

A New Global Palaeobiogeographical Model for the Late Mesozoic and Early Tertiary

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Received 22 January 2011; reviews returned 25 March 2011; accepted 10 August 2011

Associate Editor: Adrian Paterson

Abstract.—Late Mesozoic palaeobiogeography has been characterized by a distinction between the northern territories of Laurasia and the southern landmasses of Gondwana. The repeated discovery of Gondwanan lineages in Laurasia has led to the proposal of alternative scenarios to explain these anomalous occurrences. A new biogeographical model for late Mesozoic terrestrial ecosystems is here proposed in which Europe and “Gondwanan” territories possessed a common Eurogondwanan fauna during the earliest Cretaceous. Subsequently, following the Hauterivian, the European territories severed from Africa and then connected to Asiamerica resulting in a faunal interchange. This model explains the presence of Gondwanan taxa in Laurasia and the absence of Laurasian forms in the southern territories during the Cretaceous. In order to test this new palaeobiogeographical model, tree reconciliation analyses (TRAs) were performed based on biogeographical signals provided by a supertree of late Mesozoic archosaurs. The TRAs found significant evidence for the presence of an earliest Cretaceous Eurogondwanan fauna followed by a relatively short-term Gondwana–Laurasia dichotomy. The analysis recovered evidence for a biogeographical reconnection of the European territories with Africa and South America–Antarctica during the Campanian to Maastrichtian time-slice. This biogeographical scenario appears to continue through the early Tertiary and sheds light on the trans-Atlantic disjunct distributions of several extant plant and animal groups. [Archosauria; Atlantogea; Cretaceous; Eurogondwana; palaeobiogeography; Tertiary.]

Since the development of the plate tectonics theory, the sequence of severing of ancient landmasses and the effect of this process on terrestrial ecosystems has attracted the attention of generations of historical biogeographers. One of the most intriguing chapters of palaeobiogeographical history was the final breakup of the Pangaeon supercontinent during the late Mesozoic (161–65.5 Ma). The earliest late Mesozoic palaeobiogeographical studies recognized a sharp distinction between the northern territories of Laurasia (North America, Europe, and Asia) and the southern landmasses of Gondwana (South America, Africa, Antarctica, India, Madagascar, and Australia) based on geological and biotic evidence (Lillegraven et al. 1979; Smith et al. 1981; Bonaparte 1986; Bonaparte and Kielan-Jaworowska 1987). This first palaeogeographical model is still currently widely followed by most authors and accepted as a palaeobiogeographical paradigm (Colbert 1973; Doré 1991; Russell 1993; Sereno 1997, 1999; Chatterjee and Scotese 1999), driving most research efforts in unveiling the sequence of breakup of the Gondwanan and Laurasian supercontinents (Sereno 1999; Upchurch et al. 2002; Sereno et al. 2004; Turner 2004; Krause et al. 2007; Brusatte and Sereno 2008; Sereno and Brusatte 2008). Most of the previous Cretaceous biogeographical analyses were based on information provided by archosaurs, primarily that from dinosaur faunas (Sues and Taquet 1979; Rage 1981; Bonaparte 1984; Bonaparte et al. 1984; Buffetaut 1989; Rich and Vickers-Rich 1989, 1994; Le Loeuff 1991; Russell and Dong 1993; Upchurch et al. 2002; Holtz et al. 2004; Turner 2004; Smith et al. 2008; Upchurch 2008), the best sampled tetrapod clade in the terrestrial ecosystems of this time span.

The continuous increment of Cretaceous palaeontological data has obscured this initially clear palaeobiogeographical signal (Wu and Sues 1996; Upchurch et al. 2002; Naish et al. 2004; Novas and Pol 2005; Fiorelli and Calvo 2007; Ösi et al. 2010; Xu 2010). The repeated discovery of purportedly Gondwanan lineages in Laurasian territories has required the proposal of alternative scenarios to explain these anomalous occurrences, such as the presence of “terrestrial bridges” allowing faunal north–south interchange between Europe–Africa, North America–South America, and Asia–Australia during different moments of the Cretaceous (Casamiquela 1964; Sues and Taquet 1979; Rage 1981; Bonaparte et al. 1984; Rich and Vickers-Rich 1989, 1994; Le Loeuff 1991; Russell and Dong 1993; Rage 2003; Sereno et al. 2004). However, none of these proposals match completely with the current knowledge of Cretaceous biotic distributions. Here, we propose a new biogeographical model for late Mesozoic and early Tertiary terrestrial ecosystems based on the spatial and temporal distribution of Cretaceous archosaurian reptiles, the tetrapod clade that ruled over Cretaceous continental assemblages.

MATERIALS AND METHODS

In order to test late Mesozoic palaeobiogeographical hypotheses, we carried out the most comprehensive time-sliced historical cladistic biogeographical analysis to date (tree reconciliation analysis [TRA]; see Page 1988, 1994; Hunn and Upchurch 2001; Upchurch et al. 2002, among others for a detailed discussion of the method), based on the spatial and temporal

distribution of Late Jurassic and Cretaceous continental archosaurs. The TRA was based on a semistrict supertree constructed with the topologies found by 33 archosaur phylogenetic analyses (see Appendix 1 at <http://datadryad.org>, doi: 10.5061/dryad.d47h94c9). A semistrict supertree was chosen over other methodologies because the resultant topology will not contain groupings not recovered in the original phylogenetic analyses (Goloboff and Pol 2002). Some taxonomic units were pruned from selected topologies because of their conflicting phylogenetic positions when compared with more comprehensive analyses employed here (see Appendix 1). A few outgroup taxa were added to the topologies employed here in order to link the different phylogenies. Finally, several biogeographically important taxa were added by hand following strong qualitative statements raised by previous authors based on synapomorphies (see Appendix 1). The semistrict supertree was constructed with TNT 1.1 (Goloboff et al. 2008) and the resultant supertree was composed of 557 Late Jurassic and Cretaceous archosaur taxa (see Appendix 2). The recovered semistrict supertree is generally well resolved but a few major polytomies are present, such as among basal titanosauriforms, derived eusuchians, basal stegosaurs, basal ankylopollexians, and basal hadrosauroids.

