaurid hadrosauroids in North America.

### **Institutional abbreviations**

AEHM	Amur Natural History Museum, Blagoveschensk, Russia
AMNH	American Museum of Natural History, New York, USA
CM	Carnegie Museum of Natural History, Pittsburgh, USA
CMN	Canadian Museum of Nature, Ottawa, Canada
CPC	Paleontological Collection of Coahuila, Saltillo, Argentina
FGGUB	Facultatea de Geologie si Geofizica, Universitatea Bucuresti, Bucharest, Romania
FMNH	The Field Museum of Natural History, Chicago, USA
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
LACM	Natural History Museum of Los Angeles County, Los Angeles, USA
MOR	Museum of the Rockies, Bozeman, USA
MSNM	Museo Civico di Storia Naturale di Milano, Milan, Italy
NHM	The National History Museum, London, UK
OMNH	Sam Noble Oklahoma Museum of Natural History, Norman, USA
OTM	Old Trail Museum, Choteau, USA
PIN	Palaeontologiceski Institut, Akademii Nauk, Moscow, Russia
RAM	Raymond M. Alf Museum, Claremont, USA
ROM	Royal Ontario Museum, Toronto, Canada
SBDE	Sino-Belgian Dinosaur Expedition (specimens are property of the Inner Mongolian Museum in Hohhot, China; casts and part of the material are temporarily housed at the Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium)
SC	Italian State Collections (specimens housed at the Museo Civico di Storia Naturale, Trieste, Italy)
SM	Naturmuseum Senckenberg, Frankfurt, Germany
SMU	Shuler Museum of Paleontology, Southern Methodist University, Dallas, USA
TMM	Texas Memorial Museum, Austin, USA
TMP	Royal Tyrrell Museum of Paleontology, Drumheller, Canada
UCM	University of Colorado Museum, Boulder, USA
UCMP	University of California Museum of Paleontology, Berkeley, USA
USNM	National Museum of Natural History, Washington D.C., USA
YPM	Yale Peabody Museum of Paleontology, New Haven, USA
ZPAL	Instytut Paleobiologii, Polska Akademia Nauk, Warsaw, Poland

### **Systematic Paleontology**

#### **Dinosauria Owen, 1842**

#### **Ornithischia Seeley, 1887**

#### **Ornithopoda Marsh, 1881**

#### **Hadrosauroidea Cope, 1870**

## *Glishades* gen. nov.

**Etymology:** “Glis” is the Latin for “mud” and “hades” means “unseen” in Greek; thus, the generic name may be translated as “concealed in mud”, in reference to its being found in sedimentary strata. Also, “Hades” was the dark lord of the underworld in Greek mythology, here metaphorically referring to the “world” beneath the surface where fossils occur.

**Type and only species:** *Glishades ericksoni* sp. nov.

**Diagnosis:** As for the type species (below).

## *Glishades ericksoni* gen. et sp. nov.

Fig 1

**Etymology.** The specific name honors Dr. Gregory M. Erickson, for his important contributions to the knowledge of archosaur paleobiology.

**Holotype.** AMNH 27414, partial left and right premaxillae.

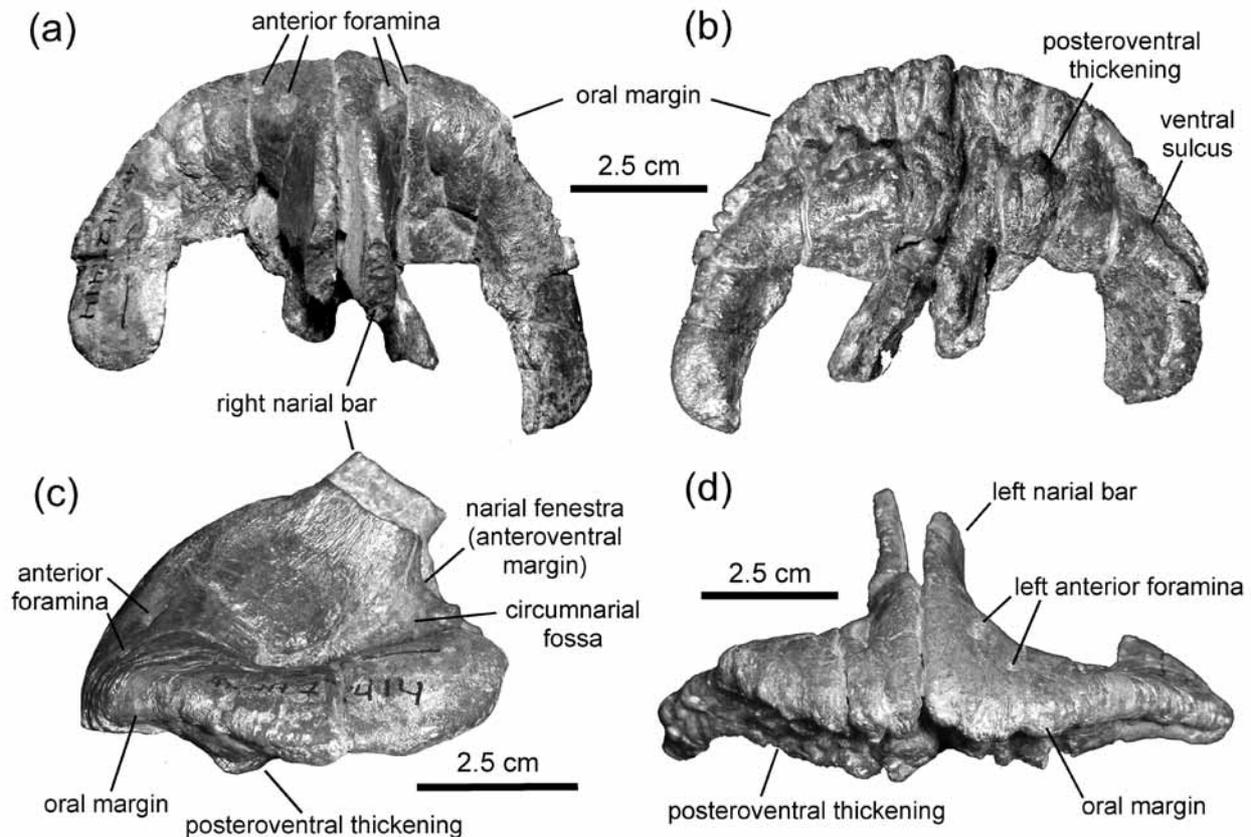
**Type locality and horizon.** The specimen was collected by Brown, Kaiser, and Johnson ca. 1915 in South Milk River, 30 miles west of Sweetgrass, Glacier County, Montana (United States of America), from strata corresponding to the Two Medicine Formation (Campanian, Upper Cretaceous).

