

# An analysis of dinosaurian biogeography: evidence for the existence of vicariance and dispersal patterns caused by geological events

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As the supercontinent Pangaea fragmented during the Mesozoic era, dinosaur faunas were divided into isolated populations living on separate continents. It has been predicted, therefore, that dinosaur distributions should display a branching ('vicariance') pattern that corresponds with the sequence and timing of continental break-up. Several recent studies, however, minimize the importance of plate tectonics and instead suggest that dispersal and regional extinction were the main controls on dinosaur biogeography. Here, in order to test the vicariance hypothesis, we apply a cladistic biogeographical method to a large dataset on dinosaur relationships and distributions. We also introduce a methodological refinement termed 'time-slicing', which is shown to be a key step in the detection of ancient biogeographical patterns. These analyses reveal biogeographical patterns that closely correlate with palaeogeography. The results provide the first statistically robust evidence that, from Middle Jurassic to mid-Cretaceous times, tectonic events had a major role in determining where and when particular dinosaur groups flourished. The fact that evolutionary trees for extinct organisms preserve such distribution patterns opens up a new and fruitful direction for palaeobiogeographical research.

**Keywords:** component analysis; Dinosauria; Mesozoic; palaeobiogeography; plate tectonics; vicariance

## 1. INTRODUCTION

Dinosaurs were diverse, geographically widespread, stratigraphically long lived and largely terrestrial: they therefore provide an almost 'ideal' case study in Mesozoic biogeography. Unfortunately, the biogeographical history of dinosaurs remains obscure and controversial, partly because of differences in the datasets studied and the methods applied. Many workers (Milner & Norman 1984; Russell 1993; Fastovsky & Weishampel 1996; Sampson *et al.* 1998) have proposed 'vicariance', driven by continental fragmentation, as the dominant factor that determined dinosaur distributions, especially during the Cretaceous. Under this hypothesis, continental break-up and the formation of epicontinental seas created barriers to the dispersal of terrestrial organisms. A once 'cosmopolitan' dinosaurian fauna began to fragment and differentiate, until eventually each isolated region acquired its own endemic dinosaurs. However, recent failures to detect this pattern led Sereno (1997, 1999*a,b*) to conclude that continent-level vicariance was rare and relatively unimportant: faunal differentiation is instead interpreted as the result of extinction events affecting different dinosaurs in each of the isolated areas.

Most attempts to study dinosaurian biogeography (Cox 1974; Galton 1977, 1982; Colbert 1984; Pereda-Suberbiola 1991; Le Loeuff *et al.* 1992; Russell 1993; Le Loeuff & Buffetaut 1995; Upchurch 1995; Fastovsky & Weishampel 1996; Sereno *et al.* 1996; Buffetaut & Suteethorn 1998; Casanovas *et al.* 1999; Pereda-Suberbiola & Sanz 1999; Pérez-Moreno *et al.* 1999) have been based on a literal interpretation of distributions in the fossil record. Such an

approach to palaeobiogeographical analysis, however, is prone to severe error because of the ambiguity inherent in 'missing data'. For example, an organism might be absent from a particular geographical region because:

- (i) it never lived in the area ('primitive absence');
- (ii) it once lived there but became extinct ('regional extinction'); or
- (iii) it lived there but has not been discovered yet ('pseudo-absence').

Several studies (Brett-Surman 1979; Milner & Norman 1984; Sereno 1997, 1999*a,b*; Weishampel & Jianu 1997; Sampson *et al.* 1998) have noted that information on phylogenetic relationships can alleviate the effects of missing data; however, none of these investigations have applied a cladistic biogeographical method coupled with statistical evaluation. The current study, therefore, has drawn together the most recent and detailed dinosaur phylogenies and geographical-stratigraphical range data (figure 1). This large dataset was subjected to the cladistic biogeographical method known as 'tree reconciliation analysis' (TRA: Page 1988, 1993, 1994, 1995) in order to test for the presence of the repeated area relationships that are potentially indicative of a vicariance signal.

