The first duckbill dinosaur (Hadrosauridae: Lambeosaurinae) from Africa and the role of oceanic dispersal in dinosaur biogeography

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A B S T R A C T

The Late Cretaceous saw distinctly endemic dinosaur faunas evolve in the northern and southern hemispheres. The Laurasian continents of North America and Asia were dominated by hadrosaurid and ceratopsian ornithischians, with tyrannosaurs as apex predators. In Gondwanan communities, including Africa, South America, India and Madagascar, titanosaurian sauropods dominated as herbivores and abelisaurids as predators. These patterns are thought to be driven by the breakup of Pangaea and formation of seaways limiting dispersal. Here, we report a lambeosaurine hadrosaurid from the late Maastrichtian of Morocco, North Africa, the first Gondwanan representative of a clade formerly thought to be restricted to Laurasia. The new animal shows features unique to Hadrosauridae and specifically Lambeosaurinae. Phylogenetic analysis recovers it within Arenysaurini, a clade of lambeosaurines previously known only in Europe. Biogeographic modelling shows that lambeosaurines dispersed from Asia to Europe, then to Africa. Given the existence of large, persistent seaways isolating Africa and Europe from other continents, and the absence of the extensive, bidirectional interchange characterizing land bridges, these patterns suggest dispersals across marine barriers, similar to those seen in Cenozoic mammals, reptiles, and amphibians. Dispersal across marine barriers also occurs in other hadrosaurid lineages and titanosaurian sauropods, suggesting oceanic dispersal played a key role in structuring Mesozoic terrestrial dinosaur faunas.

1. Introduction

The Mesozoic saw the breakup of Pangaea and the separation of Gondwana and Laurasia in the Jurassic (Blakey, 2008), then increasing fragmentation and isolation of continents in the Cretaceous (Dercourt et al., 2000; Smith et al., 2004). By the Late Cretaceous Gondwanan breakup was complete (Blakey, 2008), and sea levels stood ~100 m higher than today (Miller et al., 2005), creating wide marine barriers. The Western Interior Seaway divided North America into a western landmass, Laramidia, and an eastern continent, Appalachia; Europe formed an archipelago, separated from Asia by the Turgai Strait. Africa, South America, India, Madagascar, and the Australo-Antarctic landmass formed island continents (Smith et al., 2004; Blakey, 2008; Scotese and Wright, 2018). Isolation by straits, seas and oceans (Blakey, 2008; Scotese and Wright, 2018) constrained dispersal (Sampson et al., 2001; Longrich et al., 2017).

Consequently, Late Cretaceous dinosaurs evolved distinct faunas in different regions (Bonaparte, 1986; Bonaparte and Kielan-Jaworowska, 1987; Sampson et al., 1998; Weishampel et al., 2004; Ezcurra and Agnolín, 2012; Longrich et al., 2017). In Asia and North America, ornithischians, including hadrosaurids and ceratopsians, dominated herbivore niches; tyrannosaurids were top predators. Meanwhile, in the Gondwanan continents of Africa, South America, India, and Madagascar, titanosaurian sauropods dominated as herbivores, and abelisaurids as predators (Rogers and Forster, 2001; Sampson et al., 2001; Longrich et al., 2017; Sallam et al., 2018). Europe combined characteristic Laurasian and Gondwanan lineages with endemics (Ezcurra and Agnolín, 2012; Csiki-Sava et al., 2015; Longrich et al., 2017). However despite continuing isolation, the latest Cretaceous saw dispersal between Gondwana and Laurasia.

Large herbivores show striking biogeographic patterns. Sauropods disappeared from North America in the mid-Cretaceous and declined in Asia, but radiated in Gondwana, then dispersed into North America and Asia (Sallam et al., 2018). Ornithopods did the opposite. Large iguanodontians disappeared from Gondwana in the mid-Cretaceous, but radiated in Laurasia. There they gave rise to the Hadrosauridae (Horner et al., 2004), specialized herbivores characterized by elaborate dental batteries (Erickson et al., 2012) and cranial crests. In the latest Cretaceous, hadrosaurids dispersed to South America (Brett-Surman, 1975; Prieto-Márquez, 2010b; Cruzado-Caballero and Powell, 2017) and Antarctica (Chatterjee, 2002).

No definitive evidence for hadrosaurids is known from eastern Gondwana. Hadrosauroids are reported from the Late Cretaceous island of Oman, but it is unclear whether they are hadrosaurids, or basal hadrosauroids (Buffetaut et al., 2015). A pedal phalanx from Angola was described as a hadrosauroid (Mateus et al., 2012), but it has proven impossible to make a more specific identification (Mateus et al., 2012; Buffetaut et al., 2015).

Here, we report the first hadrosaurid from Africa, from the late Maastrichtian of Morocco (Figs. 1, 2). We show that hadrosaurids dispersed from Laurasia into Africa despite extensive, persistent marine barriers, and propose dispersal across marine barriers played an important role in latest Cretaceous biogeography.

2. Materials and Methods

Fossil. The holotype, MHNM.KHG.222, is accessioned in the Marrakech Museum of Natural History under the auspices of the Université Cadi Ayyad, Marrakech, Morocco.

Phylogenetic analysis. MHNM.KHG.222 was added to an existing character-taxon matrix (Kobayashi et al., 2019) with the lambeosaurines *Koutalisaurus kohlerorum*, *Adynomosaurus arcanus*, and *Angulomastacator daviesi*, the hadrosaurines *Bonapartesaurus rionegrensis* and *Laiyangosaurus youngi*, and the hadrosauroids *Eotrachodon orientalis*, *Jeyawati rugoculus*, and *Huehuecanauhtlus tiquichensis* for 73 taxa in total. 13 characters were added for a total of 364 characters. 247 were binary and polarized (i.e., 0 was the hypothesized ancestral state; see (Pyron, 2017)); 116 were multistate, of which 86 were ordered. For tip-dating analyses, we excluded the biogeographic character. Tip-dating analyses require a series of steps (see (Pyron, 2011); (Ronquist et al., 2012a); (Pyron, 2017)). They were performed in MrBayes v3.2.6 (Ronquist et al., 2012b).

First, we conducted an ordinary, uncalibrated analysis of the matrix as a whole, with ordering of multistate characters the only additional constraint. Second, we repeated this analysis with a strict-clock prior on branch lengths. Third, we used these two analyses to generate priors for IGR (exp[14.41789]) and relaxed-clock models (lognorm[-5.498652,0.2259837]), following Ronquist et al.(Ronquist et al., 2012a), and performed a tip-calibrated, relaxed-clock analysis. Finally, we performed a tip-dated MkA analysis (Pyron, 2017) by separating binary characters into a separate partition with parsimony-informative coding and applying the F81-like restriction model to this partition. This strategy allows for asymmetric transition rates in binary characters, which is more plausible biologically and has been shown to increase likelihoods, support, and stratigraphic precision, and to reduce influence of rogue taxa.

Biogeographic Analysis. We estimated biogeographic history of Hadrosauroidea using the BioGeoBEARS package (Matzke, 2013), which incorporates a large number of alternative models for dispersal, extinction, cladogenesis, and founder events (Matzke, 2014). We used the maximum clade credibility tree from the MkA analysis, with polytomies randomly resolved, and resulting 0-length branches arbitrarily set to 0.01Ma. Terminal species were coded to six Late Cretaceous biogeographic provinces: Africa, Appalachia, Asia, Europe, Laramidia, and South America. We set the dispersal matrix to account for variable connections between them (Table 1).

Weights were derived from: 0.75 for land masses with extensive evidence of faunal exchange; 0.5 for land masses where there is evidence for limited exchange; 0.1 for dispersal routes with little fossil evidence for exchange; and 0 for distances presumed too great for dispersal (Table 1).

We also estimated the "+w" parameter (Dupin et al., 2017), which scales the dispersal matrix exponentially to optimize the magnitude of the multipliers, though relative rates remain the same. We tested the standard suite of models: DEC and DEC+j(Ree and Smith, 2008), DIVA-like and DIVA-like+j (Ronquist, 1997), and BAYAREA-like and BAYAREA-like+j (Landis et al., 2013), then compared models using sample-size corrected AICc weights and selected the model with the highest overall weight. We allowed four simultaneous areas; no terminal species occurred in more than one. We repeated the analysis multiple times to ensure ML convergence.

3. Systematic Palaeontology

Dinosauria Owen, 1842
Ornithischia Seeley, 1887
Iguanodontia, Baur, 1891
Hadrosauridae Cope, 1869

Lambeosaurinae Parks 1923

Arenysaurini n. tax.: Arenysaurini includes all hadrosaurids closer to *Arenysaurus ardeveoli* than to *Tsintaosaurus spinorhinus*, *Parasaurolophus walkeri*, or *Lambeosaurus lambei*.

Ajnabia odysseus new genus and species

Etymology. Ajnabia, from Arabic *ajnabi*, foreigner + *odysseus*, after Odysseus, the mythical voyager.

Holotype. MHNM.KHG.222, partial left maxilla with teeth (Fig. 3-7), fragments of right maxilla, partial left dentary (Fig. 9).

Diagnosis. Lambeosaurine hadrosaurid diagnosed by the following character combination: strong downturn of premaxillary process of maxilla; maxillary neurovascular foramina with a hypertrophied foramen below jugal articulation with a smaller, accessory foramen below that; ectopterygoid ridge ventrally positioned on maxilla and weakly inclined relative to the dentigerous process; ectopterygoid ridge developed as a massive, dorsoventrally thick, rounded, lip-like structure; ectopterygoid ridge reduced anteriorly, failing to contact jugal articulation. Maxillary tooth crowns with tips curled medially, accessory ridges absent, median ridge offset posteriorly; denticles highly reduced.

