REPLY: TOWARDS A BIOGEOGRAPHY OF THE CARIBBEAN

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Introduction

During the last two decades, a subfield of historical biogeography termed "cladistic biogeography" has emerged (Humphries, 1992). Its central method is the comparison of phylogenetic trees in which taxonomic names have been replaced by geographic distributions of the taxa (areas of endemism). These "area cladograms" for different elements of a biota can be compared with each other and with models of geologic history in search of patterns of congruence that might suggest a common mechanism for their origin.

An area cladogram presents branching order, as does any phylogenetic tree, but does not convey information on times of divergence. In analyses of cladistic biogeography, time of divergence thus has taken on a secondary role and is often neglected in drawing conclusions. While we recognize the importance of phylogenetic relationships in biogeographic analysis (e.g. Hedges, 1989b; Hass and Hedges, 1991), we feel that the biogeographic history of a group is best assessed through a consideration of all available information.

Attempts to explain the origin of the fascinating biota of the West Indies have attracted the attention of numerous biogeographers over the years, and Rosen's (1975) study stimulated renewed interest in Caribbean biogeography. Nonetheless, robust phylogenetic trees for West Indian groups still are not widely available to examine the two competing theories of vicariance and dispersal. The pre-Quaternary fossil record, consisting mostly of mid-Tertiary amber fossils, also is limited and presently can contribute little to resolving this question. However, molecular systematic studies on West Indian groups, in addition to providing new insights into the phylogenetic histories of these groups, have generated considerable data on times of divergence by employing the chronometric properties of some biomolecules (e.g. Yang et al., 1974; Shochat and Dessauer, 1981; Hedges, 1989a; Hass and Hedges, 1991). In a recent study (Hedges et al., 1992), we analyzed albumin immunological distance data from a diverse set of West Indian terrestrial vertebrates. In all comparisons involving mainland and West Indian taxa, these distances were smaller than would be predicted by a late Mesozoic vicariant event, thus supporting an origin for these West Indian taxa by overwater dispersal.

Page and Lydeard (1994) have criticized our recent molecular systematic studies, and Hedges et al. (1992) in particular. Their main criticism is that we have neglected to present area cladograms for our taxa. However, it was not our goal in that study to do a cladistic biogeographic analysis and therefore we had no need to present area cladograms. Our focus was on the dimension of time and how that information can bear on an important biogeographic question. We contend that, at least in this

case, knowledge of time of divergence is sufficient to distinguish between these two biogeographic hypotheses.

BIOGEOGRAPHY INCLUDES DISPERSAL

The prior name for the subfield of cladistic biogeography was "vicariance biogeography" (Nelson and Platnick, 1981), which illustrates the importance that has been placed on this one particular biogeographic mechanism. For example, Croizat et al. (1974:278) stated that:

> "Vicariance is, therefore, of primary importance in historical biogeography, and dispersal is a secondary phenomenon of biotic distribution".

Dispersal has been labeled as "unscientific" and untestable by cladistic biogeographers (e.g. Nelson and Platnick, 1981:50) and the general assumption in cladistic biogeography is that congruence between area cladograms and geologic models indicates vicariance (Rosen, 1978:186; Humphries, 1992:140–141).

However, as noted by Page and Lydeard (1994), concordant dispersal patterns also can explain congruence between phylogenetic relationships and geologic history. In part, this is because dispersal can occur much more readily between land areas in close proximity compared with those separated by a greater distance. Also, land areas in close proximity often are those that share a more recent geologic history. Thus, dispersal over time can be expected, in many cases, to result in the same pattern of phylogenetic relationships (see also Endler, 1982, for a similar view).

A TEST OF TIME

Platnick and Nelson (1978:3) recognized that a test of vicariance versus dispersal could be the comparison of the age of a barrier with the time of divergence of taxa on either side of the barrier (Fig. 1). A prediction of vicariance is that the two dates should coincide. However, they considered that ages of barriers had "wide margins of error", and that the possibility of "discovery of older fossils" always casts doubt on evolutionary times of divergence. This uncertainty in estimates of time caused them to abandon their idea that dispersal and vicariance could be distinguished by time alone.

We suggest that this "test of time" is important in historical biogeography, and especially in situations where there is congruence among area cladograms. Because the vicariance hypothesis predicts that the taxonomic groups diverged at approximately the same time, and the dispersal hypothesis predicts that divergence occurred more recently (after the barrier was imposed), information on times of divergence can provide a critical test. Even in cases where the phylogenetic relationships are not well established, such as the Caribbean, this test of time can prove useful in distinguishing vicariance from dispersal (Hedges et al., 1992).

