

Phylogenetic Systematics as the Basis of Comparative Biology

V.A. Funk and Daniel R. Brooks



SMITHSONIAN INSTITUTION PRESS

Washington, D.C.

1990

ABSTRACT

Funk, V.A. and Daniel R. Brooks. *Phylogenetic Systematics as the Basis of Comparative Biology*. *Smithsonian Contributions to Botany*, number 73, 45 pages, 102 figures, 12 tables, 1990.—Evolution is the unifying concept of biology. The study of evolution can be approached from a within-lineage (microevolution) or among-lineage (macroevolution) perspective. Phylogenetic systematics (cladistics) is the appropriate basis for all among-lineage studies in comparative biology.

Phylogenetic systematics enhances studies in comparative biology in many ways. In the study of developmental constraints, the use of such phylogenies allows for the investigation of the possibility that ontogenetic changes (heterochrony) alone may be sufficient to explain the perceived magnitude of phenotypic change. Speciation via hybridization can be suggested, based on the character patterns of phylogenies. Phylogenetic systematics allows one to examine the potential of historical explanations for biogeographic patterns as well as modes of speciation. The historical components of coevolution, along with ecological and behavioral diversification, can be compared to the explanations of adaptation and natural selection. Because of the explanatory capabilities of phylogenetic systematics, studies in comparative biology that are not based on such phylogenies fail to reach their potential.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: Leaf clearing from the katsura tree *Cercidiphyllum japonicum* Siebold and Zuccarini.

Library of Congress Cataloging-in-Publication Data

Funk, V.A. (Vicki A.), 1947-

Phylogenetic systematics as the basis of comparative biology / V.A. Funk and Daniel R. Brooks

p. cm.—(Smithsonian contributions to botany ; no. 73)

Includes bibliographical references (p.)

Supt. of Docs. no.: SI 1.29:73

1. Phylogeny. 2. Evolution—Research—Methodology. 3. Cladistic analysis. I. Brooks, D.R. (Daniel R.), 1951-

II. Title. III. Series.

QQK1.S2747 no. 73 a [QH367.5] 581 s—dc20 [575] 89-600291

Contents

	<i>Page</i>
Introduction	1
Acknowledgments	2
Comparative Methods	3
Consensus Analysis	6
Character Coding	6
Methods and Research Programs in Macroevolution	8
Developmental Constraints	8
Hybridization	12
Biogeography	15
Speciation	25
Sympatric Speciation	25
Allopatric Speciation, Model I	25
Allopatric Speciation, Model II	27
Parapatric Speciation	29
Historical Ecology	29
Coevolution	29
Ecological and Behavioral Diversification	36
Concluding Statement	42
Literature Cited	43

Phylogenetic Systematics as the Basis of Comparative Biology

V.A. Funk and Daniel R. Brooks

Introduction

Along with virtually all biologists we consider evolution to be the unifying concept of biology. It follows that a wide variety of biological explanations would benefit from reference to evolutionary relationships and that studies without such a basis are missing an element that would greatly increase their information content.

The study of evolution can be viewed from a within-lineage or among-lineage perspective. Within-lineage patterns, resulting from processes operating on time scales less than the duration of individual species, are referred to as "microevolution." This is the focus of population genetics and population ecology.

There seems to be general agreement that evolutionary patterns exist among-lineages. These are frequently identified as macroevolutionary patterns, and are usually the focus of systematic analyses. Macroevolutionary patterns include a variety of phenomena such as increasing morphological complexity over time, morphological trends, repeating biogeographic patterns, and developmental and phylogenetic constraints. Controversy remains about the processes responsible for these patterns and, by extension, about the best methods for detecting them (see Cracraft, 1985a, and references therein).

In the past, two positions have been set forth. Goldschmidt (1940) and Eldredge and Cracraft (1980), among others, championed the view that macroevolutionary processes were qualitatively different from microevolutionary processes, and were independent of them. In contrast, Dobzhansky (1937), Mayr (1942), and Simpson (1944) forged a consensus that macroevolutionary patterns are simply microevolutionary patterns "writ large"; hence, there are only microevolutionary

processes. They argue that perception of macroevolutionary patterns is merely a result of the coarse scale of systematic studies: "There is only a difference in degree, not one of kind, between the two phenomena. They gradually merge into each other and it is only for practical reasons that they are kept separate" (Mayr, 1942:291). Eldredge (1985) termed this the "extrapolationist model of macroevolution."