Locality and Horizon. MHNM.KHG.222 is from the Office Chérifien des Phosphates mines at Sidi Chennane, Khouribga Province, Morocco (Fig. 1), upper Couche III. The phosphates comprise phosphatic sands, marls, and limestones deposited in shallow waters along the eastern margin of the Atlantic (Bardet et al., 2010; Bardet et al., 2017). They range from Maastrichtian to mid-Eocene in age (Kocsis et al., 2014; Bardet et al., 2017). Upper Couche III is late Maastrichtian based on selachian biostratigraphy (Noubhani and Cappetta, 1997); carbon and oxygen isotope chemostratigraphy constrain it to the final ~1 Ma of the Cretaceous (Kocsis et al., 2014). Marine vertebrates dominate the assemblage and include a diverse fauna of mosasaurids, plesiosaurs, turtles, fish, and sharks (Bardet et al., 2017). Dinosaurs are rare but include characteristic Gondwanan taxa including titanosaurians (Pereda-Suberbiola et al., 2004) and abelisaurids (Longrich et al., 2017) (Fig. 3).

Description. The maxilla is 156 mm long as preserved and broken anteriorly. Decrease in size of the alveoli and narrowing of the maxilla anteriorly suggest 20-30 mm is missing, making the maxilla around 190-210 mm when complete. The animal was small by hadrosaurid standards (Fig. 3). Despite this, it lacks the striated bone texture of rapidly growing juveniles (Tumarkin-Deratzian et al., 2006) suggesting somatic maturity.

The maxilla (Figs. 3-6) is broken dorsally. Given the dorsal displacement of the jugal facet, the bone was proportionately short and tall, as in Hadrosauridae, and especially Lambeosaurinae (Fig. 8A-D). Most non-hadrosaurids, including *Telmatosaurus* (Dalla Vecchia, 2006) and more basally diverging hadrosauroids such as *Bactrosaurus* (Prieto-Márquez, 2011) and *Gilmoreosaurus* (Prieto-Márquez and Norell, 2010) have a long, low maxilla (Fig. 8F,G). A deep maxilla, with a tall ascending process is a synapomorphy of *Eotrachodon* (Prieto-Márquez et al., 2016) plus Hadrosauridae (Fig. 8A-E). The maxilla is especially tall in lambeosaurines (Fig. 8A-D). The maxilla shape in *Ajnabia* therefore supports affinities with Hadrosauridae, and specifically Lambeosaurinae.

The premaxillary process curves ventrally, a plesiomorphy retained in arenysaurins and most other hadrosaurids. Compared to other Lambeosaurinae, the ventral curvature of the premaxilla is better developed than in *Pararhabdodon isonensis* (Prieto-Márquez et al., 2013) or *Parasaurolophus tubicen* (Wagner and Lehman, 2009); *Hypacrosaurus altispinus* (Evans,

2010) lacks a ventral curvature of the premaxillary process. However the strongly curved premaxillary process seen in *Ajnabia* is shared with *Canardia garonnensis* (Prieto-Márquez et al., 2013), *Corythosaurus casuarius* (Wagner and Lehman, 2009), *Amurosaurus riabinini* (Godefroit et al., 2004) and *Magnapaulia laticaudus* (Prieto-Márquez et al., 2012). More extreme development of this feature occurs in *Angulomastacator daviesi* (Wagner and Lehman, 2009).

The maxilla's lateral surface angles inward, displacing alveoli medially and creating a deep buccal fossa as in other Hadrosauridae and Hadrosauroidea. The jugal articulation is displaced dorsally relative to the ectopterygoid shelf, a lambeosaurine autapomorphy that is lost in some corythosaurins (Wagner and Lehman, 2009). A ridge extends posteriorly from the jugal articulation's ventral tubercle, showing that the jugal articulation extends posterodorsally above the ectopterygoid ridge, another lambeosaurine character (Wagner and Lehman, 2009). This feature correlates with elongation of the ectopterygoid ridge in Lambeosaurinae relative to Hadrosaurinae or basal Hadrosauroidea; in Lambesaurinae the ectopterygoid ridge extends below the jugal articulation, and approaches half the length of the maxilla.

Below and ahead of the jugal articulation are four neurovascular foramina. A reduced number of neurovascular foramina characterizes Hadrosauridae, and particularly Lambeosaurinae. There is a very large foramen immediately below and ahead of the jugal articulation, with a second, smaller foramen below and behind it. Two very small foramina lie anterior to the jugal articulation. This condition is seen in *Pararhabdodon isonensis* (Prieto-Márquez et al., 2013) and the Serrat del Rostiar lambeosaurine (Prieto-Márquez et al., 2013). Other lambeosaurines and hadrosaurids lack this condition. In *Canardia* (Prieto-Márquez et al., 2013) and *Amurosaurus* (Godefroit et al., 2004), foramina form a line, as in hadrosaurids. In *Parasaurolophus*, there is a large foramen posteriorly, and several smaller ones anteriorly (Wagner and Lehman, 2009). In corythosaurins, foramina are reduced to two, and lack the single, enlarged foramen. In non-hadrosaurid hadrosauroids, neurovascular foramina are small, numerous and distributed across the maxilla's lateral surface (Fig. 8). Although individual variation in these patterns exists, the pattern seen in in *Ajnabia* is seen elsewhere only among European lambeosaurines.

Posteriorly, the maxilla has an elongate posterior dentigerous process. The jugal articular facet lies roughly at the maxilla's midpoint, so the posterior dentigerous process makes up almost half the bone's length. An elongated posterior dentigerous process is derived for Hadrosauridae, being absent in basal hadrosauroids such as *Eotrachodon* and *Bactrosaurus*.

The posterior dentigerous process shows extreme transverse expansion, forming a broad ectopterygoid shelf that juts out laterally to the same extent as the jugal articulation. This strong transverse expansion is absent in basal hadrosauroids (Prieto-Márquez et al., 2016), and hadrosaurids (Zhang et al., 2017)(Wagner and Lehman, 2009; Prieto-Márquez et al., 2012) except for European lambeosaurines, including *Canardia garonnensis* (Prieto-Márquez et al., 2013) and the Serrat del Rostiar lambeosaurine (Prieto-Márquez et al., 2013).

Laterally, the ectopterygoid shelf bears a massive ectopterygoid ridge, placed low on the maxilla. The ridge is more dorsally positioned in most hadrosaurines (Wagner and Lehman, 2009) and lambeosaurines (Wagner and Lehman, 2009) but, a ventrally positioned ridge is seen in some hadrosaurids, including the Serrat del Rostiar lambeosaurine (Prieto-Márquez et al., 2013) and *Kritosaurus* (Wagner and Lehman, 2009), and in non-hadrosaurid hadrosauroids. In lateral view the ridge is slightly inclined dorsally relative to the dentigerous margin. Among lambeosaurines, this condition is shared with the Serrat del Rostiar lambeosaurine (Prieto-Márquez et al., 2013) and *Canardia garonnensis* (Prieto-Márquez et al., 2013); the ectopterygoid ridge is horizontal in *Pararhabdodon isonensis* (Prieto-Márquez et al., 2013), and more steeply inclined in most other lambeosaurines (Wagner and Lehman, 2009). The

ectopterygoid ridge is projected away from and demarcated from the body of the maxilla by an overhang, creating a thick lip. This morphology is shared with hadrosaurids and basal hadrosauroids such as *Eotrachodon* and *Telmatosaurus*; basally diverging taxa such as *Bactrosaurus* (Prieto-Márquez, 2011) have a weakly defined ectopterygoid ridge. Anteriorly, the ectopterygoid ridge is highly reduced, failing to contact the ventral tubercle. The anterior reduction of the ectopterygoid ridge contrasts with most hadrosaurids. It is more typical of basal hadrosauroids such as *Bactrosaurus* (Prieto-Márquez, 2011); but is also seen in the Serrat del Rostiar lambeosaurine (Prieto-Márquez et al., 2013).

23 alveoli are preserved. More teeth were present anteriorly and posteriorly, but likely ≤30 teeth based on comparisons with other lambeosaurines. A low maxillary tooth count is shared with *Canardia garonnensis* (Prieto-Márquez et al., 2013) and basal iguanodontians. Tooth count correlates with size in hadrosaurids (Prieto-Marquez and Guenther, 2018), so this low tooth count may reflect the animal's small size.

Alveoli form alveolar slots separated by thin bony septa, as in other hadrosaurids. Alveoli are small anteriorly, deeper and wider at the middle of the jaw, then smaller again posteriorly. The toothrow curves in ventral view, weakly anteriorly, and strongly toward the back, with the last few teeth strongly displaced laterally.

Maxillary teeth (Figs. 3, 6, 7) resemble hadrosaurids and derived hadrosauroids (Prieto-Márquez and Norell, 2010) in having narrow crowns, a prominent median ridge, and enamel only on the labial side. As in other iguanodontians, teeth are packed into a dental battery, with mesial and distal carinae buttressing adjacent tooth bases. The crown's enamelled face, rather than being planar, curls near its tip such that in anterior view the carinae are curved distally, not straight, and curve onto the tooth apex. This feature is unusual among hadrosaurids or hadrosauroids, but occurs in hadrosaurid teeth from the Netherlands and Belgium (Dalla Vecchia, 2006).

In lateral view, the median ridge and the crown curve forward, so the mesial carina is straight, and the distal carina is convex. The crown's single median ridge is offset caudally. This offset is primitive for hadrosauroids, appears to be lost within Hadrosauridae, then reacquired in *Ajnabia* and European lambeosaurines (Dalla Vecchia, 2009; Cruzado-Caballero et al., 2010; Prieto-Márquez et al., 2013). Marginal denticulation is reduced, a derived feature shared with the European lambeosaurines (Cruzado-Caballero et al., 2010; Prieto-Márquez et al., 2013), *Hypacrosaurus stebingeri* (Evans, 2010), and *Edmontosaurus* (Xing et al., 2017). Denticles form minute nodes along the carinae. Under magnification each node is seen to consist of clusters of multiple denticles. No wear facets are preserved; functional teeth appear to have fallen out of the jaw.

