Title
Historical biogeography: the relationship between phylogeny and geography

Permalink
https://escholarship.org/uc/item/8f72373f

Journal
Biogeographia – The Journal of Integrative Biogeography, 11(1)

ISSN
1594-7629

Author
Estabrook, George F.

Publication Date
1987

DOI
10.21426/B611110296

Peer reviewed

Historical biogeography: the relationship between phylogeny and geography

GEORGE G. ESTABROOK

Deparment of Biology and Herbarium. The University of Michigan, Ann Arbor, MI 48109 USA

SUMMARY

The Author argues that knowledge of geographical barriers, without additional assumptions about rates of evolutionary change including extinctions, or about the ability, likelihood or rates of dispersal, contributes little to more credibly reconstructing evolutionary relationships. A hypothetical, but typical example is given to illustrate these assumptions, with a group of 9 related species occurring in two areas presently divided geographically by a young mountain range.

INTRODUCTION

Historical biogeography seeks to explain the present day geographycal distributions of related groups of organisms by means of the properties of those organisms and of their environments, and by means of movements of those organisms (and of restrictions to such movements) in the areas in which they live. These changes and movements have occurred at different places and at different times during the past. Exactly what changed into what in which organisms where/when, and exactly which organisms moved from where to where and when, are usually unknown, and usually can never be known with great certainty. Because present day organisms *do* have observable differences, and *do* occur in different places, it is clear that changes and movements must have occurred. It is the challenge of historical biogeography to put forward hypotheses of change in organisms (evolution), movements of organisms (dispersal), changes in environments, and movements/changes in areas, that can explain the geographical distributions of groups of related organisms, and then to argue their differential credibility.

In contrast to experimental methods appropriate to test explanations of ongoing processes that occur continuously or repeatedly through time, the methods of historical biogeography are the ways in which additional ideas and data can be used to argue the differential credibility of hypothesized accounts of what happened in one particular series of specific historical events.

As a prerequisite to advancing hypotheses to explain the geographical

distribution of related groups of organisms, we need to know what are the related groups and what are their geographical distribution. These tasks belong to those who collect, identify, and classify organisms. It is important to have a good knowledge of the properties and distribution of the organisms whose historical biogeography would be explained, and for this reason the taxonomic authorities for a group of organisms are often those who would be among its biogeographers. Although good taxonomy near the species level and good knowledge of geographic distributions for the taxonomic groups under study is essential, historical biogeographical studies require more than taxonomy.

Typically, two related processes are going on simultaneously through time: changes in areas, in their locations, in their environmental conditions, and in what organisms can reach them and occur on them; and evolutionary changes in the organisms themselves. These processes are related because changes in areas provide some of the isolating mechanisms and changes in selection pressures than participate in producing evolutionary changes in organisms. In addition, changes in areas can bring together kinds of organisms formerly isolated from one another, after which a variety of new biotic interactions provide selection pressures that also participate in producing evolutionary changes in organisms. These processes are related also because evolutionary change in organisms can affect their ability to disperse, establish, and thrive in different environments, and thus come to occupy areas where they were formerly absent.

A moment's reflection should make it absolutely clear that present day geographical distribution of groups of related organisms, in and of themselves, do not in any way constrain the possibilities for the ancestor/descendant relationships through which they evolved. Similarly, ancestor/descendant relationships, in and of themselves, do not constrain possibilities for present day geographical distributions. Other assumptions, ideas or data must be considered.

The appearance and disappearance at various times of physical or environmental barriers to dispersal have been considered a fundamental determinant of the relationship between geography and the phylogeny of a groups of related organisms (Nelson and Platnick, 1981; Rosen, 1978). Nelson (1984) proposed that barriers to the dispersal of members of a group of related organisms among geographical areas have, in some sense, evolved; that these historical relationships among areas can somehow be adequately represented by a tree diagram; and that there should be some relationship between this tree diagram and the one representing aspects of the phylogeny of this group.

Here I will argue that knowledge of geographic barriers, without strong additional assumptions (or rarely knowledge) about rates of evolutionary change including extinction, or about the ability, likelihood, or rates of dis-

persal, contributes little to more credibly reconstructing evolutionary relationships. In many cases, it is more sound first to estimate evolutionary relationships among kinds of organisms, based on comparative biology and development, and on studies of ecology and adaptation; then these estimates can be used together with information and assumptions about geographical changes, dispersibility, and local extinctions, to suggest and constrain possible historical, geographical scenarios that would explain present geographical distributions.