A viewpoint that borrows from these two extremes is now emerging. Under this view, evolution results from a variety of interacting processes, variously construed as forces or constraints. These processes operate on differing time scales, so their expression may be found in within-lineage patterns or in among-lineages patterns. Microevolution and macroevolution are parts of a more inclusive whole represented by the hierarchical nature of biological systems (e.g., Salthe, 1985; Eldredge, 1985; Brooks and Wiley, 1986, 1988). From this perspective, macroevolutionary patterns are those that are better explained by reference to phylogeny than by reference to local environmental conditions; microevolutionary patterns refer primarily to local adaptive responses.

Macroevolutionary processes, because they operate so slowly, define the boundaries within which microevolution takes place. That is, macroevolutionary properties constrain the way in which, and the extent to which, populations can respond to local selection pressures over short time periods. The emphasis is not on a reductionist explanation but on a more holistic interpretation—on the relative contributions of processes operating at different rates rather than on the ability of one process to account for everything.

If there are macroevolutionary processes, or if there are microevolutionary processes having among-lineage effects (such as selection or competition acting in the past), it is important to estimate just how prevalent and influential these are. Macroevolutionary patterns, no matter what causes them, are manifested by persistent ancestral traits in descendant species. The current jargon for such occurrences is phylogenetic constraints, or historical constraints (or even phylo-

V.A. Funk, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA, and Daniel R. Brooks, Department of Zoology, University of Toronto, Toronto, Ontario, M5S 1A1 Canada.

Review Chairman: L. Skog, Smithsonian Institution.

genetic inertia). Phylogenetic trees produced by phylogenetic systematic analysis provide explicit summaries of putative historical constraints. Phylogenetic systematics refers to the method of Hennig (1966), which builds patterns of relationship among taxa based on shared derived characters. This method contrasts with traditional systematics, which has no specific method of determining relationship. The trees produced by this method can be used to partition out within-species and among-species evolutionary patterns.

The systematist's null hypothesis is the assumption that as more and more characters are sampled, no consistent pattern of relationships will emerge; as more and more characters are added to the tree you will continue to fail to have any resolution of the tree and the polytomies will persist. When a consistent pattern (or group of similar patterns) does emerge, the systematist rejects the null hypothesis in favor of the pattern(s) discovered. The accepted pattern, described in a cladogram, is the working hypothesis of historical order among species that can be used in macroevolutionary studies.

If one is skeptical about the existence of macroevolutionary processes, or of microevolutionary processes having among-species effects, the appropriate null hypothesis is that no causal agents (processes: forces or constraints) will show among-species correlations with the group being studied. That is, the cladogram is only a record of microevolutionary processes having no macroevolutionary effects. The template for comparisons with respect to this null hypothesis is the cladogram; the putative micro- and macroevolutionary processes are mapped onto the cladogram. Any autapomorphy can be investigated as a microevolutionary process. Any putative causal agents that behave like synapomorphies on the cladogram refute the null hypothesis.

Alternatively, if one thinks that phylogenetic constraints play a major role in evolution, the appropriate null hypothesis is one of historical structuralism (Brooks and Wiley, 1986, 1988). Under this view, putative causal agents that show homoplasious or autapomorphous correlations with the phylogeny of the taxa being studied refute the null hypothesis and lead one to accept current microevolutionary causes as explanatory. In this case, the template for comparisons with the null hypothesis is also the cladogram.

If one adopts the evolutionary view just discussed, it is more important to be able to document the influences of a variety of causal agents at particular points in the phylogeny than it is to try to reduce all of phylogeny to "microevolutionary" or "macroevolutionary" processes.

Evolutionary explanations that make explicit reference to phylogeny are not widely used today. One reason is the belief that there is an inherent circularity in the methods of producing estimates of evolutionary relationships from which such explanations would be drawn. Specifically, it is homologous traits that indicate phylogenetic relationships and yet it is phylogenies that are used to determine homology. Phylogenetic systematics (Hennig, 1966) represents an approach to reconstructing phylogeny that avoids this circularity. One must only

assume the existence of "descent with modification."

