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TOWARDS A CLADISTIC BIOGEOGRAPHY OF THE CARIBBEAN

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> "But to accept as true the proposals of one geological model, and to abandon the search for cladistic area-congruence in favour of some a priori notion that all distributions might be explained by guesswork liberally laced with dispersalist intuition is to ensure that future generations of biogeographers will regard such proposals lightly." (Rosen, 1985:657)

Introduction

The Caribbean has played a prominent role in the biogeographic literature of the last two decades, partly as a consequence of Rosen's (1975) application of track analysis (Croizat, 1958; 1964) to numerous distribution patterns in the region. Rosen's goal (p. 432) was to "reduce Caribbean distributions to the smallest number of vicariant patterns and to compare these with theories of the historical geology of the region." A decade later Rosen (1985) emphasised the geological and biotic complexity of the Caribbean and presented a series of area cladograms abstracted from geological reconstructions for different periods in time from mid-Cenozoic to the present (Fig. **Error! Bookmark not defined.**). He concluded (p. 657) that unravelling this complexity will require a "stupendous multidisciplinary effort." At the heart of this effort will be cladograms for Caribbean taxa, the supply of which is the primary limiting factor for cladistic biogeographic analysis.

The increasing availability of molecular data sets for Caribbean taxa and their relatives promises to provide a rich source of taxon cladograms for biogeographers. However, some molecular systematists have eschewed cladistic biogeographic analysis in favour of traditional, narrative dispersal accounts based on particular geological models. While those familiar with the cladistic biogeographic literature may regard this paper as another exercise in "arm-chair" biogeography that contributes no new data, in our opinion many of the people most likely to

contribute the relevant data (namely molecular systematists) have not appreciated the implications of the biogeographic literature of the last 15 years. This concern motivates our critique.

MOLECULES AND METEORS

Recently a number of phylogenies for Caribbean vertebrates have emerged from the laboratories of molecular systematists (Hedges, 1989; Hedges and Burnell, 1990; Burnell and Hedges, 1990; Hedges et al. 1991; Hass, 1991; Hass and Hedges, 1991; Hass et al., 1993), and more are on the way (Lydeard, et al. submitted; Bermingham pers. comm.; Crother pers. comm.). However, rather than use these cladograms to construct area cladograms some authors have erected elaborate scenarios dominated by hypotheses of transoceanic dispersal and bolide impacts (e.g., Hedges et al., 1992). It seems as though these same authors have ignored Platnick and Nelson's (1978:9) conclusion that:

> "...we cannot justify the kinds of biogeographic analysis of particular groups commonly found relegated to the back pages of systematic revisions (analyses that automatically invoke dispersal to account for all distribution patterns…and are primarily concerned with drawing scenarios of such dispersal)."

Hass' (1991) recent paper on *Sphaerodactylus* geckos exemplifies the kind of research that precipitated Platnick and Nelson's ire. After obtaining a taxon cladogram Hass (1991:546) notes that:

> "Some biogeographers believe that area and taxon/area cladograms must be constructed and their congruence tested before the

> biogeographic history of a group can be discussed objectively (Rosen, 1985). However, this requires that accurate area cladograms can be constructed based upon the available data. In the West Indies, this requirement cannot yet be fulfilled."

We share Hass' assessment of the merits of many existing cladograms for Caribbean taxa (see below). However, Hass then writes (p. 547):

> "Because of the current inability to construct area cladograms with confidence, I have chosen to examine the distribution of the groups within *Sphaerodactylus* in light of the revised classification, divergence times, and a consensus of available geological information."

In other words, Hass tells a story. Apparently her cladogram for *Sphaerodactylus* is sufficient to serve as the basis for a new classification of the genus (pp. 539-546) and an elaborate dispersal scenario (pp. 546-552), but not for an area cladogram.

Ironically, just as molecular systematics promises an ever growing supply of cladograms for biogeographic analysis some of its practitioners are overlooking the groundwork for cladistic biogeography laid in the previous decade by Nelson, Platnick, and Rosen (e.g., Platnick and Nelson, 1978; Rosen, 1978; Nelson and Platnick, 1981). The purpose of our critique is to reassert the importance of a cladistic framework for biogeographic analysis, with special emphasis on the Caribbean. We begin with a brief review of Caribbean biogeography and the vicariance versus dispersal debate. We then criticise Hedges et al.'s (1992) recent study of immunological divergence among Caribbean vertebrates. Our critique concludes with recommendations for future biogeographic studies of the region.

Caribbean Biogeography

OVERVIEW

Caribbean biogeography has been a topic of interest to naturalists for more than a century (see brief review by Liebherr, 1988b). The Caribbean islands lack of biotic diversity accompanied by a high degree of endemism compared with continental areas led to the formulation of two contrasting mechanisms to explain these patterns — dispersal and vicariance. As Williams (1989a:2) summarises:

> "1) Islands when they arise are totally without biota. Everything they eventually contain has been accumulated by colonisation across a pre-existing barrier.
> 2) Island faunas are fragments of continental faunas. Their differences are primarily the results of extinction after a barrier has arisen. "

Dispersal has been advocated as the predominant mechanism by Matthew (1915, 1919), Darlington (1938, 1957), Simpson, (1956), Williams, (1969, 1989a) and others. Originally, their strict adherence to dispersal was due to their belief in the geological concept of a stable earth (i.e. the permanence of continents and ocean basins). The "dispersalists" largely replaced the first group to advocate vicariance — the so-called landbridge builders. From the late 1800's when Wallace published (1876, 1892) his landmark biogeography studies to the early 1930's, most investigators believed that biotic distributional patterns of the Caribbean could best be explained by fragmentation of the islands from each other and the mainland (Schuchert, 1935) via vertical oscillations of the land or sea allowing for the formation and destruction of land bridges. Lack of empirical support for the geological mechanism which enabled

the landbridge builders to construct their bridges gave the dispersalists/earth stabilists the upper hand (Greene, 1985). In the late 1960's and early 1970's plate tectonics replaced the stable earth model and this, together with Croizat's (1958, 1964) work provided the basis for Rosen's (1975) vicariance model of the Caribbean. Unlike many previous attempts to explain Caribbean biogeography, however, Rosen argued that biotic data can provide a direct means to test hypotheses of geohistory — taxa with similar area cladograms probably share a common earth history, and hypotheses of this history generated from the biotic data can be compared with hypotheses generated from geological data.

Despite the development of cladistic biogeography over a decade ago and the recent publication of two symposium volumes focusing on the biogeography of the West Indies (Liebherr, 1988a; Woods, 1989) few area cladograms have been constructed for Caribbean taxa. This lack stems primarily from the lack of phylogenetic hypotheses for most of the Antillean biota. The paucity of area cladograms makes it difficult to search for congruent patterns of area relationships. Confounding the search for congruence is the lack of concordance found among phylogenetic hypotheses generated for some of the more studied taxa based on independent data sets (e.g. xantusiid lizards, Crother et al., 1986; Hedges et al., 1991). Finally, to add to this complexity, congruence among area cladograms may not necessarily mean vicariance but could also be due to concordant dispersal patterns. Likewise, incongruent patterns may not be a definite indication of dispersal, but could be due to the presence of more than one vicariant pattern.

VICARIANCE VERSUS DISPERSAL?

The energy expended on the “vicariance versus dispersal” debate might be more profitably be directed at another, more basic question. Platnick and Nelson (1978:8) argued that the fundamental question facing biogeographers

> "...is not "Is this pattern the result of vicariance or dispersal?" but "Does this pattern correspond to a general pattern of area interconnections (and thus reflect the history of those areas) or not?" What is needed is a method of analysis that will allow us to determine whether two given distribution patterns correspond to each other or not, so that we can test a hypothesis that the pattern of relationships of areas indicated by one group is a general one. After a hypothesised general pattern is corroborated, we may be able to ascribe it to vicariance or dispersal by the use of independent evidence of earth history."

Cladistic biogeographic analysis is the search for congruent patterns among area cladograms for different taxa. Detecting congruence suggests a common cause, which may or may not be vicariance. All too frequently in the literature congruence and vicariance have been conflated — congruence could be the result of dispersal (e.g., Savage, 1982; Minaka, 1987). As Tolson (1987:61-62) remarks:

> "Herein lies the major problem of this type of analysis (e.g., congruence of several multi-taxon cladograms) applied to the Caribbean: one cannot be certain if a pattern of distribution in the Antilles which includes Cuba, Hispaniola, and Puerto Rico (with more primitive forms in the west and more advanced forms in the east) was the result of multiple vicariant events trending from west to east or linear dispersal..."

For a related discussion of geographical constraints on tests of geographic congruence see Page (1991).

