

# “Time”: the neglected dimension in cladistic biogeography?

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## Abstract

The value of temporal data has been widely recognised in historical biogeography. Cladistic biogeographic methods, however, have not formally incorporated “time”. A theoretical perspective suggests that area and biotic relationships will change in a complex “reticulate” manner through time. This is because the disappearance of geographic barriers (and the concomitant mixing of biotas) is likely to occur as frequently as barrier formation and vicariance. A reticulate biogeographic history will consist of a chronological series of incongruent distribution patterns. Any attempt to depict such a reticulate history using a cladistic topology will inevitably lead to interpretational error and ambiguity. Temporal data, however, may allow incongruent spatial relationships to be “teased” apart, and may, therefore, play a vital role in rigorous analytical biogeography. A simple method for integrating “time” into cladistic biogeography is proposed and tested using a data-set on dinosaur phylogeny and distribution. The results indicate that large biogeographic data-sets can contain several genuine, but incongruent, sets of area relationships that combine to obscure each other. The new method (“temporally partitioned component analysis”) is an effective means of exploring a data-set for such signals, and allows time-specific area relationships to be detected. The proposal that temporal data should play an integral role in cladistic biogeographic analysis has major implications for area cladogram interpretation, and also enhances the value of fossil evidence. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

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## 1. Introduction

Historical biogeography, by definition, deals with patterns in the spatial distributions of organisms. Macro-evolutionary patterns, including those manifested in biogeography, are propagated in time as well as space: that is, we might expect the geographic distributions of organisms to change through time. Historical biogeographers have not ignored “time”, but there have been surprisingly few attempts to formally integrate temporal data into rigorous analytical methods. This “neglect” is particularly evident in cladistic biogeography, perhaps reflecting the neontological origins of this discipline.

Historical biogeography contains wide-ranging and contrasting attitudes to the value of temporal data: is the latter an irrelevance, a useful additional constraint or an absolutely essential component of all biogeographic analyses? Few previous studies have addressed this question directly.

Here, therefore, we briefly review current attitudes toward the use of temporal data in biogeography. We then outline a theoretical perspective that supports the view that temporal data should play a key role in cladistic biogeographic analysis. A relatively simple method, which integrates temporal data into a cladistic biogeographic technique, is then proposed and applied in an analysis of dinosaurian distributions. Finally, the importance of temporal data is considered in terms of its implications for the accuracy and rigour of various biogeographic methods.

## 2. The role of “time” in historical biogeography

Rosen (1994) divided biogeography into “palaeobiogeography” and “neobiogeography”, dealing with fossil and extant taxon spatial distributions, respectively. Both of these fields have drawn upon a variety of different “methods”, including: (1) a “narrative” approach, in which biogeographic history is reconstructed on the basis of direct observation of spatial distributions; (2) phenetic biogeography, where the overall similarity of biotas is measured and

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used to infer relationships between areas; and (3) cladistic biogeography, in which the phylogenetic relationships among taxa are used to reconstruct geographic and/or biogeographic histories. The extent to which temporal data are incorporated into biogeographic studies, therefore, depends on the researcher's choices regarding sources of spatial data and analytical methodology.

### 3. Palaeobiogeography

It is quite feasible to study an ancient biogeographic pattern using information from only a single point in time. Inevitably, however, palaeobiogeography tends to have a temporal dimension; indeed, the ability to observe apparent changes in taxon distribution through time is one of the strengths of this field (Rosen, 1994). One problem, however, concerns the uncertainty surrounding the ability of the fossil record to accurately reflect the "true" spatial distributions of extinct taxa. An observed distribution pattern will be formed from both "presence" and "absence" data, but the latter are difficult to interpret in the fossil record. A taxon could be absent from an area because: (1) it never lived there ("genuine absence"); (2) it lived there at an earlier time but subsequently became extinct ("regional extinction"); or (3) it lived there but has not been found yet ("pseudo-absence"). This problem will be magnified further when a chronological series of ancient biogeographic distributions is used directly to reconstruct the history of areas and biotas. For example, suppose taxon X is found in area A at time  $t_0$ , and a closely related form, Y, is found in area B at the later time  $t_1$ . As Fig. 1 demonstrates, these distributions can be

interpreted in at least two ways: X, or a close relative, could have dispersed from A to B (when the barrier between these two areas disappeared) and then given rise to Y; or X and Y may display a vicariant pattern, in which case the temporal difference between these taxa would reflect missing data concerning the true stratigraphic range of Y. Despite this ambiguity, palaeobiogeographic hypotheses have been dominated by the "dispersal" interpretation (see, for example, Galton, 1977; Gayet et al., 1992; Sereno, 1999a), perhaps reflecting an implicit belief that "absence" in the fossil record can be treated as real data. Thus, although temporal data play an important role in palaeobiogeography, that role has often been to give "polarity" to an essentially narrative approach (Patterson, 1981: pp. 487–488). It is precisely this aspect of palaeobiogeography that has prompted the devaluation of temporal data (i.e. fossil taxa) displayed by many vicariance or cladistic biogeographers (Rosen, 1994, and see below).