## 2. MATERIAL AND METHODS

The principles of cladistic biogeography have been explored by many workers (Nelson & Platnick 1981; Patterson 1981; Page 1988, 1994; Hunn & Upchurch 2001). The essence of these methods concerns the effect of geographical barrier formation on the phylogeny of organisms (i.e. vicariance). Consider a continuous geographical region, XYZ, that fragments through time such that portion X becomes isolated from YZ

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before the latter two portions finally separate. If, after fragmentation, we select three taxa, A, B and C, that are endemic to X, Y and Z, respectively, we would predict a taxon cladogram with the topology (A (B, C)) because of the effect of area history on cladogenesis. Even if we had no knowledge of palaeogeography, we could infer the most probable area fragmentation sequence (area cladogram) to be (X (Y, Z)) based purely on the relationships of A, B and C, coupled with the latter's endemic ranges. If this type of vicariance has occurred, we expect to see the same area relationships imposed on the phylogenies of many different clades (although see Lieberman (2000) and Hunn & Upchurch (2001) for a discussion of 'geodispersal'). Thus, vicariance creates a repeated set of area relationships that can be detected statistically in taxon cladograms (Nelson & Platnick 1981; Page 1988). A repeated set of imposed spatial patterns is not expected from regional extinction or most forms of dispersal because these processes are unlikely to simultaneously impose an identical pattern on the spatial distributions of different clades. Thus, although vicariance is detectable statistically, regional extinction and most forms of dispersal are not. It is therefore very difficult to assign a relative frequency to each of these biogeographical processes. Nevertheless, a statistically significant set of area relationships represents *prima facie* evidence that vicariance has been sufficiently 'dominant' to overcome the confounding effects of dispersal and extinction.

TRA was applied to the data shown in figure 1, using the computer program TREE-MAP (Page 1994, 1995). Such an analysis typically has two stages:

- (i) a search for the 'optimal area cladogram' (i.e. the area fragmentation history that best fits the area relationships in the organism phylogeny); and
- (ii) a randomization test that determines the probability that the observed signal could have occurred by chance.

Traditionally, analytical cladistic biogeography has used only data on organism relationships and spatial distributions (Nelson & Platnick 1981; Patterson 1981). Theoretical considerations, however, suggest that the temporal ranges of organisms are also important (Grande 1985; Page 1990; Hunn & Upchurch 2001, 2002; Upchurch & Hunn 2001). In particular, it seems that distribution patterns 'decay' through time as new ones are superimposed (Grande 1985). Analysis over an extensive stratigraphical range, therefore, may fail to find the correct area cladogram (or fail the randomization test) because conflicting signals obscure each other. In order to minimize this danger, TRA has been applied to 'time-slices' of various duration, such as the 'Mesozoic', 'Jurassic', and 'Early Cretaceous' (table 1). For each such TRA, the dinosaur phylogeny was 'pruned' so that only taxa present within the relevant time-slice were retained.

A wide array of different dinosaur cladograms are available: those used in the current analysis are listed in the legend to figure 1 and the criteria for their selection are discussed in electronic Appendix A (available on The Royal Society's Publications Web site). The geographical and stratigraphical ranges for the dinosaur genera were obtained from Weishampel (1990), and revised, where appropriate, on the basis of recent literature pertaining to individual taxa. All TREE-MAP nexus files are available from the first author on request.

### 3. RESULTS

The results of applying TRA to the dinosaur data are summarized in table 1 and figure 2. Most analyses pro-

duce only one or two optimal area cladograms, although all but three of these fail the randomization test. Several factors are potentially responsible for statistical failure:

- (i) inaccuracies in the topology of the dinosaur phylogeny;
- (ii) poor sampling of particular stratigraphical or geographical ranges;
- (iii) the superposition of several genuine signals (see § 2); and
- (iv) the genuine absence of any vicariance signal, perhaps reflecting the overwhelming effects of dispersal or regional extinction.

The failure of the Late Triassic and Early Jurassic analyses may reflect the current study's selection of areas that are suitable for the detection of continent-level vicariance: given that Pangaea remained largely intact until the mid-Jurassic (see below), it would not be surprising if the earliest time-slices showed no continent-level signal. Perhaps the most surprising instance of failure is that for the Late Cretaceous, a time that is often associated with the zenith of dinosaur endemism (Fastovsky & Weishampel 1996; Sereno *et al.* 1996). This result is consistent with, but does not provide support for, recent suggestions that the Campanian and Maastrichtian were characterized by several dispersal events between previously isolated continents (Colbert 1984; Le Loeuff & Buffet 1995; Sereno 1999a). Alternatively, poor sampling (such as the absence of Late Cretaceous European theropods and sauropods in the available cladograms) may be largely responsible for obscuring a repeated area relationship. In any case, it is not legitimate to make any biogeographical inferences on the basis of the statistically insignificant analyses. Randomization tests are essentially 'asymmetrical': a pass indicates the presence of a signal, whereas a failure only indicates an absence of evidence of a signal. Thus, the statistical failures cannot be interpreted as evidence of absence of repeated area relationships and cannot be used

