

Global historical biogeography of hadrosaurid dinosaurs

ALBERT PRIETO-MÁRQUEZ*

Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA

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Hadrosaurids were the most derived ornithopods and amongst the most diverse herbivore dinosaurs during the Late Cretaceous of Europe, Asia, and the two Americas. Here, their biogeographical history is reconstructed using dispersal-vicariance analysis (DIVA). The results showed that Hadrosauridae originated in North America and soon after dispersed to Asia no later than the Late Santonian. The most recent common ancestor of Saurolophidae (= Saurolophinae + Lambeosaurinae) is inferred to have been widespread in North America and Asia. The split between saurolophines and lambeosaurines occurred in response to vicariance no later than the Late Santonian: the former clade originated in North America, whereas the latter did so in Asia. Saurolophine biogeographical history included a minimum of five dispersal events followed by vicariance. Four of these dispersals were inferred to have occurred from North America to Asia during the Campanian and Early Maastrichtian, whereas a fifth event represented a southward dispersal from North to South America no later than the Late Campanian. The historical biogeography of lambeosaurines was characterized by an early evolution in Asia, with a Campanian dispersal to the European archipelago followed by vicariance. Reconstruction of the ancestral areas for the deepest nodes uniting the more derived lambeosaurines clades ('hypacrosaurids', 'corythosaurs', and 'parasaurolophids') is ambiguous. The split between North American and Asian clades of 'hypacrosaurids' and 'parasaurolophids' occurred in response to vicariance during the Campanian. The evolutionary history of North American 'hypacrosaurids' and 'parasaurolophids' was characterized by duplication events. The latter also characterized the Late Campanian 'corythosaurs', which remained restricted to North America.

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INTRODUCTION

Hadrosaurid dinosaurs were amongst the most common and diverse herbivores in the terrestrial ecosystems of the Late Cretaceous (Horner, Weishampel & Forster, 2004), particularly during the Campanian and Maastrichtian (Lund & Gates, 2006). Their fossil record shows that these animals had a widespread distribution, so far having been found in all continents except Africa and Oceania (Weishampel, 1990; Case *et al.*, 2000). Hadrosaurids are known from fully articulated skeletons (Lull & Wright, 1942), multi-individual assemblages (Dodson, 1971; Varricchio &

Horner, 1993), egg materials and growth series (Horner & Makela, 1979; Horner, Ricqlès & Padian, 2000), soft tissue impressions (Osborn, 1912; Murphy, Trexler & Thompson, 2007), and trackways (Currie, Nadon & Lockley, 1991). These dinosaurs were characterized by hypertrophied nasal passages that, in many species, were associated to a wide variety of supracranial crests (Ostrom, 1962; Hopson, 1975). Other remarkable attributes of hadrosaurids are their mediolaterally expanded rostra (Morris, 1970) and jaws equipped with well-developed dental batteries (Norman & Weishampel, 1985).

Over the last century, these remarkable and unique anatomical attributes, coupled with the high quantity and quality of the hadrosaurid fossil record, have

*E-mail: redshore@gmail.com

motivated numerous studies on the taxonomy (Lull & Wright, 1942; Prieto-Márquez, Weishampel & Horner, 2006), anatomy and functional morphology (Weishampel, 1981; Evans, 2006), life history (Horner, Ricqlès & Padian, 2000; Horner, Padian & Ricqlès, 2001), and evolutionary relationships (Godefroit *et al.*, 1998; Horner *et al.*, 2004) of these animals. However, our understanding of the historical biogeography of hadrosaurids is relatively poor. One of the reasons for this is that reconstructions of hadrosaurid biogeography have been nonglobal, based on phylogenies that used only a fraction of the known hadrosaurid diversity or focused only on particular geographical regions. Furthermore, only one study (that of Weishampel & Jianu, 1997) appears to have attempted to shed light into the biogeographical history of these animals using quantitative methods of historical biogeography. Instead, previous research has been based on the biostratigraphical distribution of taxa according to a time-calibrated phylogeny, with the assumption that the older of two sister taxa lived in the ancestral area of a particular clade. This approach has led to narratives of dispersal or vicariant scenarios with centres of origin for major clades (Brett-Surman, 1979; Weishampel & Weishampel, 1983; Godefroit *et al.*, 1998; Head, 1998, 2001; Casanovas *et al.*, 1999; Wagner, 2001; Godefroit, Bolotsky & Alifanov, 2003; Godefroit, Alifanov & Bolotsky, 2004b). Although useful for establishing working hypotheses, this approach lacks the rigour and testability provided by more quantitative methods of historical biogeography (Morrone & Crisci, 1995; Lieberman, 2000, 2003; Crisci, Katinas & Posadas, 2003). Whilst some authors have recently implemented quantitative methods for inferring biogeographical histories for major dinosaurian clades (Chapman, 1997; Upchurch, Huxford & Norman, 2002; Holtz, Chapman & Lamanna, 2004), they have not specifically addressed hadrosaurids.

Traditionally, Asia has been considered the most likely area of origin for hadrosaurids (Wiman, 1929; Rozhdestvensky, 1967). The primitive nature of taxa preceding the hadrosaurid radiation was first recognized in that continent (*Bactrosaurus johnsoni* Gilmore, 1933; *Probactrosaurus gobiensis* Rozhdestvensky, 1966). However, the discovery of outgroup taxa to hadrosaurids in Europe (*Telmatosaurus transylvanicus* Nopcsa, 1900) and North America (*Eolambia caroljonesa* Kirkland, 1998; *Protophadros byrdi* Head, 1998), as well as putative primitive forms in South America (*Secernosaurus koernerii* Brett-Surman, 1979), has complicated this issue by offering alternative ancestral areas to consider for hadrosaurids. Consequently, a number of authors have proposed that hadrosaurids may have originated in Europe (Weishampel, Norman & Grigorescu, 1993;

Company, Galobart & Gaete, 1998; Casanovas *et al.*, 1999), North America (Head, 1998, 2001; Kirkland, 1998; Horner *et al.*, 2004), or South America (Brett-Surman, 1979; Powell, 1987). Biogeographical reconstructions have involved dispersal and vicariance as the primary processes shaping the diversification and distribution of hadrosaurids (Brett-Surman, 1979, 1989; Weishampel & Weishampel, 1983; Russell, 1993; Head, 1998; Casanovas *et al.*, 1999; Godefroit *et al.*, 2003, 2004a).

The present study aimed to reconstruct the biogeographical history of hadrosaurid dinosaurs, establishing how they became widespread throughout the Northern and part of the Southern Hemisphere during their evolutionary history. In doing so, previous hypotheses positing a European, Asian, North or South American origin for hadrosaurids (and major subclades) are tested. These goals are accomplished within the framework of event-based historical biogeography, using dispersal-vicariance analysis (Ronquist, 1997). Ancestral area reconstruction using this method is implemented on a species-level phylogeny including nearly all known hadrosaurids and encompassing all continental regions where these animals have been recorded.

REVIEW OF PREVIOUS STUDIES ON HADROSAURID BIOGEOGRAPHY

STUDIES BASED ON PRECLADISTIC PHYLOGENIES

Early ideas on the biogeography of hadrosaurids are found in the literature nearly a century after the discovery of their first fossils. Thus, Lull & Wright (1942) briefly suggested in their classic monograph that the 'flat-headed' hadrosaurids of western North America might have dispersed from the eastern side of the continent, following a major regression of the western Interior Seaway during the Late Cretaceous. Hadrosaurid taxa known at the time from other continents were not considered.

Morris (1973) addressed the biogeography of a number of North American hadrosaurids during the Campanian and Maastrichtian. He proposed that *Lambeosaurus* Parks, 1923, *Prosaurolophus* Brown, 1916, and *Saurolophus* Brown, 1913 had dispersed from southern Canada to Baja California along the Pacific coast. Morris also suggested that *Edmontosaurus* Lambe, 1917 and *Gryposaurus* Lambe, 1914 had dispersed from southern Alberta to as far south as New Mexico, along a route that extended east to the Rockies. In contrast, *Corythosaurus* Brown, 1914 and *Hypacrosaurus* Brown, 1912 would have been restricted to the northern Rocky Mountain region of North America.

Brett-Surman (1975, 1979) presented the first global hypothesis of hadrosaurid biogeography. He

regarded Asia as the most likely region that harboured the origin of the group during pre-Santonian times. This was because various outgroup taxa to hadrosaurids, such as *Probactrosaurus* Rozhdestvensky, 1966, *Bactrosaurus* Gilmore, 1933, and *Gilmoreosaurus* Brett-Surman, 1979 had been found in Asia. He then considered possible dispersal routes to Europe and North America through the Turgai Strait. From Europe, he hypothesized connections to Africa, via the Iberian Peninsula, and to South America through the Amazon basin (Brett-Surman, 1975). An alternative route to South America from Europe, later suggested by Brett-Surman (1979), was via the east coast of North America across the Caribbean arc by means of island hopping. Dispersals to North America from Asia would have been possible through the Bering Strait or through Europe.

Furthermore, Brett-Surman (1979) also entertained the alternative hypothesis that hadrosaurids might have originated in South America. This idea was based on his interpretation of *Secernosaurus koeneri* Brett-Surman, 1979, from the Late Campanian–Early Maastrichtian of Argentina, as a primitive hadrosaurid. From South America, dispersals to Laurasia would have occurred via Africa and the Iberian Peninsula or, alternatively, through North America via Panama or the Caribbean arc. Although Brett-Surman considered the possibility that vicariance might have also been involved in the distribution of hadrosaurids in Laurasia and Gondwana, he tentatively preferred a dispersal model because of the absence of a hadrosaurid fossil record in Oceania and Africa. For hadrosaurines (saurolophines in this study; see below), Brett-Surman (1989) posited an Asian or North American origin. He based this hypothesis on the presence in those continents of taxa that he regarded as relatively primitive within the clade, such as *Hadrosaurus* Leidy, 1858, *Brachylophosaurus* Sternberg, 1953, and *Kritosaurus* Brown, 1910 in North America, and *Aralosaurus* Rozhdestvensky, 1968 in Asia.