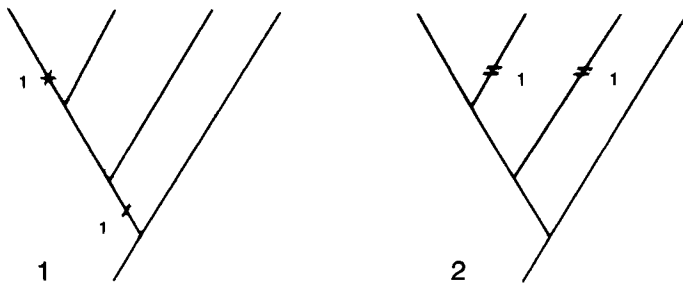
There are several components to the methodology developed by Hennig (1950, 1966). Initially, nonphylogenetic criteria (such as those of Remane, 1956; see Wiley, 1981) are used to determine homology. One asks whether two traits that *look* "the same" *are* "the same," and one assumes homology whenever possible. Having used nonphylogenetic reasoning to postulate homology, taxa are grouped according to the homologies they share. The result is a phylogenetic tree with various groupings of taxa diagnosed by the appearance of a homologous trait. For virtually every study, most presumed homologies conform, to a greater or lesser degree, to a predominant pattern, which then provides the phylogenetic hypothesis. Those traits originally thought to be homologous that do not conform to the accepted tree are reinterpreted as nonhomologies. That is, presumed homologies are determined by nonphylogenetic methods, and are used to construct phylogenetic trees that in turn determine which of the presumed homologies are not evolutionary homologies. By avoiding methodological circularity, phylogenetic systematics produces patterns of evolutionary relationships that can serve as independent explanatory templates for other evolutionary studies. As a result, we think phylogenetic systematics bridges the disciplines of developmental biology, ecology, evolution, and systematics. Indeed, it is our contention that phylogenetic systematics is the appropriate context for all studies in comparative biology.

It is not our intention here to provide an introduction to phylogenetic systematics. The three central terms of phylogenetic methodology—apomorphy, monophyly, and parsimony—have been clearly discussed elsewhere (e.g., Eldredge and Cracraft, 1980; Farris, 1974, 1983; Funk, 1984; Humphries and Funk, 1984; Oosterbrock, 1987; Platnick, 1977a, 1979; Wiley 1981).

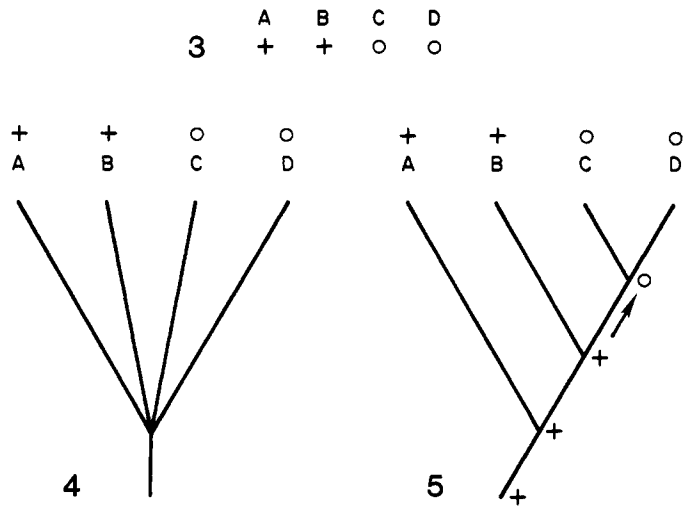
In this paper, we first present several relatively new techniques for comparing phylogenies. However, the major intention of this paper is to show how phylogenetic systematics can be used in comparative methods that have been developed for documenting macroevolutionary patterns.

ACKNOWLEDGMENTS

The authors thank the Smithsonian Institution Short-Term Visitor Program, which allowed the junior author (DRB) to travel to the Smithsonian to begin this manuscript; the Natural Sciences and Engineering Research Council (NSERC) of Canada for grant A7696 (to DRB); the Smithsonian Institution Research Opportunities Fund, which enabled the senior author (VAF) to travel to the University of British Columbia; and the following individuals for their reviews of various drafts: G. Benz, P. Cannell, G. Deets, K. Fauchald, D. McLennan, R. Mooi, J. Nix, R. O'Grady, S. Salthe, C. Starr, E. Wiley; plus J. Savage and D. Hillis and the University of Miami, Department of Biology staff and graduate students. Also, a



FIGURES 1-2.—Examples of two equally parsimonious distributions of the same apomorphic character. 1, The apomorphy gained and subsequently lost. 2, The character gained twice. In the PAUP computer program for generating phylogenies, the accelerated transformation option will produce Figure 1 and the decelerated transformation option will yield Figure 2.