The right dentary (Fig. 9) is represented by a piece from the middle of the bone. As in other hadrosauroids, the dentary's lateral surface is weakly convex anteriorly, and more convex posteriorly. Medially, platelike septa define deep, narrow alveolar slots, as in other hadrosauroids (Prieto-Márquez and Norell, 2010). Alveolar slots incline caudodorsally, as in other lambeosaurines (Prieto-Márquez et al., 2013). As in the maxilla, alveoli are broader and deeper near the middle of the toothrow, and the toothrow curves out posteriorly.

4. Analytical Results

4.1 Phylogenetic Analysis. Tip-dated Bayesian phylogenetic analysis (Fig. 10) recovers *Ajnabia* within Hadrosauridae and Lambeosaurinae. Within Lambeosaurinae, *Ajnabia* clusters within a group of European lambeosaurines, here named Arenysaurini. Congruent results placing *Ajnabia* in the Lambeosaurinae are obtained using a parsimony-based analysis, using either equal weighting or implied weighting. Numerous derived features support placement of *Ajnabia* in Hadrosauridae, and within the subclades Lambeosaurinae and Arenysaurini.

Ajnabia is united with the clade comprising *Eotrachodon* + Hadrosauridae by the arrangement of neurovascular foramina in a line anteroventral to the jugal articulation (Ch. 105:1), by strong projection of the ectopterygoid ridge (Ch 105:2), and by a tall maxillary facial process (Ch. 361:1).

Ajnabia is placed within Hadrosauridae based on the elongated ectopterygoid ridge and posterior dentigerous process of the maxilla (Ch. 112:2).

Referral of *Ajnabia* to Lambeosaurinae is based on the shape of the jugal articulation (Ch 104:3), posterodorsal extension of the jugal articulation over the ectopterygoid ridge (Ch 362:1), and dorsal displacement of the jugal articulation relative to the ectopterygoid ridge (Ch 363:1).

Within Lambeosaurinae, reduced maxillary denticles (Ch 23:2) and a broad ectopterygoid shelf are derived features shared with European lambeosaurines. The configuration of the neurovascular foramina (Ch 362:1) is shared with *Pararhabdodon* and the Serrat del Rostiar lambeosaurine. The Serrat del Rostiar lambeosaurine and *Ajnabia* are unique among lambeosaurines in having an anteriorly reduced ectopterygoid ridge (Ch 364:1).

Previous studies place the European species in three different clades: Lambeosaurini, Tsintaosaurini, and Aralosaurini. Our analysis recovers European lambeosaurines and *Ajnabia* as a basally diverging lambeosaur clade, the Arenysaurini, characterized by a unique combination of primitive and derived characters. Primitive characters include a broad dorsal process of the maxilla (Ch 99:0), as in *Aralosaurus*; in *Tsintaosaurus*, Parasaurolophini, and Lambeosaurini, the lateral exposure of the dorsal process of the maxilla is reduced to a narrow, finger-like process between the premaxilla and jugal. The diastema is short (Ch 38:0), a primitive character. The dentary battery does not project caudal to the coronoid process (Ch 56:1) in most taxa, with the exception of *Adynomosaurus arcanus*. Other characters of Arenysaurini include reduced denticles (Ch 23:2) and a dentary with a tip that is triangular and strongly tapered in lateral view (Ch 352:1), an autapomorphy of the group. Fragmentary teeth, jaws, and postcrania from Europe (Dalla Vecchia, 2009) show similar characters, consistent with the idea that all European lambeosaurines represent a single clade.

Two European hadrosauroids, *Telmatosaurus transylvanicus* and *Tethyshadros insularis*, are here recovered outside of Hadrosauridae, as basal members of the Hadrosauroidea.

4.2 Biogeographic Analysis. The overall best-fit model is the DIVA-like+j model, which accounts for dispersal and vicariance, with an AICc weight of 48%. The superiority of this model over the DEC model indicates that extinction within areas is not a strong driver of biogeographic patterns over this time frame. However, this signal is modest, as DEC+j has an AICc weight of 39% The "+j" estimate for jump dispersal dominates parameter space, suggesting a strong role for single long-distance events in hadrosauroid biogeography. The relatively high value of the "+w" parameter (2-3 across models) indicates that spatial proximity is strongly related to dispersal between areas, as the higher relative weights for adjacent areas have an exponentially disproportionate influence on the final model.

Our analyses agree broadly with previous analyses that hadrosaurid biogeography involves extensive dispersal (Prieto-Márquez, 2010a; Prieto-Márquez et al., 2013; Kobayashi et al., 2019), but differ in the precise patterns of dispersal.

This model suggests a complex pattern of frequent back-and-forth dispersal between Asia and Laramidia, and less frequent, unidirectional dispersals to Europe, Africa, Appalachia, and South America (Fig. 10). The total number and direction of the dispersal events between North America is unclear, owing to continued uncertainty about the placement of taxa, but even using alternative phylogenies (Prieto-Márquez et al., 2013) multiple dispersal events occured.

Basal Hadrosauroidea radiated in Asia. At least one dispersal into Europe is represented by the basal hadrosauroids *Telmatosaurus transylvanicus* and *Tethyshadros insularis*. Hadrosauroids then dispersed into North America, giving rise to Hadrosauridae, as previously found (Prieto-Márquez, 2010a).

Lambeosaurinae subsequently dispersed into Asia and diversified. North American lambeosaurines represent back-dispersal from Asia into North America, followed by another dispersal into Asia. Arenysaurini dispersed from Asia to Europe in the Campanian and radiated. *Ajnabia* represents a Maastrichtian dispersal of Arenysaurini from Europe to Africa (Figs. 11, 12). In light of the existence of hadrosaurids in North Africa, the previous report of a small hadrosauroid from Angola likely represents a hadrosaurid, but more fossils are required.

Hadrosaurinae are a North American radiation that saw at least three dispersals into Asia, represented by *Wulagasaurus dongi*, *Saurolophus angustirostris*, and the Edmontosaurini, with edmontosaurs subsequently dispersing back into North America. Hadrosaurines apparently dispersed twice into Appalachia, represented by *Hadrosaurus foulkii* and *Lophorhothon atopus*, followed by dispersal into South America.

5. Discussion

The theory of natural selection of Darwin (1859) and Wallace (1902) sought to describe not only the origin of species, but also their geographic distributions, invoking oceanic dispersal and land bridges to explain the modern ranges of plants and animals. Later, the discovery of continental drift spurred the development of vicariant biogeographic models, with continental fragmentation seen as the main driver of biogeography (De Queiroz, 2005). The vicariant paradigm heavily influences palaeontology. Vicariance is often assumed to be the main driver of dinosaur distributions, with faunal similarities between land masses used to infer past connections (Sampson et al., 1998; Rogers and Forster, 2001). Oceanic dispersal is not thought to play a major role.

However, evidence increasingly suggests that dispersal between isolated land masses occurred in the Cretaceous. Hadrosaurids (Prieto-Márquez, 2010a; Prieto-Márquez et al., 2013) and sauropods (Sallam et al., 2018) both dispersed between Gondwana and Laurasia in the Late Cretaceous. No explanation has been given for how dispersal occurred without land connections linking isolated land masses. The discovery of lambeosaurines in Africa highlights this paradox. We suggest oceanic dispersal may explain the presence of African hadrosaurids, and other Late Cretaceous exchanges between Gondwana and Laurasia.

Our phylogeny rejects a purely vicariant model of biogeography for hadrosaurids. Hadrosaurids diversified in the Late Cretaceous (Fig. 10), after continental breakup (Blakey, 2008), when eustatic sea levels were high (Miller et al., 2005) and seaways isolated Africa and Europe (DeConto et al., 1999; Dercourt et al., 2000; Smith et al., 2004; Blakey, 2008) (Fig. 2,10). Hadrosaurid distribution is driven by dispersal, including dispersal to continents isolated by ocean.

Dispersal of lambeosaurines from Asia to Europe requires dispersal across the Turgai Strait, then from Europe to North Africa across the Tethys (Figs. 11, 12). This dispersal likely occurred between Ibero-Occitania and Morocco- separated by 500 km of open water (Fig. 11). Hadrosaurinae furthermore dispersed from Laramidia to Appalachia across the Western Interior Seaway (Figs. 10, 12), and across ocean from Laramidia to South America (Prieto-Márquez, 2010b; Cruzado-Caballero and Powell, 2017) and Antarctica (Case et al., 2000) (Figs. 10, 12).

Other dinosaurs show similar patterns. After the mid-Cretaceous disappearance of sauropods in North America, titanosaurs dispersed to North America from South America

(Tykoski and Fiorillo, 2017; Sallam et al., 2018). Phylogenetic analyses suggest Asian titanosaurians originated in Europe (Sallam et al., 2018), crossing the Turgai Strait (Fig. 12).

Dispersal of dinosaurs can be accomplished either across land bridges, or over water. Given the inferred terrestrial habits of hadrosaurids (Horner et al., 2004) and sauropods (Upchurch et al., 2004), land bridges initially seem more likely. Shallow seas separating European islands could conceivably have been bridged by intermittent land connections, particularly during regression events. Late Cretaceous eustatic sea levels were ~100 m above current levels (Miller et al., 2005), but large (>25 m), brief (≤1 Ma) lowstand events occurred in the mid-Santonian, mid-Campanian, and near the Campanian-Maastrichtian boundary driven by glaciation in Antarctica (Miller et al., 2003; Miller et al., 2005) .