**Diagnosis.** Hadrosauroid dinosaur with the following unique combination of premaxillary characters: absence of recurvature (“reflection”) of oral margin; arcuate oral margin with wide and straight, obliquely oriented, and undeflected anterolateral corner; foramina on anteromedial surface above oral edge and adjacent to proximal end of narial bar; and grooved transversal thickening on ventral surface of premaxilla posterior to denticulate oral margin.

**Nomenclatural note.** Clade names and phylogenetic definitions follow the comprehensive recent revision of hadrosaurid interrelationships by Prieto-Márquez (in press) (Figs 2–3). Accordingly, Hadrosauroidea consists of *Hadrosaurus foulkii* and all taxa most closely related to it than to *Iguanodon bernissartensis*, including Hadrosaurinae (represented solely by *Hadrosaurus*) and Saurolophidae. The latter is defined as the last common ancestor of *Saurolophus osborni*, *Lambeosaurus lambei*, and all its descendants, which includes the two major hadrosaurid clades: Saurolophinae and Lambeosaurinae.

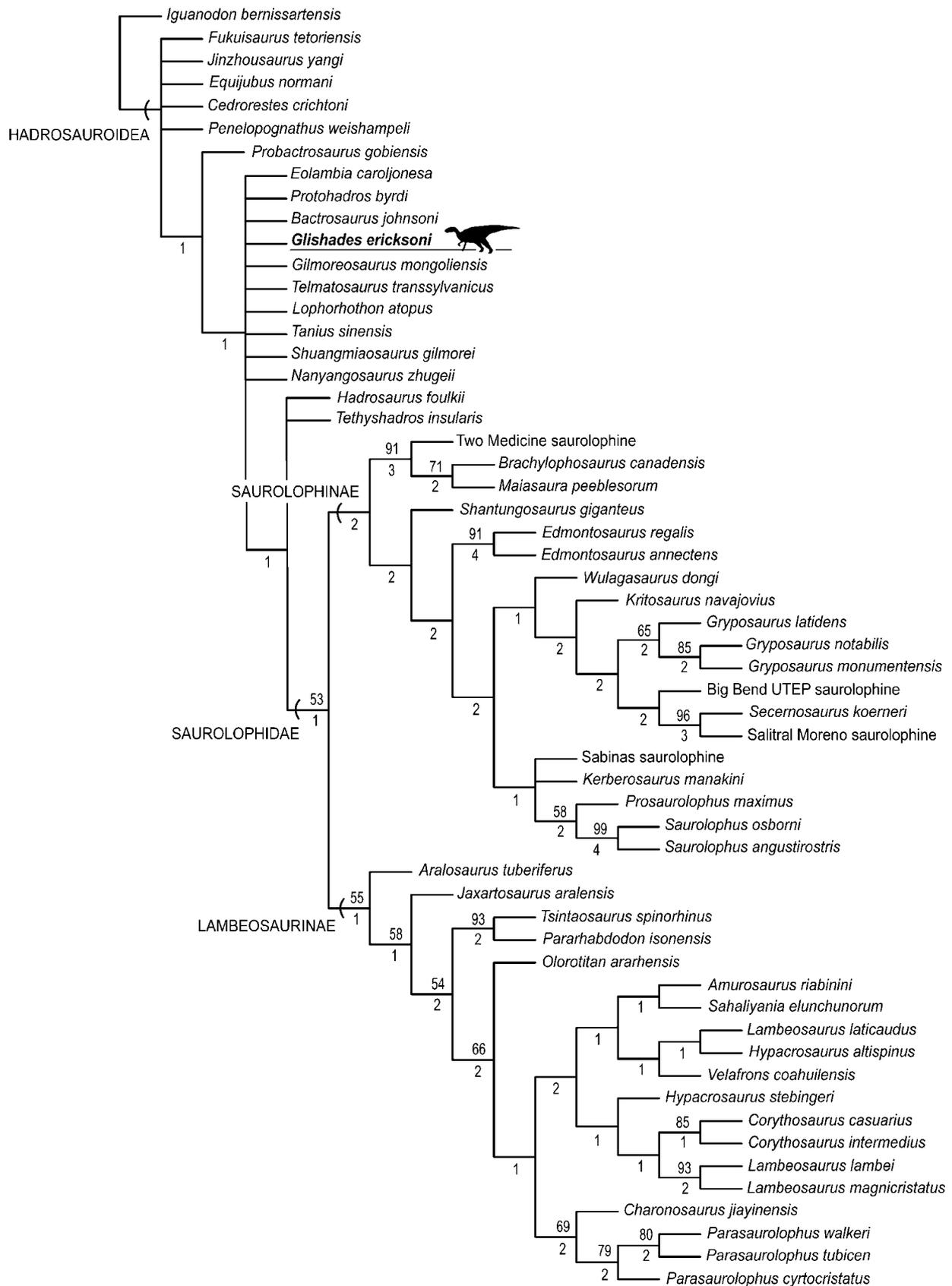
**Description.** Only the anterior regions of the articulated left and right premaxillae are preserved. In dorsal view, the oral margins of both premaxillae display an arcuate contour. This contour is not perfectly smooth, but is slightly truncated by the oblique orientation and nearly straight dorsal profile of the anterolateral corners of the oral margin (Fig. 1a). The anterior and lateral regions near the oral margin are ventrally deflected. In contrast, the anterolateral region is dorsoventrally compressed and slightly convex dorsally at the oral margin (Fig. 1c–d). There are transversal fractures across the lateral oral margin. Each fracture separates a posterior and anterior portion, so that the posterior portion is slightly offset ventrally relative to the anterior one. This displacement only affects the lateral half of the mediolateral width of the oral margin. When the posterior segment is restored to its original position by having its anterior edge meet the posterior edge of the anterior portion, the oral margin remains smooth and ventrally deflected. Adjacent and lateral to the interpremaxillary joint, each element is anteroposteriorly expanded to form the anteriormost extent of the narial bar. The anterior surface of this expanded area is triangular and faces anterodorsally and slightly laterally. It is pierced in each premaxilla by two foramina (Fig. 1a, d). A larger oval foramen is located a short distance from the narial bar; the second, much smaller foramen is located anteroventrally to the larger foramen. In addition to AMNH 27414, similarly located foramina are only unambiguously present in small (e.g., AMNH 6501 and 6575) to larger (e.g., Godefroit *et al.* 1998: plate 3, fig 4A) individuals of *Bactrosaurus johnsoni*, a subadult specimen of *Edmontosaurus cf. annectens* (CMN 8509), and a subadult *Gryposaurus* sp. (CMN 8784), along with additional foramina in *Brachylophosaurus canadensis* (e.g., MOR 794) and *Maiasaura peeblesorum* (e.g., OTM F138).