Casamiquela (1964), Weishampel & Weishampel (1983), and Bonaparte *et al.* (1984) explained the presence of South American hadrosaurids (*Kritosaurus australis* Bonaparte *et al.*, 1984) as dispersals from North America. Weishampel & Weishampel (1983) found support for this hypothesis in the finding of a femur with hadrosaurian affinities in the Cenomanian of Honduras (Horne, 1994). Weishampel & Weishampel (1983) pointed out that the Nicoya Complex, a volcanic chain of Late Cretaceous age that extended from Central America to Ecuador, might have served as a land connection between the two Americas. As these authors regarded *K. australis* as a primitive hadrosaurid, they proposed that the dispersal took place early in the evolutionary history of

the clade. However, Bonaparte *et al.* (1984) posited that these dispersals were part of a bidirectional faunal exchange between North and South America, including many other groups of vertebrates such as titanosaurs, sauropods, snakes, birds, and mammals. This faunal exchange would have occurred during the Campanian–Early Maastrichtian. In their view, the dispersals most probably took place through Central America, rather than through the Antilles, because the North American vertebrate fauna most closely related to that in South America had been found in the western region of Central America.

STUDIES BASED ON PHYLOGENIES DERIVED FROM CLADISTIC ANALYSES

Soon after cladistic analyses were applied to the reconstruction of hadrosaurid interrelationships, palaeontologists began to compare the topology of their cladograms with the geographical and stratigraphical distributions of these animals to infer biogeographical patterns. This resulted in more elaborate and testable biogeographical hypotheses on the origin and widespread distribution of hadrosaurids.

Thus, Milner & Norman (1984) proposed that hadrosaurids originated in eastern Asia during the Bajocian from iguanodontian ancestors through vicariance. Support for this hypothesis came from the finding of hadrosaurid outgroup taxa in central Asia. These authors also suggested that the split of hadrosaurids into hadrosaurines and lambeosaurines took place in Asia through vicariance. This would have been followed by dispersals during the later stages of the Cretaceous. The occurrence of *Saurolophus* and lambeosaurines in eastern Asia and western North America was explained by dispersal events eastwards from Asia through the Bering Strait. Later, Russell (1993) would support the existence of a faunal exchange through the Bering corridor not only for hadrosaurids, but also for many other dinosaur clades.

In one of the few studies of the European hadrosaurid fossil record, Weishampel, Grigorescu & Norman (1991) and Weishampel *et al.* (1993) regarded *Telmatosaurus transsylvanicus* Nopcsa, 1900, from the Maastrichtian of Romania, as the most basal hadrosaurid, a relict form that had become isolated in the European archipelago during most of the Late Cretaceous. Based on the latter phylogenetic hypothesis, Weishampel & Jianu (1997) undertook the task of elucidating whether this species migrated to Europe from North America or Asia, or whether the ancestral area of North American and Asian hadrosaurids was located in Europe. These authors considered four areas: North and South America, Asia, and a peri-Tethyan region (composed of Europe and northern

Africa). Ancestral areas for a few major iguanodontoid clades were reconstructed using parsimony optimization on the phylogeny, following the method described by Brooks & McLennan (1991). The analysis resulted in a peri-Tethyan origin for hadrosaurids.

Head (1998, 2001) also supported the survival of primitive hadrosaurids in South America (*Secernosaurus koernerii*) and Europe (*Pararhabdodon isonensis* Casanovas-Cladellas, Santafé-Llopi & Isidro-Llorens, 1993) into the latest Cretaceous. In addition, he proposed that hadrosaurids might have originated in North America during the Cenomanian (Head, 1998). From there, they would have dispersed to Asia by the Turonian and to South America during the Campanian–Maastrichtian. He suggested also that short-term regressions of the western Interior Seaway in North America during the Albian and Cenomanian might have opened areas for potential dispersals from eastern to western North America, as well as to Asia through the Bering Strait. He contended that this North American origin for hadrosaurids was as likely as the Asian origin that was the paradigm at the time. In support of his North American origination hypothesis he alluded to the presence of iguanodontians in the Early Cretaceous of this continent and the finding of what he considered the most basal hadrosaurid known at the time, *Protophadros byrdi* Head, 1998, from the Cenomanian of Texas. He favoured a dispersal model rather than vicariance because no conclusive hadrosaurid remains had been found in strata old enough to allow congruence between the sequence of continental break-up and the hadrosaurid distribution. However, he recognized the ambiguity in choosing between a North American and Asian origin for hadrosaurids. This is because although the oldest and most primitive hadrosaurid (*Protophadros*) was found in North America, the closest outgroup taxa to Hadrosauridae were recorded from Asia.

Nearly at the same time, Casanovas *et al.* (1999) regarded *Pararhabdodon isonensis*, from the Maastrichtian of northern Spain, as the most primitive lambeosaurine. These authors explained the presence of a basal lambeosaurine in Europe as the result of vicariance, after the onset of geographical barriers that isolated the western part of the continent during a transgressive period spanning from the Albian to the Maastrichtian. The presence of primitive lambeosaurines in Europe has been recently supported by Pereda-Suberbiola *et al.* (2009). According to these authors, another lineage of these animals dispersed to Europe from Asia during the Latest Cretaceous.

With the re-evaluation of *Eolambia* Kirkland, 1998, from the Cenomanian Cedar Mountain Formation of Utah, as a hadrosauroid closely related to the Mongolian genus *Probactrosaurus*, Head (2001) expanded

the North American record of these animals. He considered two biogeographical scenarios. In the first, *Eolambia* figured as the sister taxon to *Probactrosaurus*. This implied multiple dispersal events of hadrosauroids from Asia to North America from the Early to Late Cretaceous. In a second scenario, *Eolambia* was placed higher in the tree relative to *Probactrosaurus*. This would only require a single hadrosauroid dispersal event from Asia to North America to explain the presence of *Eolambia* in the latter continent.

The subsequent discovery of another nonhadrosauroid hadrosauroid, *Equijubus normani* You *et al.*, 2003, from the Late Barremian–Aptian of China, provided You and colleagues with new evidence in support of the Asian origin hypothesis. In contrast, Horner *et al.* (2004) supported a North American origin for hadrosaurids based on the geographical distribution of the closest outgroup taxa to their Hadrosauridae, *Protophadros* and *Eolambia*. Based on their hadrosaurid phylogeny, these authors explained the presence of *Telmatosaurus* in Europe as a dispersal event in the mid-Cretaceous. Horner *et al.* (2004) also thought that the divergence of hadrosaurines and lambeosaurines took place in North America in the mid-Cretaceous. Within hadrosaurines, these authors posited a dispersal event into Asia no later than the Early Maastrichtian (*Saurolophus angustirostris* Rozhdestvensky, 1952) and another dispersal event into South America no later than the Campanian (*K. australis*). Within lambeosaurines, they hypothesized a dispersal to Asia no later than the Campanian, thus explaining the presence in China of *Tsintaosaurus spinorhinus*.

Godefroit, Zan & Jin (2001) and Bolotsky & Godefroit (2004) proposed that several lineages of Asian hadrosaurids dispersed to North America no later than the Campanian via the Bering Strait. Amongst hadrosaurines, *Kerberosaurus manakini* Bolotsky & Godefroit, 2004, from the Late Maastrichtian of eastern Russia, would have occupied Asia before the cladogenesis of the *Prosaurolophus*–*Saurolophus* clade. Within lambeosaurines, *Charonosaurus jiyinensis* Godefroit, Zan & Jin, 2000, the sister taxon to the genus *Parasaurolophus* Parks, 1922, would have also dispersed to North America before the evolution of the latter.

Gates & Evans (2005) and Gates (2007) reported finer scale patterns in the distribution of hadrosaurids during the Campanian of western North America. They noted that, at a given time and for a particular region, at least one hadrosaurine and one lambeosaurine lived contemporaneously (e.g. *Prosaurolophus maximus* Brown, 1916–*Hypacrosaurus stebingeri* Horner & Currie, 1994 in the Upper Two Medicine Formation of Montana and *Kritosaurus navajovius* Brown, 1910–*Parasaurolophus tubicen*

Wiman, 1931 in the Kirtland Formation of New Mexico). The number of contemporaneous taxa however, was greater in the fauna from Dinosaur Park Formation in southern Canada. They showed that there was considerable variation in the size of the geographical ranges for some hadrosaurid genera. *Edmontosaurus* was found from southern Alberta to Alaska and *Gryposaurus* and *Parasaurolophus* were recorded from southern Alberta to the south-west of the United States. In contrast, other taxa such as *Maiasaura* Horner & Makela, 1979, and *Corythosaurus* and *Lambeosaurus* were restricted to smaller areas, such as the Western Interior of the United States and southern Canada, respectively.

Gates (2007) noted that in general hadrosaurines seemed to have larger geographical ranges than lambeosaurines. He identified the highest diversity of hadrosaurids in the Western Interior Basin of North America at approximately 75 million years ago, during the Late Campanian, with eight species recorded. During that time frame, he revealed the existence of a faunal turnover within the *Prosaurolophus*–*Edmontosaurus* and the *Brachylophosaurus*–*Gryposaurus* clades. Likewise, Gates (2007) supported a connection between North America and Asia no later than the Early Maastrichtian (age of *Saurolophus*, found in both continents). The lack of pre-Maastrichtian derived hadrosaurids in Asia, combined with the record in this continent of Maastrichtian taxa closely allied to the North American forms, led him to posit a direction of dispersal from North America to Asia.