Yet palaeogeographic reconstructions argue that land bridges cannot explain dispersal of hadrosaurids into Africa. The Tethys Sea isolated Africa from Europe (Figs. 11, 12) (Dercourt et al., 2000; Smith et al., 2004) throughout the Cretaceous (DeConto et al., 1999; Dercourt et al., 2000; Csiki-Sava et al., 2015). Lowstand events must have narrowed these barriers, narrowing seaways and straights, extending peninsulas, and exposing reefs and shoals to act as stepping stones to dispersal. But they would not have created emergent land given the presence of deep ocean passages surrounding Africa (DeConto et al., 1999; Dercourt et al., 2000; Csiki-Sava et al., 2015). Likewise, Europe appears to exist as a series of islands during the Late Cretaceous (Smith et al., 2004; Csiki-Sava et al., 2015).

Similarly, in North America, the Western Interior Seaway separated Appalachia from Laramidia from the Albian to the Maastrichtian (Hay et al., 1993); South America remained isolated by ocean through the Late Cretaceous (Smith et al., 2004; Blakey, 2008; Scotese and Wright, 2018). Scenarios involving dispersal between North and South America have envisioned land bridges (Prieto-Márquez, 2010a) for which there is currently no geological evidence (Fig. 12).

Biogeography also argues against land bridges. Because land bridges eliminate geographic barriers to dispersal, they are characterized by extensive, bidirectional faunal interchange (Gibert et al., 2013). The Great American Interchange exemplifies this pattern: following the formation of the Panamanian Isthmus, North American taxa (horses, tapirs, gomphotheres, peccaries, deer, camels, mustelids, racoons, dogs, cats, rabbits, squirrels, pocket gophers) moved south. South American taxa (opossums, armadillos, ground sloths, anteaters, toxodonts, caviimorph rodents, phorusrhacids) moved north (Marshall, 1988; Woodburne, 2010).

Similarly, existence of a high-latitude land corridor linking North America and Asia in the Late Cretaceous (Russell, 1993) is suggested by shared dinosaur groups (e.g. tyrannosaurids, lambeosaurine and hadrosaurine hadrosaurids, ankylosaurids, ceratopsids, leptoceratopsids, ornithomimids, caenagnathids, alvarezsaurids, and troodontids) (Weishampel et al., 2004). Hadrosaurids show this pattern: our model implies ten dispersals between Asia and North America via Beringia, with multiple back-dispersals. By contrast, hadrosaurid dispersal into Europe, Africa, South America, and Appalachia are limited and unidirectional, as are dispersals of titanosaurs into North America and Asia, suggesting geographic barriers existed.

Neither is it probable that the fossils described here come from another continent. Dinosaurs sometimes drift far out to sea (Carpenter et al., 1995) but intercontinental dispersal of vertebrate skeletons has not been documented, to our knowledge. It is far more likely that a fossil comes from the nearest shoreline, not hundreds of kilometres away. Futhermore, palaeogeographic reconstructions show that the *Ajnabia* was deposited in an embayment (Fig. 11). This limited the amount of drift from the open ocean, and because the embayment opened to the Atlantic, it is unlikely that a carcass could have drifted from Europe. Dinosaur remains are also relatively common in the Ouled Abdoun Basin (Longrich et al., 2017)(Pereda-

Suberbiola et al., 2004): dinosaurs were frequently transported from nearby land. Neither is *Ajnabia* referable to coeval species known from Europe.

Long distance oceanic dispersal therefore appears necessary to explain dispersal of dinosaurs between Laurasia and Gondwana. Oceanic dispersal can be accomplished by swimming, drifting, or rafting.

Many large mammals swim long distances (Ali and Vences, 2019). Deer swim long distances over water (Schemnitz, 1975; Miller, 1995; Quigley and Moffatt, 2014), routinely swimming up to 5 km in the ocean and 25 km in lakes to forage on islands (Miller, 1995; Quigley and Moffatt, 2014). Elephants are strong swimmers, and can swim at almost 3 km/hr for distances approaching 50 km (Johnson, 1980). Polar bears can swim hundreds of kilometres (Durner et al., 2011; Pagano et al., 2012), the record being a 9 day, 687 km swim (Durner et al., 2011).

Fossils support the idea that animals swim long distances. In the Pleistocene, elephants colonized oceanic islands including Crete, Cyprus (van der Geer et al., 2006), Sardinia (Palombo et al., 2017) and California's Channel Islands (Johnson, 1978; Muhs et al., 2015); deer dispersed to Crete (van der Geer et al., 2006) and Sardinia (Palombo et al., 2017). Duckbills were likely better adapted than mammals to disperse over water. Their large feet and tails probably made them powerful swimmers; some species may have been semi-aquatic (Weishampel and Horner, 1990).

Some animals passively drift long distances. An Aldabra tortoise washed ashore alive in Africa after drifting from Aldabra, a distance of over 700 km (Gerlach et al., 2006). Tortoises colonized the Galapagos from South America (Caccone et al., 1999), > 1000 km away, and colonized Madagascar, the Comoros, Aldabra, Mauritius, and the Seychelles (Austin et al., 2003), likely by drifting. Crocodilians swim well over short distances, but ride ocean currents to travel long distances (Campbell et al., 2010). Drifting likely explains oceanic dispersal of crocodilians to Madagascar (Brochu, 2007) and Aldabra (Brochu, 2006), and trans-Atlantic dispersal of crocodiles (Meredith et al., 2011) and gharials (Vélez-Juarbe et al., 2007). Hippos swim poorly (Coughlin and Fish, 2009; Geer et al., 2016) yet colonized oceanic islands including Crete and Cyprus (Stuenes, 1989) and crossed the Mozambique channel to Madagascar, a distance of 300 km (Samonds et al., 2012), and may have drifted. Semi-aquatic habits, large fat reserves, and the ability to sleep in water (Stuenes, 1989; Samonds et al., 2012) likely let them survive long periods at sea.

Even assuming hadrosaurids swam well, favourable currents likely aided dispersal. Sauropod dinosaurs may have been uniquely well adapted to drifting. While unspecialized for life in water, the pneumatized neck and back of titanosaurs (Currie Rogers, 2009) likely made them buoyant. Moreover, a combination of light vertebrae and heavy limb bones would have caused them to float upright, keeping the head out of the water even when exhausted or asleep.

Rafting, either on flotsam or floating islands, offers another means of oceanic dispersal. Large iguanas washed ashore on a flotsam raft on Anguilla after a hurricane, apparently travelling from Guadeloupe, > 200 km away (Censky et al., 1998). Historically, floating islands 10-60 m across have been observed (Houle, 1998), and floating islands apparently originating from Africa have been seen off of South America (Houle, 1998). Rafting probably explains dispersal of iguanas from South America to the Galapagos (Higgins, 1978) and Fiji (Gibbons, 1981), dispersal of rodents to the Galapagos (On, 1966) and Australia (Rowe et al., 2008), and dispersal of platyrrhine monkeys and hystricomorph rodents from Africa to South America (Poux et al., 2006). Similar patterns are seen in frogs, long thought unlikely candidates for rafting due to poor saltwater tolerance (Vences et al., 2003; Pyron, 2014). Large dinosaurs seem unlikely to disperse via rafting. However, even giant dinosaurs had small hatchlings (Prieto-Marquez and Guenther, 2018). These could conceivably have rafted.

Swimming, drifting, or rafting therefore could explain oceanic dispersal in dinosaurs. Dinosaur reproductive biology may improve the odds of a dispersal events leading to successful colonization. Large mammals have low reproductive rates, meaning a herd must disperse to establish a viable population. Dinosaurs' large clutch size (Horner, 1999) likely improved the odds of a dispersal event becoming established, because a single gravid female could establish a population.

The odds of dinosaurs crossing ocean barriers are low, but improbable is different from impossible. If vicariance and land bridges cannot explain biogeographic patterns, then oceanic dispersal, no matter how improbable, becomes the only viable hypothesis. Importantly, over millions of years, highly improbable, once-in-million-years events become likely, even probable.

6. Concluding Remarks

Fossils from the late Maastrichtian of Morocco represent a new hadrosaurid species, *Ajnabia odysseus*. Phylogenetic analysis places *A. odysseus* within Lambeosaurinae, within a clade of lambeosaurines, Arenysaurini, otherwise endemic to Europe. Biogeographic analysis suggests lambeosaurines dispersed to Africa from Asia via Europe. Palaeogeographic reconstructions suggest that oceans isolated the Gondwanan landmasses, and biogeographic patterns are also inconsistent with land bridges linking Laurasia and Gondwana. Colonization of Africa by hadrosaurids implies oceanic dispersal, with the European archipelago forming a biogeographic corridor between Asia and Africa. Together with exchange of hadrosaurids and titanosaurs between Gondwana and Laurasia, this suggests that oceanic dispersal was more common than thought in the Cretaceous, and played an important role in structuring terrestrial faunas (De Queiroz, 2005) in the Cretaceous.

Author Contributions
NRL, XPS, NEJ and RAP wrote the paper; NRL and RAP designed research, NRL and RAP conducted phylogenetic analyses, RAP conducted biogeographic analyses.