The anteromedial border of each premaxilla forms an angle of 65 degrees with the ventral surface. Posterodorsally, this border curves gently, forming a less steep angle with the ventral surface of the premaxilla. Posteriorly and dorsally, the anteromedial region of each premaxilla is extremely compressed mediolaterally to form the anterior terminus of the narial bar and the medial wall of the circumnarial fossa. Only a very small portion of the latter is preserved in each premaxilla, marked by a slightly and medially recessed surface (Fig. 1c). Posterodorsally, that surface is bounded by a crescentic edge, which constitutes a small part of the anteroventral terminus of the narial fenestra. The dorsal surface of each premaxilla, posterior to the oral margin and lateral to the narial fenestra, is only preserved anteriorly. There is no evidence of the presence of premaxillary foramina in this surface, as in non-hadrosaurid hadrosauroids and lambeosaurine hadrosaurids.

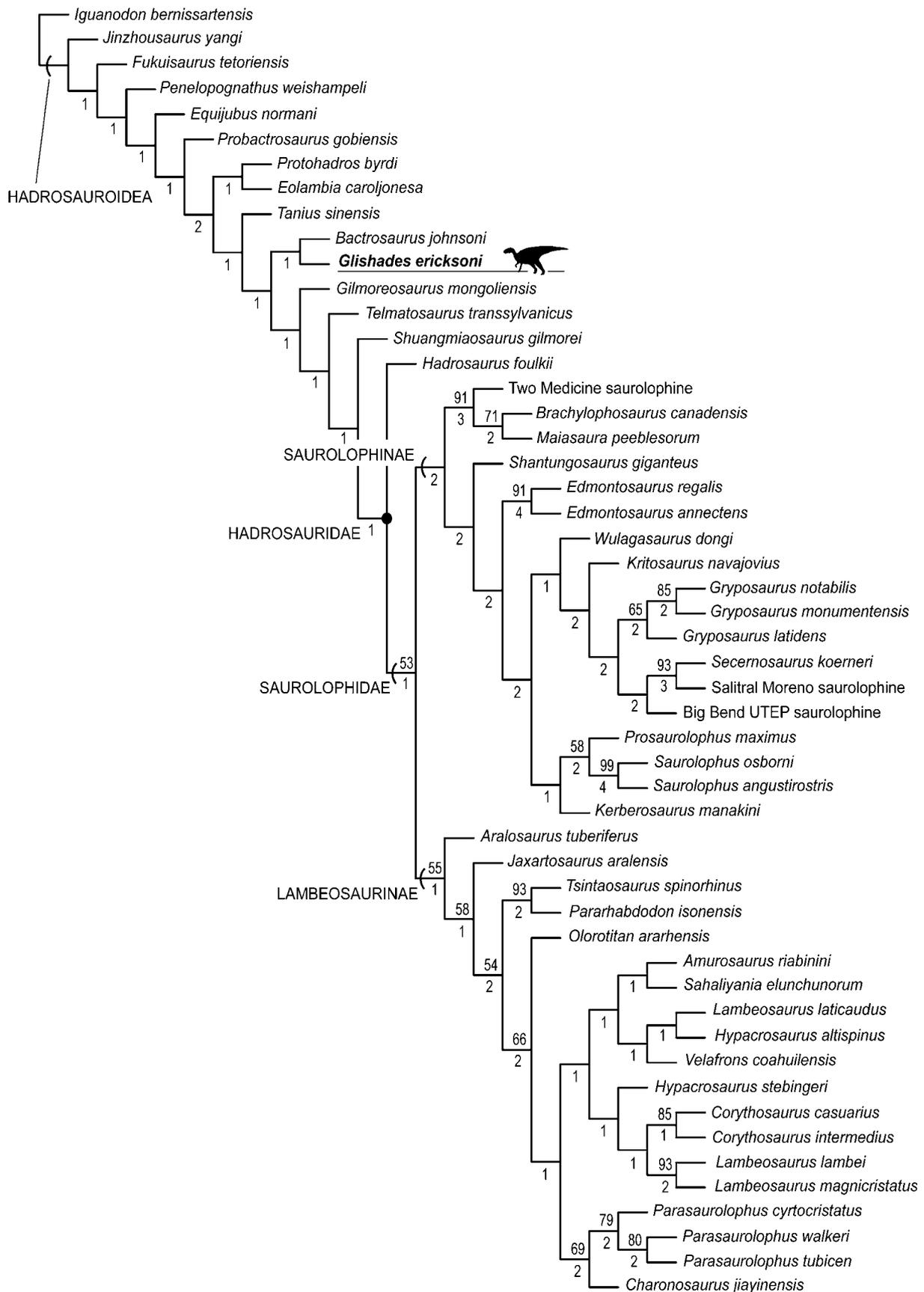


**FIGURE 1.** Paired premaxillae from the holotype specimen of *Glishades ericksoni* (AMNH 27414) in dorsal (a), ventral (b), left lateral (c), and anterior (d) views.

