Crocodyliform biogeography during the Cretaceous: evidence of Gondwanan vicariance from biogeographical analysis

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Explanations of the distributions of terrestrial vertebrates during the Mesozoic are currently vigorously contested and debated in palaeobiogeography. Recent studies focusing on dinosaurs yield conflicting hypotheses. Dispersal, coupled with regional extinction or vicariance driven by continental break-up, have been cited as the main causal factors behind dinosaur distributions in the Mesozoic. To expand the scope of the debate and test for vicariance within another terrestrial group, I herein apply a cladistic biogeographical method to a large sample of Cretaceous crocodyliform taxa. A time-slicing methodology is employed and a refinement made to account for the divergence times of the analysed clades. The results provide statistically significant evidence that Gondwana fragmentation affected crocodyliform diversification during the Mid–Late Cretaceous. Detection of a vicariant pattern within crocodyliforms is important as it helps corroborate vicariance hypotheses in other fossil and extant groups as well as furthers the move towards more taxonomically diverse approaches to palaeobiogeographical research.

Keywords: crocodyliforms; Cretaceous; palaeobiogeography; vicariance; tree reconciliation analysis; Gondwana

1. INTRODUCTION

The relative roles that vicariance and dispersal have played in shaping the biogeographical patterns seen during the Mesozoic remain controversial, owing in large part to the poor understanding of the biogeographical histories of most terrestrial vertebrate clades living at the time. While some modern biotas, such as *Nothofagus* (Swenson *et al.* 2001), ratites and other neornithine birds (Van Tuinen *et al.* 1998; Cracraft 2001) and fishes (cichlid fish (Sparks 2004); and killifish (Murray & Collier 1997)) suggest that vicariant processes may have been significant, ambiguity from fossil data persists (also see Sanmartín & Ronquist 2004). Failures to uncover palaeobiogeographical patterns and/or disagreements among workers on the interpretation of those patterns that are recovered are prevalent and stem, in part, from methodological deficiencies and dataset size (Upchurch *et al.* 2002).

Palaeobiogeographical analysis has consisted predominantly of narrative approaches (Cox 1974; Buffetaut & Taquet 1979; Colbert 1984; Buffetaut & Rage 1993; Upchurch 1995; Gasparini 1996; Sereno *et al.* 1996, 2004; Pol *et al.* 2002). Generally, these methods are based on either a literal reading of fossil distributions or scenario construction constrained by phylogenetic data. Although effective for hypothesis building, this yields scenarios that are difficult to evaluate for consistency with the biogeographical data. Cladistic biogeographical methods provide an alternative, analytically rigorous means of inferring historical patterns. These methods, coupled with statistical and topological evaluation of the recovered biogeographical patterns, facilitate comparison of patterns between different biotas and different analyses. Most analytical studies of Mesozoic palaeobiogeography have been taxonomically limited, with attempts focused primarily on

dinosaurian clades (Cox 1974; Galton 1977; Colbert 1984; Le Loeuff *et al.* 1992; Russel 1993; Le Loeuff & Buffetaut 1995; Upchurch 1995; Fastovsky & Weishampel 1996; Sampson *et al.* 1998; Sereno *et al.* 1998, 2004; Pereda-Suberbiola & Sanz 1999; Pérez-Moreno *et al.* 1999; Upchurch *et al.* 2002). Moreover, few comparisons between fossil taxa can be made, owing to the paucity of analytical biogeography work on other groups (though see Buffetaut & Taquet 1979; Buffetaut & Rage 1993; Gasparini 1996; Krause & Grine 1996; Krause *et al.* 1999; Krause 2001; Pol *et al.* 2002). Dinosaur palaeobiogeographical work has led to a wealth of biogeographical hypotheses, many proposing continent-level vicariance processes as the dominant causal factor (Milner & Norman 1984; Russel 1993; Sampson *et al.* 1998; Upchurch *et al.* 2002). Sereno (1997, 1999) and Sereno *et al.* (1998, 2004) have contested these claims, suggesting that current dinosaur data does not satisfy the minimal conditions necessary to be interpreted as vicariance and therefore cannot reject a ‘null’ scenario in which dispersal and regional extinction are the driving factors. However, a cladistic biogeographical analysis by Upchurch *et al.* (2002) indicates that at least for portions of the Mesozoic, dinosaur distributions are consistent with vicariant origins.