Figure 1 (opposite). Two cladograms, (a) Ornithischia and (b) Saurischia, showing the phylogenetic relationships of dinosaurs and geographical-stratigraphical ranges used in this study. Sources for these cladistic analyses are: Dinosauria as a whole (Sereno 1997, 1999a); Thyreophora (Lee 1996; Sullivan 1999; Galton & Upchurch 2002b); Marginocephalia (Sereno 2000); Ornithopoda (D. B. Norman, unpublished data); Theropoda (Barsbold & Osmolska 1990; Barsbold *et al.* 1990; Novas 1997; Sereno 1999c; Sereno *et al.* 1996, 1998); Sauropodomorpha (Upchurch 1998; P. Upchurch, unpublished data; Galton & Upchurch 2002a). Abbreviations for geographical areas: AF, Africa; AS, Asia (excluding India); AN, Antarctica; AU, Australia; EU, Europe; IN, India; NA, North America; SA, South America. Abbreviations for stratigraphical ranges: Aal, Aalenian; Alb, Albian; Apt, Aptian; Baj, Bajocian; Bar, Barremian; Bat, Bathonian; Ber, Berriasian; Cal, Callovian; Cam, Campanian; Car, Carnian; Cen, Cenomanian; Con, Coniacian; EC, Early Cretaceous; EJ, Early Jurassic; Hau, Hauterivian; Het, Hettangian; Kim, Kimmeridgian; LC, Late Cretaceous; LJ, Late Jurassic; LT, Late Triassic; Maa, Maastrichtian; MJ, Middle Jurassic; Nor, Norian; Oxf, Oxfordian; Rha, Rhaetian; San, Santonian; Sin, Sinemurian; Tth, Tithonian; Toa, Toarcian; Val, Valanginian.