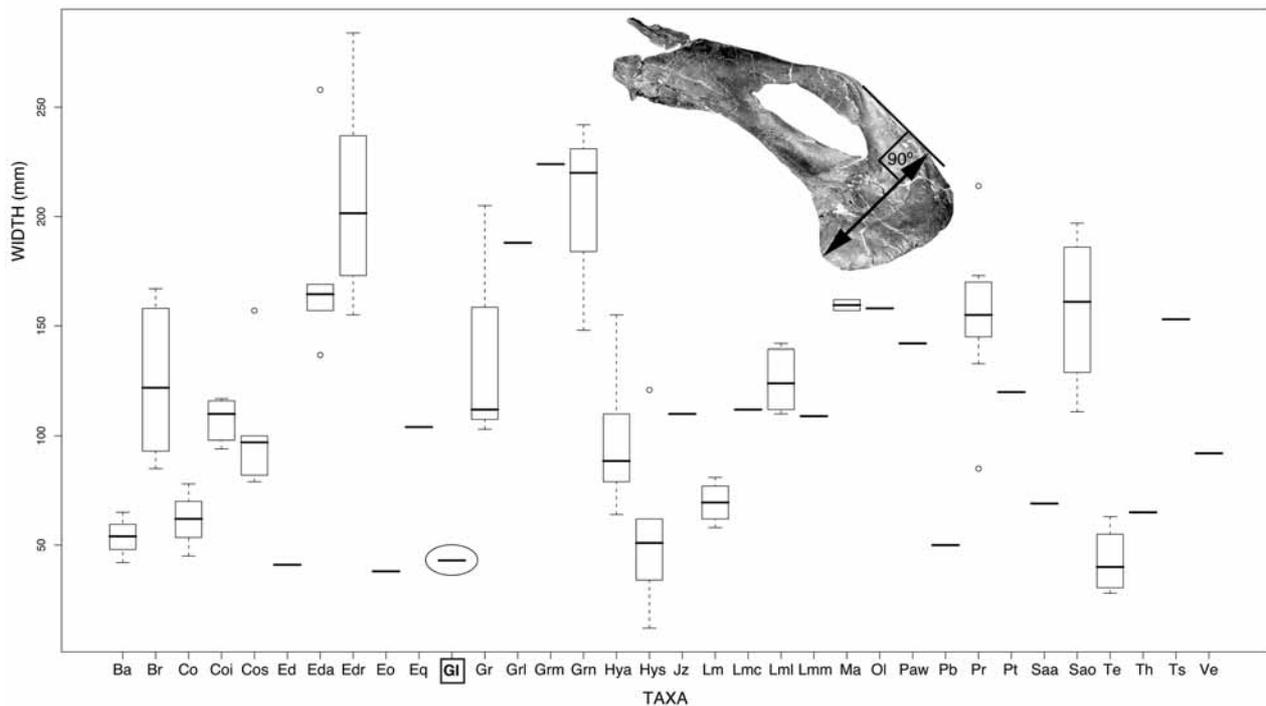
The ventral surface of each premaxilla is carved with deep anteroposteriorly-oriented grooves (Fig. 1b). The prominent ridges that lie between the grooves extend anteriorly into the oral margin of each premaxilla, forming denticle-shaped structures (Fig. 1d). Posterior to this denticulate margin, there is another thick and transversal layer of bone. This thickening protrudes ventrally and contains the posterior extent of the series of grooves and ridges that cross most the ventral surface of each premaxilla (Fig. 1b–d). A deep transversal sulcus separates the oral denticulate layer from this posterior thickening. This configuration of sulcus and “double denticulate layering” of the premaxilla is typically found in hadrosaurids; among non-hadrosaurid hadrosauroids it is also present in *Bactrosaurus johnsoni* (e.g., AMNH 6501 and 6575). Outside Hadrosauroidea, a posterior thickening also occurs in the basal iguanodontoidean *Ouranosaurus nigeriensis* (e.g., cast of GDF 300).



**FIGURE 2.** Strict consensus cladogram of the 80 most parsimonious trees derived from maximum parsimony analysis of 56 hadrosauroid taxa, showing the phylogenetic position of *Glishades ericksoni*. Numbers above branches indicate bootstrap proportions, whereas those below indicate decay indices.



**FIGURE 3.** Maximum agreement subtree derived from maximum parsimony analysis of 56 hadrosauroid taxa, showing the phylogenetic position of *Glishades ericksoni*. Numbers above branches indicate bootstrap proportions, whereas those below indicate decay indices.



**FIGURE 4.** Boxplot showing the known range of sizes for the premaxilla for the majority of hadrosauroid taxa for which this element is known. Premaxillary width is used as an indicator of the size of this bone. It is measured perpendicular to the proximal region of the narial bar, as indicated in the inserted photograph of the left premaxilla of *Maiasaura peeblesorum* (OTM F138). For each taxon, the box plot displays up to five statistical summary measures: smallest value of the sample, lower quartile, median (darkest horizontal line), upper quartile, and largest value. Each box contains the middle 50% of the values; its upper edge indicates the 75<sup>th</sup> percentile (upper quartile) and the lower edge represents the 25<sup>th</sup> percentile (lower quartile). The darkest horizontal line inside each box represents the median value of the sample. The ends of the vertical lines (“whiskers”) indicate the minimum and maximum values of the sample for a given taxon. Outliers are indicated by small circles. Taxon abbreviations: Ba, *Bactrosaurus johnsoni*; Br, *Brachylophosaurus canadensis*; Co, *Corythosaurus* sp., Coi, *C. intermedius*; Cos, *C. casuarius*; Ed, *Edmontosaurus* sp.; Eda, *E. annectens*; Edr, *E. regalis*; Eo, *Eolambia caroljonesa*; Eq, *Equijubus normani*; Gl, *Glishades ericksoni*; Gr, *Gryposaurus* sp.; Grl, *G. latidens*; Grm, *G. monumentensis*; Grn, *G. notabilis*; Hya, *Hypacrosaurus altispinus*; Hys, *H. stebingeri*; Jz, *Jinzhouosaurus yangi*; Lm, *Lambeosaurus* sp.; Lmc, *L. laticaudus*; Lml, *L. lambei*; Lmm, *L. magnicristatus*; Ma, *M. peeblesorum*; Ol, *Olorotitan ararhensis*; Paw, *Parasaurolophus walkeri*; Pb, *Probactrosaurus gobiensis*; Pt, *Protohadros byrdi*; Saa, *Saurolophus angustirostris*; Sao, *S. osborni*; Te, *Telmatosaurus transsylvanicus*; Th, *Tethyshadros insularis*; Ts, *Tsintaosaurus spinorhinus*; Ve, *Velafrons coahuilensis*.