In order to analyze the Late Jurassic and Cretaceous biogeographical patterns, 8 continental geographic areas were chosen: (1) South America, (2) North America, (3) Asia, (4) Europe, (5) Africa (absent in the Campanian–Maastrichtian time-slice), (6) Australia (only in the Aptian–Albian time-slice), (7) Madagascar, and (8) India (only in the Campanian–Maastrichtian time-slice). Africa was excluded from the Campanian–Maastrichtian time-slice because its tetrapod fossil record is very poor and most of the few known specimens lack restricted taxonomic assignments. Thus, the addition of latest Cretaceous African archosaurs in the TRA may result in a poorly supported and statistically nonsignificant result. We chose these areas because we aimed to test biogeographical hypotheses and the probable implications that can be observed through vicariant distributions during the breakup of the ancient Mesozoic supercontinents (Upchurch et al. 2002). Accordingly, a finer division of geographic areas was not necessary. The selection of more restricted geographic areas would limit the statistical power of the TRA and avoiding an overdivision of areas is usually suggested when performing geographical analyses (Ree and Smith 2008). The 8 geographic areas selected here agree with those employed in previous biogeographical analyses of the same kind (e.g., Upchurch et al. 2002; Turner 2004; Butler et al. 2006; Upchurch 2008) and maintain their identity through the entire analyzed time span.

The time slicing protocol introduced by Upchurch et al. (2002) for TRAs was implemented here. Six time-slices were selected to conduct the palaeobiogeographical analysis: Late Jurassic (161–145.5 Ma), Berriasian–Hauterivian (145.5–130 Ma), Barremian (130–125 Ma), Aptian–Albian (125–99.6 Ma), Cenomanian–Santonian

(99.6–83.5 Ma), and Campanian–Maastrichtian (83.5–65.5 Ma). These time-slices were selected because: (1) they are based on the geological stages recognized by the International Stratigraphic Chart and taxa can be easily located within them; (2) biotic changes have been recognized by previous authors in several boundaries among these time-slices; (3) the subdivision of the early Cretaceous into the 3 proposed time-slices will allow the Eurogondwanan biogeographical hypothesis proposed here to be tested; and (4) the subdivision of the Late Cretaceous into Cenomanian–Santonian and Campanian–Maastrichtian would allow to recognize biogeographical changes occurring toward the end of the Mesozoic.

The search for optimal area cladograms (OACs) was conducted using COMPONENT 2.0 (Page 1993; see Appendix 3). This program cannot cope with polytomies in the input cladogram, and the cladogram therefore had to be manipulated to produce fully resolved topologies. Some of the polytomies present in the semistrict supertree disappeared when the time-slicing protocol was applied (Upchurch et al. 2002). However, in cases in which polytomies persisted we applied 3 sequential criteria in the following order: (1) we pruned taxa that shared redundant geographical areas with other taxa present within the same polytomy, (2) we pruned taxa in order to preferentially retain branches that have more than one terminal, and (3) we favor the presence of taxa from geographic areas with a low number of representatives for that time-slice. COMPONENT 2.0 cannot manage data sets larger than 100 taxa because of software constraints. In consequence, we had to condense some monophyletic or paraphyletic terminals with redundant geographical areas for the Campanian–Maastrichtian time-slice. Details of the application of these criteria on each time-sliced supertree are provided in Appendix 1. The OACs were found through a heuristic search employing nearest neighbor interchanges as the branch swapping algorithm and the number of losses was used as the optimal criterion (see Appendix 3).

Subsequently, reconstructions of biogeographical events were conducted for each time-slice in TREEMAP 1.0 using heuristic searches (Page 1995; see Appendix 3). Randomization tests for each time-slice were conducted using TREEMAP 1.0 in order to test the null hypothesis that the observed biogeographical pattern of this time-slice could not occur by chance only and determine its probability (Page 1994, 1995; see Appendix 3). The statistical analysis generates random taxa cladograms and reconciles each of them with the phylogenetic cladogram (Page 1991). Ten thousand randomized replications were conducted for each time-slice using the “proportional to distinguishable” algorithm. The topology recovered in the OACs was considered as statistically significant if <5% of the replicates ($\alpha = 0.05$) included the same number or more codivergences than found in the original TRA.

The results of these analyses were complemented with tests of the fit of different biogeographical hypotheses to the phylogeny (e.g., Laurasia–Gondwana

dichotomy in the Aptian–Albian supertree). In order to obtain a quantitative measure of the relationships between the different palaeobiogeographical hypotheses and the topology of the time-sliced archosaur supertree for each time-slice, a “consistency index of the hypothesis” was calculated. First, each biogeographical hypothesis was scored as the binary or multistate character “biogeographical hypothesis” (e.g., Berriasian–Hauterivian model: Asiamerica [0]; Eurogondwana [1]). Then, this character was optimized following a maximum parsimony criterion on the topologies of the archosaur supertree for each time-slice using the program TNT 1.1. (Goloboff et al. 2008). The consistency index of each biogeographical hypothesis character (BHCI) was calculated (see Equation 1). A closer value of the consistency index to 1 indicates a lower degree of homoplasy for the character (Kluge and Farris 1969). Accordingly, the inferred biogeographical signal in the time-sliced archosaur supertree is stronger as the BHCI approaches 1 following Equation 1.

$$\text{BHCI} = \text{BHm}/\text{BHs} \quad (1)$$

in which BHCI is the biogeographical hypothesis consistency index, BHm is the number of states of the biogeographical hypothesis character—1 (i.e., minimum number of changes in any tree), and BHs is the number of steps recovered in the optimization of the biogeographical hypothesis character on the tree.

Finally, a statistical analysis generating *P* values was performed utilizing a sample of randomized trees in order to test the likelihood of recovering the biogeographical signal by chance alone. Ten thousand pseudoreplicates of Monte–Carlo randomizations, with the permutation of all the terminals from the original tree, were conducted with a script written for TNT 1.1 (script under request to the corresponding author). The character biogeographical hypothesis was optimized onto this new set of randomized cladograms and the consistency index of the character was calculated with TNT 1.1. A *P* value was generated with the number of times that the same or higher BHCI to the original time-sliced archosaur supertree was recovered (i.e., the number of times that recovered an equal or stronger biogeographical signal by chance alone) divided by the total number of randomized trees (10,000 in this case). Bonferroni corrections were applied for these analyses because multiple tests were performed for different biogeographical hypotheses within the same time-slice (see Appendix 3). It must be noted that comparisons among the results of these significance tests must be restricted to a single time-slice (e.g., Eurogondwana vs. Laurasia–Gondwana hypotheses for the Berriasian–Hauterivian time-slice), and they cannot be compared between different time-slices because of tree shape biases related to the usage of a consistency index (Kluge and Farris 1969).