EXAMPLE

To illustrate these points more concretely, I will describe a hypothetical, but typical example. A distinct group of 9 related species occurs in two areas presently divided geographically by a young mountain range that is now a physical and ecological barrier to the dispersal of these species. Formerly this range was not sufficiently well developed to present a barrier to the dispersal of the ancestors of this group, and they all occupied appropriate niches in these two areas (then only one area). Presently, species e, f, and y occur in one area, and species a, b, c, d, x, and z occur in the other area. The one area has only limestone soils: y occupies drier sites with shorter growing seasons; f occupies wetter sites, and e is a weed associated with agricultural disturbance. The other area also has limestone soils where d occupies drier sites with shorter growing seasons, z occupies wetter sites, and x is a weed associated with agricultural disturbance. In addition, this area has forest-covered acid soils that extend into the higher altitudes: x occurs in the understory; b occurs at the higher altitude ecotone where the growing season is shortened by the harsh winters; and a occurs at the low altitude ecotone.

Some characters of these species reflect their adaptations to the various conditions in which they grow; other characters reflect their common ancestry and evidence their phylogenetic relationships at various temporal scales. Typically, the observations made in a study of comparative biology and development can be the basis for characters that reflect either or both types of information, and which type is reflected in any particular character will not be immediately clear. To illustrate the possibilities, I will describe a hypotetical evolutionary scenario for the 9 species mentioned above.

Eight milion years ago, x grew on acid soils in the forest understory. Seven million years ago y evolved to exploit drier, unforested, limestone soils. Six million years ago z evolved from y to occupy newly formed, wetter limestone soil habitats. The three species underwent range expansion and came to occupy habitats appropriate for them over a large geographic area. Five million years ago this area was effectively divided into two areas by the increasing height and harshness of a growing mountain range. This barrier prevented all dispersal from one side to the other. All the acid forest soils were on one side of this mountain range, confined to the lower slopes where

there was somewhat more rain. In consequence, x was found only on this side of the mountains. But both wet and dry limestone soil habitats were to be found on both sides of the mountains and so were y and z.

The side with acid forest became wetter and so dry limestone soil sites became rare, isolated, and small, with some lacking members of y, while z became common and continuous. When conditions became drier again, 3 million years ago, species d evolved from z to occupy the largely unoccupied, expanding, drier, limestone soil habitat. As the newly evolved d spread, it encountered y and excluded it competitively. By two million years ago y had become extinct on this side of the barrier. Increasing mountain height produced a high altitude limit to acid forests and species b evolved from x to exploit this high altitude ecotone.

Five million years ago, the drier side, which lacked the acid forest habitat, became even drier with habitats for z becoming rare, isolated, and smaller, with some lacking the wet adapted z altogether, while y became widespread and common. Four million years ago conditions became somewhat wetter again and f evolved from y to fill the expanding but largely unoccupied wetter limestone soil habitats. As the newly evolved f spread, it encountered z and excluded it competitively, so that by 3 million years ago z was extinct on this side of the barrier.

Twenty thousand years ago forest clearance by humans opened low altitude, acid soil, forest ecotone habitat and a evolved from the forest dwelling x to exploit this habitat. Seven thousand years ago when human disturbance for early agriculture in the wetter, limestone sites opened a niche for weeds, on one side of the barrier the weedy c evolved from the wet, limestone soil dwelling z, and on the other side of the barrier the weedy e evolved from the wed, limestone soil dwelling f, to fill these niches.

These historical events have produced the present day species and their geographical distributions. Their phylogenic tree is shown in Figure 1 and their Haase diagram of ancestor/descendant relationships (Estabrook, 1984) is shown in Figure 2. Table 1 presents their adaptive/ecological characters and Figure 3 is the average link phenogram of simple mismatching distances using the data of Table 1. If we suppose that one unique, observable, new property arose at each speciation and that this property was inherited without change by all subsequent descendants, then characters based on these properties would evidence ancestor/descendant relationships among the species. Table 2 presents such characters; their sum (Estabrook, 1984) would reconstruct the diagram of Figure 2. Figure 4 is the average link phenogram of simple mismatching distances using the data of both Table 1 and Table 2 together. Figures 5A and 5B are two parsimony reconstructions of undirect ancestor/descendant relationships (made by WAGNER78, written by J.S. Farris) based on the data of Tables 1 and 2. They each require 17 steps, only three extra steps above the minimum of one per character.