Crocodyliform phylogeny indicates a late Gondwanan division among many of its constituent clades and therefore would be subject to any biogeographical events occurring and affecting other groups at the time (e.g. dinosaurs). Additionally, crocodyliforms possess many of the same attributes that make dinosaurs ‘an almost ‘ideal’ case study in Mesozoic biogeography’ (Upchurch *et al.* 2002, p. 613)—namely high diversity, widespread geography and a largely terrestrial habit, and thus represent an intuitive next step in examining Mesozoic palaeobiogeography.

Figure 1. Temporally calibrated portion of taxon-area cladogram of crocodyliform taxa. The shapes above the names denote the area in which the taxon occurs. Thickened lines are observed ranges, with thin lines marking ghost lineages inferred from phylogeny.

Unfortunately, crocodyliform biogeography remains ambiguous, with much of the work drawing attention to faunal similarities between continents (Buffetaut & Taquet 1979; Buffetaut & Rage 1993; Gasparini 1996; Buckley & Brochu 1999; Pol *et al.* 2002), but having yet to apply rigorous methods and statistical evaluation. The present study now considers the crocodyliform data from a cladistic biogeographical perspective. A phylogeny of 29 crocodyliforms (figure 1) was examined using 'tree reconciliation analysis' (TRA)—a method that tests for the presence of repeated patterns of area relationships (Page 1988, 1990a, 1993, 1994a,b; see also Hunn & Upchurch 2001). Evaluation of the resultant pattern can indicate the presence of a vicariant biogeographical signal (Nelson & Platnick 1981; Page 1988).

2. MATERIAL AND METHODS

The philosophy of cladistic biogeography has been discussed in detail by numerous authors (Nelson & Platnick 1981; Patterson 1981; Grande 1985; Page 1988, 1994a; Lieberman 2000; Hunn & Upchurch 2001; Upchurch & Hunn 2002; Upchurch *et al.* 2002) and thus will not be covered here. TRA was conducted on the data shown in figure 1. A time-slicing protocol was adapted from that described by Upchurch *et al.* (2002) and a refinement made in which time-slicing pruned not only the taxa absent during the time-slice, but also those taxa that did not diverge during the interval (Turner 2003). This refinement accounts for divergence timing in cladistic biogeographical analysis, thus incorporating a crucial data source necessary for constraining patterns of vicariance (Grande 1985; Page 1990b). A pattern of distributions may appear to be explained by vicariance, but if the divergence times of the clade in question do not coincide with the timing of a

separation event, then a hypothesis of vicariance is only poorly supported.

The crocodyliform phylogeny was 'time-sliced' for three different intervals (figure 2); the first time-slice (Late Jurassic–Late Cretaceous: figure 2a) incorporates the entire crocodyliform phylogeny, the second time-slice (Late Jurassic–Early Cretaceous: figure 2c) incorporates the early biogeographical history of the clade, and the third time-slice (Mid–Late Cretaceous: figure 2e) incorporates the time-frame in which most of the Gondwanan divisional events are proposed to have occurred (Smith *et al.* 1994; Smith & Rush 1997; Scotese 1998; Hay *et al.* 1999). Searches for the optimal area cladogram were conducted in COMPONENT, v. 2.0 (Page 1993). Randomization tests, which determine the probability that the observed biogeographical pattern could have occurred by chance alone, were run using TREEMAP's 'randomize parasite tree' function with 10 000 random topologies generated (Page 1994a, 1995).

Topological sensitivity and taxon-sampling effects were explored for the Mid–Late Cretaceous time-slice using sequential pruning and addition (grafting) protocols implemented in PRUNE (J. A. Callery, A. H. Turner and N. D. Smith, unpublished software). First, taxa were sequentially pruned to yield the set of all possible $n - 1$ trees (where n equals the number of taxa present in the original taxon cladogram). Subsequently, two randomly selected taxa are pruned. This is repeated 100 times to approximate the range of $n - 2$ trees. The frequencies at which these data recover the optimal area relationships are then recorded. These data represent an asymmetrical test; a high recovery percentage using this index is informative and indicates a robust and redundant pattern insensitive to any given taxon's presence, while a low value is equivocal, i.e. sensitivity of a pattern to the presence of certain taxon does not lessen the validity of that pattern.