With the aim of determining the presence and direction of trans-Atlantic dispersal events between South America and Africa during the early Tertiary we conducted dispersal–vicariance analyses in S-DIVA 1.5c

(Yu et al. 2010). The analyses allowed the inference of ancestral distributions and historical events based on the phylogeny of 3 emblematic groups with supposed trans-Atlantic dispersals during the early Tertiary (caviomorph rodents: Coster et al. 2010; amphisbaenian lepidosaurs: Vidal et al. 2008; and malpighiacean angiosperms: Davis et al. 2004; see Appendix 4). In the dispersal–vicariance analyses, the geographic areas of (1) South America and Caribbean, (2) North America, (3) Africa, (4) Europe, and (5) Asia were employed. The dispersal–vicariance analysis reconstructs the ancestral geographic areas of each node of the phylogenetic tree by optimizing a three-dimensional cost matrix in which extinctions and dispersals “cost” more than vicariance (Ronquist 1997; Lamm and Redelings 2009). S-DIVA also recovers the statistical support for ancestral range reconstructions (Yu et al. 2009). In all cases, the analyses were not performed by generating a random number of trees but through an existing optimal tree taken from published studies (Davis et al. 2004; Vidal et al. 2008; Coster et al. 2010). Reconstructions were allowed and a maximum of 5 areas at each node were considered. Other options followed the default settings of the program. In the amphisbaenian and malpighiacean analyses, the phylogenetic trees did not contain polytomies. However, in the histicognath phylogeny, some unresolved nodes were present in the strict consensus tree. As a result, we reanalyzed the data set of Coster et al. (2010) in order to obtain each MPT. The analysis was conducted using a heuristic search of 1000 replications of Wagner trees (with random addition sequence) followed by tree bisection reconnection branch swapping algorithm (holding 10 trees per replicate) with TNT 1.1 (Goloboff et al. 2008). The results were 2 most parsimonious trees (MPTs) of 250 steps (CI = 0.368; RI = 0.682), and the best score was hit 298 times out of 1000, which are consistent with the original analysis performed by Coster et al. (2010). One of these MPTs was selected for the S-DIVA analysis. The selected tree was that in which *Phiomys sensu stricto* was recovered as a monophyletic genus, but the usage of the alternative phylogeny did not change the results of the analysis.

RESULTS

The TRA for the Late Jurassic time-slice (Fig. 1a) failed to find a significant biogeographical pattern (*P* = 0.1131; Table 1). However, in earliest Cretaceous times (Berriasian–Hauterivian), a significant and distinct dichotomy between an European–Gondwanan clade (Europe, South America, and Africa) and an Asiamerican one was found in the recovered OAC (*P* = 0.0070; Fig. 1b), a pattern also significantly supported in the archosaur phylogeny (*P* = 0.0069; see Appendix 3). Subsequently, within the Barremian time-slice (Fig. 1c), Europe was recovered in the OAC as sharing closer biogeographical affinities with Asia and North America than with southern territories (Africa and South America), as was also recovered by previous authors (Russell 1993; Smith et al. 1994; Upchurch 1995; Smith and Rush

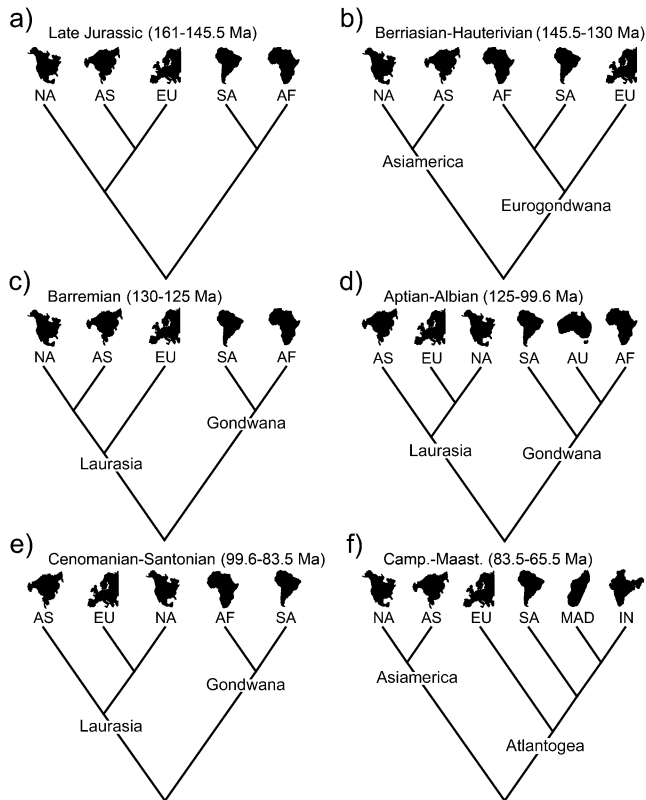


FIGURE 1. Recovered cladograms of optimized geographic areas for the (a) Late Jurassic, (b) Berriasian–Hauterivian, (c) Barremian, (d) Aptian–Albian, (e) Cenomanian–Santonian, and (f) Campanian–Maastrichtian time-slices. Abbreviations: AF, Africa; AS, Asia; AU, Australasia; EU, Europe; IN, India; MAD, Madagascar; NA, North America; SA, South America.

1997; Norman 1998; Upchurch et al. 2002). However, we failed to recover a statistically significant biogeographical signal in the TRA ($P = 0.1508$; Table 1). In contrast, in the archosaur phylogeny we obtained significant results for the fit of both Gondwana–Laurasia and Eurogondwana–Asiameica dichotomies in the topology of this time-slice ($P = 0.0118$ and $P = 0.0014$, respectively; see Appendix 3). As in the Barremian OAC, in the Aptian–Albian and Cenomanian–Santonian time-slices a monophyletic Laurasia was recovered, but with significant support ($P = 0.0289$ and $P = 0.0333$, respectively; Fig. 1d,e; Table 1). It must be noted that Australia was found nested within the Gondwanan clade in the Aptian–Albian time-slice. Finally, Europe was depicted as sharing stronger common vicariant distributions with South America, India, and Madagascar than with

Asiameica in the Campanian–Maastrichtian time-slice ($P = 0.0373$; Fig. 1f and Table 1). In addition, in the Aptian–Albian and Late Cretaceous time frames significant results ($P = 0.0001$) were recovered for the fitting of both Gondwana–Laurasia and Eurogondwana–Asiameica dichotomies in the time-sliced archosaur phylogenies.