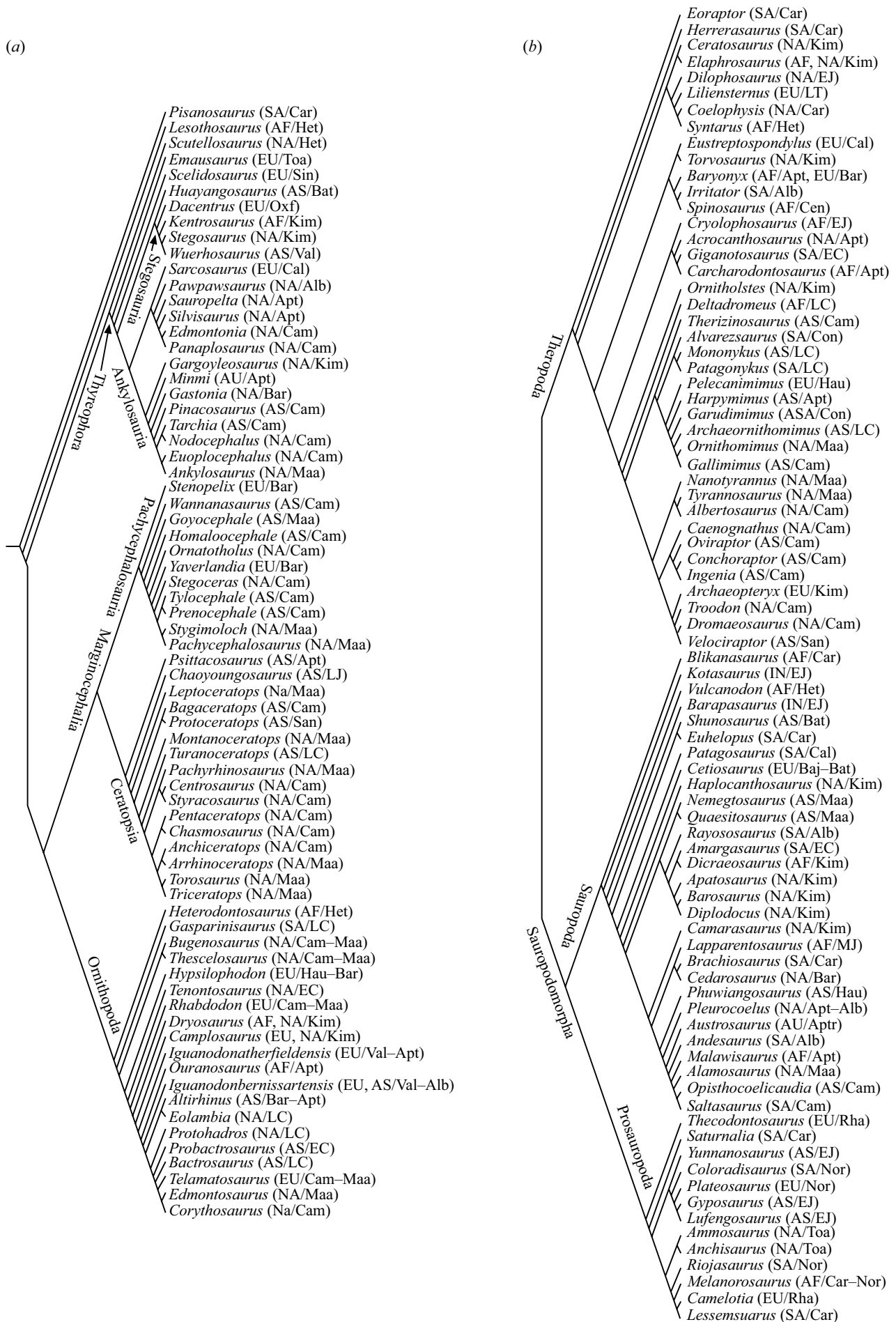


Table 1. Results of tree reconciliation analyses.

(This table summarizes the results of time-sliced TRAs of the dinosaur phylogenies and distributions shown in figure 1. The optimal area cladogram topologies are shown using standard parenthetical notation. Areas and stratigraphical ranges are denoted by the same abbreviations listed in the legend for figure 1. The *p*-values for each optimal area cladogram were obtained via reconciliation with 10 000 randomized versions of the taxon cladograms (see § 2 and electronic Appendix A). The stratigraphical units and boundaries used here are based on the Geological Society of America Geological Time-scale (Geological Society of America 1998). For the 'Mesozoic' time-slice analysis only, the dinosaur cladogram was partitioned into 'Saurischia' and 'Ornithischia' because software constraints in TREEMAP (Page 1995) prevent the analysis of cladograms with more than 100 taxa.)

time-slice	optimal area cladogram topology	<i>p</i> -value
Mesozoic (Car–Maa)	Saurischia (IN (AU (AN (AF (SA (EU (AS, NA))))))) Ornithischia <sup>a</sup> (SA (AU (AF (EU (AS, NA))))))	0.98 0.99
Late Triassic (Car–Rha)	<sup>a</sup> (AF (NA (EU, SA)))	0.81
Jurassic (Het–Tth)	(IN (AS (SA (EU (AF, NA))))))	0.23
Early Jurassic (Het–Toa)	((AF, IN), (EU (AS, NA)))	0.21
Middle Jurassic (Aal–Cal)	(AS (SA (AF, EU)))	0.0096
Late Jurassic (Oxf–Tth)	(AS (EU (AF, NA)))	0.001
Cretaceous (Ber–Maa)	(AU (AF ((AS, SA), (EU, NA)))) (AU (AF (EU (NA (SA, AS))))))	0.157 0.157
Early Cretaceous (Ber–Alb)	((AS, EU), (NA (AU (AF, SA))))	0.0047
Late Cretaceous (Cen–Maa)	(AF (SA (AS (EU, NA))))	0.84

<sup>a</sup> 'General area cladograms', i.e. Nelson consensus trees (Nelson & Platnick 1981), that have been constructed using multiple optimal area cladograms.

to claim that vicariance was not important during the times concerned.

Three analyses (Middle Jurassic, Late Jurassic and Early Cretaceous) passed the randomization test ( $p < 0.05$ , table 1, figure 2), indicating that the data for these periods contain biogeographical patterns that are highly unlikely to have arisen by chance. The optimal area cladograms for the Middle and Late Jurassic (figure 2*b,d*) each contain only four areas, reflecting the poor sampling of dinosaurs for several continents. These two area cladograms display the same relationships between the three areas that they share in common; i.e. Europe and Africa were more recently in contact than either was with Asia. The Early Cretaceous area cladogram (figure 2*f*) contains six areas and differs from that for the Late Jurassic regarding the 'relationships' of the European area. Incongruence between these three area cladograms is produced by shifts in the relationships of Europe and South America relative to other continents, a phenomenon that is probably caused by both an artefact of area designation and genuine biogeographical processes (see § 4).

#### 4. COMPARISONS WITH PALAEOGEOGRAPHY

Cladistic biogeographers generally regard vicariance as the only process capable of producing a repeated set of area relationships in an organism cladogram (Nelson & Platnick 1981; Patterson 1981). Although vicariance is the most probable cause of such patterns, recent work has suggested that there exist a number of 'vicariance-mimicking' phenomena that can affect area cladogram topology (Hunn & Upchurch 2001, 2002; Upchurch & Hunn 2001). For example, the formation of a connection between two previously separate geographical areas allows the dispersal of many different types of organism, potentially causing the two areas to cluster together in the area cladogram. Thus, it is highly desirable that we test our apparent vicariance patterns against palaeogeography.