FIGURES 3-5.—Cladograms demonstrating the difference between independent origin and mapping of characters. 3, Distribution of two traits (0, +) among four species (A-D). 4, Cladogram if each trait occurred independently in each species. 5, Cladogram if trait “+” occurred in common ancestor of all four species, and trait “0” arose in common ancestor of C and D.

special thanks to D. Futuyma and B. Simpson for reviewing the completed manuscript and providing numerous corrections, additions, and comments. The listing of these reviewers names is not meant to imply their agreement with the various assertions in this paper.

Comparative Methods

There are two kinds of “comparative methods.” The first consists of finding a trait of interest in a particular species, then examining unrelated species having similar ecological requirements to see if any of them have evolved similar traits. If they have, that trait may be considered to be a convergent adaptive response to a common selection regime (see Alcock, 1984). An example is the succulent nature of the stems and/or leaves of many unrelated plants that grow in deserts. Another is the blindness of many animals that live in perpetual darkness.

The second comparative method is rooted in the discipline of systematics. It consists of documenting genealogical

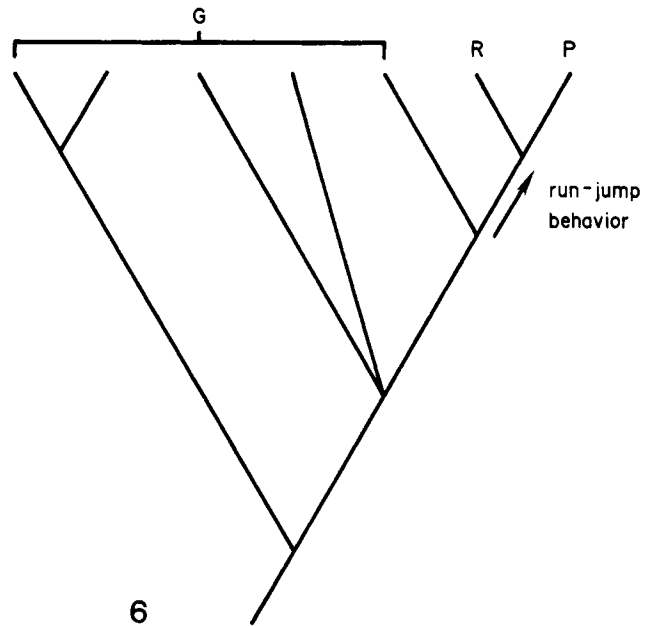


FIGURE 6.—Phylogeny of ground squirrels plus prairie dogs showing distribution of run-jump behavior. As represented on this tree, the run-jump behavior arose in common ancestor of Richardson’s ground squirrels (R) and prairie dogs (P). All other ground squirrels (G) lack this behavior. (After Dobson, 1985.)

relationships and then asking if shared traits arose in a common ancestor and have persisted, or if they arose independently in the species of interest. This method can be referred to as the phylogenetic comparative form.

For the first kind of comparative method, an assumption is made that similarities arise through adaptive response to common selection pressures. No provision, however, is made for animals that live in darkness but can still see and for plants that grow in the desert and are not succulent. Also, no explicit provision is made for explaining some similarities as persistent ancestral traits, although such “phylogenetic constraints” are sometimes explained post hoc as the result of selection in the past. And yet, if replication rates are higher than mutation rates (a microevolutionary observation), we might expect more persistent ancestral traits than newly evolved traits to be expressed in similarities among related species (a macroevolutionary pattern). Therefore, we believe that the appropriate general comparative method for evolutionary biology, and certainly for studies in macroevolution, is the second type, the phylogenetic form. This agrees with the argument of Hennig (1966), who asserted that the preferred “general system” for biology should be one based on phylogeny.