An undirect compatibility analysis of the same characters (using

x   a   b   z   c   d   f   e   y

BARRIER
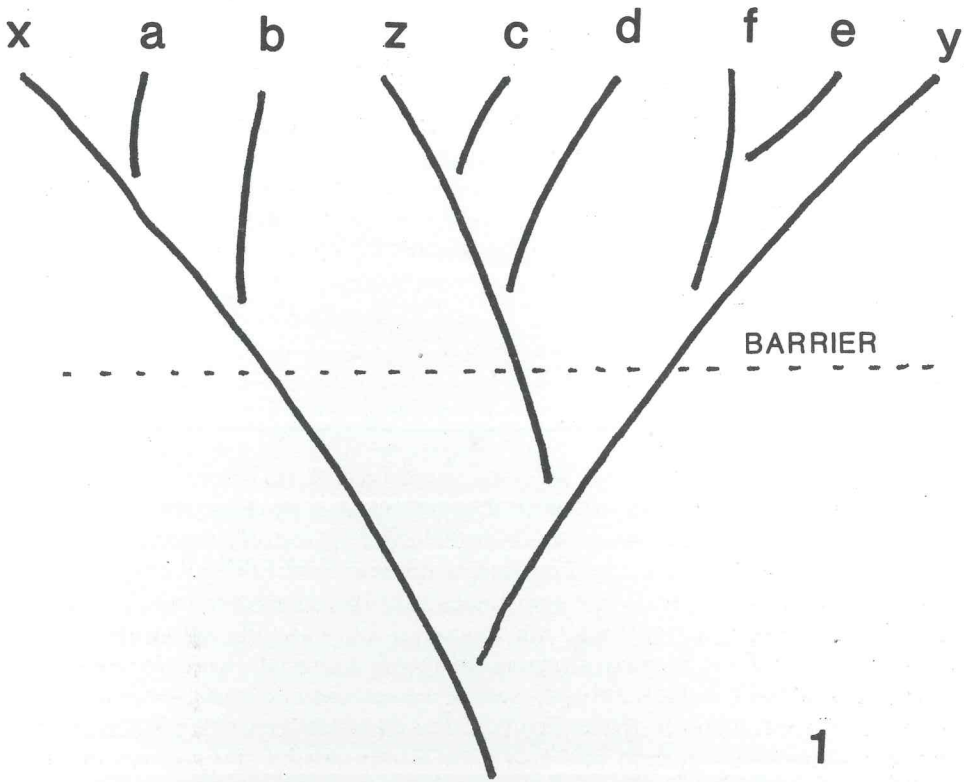
1
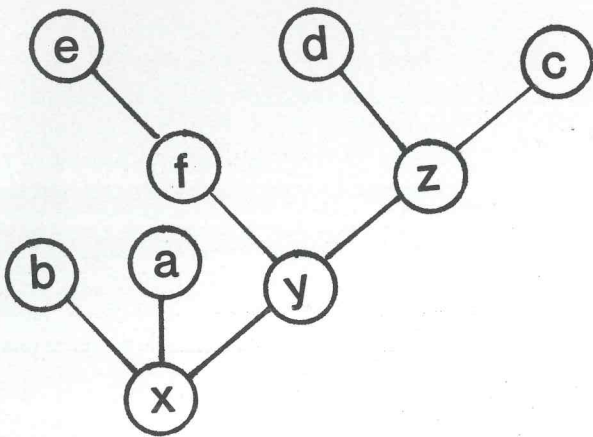
2

FIG. 1-2

TABLE 1 - The columns of Table 1 show the states of the adaptive/ecological characters for the species labeling the rows. The first row shows the character numbers used in Figures 6A, 6B, and 6C. The second row shows the character names used in the text.