Finally, Godefroit *et al.* (2008) supported an Asian origin for both hadrosaurines and lambeosaurines after inferring a phylogeny where the most basal members of each clade lived in Asia. From Asia, lambeosaurines and hadrosaurines were postulated to have dispersed to North America no later than the Campanian. This would have occurred through the Beringian isthmus, which would have remained operative from the Albian–Aptian until the end of the Cretaceous.

MATERIAL AND METHODS

BIOGEOGRAPHICAL INFERENCE AND AREAS OF ANALYSIS

Event-based methods of cladistic biogeography integrate phylogenetic information with explicit models of the processes that shape the distribution of taxa (Crisci *et al.*, 2003). In contrast to other approaches, event-based methods incorporate optimality criteria in their procedures. One such methodology, dispersal–vicariance analysis (DIVA), is used here to infer ancestral areas for all the internal nodes of the phy-

logeny shown in Figure 1 (Prieto-Márquez, 2010). DIVA was developed by Ronquist (1996, 1997) as an extension of the ideas presented by Ronquist & Nylin (1990) for host–parasite coevolutionary studies. Although DIVA assumes allopatric speciation as a result of vicariance as a null hypothesis, the method also considers dispersal and extinction as alternative processes influencing the resulting distribution of taxa (Ronquist, 1997). An advantage of DIVA is that it allows for the inference of biogeographical histories of clades in the absence of previous knowledge of the history of the areas (Nylander *et al.*, 2008). This is particularly useful when dealing with the hypothetical reconstructions of the palaeogeography during geological times, as well as in complex geological settings where the history of the areas may have split and re-united repeatedly through time (Sanmartín & Ronquist, 2004).

DIVA uses a model in which vicariance, sympatric speciation, dispersal, and extinction events are given different costs. These costs are inversely related to the likelihood of occurrence of these events (Sanmartín & Ronquist, 2004). Specifically, vicariance (speciation because of 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 is implemented in the program DIVA 1.1 (Ronquist, 1996) using the exact search according to the optimization algorithm of Ronquist (1997). The latter 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). This procedure is accomplished via optimization of a three-dimensional cost matrix, where the cost of an event depends on the combination of the distributions of the sister taxa descended from a common ancestor (Ronquist, 1997). In order to allow for the possibility of widespread ancestors, the number of ancestral areas optimized for a particular node is left unrestricted. Walking up the tree, the splitting of areas is interpreted as vicariance (e.g. a situation in which the ancestor at a given node shows area ‘ab’ and one of the two descendants is present only in area ‘a’ whereas the other descendant is recorded in area ‘b’). Likewise, the addition of areas is interpreted as dispersal (e.g. ancestor is present in area ‘a’ and a particular descendant is found in area ‘ab’; that means that the taxon at ‘ab’ has expanded its range, or dispersed, from ‘a’ to include also ‘b’). Those instances in which the same area is reconstructed for an ancestor and its descendant taxa are interpreted as duplication (e.g. a situation in which

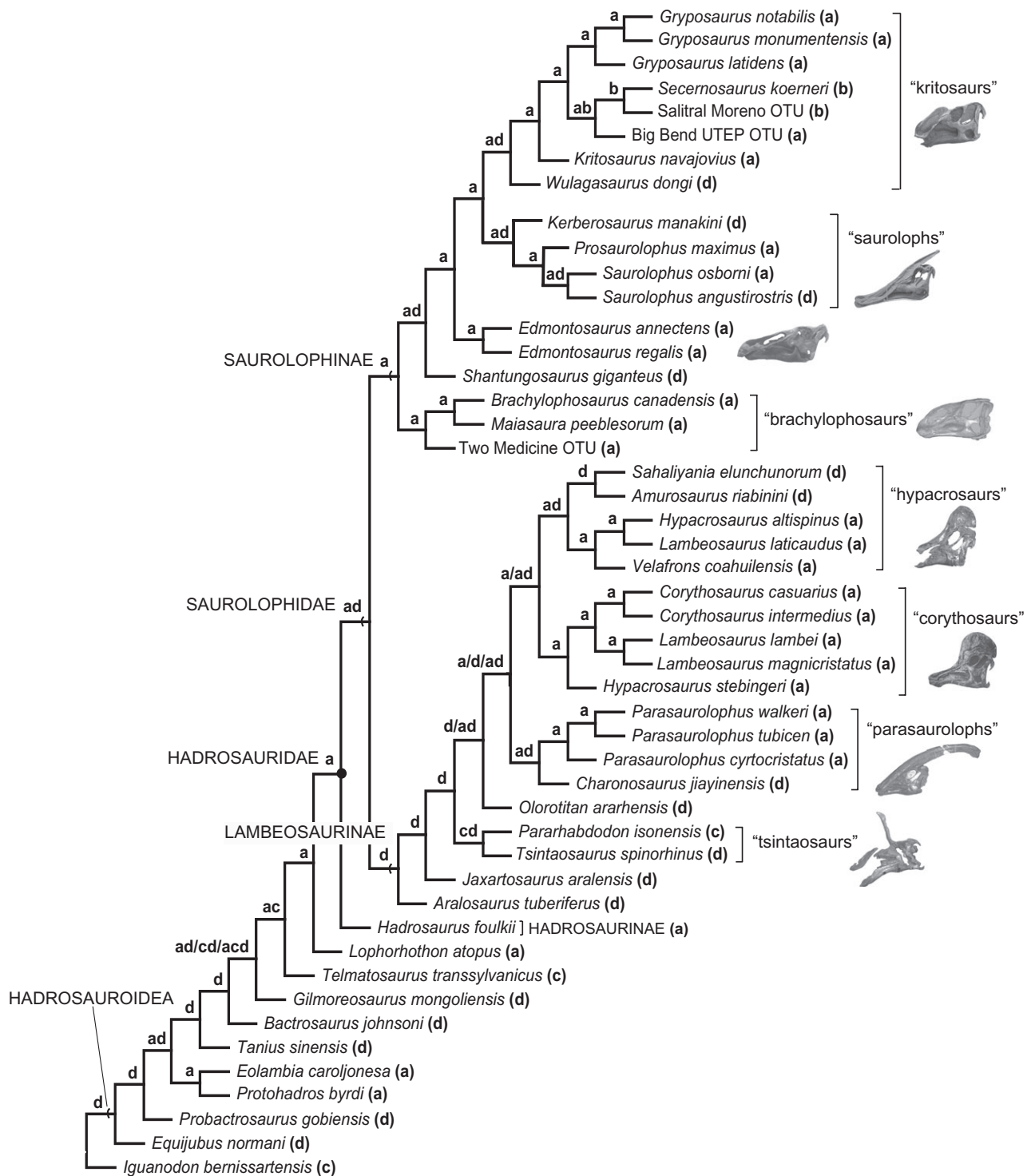


Figure 1. Reduced strict consensus tree derived from parsimony analysis of hadrosauroid dinosaurs by Prieto-Márquez (2010), showing ancestral area reconstructions for all the nodes. Words between quotation marks are informal names created to facilitate the reference to specific clades throughout the text. Abbreviations: a, North America; b, South America; c, Europe; d, Asia; ab, North and South America; ac, North America and Europe; ad, North America and Asia; cd, Eurasia.

ancestor is found in 'a' and both descendants are also in 'a'). However, the recognition of extinction events is much less straightforward. Nylander *et al.* (2008) noted that in those clades where a descendant taxon shows a more restricted distribution than its sister taxon, it would be erroneous to infer extinction as the process causing the loss of the area for one of the taxa. According to these authors, this is because DIVA assumes that widespread distributions cannot be maintained through speciation, which implies that duplication is not allowed in ancestors with widespread distributions and that, instead, these would speciate allopatrically at each node. In addition, a relatively more restricted distribution of a descendant taxon might be the result of a negatively biased fossil record rather than to actual extinction from a particular area.

In this large-scale biogeographical analysis only four general areas are considered. These are the four continental landmasses where all hadrosaurids have

been recorded: Europe, Asia, and the two Americas. The geographical distribution of terminal taxa is displayed in Figure 1.