Notwithstanding such reservations concerning "traditional" palaeobiogeography, temporal data remain vital in order to "tease" apart potentially different biogeographic patterns. This has led many palaeobiogeographers to examine their data as a series of temporally constrained samples (Rosen, 1988; Rosen and Smith, 1988; Grande, 1985; Cocks and Fortey, 1990; Beadle, 1991; Dhondt, 1992; Jablonski, 1993; Grande and Bemis, 1998). Perhaps the most rigorous and formalised attempt to utilise time in palaeobiogeography was introduced by Rosen (1988) and Rosen and Smith (1988) in the method known as "parsimony analysis of endemism" (PAE). Concerned about the drawbacks of the narrative approach, these authors proposed a method in which presence/absence data, for a wide range of taxa from

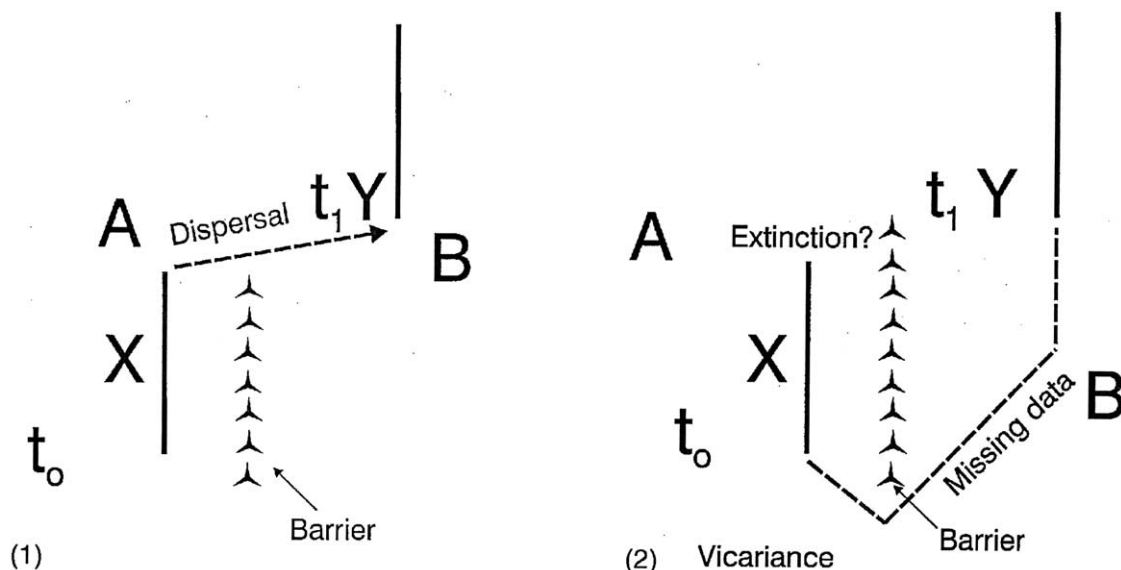


Fig. 1. An illustration of how the same combination of presence/absence data can be explained by alternative biogeographic hypotheses. In both (1) and (2), taxa X and Y have stratigraphic ranges commencing at  $t_0$  and  $t_1$ , respectively. X is only known from area A, and Y is only known from area B. A barrier separates A from B from  $t_0$  onwards, but disappears at  $t_1$ . In (1), X originates in area A and then disperses to B when the barrier disappears, where it then gives rise to Y. In (2), an ancestral taxon occupies A + B prior to  $t_0$ . At  $t_0$ , creation of the geographic barrier results in vicariant speciation and the appearance of two daughter species, one in A and one in B. The later appearance of Y in B is explained by a missing, or unsampled, portion of the fossil record in B.

a single time-plane, are analysed using a cladistic algorithm. Thus, areas are clustered together hierarchically for each time-plane, and observation of the results in chronological order yields information on area and biotic histories. The fact that “absences” are coded as ‘0’s (i.e. genuine absence) rather than ‘?’s (i.e. uncertainty) means that PAE is essentially a phenetic technique which builds “area phenograms” based on overall biotic similarities (Rosen and Smith, 1988). Nevertheless, the results of PAE suggest that biogeographic distributions change through time, and that consecutive area relationships are not always congruent with each other (see below).

In recent years, workers have started using cladistic techniques in palaeobiogeography. In particular, attention has focussed on the application of “Brooks parsimony analysis” (BPA) (Lieberman, 2000, and references therein) and “dispersal–vicariance analysis” (DIVA) (Ronquist, 1997; Sereno et al., 1998). All of these studies applied these methods to their entire taxon cladograms, without any evaluation of temporal distributions.

#### 4. Neobiogeography

Almost by definition, neobiogeography does not have a formal temporal component, because it focuses on the spatial distributions of extant taxa. As Rosen (1994) noted, however, neobiogeographers have frequently utilised palaeobiogeographic and palaeogeographic data in order to “test” hypotheses of how current distributions were formed. As in palaeobiogeography, the use of temporal data in neobiogeography has not been formally scrutinised in any detail; most attempts to use such data tend to be more narrative than analytical, largely because of the problems associated with the interpretation of “absence” discussed above.