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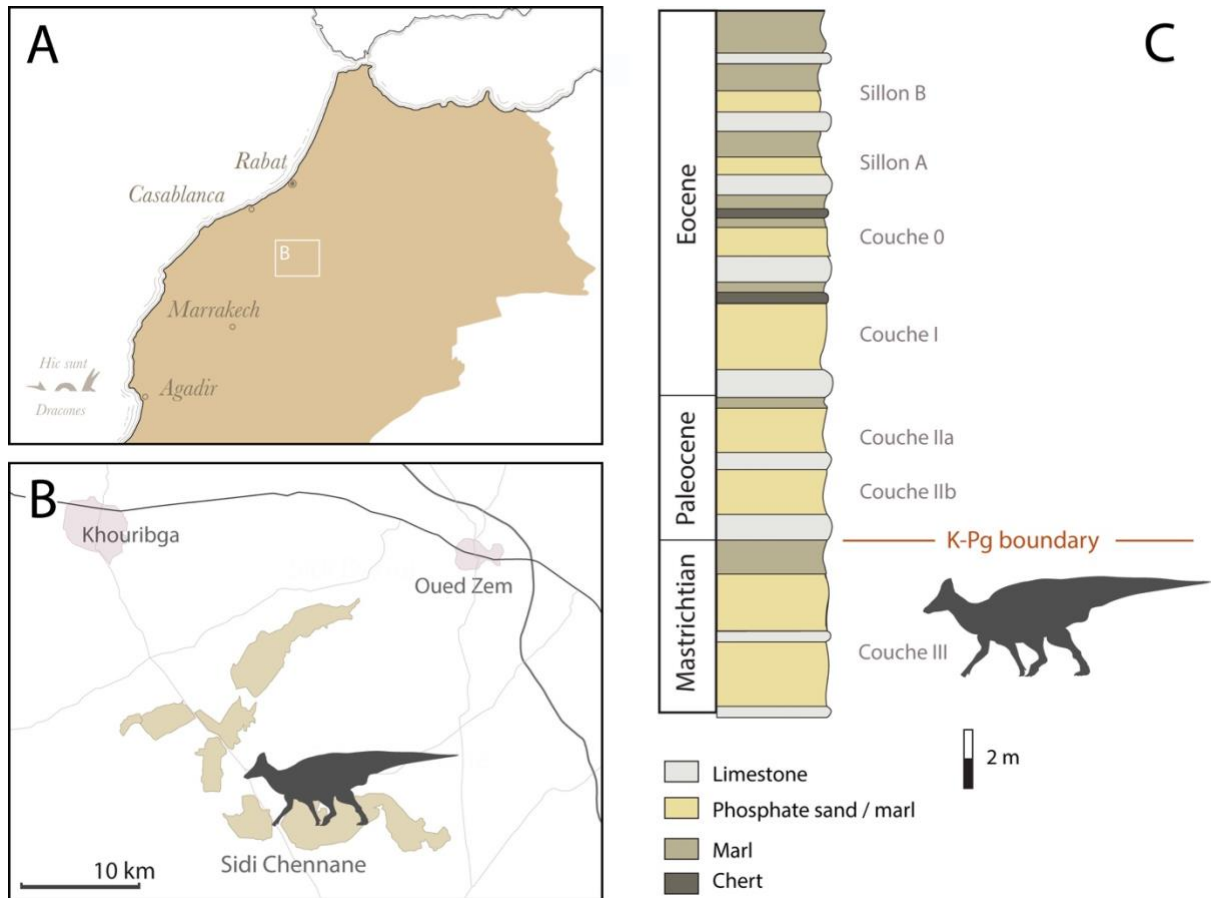
Figures