##### (a) *South America in the Middle Jurassic*

The greatest incongruence between the area cladograms and palaeogeography concerns the position of South America during the Middle Jurassic. According to the area cladogram (figure 2*b*), Europe and Africa were more recently in contact with each other than either was with South America. This conflicts with palaeogeographical reconstructions (figure 3), which suggest that Africa and South America formed a continuous area throughout the Jurassic and into the Cretaceous (Smith *et al.* 1994; Smith & Rush 1997). It is conceivable that some form of non-marine barrier separated South America and Africa during the Middle Jurassic, but there is no geological evidence to support this at present. It seems more probable, therefore, that the problem lies with the apparent biogeographical signal. One possibility is that the complexity of the European region (see § 4*b*) has produced an incorrect set of area relationships.

##### (b) *Laurasian fragmentation*

Traditionally, the initial phase of Pangaeon fragmentation is believed to involve a Callovian age (about 160 million years (Myr)) separation into Laurasian and Gondwanan land masses (Serenio 1997, 1999*b*), which prompted the appearance of distinct endemic northern and southern biotas (Bonaparte & Kielan-Jaworowska 1987). Several recent studies (Serenio 1997, 1999*b*) have noted that dinosaurian distributions do not conform to this north–south division and have used this observation as evidence against the vicariance hypothesis. The topologies of the area cladograms in figure 2 do not contain a 'monophyletic' cluster of Laurasian areas and are therefore also incompatible with an initial north–south palaeogeographical separation. However, an examination of palaeocoastline reconstructions (Smith *et al.* 1994; Smith & Rush 1997) suggests that this incongruence is more apparent than real. Although Laurasia may have been formed from a single continuous area of continental

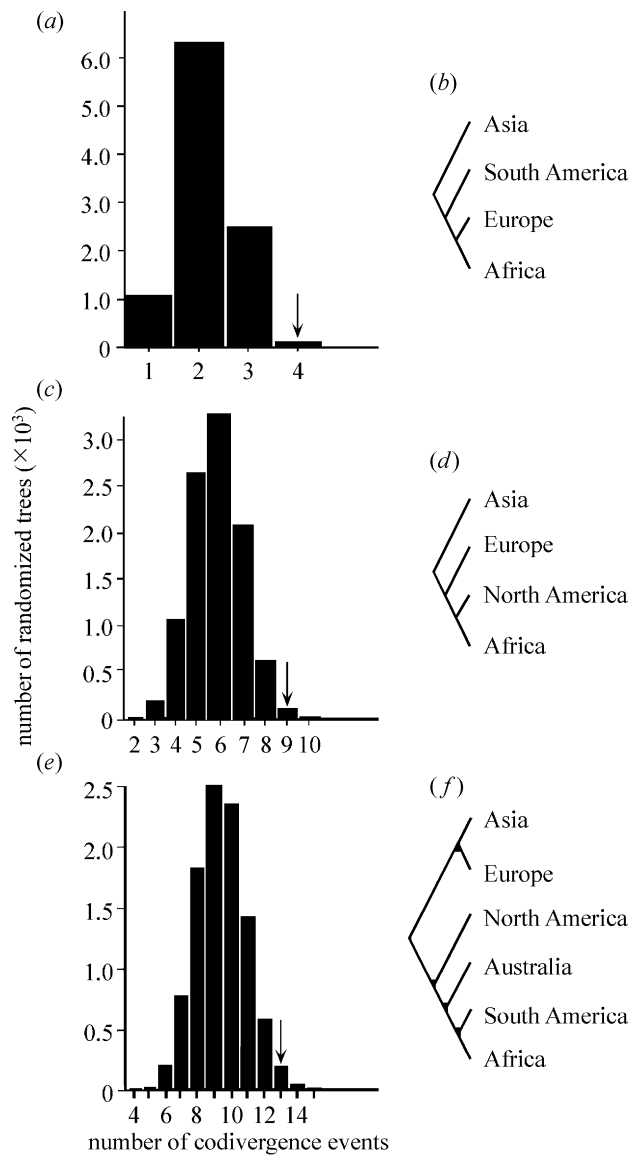


Figure 2. Statistically significant results of tree reconciliation and randomization tests for the Middle Jurassic (a, b), Late Jurassic (c, d) and Early Cretaceous (e, f) time-slices. (a, c, e) Histograms showing the degree of congruence (measured as 'number of codivergence events') between the optimal area cladogram and the 10 000 randomized versions of the original taxon cladogram. The arrows mark the number of codivergence events present when the original taxon cladogram is reconciled with the optimal area cladogram. (b, d, f) Optimal area cladogram topologies for the Middle Jurassic, Late Jurassic and Early Cretaceous, respectively.