## Discussion

### Ontogenetic variation of the hadrosauroid premaxilla

The premaxilla of *Glishades ericksoni* differs from that of any hadrosaurid. It is distinct from Lambeosaurinae, *Edmontosaurus* spp., *Brachylophosaurus canadensis*, and *Maiasaura peeblesorum* in lacking an expanded and ventrally deflected anterolateral corner of the oral margin (APM pers. obs; Table 1). The new taxon also differs from those hadrosaurids that do not have expanded and deflected anterolateral corners (*Gryposaurus* spp., *Prosaurolophus maximus*, and *Saurolophus* spp.) in lacking the thin and everted oral margin that is so characteristic of those taxa (APM pers. obs; Table 1). Outside Hadrosauridae, *G. ericksoni* differs from non-hadrosauroid iguanodontians and hadrosauroids *Equijubus normani*, *Probactrosaurus gobiensis*, *Protohadros byrdi*, *Eolambia caroljonesa*, and *Telmatosaurus transsylvanicus* in possessing the posteroventral thickening (i.e., “extra denticulate layer”) on the ventral surface of the premaxilla (APM pers. obs; Table 1) (note: it is unknown whether this condition is present in *Lophorhothon atopus*, *Gilmoresaurus mongoliensis*, *Claosaurus agilis*, *Jinzhouosaurus yangi*, *Nanyangosaurus zhugeii*,

**TABLE 1.** Distribution of the four premaxillary characters relevant to the diagnostic combination of *Glishades ericksoni* in a sample of hadrosauroid species. This sample includes the vast majority of known hadrosauroid premaxillae. MG: morphology of the oral margin of the premaxilla (0 = moderately expanded border, dorsoventrally thicker towards the parasagittal plane of the snout, and slightly deflected ventrally; 1 = moderately expanded border, becoming thinner towards the parasagittal plane of the snout; 2 = folded caudodorsally into a thin recurved margin; 3 = ventrally deflected and dorsoventrally expanded, forming a very broad “lip-like” margin). VP: ventral projection of the anterolateral corner of the premaxilla (0 = absent; 1 = present). VT: grooved ventral thickening of the premaxilla (0 = absent; 1 = present). F = one or more foramina on the anterior surface of the premaxilla, near the proximal end of the narial bar (0 = absent; 1 = present). W: maximum mediolateral width of the premaxilla, perpendicular to the narial bar (Fig. 4). The data displayed in this table are based on first hand examination of actual specimens by the author, except in the following cases in which it was based on literature sources: (1) Godefroit et al. (1998); (2) Head (2001); (3) Norman (2002); (4) Dalla Vecchia (2009); (5) Brown (1916); (6) Brown (1912); (7) Brown (1914); (8) Evans (2007).

TAXA	SPECIMEN	W (mm)	MG	VP	VT	F
NON-HADROSAURID HADROSAUROIDS						
<i>Bactrosaurus johnsoni</i>	AMNH 6501	54	0	1	1	1
<i>Bactrosaurus johnsoni</i>	AMNH 6575	42	0	?	1	1
<i>Bactrosaurus johnsoni</i>	SBDE 95E5/4-4bis <sup>(1)</sup>	65	0	1	?	1
<i>Eolambia caroljonesa</i>	OMNH 4218 <sup>(2)</sup>	38	0	0	0	0
<i>Equijubus normani</i>	IVPP V12534	104	0	0	0	0
<i>Glishades ericksoni</i>	AMNH 27414	43	0	0	1	1
<i>Jinzhousaurus yangi</i>	IVPP V12691	110	0	1	?	0
<i>Probactrosaurus gobiensis</i>	PIN 2232/1 <sup>(3)</sup>	50	0	0	?	0
<i>Protohadros byrdi</i>	SMU 74582	120	0	1	0	0
<i>Telmatosaurus transsylvanicus</i>	NHM R3386	63	0	0	0	0
<i>Telmatosaurus transsylvanicus</i>	FGGUB 1015	28	0	0	0	0
<i>Telmatosaurus transsylvanicus</i>	FGGUB 1008	47	0	0	0	0
<i>Telmatosaurus transsylvanicus</i>	NHM R4911	33	0	0	0	0
<i>Tethyshadros insularis</i>	SC 57021 <sup>(4)</sup>	65	0	0	0	0
SAUROLOPHINE HADROSAURIDS						
<i>Brachylophosaurus canadensis</i>	MOR 794	167	3	1	?	1
<i>Brachylophosaurus canadensis</i>	CMN 8893	158	3	1	1	1
<i>Brachylophosaurus canadensis</i>	TMP 90.104.1	144	3	1	1	?
<i>Brachylophosaurus canadensis</i>	MOR 1071-7-5-98-66	85	3	1	1	?
<i>Brachylophosaurus canadensis</i>	MOR 1071-7-7-98-84	100	3	1	1	1
<i>Brachylophosaurus canadensis</i>	MOR 1071-7-23-99-179	93	3	1	1	0
<i>Edmontosaurus annectens</i>	AMNH 5730	165	3	0	1	0
<i>Edmontosaurus annectens</i>	SM R4036	169	3	0	1	0
<i>Edmontosaurus annectens</i>	CMN 8399	157	3	0	?	0
<i>Edmontosaurus annectens</i>	MOR 003	258	3	0	1	0
<i>Edmontosaurus annectens</i>	CMN 8509	137	3	0	1	1
<i>Edmontosaurus annectens</i>	UCM 20892	164	3	0	1	0
<i>Edmontosaurus regalis</i>	ROM 801	284	3	0	?	0
<i>Edmontosaurus regalis</i>	NHM R8927	155	3	0	1	0
<i>Edmontosaurus regalis</i>	CMN 2288	237	3	0	1	0
<i>Edmontosaurus regalis</i>	CM 26258	176	3	0	1	0

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**TABLE 1.** (continued)