The task confronting biogeographers is to first establish whether or not the Caribbean biota displays geographic congruence. Hedges, Hass, Maxson, and colleagues attempt to avoid this task by comparing estimates of time of divergence based on immunological distance with estimates based on a particular geological scenario.

GEOLOGICAL SCENARIOS

> "It is ironic that vicariance cladists accept and use the geological equivalent to what they scornfully dismiss as "narrative" in biological systematics."(Craw, 1988:296-297)

Hedges et al.'s (1992) conclusion that dispersal as been the primary biogeographic process in the Caribbean relies heavily on the hypothesised timing of vicariant events based on studies of the geohistory of the region. However, as Lewis and Draper (1990:77) assert: "Even today, the [geological] models based on modern theories of plate tectonics are still vigorously debated, and no single hypothesis has met with widespread acceptance." For instance, Hedges et al. hypothesised the separation of the proto-Antilles from the mainland occurred in the late Cretaceous (70-80mya) based on the models of Burke (1988), Ross and Scotese (1988), and Pindell and Barrett (1990). However, Burke (1988) actually depicts Jamaica as being in contact with the mainland as late as 59 mya (his fig. 10). Furthermore, other geological models suggest Cuba and the Yucatan peninsula were in contact or close approximation as late as the early Eocene some 55 mya (Pindell and Dewey, 1982; Coney, 1982; Sykes et al., 1982; Donnelly, 1988). In fact, other than from the Pliocene to the present, Perfit and Williams (1989: 65) assert that "geologists do not have the kind of information required to determine the paleogeographic positions of most of the islands nor the total area above sea level at any given time interval."

Clearly we should not underestimate the difficulties in extracting biologically relevant information from the geological literature, nor should we overestimate the precision of geological reconstructions.

Pairwise Immunological Distance

Hedges et al.'s (1992:table 1; see our Fig. 11) data comprise 38 pairwise albumin immunological distances (IDs) among Caribbean vertebrate taxa, from which they concluded (pp. 1909-1910):

> "Most comparisons indicate evolutionary divergence in the mid-Cenozoic (Eocene to Miocene), not in the late Cretaceous. The wide variation in observed values for the comparisons further suggests that a single event was not responsible for the divergences."

Their first conclusion requires that albumin IDs are clock-like and can be accurately calibrated. Their second conclusion requires that the observed variation exceeds that attributable to other sources, such as experimental error, variation in rates of evolution, and taxonomic sampling. We consider these sources of variation below.

RECIPROCITY

Of the 38 pairwise comparisons reported by Hedges et al. (1992) 30 were based on one-way comparisons only, that is, the distance D_{AB} between taxa A and B is estimated using the distance d_{AB} between antisera to A and serum from B. For one-way comparisons to be useful the reciprocal distance d_{BA} between antisera to B and serum from A should not differ significantly from d_{AB}. Hedges et al. (1992:1910) assert that

> "The reciprocal estimation of ID between two taxa has an average deviation of about 10% and would not cause a consistent underestimation of distance across many taxonomic groups."

They do not, however, present any values for the taxa they themselves examined. While the percent standard deviation from reciprocity (Maxson and Wilson, 1975) for some taxa is "low" (e.g., 8.7% in *Eleutherodactylus*) for others it is rather higher (e.g., 19.3% in *Sphaerodactylus*). Interestingly, Guyer (1992) has argued that percent standard deviation is an inappropriate measure of nonreciprocity as observed IDs will tend to underestimate the actual distance, D_{AB}. He advocates using the larger of d_{AB} and d_{BA} as the best estimate of D_{AB}, and presents an alternative formula for calculating nonreciprocity. Using Guyer's formula the nonreciprocities for *Eleutherodactylus* and *Sphaerodactylus* are 13.1% and 26.4%, respectively. If Guyer (1992) is correct, then the variation in IDs attributable to nonreciprocity may be substantially more than allowed by Hedges et al. (1992; but see Hass and Maxson [1993] for a response to Guyer).

MOLECULAR CLOCK

We do not intend to rehearse the arguments for and against molecular clocks (the reader is directed to Gillespie's [1991] account for a recent appraisal). For our purposes the question is whether the variation in rate of albumin evolution between taxa is sufficient to be a significant source of error in estimating divergence times.

For a distance measure to be clock-like it must be an *ultrametric*, that is, given two taxa A and B more closely related to each other than to taxon C, the distances between the three taxa must satisfy the inequality $D_{AB} \leq D_{AC} = D_{BC}$ (Fig. 11). To the extent that $D_{AC} \neq D_{BC}$ the distance measure departs from being clock-like.

Hedges et al. (1992:1910) cite Cadle's (1988) study of albumin evolution in snakes as evidence that rates vary by 10-15% and state that "[d]eviations of this magnitude would not affect the interpretation of the data..." However, other studies have shown substantial variation in rates of albumin evolution (e.g., Baverstock et al., 1989). Indeed, Cadle's (1988: fig 4) trees show pairs of taxa where one lineage has accumulated between 50-77% more ID than the other lineage since they last shared a common ancestor. Hass et al.'s (1993:fig 1) trees for *Anolis* (one of the taxa used by Hedges et al.) albumin IDs show pairs of taxa with branches varying up to 44% in length.

Molecular clock hypotheses postulate a stochastic clock, so that there will always be some variation in amounts of divergence between pairs of taxa of the same age. This variation may be so great as to falsify the clock hypothesis itself. One of the authors of Hedges et al. (1992) has previously cautioned that "…the existence of an albumin clock cannot be assumed; it must be documented for the particular group being studied" (Maxson et al., 1975:398). Yet Hedges et al. (1992) have not documented a clock for any of the taxa they studied. As with their estimates of nonreciprocity, they have chosen to cite values for other taxa and assume that these values hold for the taxa they studied. Given that Hedges et al. use the variation in IDs between islands as evidence for multiple inter-island dispersal events it is incumbent upon them to show that the observed variation in their data exceeds that which could be attributed to nonreciprocity and variation in evolutionary rates.

CALIBRATION

Hedges et al. (1992:1909) used a "standard" calibration of 1 ID unit = 0.6 Myr "derived for a number of different vertebrate groups based on both fossil and geological information, including a group of West Indian frogs." The frog in question is *Eleutherodactylus*, which Hass and Hedges (1991) calibrated using the timing of

three geological events in the history of the Caribbean. That Hedges et al. then used the same *Eleutherodactylus* to test the relationship between the timing of geological events and albumin divergence introduces an element of circularity into their study.

Ideally a molecular “clock" would be calibrated using independently dated fossils, taking into consideration that fossils provide only a minimum age for a taxon (Hennig, 1966). Unfortunately relevant fossils are scarce, and those that are known are of uncertain age. For example, Böhme (1984) described an extinct *Sphaerodactylus* gecko from Dominican amber, which may be 40 Myr old (Lambert et al., 1985), predating Hass’ (1991:547-548) estimate of 27 Myr for the age of origin of *Sphaerodactylus* based on albumin divergence. However, the age assigned to the amber is based on a “highly speculative” (Lambert et al., 1985: 50) interpretation of ^{13}C nuclear magnetic resonance spectra.

Important considerations when calibrating a molecular clock include whether divergence is linearly correlated with time, whether rates vary between clades, how much error is associated with estimates of molecular divergence, and the confidence limits around the predicted time of divergence based on the calibration (Hillis and Moritz, 1990; Wayne et al., 1991). This last point is particularly relevant here. In the absence of confidence limits we have no way of knowing how precise are Hedges et al.'s (1992) estimates of divergence time. We note that Hillis and Moritz (1990: 511) found that confidence limits for predicted divergence times are typically broad, sometimes “so large as to not exclude any reasonable possibility.”

Taxonomic Sampling

If the problems of calibration were addressed then a sufficiently precise distance measure that conformed to an ultrametric (i.e., was clock-like) could be a powerful test of specific biogeographic hypotheses (see also Page, 1990b, 1993). This is particularly true if one suspects the presence of superimposed biogeographic

patterns of different age. However, using a molecular clock (or clocks) does not obviate the need to consider the cladistic relationships of the taxa in question.

If all the representatives of a given clade in each area of endemism comprise a monophyletic group with respect to members of the same clade found in all other areas of endemism being studied, then (assuming a clock) we could estimate the genetic distance between taxa from the different areas of endemism by sampling any taxon from each area. For example, in Figure 11a the distance between any of the taxon pairs (1, 3), (1, 4), (2, 3), or (2, 4) would estimate the genetic divergence between lineages in areas A and B. However, if some taxa within an area of endemism are more closely related to taxa in other areas than to representatives of the same clade found in the same area then the taxa used to estimate genetic distance need to be chosen with great care. To illustrate, given the tree in Figure 11b, only taxon pairs (6,7) and (8, 9) are relevant — the distances between taxa (6, 9) and (7, 8) are irrelevant to the problem at hand. Molecular systematists may recognise this distinction as analogous to that between orthologous and paralogous genes (Fitch, 1970). Using this terminology, taxa 6 and 7 are orthologous, as are taxa 8 and 9, but the pairs (6, 7) and (8, 9) are paralogous (Page [1993] explores this analogy further).