Figure 2. Results of TRA on various time-sliced crocodyliform cladograms and randomization test for (a,b) the Late Jurassic–Late Cretaceous time-slice, (c,d) Early Cretaceous time-slice, and (e,f) Mid–Late Cretaceous time-slice. Histograms (b, d, f) show degree of congruence between the number of codivergences present in the time-sliced cladograms and the 10 000 randomized versions of the original taxon cladogram. The highlighted arrow marks the number of codivergence events implied by the optimal area cladogram. (a, c, e) Optimal area cladogram topologies for the three time-slices in the analysis.

Next, a set of $n+1$ trees is generated for every area in the analysis to test the current signal against potential future sampling. Each of the $n+1$ sets contain the complement of all possible tree topologies incorporating a hypothetical novel taxon. In this case, three sets were generated. As before, the frequencies at

which these data recover the optimal area relationship are then recorded. Unlike the previous test, this test is symmetrical; thus a high recovery percentage denotes a robust signal insensitive to taxon-sampling failure, while low values indicate a signal sensitive to future sampling.

The crocodyliform cladogram used in the analysis was selected from one of the 19 most parsimonious trees, which varied little from the strict consensus tree of a phylogenetic analysis of 29 geographically widespread crocodyliform taxa and 127 morphological characters (see electronic Appendix A for further discussion of phylogenetic analysis, taxon sampling and tree selection). The preferred topology was selected because it maximizes the conflict in biogeographical signal among the crocodyliform clades. It therefore serves as a conservative test as it maximizes the chance of failure in detecting a repeated biogeographical pattern. It should be noted, however, that all of the most parsimonious trees recover the same biogeographical pattern. Geographical and stratigraphic ranges for the taxa were obtained directly from the literature. All nexus files are available from the author upon request.

3. RESULTS AND DISCUSSION

(a) *Optimal area cladograms*

TRA of the crocodyliform data recovers a single optimal area cladogram for each of the three time-slices (figure 2*a,c,e*). Each of the three area cladograms shows the same relationships between the areas in common. Two of the phylogenies passed randomization tests: the large Late Jurassic–Late Cretaceous time-slice ($p = 0.0017$; figure 2*b*) and the Mid–Late Cretaceous time-slice ($p = 0.0012$; figure 2*f*). The Late Jurassic–Early Cretaceous time-slice failed a randomization test ($p = 0.1020$; figure 2*d*). That two analyses passed the randomization test indicates that the data for these biogeographical patterns are highly unlikely to have arisen by chance alone. Limited taxon sampling in the Late Jurassic–Early Cretaceous probably contributed to failure of the randomization test. It should be noted, however, that this failure only indicates an absence of evidence of a signal and should not be interpreted as evidence of absence (Upchurch *et al.* 2002).

The large time-slice, given its scale and insensitivity of divergence times, is a weaker test of vicariance among the crocodyliforms in this analysis than the finer time-slices. All tree analyses recovered a Gondwanan clade, which is sister to a North America + Europe clade in two of the time-slices (figure 2*a,c*). Given that the general interest of this study is to examine Gondwanan biogeography, coupled with the failure of the Late Jurassic–Early Cretaceous time-slice to pass a randomization test, the Mid–Late Cretaceous time-slice warrants further examination to explore the crocodyliform biogeographical signal present in the dataset.

(b) *Do crocodyliforms show vicariance?*

Two biogeographical processes are considered likely to produce statistically significant patterns of repeated area relationships. Area separation, often through the emplacement of geographical barriers, can divide continuous species populations. This results in repeated area relationships across a wide taxonomic range if allopatric speciation occurs between the now isolated populations (Rosen 1978; Wiley 1980; Nelson & Platnick 1981; Patterson 1981). This is the essential vicariance pattern.

The other process capable of generating repeated patterns of area relationship is area coalescence. This can result in a phenomenon known as ‘mass coherent dispersal’ (geodispersal of Lieberman (2000)) in which previously separated taxa on geographically isolated areas come into

contact with one another, dispersing to fill the newly formed area (Upchurch & Hunn 2002). This, like vicariance, allows a large number of taxonomically diverse groups to all depict the same change in their range data (Lieberman & Eldredge 1996; Lieberman 1997; Hunn & Upchurch 2001; Upchurch & Hunn 2002).