crust, the formation of epicontinental seas divided it into a number of separate land masses. For example, a narrow marine barrier existed between Asia (and perhaps part of eastern Europe) and the rest of Pangaea throughout the Late Triassic and Early Jurassic. During the Callovian (ca. 160 Myr), Asia became fully isolated as a result of the formation of the Turgai epicontinental sea along its western margin. The palaeogeographical history of Europe is complex. For much of the Jurassic and Cretaceous, Europe was composed of several major islands (e.g. Britain, Iberia and Eastern Europe), some of which had occasional contact with North America or Asia (figure 3). North America

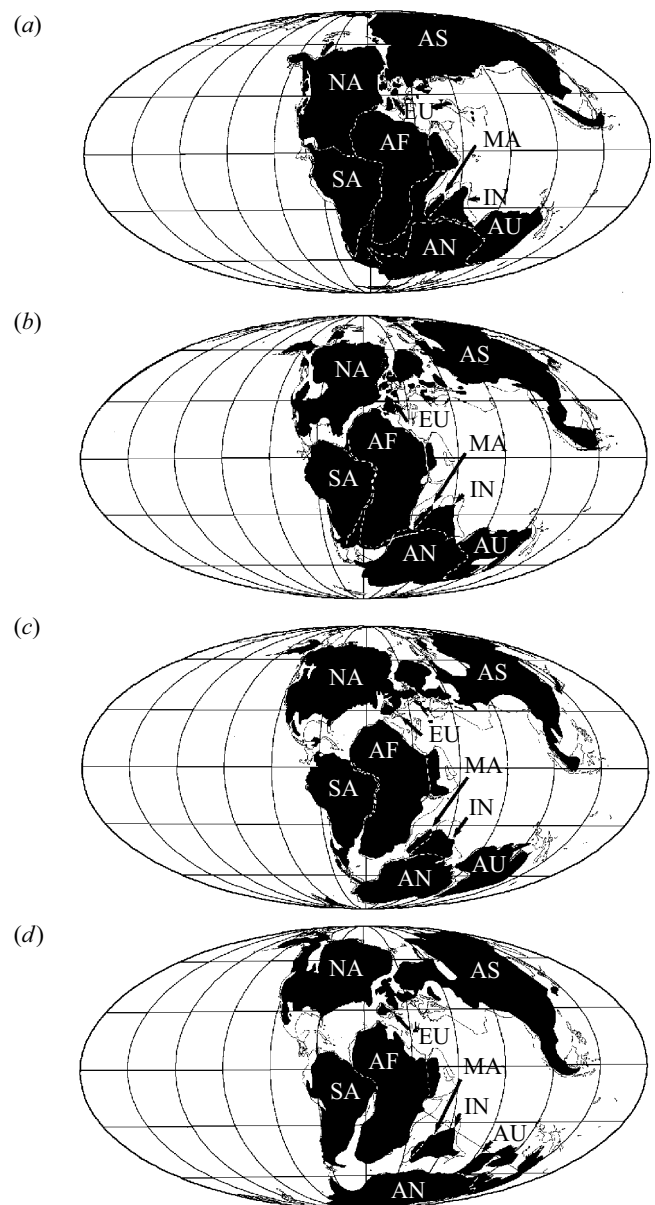


Figure 3. Palaeocoastline reconstructions after Smith *et al.* (1994) and Smith & Rush (1997): (a) Late Triassic (220 million years (Myr)); (b) Callovian (160 Myr); (c) Berriasian-Valanginian (138 Myr); (d) Aptian (120 Myr). Black regions mark emergent land; dashed white lines depict approximate positions of present-day continental margins. Area abbreviations are defined in the legend to figure 1; MA, Madagascar.

seems to have maintained a substantial connection with Gondwana (via northwest Africa) during the Early Jurassic until their separation in the Callovian (figure 3a,b). Thus, palaeogeography indicates that the initial phase of Pangean fragmentation involved the isolation of Asia (a state maintained until the mid-Cretaceous), followed by a later separation of North America from Gondwana. Although uncertainty surrounds the role of European island areas, the above palaeogeographical history predicts that the area cladograms should have the form (Asia (North America, Gondwana)), as indeed is the case for the Late Jurassic and Early Cretaceous (figure 2d,f). Furthermore, the area cladograms are also congruent in terms of the timing of these events, with the isolation of Asia occurring prior to

the Middle Jurassic, and the separation of North America from Africa being established by the Late Jurassic at the latest. Thus, there appears to be considerable congruence between area cladogram topology and palaeogeographical fragmentation, supporting the interpretation that the former depicts vicariance events.