STATISTICS IN BIOGEOGRAPHIC ANALYSIS

We find it curious that Page and Lydeard (1994) have raised the issue of statistics (with regard to confidence intervals), considering that cladistic biogeography lacks a statistical framework. In cladistics, the tree with the fewest required changes is
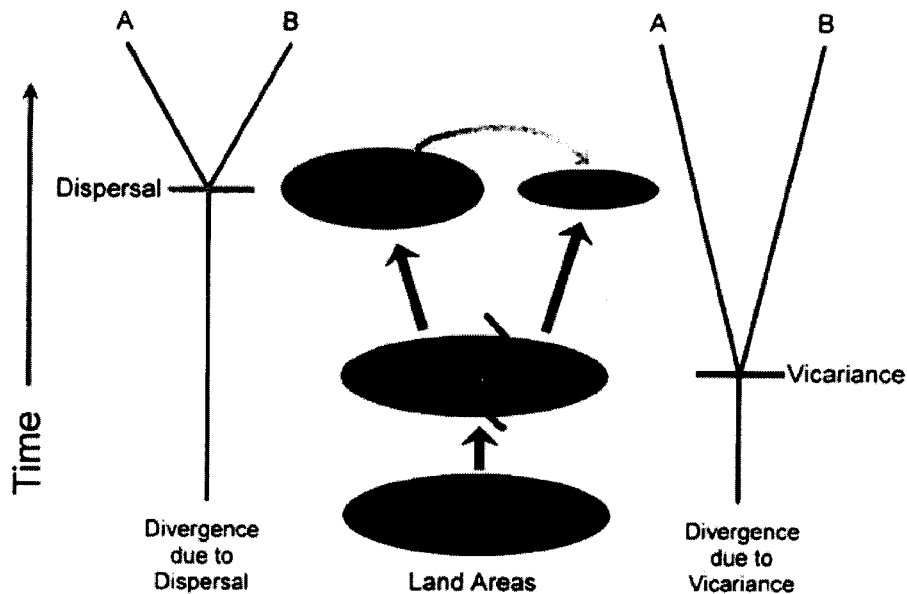
Fig. 1. Application of the time test in biogeographic analysis. Two groups on either side of a barrier are found to be sister taxa. Because the same phylogenetic relationships are expected with both models, examination of divergence times (through fossil evidence or molecular divergence) is necessary to distinguish between vicariance and dispersal. If the time of divergence between the two groups is shown to be significantly more recent than would be predicted by a vicariant event, then that vicariant event is rejected.

favored, usually without regard to whether it is significantly better (statistically) than alternative trees, or to the statistical significance of individual groups within the tree. For example, Page and Lydeard (1994) consider the study of Kluge (1989) on Caribbean boid snakes to be an example of a "robust" phylogeny. It may in fact be "robust", but Kluge did not present any statistical evidence that it is, and Swofford's (1991) reanalysis of those data lead one to question the robustness of the results.

Examination of congruence among area cladograms is central to cladistic biogeographic analysis, but as Page (1988) noted, "cladistic biogeographers have shown a marked reluctance to respond to the [statistical] issues raised by Simberloff et al. (1981; see also Simberloff, 1987)". While we applaud Page's (1988) efforts towards developing statistical tests for comparing area cladograms, these tests do not account for the error involved in estimating individual phylogenies upon which area cladograms are based. As noted above in the boid snake example, Page and Lydeard (1994) and other cladistic biogeographers have assumed that phylogenetic trees of individual taxonomic groups are accurate representations of evolutionary histories and can be treated as such for area cladograms. In reality, few phylogenetic trees exhibit well-supported, highly significant nodes throughout when statistical tests (e.g. Felsenstein, 1985) are applied.

BIOGEOGRAPHY—A SYNTHESIS

Page and Lydeard (1994) have acknowledged that the concordance of area cladograms can indicate either vicariance or concordant dispersal patterns. At the same time, they also acknowledge that the lack of concordance among area

cladograms may be due to either dispersal, or more than one vicariant pattern. If this is the case, then what inference can be made with area cladograms?