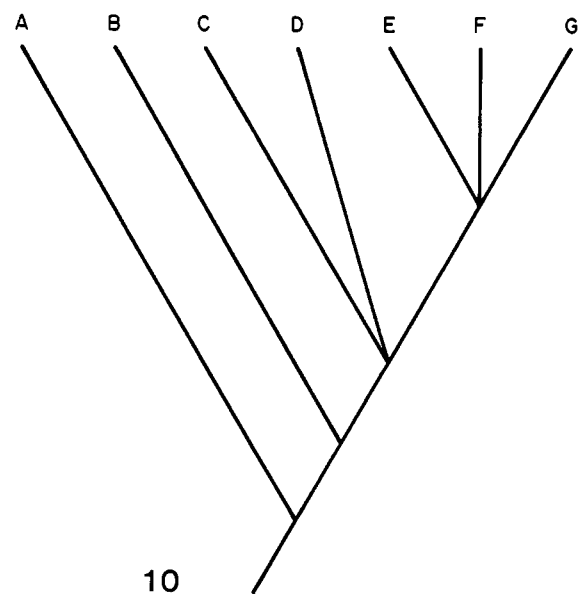
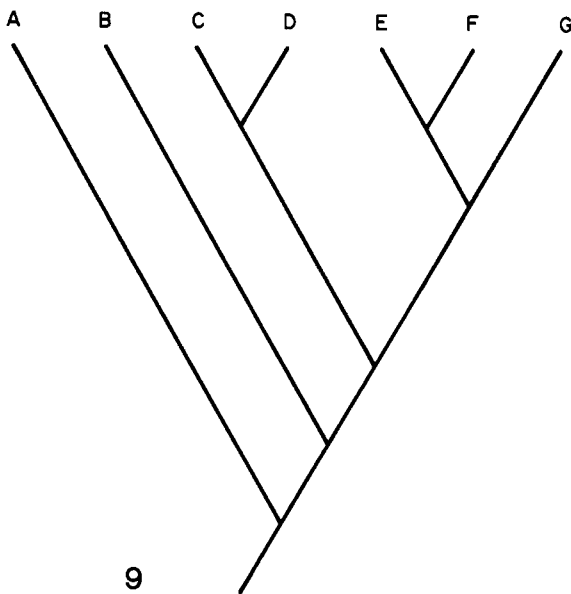
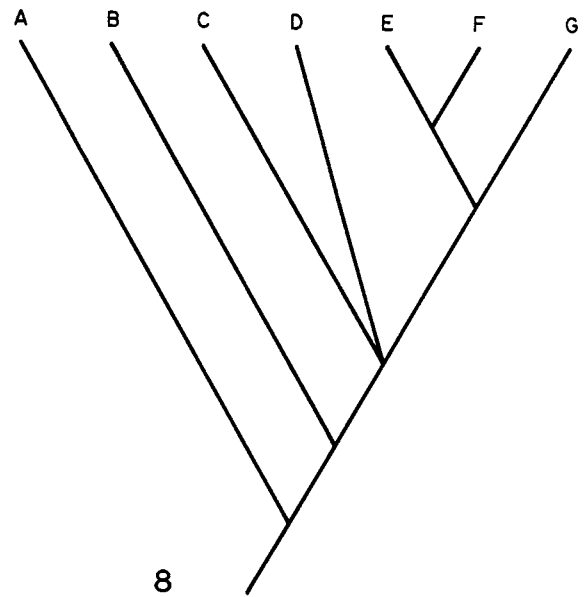
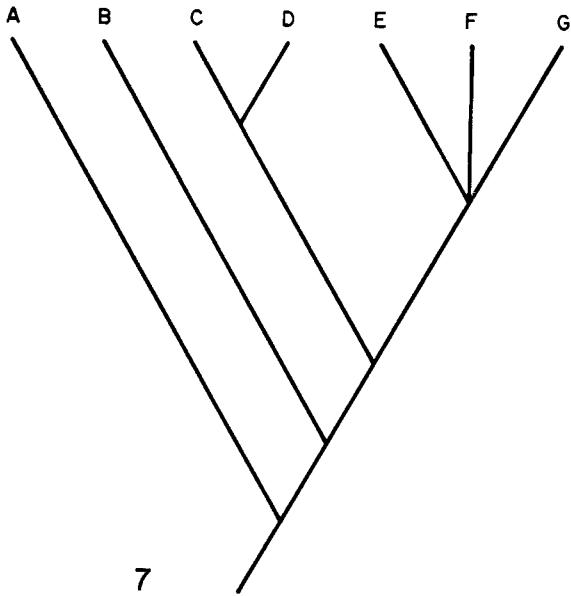
There are two general ways to use comparative phylogenetics to examine macroevolutionary patterns. One way to use cladograms involves comparing more than one cladogram to see if there is evidence of processes affecting more than one lineage at a time. Within this realm of comparing cladograms, we may ask two different types of questions.

TABLE 1.—Components for Figures 7 and 8.