The dispersal–vicariance analyses successfully reconstructed the ancestral distribution and historical biogeographical events for the phylogeny of the 3 analyzed groups. In the case of the hystricognath rodents, Asia was reconstructed as the ancestral geographic area of the group and with a subsequent dispersal toward Africa in the node that includes the polyphyletic *Phiomys sensu lato*. A migration within these African hystricognaths to South America was reconstructed at the base of the caviomorph clade, a node which was temporally dated by Coster et al. (2010: based on the fossil record) as latest Middle to latest Late Eocene. Within this South American caviomorph clade, a return to Africa was reconstructed for the deeply nested caviomorph *Gaudeamus* between the latest Eocene and earliest Oligocene (see Appendix 4). Regarding the Amphisbaenia, the most probable ancestral area reconstructed for the node including the families Bipediidae, Blanidae, and Cadeidae was South and Central America and a subsequent dispersal event of blanids to Africa and Europe was reconstructed (see Appendix 4). The origin of blanids and probably the dispersal event was dated through molecular clocks as early Late Eocene (Vidal et al. 2008). Finally, the ancestral area for the node including the malpighiaceans *Mcvaughia* and *Barnebya* was reconstructed as South and Central America. Within this New World clade, a dispersal event from South America to Africa, dated as earliest Oligocene (Davis et al. 2004: based on molecular evidence), was reconstructed within the *Tristellateia* lineage (see Appendix 4).

DISCUSSION

Evidence for the Eurogondwanan Hypothesis: A New Explanation for the Gondwanan–Laurasian Faunal Anomalies

In contrast to the traditional Gondwana–Laurasia model, there have been increasing discoveries in the last two decades of purported endemic Gondwanan clades in Laurasian Cretaceous outcrops. Outstanding examples of these lineages include the abelisaurid, spinosaurid, carcharodontosaurid, and alvarezsaurid

TABLE 1. Parenthetical topologies of the OACs recovered in the TRAs of each time-slice and their respective P values

Time-slice	OAC topology	TRA P value	Ma
Late Jurassic	((NA, (AS, EU)), (SA, AF))	0.1131	161–145.5
Berr–Haut	((EU, (SA, AF)), (NA, AS))	0.0070^d	145.5–130
Barremian	((SA, AF), (EU, (NA, AS)))	0.1508	130–125
Aptian–Albian	((AS, (EU, NA)), (SA (AU, AF)))	0.0289^d	125–99.6
Ceno–Sant	((AS, (EU, NA)), (AF, SA))	0.0333^d	99.6–83.5
Camp–Maast	((NA, AS), (EU, (SA, (MAD, IN))))	0.0373^d	83.5–65.5

^dStatistical significant results in bold.

theropods; rebbachisaurid and derived titanosaurian sauropods; notosuchian and sebecosuchian crocodylomorphs; anhanguerid pterosaurs, madtsoiid, boid, and anilioid snakes; and podocnemidid, pelomedusid, and stem-meiolaniid turtles, among others (Antunes 1975; de Broin 1977, 1980; Rage 1981; Galton and Taquet 1982; Buffetaut et al. 1988; Lucas and Hunt 1989; Le Loeuff and Buffetaut 1991; Le Loeuff 1993, 1995; Wu et al. 1995; Novas 1996; Ortega et al. 1996; Wu and Sues 1996; Salgado et al. 1997; Hirayama et al. 2000; Chiappe et al. 2002; Allain and Pereda Suberbiola 2003; Pereda-Suberbiola et al. 2003; Naish and Dyke 2004; Company et al. 2005; Joyce 2007; Milner et al. 2007; Rose 2007; Vullo et al. 2007; Canudo et al. 2008, 2009; Sterli 2008, 2010; Brusatte et al. 2009; Longrich and Currie 2009; Mannion 2009). However, most of the purported endemic Laurasian tetrapod clades have not yet been found in Gondwana through the entire Cretaceous, including ornithomimosaur, oviraptorosaur, therizinosaurid, tyrannosaurid (see Herne et al. 2010), troodontid, and microraptoran theropods, pachycephalosaur and ceratopsian ornithischians, and solemydid and trionychid turtles (Bonaparte 1986; Bonaparte and Kielan-Jaworowska 1987; Weishampel 1990; Russell 1993; Lapparent de Broin and Murelaga 1996; Lapparent de Broin 2000; Weishampel et al. 2004; Lipka et al. 2006; Longrich and Currie 2009). Due to these incongruences, several alternative and complex ad hoc biogeographical hypotheses were proposed as possible explanations, including intercontinental bridges, stepping stones, and discontinuous filter dispersal routes, with the aim of explaining the data within the traditional Gondwana–Laurasia paradigm (Casamiquela 1964; Sues and Taquet 1979; Rage 1981; Bonaparte 1984; Bonaparte et al. 1984; Buffetaut 1988, 1989; Rich and Vickers-Rich 1989, 1994; Le Loeuff 1991, 1993; Russell 1993; Rage 2003; Gheerbrant and Rage 2006). However, most of these explanations necessarily imply a massive south–north biotic interchange, a fact that it is not supported by the fossil record because the above-mentioned northern taxa are not yet recorded in southern assemblages (Bonaparte 1986; Bonaparte and Kielan-Jaworowska 1987; Weishampel 1990; Russell 1993; Lapparent de Broin and Murelaga 1996; Lapparent de Broin 2000; Juárez Valieri and Fiorelli 2003; Weishampel et al. 2004; Lipka et al. 2006; Longrich and Currie 2009; but see below for the latest Cretaceous biogeographical pattern). Furthermore, if a dispersal route between northern and southern continents was present, the presence of a unidirectional dispersal of several disparate southern clades toward the north but not in an opposite direction sounds very unlikely. More recently, it has been proposed a world-wide cosmopolitanism of Cretaceous dinosaur faunas (Barrett et al. 2011). However, the latter hypothesis or a retention of a Jurassic cosmopolitanism neither explain the absence of several northern lineages in the southern continents. As a result, we propose here an alternative new model, the Eurogondwanan hypothesis, in order to explain the presence of “Gondwanan” taxa in Laurasia but, at the same time, the absence of