During the past decade, the rapid rise of molecular phylogenetics has facilitated the development of new approaches in neobiogeography. A typical study (e.g. Noonan, 2000; Trewick, 2000; Cooper et al., 2001) first involves the use of molecular sequences to infer the phylogenetic relationships of a group of taxa. Statistical tests are then applied in order to determine whether the sequence evolution conforms to a “clock-like” model. If a molecular “clock” is supported, it can then be used to determine the relative divergence times between the various lineages. Ideally, the molecular “clock” is calibrated using either fossil taxa or a knowledge of palaeogeography to date one or more of the nodes, allowing the absolute ages of all nodes to be inferred. These temporal and phylogenetic data can then be combined with the spatial distributions of the terminal taxa to reconstruct biogeographic history and “test” hypotheses of dispersal and/or vicariance. For example, consider three taxa, X, Y and Z, with the relationships (X (Y, Z)), which are endemic to the areas A, B and C, respectively (Fig. 2). Suppose that a molecular “clock” indicates that the diver-

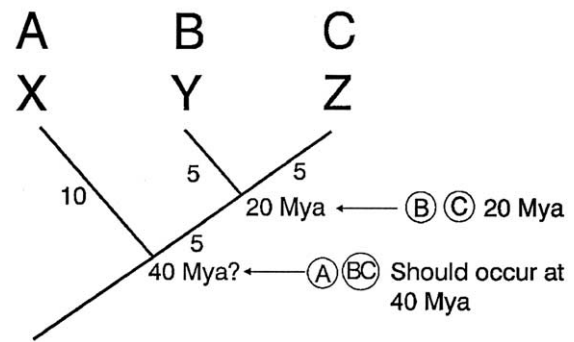


Fig. 2. An example of the use of temporal data in molecular biogeography. Taxa X, Y, Z are inferred to have the phylogenetic relationships shown, based on molecular sequence data. The number of sequence changes along each branch is shown, and indicates that the molecular evolution conforms to a “clock”-like model. Palaeogeographic data indicate that the separation of areas B and C occurred 20 million years ago (Mya), allowing the molecular “clock” to be calibrated. This, in turn, allows the divergence time for X from YZ to be estimated at 40 Mya. The cladogenetic event X/YZ can be interpreted in terms of vicariance caused by the separation of area A from B + C, provided there is correspondence between the timings of these two events. See text for further details.

gence time (relative to the present), for the separation of the X and YZ lineages, is 10 time units, and the divergence time for the separation of the Y and Z lineages is 5 time units. Suppose also that we know that areas B and C separated from each other 20 million years ago (Mya). We can now calibrate the molecular “clock” and infer that the cladogenetic separation between the X and YZ lineages occurred 40 Mya. At this point, the researcher may have a choice in terms of how to proceed. If the age of the geographic event that separated A from BC is known, this can be compared to the estimated divergence time for X from YZ: this provides a “test” of both the “clock-like” nature of the molecular evolution and the hypothesis that cladogenesis was caused by area fragmentation. If the timing of the cladogenetic and area fragmentation events is different, taxon dispersal may be invoked to explain the observed biogeographic distributions (Noonan, 2000; Trewick, 2000; Cooper et al., 2001). Alternatively, if palaeogeographic data are lacking concerning the timing of the separation of A from BC, then the molecular biogeographic approach can be used to supply an estimate of the age of this geographic event. Clearly, molecular phylogenies represent an important new source of temporal data in the context of historical biogeography. However, it should be remembered that the linkage between temporal and spatial data is somewhat indirect: the prior existence of a taxon at a particular locus in time and space is inferred in molecular biogeography, whereas it can be directly observed from fossil evidence. We return to the usage of temporal data by molecular studies in Section 7.

#### 5. Cladistic versus reticulate systems

Vicariance biogeography is based on a simple fundamental premise (Nelson and Platnick, 1981; Rosen, 1978; Wiley,

1980; Patterson, 1981): when geographic barriers form, they have the potential to divide once continuous biological populations into two or more isolated sub-populations. Since isolation, by definition, prevents gene flow, these sub-populations are free to evolve in different directions, eventually resulting in allopatric speciation. This provides a clear linkage between geographic and cladogenetic events. Furthermore, the emplacement of a barrier will potentially affect many different species simultaneously, so that the same set of area relationships is imposed across many different clades. Such a “vicariance” pattern can then be detected statistically. Dispersal, in contrast, is often viewed as a biogeographic process that affects particular species in different ways at different times: this is because the ability of organisms to disperse across geographic barriers (i.e. “jump” dispersal) will depend on factors peculiar to individual species (e.g. environmental tolerances, locomotor ability, etc.). Thus, vicariance is often regarded as a “coherent” pattern-forming process, whereas dispersal lacks coherence across different clades and, therefore, tends to destroy or obscure vicariance patterns (Croizat, 1958; Craw, 1983). If this set of underlying assumptions is correct, then area and biotic histories will tend to have a branching “tree”-like structure that can be adequately represented using a cladistic topology.

Recent work (Lieberman and Eldredge, 1996; Lieberman, 1997, 2000; Hunn and Upchurch, 2001), however, has suggested that there is a form of coherent dispersal that can impose a repeated set of area relationships on taxon cladograms. There is no a priori reason to assume that area coalescence (i.e. the removal of barriers between areas) occurs any less frequently than area fragmentation. Indeed, our knowledge of palaeogeographic history indicates that area coalescence is common. When areas coalesce, there will be an opportunity for the previously isolated biotas to mix and expand their ranges to include the newly available areas. This “range expansion” is, in fact, a key assumption underlying vicariance: organisms must disperse across an ancestral area in order to be affected by subsequent vicariance events. Furthermore, the removal of a barrier between two areas potentially allows many different species to change their area relationships in a similar way and at the same time. This phenomenon has been called “geodispersal” (Lieberman, 2000), though here we prefer the term “mass coherent dispersal” (MCD). Area coalescence, and the concomitant MCD, therefore, means that the histories of areas and biotas will have a reticulate rather than branching structure, raising the question as to how well cladistic biogeographic techniques will be able to accurately analyse and depict a reticulate system.