TAXA	SPECIMEN	W (mm)	MG	VP	VT	F
<i>Edmontosaurus regalis</i>	FMNH P15004	227	3	0	?	0
<i>Edmontosaurus regalis</i>	LACM 23502	173	3	0	1	0
<i>Edmontosaurus sp.</i>	UCMP fldAK-83-V-168	41	3	0	1	1
<i>Gryposaurus latidens</i>	AMNH 5465	188	2	0	1	0
<i>Gryposaurus monumentensis</i>	RAM 6797	224	2	0	1	0
<i>Gryposaurus notabilis</i>	CMN 2278	220	2	0	1	0
<i>Gryposaurus notabilis</i>	MSNM V345	242	2	0	1	0
<i>Gryposaurus notabilis</i>	TMP 80.22.1	148	2	0	1	0
<i>Gryposaurus notabilis</i>	ROM 873	205	2	0	1	0
<i>Gryposaurus sp.</i>	MOR 553S-7-18-91-107	103	2	0	1	0
<i>Gryposaurus sp.</i>	MOR 553S-7-23-8-57	112	2	0	1	0
<i>Gryposaurus sp.</i>	ROM 8784	74	2	0	1	1
<i>Maiasaura peeblesorum</i>	ROM 44770	162	3	1	1	1
<i>Maiasaura peeblesorum</i>	OTM F138	157	3	1	1	1
<i>Prosaurolophus maximus</i>	ROM 787	173	2	0	?	0
<i>Prosaurolophus maximus</i>	CMN 2277	160	2	0	1	0
<i>Prosaurolophus maximus</i>	CMN 2870	146	2	0	1	0
<i>Prosaurolophus maximus</i>	AMNH 5386 <sup>(5)</sup>	214	2	0	1	0
<i>Prosaurolophus maximus</i>	TMM 41262-1	145	2	0	?	0
<i>Prosaurolophus maximus</i>	ROM 1928	133	2	0	1	0
<i>Prosaurolophus maximus</i>	TMP 84.1.1	170	2	0	1	0
<i>Prosaurolophus maximus</i>	TMP 83.64.3	85	2	0	1	0
<i>Prosaurolophus maximus</i>	MOR 454-7-8-2-9	155	2	0	1	0
<i>Saurolophus angustirostris</i>	ZPAL MgD-I 159	69	2	0	1	0
<i>Saurolophus osborni</i>	AMNH 5220 <sup>(6)</sup>	197	2	0	?	0
<i>Saurolophus osborni</i>	AMNH 5221	147	2	0	1	0
<i>Saurolophus osborni</i>	LACM 2852	111	2	0	1	0
<i>Saurolophus osborni</i>	CMN 8796	175	2	0	1	0
<b>LAMBEOSAURINE HADROSAURIDS</b>						
<i>Corythosaurus casuarius</i>	AMNH 5240 <sup>(7)</sup>	157	1	1	1	0
<i>Corythosaurus casuarius</i>	CMN 8676	97	1	1	1	0
<i>Corythosaurus casuarius</i>	ROM 868	100	1	1	1	?
<i>Corythosaurus casuarius</i>	ROM 870	79	1	1	1	0
<i>Corythosaurus casuarius</i>	ROM 1933	82	1	1	1	0
<i>Corythosaurus intermedius</i>	ROM 845	98	1	1	?	0
<i>Corythosaurus intermedius</i>	CMN 8503	94	1	1	1	?
<i>Corythosaurus intermedius</i>	CMN 8704	110	1	1	1	0
<i>Corythosaurus intermedius</i>	ROM 776	117	1	1	1	0
<i>Corythosaurus intermedius</i>	ROM 777	116	1	1	1	0
<i>Corythosaurus sp.</i>	ROM 759	45	1	1	1	?
<i>Corythosaurus sp.</i>	TMP 97.12.232	62	1	1	1	0

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**TABLE 1.** (continued)

TAXA	SPECIMEN	W (mm)	MG	VP	VT	F
<i>Corythosaurus</i> sp.	TMP 82.37.1	78	1	1	1	0
<i>Corythosaurus</i> sp.	CMN 34845	74	1	1	1	?
<i>Hypacrosaurus altispinus</i>	CMN 8501	155	1	1	1	0
<i>Hypacrosaurus altispinus</i>	ROM 702	106	1	1	1	0
<i>Hypacrosaurus altispinus</i>	CMN 8673	88	1	1	1	0
<i>Hypacrosaurus altispinus</i>	CMN 8675	114	1	1	1	0
<i>Hypacrosaurus altispinus</i>	USNM 299718	64	1	1	1	0
<i>Hypacrosaurus altispinus</i>	CMN 2246	87	1	1	1	0
<i>Hypacrosaurus altispinus</i>	CMN 2247	71	1	1	?	0
<i>Hypacrosaurus altispinus</i>	TMP 82.10.1	89	1	1	1	0
<i>Hypacrosaurus stebingeri</i>	MOR 549	121	3	1	1	0
<i>Hypacrosaurus stebingeri</i>	AMNH 5461	51	?	1	1	0
<i>Hypacrosaurus stebingeri</i>	TMP 89.79.52	12	1	1	?	0
<i>Hypacrosaurus stebingeri</i>	TMP 94.385.1	62	?	1	1	0
<i>Hypacrosaurus stebingeri</i>	MOR 548	34	1	1	1	0
<i>Lambeosaurus lambei</i>	CMN 2869	110	1	1	1	0
<i>Lambeosaurus lambei</i>	YPM 3222	132	1	1	1	0
<i>Lambeosaurus lambei</i>	TMP 81.37.1	110	1	1	1	0
<i>Lambeosaurus lambei</i>	ROM 794	140	1	1	1	0
<i>Lambeosaurus lambei</i>	FMNH PR380	139	1	1	1	0
<i>Lambeosaurus lambei</i>	CMN 8703	114	1	1	1	0
<i>Lambeosaurus lambei</i>	ROM 1218	142	1	1	?	0
<i>Lambeosaurus lambei</i>	TMP 82.38.1	116	1	1	?	0
<i>Lambeosaurus magnicristatus</i>	TMP 66.4.1	109	1	1	1	0
<i>Lambeosaurus laticaudus</i>	LACM 17712	112	1	1	1	0
<i>Lambeosaurus</i> sp.	AMNH 5340 <sup>(8)</sup>	66	1	1	?	0
<i>Lambeosaurus</i> sp.	CMN 8633	73	1	1	1	0
<i>Lambeosaurus</i> sp.	ROM 758	58	1	1	1	0
<i>Lambeosaurus</i> sp.	ROM 869	81	1	1	1	0
<i>Olorotitan ararhensis</i>	AEHM 2/845	158	3	1	1	0
<i>Parasaurolophus walkeri</i>	ROM 768	142	3	1	?	0
<i>Tsintaosaurus spinorhinus</i>	IVPP V725	153	3	0	1	0
<i>Velafrons coahuilensis</i>	CPC-59	92	1	1	1	0