This problem stresses the limitations of trying to infer something as complex as historical biogeography with only one piece of information—phylogenetic relationships. Non-cladistic biogeographers often use a variety of information, including time, distribution, ecology, as well as phylogeny, to infer historical biogeography. Yet cladistic biogeographers, including Page and Lydeard, have criticized this type of research as "story telling". We should point out that a story may be fictitious, or it may be true. A biogeographic "story" that accounts for all of the available data (including time) will have a higher probability of being correct than one which is based on phylogenetic relationships alone. While we acknowledge the importance of phylogeny, we favor an approach to biogeography that utilizes all available information and makes no assumptions about the primacy of one mechanism over another.

Specific Replies to Page and Lydeard (1994)

GEOLOGICAL SCENARIOS

In their introduction and fig. 1, Page and Lydeard (1994) appear to have accepted an erroneous model of Caribbean geologic history. Rosen (1985), in his "cladistic analysis" of Caribbean biogeography, made an error in a figure legend. Rosen's fig. 35 shows a "diagrammatic consensus map of the mid-Cenozoic relations among some main components of the Caribbean heartland and a branching diagram that summarizes these relations". However, his diagram clearly shows the "proto-Antilles" connected to northern Central America in an orientation that appears in most of his geologic references as late Mesozoic, and his discussion in the text indicates that. Furthermore, the next time period figured by Rosen is "late Eocene" (=mid-Cenozoic), confirming that Rosen's label of "Mid-Cenozoic" for his fig. 35 was simply an error.

Page and Lydeard (1994) are correct to point out that many details of the geologic history of the Caribbean are poorly known. However, the complex nature of Caribbean geology has not escaped our notice (e.g. Hedges, 1982), and the geological history used in our recent study (Hedges et al., 1992) was based upon a synthesis of the latest geologic models (Pindell and Barrett, 1990).

The time span that we assigned to the separation of the proto-Antilles from the mainland, 76–80 Mya, was criticized by Page and Lydeard, who claim that Ross and Scotese (1988 : fig. 10) depict Jamaica in contact with the mainland "as late as 59 Mya". However, Ross and Scotese (1988) and their source (Pindell and Barrett, "in press" = 1990) show only close proximity, not direct contact, between Jamaica and the mainland at that time. Information such as "contact" between these ancient land masses, critical for biogeographic analysis, is largely unavailable from the present geologic evidence. Regardless, it would not matter for the vicariance theory because all of our IDs between taxa on Jamaica and the mainland indicated divergence after 42 Mya (Hedges et al., 1992 : fig. 1), which also is consistent with the geologic evidence for mid-Tertiary submergence of that island (see Hedges, 1989a, for discussion).

Page and Lydeard also mention that some other geologic models have placed Cuba in close contact with the Yucatan peninsula as late as 55 Mya. However, three

of the four studies cited are more than 12 years old, whereas we have placed emphasis on the most recent synthesis (Pindell and Barrett, 1990) of the ever-expanding geologic database. And again, even this date would not have a significant effect on our conclusions.

One consistent feature of geologic syntheses of the Caribbean is that an island-arc (=proto-Antilles) was situated roughly between North and South America in the late Cretaceous (Pindell and Barrett, 1990). Unfortunately, there is no geologic evidence that this island arc formed an emergent and continuous connection between the two continents. However, we interpret the existence of this island arc as establishing the possibility and approximate timing of vicariance, as suggested by Rosen (1975) nearly two decades ago.

IMMUNOLOGICAL DISTANCE

Page and Lydeard (1994) question three aspects of our use of estimates of amino acid sequence divergence obtained by the immunological technique of micro-complement fixation (MC'F). The first is the ability of one-way immunological distances (IDs) between pairs of taxa to provide an accurate estimate of actual amino acid sequence divergence. Hass and Maxson (1993) discussed this problem at length and we will briefly summarize that discussion here.

In most immunological studies, there is some deviation from perfect reciprocity (the ID measured from taxon A to B is not identical to that measured from B to A). The degree of this deviation can be calculated and usually is reported as the per cent standard deviation from reciprocity (Maxson and Wilson, 1975); this averages between 10 and 15% (see Hass and Maxson, 1993; table 1). If the degree of deviation is large, the data set can be corrected by assuming the mean between two ID estimates of the actual amino acid sequence divergence is the most accurate estimate (Cronin and Sarich, 1975).