Let us consider the possible effect of an instance of area coalescence on the topology of an area cladogram. Fig. 3 shows a hypothetical history for the areas A, B and C. At time  $t_0$ , ABC forms a single continuous area. At time  $t_1$ , A becomes isolated from BC by the formation of a barrier. At time  $t_2$ , B and C become isolated from each other. Finally,

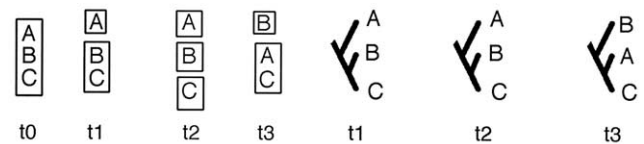


Fig. 3. (Left) A hypothetical history for the areas A, B and C, from time  $t_0$  to  $t_3$ . (Right) The expected area cladograms for times  $t_1$  to  $t_3$ . See text for details.

at time  $t_3$ , A and C come into contact. Fig. 3 also shows the area cladograms we would expect to be generated at each point in this history. At  $t_2$ , taxa from areas B and C should be more closely related to each other than they are to taxa from A; but at  $t_3$ , taxa from A and C should be more closely related to each other than they are to taxa from B. As a result, area relationships change in a non-branching (i.e. non-hierarchical) way when we compare the area cladogram topologies for  $t_2$  and  $t_3$ . Thus, provided MCD occurs, area relationships will change in a non-hierarchical way every time there is an instance of area coalescence. Clearly, this will create a reticulate area and biotic history that cannot be accurately depicted in any one area cladogram. Indeed, the only way to fully and unambiguously describe this history is to have two area cladograms, one for  $t_2$  and one for  $t_3$ , and compare them in chronological sequence. Note, also, that any attempt to analyse a data-set that contains phylogenetic and distribution data from  $t_2$  and  $t_3$  will effectively combine two incongruent patterns, potentially resulting in confusion and the failure to detect any clear, statistically supported, signal.

From this simple theoretical perspective, it is clear that temporal data could play a major role in cladistic biogeographic analysis, since such data will be necessary if we wish to sample the different, incongruent, area relationships that occur at different time periods. A similar, though less explicit, line of reasoning was followed by Grande (1985). Grande suggested that biogeographic history is likely to be “complex” (i.e. reticulate), and noted that such patterns would not be easily or accurately resolved using a cladistic biogeographic technique. This problem could be alleviated, however, if time-specific samples of fossils are used to determine the prevalent biogeographic relationships for a series of points through time. Examination of these different patterns, in chronological order, would then reveal the complex biogeographic history (Grande, 1985).

In short, the work of Grande (1985), Lieberman (1997, 2000) and Hunn and Upchurch (submitted) suggests that the fundamental assumptions of cladistic biogeography are too narrow because of the emphasis on vicariance being the sole process capable of producing a coherent set of repeated area relationships. Two hypotheses arise from this new theoretical perspective: (1) biogeographic history has a reticulate rather than branching structure; and (2) temporal data can be used to “tease” apart the superimposed incongruent distribution patterns caused by this reticulate history. Below, we



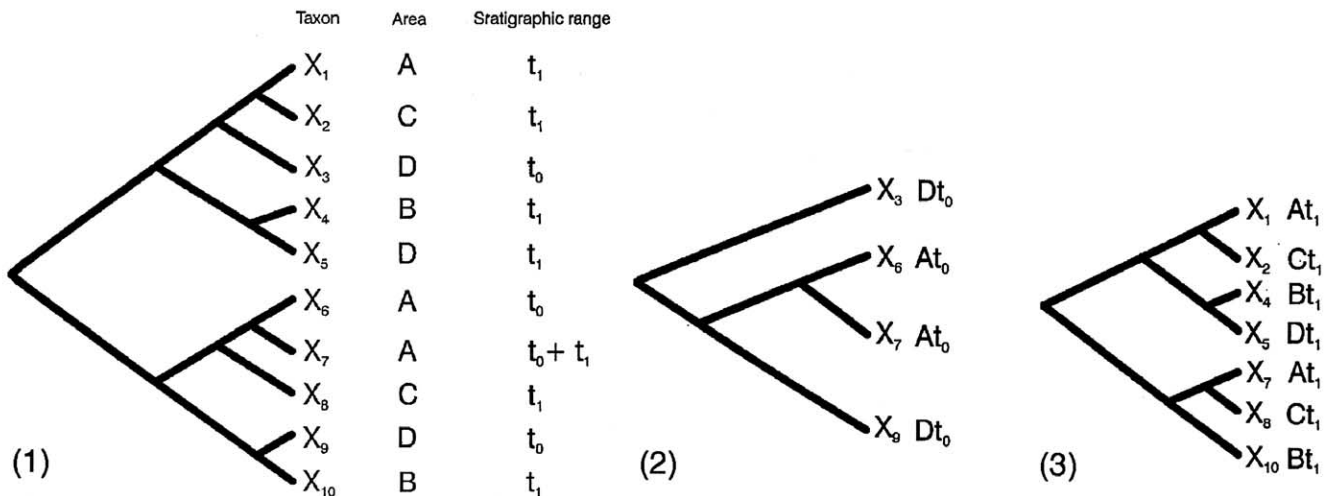


Fig. 4. A schematic representation of how to temporally partition a taxon cladogram. (1) The original taxon cladogram contains 10 taxa (X<sub>1</sub>-X<sub>10</sub>) from four areas (A-D) and two time periods (t<sub>0</sub> and t<sub>1</sub>). (2) and (3) are the temporally partitioned cladograms, containing only taxa from t<sub>0</sub> and t<sub>1</sub>, respectively. See text for details.