The implications for Hedges et al.'s (1992) study are clear; their data will be relevant only if the comparisons are between orthologous taxa. They are aware of this problem (pp. 1910-1911):

> "The species used here may not be representative of the most recent divergence event between the lineages examined...this type of error always will result in an overestimation of the time of lineage divergence for the taxa from different land masses."

This is correct, but overlooks the implications for their conclusion (p. 1910) that "[t]he wide variation in observed values for the comparisons further suggests that a single event was not responsible for the divergences." Without knowing what kinds of

comparisons are being made this conclusion does not follow; the variation could be due to comparing a mixture of orthologous and paralogous pairs of taxa. For many of the taxa Hedges et al. (1992) sampled the cladistic relationships are poorly understood, making it difficult to assess whether valid comparisons were made (consider the ongoing controversy over relationships within *Anolis* [Guyer and Savage, 1986; Cannatella and de Queiroz, 1989; Williams, 1989b; Guyer and Savage, 1992]). We look at one taxon, *Sphaerodactylus*, in more detail.

SPHAERODACTYLUS

Albumin immunological distances obtained by Hass (1991:table 2) for the gecko *Sphaerodactylus* featured in all five pairwise geographic divergences considered by Hedges et al. (1992). Using a cladogram for the genus obtained by Hass using electrophoretic data (Fig. 11) we can locate these taxa and see whether the divergences being compared are between orthologous or paralogous taxa (we follow Hedge et al.'s convention of using boldface for taxa represented by antisera).

The Jamaica-Hispaniola divergence is represented by the pairs ***S. asterulus*** and *S. parkeri* (ID=7), ***S. asterulus*** and *S. richardsoni* (ID=10), and ***S. asterulus*** and ***S. argus*** (ID=18, the mean of 14 and 22). In Figure 11 we see that ***S. argus*** is more closely related to other Hispaniolian *Sphaerodactylus* than it is to ***S. asterulus***, hence the ID of 18 between Jamaica and Hispaniola is not a measure of a Jamaica-Hispaniola event. Likewise the Hispaniola-Puerto Rico estimate is not made using orthologous pairs of taxa. The Puerto Rican taxa *S. klauberi* and *S. roosevelti* are more closely related to other *Sphaerodactyus* on Hispaniola than they are to species ***S. asterulus*** and ***S. copei*** used by Hedges et al. (1992).

Furthermore, if the tree in Figure 11 is correct then albumin distances between *Sphaerodactylus* taxa are markedly *non*ultrametric. If the distances were ultrametric then all IDs among taxa within a clade would be less than any ID between those taxa

and more remotely related taxa (see Fig. 11). This is not the case for *Sphaerodactylus*; to give one example, ***S. asterulus*** and ***S. copei*** both belong to the *cinereus* series, yet ***S. asterulus*** albumin differs more from ***S. copei*** albumin (ID=34) than albumin from the more distantly related ***S. argus*** (ID=18). This discrepancy between the supposedly ultrametric albumin IDs and the electrophoretic tree raises the possibility that either the albumin distances are not ultrametric and hence not clock-like, or the electrophoretic tree is grossly in error. If the former is true then for this genus albumin ID cannot be used as molecular clock to estimate time of divergence. If the second is true then we lack a cladistic framework interpreting the pairwise distances between *Sphaerodactylus* and so are unable to decide whether the comparisons made by Hedges et al. (1992) are legitimate.

Hass (1991:530) reported finding 1000 equally parsimonious trees for her electrophoretic data, but did not present a consensus summary of those trees. As an exercise we reanalysed Hass' data (her appendix 2) using PAUP 3.0s (Swofford, 1990). All 15 loci were coded as unordered multistate characters with the alleles as character states. Heterozygous individuals were treated as polymorphic (MSTAXA=POLYMORPH), TBR branch swapping was used on a starting tree obtained using the CLOSEST addition sequence. PAUP found 1000 trees (corresponding to the value of MAXTREES used) of 156 steps (ci=0.897, ri=0.874), before running out of memory. The strict and Adams consensus trees of these 1000 trees are shown in Figure 11. We do not pretend that this is an exhaustive analysis of this data set, but our results, together with Hass', inspire little confidence in our knowledge of the relationships of these geckos.

We note in passing that one reason for the multiplicity of equally parsimonious trees is the large number of character states relative to taxa in Hass' data set (this is also a feature of Burnell and Hedges' [1990] *Anolis* data set). This is a consequence of the use of sequential electrophoresis in an attempt to minimise homoplasy due to incorrectly homologised alleles (Hedges, 1989). Unfortunately this laudable goal has undesirable consequences given that the relationship between the character states (i.e.,

the alleles) is unknown. In the absence of character state trees for the alleles each locus is treated as unordered multistate character, and so as the number of character states increases the informativeness of the character decreases.

Designing a Cladistic Biogeographic Study

The cladistic biogeographic literature is at times obscure and seemingly preoccupied with technical questions of interest solely to "the crazed devotee of cladistics" (Nelson, 1984:280). With this in mind we offer some suggestions a reader contemplating undertaking a cladistic biogeographic study may find helpful.

TAXON CLADOGRAMS

A cladistic biogeography of the Caribbean will require robust phylogenies of Caribbean taxa. This requirement is not trivial. Ideally we would like cladograms based on independent data sets, such as exist for *Epicrates* (Tolson, 1987; Kluge, 1989).

The *Epicrates* example is instructive. For the lipid data set there are 10 equally parsimonious trees whereas the morphological data set supports 2 trees (Kluge, 1989). None of these trees is identical, nor are any of the trees with lengths within 5% of the shortest trees (Swofford, 1991) the same. However, the most parsimonious trees are very similar. Swofford's observation that the agreement subtrees (= common pruned trees) for the 12 shortest contain just six of the 10 taxa overstates the dissimilarity between the two sets of trees by confounding within data set ambiguity (each data set supports more than one tree) with between data set differences. By computing agreement subtrees for each pair of lipid and morphological tree we found that two pairs of trees differ solely in the placement of one taxon. To the extent that the best trees from the two data sets are very similar we should be encouraged that robust

phylogenies are obtainable; to the extent that the trees are nevertheless different we should be cautious about accepting trees inferred from a single data set.

That trees for different data sets can differ serves to remind us that our cladograms are based on samples of characters and hence subject to sampling error. As biogeographers we are consumers of cladograms and hence we need to pay particular attention to the strengths and weakness of the cladograms upon which we base our conclusions. DeBry (1992) is one of few authors who have explicitly attempted to incorporate uncertainty about taxonomic relationships in a biogeographic analysis.

The existence of multiple equally parsimonious taxon trees for a given data set, or incongruent trees for the same taxa from different data sets raises the problem of how to proceed in the face of such uncertainty. Lydeard et al. (submitted) encountered these problems in their study of *Gambusia* fishes. One approach adopted was to construct area cladograms from each taxon cladogram separately, and then retain the most informative area cladograms (i.e., those obtained from the taxon cladogram that permitted the fewest, least different area cladograms). This is a useful strategy when area cladograms for other taxa are in short supply as it allows the formulation of the most explicit hypothesis which can subsequently be tested using other taxa. By comparing the area cladograms for different trees for *Gambusia* Lydeard et al. were also able to assess the impact of phylogenetic uncertainty on their hypothesis of biogeographic relationships.

DEFINITION OF AREAS

Platnick (1991) stressed the need for maximally endemic taxa for a meaningful biogeographic analysis. Large, purely geographically defined areas are unlikely to be natural areas (Platnick and Nelson, 1984). Hedge's et al.'s (1992) lumping of North, Central, and South America into one category called “Mainland,” and all the Caribbean islands into the second category “West Indies” is a particularly egregious example that

presupposes the monophyly of all Caribbean taxa with respect to their mainland relatives. Indeed, the considerable range in albumin IDs between "Mainland" and "West Indian" taxa may well in part reflect the artificial nature of those areas (in addition to the other reasons discussed above).

COMPOSITE AREAS

A number of Caribbean islands (e.g., Cuba, Hispaniola) are thought to be geological composites, raising the possibility that their biotas are also composites. The implications of composite areas for cladistic biogeography have been discussed by Craw (1982, 1988), Platnick and Nelson (1984), and Rosen (1985) among others. Foremost among these is that different taxa may support different sets of area relationships. Consequently, discovering that two taxa have quite different area cladograms need not necessarily imply that one or other taxon has dispersed. At the same time, there is a danger that once we allow for the existence of multiple patterns we might regard any number of patterns as all equally valid. If a set of area cladograms fall into groups such that within each group the cladograms agree but between groups the cladograms conflict then we could argue that we have evidence of multiple but replicated patterns (e.g., Cracraft, 1988). If however the set of cladograms are all mutually quite different then the hypothesis of one or more underlying patterns becomes less tenable.