PHYLOGENETIC HYPOTHESIS

Ancestral areas are reconstructed for all the internal nodes of the phylogeny inferred by Prieto-Márquez (2010), Figs. 2–4. In particular, this phylogeny consists of the reduced strict consensus tree derived from maximum parsimony analysis of a nearly complete taxonomic sample of hadrosaurid species. As DIVA requires fully bifurcated trees (Ronquist, 1996), the only two polytomic relationships in the reduced strict consensus tree presented by Prieto-Márquez (2010) are omitted by pruning the Sabinas operational taxonomic unit (OTU; Kirkland *et al.*, 2006) and *Mantellisaurus atherfieldensis* Hooley, 1925 from the topology. Thus, the tree included a total of 48 species (Tables 1, 2), consisting of one distant

Table 1. Outgroup hadrosauroid taxa used in the biogeographical analysis, showing the occurrence and age considered in this study

Hadrosauroid outgroup taxa	Occurrence	Age
<i>Bactrosaurus johnsoni</i> Gilmore, 1933	Iren Dabasu Fm., Inner Mongolia, China	Late Campanian–?Early Maastrichtian (Van Itterbeek <i>et al.</i> , 2005)
<i>Eolambia caroljonesa</i> Kirkland, 1998	Cedar Mountain Fm., Utah, USA	Late Albian–Early Cenomanian (Lund & Gates, 2006)
<i>Equijubus normani</i> You <i>et al.</i> , 2003	Xinnminbao Group (middle Grey Unit), Gongpoquan Basin, Mazongshan region, Gansu Province, China	Late Barremian–Aptian (Tang <i>et al.</i> , 2001)
<i>Gilmoreosaurus mongoliensis</i> Gilmore, 1933; Brett-Surman, 1979	Iren Dabasu Fm., Inner Mongolia, China	Late Campanian–?Early Maastrichtian (Van Itterbeek <i>et al.</i> , 2005)
<i>Iguanodon bernissartensis</i> Boulenger in Beneden, 1881	Upper Hainaut Group, south-western Belgium	mid-Late Barremian to earliest Aptian (Paul, 2008)
<i>Lophorothon atopus</i> Langston, 1960	Mooreville Chalk Fm. (lower unnamed member), Alabama, USA	Santonian–Campanian boundary (J. Lamb, pers. comm.)
<i>Probactrosaurus gobiensis</i> Rozhdestvensky, 1966	Dashiguo Fm., Mongolia	Barremian–Albian (Norman, 2002)
<i>Protophadros byrdi</i> Head, 1998	Woodbine Fm., Texas, USA	Middle Cenomanian (Head, 1998)
<i>Tanaisius sinensis</i> Wiman, 1929	Jiangjun Fm. (Hu <i>et al.</i> , 2001), Wangshi Group, Shandong Province, China	Early Campanian (Hong & Miyata, 1999)
<i>Telmatosaurus transsylvanicus</i> Nopcsa, 1900, 1903	?Sampetru Fm., near Sampetru (= Szentpeterfalva), Sibisel River valley, Romania	Early Maastrichtian (F. M. Dalla Vecchia, pers. comm.)

Fm., Formation.

In the first column, when two citations accompany the taxonomic name the first one refers to the specific and the second to the generic name. Unless otherwise specified, the occurrences of the second column are taken from the literature references noted in the third, age column.

Table 2. Ingroup hadrosaurid taxa used in the biogeographical analysis, showing the occurrence and age considered in this study

Hadrosaurid ingroup taxa	Occurrence	Age
<i>Amurosaurus riabinini</i> Bolotsky & Kurzanov, 1991	Udurchukan Fm., Amur Region, Russia	Middle–Late Maastrichtian (Godefroit <i>et al.</i> , 2004a)
<i>Aralosaurus tuberiferus</i> Rozhdestvensky, 1968	Bostobe (Bostobynskaya) Fm., Shak Shak locality, north-eastern Aral Sea region, south-western Kazakhstan	Late Santonian–Early Campanian (Kordikova <i>et al.</i> , 2001; Averianov, 2007)
<i>Brachylophosaurus canadensis</i> Sternberg, 1953	Judith River Fm., Montana, USA; Oldman Fm., Alberta, Canada	Late Campanian (LaRock, 2000)
<i>Charonosaurus jiayinensis</i> Godefroit <i>et al.</i> , 2000	Yuliangze Fm., near Jiayin, Heilongjiang Province, north-eastern China	Late Maastrichtian (Godefroit <i>et al.</i> , 2000)
<i>Corythosaurus casuarius</i> Brown, 1914	Dinosaur Park Fm. (lower third), Alberta, Canada	Late Campanian (Evans, 2007)
<i>Corythosaurus intermedius</i> Parks, 1923	Dinosaur Park Fm. (middle third), Alberta, Canada	Late Campanian (Evans, 2007)
<i>Edmontosaurus annectens</i> Marsh, 1892	Hell Creek Fm., Montana and South Dakota, USA; Lance Fm., South Dakota and Wyoming, USA; Laramie Fm., Colorado, USA; Scollard Fm., Alberta, Canada	Late Maastrichtian (Horner <i>et al.</i> , 2004)
<i>Edmontosaurus regalis</i> Lambe, 1917	Hell Creek Fm., Montana, North and South Dakota, USA; Lance Fm., Wyoming, USA; Laramie Fm., Colorado, USA; Scollard Fm., St. Mary River Fm. and Horseshoe Canyon Fm., Canada	Early–Late Maastrichtian (Horner <i>et al.</i> , 2004)
<i>Gryposaurus notabilis</i> Lambe, 1914	Dinosaur Park Fm. (lower third), Alberta, Canada	Late Campanian (Evans, 2007)
<i>Gryposaurus latidens</i> Horner, 1992	Two Medicine Fm. (lower section), near Two Medicine River, Pondera County, Montana, USA	Late Santonian–Early Campanian (Horner, 1992)
<i>Gryposaurus monumentensis</i> Gates & Sampson, 2007	Kaiparowits Fm., southern Utah, USA	Late Campanian (Gates & Sampson, 2007)
<i>Hadrosaurus foulkii</i> Leidy, 1858	Woodbury Fm., Haddonfield, New Jersey, USA	Campanian (Prieto-Márquez <i>et al.</i> , 2006)
<i>Hypacrosaurus altispinus</i> Brown, 1912	Horseshoe Canyon Fm., Alberta, Canada	Early Maastrichtian (Evans, 2007)
<i>Hypacrosaurus stebingeri</i> Horner & Currie, 1994	Two Medicine Fm. (upper section), Montana, USA; Oldman Fm., Alberta, Canada	Middle–Late Campanian (Horner <i>et al.</i> , 2004)
<i>Jaxartosaurus aralensis</i> Riabinin, 1939	Syuksyuk Fm., Kazakhstan	Santonian (Averianov & Nesson, 1995)
<i>Kerberosaurus manakini</i> Bolotsky & Godefroit, 2004	Tsagayan Fm. (upper section), Nagornaia street in Blagoveshensk city, Amur Region, Russia	?Late Maastrichtian (Bolotsky & Godefroit, 2004)
<i>Kritosaurus navajovius</i> Brown, 1910	Kirtland Fm. (De-Na-Zin Member), San Juan Basin, New Mexico, USA	Late Campanian (Sullivan, 1999)
<i>Kritosaurus australis</i> Bonaparte <i>et al.</i> , 1984	Los Alamitos Fm., Rio Negro Province, north-eastern Patagonia, Argentina	Late Campanian–Early Maastrichtian (Apesteguia, 2005)
<i>Lambeosaurus lambei</i> Parks, 1923	Dinosaur Park Fm. (middle–upper sections), Alberta, Canada	Late Campanian (Evans, 2007)

Table 2. Continued

Hadrosaurid ingroup taxa	Occurrence	Age
<i>Lambeosaurus magnicristatus</i> Sternberg, 1935	Dinosaur Park Fm. (upper section), Alberta, Canada	Late Campanian (Evans, 2007)
<i>Lambeosaurus laticaudus</i> Morris, 1981	El Gallo Fm., north of Arroyo del Rosario, El Rosario, northern Baja California, Mexico	Campanian (Horner <i>et al.</i> , 2004)
<i>Maiasaura peeblesorum</i> Horner & Makela, 1979	Two Medicine Fm., Montana, USA	Middle–Late Campanian (Horner <i>et al.</i> , 2004)
<i>Olorotitan ararhensis</i> Godefroit <i>et al.</i> , 2003	Kundur, Amur Region, Far Eastern Russia	Middle–Late Maastrichtian (Godefroit <i>et al.</i> , 2003)
<i>Pararhabdodon isonensis</i> Casanovas-Cladellas <i>et al.</i> , 1993	Tremp Fm., Catalunya, north-eastern Spain	Late Maastrichtian (Prieto-Márquez <i>et al.</i> , 2006)
<i>Parasaurolophus walkeri</i> Parks, 1922	Dinosaur Park Fm. (lower third), Alberta, Canada	Late Campanian (Evans, 2007)
<i>Parasaurolophus tubicen</i> Wiman, 1931	Kirtland Fm. (lower section), New Mexico, USA	Late Campanian (Horner <i>et al.</i> , 2004)
<i>Parasaurolophus cyrtocristatus</i> Ostrom, 1961	Kaiparowits Fm., Utah, USA; Fruitland Fm., New Mexico, USA	Late Campanian (Horner <i>et al.</i> , 2004)
<i>Prosaurolophus maximus</i> Brown, 1916	Dinosaur Park Fm. (upper half), Alberta, Canada	Late Campanian (Evans, 2007)
<i>Sahaliyana elunchunorum</i> Godefroit <i>et al.</i> , 2008	Yuliangze Fm., near Wulaga, Heilongjiang Province, north-eastern China	?Late Maastrichtian (Godefroit <i>et al.</i> , 2008)
<i>Saurolophus osborni</i> Brown, 1913	Horseshoe Canyon Fm., Alberta, Canada	Early Maastrichtian (Horner <i>et al.</i> , 2004)
<i>Saurolophus angustirostris</i> Rozhdestvensky, 1952	Nemegt Fm. (white beds of Hermin Tsav), North Sayr, Nemegt, Mongolia	Middle Maastrichtian (Wilson, 2005)
<i>Secernosaurus koeneri</i> Brett-Surman, 1979	Upper Bajo Barreal Fm., Lago Colhue Huapi, Rio Negro Province, Argentina	Late Campanian–Early Maastrichtian (G. Salinas, pers. comm.)
<i>Shantungosaurus giganteus</i> Hu, 1972	Xingezhuang Fm. (Hu <i>et al.</i> , 2001), Wangshi Group, Shandong Province, China	Early Campanian (Hong & Miyata, 1999)
<i>Tsintaosaurus spinorhinus</i> Young, 1958	Jingangkou Fm. (Hu <i>et al.</i> , 2001), Wangshi Group, Shandong Province, China	Early Campanian (Hong & Miyata, 1999)
<i>Velafrons coahuilensis</i> Gates <i>et al.</i> , 2007	Cerro del Pueblo Fm., Coahuila, Mexico	Late Campanian (Gates <i>et al.</i> , 2007)
<i>Wulagasaurus dongi</i> Godefroit <i>et al.</i> , 2008	Yuliangze Fm., near Wulaga, Heilongjiang Province, north-eastern China	?Late Maastrichtian (Godefroit <i>et al.</i> , 2008)
Unnamed hadrosaurid from Big Bend National Park (Davies, 1983)	Aguja Fm. (upper shale member), Texas, USA	Campanian–?Early Maastrichtian (Wagner, 2001)
Unnamed hadrosaurid from the Two Medicine and Wahweap Fm. (T. A. Gates, pers. comm.)	Two Medicine Fm.; Wahweap Fm (upper section)	Late Campanian (Gates, 2007)
Unnamed hadrosaurid from Salitral Moreno (Powell, 1987)	Allen Fm., Rio Negro Province, Argentina	Late Campanian–Early Maastrichtian (Salgado <i>et al.</i> , 2007)

Fm., Formation.