Page and Lydeard suggest that we have misrepresented the magnitude of this problem and cite a method for calculating this deviation that was proposed by Guyer (1992). However, Hass and Maxson (1993) demonstrated that Guyer's assumptions, which are based largely upon a theoretical model of the role of the host animal in the immune response (Faith, 1985), are not supported by the available data. In addition, Guyer's equation for his improved estimate of non-reciprocity was mathematically incorrect. He suggested that the denominator should be divided by two, but the original equation is correct for this case in which the two values (for each reciprocal comparison) are being tested individually against their mean (Hass and Maxson, 1993). Because the average level of deviation from reciprocity, calculated using the correct equation, would not affect the conclusions that we drew from the immunological data, we were justified in using one-way IDs to provide estimates of the divergence time between taxa (Hedges et al., 1992).

The second and third aspects that Page and Lydeard (1994) discuss, use of albumin as a molecular clock and the calibration of that clock, also are tied to the experimental error inherent in estimation techniques. They state that for the data to be used as a clock, they must be ultrametric. In studies where that information has been calculated, such as felid carnivores (Collier and O'Brien, 1985) and West Indian eleutherodactyline frogs (Hass and Hedges, 1991), the albumin IDs are highly metric (95% of all possible comparisons met the triangle inequality).

While most of the observed variation in rates of albumin evolution appears to be technical, as has been discussed previously (Hass et al., 1992; Hass and Maxson, 1993), there are cases where albumin evolution appears to have accelerated or decelerated along a specific lineage. However, this change can be detected by looking "into" the specific group using an antiserum against a taxon outside that lineage. For example, Cadle (1988) used this method, a relative rate test, to detect a slowdown in the rate of albumin along the viperid snake lineage, particularly in the pit vipers.

In pointing out extreme cases of rate differential in some data sets, Page and Lydeard fail to make a case because, by definition, those examples are atypical of most data sets. Page and Lydeard cite our study on West Indian *Anolis* (Hass et al., 1993) to show that one of the data sets we used to investigate Caribbean biogeography (Hedges et al., 1992) exhibits large variation in rates of albumin evolution. However, that data set had a lower than average standard deviation from reciprocity (8.05%), and only one antiserum of the eight used had a directional bias in ID estimates.

Page and Lydeard criticize the absence of confidence limits on the data points shown in our figure (Hedges et al., 1992:fig. 1), However, as we mentioned in that paper, there is no known error that would cause a "consistent underestimation of distance across many taxonomic groups". The typical errors in ID (discussed above) are not sufficiently large to have affected our conclusions. Nonetheless, we have calculated these confidence limits on the data presented in Maxson (1992) using the intercept model of linear regression, without constraining the regression line to pass through the origin (which would underestimate the error in divergence values at the lower end of the range). The intercept is 3.53, which is not significantly different from zero at the 95% level (t = 1.41, 34 degrees of freedom). Confidence intervals (95%) were obtained for the divergence times predicted ($\hat{Y}$ values) from ID (X values) using the Working–Hotelling approach to simultaneously estimate Ys across a number of Xs (Neter et al., 1990:163). The data points with these confidence limits appear in Fig. 2. It is clear that our interpretation of the data would not have been affected by the level of error in estimates of divergence time.

Page and Lydeard state that our inclusion of some Caribbean frogs in the albumin clock calibration adds an "element of circularity" in our study. However, the inclusion or exclusion of those three data points did not change the "standard" calibration that we used.