present the first explicit tests of these hypotheses, based on a cladistic biogeographic analysis of dinosaurian distribution.

## 6. An implementation of temporal partitioning

### 6.1. Temporally partitioned taxon cladograms

We have developed a simple method, known as “temporally partitioned component analysis” (TPCA), which incorporates temporal data into a conventional cladistic biogeographic technique. Component analysis (Nelson and Platnick, 1981; Page, 1988) has been implemented in the computer programs Component (Page, 1993) and TreeMap (Page, 1995). This method has two stages: (1) “optimal area cladograms” (OACs) are found by determining which area relationships provide the “best” (under some designated optimality criterion) explanation for the spatial distributions observed in the taxon cladogram; and (2) a randomisation test is then used to determine whether the degree of fit between area and taxon cladogram topologies is greater than would be expected by chance (Page, 1991). TPCA adds an extra stage prior to the application of CA itself: the taxon cladogram is temporally partitioned by deleting all taxa that lie outside a particular designated time-range (Fig. 4). It should be noted that taxon deletions take place after phylogenetic analysis, not before. Once the taxon cladogram has been temporally partitioned, it can then be subjected to CA, so that the analysis is constrained to find only the biogeographic pattern that existed during the particular designated time-range. Since we do not know, a priori, the number or duration of the different biogeographic patterns contained within the total data-set, it is recommended that temporal partitioning be viewed as a heuristic approach that “explores” the data for possible signals. In

other words, a biogeographer should use a variety of different temporal partitions, as illustrated in the example below.

### 6.2. The dinosaurian data-set

Upchurch et al. (2002) created a biogeographic data-set for dinosaurian taxa, consisting of the phylogenetic relationships and stratigraphic/geographic distributions for approximately 150 genera (Fig. 5). The stratigraphic age of each taxon is identified to Standard European Stage level if possible. Each taxon is assigned to one or more of eight continental areas, such as “North America”, “Antarctica”, etc. These areas were selected so that the possible impact of Pangaeian fragmentation, on dinosaurian distributions, could be observed. Temporal partitioning was applied using major stratigraphic divisions as the boundaries between different time-ranges. Thus, the cladograms in Fig. 5 were “pruned” so that they contained, for example, only taxa from the “Jurassic” or “Early Cretaceous”. Each “pruned” cladogram was then subjected to a conventional CA, and the resulting OACs were then evaluated using the randomisation test available in TreeMap (Page, 1995) (see Table 1).

### 6.3. Results

As Table 1 shows, most analyses produced only one or two OACs, but the majority of these topologies failed the randomisation tests ( $P > 0.05$ ). There are many reasons why no apparent biogeographic signal is detected: (1) there could be errors in the taxonomy or phylogenetic relationships of dinosaurs that obscure genuine area relationships; (2) patterns may have been obscured by non-coherent, “jump”, dispersal events in which individual taxa cross geographic barriers; (3) statistically significant patterns may not be detectable because of extinction and/or missing data; (4) the