Is the crocodyliform biogeographical pattern therefore best explained by vicariance or mass coherent dispersal? It is widely accepted that the Cretaceous marks one of the most tectonically active times in the Phanerozoic, with most of Gondwana’s separation occurring between 145 Myr ago and 80 Myr ago (Smith *et al.* 1994; Storey 1995; Scotese 1998; Smith & Rush 1997; Hay *et al.* 1999). Perhaps with the exception of India establishing contact with Asia in the latest Cretaceous (Jaeger *et al.* 1989; Rage 1996; Chemenda *et al.* 2000), it is unlikely that coalescence of large continent-scale areas was occurring during the time period in which this analysis examined crocodyliform biogeography. Therefore, the most parsimonious explanation for the crocodyliform’s biogeographical pattern during the Mid–Late Cretaceous is vicariance. This is important as it marks one of the few documented instances in which biogeographical analysis of the fossil members of a clade yields statistically significant evidence for vicariance as an important factor affecting the diversification of the group.

(c) *Effects of missing data*

Previous examinations of the crocodyliform data have suggested that crocodyliforms present differing lines of evidence. Early Cretaceous crocodyliforms seem to show a close South America–Africa relationship (Buffetaut & Taquet 1977; Larsson & Gado 2000; Sereno *et al.* 2001, 2003) while those from the Late Cretaceous show a close South America–Madagascar relationship (Buckley *et al.* 1997, 2000; Buckley & Brochu 1999). While these conjectures are not mutually exclusive because of an absence of Indo-Malagasy crocodyliforms correlative with the African taxa, resolution has remained ambiguous. The early Cretaceous crocodyliforms may well be providing an accurate indicator of the separation of Africa and South America from other Gondwanan landmasses. With no correlative Indo-Malagasy crocodyliforms, however, any faunal similarity between Indo-Madagascar and South America will not be recovered by these analyses looking at the fossil distributions. This renders the South America–Africa relationship untested in these cases.

Phylogenetic approaches can alleviate some ambiguities resulting from missing data (Brett-Surman 1979; Sereno 1997; Sampson *et al.* 1998; Sereno 1999). Indeed, if a large number of a clade’s members are known from a later time period (e.g. the Late Cretaceous), but the clade itself diverged during an earlier period (e.g. the Early Cretaceous), then the biogeographical pattern of the clade’s temporally later members is the result and illustrative of the geographical events of the early time period. In other words, taxa can reveal biogeographical data of a temporally earlier event given that the taxa belong to a clade that diverged during the earlier time period and the clade’s phylogenetic pattern is consistent with a vicariant origin. Additionally, this illustrates the importance of incorporating divergence times into biogeographical analyses. Taxa with divergences older than the time period of interest cannot play a role in biogeographical pattern recognition in

Figure 3. Optimal area cladogram from the Mid–Late Cretaceous time-slice depicting the close area relationship between South America and Indo-Madagascar to the exclusion of Africa. The values below the node represent the average percentage recovery for $n + 1$ trees (top value) and $n - 1/n - 2$ trees (bottom value). Percentage recovery for $n + 1$ tree per area is as follows: Indo-Mad., 85%; South America, 89%; Africa, 70%.

situations where vicariance is being tested as a potential causal factor because these taxa will represent older events.

As discussed above, the taxa from the temporally later period are understood to have existed in the temporally earlier period only as ghost lineages. While ghost lineages are valid inferences of presence or absence of data for a taxon (Norell 1992), they do not carry geographical information *per se*. This proves trivial, as even infinite conjectures of dispersal between an area and its sister area along a ghost lineage do not alter the biogeographical signal from that implied by the much more parsimonious assumption of ‘no dispersal’ along the ghost lineage; i.e. the two areas, regardless of dispersal, share a closer area relationship with each other than either with a third area.

Variation in tree topology and/or discovery of a novel fossil taxon may alter the biogeographical pattern of a clade regardless of whether ghost lineages are present within the clade during the time-slice of interest. Such topological sensitivity and taxon sampling effects were quantitatively evaluated using sets of pruned and grafted trees.