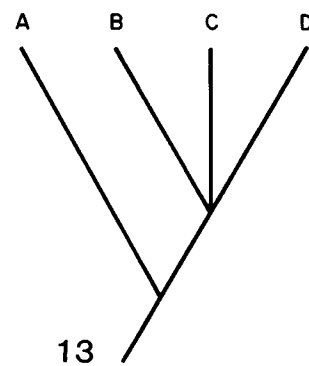
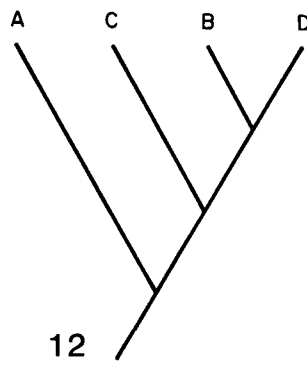
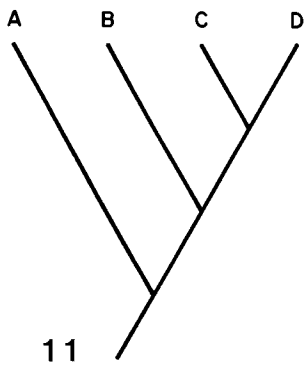
Figure 7	Figure 8
EFG	EF
CD	EFG
CDEFG	CDEFG
BCDEFG	BCDEFG
ABCDEFG	ABCDEFG

TABLE 2.—Components for Figures 14 and 15.

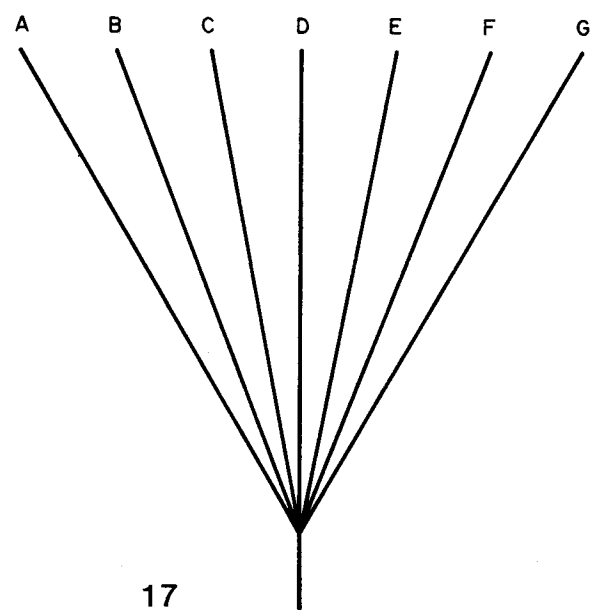
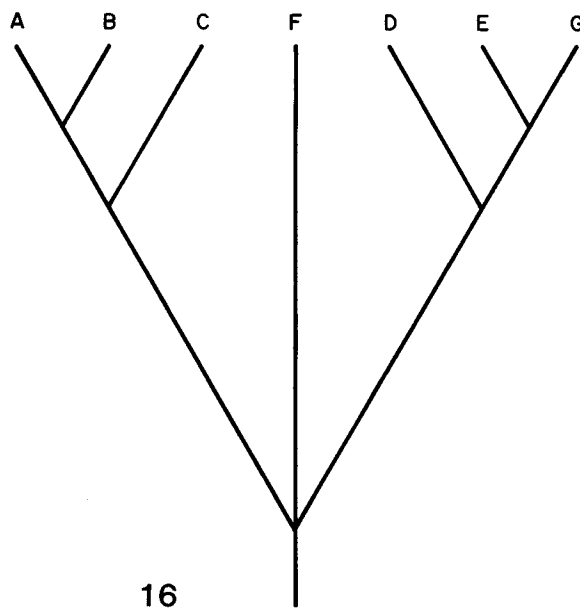
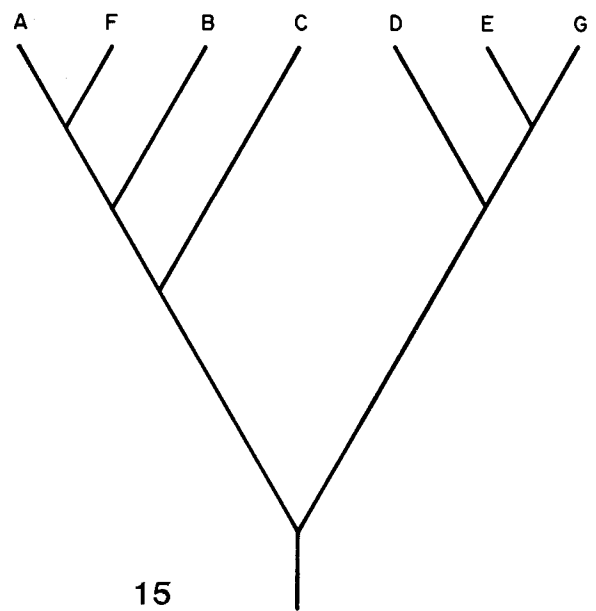
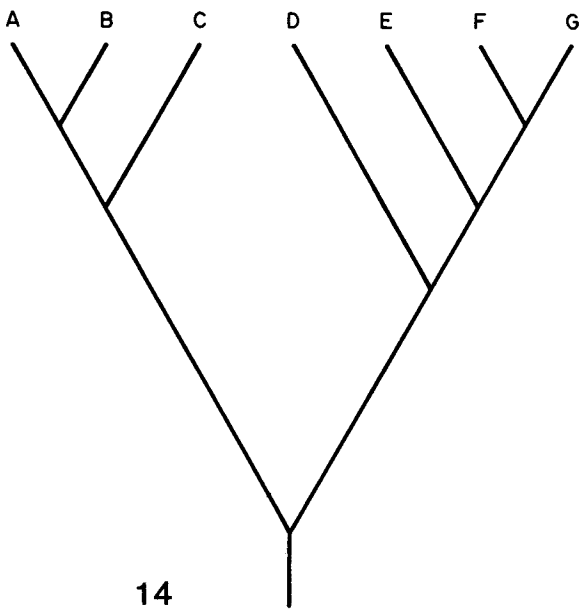
Figure 14	Figure 15
AB	AF
ABC	AFB
	AFBC
FG	EG
EFG	DEG
DEFG	AFBCDEG
ABCDEFG	