	1 Forest	2 Ecotone	3 Acid	4 Wet	5 Short season	6 Weed
x	1	0	1	1	0	0
y	0	0	0	0	1	0
z	0	0	0	1	0	0
a	1	1	1	1	1	0
b	1	1	1	1	0	0
c	0	0	0	1	0	1
d	0	0	0	0	1	0
e	0	0	0	1	0	1
f	0	0	0	1	0	0

CLINCH, written by K.L. Fiala) revealed three groups of 11 characters each. One contains all 8 characters of Table 2 together with the first three characters of Table 1. The reconstruction of undirected ancestor/descendant relationship based on it is shown in Figure 6A. Characters FOREST and ACID, although adaptive/ecological, are also historically true and accurately reflect ancestor/descendant relationships. But character ECOTONE, although compatible with the rest, is historically false; in fact it *did* arise twice, in parallel, and thus incorrectly suggests the existence of an extinct common ancestor for *a* and *b*. But each of these evolved the ecotone character state from understory dwelling *x*, and so this character falsely refines the true ancestor/descendant diagram. This false refinement is also present in the parsimony reconstructions of Figure 5A and 5B.

Another group of compatible characters is the result of the reversed and parallel character WET displacing the historically correct character EVOLVED FROM *z*. This gives the diagram of Figure 6B, which resembles somewhat the parsimony reconstructions of Figures 5A and 5B. The third group of 11 compatible characters is the result of additionally replacing historically correct character EVOLVED FROM *f* with the parallel, adaptive/ecological character WEED. This gives the diagram of Figure 6C, which suggests relationships similar to the ecological relationships of phenogram of Figure 3. This is because there are only three informative (contradictable) historical characters; removing two from the group of 11 leaves only one, EVOLVED FROM *y*, which is equivalent to the adaptive/ecological characters ACID and FOREST; and among adaptive/ecological characters, only the very incompatible SHORT SEASON is excluded. The parsimony reconstructions of Figures 5A and 5B resemble somewhat the phenogram of Figure 4, which is based on all the characters; this is expected because parsimony shares with phenetic techniques the requirement that all the characters be accomodated in the reconstruction.
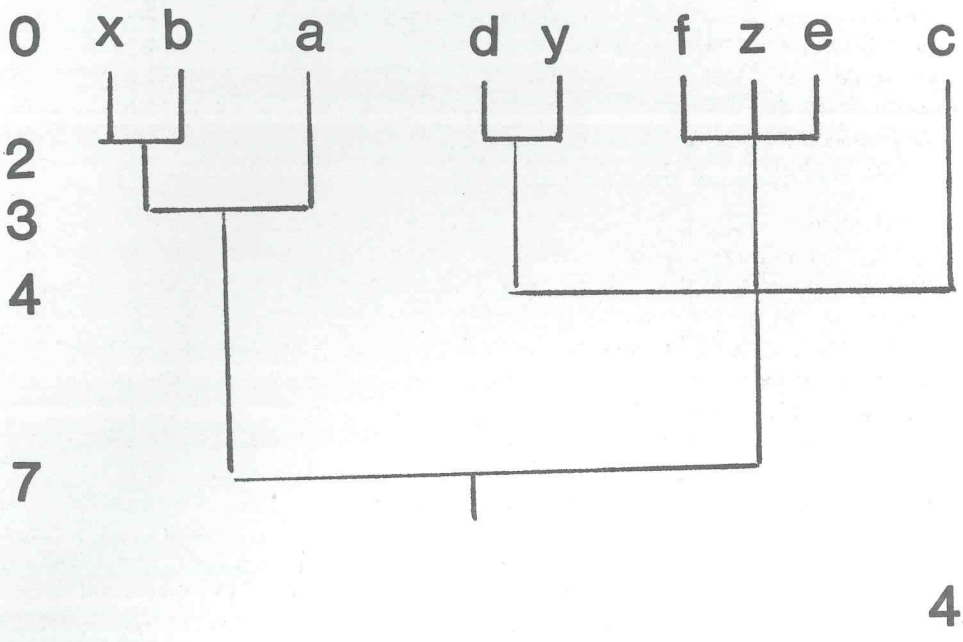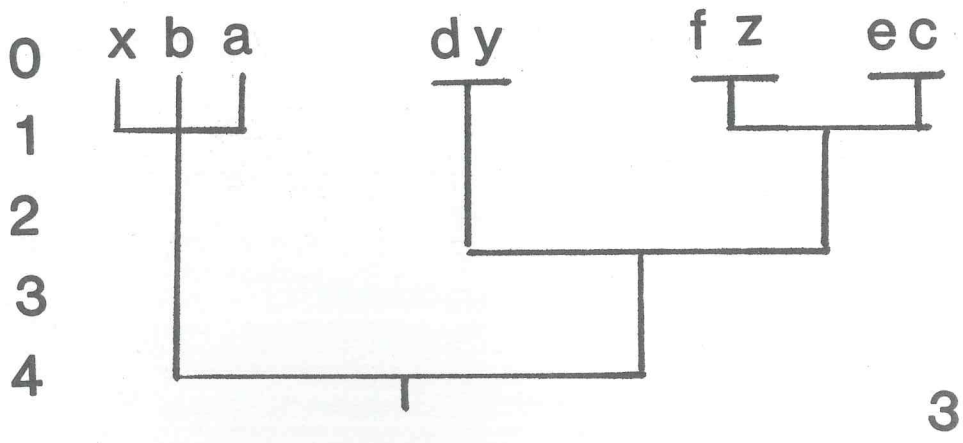
FIG. 3-4