Pruned sets of $n - 1$ and $n - 2$ trees for the Mid–Late Cretaceous time-slice recovered the vicariant South America–Indo-Madagascar biogeographical pattern in nearly 62% of the trials (figure 3). Unfortunately, given the asymmetry of this test, this value indicates little regarding the robustness of the biogeographical signal within the crocodyliform dataset. Nonetheless, this protocol demonstrates that six taxa (Peirosauridae, *Uruguaysuchus*, *Mahajangasuchus*, *Malawisuchus*, *Trematochamps* and *Simosuchus*) are critical to recovery of the pattern.

The three grafted sets of $n + 1$ trees, one for each of the three areas in the study, were analysed using the same time-slicing TRA method as the actual analysis. A novel taxon from either South America or Indo-Madagascar had minimal affect on recovering a South America–Indo-Madagascar pattern: 85% of Indo-Malagasy additions and

89% of South American additions (figure 3). A novel African taxon had slightly more effect, as might be expected, with 70% of the trees from the set recovering the South America–Indo-Madagascar biogeographical pattern seen in the actual analysis. Thus, these tests provide a powerful metric for assessing the robustness of a palaeobiogeographical signal. Considered together with statistical evaluation, it establishes the crocodyliform biogeographical pattern in the Mid–Late Cretaceous as topologically robust with a relatively insensitive signal to future taxonomic sampling.

4. CONCLUSION

While it remains true that a paucity of Late Cretaceous African and Early Cretaceous Indo-Malagasy crocodyliforms persists, re-examination of these data using a cladistic biogeographical method provides a means to clarify the ambiguous Cretaceous crocodyliform signal. The optimal area cladogram recovered for the Mid–Late Cretaceous in this analysis possesses two nodes, interpreted here as two separate continent-level vicariant events. The first represents the separation of Africa, South America and Indo-Madagascar from other landmasses. The second, later, event represents the division of Africa from South America and Indo-Madagascar. This later event depicts a rather non-traditional biogeographic relationship and, in that respect, this study’s results are similar to and support the conclusions of Sampson *et al.* (1998), Buckley & Brochu (1999), Krause *et al.* (1999), Krause (2001) and the geological data of Hay *et al.* (1999).

These results have implications for understanding crocodyliform evolutionary and biogeographical history. For crocodyliforms, as with most other terrestrial vertebrate groups, the relative importance of vicariance, dispersal, and regional extinction in shaping their evolutionary history and biogeographical pattern has remained difficult to estimate. Refining a ‘time-slicing’ cladistic biogeographical approach to include divergence data marks an important advance, which strengthens the method’s ability to recognize repeated patterns of area relationships that fulfil the necessary condition for hypothesizing vicariance as a causal process: namely, concomitant taxonomic divergence and geographical division (Grande 1985; Page 1990b). The demonstration of a vicariant biogeographical pattern among the examined Cretaceous crocodyliforms suggests that the process played a major role in determining their geographical distribution, in spite of other potentially analytically confounding processes such as dispersal and regional extinction. Although dispersal and regional extinction cannot be dismissed as insignificant factors, a vicariant pattern within crocodyliforms suggests that vicariant patterns detected in other groups (e.g. dinosaurs, cichlid fish, *Nothofagus*) indeed represent real patterns and further predicts that similar vicariant patterns should be present in other Cretaceous terrestrial clades.

Whatever the source, fossil biogeographical data will suffer from missing data in the form of temporal ambiguities and imperfect taxon sampling. Phylogenetic information provides a means to alleviate some of the temporal issues by constraining divergence times and taxonomic range data. However, imperfect taxon sampling is more problematic, as phylogeny cannot predict completely novel taxa with their own unique evolutionary history. At smaller clade

scales, it is likely that the effects of poor taxon sampling will be the strongest. Cladistic biogeographical methods provide biogeographical patterns that can be evaluated using statistical procedures and topological manipulation to gauge the relative effect that sampling may have on a pattern, and thus provide a framework of testability. Nevertheless, it is paramount that studies of biogeography broaden their scope past that of an individual group's pattern. Beyond the necessity of continued fieldwork and the fine-tuning of geophysical data, the addition and combination of biogeographical data from methodologically rigorous analyses of other fossil and extant clades, and from molecular as well as morphological datasets, represents the best means towards uncovering truly global patterns of dispersal and vicariance that may have existed during the time of Gondwanan fragmentation.

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