FIGURES 7–10.—Consensus Trees. 7 and 8, Two alternative cladograms for the same seven taxa. 9, Adams consensus tree for Figures 7 and 8. 10, Strict consensus tree for Figures 7 and 8. (See Table 1.)



FIGURES 11-13.—Consensus trees. 11 and 12, Two cladograms for the same four taxa. 13, Adams and strict consensus trees identical for Figures 11 and 12.



FIGURES 14-17.—Consensus trees. 14 and 15, Two cladograms for the same seven taxa. 16, Adams consensus tree for Figures 14 and 15. 17, Strict consensus tree for Figures 14 and 15. (See Table 2.)

We may ask what parts of different cladograms agree with each other (or conversely, what parts of cladograms are responsible for any ambiguity). Alternatively, we may ask how the history of one clade or of a set of areas explains the history of another clade or clades. Portions of the cladograms that behave as homologies are the historically determined variation (macroevolutionary contribution) and portions that behave as homoplasies are the proximally determined variation (microevolutionary contribution).

The second way is to map a trait of interest on the cladogram (Figures 1 and 2) and to estimate both when, and how many times, a trait arose in the group being studied (Figures 3–5). Macroevolutionary patterns that emerge from this level of analysis are those affecting particular clades. Dobson (1985) used just such a procedure when commenting on the evolution of the “run-jump” behavior found only in prairie dogs and the Richardson’s ground squirrel. His hypothesis was that the run-jump behavior is a result of a common history of the two groups. He tested the hypothesis by mapping it on the phylogeny for ground squirrels and prairie dogs. Dobson found that Richardson’s ground squirrel is more closely related to the prairie dog than to other ground squirrels (Figure 6), thereby supporting, through parsimony, the common history hypothesis.

CONSENSUS ANALYSIS

Consensus trees provide a summary when more than one cladogram is available. Sometimes the topology of the consensus tree will be the same as one of the original cladograms, but it often contains branching sequences not found in any of the original ones. Although consensus trees are not a valid summary of the data and should not be used as such (Miyamoto, 1983), they are an excellent way to locate problem taxa and characters and to illustrate areas of agreement and nonagreement.