In the first column, when two citations accompany the taxonomic name the first one refers to the specific and the second to the generic name. Unless otherwise specified, the occurrences of the second column are taken from the literature references noted in the third, age column.

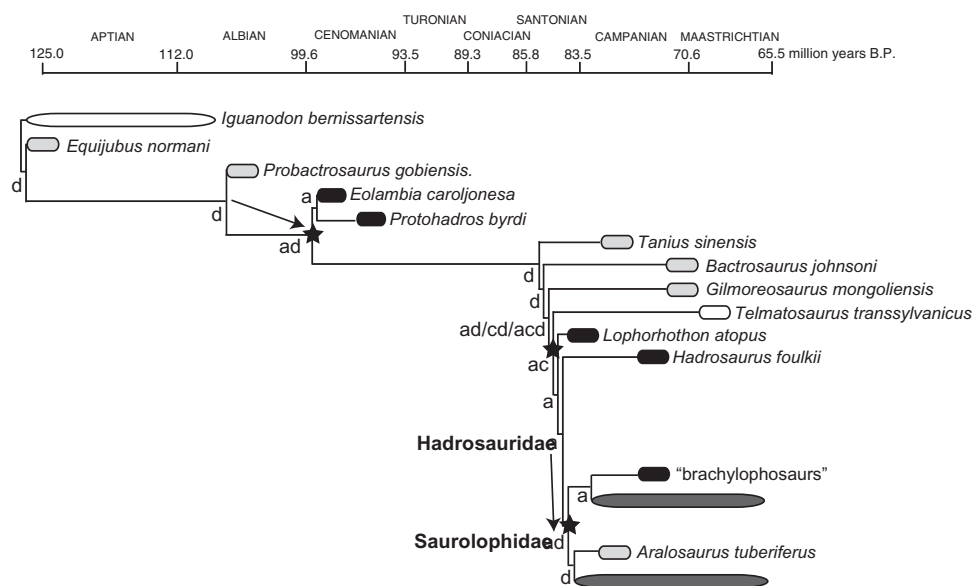


Figure 2. Time-calibrated phylogram of Hadrosauroidea based on the reduced strict consensus tree of Prieto-Márquez (2010). Letters at each node represent ancestral areas as inferred in the dispersal–vicariance analysis; their meaning is as in Fig. 1. The colours of the stratigraphical ranges of taxa indicate the following areas: white, Europe; black, North America; light grey, Asia; dark grey, range of an entire clade. Black stars indicate vicariance. Arrows indicate the direction of dispersal events. Note that the stratigraphical ranges for each species are not point estimates, but just extend to indicate divisions of particular geochronological stages. Geochronological ages from Gradstein, Ogg, Smith (2004). Abbreviations: a, North America; b, South America; c, Europe; d, Asia; ab, North and South America; ac, North America and Europe; ad, North America and Asia; cd, Eurasia.

outgroup to hadrosaurids (*Iguanodon bernissartensis* Boulenger in Beneden, 1881), nine nonhadrosaurid hadrosauroids, and 38 hadrosaurids (including, but not restricted to, 18 saurolophines and 19 lambeosaurines). The taxonomic nomenclature and clade definitions follow those of Prieto-Márquez (2010), who used different names to refer to some major hadrosaurid clades; notably, Saurolophidae was used for Lambeosaurinae plus Saurolophinae and Saurolophinae instead of Hadrosaurinae (Fig. 1). Informal names, written between quotation marks, are created here to facilitate reference to the main less inclusive clades of the tree (Fig. 1). The stratigraphical ages of the 48 species of hadrosauroids considered here are taken from the literature (Tables 1, 2).

RECONSTRUCTING THE HADROSAURID BIOGEOGRAPHICAL HISTORY

HADROSAUROID OUTGROUP TAXA AND HADROSAURIDAE

The inference of ancestral areas for nonhadrosaurid hadrosauroids is presented in Figure 2. DIVA inferred the origin of Hadrosauroidea in Asia no later than the Early Aptian, as well as a subsequent dispersal of these animals to North America during the

Cenomanian. The most recent common ancestor of the *Eolambia*–*Protohadros* clade and remaining hadrosauroids is reconstructed as widespread between Asia and North America. The split of the North American *Eolambia*–*Protohadros* clade from the other Asian hadrosauroids occurred after a vicariant event. The next two clades that evolved within Hadrosauroidea originated in Asia no later than the Santonian and are represented by forms discovered in Campanian to Early Maastrichtian formations of China (*Tanius sinensis* Wiman, 1929 and *Bactrosaurus johnsoni*).

Only ambiguous reconstructions are provided for the area occupied by the most recent common ancestor of *Gilmoreosaurus mongoliensis* (Late Campanian–Early Maastrichtian of China) and remaining hadrosauroids, with possible ancestral distributions widespread between Asia and North America, Eurasia, or North America and Eurasia. The most recent common ancestor of *Telmatosaurus transsylvanicus* (Maastrichtian of eastern Europe) and the clade including *Lophorhothon atopus* Langston, 1960 and Hadrosauridae is inferred to have been widespread throughout North America and Europe. Likewise, speciation of *T. transsylvanicus* is likely to have been because of vicariance, preceded perhaps by a

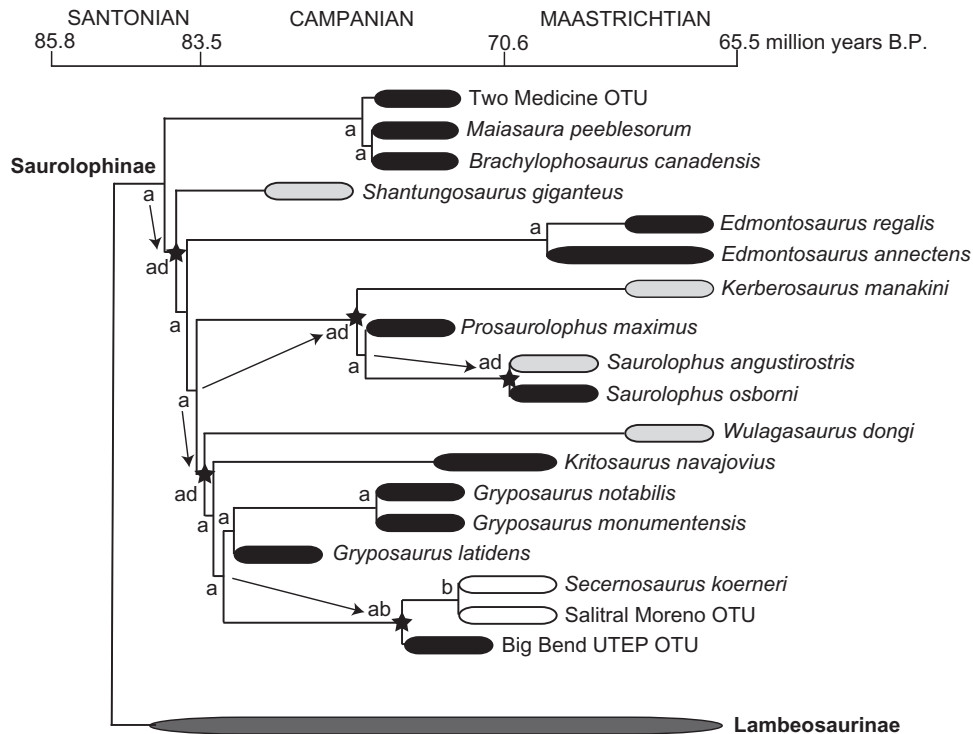


Figure 3. Time-calibrated phylogram of Saurolophinae based on the reduced strict consensus tree of Prieto-Márquez (2010). Letters at each node represent ancestral areas as inferred in the DIVA analysis; their meaning is as in Fig. 1. The colors of the stratigraphic ranges of taxa indicate the following areas: white = South America; black = North America; light grey = Asia; dark grey = range of an entire clade. Black stars indicate vicariance. Arrows indicate the direction of dispersal events. Note that the stratigraphic ranges for each species are not point estimates, but just extend to indicate divisions of particular geochronological stages. Geochronological ages from Gradstein *et al.* (2004).

dispersal event of hadrosauroids from Asia or Asiamerica. However, the sister taxon to Hadrosauridae, *Lophorhothon atopus* (Late Santonian of Alabama), evolved from an ancestor that lived in the eastern half of North America no later than the Late Santonian.