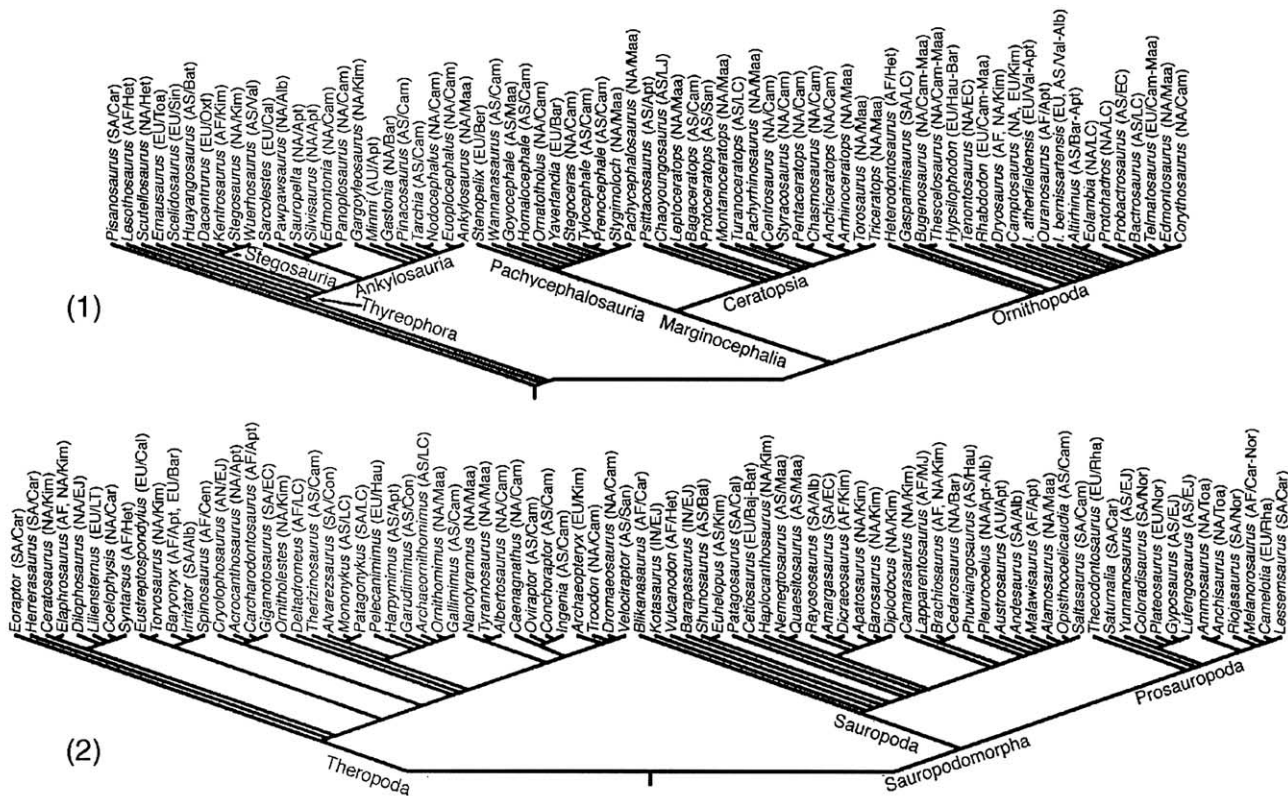


Fig. 5. Two cladograms, (1) Ornithischia (2) Saurischia, showing the phylogenetic relationships and geographic/stratigraphic ranges for Dinosauria (based on Upchurch et al., 2002). Sources for these cladistic analyses are: Dinosauria as a whole (Sereno, 1997, 1999b); Thyreophora (Lee, 1996; Sullivan, 1999); Marginocephalia (Sereno, 2000); Ornithomimipoda (D.B. Norman, unpublished data); Theropoda (Barsbold and Osmólska, 1990; Barsbold et al., 1990; Novas, 1997; Sereno, 1999c; Sereno et al., 1996, 1998); Sauropodomorpha (Upchurch, 1998). The main source for stratigraphic/geographic ranges is Weishampel (1990), with revisions based on more recent literature pertaining to each taxon and personal communications from P.M. Barrett (2000–2001). Abbreviations for geographic areas: AF, Africa; AS, Asia (excluding India); AN, Antarctica; AU, Australia; EU, Europe; IN, India; NA, North America; SA, South America. Abbreviations for stratigraphic ranges: Aal, Aalenian; Alb, Albanian; 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. Note that *I. atherfieldensis* and *I. bernissartensis* are species of the genus *Iguanodon*.

selection of the eight areas of endemism may not correspond to the true palaeogeography of the times concerned; (5) the larger time-slices may have failed the randomisation test because they contain several conflicting patterns (see below); and (6) there may simply be no pattern to detect (i.e. dinosaurian distributions during the relevant time-periods were not shaped by sea-level changes and tectonic motions at the continental level). It should be noted, therefore, that randomisation tests are “one-sided” or “asymmetrical”: that is, a statistically significant result indicates the existence of a non-random pattern, but a statistically insignificant result is ambiguous because it can reflect the non-existence of pattern, the obliteration of a pattern or the conflict between incongruent patterns.

Three time-ranges, the Middle and Late Jurassic and Early Cretaceous, yield OAC topologies that pass the randomisation test ( $P = 0.0096–0.012$ ), indicating the presence of a statistically significant level of area relationship repetition across the dinosaurian clades (Table 1). The statistically supported OACs are shown in Fig. 6. Note that

these OACs do not contain all eight of the original designated continental areas: one by-product of temporal partitioning, of course, is that smaller time-ranges may contain taxa that do not occupy all the areas available in the total data-set.

**7. Discussion**

*7.1. The implications of the TPCA results for cladistic biogeography*

The results outlined above have implications for dinosaurian biogeographic history and Mesozoic palaeogeography, but these are discussed in detail elsewhere (Upchurch et al., 2002). Here, we are concerned with more general issues, such as what the results of TPCA reveal about the importance of temporal data in cladistic biogeographic analysis.

**Table 1**  
 Summary of the results of TPCA of the dinosaurian data-set shown in Fig. 5. The optimal area cladogram topologies are shown using standard parenthetical notation. Areas and stratigraphic ranges are denoted by the same abbreviations listed in the legend for Fig. 5. The *P* values for each optimal area cladogram were obtained via reconciliation with 10 000 randomised versions of the taxon cladograms (see Page, 1991, 1993, 1995). The stratigraphic units and boundaries employed here are based on the Geological Society of America Geological Time Scale (Geological Society of America, www.geosociety.org 1998). Asterisks mark “general area cladograms”, i.e. Nelson consensus trees (Nelson and Platnick, 1981), that have been constructed using multiple optimal area cladograms