*Shuangmiaosaurus gilmorei*, *Levnesovia transoxiana*, and *Tanius sinensis* due to either lack of preservation of their premaxillae or because the ventral surface of the bone is concealed in articulated skulls). The latter feature is shared with the hadrosauroid *Bactrosaurus johnsoni*; however, *B. johnsoni* differs from *G. ericksoni* in possessing an expanded and deflected anterolateral corner of the oral premaxillary margin (e.g., AMNH 6501).

However, could it be that, given its relatively small size, the distinctive combination of characters in AMNH 27414 reflects the subadult nature of the specimen rather than the morphology present in the adult form? Subadult premaxillae of a wide range of sizes are known for a number of hadrosauroid genera, including *Bactrosaurus*, *Brachylophosaurus*, *Gryposaurus*, *Prosaurolophus*, *Saurolophus*, *Edmontosaurus*,

*Corythosaurus*, *Lambeosaurus*, and *Hypacrosaurus* (APM pers. obs.; Fig. 4). In all these taxa, subadult premaxillae (from neonate juvenile to large subadult size) display the morphological characters that are diagnostic of the adult specimens, particularly those characters that compose the diagnostic combination of *Glishades ericksoni*; comparisons between the latter taxon and most known hadrosauroids, including North American forms, are summarized in Table 1. Aside from *G. ericksoni*, the hadrosaurid fossil record of the Two Medicine Formation consists of the saurolophines (sensu Prieto-Márquez in press) *Maiasaura peeblesorum* (Horner & Makela 1979; Horner 1983), *Gryposaurus latidens* and *Prosaurolophus maximus* (Horner 1992), and the lambeosaurine *Hypacrosaurus stebingeri* (Horner & Currie 1994). The oral margin of the premaxilla of *Gryposaurus latidens* (e.g., AMNH 5465) is everted, unlike that of *G. ericksoni*. No juvenile specimen is known for *Gryposaurus latidens*. However, a few subadult disarticulated premaxillae collected from Two Medicine strata might be referable to *Gryposaurus* sp. or *Prosaurolophus* sp. because of their characteristic rounded and everted oral margins (e.g., MOR 553S-7-18-91-107 and MOR 553S-7-23-8-57) and thus, are distinct from the premaxilla of *G. ericksoni*. Waldman (1969) described an immature articulated skull collected from the Campanian Oldman Formation of southern Canada. The specimen, CMN 8784, has a premaxilla of comparable size to that of *G. ericksoni*. Despite its relatively small size (Table 1 and Fig. 4), the premaxilla of CMN 8784 shows the diagnostic morphology present in the adult exemplars of the genus *Gryposaurus* (e.g., ROM 873 or CMN 2278), with its rounded and everted oral margin and ventral transversal thickening (APM pers. obs.).

The Two Medicine Formation has also provided some of the smallest known hadrosaurid specimens, which correspond to *M. peeblesorum* (e.g., YPM-PU 22400) and *H. stebingeri* (e.g., MOR 548 and TMP TMP 89.79.52). As already noted, both the premaxilla of *M. peeblesorum* and *H. stebingeri* differ from that of *G. ericksoni* in possessing a strongly projected anteroventral corner. Unfortunately, no subadult or juvenile premaxilla is available for *M. peeblesorum*, not even in the extensive collection of neonates or small juveniles YPM-PU 22400 (APM pers. obs.). However, several growth stages are known for *H. stebingeri* (Horner & Currie 2004; Evans 2007). It is worth noting that the size of the *M. peeblesorum* small juveniles (YPM-PU 22400) is comparable to those of *H. stebingeri* (MOR 548), which, judging from the size of their premaxillae and rest of facial elements, likely correspond to an earlier ontogenetic stage than that of *G. ericksoni* (Table 1 and Fig. 4). In all of the available specimens of *H. stebingeri*, from the larger MOR 549 to the subadult TMP 94.385.1, the juvenile AMNH 5461, and smaller juveniles MOR 548, the premaxilla is morphologically consistent and shows little variation other than size-related proportions; all these specimens in this growth series show a projected anteroventral corner, ventral thickening, lack of foramina on the anteromedial surface, and absence of eversion of the oral margin (APM pers. obs.). Therefore, the available fossil data suggests that it is unlikely that the diagnostic combination of characters present in the premaxilla of *Glishades ericksoni* would differ substantially throughout ontogeny.

### Phylogenetic relationships of *Glishades ericksoni*

The phylogenetic position of *Glishades ericksoni* was inferred via parsimony analysis using the character data set of Prieto-Márquez (in press) (Appendices 1 and 2). Including *G. ericksoni*, the taxonomic sample consisted of 56 hadrosauroid species (39 Hadrosauridae and 17 non-hadrosaurid Hadrosauroidea), providing a wide representation of the diversity of the clade. The basal iguanodontoidean *Iguanodon bernissartensis* served as outgroup taxon to hadrosauroids. The character data of Prieto-Márquez (in press) consisted of 287 equally weighted morphological characters (197 cranial and 90 postcranial). One additional character was added: presence (0) or absence (1) of at least one foramen on the anteromedial surface of the premaxilla (Appendix 2). Characters 1, 4, 16, and 19 were ordered, following the recommendation of Prieto-Márquez (in press). The search for the optimal tree(s) using maximum parsimony was conducted in TNT version 1.0 (Goloboff *et al.* 2003). A heuristic search of 10,000 replicates using random additional sequences was performed, followed by branch swapping by tree-bisection-reconnection holding 10 trees per replicate. The results were summarized in a strict consensus tree and a maximum agreement subtree using TNT algorithms (Goloboff *et al.* 2008). A maximum agreement subtree is a consensus method and, thus, it is performed a posteriori of the parsimony tree search. It results from pruning the minimum number of labile taxa to expose

the underlying structure that is present in all the most parsimonious trees; pruning is accomplished through the computation of specific algorithms (Kubicka *et al.* 1995; Amir & Keselman 1997). Bremer support was assessed by computing decay indices using the TNT software. Bootstrap proportions were calculated using 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.