At the same time, we should ask what constitutes evidence for composite biotas. Cladograms for relict biotas that differentiated prior to the most recent geological events may on first glance suggest the presence of composite areas. To illustrate, Figure **Error! Bookmark not defined.**a shows a taxon-area cladogram for seven taxa in four areas. If we have just taxa 1, 2, 5, 6, and 7 (perhaps our sample was incomplete, or the other taxa are extinct) we might interpret the resulting cladogram (Fig. **Error! Bookmark not defined.**b) as suggesting that area B was composite as

the nearest relatives of its two resident taxa (2 and 5) occur in different areas. Yet this interpretation would be wrong. Merely finding an area grouped with one set of areas by one subclade and then grouped with another set of areas elsewhere in the cladogram is not, in itself, evidence for a composite area.

As an empirical example consider Figure 11 which shows one of Liebherr's (1988d:fig 6) taxon-area cladograms for Caribbean *Platynus* beetles. This cladogram shows substantial redundancy, that is, the same areas appear more than once on the cladogram. The two parts of Hispaniola appear together in two different places on the cladogram, grouped with either northern Central American taxa, or with Cuban taxa, leading Liebherr (1988d: 403) to conclude that Hispaniola is a "hybrid" island. However, if we decompose the cladogram into subtrees that minimise redundancy (this can be likened to identifying the sets of biogeographically orthologous taxa; see Nelson and Ladiges, 1991:481, and Page, 1993) we see that all the subtrees are mutually consistent (Fig. 11), that is, we could combine them all to create one or more area cladograms that all subtrees would agree with. Figure 11 shows the area cladogram for *Platynus* that has the fewest items of error (Nelson and Platnick, 1981; Page, 1990a). This area cladogram is consistent with the four subtrees shown in Figure 11.

CHOOSING TAXA

Many problems confronting a cladistic biogeographic study could be avoided if the taxa chosen were sampled with the biogeographic analysis in mind. As Platnick (1991) notes, the substantial investment of time, effort and money that a systematic analysis entails can create the expectation that the study group will be biogeographically informative, regardless of how poorly chosen for that purpose the group may be. We offer three suggestions:

(1) ENDEMICITY

The first requirement for biogeographic analysis is that the clade is maximally endemic. Widespread taxa are a source of ambiguity (as well as an inspiration for underemployed biogeographers to invent ever cleverer ways of combating them) as two or more areas can share the same taxon due to relatedness, geographic proximity, or dispersal (Platnick and Nelson, 1978; Page, 1989). Maximising endemicity minimises the potential for ambiguity.

(2) SAMPLING EXHAUSTIVELY WITHIN A CLADE

The second requirement is to maximise the thoroughness of within clade sampling. This requirement can conflict with the systematist's desire to characterise the relationships of a speciose clade by using exemplar taxa to represent subclades thought to be monophyletic. For example, *Anolis* species are typically grouped into putatively monophyletic "series" (e.g., Burnell and Hedges, 1990) which have served as the basis for sampling taxa for DNA sequencing (Hass et al. 1993), amongst other characters.

While this is a perfectly reasonable strategy for maximising the systematic informativeness of a finite sample of taxa, it need not result in biogeographically informative data. Consider the hypothetical example in Figure 11 of a clade of nine taxa thought to comprise three monophyletic subclades. A systematist wishing to characterise the broad pattern of relationships in a clade of nine taxa may choose a single exemplar taxon from each subclade and arrive at the tree in Figure 11b. This tree correctly depicts the taxonomic relationships but is quite misleading about the biogeographic relationships. If we were to take into account that each clade in the subsample has closer relatives found in the other areas (i.e., taxon 3 in area C is more closely related to taxa 1 and 2 in areas A and B than it is to taxon 5) then the taxon cladogram is no longer misleading but merely uninformative about biogeographic

relationships. A biogeographer would prefer to sample exhaustively within one of the subclades in Figure 11, in this example recovering the correct biogeographic relationships (Fig. 11c). Ideally, of course, both systematist and biogeographer want to sample all taxa within a clade. However, when limited to sampling a subset of taxa they may differ in their preferred choice of taxa.

(3) Including All Relevant Areas

The third requirement is to include taxa from as many relevant areas as possible. Many biogeographic discussions of the Caribbean implicitly assume that the island taxa are monophyletic with respect to their mainland relatives. This need not be the case, and inclusion of mainland taxa can have a dramatic impact on biogeographic interpretations. For example, Liebherr's (1988d) inclusion of mainland taxa of *Platynus* beetles changed the hypothesised phylogeny of the Antillean taxa enough to alter his interpretation from one of predominantly overwater dispersal (Liebherr, 1988c) in his analysis of only Antillean taxa, to one of predominantly vicariance (Liebherr, 1988d).

Summary

> "It is incumbent on us as systematists to present our data as explicitly as possible (preferably through the use of maps and cladograms), but unless we are willing to consider more than single groups at a time, we cannot adequately analyse that data." (Platnick and Nelson, 1978: 5)

Understanding the history of the Caribbean poses a considerable scientific challenge requiring carefully selected data for different taxa, coupled with rigorous analysis. We have focused our critique on Hedges et al. (1992) because in our opinion it meets neither of these two requirements. Lest we be misunderstood, we emphasise

that we do not reject the possible utility of estimates of genetic divergence and molecular clock hypotheses in biogeographic analysis (quite the contrary, see Page, 1990b; 1993) — rather we appeal for careful analysis. In particular we stress the need for estimates of genetic distance and time of divergence to be accompanied by confidence intervals. Omitting confidence intervals lends the data an appearance of precision it does not possess. Furthermore, the interpretation of genetic distances requires a cladistic framework, which Hedges et al. do not provide.

Perhaps the most troubling aspect of the kind of study typified by Hedges et al. (1992) is that the absence of area cladograms makes it difficult for other workers to compare their data with Hedges et al.'s, unless the data also consists of albumin IDs (or some other measure of distance that is correlated with ID). A biogeography based solely on estimates of genetic distance excludes a large class of potential data, namely area cladograms derived from morphologically based taxon cladograms.

The language of cladistic biogeography is the area cladogram, its goal is testing hypotheses of general pattern(s). Currently many authors, whether advocating dispersal or vicariance, simply offer best-guess scenarios based on distributional patterns of hypothesised geological models without ever attempting to construct area cladograms. Unless systematists are willing to present area cladograms for their taxa (whatever the source of data) and seek to compare the results with area cladograms for other taxa, cladistic biogeography will remain in the doldrums and biogeography itself will remain the province of story telling. The subject deserves better.

Acknowledgments

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Figure captions:

Fig. 1. Geological area cladograms for the Caribbean for five different time periods from mid-Cenozoic to the present day (from Rosen, 1985: figs 35, 37, 39, 41, and 43). Area abbreviations are Central America (CA), nuclear Central America (NCA), Jamaica (JAM), south western Hispaniola (SW HISP), central Hispaniola (C HISP), western Cuba (W CUB), eastern Cuba (E CUB), and south Bahamas (S BAH).

Fig. 2 Albumin immunological distances (ID) between Caribbean and mainland taxa, and between taxa from different islands in the Caribbean region. The vertical axis is calibrated in both ID and absolute time (in millions of years ago, mya), assuming 1ID = 0.6 million years. Shaded regions indicate IDs predicted if divergence between taxa was due to vicariance, other geological events are also indicated (redrawn from Hedges et al., 1992: fig 1). Area abbreviations are Jamaica (Jam), Hispaniola (Hsp), and Puerto Rico (PR).

Fig. 3. An illustration of the ultrametric inequality $D_{AB} \leq D_{AC} = D_{BC}$. In this example $D_{AB} = 2$, and $D_{AC} = D_{BC} = 4$.

Fig 4. Two taxon-area cladograms for two sets of taxa (1-5) and (6-10) occurring in three areas and the geographic event(s) distinguishing areas A and B. In cladogram (a) the genetic distance between any taxon from area A with any taxon from area B will be related to the geographic event between areas A and B. However, for cladogram (b) only the distances between taxa 6 and 7, and between taxa 8 and 9 will correspond to the desired event. The genetic distances between taxon 6 with 9, or between taxon 7 with 8 correspond to an earlier event.