TAXONOMIC SAMPLING

Page and Lydeard (1994) suggest that possible errors in our taxonomic sampling may have affected our conclusions. But as we pointed out (Hedges et al., 1992:1910–1911), such errors—if they exist—will result in an overestimation of the time of lineage divergence for taxa from different areas. Because we found low immunological distances, indicating overwater dispersal, an error of this type could only mean that the actual distances are even lower—strengthening the support for dispersal. Furthermore, whether the IDs coincide or not would not affect that conclusion, because mid-Cenozoic vicariance involving the proto-Antilles and the mainland is not a geologic possibility given current evidence (Pindell and Barrett, 1990).
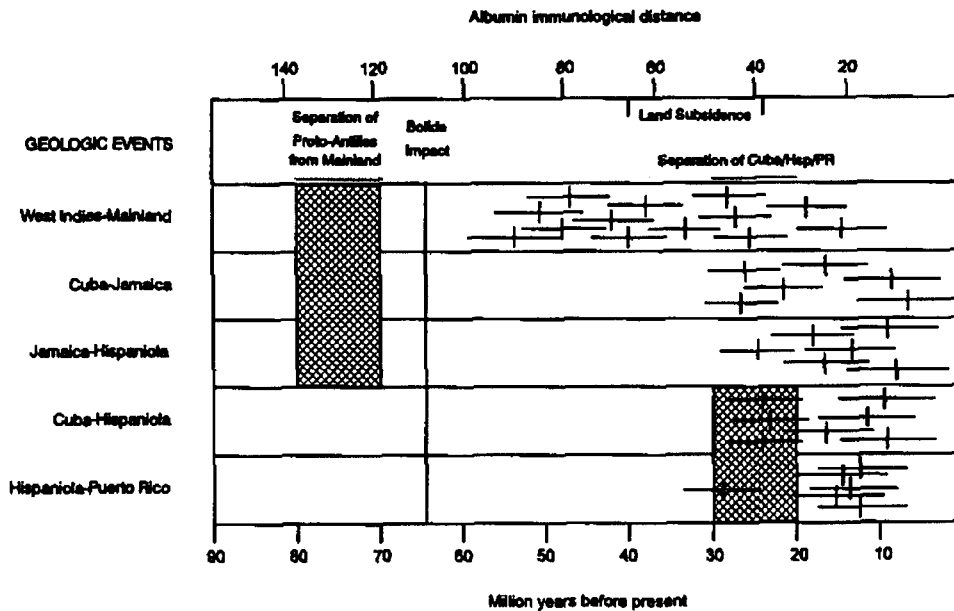
Fig. 2. Estimation of times of divergence between terrestrial vertebrate taxa based on albumin immunological distance values (after Hedges et al., 1992: fig. 1). The horizontal error bars indicate the range of divergence time for each estimate (method described in text) at the 95% confidence level. The shaded regions denote the range of IDs predicted by vicariance. HSP—Hispaniola, PR—Puerto Rico.

We attributed the variability in IDs as further support that a single event was not responsible for the divergences because we did not feel that taxonomic sampling errors were so pervasive that they affected every comparison. On the contrary, our previous and ongoing systematic studies of West Indian vertebrate groups have given us some insight into which taxa constitute valid sister-group comparisons. For example, our molecular data for frogs of the genus *Eleutherodactylus* (Hedges, 1989b; Hass and Hedges, 1991) have identified the subgenera *Syrrhophus* (Middle America) and *Euhyas* (Western Caribbean) as sister groups, and thus the ID of 62 between them is not likely to be subject to taxonomic sampling error. Likewise, the lizard genera *Iguana* (mainland) and *Cyclura* (West Indies) are considered to be sister groups based on morphological (Norell and de Queiroz, 1991) and molecular (Gorman et al., 1971) data, and therefore the ID between them (20) is unlikely to be affected by taxonomic sampling. The IDs for the comparisons in these two groups are considerably lower than the range predicted for vicariance (117-133), and yet they differ by a factor of three. We suggested that such wide variation is due to different times of dispersal between the mainland and the West Indies. While we are far from knowing the complete phylogenetic relationships of any of these groups with certainty, we feel that sufficient data are available to reject the criticism of Page and Lydeard (1994) that we do not know "which kinds of comparisons are being made".

Page and Lydeard (1994) discuss in detail our comparisons involving lizards of the genus *Sphaerodactylus* with respect to taxonomic sampling error. Considering that such error, if it exists, would not affect the conclusions of our study (as noted above), we are surprised to see so much discussion devoted to this topic. Nonetheless, we will point out why even these specific criticisms regarding *Sphaerodactylus* are not valid.

Unfortunately, Page and Lydeard use the terms orthologous and paralogous when discussing taxa (see also Page, 1993). However, these terms have very specific meanings in molecular evolution (comparison of genes which are identical by descent versus comparison of genes which are the result of duplication) and we feel that such usage will only lead to confusion when discussing phylogenetic trees constructed from molecular data.

The immunological comparisons involving *Sphaerodactylus* were limited by the number of antisera available. Because at least 0.5 ml of plasma is required to produce a single rabbit antiserum with sufficient material left to use as homologous antigen in the MC'F experiments, plasma had to be pooled from numerous individuals of these very small animals from a single locality. Thus, the taxa used for antiserum production were chosen by the ability to collect sufficient specimens. Ideally, we would like to have IDs from all pairs of taxa. Although technical limitations prevent that goal from being achieved, this does not mean that the present data are insufficient to draw phylogenetic or biogeographic conclusions. On the contrary, the errors in taxonomic sampling claimed by Page and Lydeard, even if valid, would only strengthen our conclusions that dispersal was the mechanism responsible for the origin of the groups.