northern lineages in Gondwana (Fig. 2). The Eurogondwanan hypothesis proposes that most of the areas that currently compose the European region (an archipelago during the late Mesozoic; Scotese 2001; Bosellini 2002) had a close biogeographical affinity with Gondwana via Africa during the earliest Cretaceous (Berriasian–Hauterivian: ca. 15 Mya; Fig. 2b). Following the Hauterivian, when several tetrapod lineages previously recorded in Gondwana and Europe appeared in Asiamerica for the first time, Europe severed from Africa (Fig. 2c) and after that coalesced with western Asia, allowing a biotic interchange between both landmasses (Fig. 2d). Thus, this model explains the migration of Eurogondwanan lineages to Laurasia and does not require two necessary conditions of the previous model which are weakly supported by the fossil and palaeogeographic record: first, the migration of Laurasian taxa to Gondwana during the Early Cretaceous and second, the presence of several intercontinental bridges, stepping stones, discontinuous filter dispersal routes, or world-wide cosmopolitanism.

The Eurogondwanan hypothesis was not rejected by the results of our biogeographical quantitative analyses and perfectly matches it (Fig. 1). The Eurogondwanan fauna is supported by the sharing of a common biota between Europe and Gondwana but still unrecorded in Asiamerica, during the earliest Berriasian–Hauterivian times, contrasting with the Late Jurassic pattern (e.g., spinosaurid theropods, rebbachisaurid and derived titanosaurian sauropods, basal dryomorph ornithopods, and boreosphenidan, peramurid, and thereuodontid mammals; Rage 1988; Buffetaut 1989; Le Loeuff 1991; Russell 1993; Martill and Hutt 1996; Charig and Milner 1997; Martill and Naish 2001; Dalla-Vecchia 2003; Torcida et al. 2003; Juárez Valieri et al. 2004; Kielan-Jaworowska et al. 2004; Ruiz-Omeñaca et al. 2005; Gheerbrant and Rage 2006; Canudo et al. 2008, 2009; Coria et al. 2010). The latter suggests that Europe maintained a close palaeobiogeographical connection allowing biotic interchanges with Gondwanan territories until the Hauterivian, at least. It must be noted that the biogeographical model here proposed is supported with the currently available Berriasian–Hauterivian fossil record, but archosaur taxa from this time-slice are poorly sampled and chronostratigraphically constrained outside Europe. Accordingly, any new discovery and more accurate dating will definitely shed light on the suitability of the hypothesis here proposed.

The recovery of Europe as more closely related to Asiamerica than to southern landmasses in the late Early Cretaceous TRA (Fig. 1d) supports the coalescence of Europe with Asiamerica during this time-span. Several Eurogondwanan tetrapod clades should have made their appearance during post-Hauterivian times in Asiamerican assemblages, such as titanosauriforms and possibly neovenatorid, carcharodontosaurid, and spinosaurid dinosaurs, notosuchian crocodylomorphs, and boreosphenidan mammals (Wu and Sues 1996; Salgado and Calvo 1997; Wilson 2000; Juárez Valieri et al. 2004; Gheerbrant and Rage 2006; Milner et al.

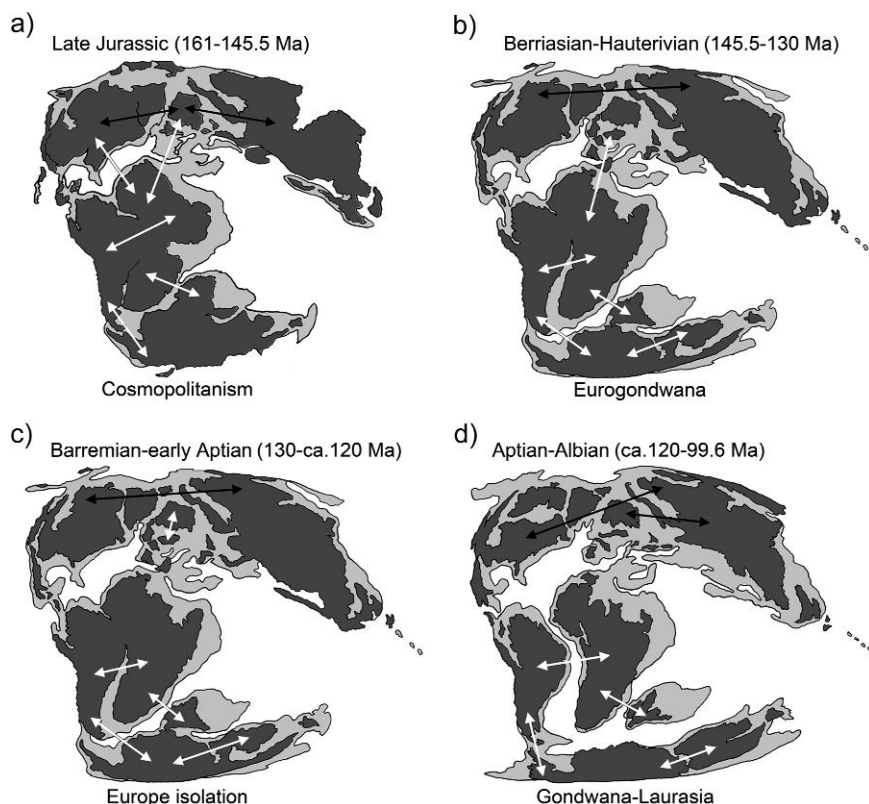


FIGURE 2. Global palaeogeographic reconstructions showing the main biogeographical model and connections here proposed for the (a) Late Jurassic, (b) Berriasian–Hauterivian, (c) Barremian–earliest Aptian, and (d) Aptian–Albian time-slices. The white arrows depict biogeographical connections among southern landmasses and/or Europe and the black arrows between Asia and North America or within Laurasia (a–d redrawn from Blakey 2006 and modified following Canudo et al. 2009 regarding the position of the Apulian Plate).