Fig. 1. Map showing **A**, location of the Khouribga region, Ouled Abdoun Basin; **B**, Sidi Chennane mines; **C**, stratigraphy of the phosphatic series, Sidi Chennane, Khouribga Province, Morocco.
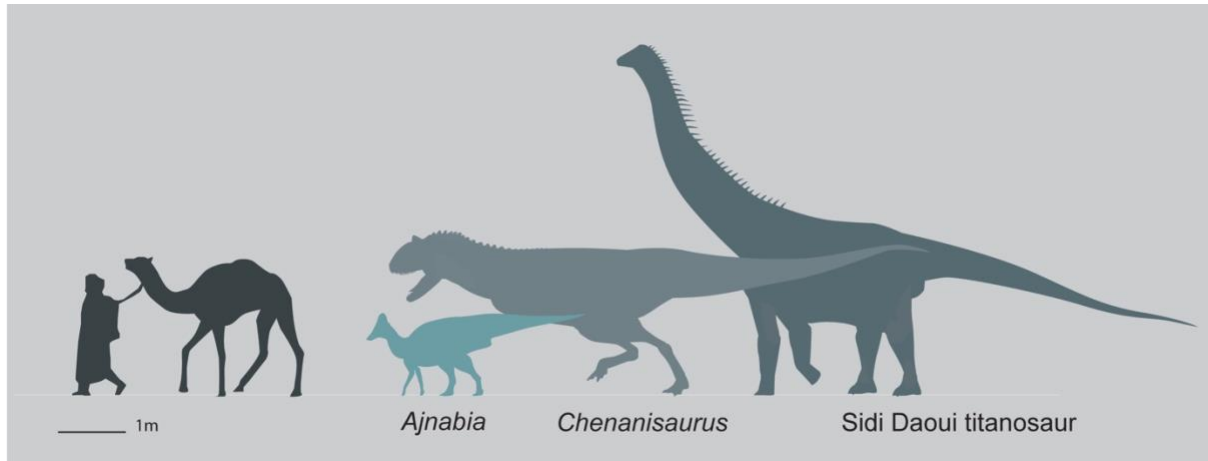
Fig. 2. Late Maastrichtian dinosaurs from the Moroccan phosphates, showing relative sizes of *Ajnabia odysseus*, *Chenanisaurus barbaricus*, and an unnamed titanosaur.
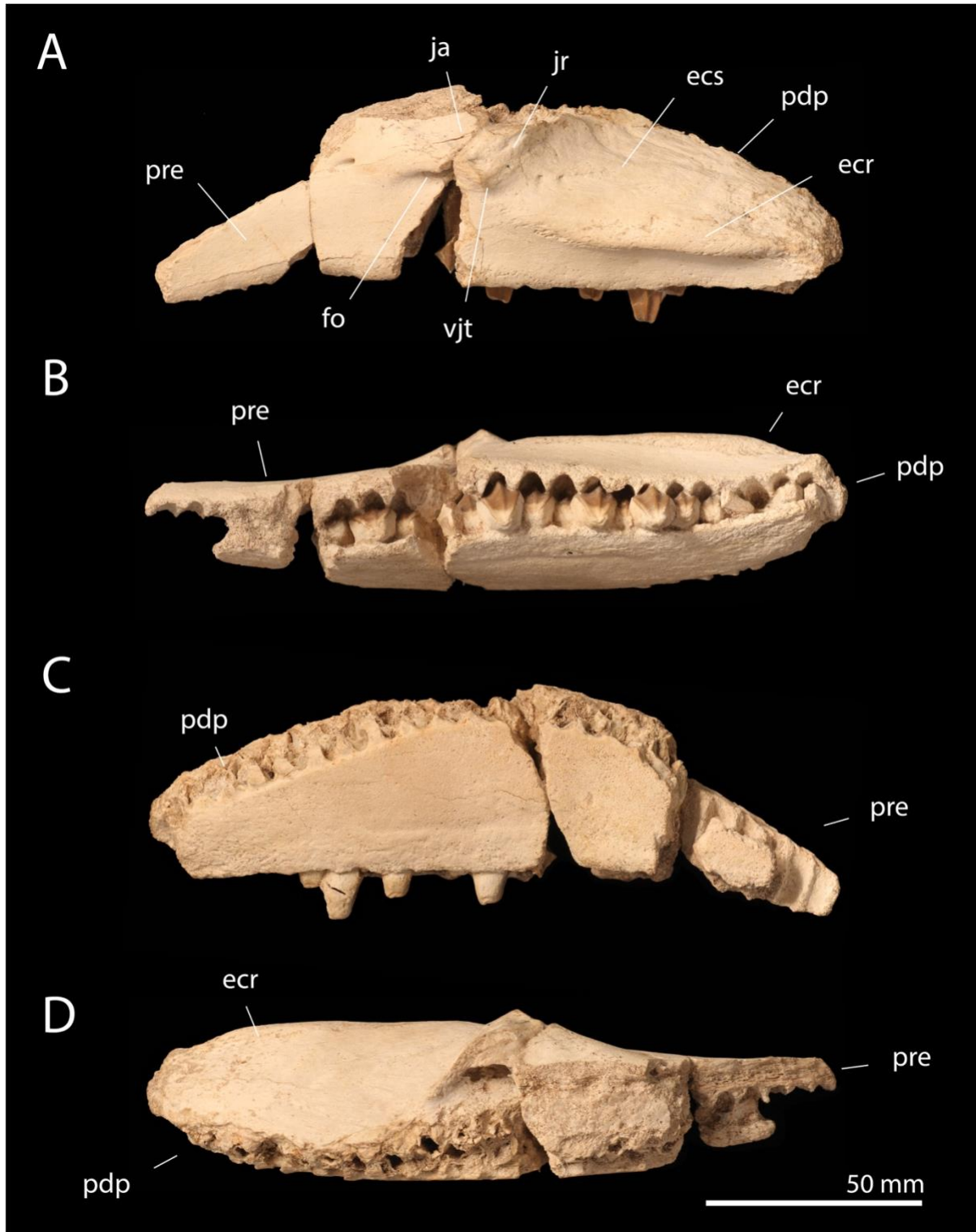
Fig 3. *Ajnabia odysseus*, holotype MHNM.KHG.222, left maxilla in **A**, lateral; **B**, ventral; **C**, medial and **D**, dorsal views. Abbreviations: ecr, ectopterygoid ridge; ecs, ectopterygoid shelf; fo, foramen; ja, jugal articulation; idr, interdental ridge, ja, jugal articulation; jr, jugal ridge; pdp, posterior dentigerous process; pre, premaxillary process, vjt, ventral jugal tubercle.
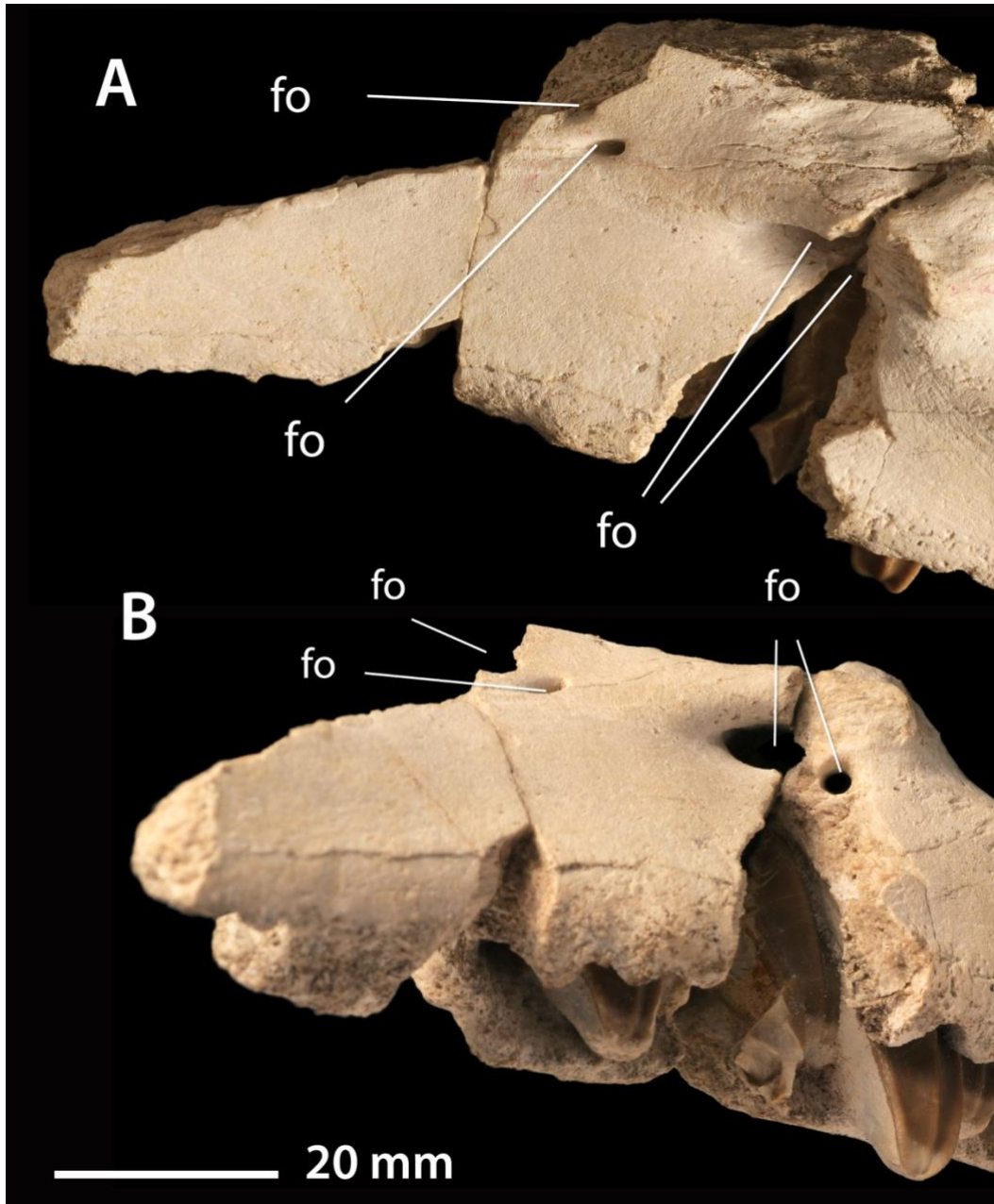
Fig. 4. Anterior maxilla, *Ajnabia odysseus*, holotype MHNM.KHG.222. **A**, Lateral view; **B**, ventrolateral view.
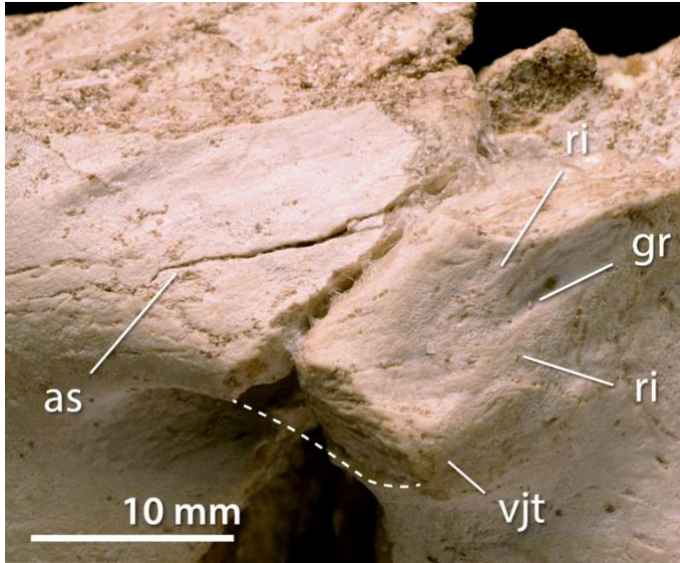
Fig. 5. Maxilla of *Ajnabia odysseus*, holotype MHNM.KHG.222, jugal articulation. Abbreviations: as, articular surface, gr, groove, ri, ridge, vjt, ventral jugal tubercle.
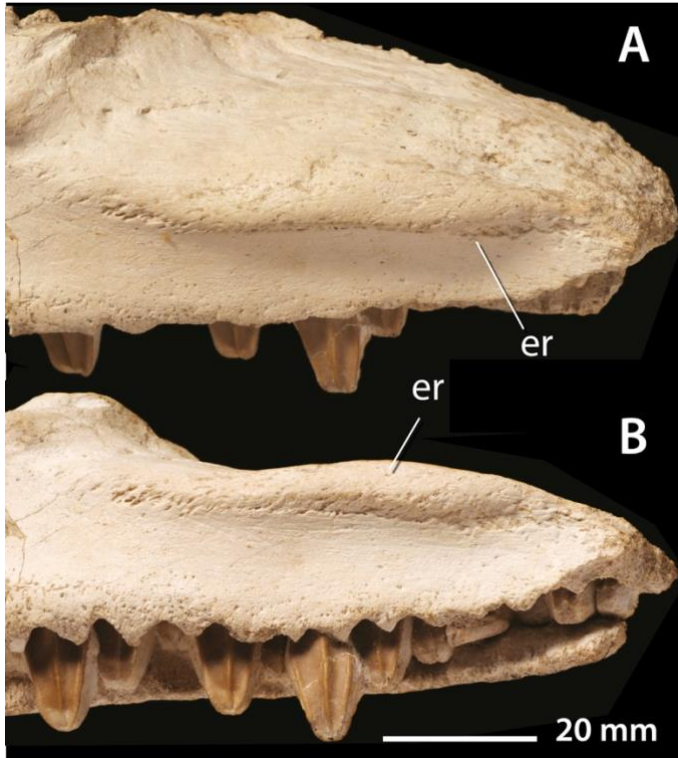
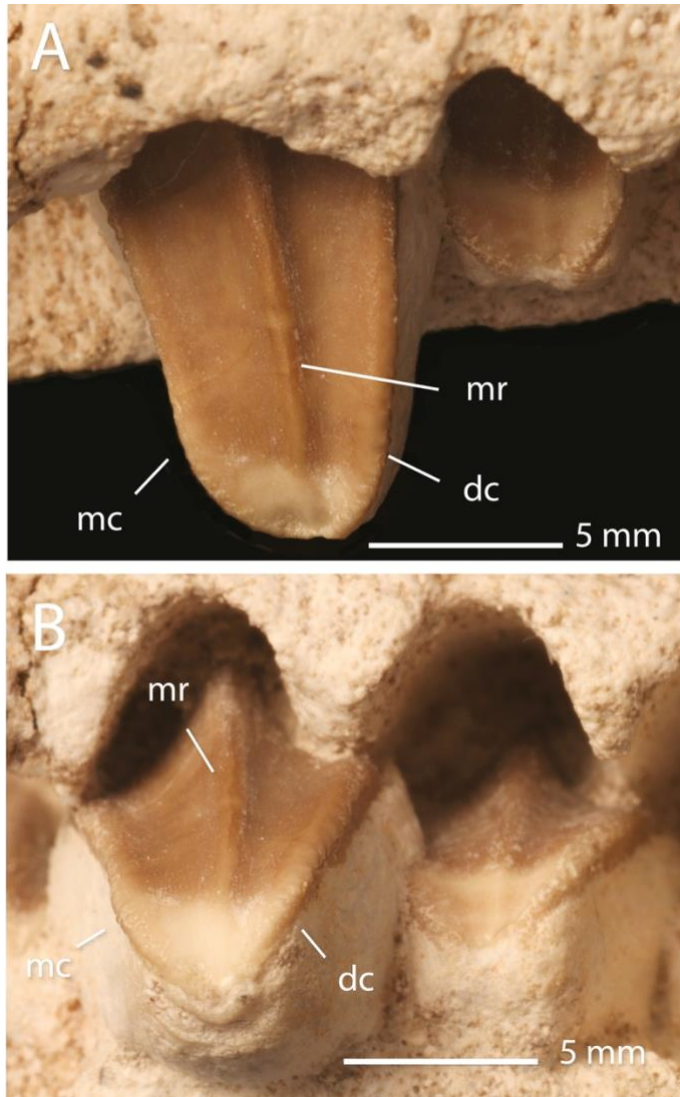**Fig. 6.** Maxilla of *Ajnabia odysseus*, holotype MHNM.KHG.222, ectopterygoid ridge. A, lateral