Page and Lydeard (1994) also question the robustness of the phylogeny generated for West Indian *Sphaerodactylus* based on the electrophoretic data (Hass, 1991). They incorrectly state that a consensus summary of the MPTs was not provided. A strict consensus tree was described at the end of the character analysis section in the Results (Hass, 1991 : 536) and was essentially the same as fig. 6 in Page and Lydeard (1994). Unfortunately, in their reanalysis of the character data, they entered the data differently than was described in the Methods section of the original paper in which taxa with identical character states were combined (as were the outgroup taxa) into composite OTUs. Because of this, the length of the tree they obtained is much longer and their results cannot be compared directly to those reported previously (Hass, 1991).

Oddly, Page and Lydeard (1994:fig. 5) discuss the detailed phylogenetic tree of *Sphaerodactylus* relationships (from Hass, 1991) as if it represented the true phylogenetic relationships of the group, and then go on to accept a consensus tree for the same data showing virtually no resolution of relationships (their fig. 6). This contradiction makes it difficult to understand what Page and Lydeard are actually criticizing, but clearly they are not comfortable with Hass' (1991) study. We should simply point out that: (1) Hass never claimed to be writing the final word on *Sphaerodactylus* relationships; (2) Page and Lydeard have restricted their discussion to parsimony analyses of her allozyme data, whereas Hass also draws conclusions from her distance analyses; and (3) none of Page and Lydeard's extensive criticisms of her study are relevant, because the very low immunological distances between pairs of *Sphaerodactylus* in Hedges et al. (1992) would only be lower (supporting dispersal more strongly) if taxonomic sampling errors were present!

Page and Lydeard (1994) criticize the use of sequential electrophoresis, in Hass (1991) and Burnell and Hedges (1990), because it produces more character states and hence more parsimonious trees. This is analogous to criticizing a microscope that has a clean objective lens in favor of one with a dirty lens. Sequential electrophoresis allows one to discriminate genetic variation that would otherwise be hidden. *The consequences of hidden variation in a phylogenetic analysis are*

obvious, and thus one should strive to reduce the amount of this hidden variation as much as is possible. That more character states are produced is not a problem with sequential electrophoresis, but a problem for the method of analysis (here, parsimony).

DEFINITION OF AREAS

Page and Lydeard have criticized our distributional categories of "mainland" (North, Central and South America) and "West Indies" because they presuppose "the monophyly of all Caribbean taxa with respect to their mainland relatives". This is not true. Previous and ongoing systematic studies of these vertebrate groups allow for some informed decisions regarding monophyly of groups. For example, West Indian frogs of the genus *Eleutherodactylus* probably are not monophyletic (Hedges, 1989b). Rather, there are three major groups present, and our comparison involved one of those groups (subgenus *Euhyas*) with its mainland sister group (subgenus *Syrrhophus*). Similar informed decisions were made with the other vertebrate groups compared.

Furthermore, our study involved a test of timing, and therefore categories of mainland versus West Indies were specifically designed to test the two theories (vicariance and dispersal). That the sister group of the West Indian frog subgenus *Euhyas* occurs in Central America and the sister group of West Indian snakes of the genus *Tropidophis* (a monophyletic group; Hedges et al., unpubl.) occurs in South America was recognized by us and incorporated in the test, but it did not require separate delineation of those areas. As noted elsewhere in this paper (see "Taxonomic Sampling"), failure to identify all of the sister groups would not effect our conclusions.

XANTUSIID AND ANOLINE LIZARDS

Two groups of lizards have played a significant role in the literature on Caribbean biogeography, but this role was misstated by Page and Lydeard (1994). In both cases (xantusiids and anolines) they have assumed that the existence of alternative viewpoints in the literature indicates that the "relationships are poorly understood". However, very little progress in systematics could be made if this assumption were applied for every disputed phylogeny. We believe that it is better to look at the available evidence and make an informed decision.