Fig. 5. Hass' (1991:fig. 2) cladogram for *Sphaerodactylus* geckos showing the distribution of the Caribbean taxa. The pairwise albumin immunological distances between taxa used by Hedges et al. (1992) to date the Hispaniola-Jamaica and Hispaniola-Puerto Rico divergences are shown. Note that the comparisons between *S. asterulus* and *S. argus*, and between *S. asterulus/copei* and *S. klauberi/roosevelti* are not valid estimates of the age of divergence between the areas those taxa occur in (compare with Fig. 11 and see text).

Fig. 6. Strict and Adams consensus of 1000 trees for *Sphaerodactylus* computed from Hass' (1991) data.

Fig. 7. (a) A taxon-area cladogram for seven taxa occurring in four areas and (b) a subtree of that cladogram. Cladogram (b) could be interpreted to suggest that area B is composite as its resident taxa (2 and 5) have their nearest relatives in different areas. However, in this case it is simply the result of incomplete sampling (see text).

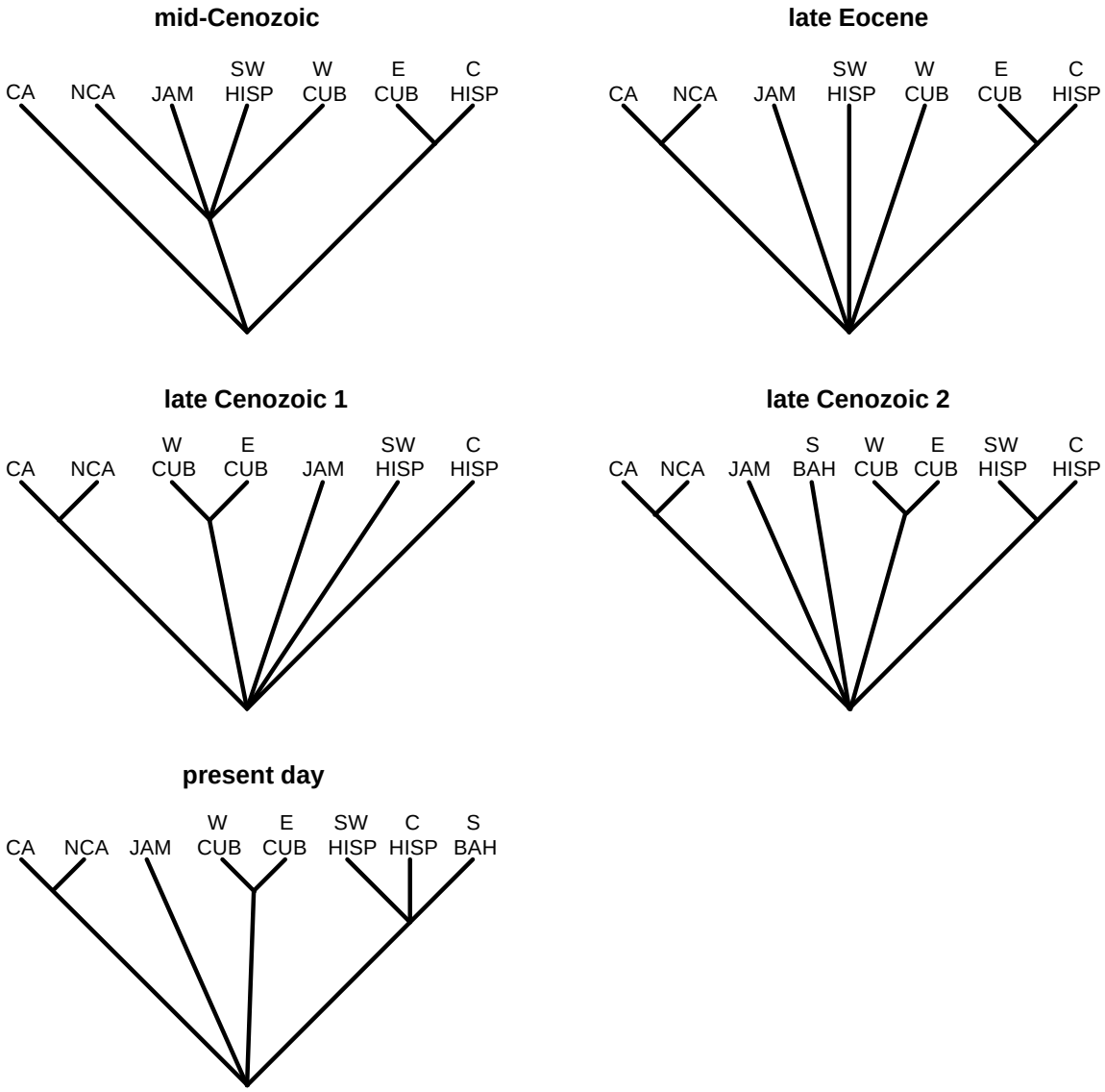
Fig. 8. Cladogram for *Platynus* beetles showing their distribution in the Caribbean (after Liebherr, 1988d: fig 6, with museum collection numbers for undescribed species replaced by names published in Liebherr, 1989).

Fig. 9. Four informative area cladograms for subsets of the areas occupied by *Platynus* obtained from the taxon-area cladogram in Figure 11. The number assigned to the root of each subtree corresponds to the node with the same number in Figure 11. Area abbreviations are Central America (CA), northern Central America (NoCA), Jamaica (J), south western Hispaniola (SH), central Hispaniola (CH), western Cuba (WC), eastern Cuba (EC), and the Lesser Antilles (LA).

Fig. 10. Area cladogram for the *Platynus* beetle cladogram in Fig. 11 that minimises the number of items of error. This tree is consistent with the four subtrees

shown in Figure 9. Note that the island areas do not form a clade with respect to the mainland areas NoCA and CA, so that some islands are more closely related to part of the mainland than they are to other islands (area abbreviations as in Figure 11).

Fig. 11. The importance for biogeographic analysis of thoroughly sampling within a clade. (a) shows a clade of nine taxa (1-9) found in three areas (A-C). A systematist wishing to characterise the broad pattern of relationships within the clade might assume that subclades 1-3, 4-6, and 7-9 are monophyletic and then sample a single exemplar taxon from within each clade, e.g. taxa 3, 5, and 7. In this example the result (b) accurately reflects the taxonomic relationships but distorts (or is at best uninformative about) the relationships between the areas occupied by the taxa. The correct area relationships (c) are obtained by sampling exhaustively within one of the subclades (e.g., taxa 1-3).



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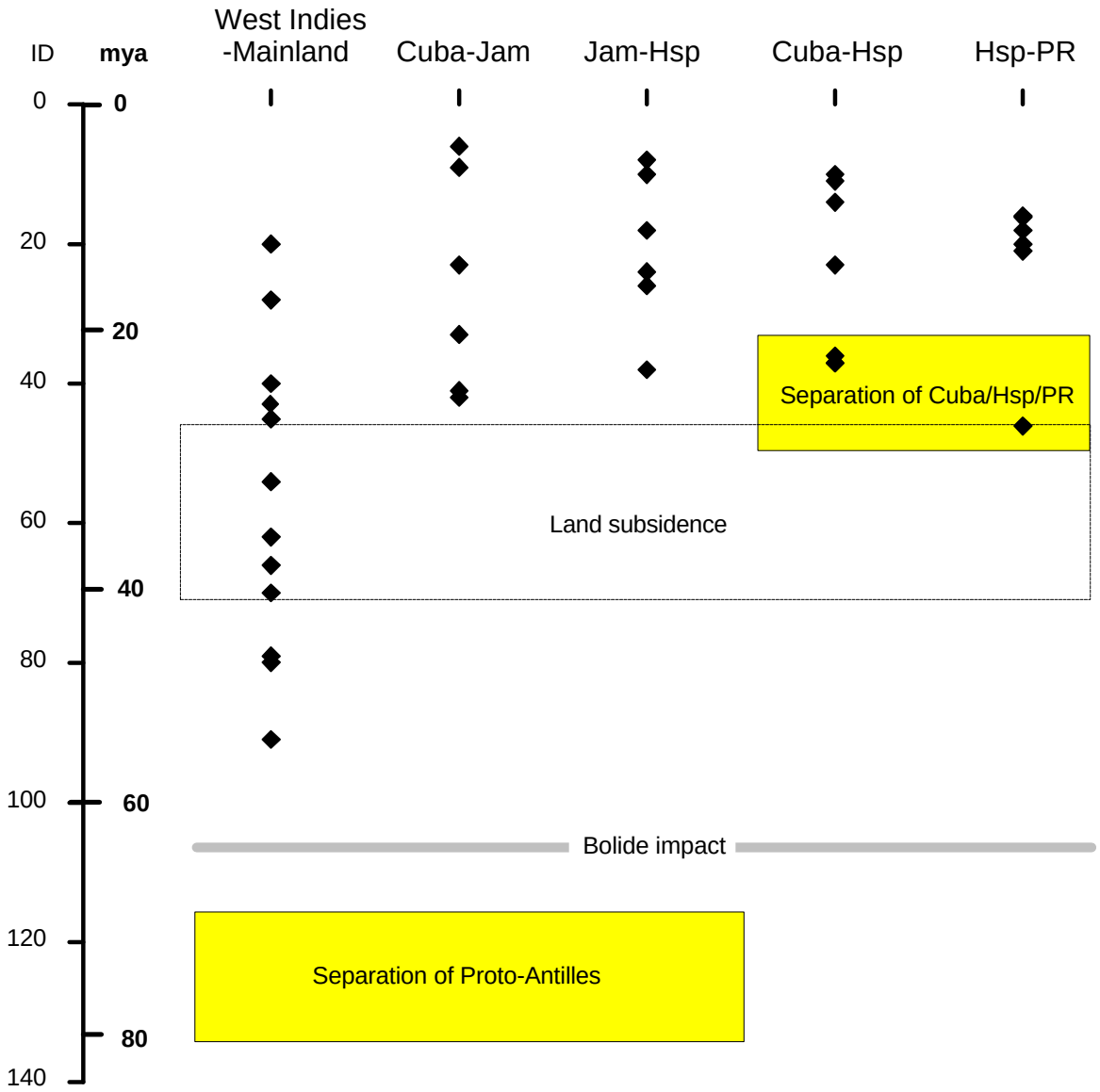
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Land subsidence
Bolide impact
Separation of Proto-Antilles