The analysis resulted in 191 most parsimonious trees of 976 steps each (C.I. = 0.49; R.I.= 0.77). The strict consensus tree positioned *Glishades ericksoni* as part of a polytomy of derived hadrosauroids (Fig. 2). However, the maximum agreement subtree (Fig. 3) showed *G. ericksoni* forming a sister-relationship with *Bactrosaurus johnsoni*, from the Iren Dabasu Formation of northern China (Gilmore 1933). Two unambiguous synapomorphies supported the *Glishades-Bactrosaurus* clade: posteroventral thickening on the ventral surface of the premaxilla (independently derived in saurolophid hadrosaurids and *Ouranosaurus nigeriensis*) and having a foramen on each premaxilla on the anterior surface, adjacent to the parasagittal plane of the rostrum (reconstructed as independently derived in *Brachylophosaurus canadensis*, *Maiasaura peeblesorum*, and *Edmontosaurus annectens*). Exclusion of *G. ericksoni* from Hadrosauridae was unambiguously supported by the lack in AMNH 27414 of a dorsomedially reflected premaxillary oral margin.

The basal hadrosauroid species of North America that are most closely related to Hadrosauridae, *Claosaurus agilis* and *Lophorhodon atopus* (Figs 1–2; see also Prieto-Márquez in press), are recorded in the southern region of the continent (Langston 1960; Carpenter *et al.* 1995). The northern-most species recognized so far, *Eolambia caroljonesa* and *Cedrorestes crichtoni* (Kirkland 1998; Gilpin *et al.* 2007) are distantly related to Hadrosauridae (Figs 1–2). Thus, *Glishades ericksoni* extends the distribution of derived non-hadrosaurid hadrosauroids in North America further north than previously recognized, documenting the presence of *Bactrosaurus*-grade forms in the continent as recently as the Campanian.

## Acknowledgments

I am grateful to M. Norell for the opportunity to study AMNH 27414. Character state codings for *Tethyshadros insularis* were obtained in collaboration with F. M. Dalla Vecchia (Institut Català de Paleontologia) as part of a project on European Cretaceous dinosaurs supported by the Ministry of Education and Science of Spain (CGL2005-07878-C02-01 grant presented to A. Galobart). I thank R. J. Butler, A. T. McDonald, and two anonymous reviewers for their assistance in various aspects of the manuscript. Funds for this study were provided by a Kalbfleisch Research Fellowship from the American Museum of Natural History and the National Science Foundation (EAR 0207744 and DBI 0446224 grants presented to G. Erickson).

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## Appendix 2

Codings for the absence (0) or presence (1) of at least one foramen on the anteromedial surface of the premaxilla (character 287) for the 56 hadrosauroid taxa included in this study.

Taxa	Character 287
<i>Iguanodon bernissartensis</i>	0
<i>Eolambia caroljonesa</i>	0
<i>Equijubus normani</i>	0
<i>Probactrosaurus gobiensis</i>	0
<i>Protohadros byrdi</i>	0
<i>Bactrosaurus johnsoni</i>	1
<i>Gilmoreosaurus mongoliensis</i>	?
<i>Tanius sinensis</i>	?
<b><i>Glishades ericksoni</i></b>	<b>1</b>
<i>Cedrorestes crichtoni</i>	?
<i>Fukuisaurus tetoriensis</i>	0
<i>Shuangmiaosaurus gilmorei</i>	?
<i>Nanyangosaurus zhuchei</i>	?
<i>Jinzhouosaurus yangi</i>	0
<i>Penelopognathus weishampeli</i>	?
<i>Tethyshadros insularis</i>	0
<i>Hadrosaurus foulkii</i>	?
<i>Telmatosaurus transsylvanicus</i>	0
<i>Lophorhothon atopus</i>	?
<i>Wulagasaurus dongi</i>	?
<i>Sahaliyana elunchunorum</i>	?
<i>Amurosaurus riabinini</i>	?
<i>Aralosaurus tuberiferus</i>	?
<i>Brachylophosaurus canadensis</i>	0&1
<i>Maiasaura peeblesorum</i>	1
Two Medicine saurolophine	?
<i>Charonosaurus jiayinensis</i>	?
<i>Corythosaurus casuarius</i>	0
<i>Corythosaurus intermedius</i>	0
<i>Hypacrosaurus stebingeri</i>	0
<i>Hypacrosaurus altispinus</i>	0
<i>Lambeosaurus lambei</i>	0
<i>Lambeosaurus magnicristatus</i>	0
<i>Edmontosaurus annectens</i>	0&1
<i>Edmontosaurus regalis</i>	0
<i>Kerberosaurus manakini</i>	?
<i>Lambeosaurus laticaudus</i>	?
<i>Velafrons coahuilensis</i>	0
<i>Jaxartosaurus aralensis</i>	?
<i>Kritosaurus navajovius</i>	?
<i>Gryposaurus notabilis</i>	0

continued next page

**Appendix 2.** (continued)

Taxa	Character 287
<i>Gryposaurus latidens</i>	0
<i>Gryposaurus monumentensis</i>	0
<i>Olorotitan ararhensis</i>	0
<i>Parasaurolophus walkeri</i>	0
<i>Parasaurolophus cyrtocristatus</i>	?
<i>Parasaurolophus tubicen</i>	?
<i>Prosaurolophus maximus</i>	0
<i>Secernosaurus koernerii</i>	?
Salitral Moreno saurolophine	0
Big Bend UTEP saurolophine	?
<i>Saurolophus osborni</i>	0
<i>Saurolophus angustirostris</i>	0
<i>Shantungosaurus giganteus</i>	?
<i>Pararhabdodon isonensis</i>	?
<i>Tsintaosaurus spinorhinus</i>	0
Sabinas saurolophine	?