### (c) *Europe–Asia convergence*

Comparison of the area cladograms for the Late Jurassic and Early Cretaceous (figure 2*d,f*) reveals that Europe has ‘shifted’ its position in the latter to become the ‘sister-area’ of Asia. Such a change in area relationships through time could be caused by a convergence of two previously separate areas, allowing an interchange of biotic components (Hunn & Upchurch 2002). This result is consistent with several previous studies (Russell 1993; Upchurch 1995; Norman 1998), which have proposed that a major dispersal event between Europe and Asia occurred during the Aptian–Albian (120–95 Myr). Palaeocoastline reconstructions (Smith *et al.* 1994; Smith & Rush 1997) provide a potential explanation for this pattern because the Turgai Sea underwent regression during the Aptian and Albian, allowing a Europe–Asia ‘land bridge’ to form (figure 3*d*). There is slight incongruence in terms of the timing of these events because the biogeographical signal for the Early Cretaceous has been established on data that contain many pre-Aptian dinosaurs. One possible explanation for this anomaly is that the Early Cretaceous time-slice contains two superimposed biogeographical signals:

- (i) an earlier pattern more closely resembling that from the Late Jurassic; and
- (ii) an Aptian–Albian pattern in which Europe has shifted position.

This hypothesis could be tested through further time-slicing of the data, but this would require improved sampling of mid-Cretaceous dinosaurs.

### (d) *Gondwanan fragmentation*

Unlike Laurasia, Gondwana did exist as a single separate land area from the Callovian to at least the Tithonian (*ca.* 160–148 Myr) (figure 3*b*), an observation that is congruent with the monophyletic clustering of Africa, South America and Australia in the Early Cretaceous area cladogram (figure 2*f*). However, comparison of the biogeographical pattern with palaeogeography is complicated by the existence of two competing tectonic models for Gondwanan fragmentation. Smith *et al.* (1994) and Smith & Rush (1997) have proposed that western Gondwana (Africa + South America) became separated from eastern Gondwana (Indo-Madagascar + Antarctica + Australia) from the Valanginian (138 Myr) onwards. The South Atlantic started to open up between Africa and South America in Valanginian–Barremian times and these two continents became completely separated from each other by the Cenomanian (*ca.* 100 Myr). Hay *et al.* (1999), however, have suggested that Africa became isolated from the rest of Gondwana during the Aptian (*ca.* 120 Myr), whereas South America remained in contact with eastern Gondwana until the Late Cretaceous. The Early Cretaceous area cladogram (figure 2*f*) is congruent with the palaeocoastline reconstructions of Smith *et al.*

(1994) in terms of the fragmentation sequence and the Valanginian timing of the separation between western and eastern Gondwana. The timing of the separation between Africa and South America, however, appears to be different in the area cladogram and the reconstructions of Smith *et al.* (1994) (pre-Albian versus Cenomanian, respectively). This discrepancy may reflect errors in geological dating, or could indicate that the initial stages of vicariance (between Africa and South America) occurred soon after the South Atlantic started to open up.

## 5. DISCUSSION AND CONCLUSION

The three statistically significant area cladograms (figure 2) contain 11 nodes. However, some of these nodes, in different cladograms, potentially represent the same geographical event. For example, all three area cladograms contain a basal node representing the separation of Asia from the rest of Pangaea: this is most parsimoniously interpreted as only a single geographical event, in the absence of evidence to the contrary. When such ‘equivalent’ nodes are accounted for, we find that the three area cladograms contain information on seven geographical events that have apparently produced the repeated area relationships in the taxon cladograms. Four of these events are well-supported instances of continent-level vicariance:

- (i) separation of Asia from Pangaea in the Early or Middle Jurassic;
- (ii) fragmentation of North America from Gondwana prior to the Callovian;
- (iii) separation of Australia (as part of eastern Gondwana) from western Gondwana (Africa + South America) during the Valanginian; and
- (iv) fragmentation of Africa from South America during the Early or mid-Cretaceous.

The Europe–Asia connection, shown by the Early Cretaceous area cladogram (figure 2*f*), represents a well-supported example of biotic interchange brought about by ‘area coalescence’. The apparent separation of Europe from North America + Gondwana (or perhaps just Gondwana), present in the Middle and Late Jurassic area cladograms (figure 2*b,d*) is neither supported nor contradicted by palaeogeography because of the complex nature of the European region. Finally, one ‘event’, the apparent separation of South America from a Europe + Africa area during the Middle Jurassic, is contradicted by palaeogeography. Thus, five out of seven geographical events, predicted on the basis of biogeographical analysis, correspond well with the sequence and timing of palaeogeographical changes.