2007; Buffetaut et al. 2008; Brusatte et al. 2009; Benson et al. 2010). At the same time, groups that up to that moment were only present in Asiamerica should have entered into Europe during late Early Cretaceous to early Late Cretaceous times, such as eudromaeosaurian, troodontid, hadrosaurid, euhelepodid, ceratopsian and nodosaurid dinosaurs, and amphilestid and gobiconodontid mammals (Buffetaut 1989; Osmólska and Barsbold 1990; Howse and Milner 1993; Canudo et al. 2002; Cuenca-Bescós and Canudo 2003; Ösi 2005; Prieto-Marquez et al. 2006; Lindgren et al. 2007; Dalla-Vecchia 2009; Ösi and Makádi 2009; Cruzado-Caballero et al. 2010; Ösi et al. 2010).

The Eurogondwanan model is also supported by micropalaeontological (Cherchi and Schroeder 1973) and geological evidence (Dercourt 1972; Zappaterra 1994; Stampfli and Mosar 1999; Bosellini 2002). In this regard, a series of microplates allowed a land connection between Africa and Europe during the Early Cretaceous by the so-called “Apulian Route” (Gheerbrant and Rage 2006; Canudo et al. 2009; Knoll and Ruiz-Omeñaca 2009). Among them, the Adriatic–Dinaric Carbonate Platform seems to have connected Afro-Arabia (Bosellini 2002) and was isolated in the Tethys at least since the Aptian (Dercourt et al. 1993; Dalla-Vecchia 2009). The discovery of dinosaur trackways in this region demonstrated the presence of aerial

exposures during this time (Bosellini 2002; Skelton et al. 2003; Dalla-Vecchia 2005; Nicosia et al. 2007). In addition, a drastic sea-level fall is documented during the Berriasian–Hauterivian time span (Miller et al. 2005) and perfectly matches with the point at which a Eurogondwanan signal is recovered (see Appendix 3). Finally, the subsequent post-Hauterivian biotic interchanges between the European archipelago and southern Asia across the Turgai Strait has been repeatedly proposed by several authors and supported by the presence of tectonic crustal uplift and volcanism along the northern margin of the Tethys (Sues and Averianov 2009; Dalla-Vecchia 2009; Cruzado-Caballero et al. 2010).

A Nontraditional Fleeting Gondwana–Laurasian Dichotomy

Our cladistic biogeographical analysis recovered both monophyletic Gondwanan (including South America, Australia, and Africa) and Laurasian groupings (Europe, North America, and Asia) after Hauterivian times (Fig. 1c–e and Table 1). In contrast, previous hypotheses proposed an isolation of more than 100 myr between Gondwana and Laurasia (Bonaparte 1984), but the presence of endemic clades for each supercontinent is weak as a whole during the entire Late Cretaceous (99.6–65.5 Ma; Wu and Sues 1996; Naish et al. 2004; Fiorelli and Calvo 2007; Barrett et al. 2011). In this regard, unenlagiid and noosaurid theropods,

mahajangasuchid and peirosaurid crocodylomorphs, and gondwanatherian mammals are the only unambiguous endemic terrestrial clades widely distributed in Gondwanan continents after Hauterivian times (Krause et al. 1997; Makovicky et al. 2005; Candeiro and Martinelli 2007; Larsson and Sues 2007; Carrano and Sampson 2008; Novas et al. 2009; Sereno and Larsson 2009). On the other hand, in Laurasian territories the only endemic Late Cretaceous archosaur lineages are ornithomimosaurian, mononykine alvarezsaurid, tyrannosaurid, and troodontid theropods, nodosaurid, and marginocephalian ornithischians (Buffetaut 1989; Barsbold and Osmólska 1990; Barsbold et al. 1990; Chiappe et al. 1998; Hutchinson and Chiappe 1998; Dodson et al. 2004; Makovicky and Norell 2004; Maryanska et al. 2004; Osmólska et al. 2004; Vickaryous et al. 2004; Weishampel et al. 2004; Ösi 2005; Chinnery and Horner 2007; Longrich and Currie 2009; Ösi and Makádi 2009; Ösi et al. 2010; Xu et al. 2011). Thus, the presence of only limited endemic clades in Gondwana and Laurasia contrasts with traditional views, which indicated a larger number of endemic forms for each supercontinent (Bonaparte 1999). The meagre presence of endemic northern and southern tetrapod taxa could be explained with the model here proposed. The late formation of Laurasia and Gondwana in post-Hauterivian times, together with the flow of Eurogondwanan clades discharged by Europe into Asiamerica, would have acted against a deeper endemism of both Gondwanan and Laurasian faunas (Figs. 2 and 3).

The biogeographical relationships of Australia during the Cretaceous are currently a matter of debate (Molnar 1992; Rich and Vickers-Rich 1994, 2003; Rich 1996; Vickers-Rich 1996; Smith et al. 2008; Agnolín et al. 2010; Barrett et al. 2011). In our palaeobiogeographical analysis, Australia is recovered as deeply nested within Gondwana during the Aptian–Albian time-slice (Fig. 1d) in agreement with recent studies that highlighted the presence of Eurogondwanan tetrapods in this landmass (e.g., megaraptoran, *Chubutisaurus–Wintonotitan* clade, and probable baurusuchid crocodylomorphs; Smith et al. 2008; Agnolín et al. 2010; Carballido et al. 2011).

In addition to the late biogeographical distinction between Gondwana and Laurasia, the dichotomy between these faunas is not recorded here up to the end of the Mesozoic sharply contrasting with the currently widely accepted palaeobiogeographical paradigm. Accordingly, the Gondwana–Laurasia dichotomy (Figs. 1c–e and 3a,b) seems to have been a relatively fleeting scenario culminating with a peculiar biogeographical pattern in the second half of the Late Cretaceous (Campanian–Maastrichtian time-slice).