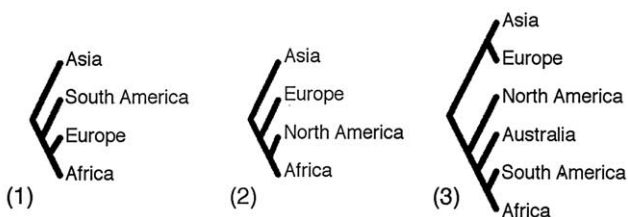
Time-range	Optimal area cladogram topology	<i>P</i> value
Mesozoic (Car–Maa)	Saurischia (IN (AU (AN (AF (SA (EU (AS, NA))))))) Ornithischia *(SA (AU (AF (EU (AS, NA))))))	0.98 0.99
Late Triassic (Car–Rha)	*(AF (NA (EU, SA)))	0.81
Jurassic (Het–Tth)	(IN (AS (SA (EU (AF, NA)))))	0.23
Early Jurassic (Het–Toa)	((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)))	0.0097
Cretaceous (Ber–Maa)	(AU (AF ((AS, SA), (EU, NA))))	0.82
Early Cretaceous (Ber–Alb)	(AU (AF (EU (NA (SA, AS)))))	0.82
Late Cretaceous (Cen–Maa)	((AS, EU), (NA (AU (AF, SA)))) (AF (SA (AS (EU, NA))))	0.012 0.99

(1) The results of TPCA show that all of the more extensive time-ranges (e.g. “Mesozoic”, “Jurassic”, “Cretaceous”, etc.) fail to produce a statistically significant OAC. Normally, such failures would be interpreted as meaning that the data contain no detectable signal, either because a genuine biogeographic pattern has been degraded by “noise” (e.g. dispersal, missing data or phylogenetic error) or because no pattern was imposed on the taxon phylogeny in the first place. However, the fact that some of the shorter time-ranges (“Middle” and “Late Jurassic”, and “Early Cretaceous”) pass the randomisation test suggests an additional explanation: statistical failure of the larger time-ranges could have been caused by the analysis of data that contain several genuine, but incongruent, distribution patterns. One of the key benefits of applying a temporal constraint in a cladistic biogeographic analysis, therefore, is that it enhances the probability that statistically significant area relationships will be detected.

(2) The statistically significant OACs for the Middle Jurassic, Late Jurassic and Early Cretaceous (Fig. 6) have partially incompatible topologies. For example, the Late Jurassic OAC places Europe closer to North America + Africa than to Asia, whereas the Early Cretaceous OAC clusters Europe and Asia as “sister-areas”. This represents a non-hierarchical change in area relationships through time, suggesting a possible area coalescence event (and MCD of dinosaurian taxa) involving Europe and Asia during the Early Cretaceous (N.B. in this case, there is

geological evidence supporting area coalescence: see Upchurch et al., 2002). We cannot explain non-hierarchical shifts in area relationships in terms of vicariance. Thus, such a result provides direct support for the hypotheses that MCD can act as a pattern-forming process, and that biogeographic histories can, therefore, display a reticulate structure.

(3) The MCD phenomenon has profound implications for OAC interpretation. If we only have access to one OAC, then it is no longer possible to interpret each of its nodes in terms of area fragmentation and vicariance: this is because area coalescence and MCD provide an equally plausible explanation for the observed area relationships. Such ambiguity may be removed if we compare the area cladogram with independently derived palaeogeographic data. For example, in Fig. 3, we “know” that areas B and C separate from each other during  $t_2$ , so the node linking B and C in the area cladogram for that time can be plausibly interpreted as a vicariance event associated with area fragmentation. There will, however, be occasions when palaeogeographic data are unavailable, or we wish to test palaeogeographic hypotheses using biogeographic patterns. Furthermore, Hurn and Upchurch (submitted) demonstrate that the “deeper” nodes in an area cladogram become ambiguous even when palaeogeographic data are available. Under these circumstances, we would like to be able to interpret area cladograms accurately without the aid of extrinsic sources of data. This can be achieved provided we have access to two or more consecutive OACs, so that the evolution of area relationships through time can be assessed.



**Fig. 6.** Statistically significant optimal area cladograms, obtained from the TPCA of the dinosaurian data-set, for the: (1) Middle Jurassic; (2) Late Jurassic; and (3) Early Cretaceous. See text for details.

## 7.2. Fossil taxa in historical biogeography: irrelevant or indispensable?

Although palaeogeography and molecular “clocks” have an important role to play in providing historical biogeography with temporal data, fossil taxa remain the most significant source of such information. However, the manner in which fossil taxon distributions should be interpreted, and