Clearly, there is not a perfect fit between the biogeographical patterns and palaeogeographical history, but there are several reasons why it would be premature to reject the biological signal:

- (i) palaeogeographical reconstructions are themselves hypotheses that potentially contain errors;
- (ii) congruence may increase as time-slicing and area selection are refined;
- (iii) the degree of congruence partly depends on *a priori*

expectations regarding the effect of barriers on dispersal (e.g. phylogenetic divergence may commence before a barrier is fully developed); and

- (iv) the repeated area relationships are statistically supported signals that stand by themselves as patterns that require explanation.

Given current limitations on both data and methods, the biogeographical and palaeogeographical histories display close correspondence in terms of both fragmentation–convergence sequence and timing.

The ‘detection’ of the biogeographical impact of regional extinction and dispersal in the fossil record is difficult to achieve using rigorous statistical methods: these processes are less likely to produce repeated area relationships and their ‘signals’ are heavily confounded by interpretations of ‘absence’ data. Thus, it has been impossible to discover a satisfactory way to estimate the relative importance of vicariance, dispersal and extinction using historical biogeography. The current study does not solve this problem, but some simple qualitative and quantitative comparisons can be made. First, the presence of statistically robust repeated area relationships suggests that vicariance was not overwhelmed by dispersal or regional extinction (at least during the mid-Jurassic to mid-Cretaceous time-frame). Second, the discovery of four vicariance events and one instance of biotic interchange also suggests that the former process had the major role in determining dinosaurian distributions.

From the Middle Jurassic to Early Cretaceous, dinosaurian faunas were fragmented and became isolated in the order: Asia, Europe, North America, Australia, Africa and South America. Each of these fragmentations represents an important continent-level vicariance event in response to changes in palaeogeography. Continent-level vicariance, therefore, was not a rare or unimportant phenomenon; rather, it seems to have had a major role in shaping dinosaurian distributions. Regional extinction and dispersal cannot be dismissed as insignificant factors; indeed, the results reported here indicate a major role for biotic interchange in at least the mid-Cretaceous. Although no positive conclusions can be drawn from failed statistical tests, the absence of a repeated area signal for the Late Cretaceous leaves open the possibility that the original vicariance pattern was ultimately overwhelmed by dispersal or regional extinction. Nevertheless, our analyses provide the first statistically robust support for the hypothesis that Pangaeon fragmentation and the formation of epicontinental seas, during the Jurassic and Early Cretaceous, imposed a fundamentally vicariant pattern on dinosaurian evolution.

These results have implications for our understanding of dinosaur evolutionary and biogeographical history. For example, the apparent faunal similarity between the Late Jurassic Morrison and Tendaguru Formations of North America and Africa, respectively, has led many authors to suggest that these areas were still in contact during the Late Jurassic (Cox 1974; Galton 1977, 1982; Russell 1993; Upchurch 1995; Fastovsky & Weishampel 1996). Proposed dispersal between North America and Africa has involved routes via either Europe (Iberia–North Africa) or central and South America. The existence of these land connections, however, is contradicted by palaeogeographi-

cal evidence (Smith *et al.* 1994; Smith & Rush 1997). This problem has been created by the erroneous belief that biotic similarity indicates continuity of geographical areas. In fact, these faunal similarities are best explained by the vicariance event associated with the separation of North America and Africa during the Callovian.

The demonstrable presence of non-random biogeographical patterns in evolutionary trees has important implications for palaeobiogeographical research. To date, this field has been dominated by a ‘narrative’ approach, based either on direct observation of the fossil record or scenario building constrained by knowledge of phylogenetic relationships and distributions. Although these methods have proved useful in terms of hypothesis creation, they are ultimately severely limited with regard to hypothesis testing. The introduction of ‘time-slicing’ into cladistic biogeography represents an important advance because, as the current study demonstrates, significant area relationships may not be detected due to the phenomenon of pattern superposition.

The wealth of information concerning palaeogeography and evolutionary relationships, combined with the introduction of new biogeographical techniques, creates an opportunity to place palaeobiogeographical research on a more analytical and statistically robust footing. We would predict that the same area relationships should also have been imposed on the phylogenies of other terrestrial Mesozoic taxa. If future studies verify that the same vicariance patterns are widespread across many Mesozoic clades, Pangaeon fragmentation will provide a major unifying explanation for the distributions of taxa seen in the fossil record and today.

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