A Peculiar Latest Cretaceous–Palaeogene Biogeography and the Atlantogea Biogeographical Palaeoprovince

Perhaps, the most unexpected result of our TRA was the recovery of Europe as more closely related

to southern landmasses than to Asiamerica during the Campanian–Maastrichtian time-slice (Figs. 1f and 3c,d; Table 1). This palaeobiogeographical signal is based in our analysis on the common presence of baurusuchid crocodylomorphs and carnosaurine and derived titanosaurian dinosaurs in Europe and southern landmasses (see Appendix 1 for details on the latest Cretaceous European carnosaurine assignment). In addition, this hypothesis is also supported by the distribution of trematochampsid crocodylomorphs, madtsoiid and boid snakes, podocnemidoid turtles, and basal didelphoids and ungulatormorph mammals (e.g., Lavocat 1977; de Broin 1980; Crochet and Sigé 1983; Buffetaut 1985, 1989; Astibia et al. 1990; Le Loeuff 1991, 1995; Lapparent de Broin and Murelaga 1996; Rage 1996; Allain and Pereda Suberbiola 2003; Kielan-Jaworowska et al. 2004; Rasmusson and Buckley 2009; Cadena et al. 2010; Williamson et al. 2010). The close biogeographical affinities between European and South American faunas necessarily implies that both landmasses had biogeographical connections with Africa in latest Cretaceous times, as suggested by some previous authors (Tarling 1980; Bonaparte 1984; Morley 2000, 2003; Morley and Dick 2003; also see Mannion and Upchurch 2011; Fig. 3c). The presence of a European–Africa–South American connection deep in the Late Cretaceous contrasts with the Africa First (Hay et al. 1999; Krause et al. 2007) and Pan-Gondwanan models (Sereno et al. 1996; Scotese 2001; Sereno et al. 2004; Sereno and Brusatte 2008), which suggested a biogeographical severing between Africa and South America during the late Early Cretaceous and Cenomanian, respectively.

Geological evidence suggests that the epicontinental Ural seaway that separated Asia from Europe was an uncrossable barrier preventing biotic interchange during the latest Cretaceous (ca. 90 Ma; Le Loeuff 1991; Blakey 2006). Conversely, it has been proposed that at least some European regions reacquired terrestrial connections with Africa during this time span through the Alboran or Apulian plates (Buffetaut 1989; Philip and Floquet 2000), allowing a faunal interchange between these areas (Le Loeuff 1991; Fig. 3c). Regarding the African and South American geographic relationships during the latest Cretaceous, most recent palaeogeographic reconstructions indicate that in post-Cenomanian times the severing between both landmasses was complete (Scotese 2004). However, multiple lines of geological evidence (e.g., magnetic anomalies, reef limestones as records of carbonate shelves, and direct drilling data) indicate the existence of large islands in the South Atlantic between Africa and South America since the late Maastrichtian, at least, up to the Eocene (Kastens et al. 1998; Lawver and Gahagan 2003; Markwick and Valdes 2004; Oliveira et al. 2010). The latter is in accordance with the presence of distinct southern and northern South Atlantic foraminifer assemblages until the latest Cretaceous (Beurlen 1967; Tinoco 1967) and the presence of red algae remains, shallow water animals, and rocks formed under aerial exposure (Oliveira et al. 2010). Finally, the Rio Grande Rise (Brazil) and the

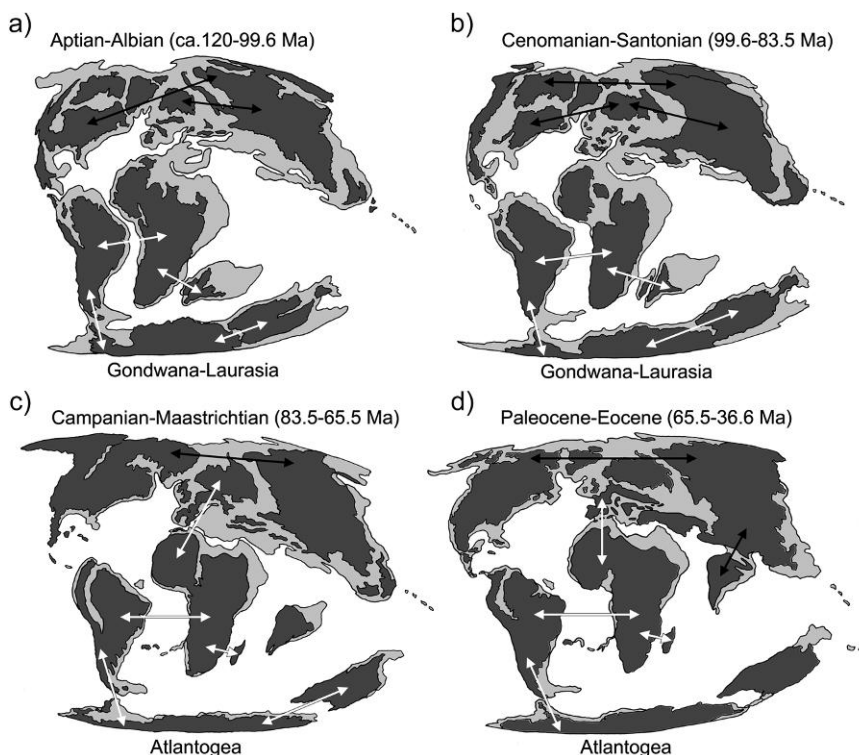


FIGURE 3. Global palaeogeographic reconstructions showing the main biogeographical model and connections here proposed for the (a) Aptian–Albian, (b) Cenomanian–Santonian, (c) Campanian–Maastrichtian, and (d) Paleocene–Eocene time-slices. The white arrows depict biogeographical connections within Gondwana and Atlantogea and the black arrows within Laurasia and Asiamerica (a–d redrawn from [Blakey 2006](#) and modified following [Oliveira et al. 2010](#) regarding the South Atlantic palaeogeography).

Walvis Ridge (Africa) have been interpreted as part of a hotspot track generated during the latest Cretaceous and Paleogene ([Le Pichon and Hayes 1971](#); [O'Connor and Duncan 1990](#); [Parrish 1993](#); [Ferrari and Riccomini 1999](#); [Schettino and Scotese 2005](#)). All this evidence indicates the presence of an island chain allowing the establishment of palaeobiogeographical connections between Africa and South America across the South Atlantic from Campanian to Eocene times ([Oliveira et al. 2010](#); Fig. 3c,d).