The present analysis indicates that the ancestral area of Hadrosauridae was located in North America (Fig. 2), in agreement with Head (1998), Kirkland (1998), and Horner *et al.* (2004). However, the most recent common ancestor of Saurolophidae is inferred to have been widespread in Asia and North America. The latter distribution was preceded by a dispersal event from North America to Asia that occurred no later than the Late Santonian. Subsequently, also sometime during the Santonian, saurolophids split in response to vicariance into the two major subclades of hadrosaurids, Saurolophinae and Lambeosaurinae (Fig. 2).

SAUROLOPHINE ANCESTRAL AREAS

The reconstruction of ancestral areas for saurolophine hadrosaurids is presented in Figure 3. The ancestral

area of Saurolophinae is inferred to have been located in North America, where the most basal members of the clade, the Late Campanian 'brachylophosaurs' (Fig. 6), have been recorded. From North America, saurolophines dispersed to Asia no later than the Early Campanian. The shortest route for this dispersal would have been across the Bering land bridge, which may have existed during that time (Zharkov, Murdmaa & Filatova, 1998; Averianov & Archibald, 2003).

From this Asiamerican distribution, two lineages evolved through vicariance: *Shantungosaurus giganteus* Hu, 1972 (Campanian of China) in Asia and a very diverse clade in North America that included *Edmontosaurus*, 'saurolophs', and 'kritosaurs'. No later than the Early Campanian (the age of the oldest saurolophine, *Gryposaurus latidens* Horner, 1992), the latter clade diverged in North America into *Edmontosaurus* and the clade including 'saurolophs' and 'kritosaurs'. From western North America, two dispersal events to Asia occurred within the 'sauroloph-kritosaur' clade. The most obvious and shortest route from western North America to Asia for these dispersals would have been via the Bering land bridge

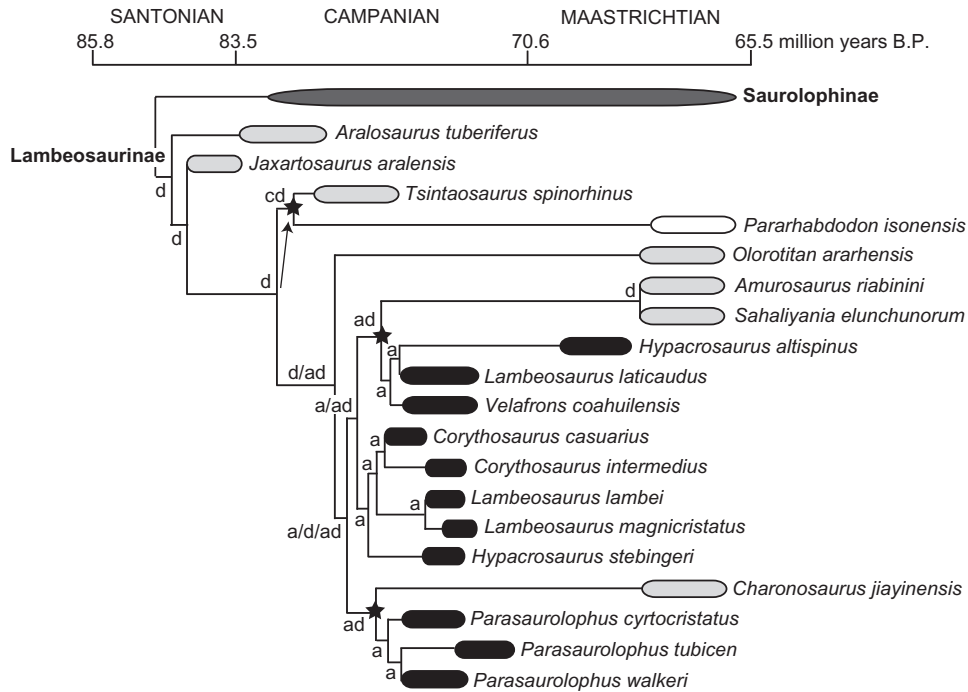


Figure 4. Time-calibrated phylogram of Lambeosaurinae based on the reduced strict consensus tree of Prieto-Márquez (2010). Letters at each node represent ancestral areas as inferred in the DIVA analysis; their meaning is as in Fig. 1. The colors of the stratigraphic ranges of taxa indicate the following areas: white = Europe; black = North America; light grey = Asia; dark grey = range of an entire clade. Black stars indicate vicariance. Arrows indicate the direction of dispersal events. Note that the stratigraphic ranges for each species are not point estimates, but just extend to indicate divisions of particular geochronological stages. Geochronological ages from Gradstein *et al.* (2004).

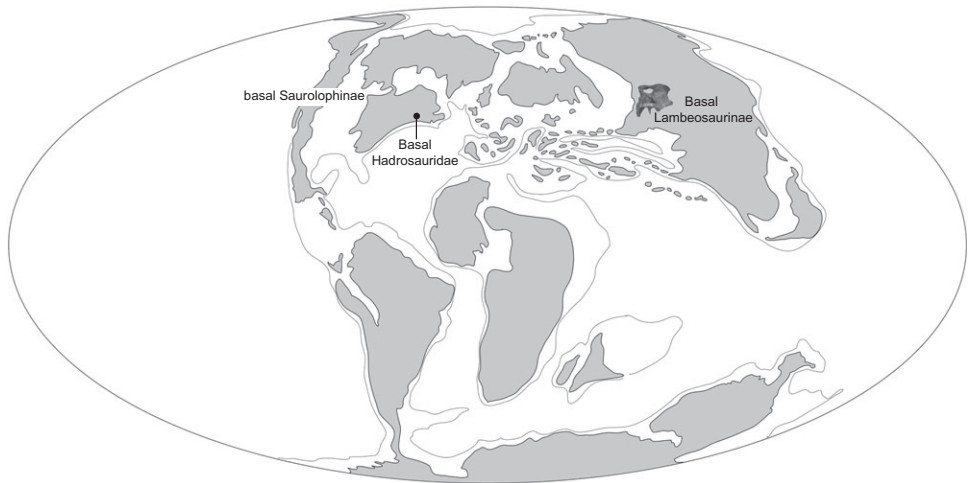


Figure 5. Distribution of the main hadrosaurid clades discussed in the text on a paleogeographic reconstruction of continental coastlines during the Santonian. Continental paleocoastlines redrawn after Smith, Smith & Funnell (1994), Hay *et al.* (1999), Blakey (2001), Pough *et al.* (2004), and Hedges (2006). The partial skull depicted to represent basal lambeosaurines is that of *Jaxartosaurus ararlensis*.



Figure 6. Distribution of the main hadrosaurid clades discussed in the text on a paleogeographic reconstruction of continental coastlines during the Campanian. Continental paleocoastlines redrawn after Smith *et al.* (1994), Hay *et al.* (1999), Blakey (2001), Pough *et al.* (2004), and Hedges (2006).

(Russell, 1993; Averianov & Archibald, 2003). The direction of these dispersals from North America to Asia agrees with Gates (2007), who also proposed such directionality to explain the distribution of the species of *Saurolophus* in both continents. According to the present analysis, one of these dispersals took place no later than the Late Campanian and led to the evolution of 'saurolophs' (Fig. 6). The common ancestor of 'saurolophs' became widespread in Asia and North America, and the split between *Kerberosaurus manakini* (Maastrichtian of Russia) and the *Prosaurolophus*–*Saurolophus* clade probably occurred through vicariance. Similarly, the most recent common ancestor of *Saurolophus osborni* and *Saurolophus angustirostris* became widespread in North America and Asia after a dispersal event inferred to have occurred from the former to the latter continent no later than the Early Maastrichtian. Subsequently, the two *Saurolophus* species evolved separately in response to vicariance.

The other dispersal event within the 'kritosaur–sauroloph' clade also is inferred to have occurred from North America to Asia, in this case no later than the Early Campanian. As a result, the most recent common ancestor of all 'kritosaurs' lived in both North America and Asia. A vicariant event led to the split between *Wulagasaurus dongi* Godefroit *et al.*, 2008 in Asia and the common ancestor of all other 'kritosaurs' in North America. From North America, a dispersal event to South America is inferred to have occurred no

later than the Late Campanian. This dispersal, previously posited by Weishampel & Weishampel (1983), Bonaparte *et al.* (1984), and Horner *et al.* (2004), led to the widespread distribution in both Americas of the most recent common ancestor of *Secernosaurus koerneri*, the Salitral Moreno OTU, and the Big Bend UTEP (Centennial Museum at the University of Texas at El Paso) OTU. The existence of a land connection between both Americas during the Late Cretaceous has recently been supported by several studies (e.g. Pough *et al.*, 2004). In particular, subduction of the southern part of the North American plate under the eastward-moving Caribbean plate may have given rise to a Proto-Antillean volcanic arc (Duellman, 2001; Pindell & Kennan, 2002; Hedges, 2006). This chain of islands would have been located between North and South America in the position currently occupied by Central America, thereby providing a dispersal route for hadrosaurids and other vertebrates during at least the Late Campanian (Hedges, 2006; Fig. 6). The Antilles are believed to have subsequently moved eastward during the migration of the Caribbean plate (Duellman, 2001). By the Maastrichtian, this connection would have been interrupted (Pindell & Kennan, 2002; Fig. 7). This scenario is congruent with vicariance being involved in the evolution of the *Secernosaurus*–*Salitral Moreno* clade in South America (Fig. 6). A similar scenario, whereby the Caribbean plate carried ancient Mesozoic biota eastwards, has previously been posited to explain the evolution of various endemic