TABLE 2 - The columns of Table 2 show the states of the characters associated with the specifications. A 1 means that the species labeling the row did evolve from (and possesses a particular property that arose during the evolution of) the species labeling the column. The first row shows the character numbers used in Figures 6A, 6B, and 6C. These character are referred to in the text as EVOLVED FROM y, etc. Because only the first have more than one species in state 1, only these make contradictable assertion about ancestor/descendant relationships. The last four serve to distinguish species from their ancestors.

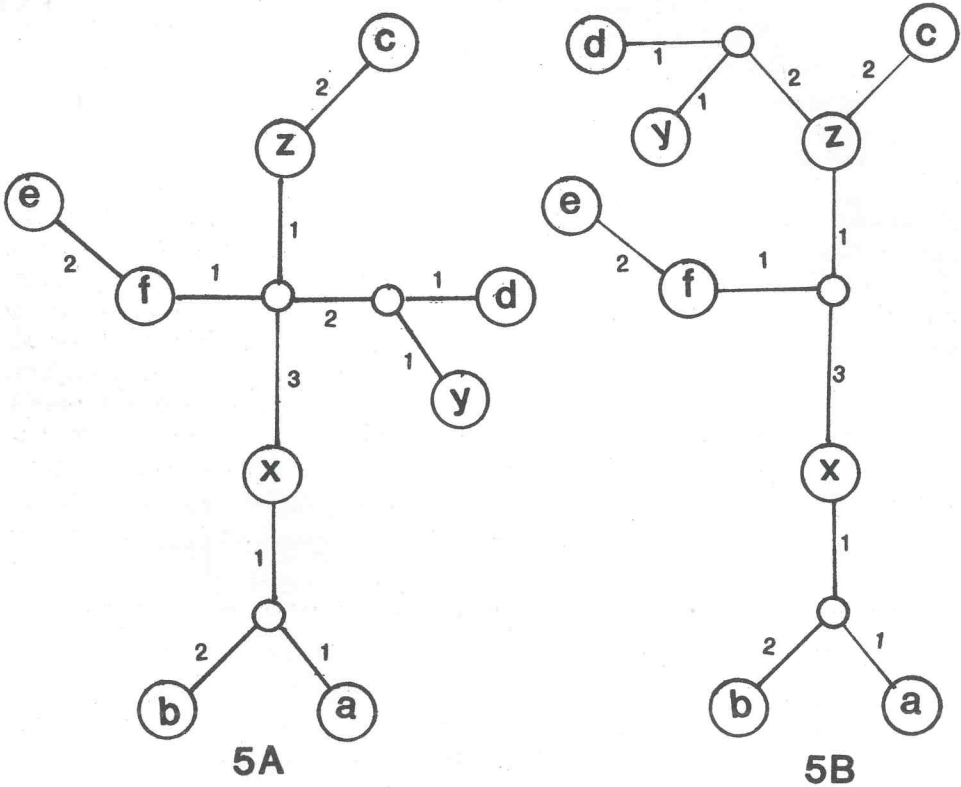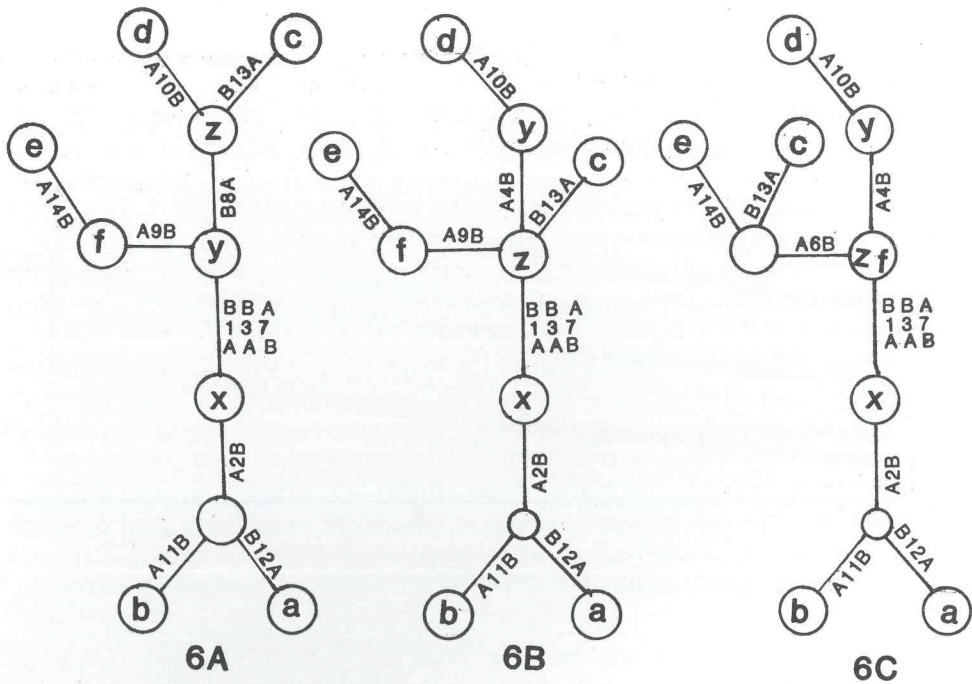| | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
	y	z	f	d	b	a	c	e
x	0	0	0	0	0	0	0	0
y	1	0	0	0	0	0	0	0
z	1	1	0	0	0	0	0	0
a	0	0	0	0	0	1	0	0
b	0	0	0	0	1	0	0	0
c	1	1	0	0	0	0	1	0
d	1	1	0	1	0	0	0	0
e	1	0	1	0	0	0	0	1
f	1	0	1	0	0	0	0	0

5A

5B

FIG. 5

FIG. 6

GEOGRAPHIC DISTRIBUTION

What information about relationships among species do we have from the fact that y, f, and e occur on one side of the barrier and z, c, d, a, b, and x occur on the other? We could try to argue that y, f, and e, were a monophyletic group because they occur on one side of a barrier and are all (or all except their ancestor) absent from the other side of the barrier. This conclusion would be correct if the barrier had by chance isolated a monophyletic group or a single species that had not yet served as an ancestor for others, and y, f, and e had been that monophyletic group or had evolved from it or had evolved from that single (monophyletic) species. In our example these conditions are not met, nor does it seem usual or probable that they be met in the history of real taxa whose members have been separated by dispersal barriers. We do not have y, f, and e monophyletic because their most recent common ancestor is y whose descendants are the monophyletic group, z, c, d, f, e, and y. The other side of the barrier is not monophyletic either; its most recent common ancestor is x whose descendants are the whole group of 9 species.

Perhaps if some species had occurred on both sides of the barrier this would be an indication of its antiquity or primitiveness. Certainly if the barrier completely blocks dispersal, any species occurring on both sides must

45

predate the barrier. But as we have seen, local extinctions make it possible for species occurring on only one side of the barrier to predate the barrier as well. Suppose, for example, that a population of z were found on the side of the barrier where f occurs, i.e., it had not gone quite locally extinct but had remained in a few isolated habitats. We know that z is not the ancestor of the entire group of 9 species, neither is it the ancestor of the group of three on one side nor of the group of 6 on the other side. It is older than some species but younger than others. No very compelling conclusions about z follow from the fact that it occurs on both sides of the barrier. In fact, no very compelling conclusions about relationships among species follow from consideration of the geographical distribution in and of itself out of the context of the biology of those species.