Fig. 7. Teeth of *Ajnabia odysseus*, holotype MHNM.KHG.222. **A**, maxillary teeth in lateral view; **B**, ventral view. Abbreviations: dc, distal carina; mc, mesial carina; mr, median ridge.
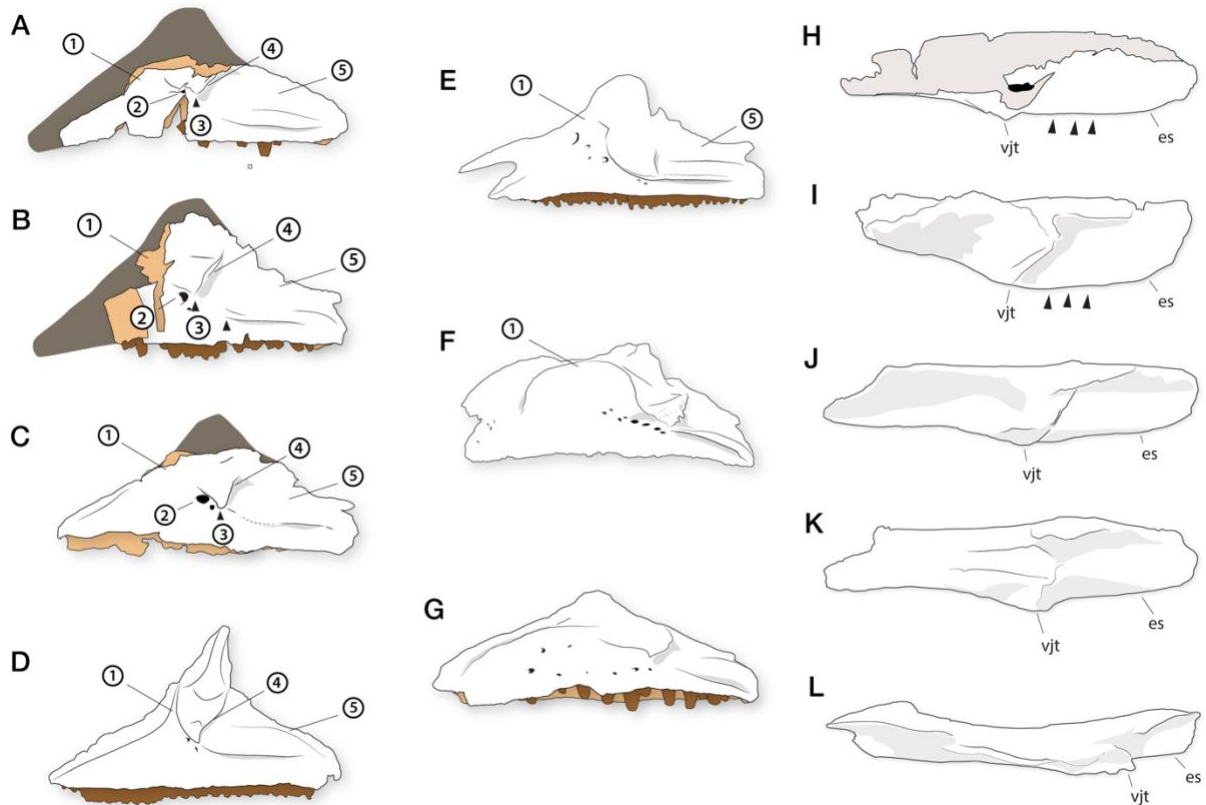
Fig. 8. Comparison of maxilla of *Ajnabia odysseus* to other Hadrosauridae and Hadrosauroidea. **A**, *Ajnabia odysseus*, MHNM.KHG.222; **B**, Serrat del Rostiar lambeosaurine (Prieto-Márquez et al., 2013), **C**, *Pararhabdodon isonensis* (Prieto-Márquez et al., 2013), **D**, *Hypacrosaurus altispinus* (Wagner and Lehman, 2009), **E**, *Edmontosaurus regalis* (Xing et al., 2017), **F**, *Eotrachodon orientalis* (Prieto-Márquez et al., 2016), **G**, *Gilmoreosaurus mongoliensis* (Prieto-Márquez and Norell, 2010) (not to scale). **H**, *Ajnabia odysseus* holotype; **I**, *Canardia garonnensis* (Prieto-Márquez et al., 2013); **J** *Magnapaulia laticaudus* (Prieto-Márquez et al., 2012); **K**, *Laiyangosaurus youngi* (Zhang et al., 2017); **L**, *Eotrachodon orientalis* (Prieto-Márquez et al., 2016) (not to scale). Abbreviations: es, ectopterygoid shelf, vjt, ventral jugal tubercle. Arrows point to strong lateral expansion of the posterior dentigerous process / ectopterygoid shelf, shared by *Ajnabia* and *Canardia*. Derived characters found in Hadrosauridae and Lambeosauridae: (1) tall facial process of the maxilla (2) one or two large foramina anterovetral to the jugal articulation, (3) elevated ventral jugal tubercle of the jugal articulation, (4) posterior margin of jugal articulation strongly extended backwards over ectopterygoid ridge, (5) tall posterior dentigerous process.
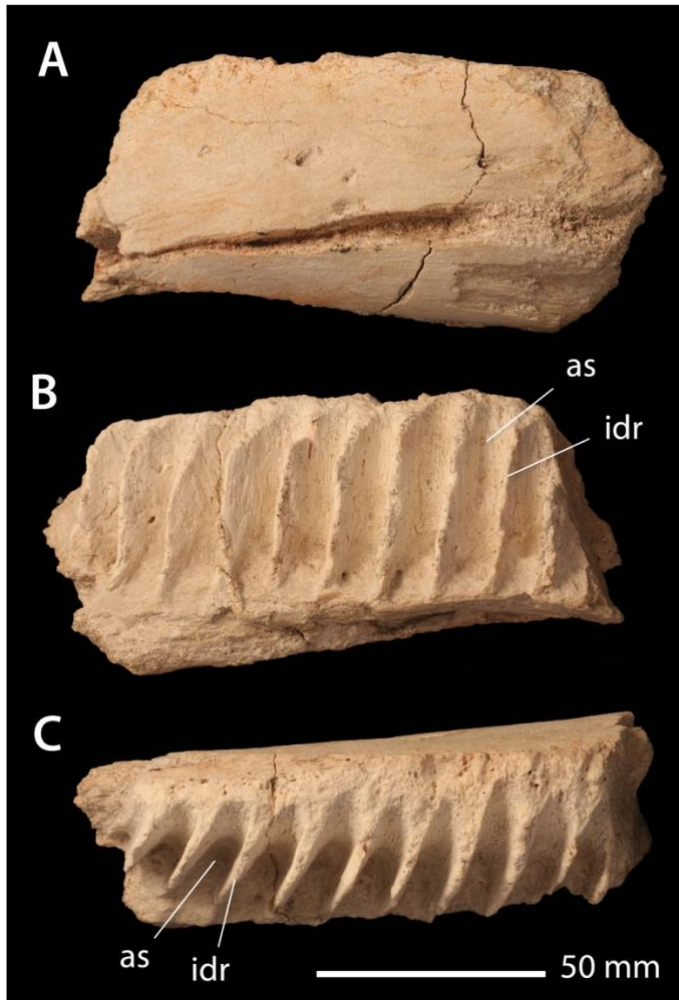
Fig. 9. Partial right dentary of *Ajnabia odysseus*, holotype MHNM.KHG.222. **A**, lateral view, **B**, medial view, **C**, dorsal view. Abbreviations: as, alveolar slot, idr, interdental ridge.