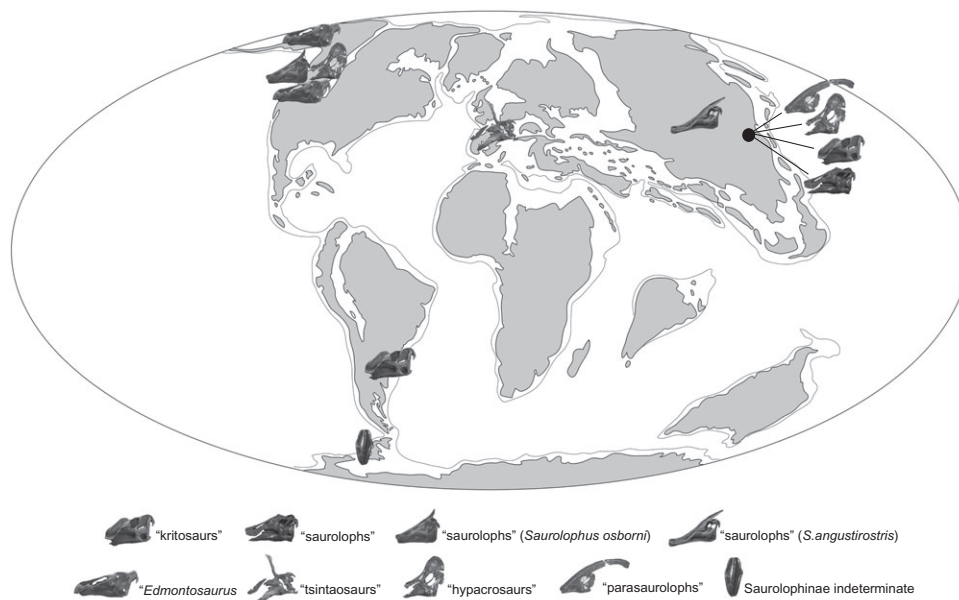


Figure 7. Distribution of the main hadrosaurid clades discussed in the text on a paleogeographic reconstruction of continental coastlines during the Maastrichtian. Continental paleocoastlines redrawn after Smith *et al.* (1994), Hay *et al.* (1999), Blakey (2001), Pough *et al.* (2004), and Hedges (2006).

terrestrial vertebrates in the Antilles (Hedges, 2006). By the Late Campanian, the South American clade is inferred to have diverged from North American 'kritosaurus' as a result of vicariance.

It is worth noting that Case *et al.* (2000) reported an isolated hadrosaurid tooth from the Late Maastrichtian Lopez de Bertodano Formation, in Vega Island, Antarctica (Fig. 7). I concur with these authors in regarding this tooth as belonging to a member of Saurolophinae (their Hadrosaurinae). My reasons for this referral are the absence of all but a median carina and the lack or very small size of marginal denticles. Hadrosaurids may have dispersed into Antarctica through an isthmus that connected this continent with South America during, at least, the Late Campanian and Early Maastrichtian (Zharkov *et al.*, 1998; Hay *et al.*, 1999).

LAMBEOSAURINE ANCESTRAL AREAS

The reconstruction of ancestral areas for lambeosaurine hadrosaurids is presented in Figure 4. The DIVA analysis indicated that the most recent common ancestor of Lambeosaurinae evolved in Asia no later than the Late Santonian. An Asian origin for lambeosaurines is in agreement with the biogeographical hypothesis of Godefroit *et al.* (2004b, 2008). Following an early diversification in Asia (*Aralosaurus tuberiferus* Rozhdestvensky, 1968 and *Jaxartosaurus aralensis* Riabinin, 1939), a dispersal event from this

continent to Europe is inferred to have occurred no later than the Early Campanian. This led to the Eurasian distribution of the most recent common ancestor of *Tsintaosaurus spinorhinus* Young, 1958 (Early Campanian of China) and *Pararhabdodon isonensis* (Late Maastrichtian of Spain). Although no continuous land connection between Asia and Europe has been reconstructed for the Late Cretaceous, 'tsintaosaurs' may have used the mosaic of small land-masses that then formed the European archipelago (Haq, Hardenbol & Vail, 1987) as stepping-stones to reach the western region of this continent. The recent discovery of another basal lambeosaurine from southwestern Europe has supported a close relationship between the Asian and European lambeosaurine faunas (Pereda-Suberbiola *et al.*, 2009). Speciation of *P. isonensis* and *T. spinorhinus* is inferred to have occurred in response to vicariance no later than the Early Campanian. This hypothesis supports similar conclusions reached by Casanovas *et al.* (1999). The mosaic palaeogeographical configuration of Europe during that time supports the possibility of vicariant events operating because of the intermittent nature of the land connections owing to relatively high eustatic sea levels (Dalla Vecchia, 2006).

Walking up the lambeosaurine tree, DIVA could only infer ambiguous ancestral areas for the most recent common ancestors of the next three more inclusive clades (Fig. 4). The results of the analysis indicate that no later than the Late Campanian

lambeosaurines occupied western North America, where they underwent extensive cladogenesis. This lambeosaurine radiation gave rise to the 'hypacrosaur–corythosaur' and 'parasauroloph' clades. However, because of the ambiguity in the ancestral area reconstruction of those internal nodes in the lambeosaurine tree, it is uncertain at which point in their phylogenetic history these animals reached North America. Yet, the ancestral areas of 'hypacrosaur', 'corythosaurs', and 'parasauroloph' are unambiguously inferred.

Thus, the most recent common ancestor of 'hypacrosaur' is inferred to have been widespread between North America and Asia. No later than the Late Campanian, Asian 'hypacrosaur' split through vicariance from the North American clade. Within the latter, it is likely that their most recent common ancestor originated in the southern region of the continent. This is suggested by a northward shift in the distribution of the three North American 'hypacrosaur' from the Late Campanian to the Early Maastrichtian (Fig. 4). Specifically, *Velafrons coahuilensis* Gates *et al.*, 2007, the outgroup to the *Lambeosaurus laticaudus* Morris, 1981–*Hypacrosaurus altispinus* Brown, 1912 clade, lived in Mexico during the Late Campanian. *Lambeosaurus laticaudus* also lived in the Late Campanian of Mexico. The occurrence of its sister taxon, *H. altispinus*, in the Early Maastrichtian of northern North America could have been the result of a northward dispersal. 'Corythosaurs' originated in North America no later than the Late Campanian and the evolution of this clade appears to have been restricted to this continent, consisting of a series of duplication events (Fig. 4).

Finally, 'parasauroloph' evolved from an ancestor that is inferred to have been present in North America and Asia no later than the Late Campanian. By that time, a vicariant event led to the speciation of *Charonosaurus jiyinensis* in Asia and the most recent common ancestor of *Parasaurolophus* spp. in North America.

DISCUSSION

There are various sources of uncertainty that may affect the accuracy of the biogeographical histories presented here. First, the accuracy of the ancestral areas inferred in the dispersal–vicariance analysis rests upon the accuracy of the phylogeny used. Although the latter resulted from the most thorough phylogenetic analysis of hadrosaurids published so far, future discoveries of new taxa may lead to changes in its topology, which in turn may result in differences in the inference of ancestral areas. Second, the optimization of areas in DIVA may result in some nodes exhibiting equally optimal parsimonious recon-

structions, especially in the presence of many widespread distributions (Nylander *et al.*, 2008). Usually, this ambiguity tends to increase towards the root node, because the latter typically includes all or most of the areas occupied by terminal taxa (Ronquist, 1996). Additionally, two other sources of uncertainty are the stratigraphical ages of the taxa of interest and the degree of completeness of their fossil record.

UNCERTAINTY IN THE STRATIGRAPHICAL DATING

The validity of the inferred time of origin and the sequence of historical biogeographical events is directly affected by the accuracy of the stratigraphical ages of the taxa under consideration. In general, there are few stratigraphical sequences that have yielded hadrosauroid material whose age is known with relatively good accuracy and precision. One of these sequences is the Late Campanian deposits of the Dinosaur Provincial Park, in southern Canada, that yielded a rich fossil record of saurolophines and lambeosaurines. Another example is the Late Maastrichtian strata of the South-Central Foredeep Pyrenean Basin of north-eastern Spain that yielded one of the only two named hadrosaurids in Europe, the lambeosaurine *Pararhabdodon isonensis*. In contrast, the age of several hadrosauroid species that occupy basal positions in the phylogeny has been contentious. Accurate ages for these basal species are important for unravelling the age of first appearance of particular clades, which constitute outgroup taxa to hadrosaurids. This is exemplified by the uncertainty that has surrounded the age of the Iren Dabasu Formation in Inner Mongolia, southern China. This formation yielded two outgroup taxa to hadrosaurids, *Bactrosaurus johnsoni* and *Gilmoresaurus mongoliensis*. The age of the Iren Dabasu Formation has been estimated as Early Cretaceous (Berkey & Morris, 1927), Cenomanian (Rozhdestvensky, 1966, 1977), pre-Turonian (Weishampel & Horner, 1986), pre-Santonian (Brett-Surman, 1979), Early Late Cretaceous (Godefroit *et al.*, 1998), Early Campanian (Jerzykiewicz & Russell, 1991; Currie & Eberth, 1993), and Maastrichtian (Chen, 1983; Liu & Wu, 1990). More recently, Van Itterbeek *et al.* (2005) re-studied the stratigraphy and sedimentology of the Iren Dabasu Formation and concluded that it is most probably latest Campanian–Early Maastrichtian in age. They based this conclusion on the age provided by microfossils, particularly four species of charophytes and eight species of ostracods.