The reconnection of Europe and South America via Africa would explain the presence of Laurasian tetrapod lineages in the Campanian–Maastrichtian of South America and Antarctica, namely lambeosaurine and ankylosaurian ornithischians, ungulatormorphs, and basal didelphoid mammals ([Casamiquela 1978](#); [Brett-Surman 1979](#); [Bonaparte 1984](#); [Bonaparte and Rougier 1987](#); [Powell 1987](#); [Case et al. 2000](#); [Coria and Salgado 2003](#); [Rage 2003](#); [Kielan-Jaworowska et al. 2004](#); [Salgado and Gasparini 2006](#)). This model is an alternative explanation to the traditional hypothesis of a dispersal event between North America and South America via a terrestrial bridge during the latest Cretaceous ([Bonaparte 1984](#); [Krause et al. 1997](#)). This Panamerican connection rests on weak and controversial palaeogeographic evidence ([Schmidt-Effing 1979](#); [Rage 1981](#); [Pitman et al. 1993](#)) and most recent geographic reconstructions do not depict such a land bridge

([Scotese 2001](#); [Blakey 2006](#)). The absence of the most abundant North American Campanian–Maastrichtian tetrapod lineages in the latest Cretaceous of South America is an incongruent pattern under the Panamerican land bridge model (e.g., tyrannosaurid, troodontid, therizinosaurid, oviraptorosaurid and velociraptorine theropods, marginocephalian ornithischians, and anguimorph lizards, with the exception of a hadrosaurine genus; [Prieto-Marquez and Salinas 2010](#)). Accordingly, since these abundant North American taxa are also absent in the latest Cretaceous of Europe, the dispersal of Laurasian forms to South America and Antarctica is considered here more likely to have occurred from the latter region rather than from North America (Fig. 3c).

The evidence for a late biogeographical reconnection between Europe, Africa, and South America is not limited to latest Cretaceous times but seems to extend through the Paleogene. Floral and faunal taxa from fossil assemblages of the early Tertiary of Europe (e.g., London Clay and Messel Pit) exhibit close phylogenetic affinities with typical African, Australian, and South American taxa, absent in coeval Asiamerican beds. Among these taxa are rhea-like ratite, quercymegapodiid, anseranatid, idiornithid, cathartid, threskiornithid, nyctibiid, falconid, psittaciform, trochilid, upupiform, trogoniform and passeriform birds, ceratophryid anurans, ercine snakes, sebecosuchian crocodylomorphs, and didelphinine and

afrotherian mammals (Crochet and Sigé 1983; Bonaparte 1984; Rage 1984; Peters and Storch 1993; Rage and Rocek 2008; Mayr 2009; Rasmusson and Buckley 2009; Agnolín and Chimento 2011). The minimal divergence times between several South American and African extant plant and animal groups are calibrated well after the purported latest separation between both landmasses (80 Ma; Scotese 2004), suggesting dispersal events between both continents after their severing. Furthermore, it is assumed that the trans-Atlantic dispersion of these groups must have occurred even more recently, as for example in platyrrhine monkeys (40 Ma; Schneider 2000), caviomorph rodents (45.4 ± 4.1 Ma; Poux et al. 2006), cichlid perciforms (58–41 Ma; Vences et al. 2001), lacantuniid siluriforms (46–45 Ma; Lundberg et al. 2007), amphisbaenian lepidosaurs (40 Ma; Vidal et al. 2008; Müller et al. 2011), inocybacean mushrooms (64 and 46 Ma; Matheny et al. 2009), and cinchonoid (53.1–44.9 Ma; Antonelli et al. 2009), annonacean (52–49 Ma; Erkens et al. 2009), lamialean (74–44 Ma; Pennington and Dick 2004), legumean (79–74 Ma; Pennington and Dick 2004), and malpighiacean angiosperms (68.76–56.83 Ma; Davis et al. 2004).

In order to explain these unexpected disjunct distributions on both sides of the South Atlantic previous authors have suggested the presence of unidirectional westward dispersals by rafting floating islands helped by palaeocurrents and palaeowinds (Hoffstetter 1972; Parrish 1993). However, the phylogenetic relationships and geographical distribution of several groups of plants and animals are incongruent with the hypothesis of a unidirectional dispersal from Africa to South America. Our dispersal–vicariance analyses of 3 paradigmatic clades indicate the presence of bidirectional (caviomorphs) and eastwards dispersion fluxes (malpighiaceans and amphisbaenians), contrasting with the westward directed floating island model (see Appendix 4). In addition, the transoceanic rafting of fossorial amphisbaenians and freshwater lacantuniid and cichlid fishes is highly unlikely. The fact that they had to achieve two transoceanic dispersals (i.e., North Atlantic and Caribbean) weakens a northern Europe–North America–South America migration route, statement that is bolstered by the complete absence of fossil remains of these numerous plant and animals groups in North America (with the exception of rhineurid amphisbaenians; Hembree 2007) during the Tertiary. Accordingly, the available geological and biological information suggests the presence of bidirectional faunistic and floristic interchanges between Africa and South America during the Campanian–Eocene time span (80–40 Ma; Fig. 3c,d). The common presence of several groups of animals and plants leads us to propose a new biogeographical palaeoprovince named here Atlantogea. The Atlantogean Biogeographical Palaeoprovince included the modern territories of South America, Caribbean, Antarctica, Africa, Europe, and Australia. In spite of the presence of several groups widely distributed across Atlantogea, other well-known clades of animals (e.g., xenarthrans, some afrotherian clades, and catarrhine monkeys)

considered to have an endemic African, European or South American distribution during the early Tertiary suggest that some kind of dispersal filter routes were present among these landmasses. The new model here proposed invites a review of the biogeographical and phylogenetic affinities of several clades of organisms in order to unveil the palaeobiogeographical scenario that modeled the distribution of extant plant and animal groups.

SUPPLEMENTARY MATERIAL

Supplementary material, including data files and/or online-only appendices, can be found at <http://data-dryad.org>, doi: 10.5061/dryad.d47h94c9.

ACKNOWLEDGEMENTS

We thank the commentaries and suggestions provided by A. Martinelli and S. Brusatte on an early draft of the manuscript, as well as enrichment discussions with N. Chimento, S. Lucero, S. Bogan, and G. Lio. The suggestions and comments provided by the editor R. DeBry, the associate editor A. Paterson, and E. Buffetaut, P. Upchurch, R. Butler, and 2 anonymous reviewers improved the quality of the manuscript and are appreciated. We thank D. Pol for help in the writing of the script for TNT 1.1 used in this study.

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