Fig. 11

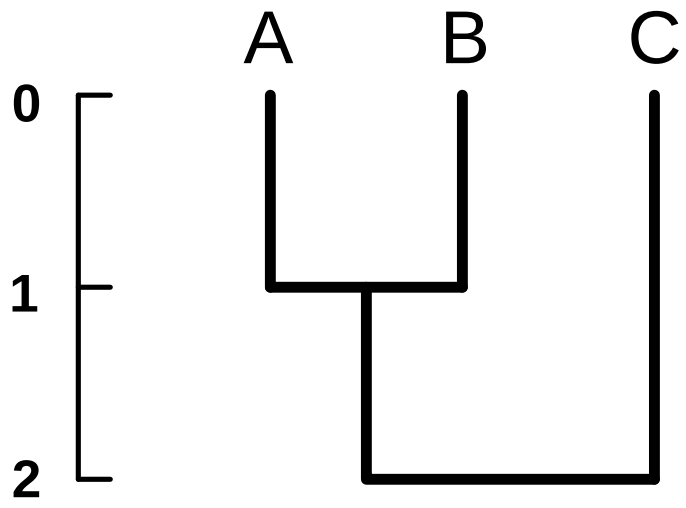

Fig. 11

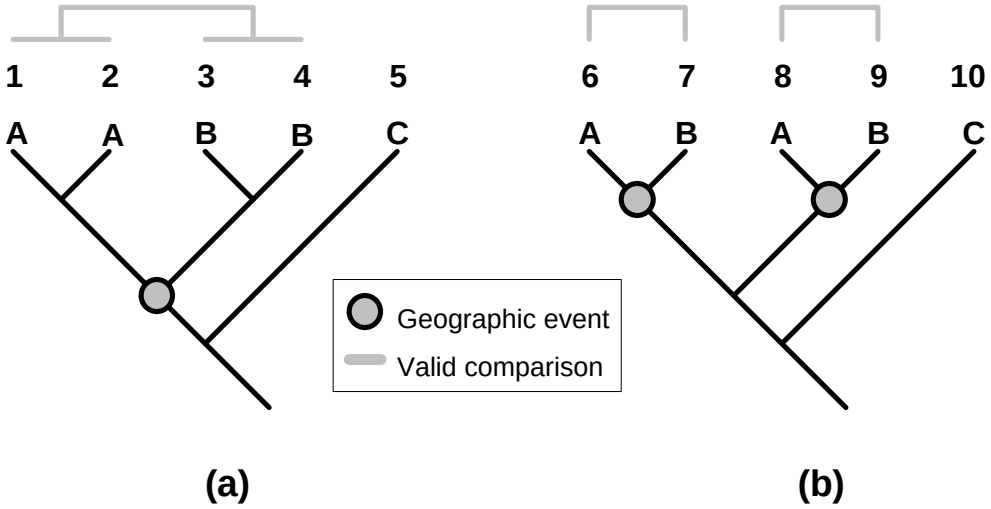
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Fig 11

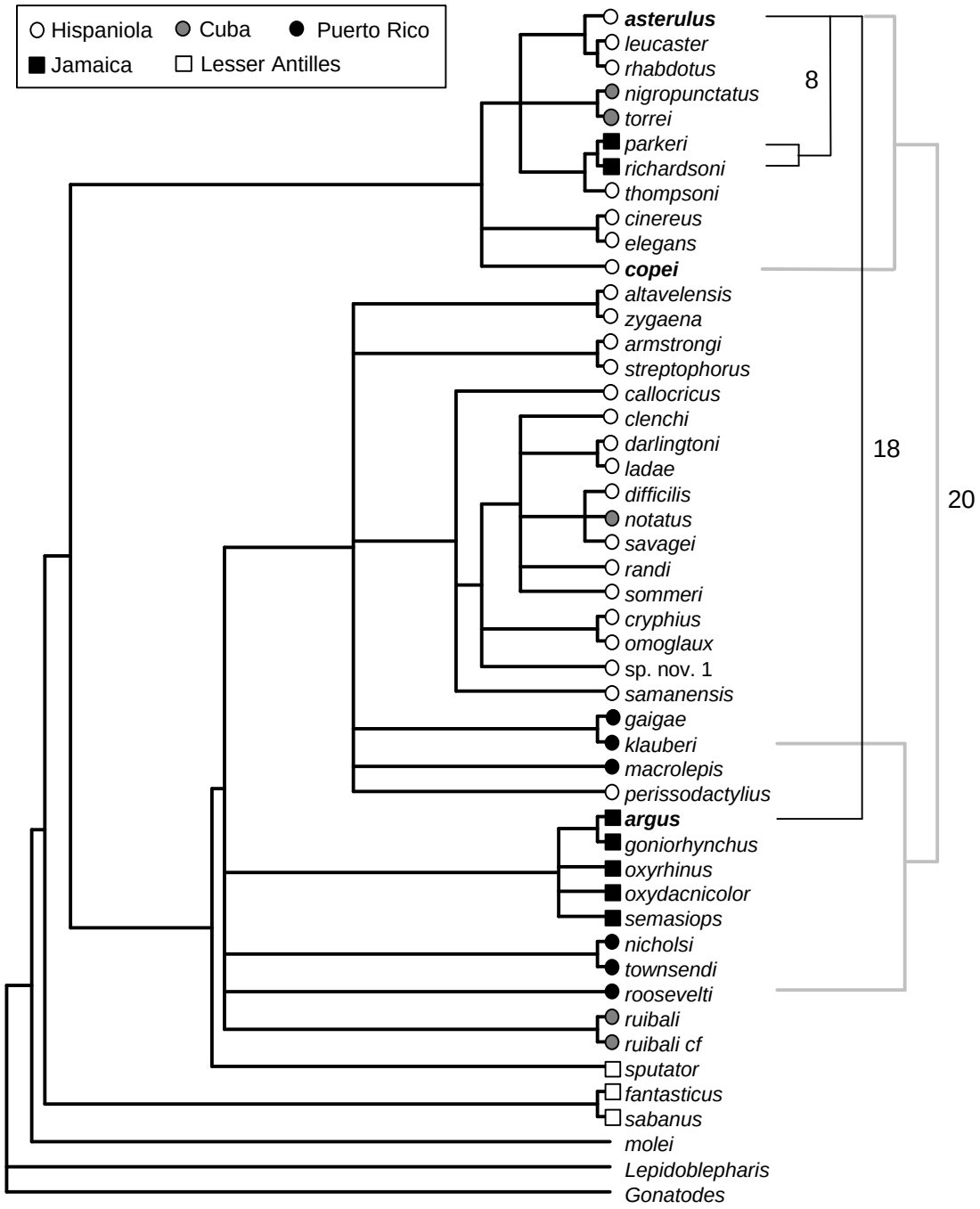
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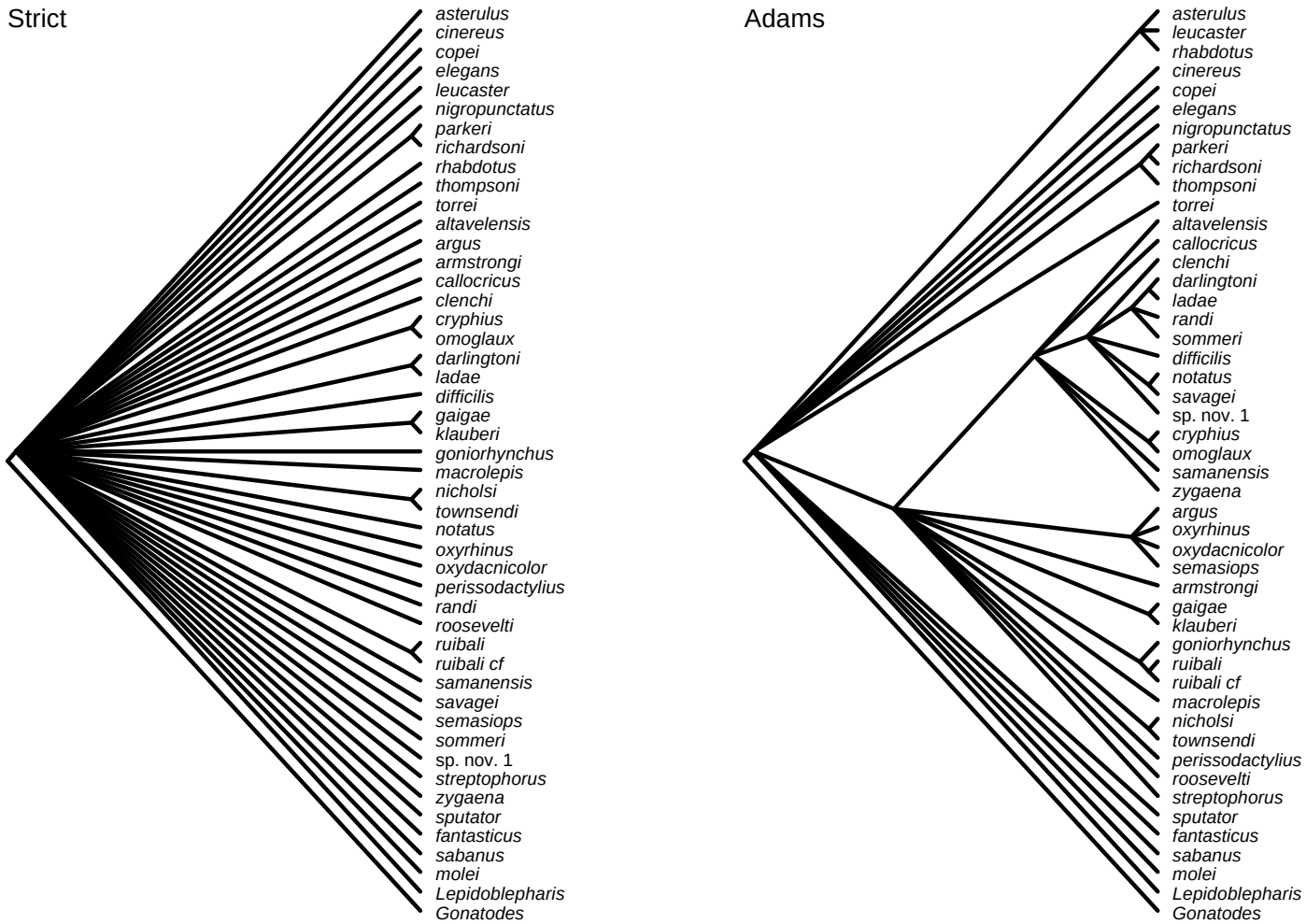
Fig. 11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armstrongi
callocricus
clenchi
cryphius
omoglaux
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ladae
difficilis
gaigae
klauberi
goniorhynchus
macrolepis
nicholsi
townsendi
notatus
oxyrhinus
oxydacnicolor
perissodactylius
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ruibali
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samanensis
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sommeri
sp. nov. 1
streptophorus
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sputator
fantasticus
sabanus
molei
Lepidoblepharis
Gonatodes
Adams
asterulus
leucaster
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Fig. 11