GEOGRAPHY AND CHARACTER ANALYSIS

Although geography may not constrain the possibilities for the phylogenetic relationships among species, it may contribute something to the phylogenetic analysis of characters in their adaptive/ecological context, that may aid in deciding which characters might more accurately reflect ancestor/descendant relationships.

In our example, we have a logical conflict between WET and EVOLVED FROM z. We have not specified in our example exactly what observable property evolved with z: we know that it is present in the dry adapted d byt absent in the dry adapted y; present in the weedy c but absent in the weedy e; and present in the wet adapted z but absent in the wet adapted f. On the other hand, WET is present in the two pairs, (z, f) and (c, e), of very similar species, with the members of each pair *separated by a dispersal barrier*. Similar selection pressures related to wet adaptations and acting on different isolated populations of the same ancestral species could produce similar, but distinct, wet limestone soil adapted species, by evolving the WET character in parallel. In this way, phenetics, adaptive/ecological considerations, and geographic isolation can all contribute to deciding that EVOLVED FROM z (whatever property that might be) might be more likely to reflect ancestor/descendant relationships than WET. Similar arguments can apply to the incompatible WEED and EVOLVED FROM f characters to suggest that the second is more likely to be historically true. In this case, however, the possibility of modern human transport of weeds cannot be overlooked.

These considerations would lead us to prefer Figure 6A as an estimate of ancestor/descendant relationships. The species presently on one side of the barrier are not even convex on this estimate. Since some of the habitats seem to be similar on both sides of the barrier, this estimate suggests that some historical environmental fluctuations since the establishment of the barrier could have resulted in extinction of ancestors on one or both sides.

This technique of using phenetics and adaptive/ecological considerations

along with geographic isolation to analyze characters to decide which might most plausibly reflect ancestor/descendant relationships can be applied with parsimony reconstructions as well, but its application is facilitated by character compatibility analysis because here the conflicts between incompatible characters are identified directly, and groups of compatible characters are explicitly revealed. In this way, additional considerations can be brought to bear directly on the resolution of conflict at the level of the characters.

The history of the environment can also make a contribution to recognizing true and false characters. All reconstructions of ancestor/descendant relationships illustrated in Figures 5 and 6 suggest an exctinct common ancestor for a and b that arose for x. The geographic range and adaptive habitat for x is contiguous with that of a and with that of b. But if the forest had a continuous existence since before the mountains, then the low and high altitude ecotones would always have been isolated from each other, making it seem more likely that the species adapted to these habitats each evolved directly from the nearby x in different parts of its range.

CONCLUSION

Where a species occurs in the world is as much a property of that species as are its morphological, developmental, biochemical, molecular, and behavioral characters. And how the present day geographical distributions for a group of related species came to be is as much a part of the natural history of the group as is how the diversity of their other properties arose during their phylogeny. Although knowledge of present day geographic distributions does not by itself constrain possibilities for ancestor/descendant relationships, estimates of relationships based on observable properties can sometimes be made more credible by considering phenetics, adaptation, ecology, and environmental history, together with geographic information. This can help resolve the character incompatibilities revealed by character compatibility analysis. More convincing phylogenetic reconstructions can then help to more plausibly construct geographic scenarios that can explain the modern geographic distribution of related species.

LITERATURE CITED

ESTABROOK G.F., (1984) - *Phylogenetic Trees and Character State Trees.* - in T. Duncan and T.F. Stuessy, eds. Cladistics. Columbia University Press, New York, pp. 135-151.
NELSON, G., (1984) - *Cladistics and Biogeography.* - In T. Duncan and T.F. Stuessy, eds. Cladistics. Columbia University Press, New York, pp. 273-293.
NELSON G. and N. PLATNICK., (1981) - Systematics and Biogeography: Cladistic and Vicariance. - Columbia University Press, New York.
ROSEN D., (1978) - *Vicariant Patterns and Historical Explanation in Biogeography* - Syst. Zool. **27**: 159-188.