their value for historical biogeographic analysis, has been a subject of considerable debate and controversy. Some neo biogeographers have expressed doubts that fossil taxa can contribute usefully to biogeographic analyses, especially with regard to the investigation of extant taxon distributions. Croizat (1964: p. 715) wrote: “Fossil life cannot of course genuinely contradict living life.” Fossil taxa were largely ignored during the early development of vicariance biogeography (Rosen, 1976, 1978; Nelson and Platnick, 1981). When fossils were discussed by vicariance biogeographers, it was normally to associate them with “dispersal biogeography” and the untestable concept of “centres of origin”. Thus, Patterson (1981: p. 447) wrote “...fossils are of subsidiary importance in vicariance biogeography, but of cardinal importance in dispersal biogeography”, and (ibid, p. 488) “That fossils can contradict Recent distributions is considered true only by dispersal biogeographers, who expect that fossils can localise centres of origin and hence directions of dispersal.” The prime reason for this attitude seems to stem from an appreciation that we do not know how faithfully the fossil record reflects true spatial and temporal distributions (see above). Patterson (1981: p. 488) argued “If it is agreed that the fossil record is incomplete, then fossils cannot decisively contradict evidence from Recent distributions. This is assumed to be true in vicariance biogeography.” As a result, vicariance biogeographers usually advocated the establishment of vicariance patterns based solely on extant taxa, with the distributions of fossil taxa being explained, a posteriori, in the light of these patterns. Such views have not been well received by most palaeobiogeographers and those who consider dispersal to be an important and detectable process (see Briggs, 1996: pp. 12–14). As a result, palaeobiogeographers have been slow to adopt cladistic biogeographic methods. Indeed, the first applications of methods such as BPA (Lieberman, 2000), DIVA (Serenó et al., 1998) and CA (Upchurch et al., 2002), to palaeontological data, have all occurred very recently. But it would be unfair to represent vicariance biogeographers as regarding fossils as having absolutely no value in biogeographic studies (see Grande (2000) for a general discussion of Patterson’s views on the significance of fossils). Patterson (1981: p. 489) noted that fossil taxa could contribute to historical biogeography in two important ways: (1) identification of changes in biogeographic patterns caused by regional extinction events; and (2) provision of minimum ages for the occupation of certain areas by particular clades. Also, Humphries and Parenti (1986: p. 60) stated “We see no special role for fossils in cladistic biogeography except to help in rejecting geological explanations for a particular pattern.”

The case for a more “active” role for fossils in historical biogeography has been stated by many workers (Grande, 1985; Rosen, 1994; Grande and Bemis, 1998). As outlined above, the most important point was raised by Grande (1985), though the significance of his argument seems to

have been completely overlooked subsequently by most cladistic biogeographers.

The debate concerning the role of fossils in historical biogeography can now be viewed in the light of the TPCA results outlined above. Clearly, Patterson (1981) was correct to argue that the distribution of fossil taxa cannot “contradict” patterns observed among living taxa: any incongruence between past and present patterns can always be explained in terms of “jump” dispersals, missing data or even MCD. In other words, extant taxa provide the most reliable estimate of current area relationships, and this pattern cannot be challenged or modified by information from fossil taxa. However, although we accept that the “extant pattern” remains unaffected by fossil data, we suggest that the interpretation of the processes responsible for that pattern will depend heavily on information from earlier time-planes. Patterson and others were not aware of the effect of MCD on OAC topology, and, therefore, overlooked the fact that area relationships must be evaluated in the light of their temporal context. This new perspective has several implications: (1) extant area relationships can only be interpreted unambiguously when compared to the immediately preceding distribution pattern; and (2) the extent to which extant area relationships reflect past events will decrease as those events increase in age relative to the present. The suggestion that fossils cannot overturn biogeographic hypotheses established on the basis of extant taxa is based on the view that area and biotic histories display a branching pattern that extends back in time to the point when all relevant areas formed a single unit. Under such circumstances, fossil taxa should indeed display distributions that largely accord with the vicariance pattern observed during the present. The existence of a reticulate biogeographic history, however, would negate this view, because distributions from the current time-plane may retain little of the hierarchical structure that existed prior to the most recent area coalescence events. The distribution patterns of fossil taxa are, therefore, highly relevant to determining the processes and events that have shaped area relationships among living taxa. Furthermore, the suggestion that vicariance patterns should be established using extant taxa, and that fossils should then be “slotted” into this pattern, appears flawed for two reasons. First, the area relationships of living taxa could have been produced by a combination of vicariance and MCD. Second, there is no guarantee that the fossil taxa had the same area relationships as living forms. This means that caution is required when the area relationships of extant forms are used to infer ancient biogeographic and palaeogeographic events: the greater the temporal difference between the present and the events concerned, the more we should expect to see interpretational errors and ambiguities.

We suggest, therefore, that past critiques of the value of fossils in historical biogeography have taken too severe a stance. Fossil taxa do have a special role to play in historical biogeography (including neobiogeography), because they



represent the only direct source of information on past area relationships. Even when the distributions of extant taxa form the focus of biogeographic investigation, it will be useful (or perhaps even essential) to use fossil data to establish the area relationships that immediately preceded those of the present. Without fossils, cladistic biogeography becomes a highly restricted and somewhat ambiguous discipline that must rely heavily on knowledge of palaeogeography in order to interpret its results.

## 8. Conclusion

A reappraisal of the fundamental premises of cladistic biogeography suggests that area coalescence and MCD should be treated on an equal footing with area fragmentation and vicariance. Simple theoretical considerations indicate that MCD is capable of producing repeated area relationships imposed across many different clades. This, in turn, means that biogeographic history can have a reticulate structure, and so a single area cladogram cannot be interpreted without ambiguity. Grande (1985) predicted that this problem could be alleviated by analysing biogeographic patterns restricted to a series of different time-planes. Implementation of this method has proved to be a useful way of “teasing” apart consecutive incongruent area relationships present in dinosaurian distributions. Since fossil taxa provide the only means for identifying simultaneously the temporal and spatial loci of evolutionary lineages, their importance for neobiogeography is greatly enhanced.

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