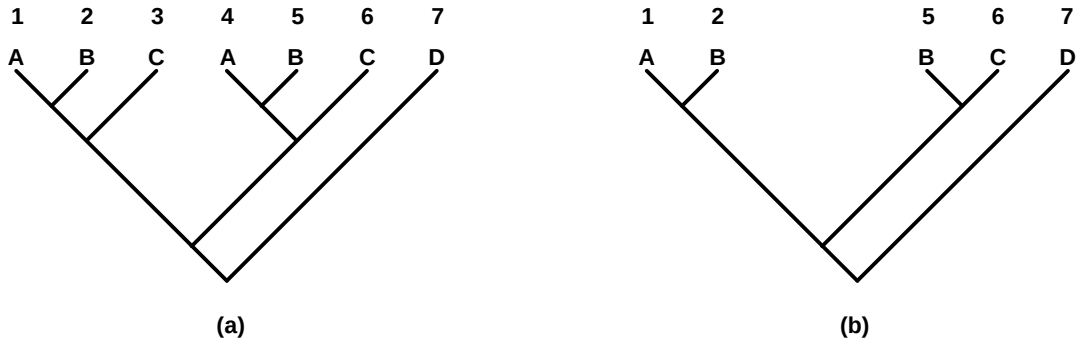
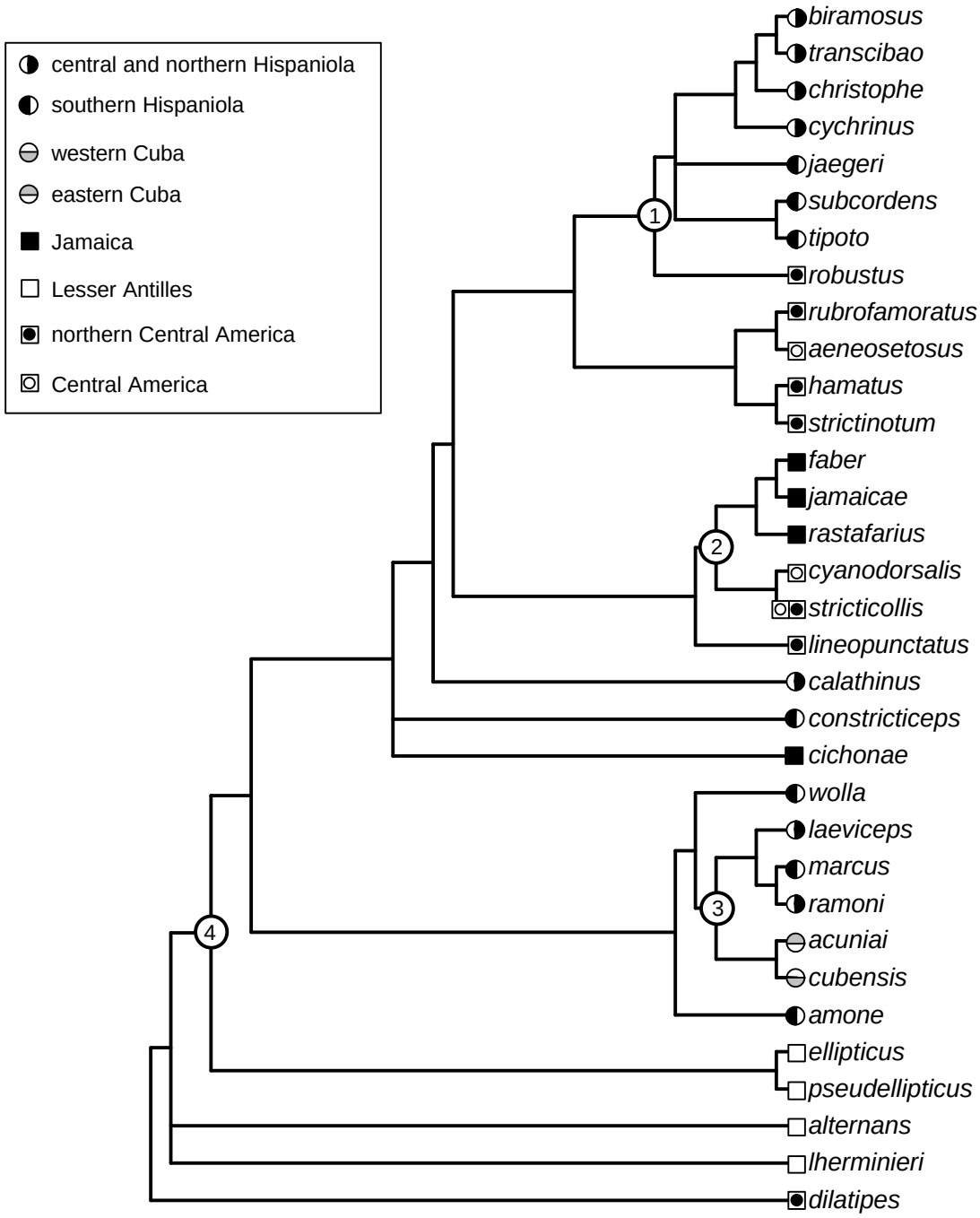