The Wangshi Group, in the Chinese Province of Shandong, yielded a primitive hadrosauroid fauna, including *Tanios sinensis*, the basal saurolophine *Shantungosaurus giganteus*, and the basallambeosaurine *Tsintaosaurus spinorhinus*. Estimations of the

age of the Wangshi Group vary from Coniacian to the Maastrichtian (Zhang, Dong & Shi, 2003; Horner *et al.*, 2004) or simply Campanian (Buffetaut, 1995; Godefroit *et al.*, 2003; Bolotsky & Godefroit, 2004). However, Zhang *et al.* (2008) recently reported that basalt floods in the Wangshi Group date back to 74 million years old, placing these strata in the Middle Campanian. Additionally, Hong & Miyata (1999) dated the Wangshi Group as being between 82.4 and 81.8 million years old on the basis of fission track zircon ages and the fossil gastropod *Campeloma liui*.

The age of *Aralosaurus tuberiferus* is very relevant for estimating the time of origin of Lambeosaurinae because this species is the outgroup taxon to all other members of the clade. *Aralosaurus tuberiferus* was collected from the Shakh Shakh locality of the Bostobe Formation, in the north-eastern Aral Sea Region, Kazakhstan (Godefroit *et al.*, 2004b). The Bostobe Formation has also been known as the Beleuta (Hwang *et al.*, 2002) or Bostobynskaya (Dyke & Malakhov, 2004) Formation. The age of this formation has received different estimates, from Turonian (Nessov & Khissarova, 1988), Turonian–Santonian (Godefroit *et al.*, 2004b), Santonian (Averianov, 2007), Santonian–Campanian (Kordikova *et al.*, 2001), and Campanian (Nessov, 1995).

COMPLETENESS OF THE HADROSAURID FOSSIL RECORD

The completeness of the fossil record of hadrosauroids (hadrosaurids and closely related outgroup taxa), as well as the stratigraphical fit of the phylogeny utilized in this analysis, can affect the accuracy biogeographical hypotheses herein presented. The time-calibrated phylograms showed a substantial amount of time represented by ghost lineages (Figs 2–4). In order to show quantitatively the extent of this apparent lack of representation in the evolutionary history of hadrosauroids, I estimated the completeness of the fossil record of these animals. This is accomplished using the method of Foote & Raup (1996). Unlike other approaches (Norell & Novacek, 1992; Benton & Storrs, 1994; Smith & Littlewood, 1994) that provide an assessment of the proportion of preserved taxa in the fossil record based on a phylogenetic hypothesis, Foote and Raup's method is based only on the duration of the taxa of interest and does not require a phylogeny. This method is preferred because it does not incorporate potential errors in the accuracy of the phylogeny.

In their approach, Foote & Raup (1996) estimated the proportion of taxa preserved in the fossil record of a given group by combining estimates of the preservation probability and estimates of the original durations of its constituent taxa. Specifically, the

completeness of the fossil record is computed using the following expression:

$$P_P = \sum_{T=1}^{\infty} P_1(T) \cdot h(T),$$

where P_P is the proportion of preserved fossil record, $P_1(T)$ the probability that a taxon is preserved at least once given an original duration of T stratigraphical units and $h(T)$ the probability that the original durations are equal to T . $P_1(T)$ is given by the following expression:

$$P_1(T) = 1 - (1 - R)^T,$$

where R is the probability that a given species is preserved at least once in one stratigraphical unit and T the number of stratigraphical units where that species was recorded. R is calculated using the following equation:

$$R = f(2)^2 / [f(1) \cdot f(3)],$$

where $f(1)$, $f(2)$ and $f(3)$ are the frequencies of species preserved in one, two, and three stratigraphical units, respectively. For the calculation of $f(t)$ (the frequencies of species with t preserved stratigraphical units), each geological stage is divided into three parts or units (Early, Middle, and Late). The next step is to compile the number of stratigraphical units recorded for every species, which is compiled from the data shown in Tables 1 and 2. Thus, for example, a species recorded from the Late Santonian to the Early Campanian would be assigned a value of two stratigraphical units and a species recorded from the Santonian would be assigned a value of three units.

Finally, the probability that the original duration of a taxon is equal to T stratigraphical units is calculated using the following expression:

$$h_1(T) = e^{-q(T-1)} - e^{-qT}.$$

The calculation of this probability assumed an exponential distribution of the original durations with constant extinction rate (Alba, Agustí & Moyà-Solà, 2001). This constant (q in the formula above) is obtained from the natural logarithm of the slope of the range of frequencies $f(t)$.

In the case of hadrosauroids, the probability that a species is recorded at least once in a stratigraphical unit is 0.61. The completeness of the hadrosauroid fossil record is 0.69. Two limitations inherent to the data used for this analysis (Tables 1, 2) should be kept in mind as potential sources of error for this estimate. First, and as explained above, hadrosauroid ages are not precise point estimates but consist of time intervals subject to error and uncertainty. Second, the slope q could only be approximated as the difference between the natural logarithms of $f(2)$ and

f(3). This is because the small (relative to other taxonomic groups such as Neogene mammals) number of hadrosauroid species did not include any taxa with longer durations than three stratigraphical units. With this in mind, the hadrosauroid fossil record appeared to be reasonably complete, a result hardly surprising given the fact that this clade is one of the best represented within non-avian dinosaurs.

Finally, Prieto-Márquez (2010) assessed the fit between the stratigraphical ages of hadrosauroid species and the order of branching events of the phylogeny considered in this study. This was accomplished by implementing the Manhattan Stratigraphic Measure (MSM; Siddall, 1998) as modified by Pol & Norell (2001; MSM*). His analysis resulted in a MSM* for Hadrosauroidea of 0.97 (P -value = 0.001) and a MSM* for Hadrosauridae of 0.91 (P -value = 0.008). These measures indicate a significant high degree of congruence between the sequence of appearance of hadrosauroid species in the stratigraphical record and the branching sequence of the phylogeny. Prieto-Márquez's results are congruent with the relatively good completeness of the hadrosauroid fossil record estimated here.

In conclusion, potential inaccuracies in the inference of the biogeographical hypotheses presented above are more likely to be caused by inaccuracies of the phylogeny and/or shortcomings of the inference of ancestral areas than by the incompleteness of the hadrosauroid/hadrosaurid fossil record and the stratigraphical fit of the phylogenetic tree.

LATE CRETACEOUS DINOSAURIAN BIOGEOGRAPHY

As suggested above, the radiation of Saurolophidae is inferred to have occurred separately in North America and Asia in response to vicariance. In a broader context, this hypothesis agrees only partially with the dinosaurian pattern of origination presented by Russell (1993). This author emphasized the importance of Asia as the ancestral area for numerous groups of non-avian dinosaurs, particularly those with well-represented distributions in North America. More recently, an Asian origin has been posited for a number of dinosaurian contemporaries of hadrosaurids, such as dromaeosaurids (Norell and Makovicky, 2004), troodontids (Makovicky & Norell, 2004), therizinosaurids (Clark, Maryanska & Barsbold, 2004), pachycephalosaurs (Maryanska, Chapman, and Weishampel, 2004), and neoceratopsians (You & Dodson, 2004). According to the results shown above, lambeosaurines (but not saurolophines) would join that list. Notably, as in for example several saurolophine subclades, dispersals between North America and Asia via the Bering land bridge have also been proposed for other Late Cretaceous dinosaurian

clades (Russell, 1993). For example, troodontids appear to have dispersed back to North America no later than the Campanian (Makovicky & Norell, 2004). Ornithomimids and therizinosaurids required dispersal events to North America to account for their biogeography (Makovicky & Norell, 2004; Clark *et al.*, 2004). By contrast, pachycephalosaurs showed a bidirectional dispersal pattern between North America and Asia (Maryanska *et al.*, 2004). However, the mammalian record is weakly in accord with the hadrosaurid pattern because faunal exchanges between North America and Asia of Late Cretaceous mammals appear to have been uncommon, with only two cases on record (one occurring before the Cenomanian and another in the Middle Campanian; Weil, 2002).

'Kritosaur' saurolophines may have been accompanied by other groups of vertebrates in their dispersal to South America. Such may have been the case of didelphid marsupials and several groups of placental mammals with North American affinities, which are also recorded in the Late Cretaceous of South America (Bonaparte & Rougier, 1987; Cox, 2000).

CONCLUSIONS

Dispersal–vicariance analysis of hadrosaurid dinosaurs indicates that their recorded distribution was mainly shaped by dispersal, vicariance, and duplication events that took place during a time spanning from the Late Santonian to the Late Maastrichtian. This study supports North America as the region harbouring the ancestral area of Hadrosauridae. Subsequently, no later than the Late Santonian, hadrosaurids dispersed to Asia. The most recent common ancestor of Saurolophidae, the major clade of hadrosaurids containing all known species with the exception of *Hadrosaurus foulkii*, is inferred to have been widespread in North America and Asia. No later than the Late Santonian, Saurolophinae *sensu* Prieto-Márquez (2010) and Lambeosaurinae split in response to vicariance. The genesis of saurolophines is inferred to have occurred in North America, whereas that of lambeosaurines was reconstructed to have occurred in Asia. Saurolophine biogeographical history was mostly influenced by dispersal events from North America to Asia and, to a lesser extent, to South America, followed by vicariant events. By contrast, the biogeographical history of lambeosaurines can be traced back to an early evolution in Asia, with at least one unambiguously reconstructed dispersal event to the European archipelago by the Early Campanian followed by vicariance. However, the ancestral areas for the deepest nodes relating the more derived lambeosaurine clades could not be unambiguously inferred. The historical biogeography of 'hypacrosaur' and 'parasauroloph' was mainly influenced by

vicariant and duplication events, whereas that of 'corythosaurs' appears to have been restricted to North America.

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