Crother et al. (1986) listed 30 morphological characters for their analysis of xantusiid relationships, but only nine (13 if ordered) were informative under parsimony, and the controversial node of *Lepidophyma* + *Cricosaura* is supported by only two unambiguous shared-derived characters (no statistical tests applied). Hedges et al. (1991) presented DNA sequence data from two genes (709 sites, 365 variable, 168 informative under parsimony) strongly supporting (99% bootstrap *P*-value) a *Xantusia* + *Lepidophyma* clade. Crother and Presch (1993) re-examined xantusiid relationships using both data sets, but gave the small morphological data set equal weight to the large molecular data set and obtained ambiguous results (actually, the results were unclear because no statistical tests were applied). Hedges and Bezy (1993) replied by demonstrating that the two pivotal morphological characters uniting *Cricosaura* and *Lepidophyma* were scored incorrectly (thus questioning the

entire morphological analysis), and that when DNA sequence data from a third mitochondrial gene were added to the previous molecular data (1028 sites total, 471 variable, 281 informative under parsimony), the same *Xantusia* + *Lepidophyma* clade found in that earlier molecular study was strongly supported (100% bootstrap P-value).

Page and Lydeard (1994) mention the controversy surrounding Guyer and Savage (1986) as evidence that the relationships of Caribbean anoline lizards are poorly known and thus questioning the validity of our anoline comparisons (Hedges et al., 1992). In fact, this is a biased subset of the enormous literature on the relationships of Caribbean anoline lizards (e.g. see review in Burnell and Hedges, 1990), and as such is misleading. Guyer and Savage (1986) reclassified these lizards based on an analysis of some data (primarily morphological) from the literature. Williams (1989) found "serious errors and confusions" in their interpretation of those data and recommended that "neither the data bases nor the taxonomic conclusions be accepted". Guyer and Savage (1992) responded to some of Williams' (1989) and Cannatella and de Queiroz's (1989) criticisms but, in doing so, have created more errors and confusion. Furthermore, the complete lack of statistics makes it impossible for the reader to understand what is significant among the results of Guyer and Savage (1986, 1992).

The relationships of some Caribbean anoline lizards are quite well established based on the congruence of morphological and molecular data, such as the monophyly of the native Jamaican species (Shochat and Dessauer, 1981; Hedges and Burnell, 1990), the monophyly of most Puerto Rican species (Gorman et al., 1983) and the definition of most species groups and series (e.g. Williams, 1976; Burnell and Hedges, 1990). Recently, we found congruence between albumin immunological distances and mitochondrial DNA sequence data indicating the paraphyly of West Indian *Anolis* with respect to the endemic Cuban genus *Chamaeleolis* (Hass et al., 1993). While there is no question that more data need to be gathered before an accurate picture of anoline lizard evolution emerges, Page and Lydeard (1994) make a superficial assessment of a complex issue.

Summary

Vicariance and dispersal both can result in the same phylogenetic relationships, and therefore in many cases an area cladogram analysis alone is not sufficient to distinguish between these two mechanisms. Time of divergence is an important factor that is typically considered in historical biogeographic analyses but usually overlooked in cladistic biogeographic analyses.

Page and Lydeard (1994) have criticized our recent study (Hedges et al., 1992) on Caribbean biogeography primarily on the grounds that we did not perform a cladistic biogeographic analysis. However, it was not our intent to do such an analysis because it would not have given us the information that we were seeking: the times of divergence between West Indian and mainland groups of terrestrial vertebrates. We found that all of the groups examined diverged from their mainland relatives more recently than would be predicted by the vicariance model and concluded that this supports an origin for those groups by overwater dispersal.

Page and Lydeard's criticisms of the geological scenarios that we used appear to be based mainly on errors in their reading of the literature. Their criticisms of

immunological distance are largely based on an erroneous model by Guyer (1992), which has been responded to elsewhere (Hass and Maxson, 1993). Their lengthy criticisms of our taxonomic sampling are ineffectual because Page and Lydeard acknowledge that such errors (if present) would not affect our rejection of the vicariance model.

Page and Lydeard state that cladistic biogeography will "remain in the doldrums" unless systematists are willing to present area cladograms. However, we suggest the reason cladistic biogeography has remained in the doldrums is that cladistic biogeographers have: (1) placed a major biogeographic mechanism—dispersal—in a secondary role; (2) focused on only one aspect of biogeography—phylogeny—without considering all of the evidence; and (3) have accepted nearly any hypothesis of phylogeny without regard to statistical significance. We believe that the field of biogeography deserves better.

Acknowledgements

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