Fig. 11


central and northern Hispaniola
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northern Central America
Central America
biramosus
transcibao
christophe
cychrinus
jaegeri
subcordens
tipoto
robustus
rubrofamoratus
aeneosetosus
hamatus
strictinotum
faber
jamaicae
rastafarius
cyanodorsalis
stricticollis
lineopunctatus
calathinus
constricticeps
cichonae
wolla
laeviceps
marcus
ramoni
acuniai
cubensis
amone
ellipticus
pseudellipticus
alternans
lherminieri
dilatipes
1
2
3
4

Fig. 11

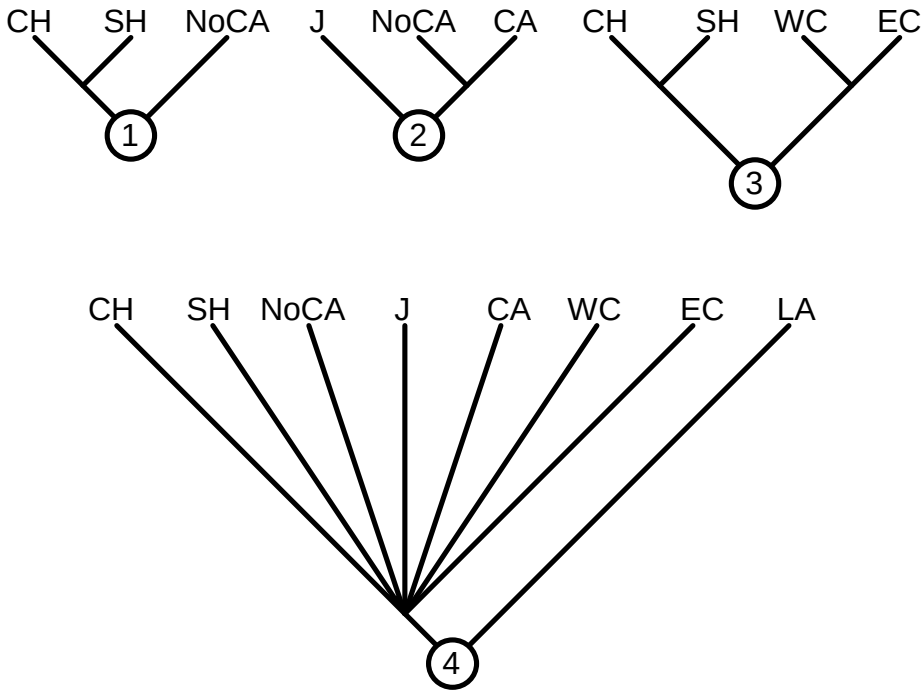

Fig. 11

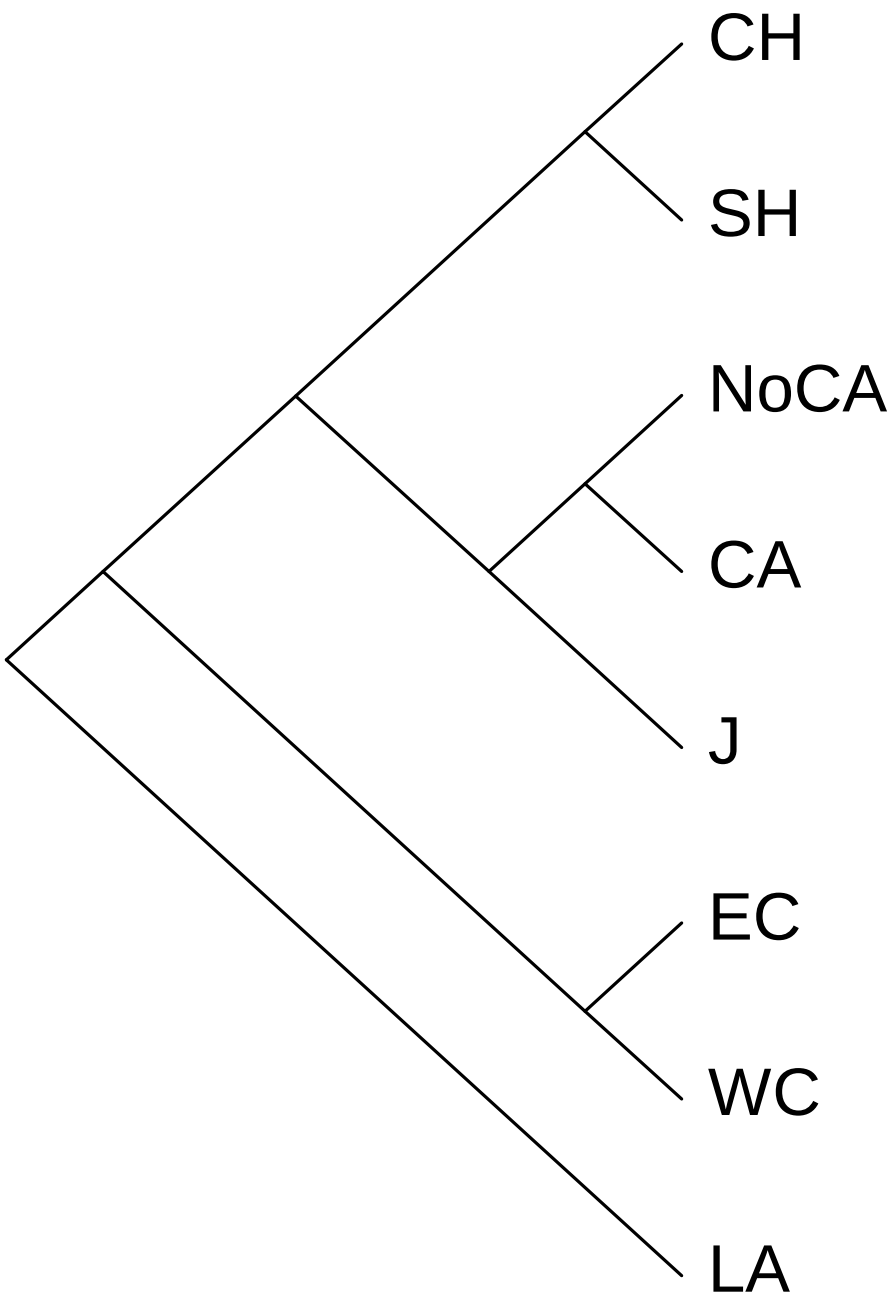

Fig. 11

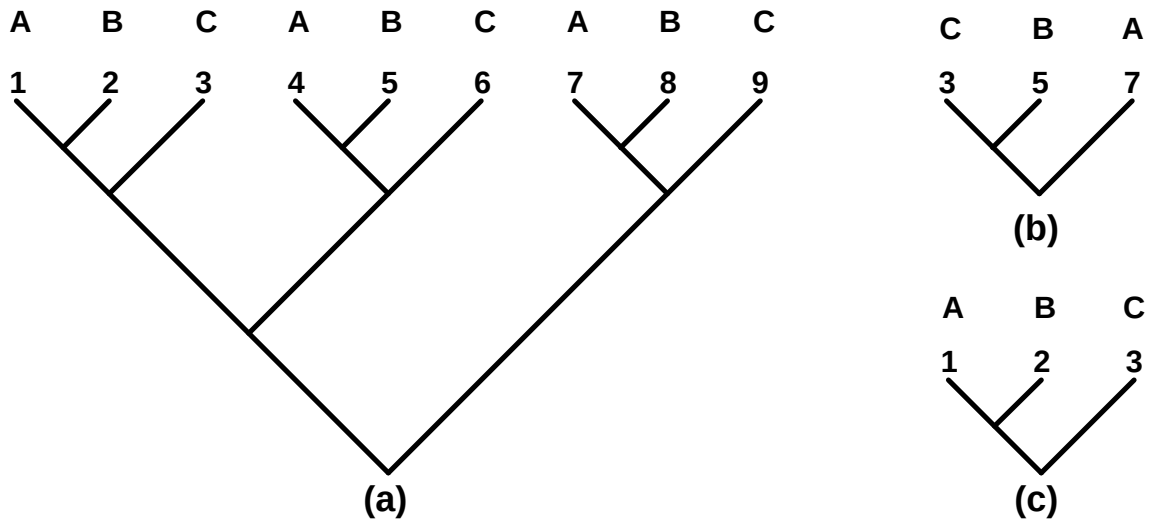

Fig. 11