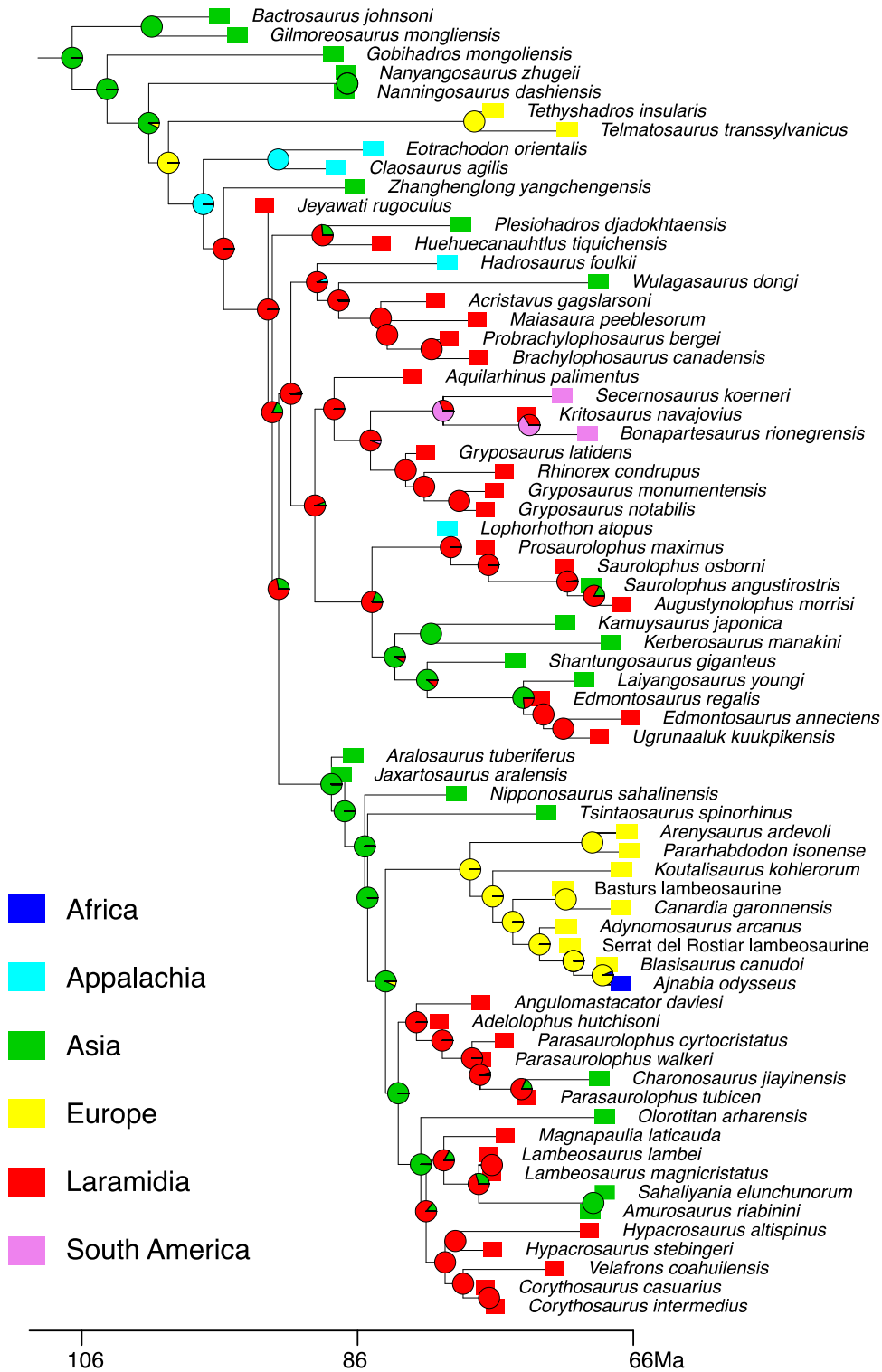
Fig. 10. Phylogenetic and biogeographic analysis of Hadrosauridae. *Ajnabia odysseus* nests within Hadrosauridae, Lambeosaurinae, and Arenysaurini. Biogeographic analysis suggests origination of Hadrosauridae in Laramidia, dispersal of Lambeosaurinae into Asia, then Arenysaurini into Europe and Africa.
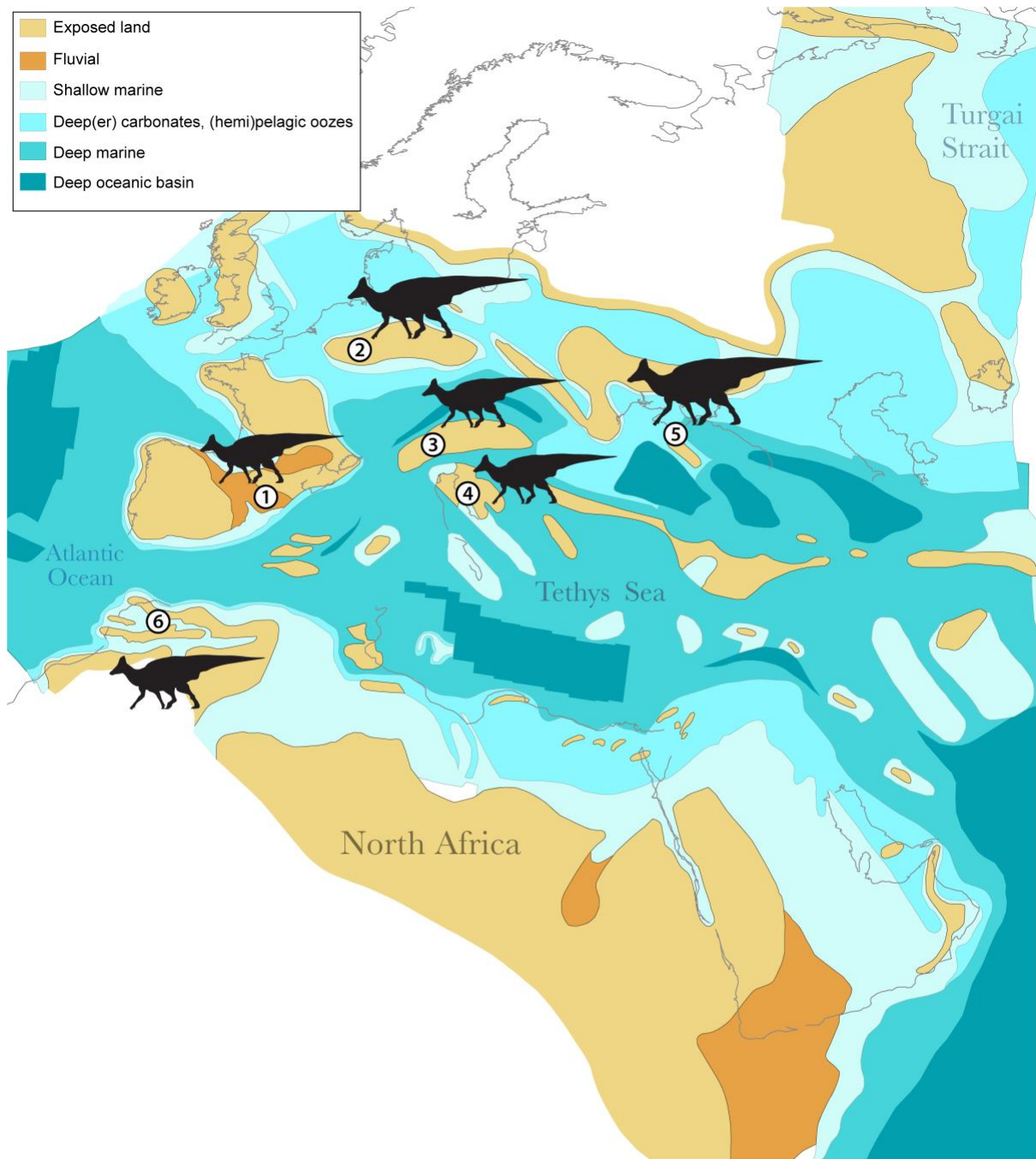
Fig. 11. Hadrosauridae in the Late Cretaceous of Europe and Africa. (**1**) France and Spain: *Arenysaurus ardeveoli*, *Blasisaurus canudoi*, *Koutalisaurus kohlerorum*, *Pararhabdodon isonensis*, *Canardia garonnensis*, *Adynomosaurus arcanus*, Basturs Poble lambeosaurine (Prieto-Márquez et al., 2013; Fondevilla et al., 2018; Prieto-Márquez et al., 2018). (**2**) Netherlands and Belgium, *Orthomerus dolloi* (Madzia et al., 2020) and unnamed hadrosaurids (Dalla Vecchia, 2009). (**3**) Germany, unnamed hadrosaurid (Dalla Vecchia, 2009); (**4**) Slovenia, unnamed hadrosaurid (Dalla Vecchia, 2009); (**5**) Crimea, unnamed hadrosaurid (Dalla Vecchia, 2009), (**6**) Morocco, *Ajnabia odysseus*. Map after (Dercourt et al., 2000).
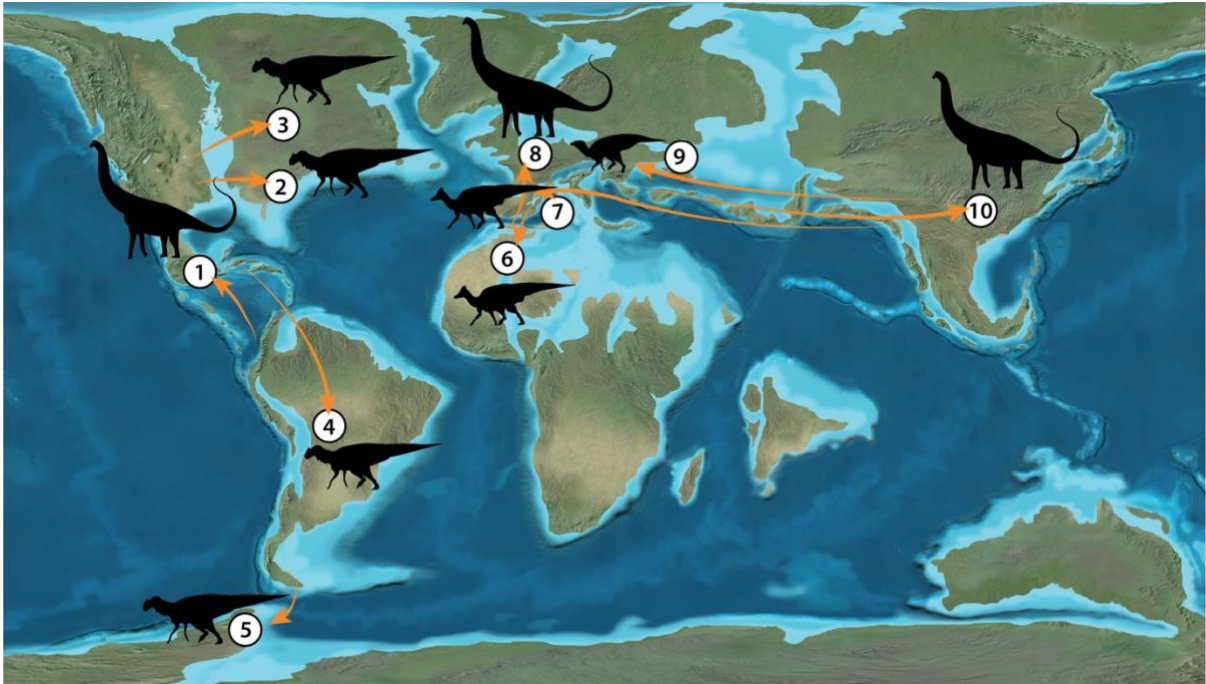
Fig. 12. Late Cretaceous dispersal of dinosaurs across marine barriers. (**1**), Titanosauria, South America to Laramidia. (**2**), Hadrosaurinae (*Hadrosaurus*), Laramidia to Appalachia. (**3**), Hadrosaurinae, (*Lophorhothon*) Laramidia to Appalachia. (**4**), Kritosaurini, Laramidia to South America. (**5**), Hadrosauridae, South America to Antarctica. (**6**), Lambeosaurinae, Europe to Africa. (**7**), Lambeosaurinae, Asia to Europe. (**8**), Titanosauria, Africa to Europe(?). (**9**), "telmatosaurs", Asia to Europe. (**10**), Titanosauria, Europe to Asia.