For our purposes there are two basic types of consensus trees: Adams consensus trees (ACT, Adams, 1972) and strict, or Nelson, consensus trees (NCT, Nelson, 1979, 1983). They differ in the manner in which they handle conflicting data. An Adams tree will give the highest resolution possible when there is no conflict in the data and a strict consensus tree will give only the branching sequences that are identical on all cladograms under consideration. For instance, Figures 7 and 8 are two alternative cladograms for the same seven taxa, A–G. The Adams tree (Figure 9) is better resolved than either of the cladograms because neither 7 nor 8 conflicts with the other. The NCT (Figure 10) recognizes only clades that are present in both trees. In some cases the Adams tree and the strict consensus tree will produce the same result (Figures 11–13). In other cases they will be very different. For instance, Figures 14 and 15 have one taxon that changes position (taxon F); in doing this it changes all of the monophyletic groups on the cladogram so that the Adams tree (Figure 16) has a trichotomy at the base but the strict consensus tree has no resolution

possible (Figure 17). These two types of consensus analysis do not give conflicting information, they answer different questions. An Adams tree answers those questions about which the clades are not in conflict, while a strict consensus tree provides information only on those areas of the cladograms that are identical.

Alternative trees can be compared by “matching” the “components” (sensu Nelson, 1983) of the different trees. A component is any monophyletic group on the cladogram. Table 1 provides the components for Figures 7 and 8. There are five components, four of which are identical in the two lists (EFG, CDEFG, BCDEFG, and ABCDEFG). A strict consensus tree contains only the four identical components (Figure 10). An Adams tree contains these four components as well as components EF and CD because they do not conflict with each other. Table 2 provides the components for Figures 14 and 15. Even though there are no identical components, it is clear from the listing that taxon F is causing the lack of agreement, demonstrating that even when the strict consensus tree approach does not produce a tree, it can indicate the problematic taxa.

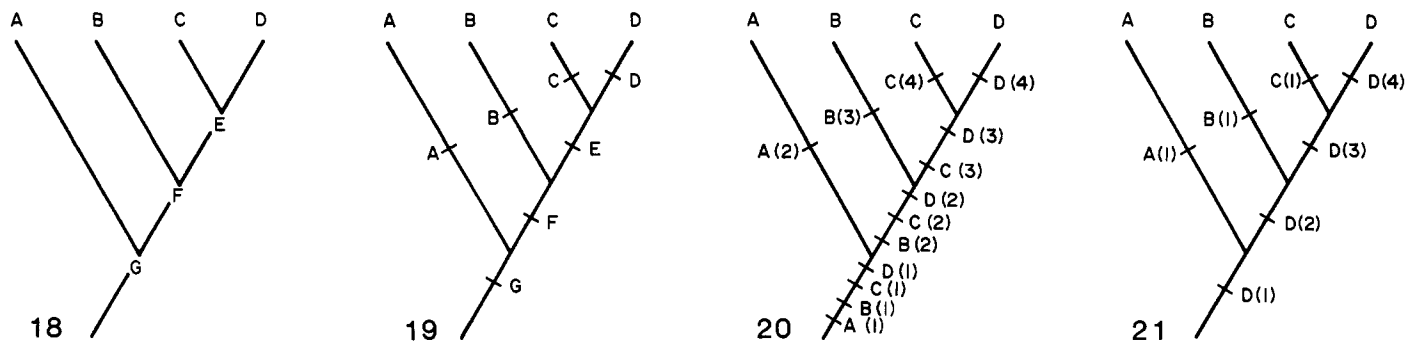
CHARACTER CODING

Species co-occur in various kinds of associations. Geographically co-occurring species are *sympatric*, ecologically associated ones can be *synecological*, *syntopic*, or even *sympatric*. Each of these association is thus diagnosed by its component species. If the associations play a role in the evolution of any of these diagnostic species, the phylogenies of the various groups will covary with respect to the associations.

In terms of phylogenetic analysis, this is accomplished by treating each cladogram as a multistate character of the association (considered “taxa,” be they areas, communities, hosts, etc.). Brooks (1981) first proposed this approach for studies in coevolution. All “characters” (cladograms coded as multistate characters) are then placed in a common data matrix. The data matrix can be handled in one of two ways. (1) Either it can be mapped onto the host phylogeny, in which case characters that covary (act as homologues) share a common history with respect to the taxa, or (2) a phylogenetic systematic analysis can be performed. In the latter approach, a cladogram (or cladograms) of “taxa” is produced with portions of the various phylogenies used as characters (for examples see “Biogeography,” below).

There are general methods available for converting a phylogenetic tree into a matrix of unit characters: Additive Binary Coding (ABC), Redundant Linear Coding (RLC), and Nonredundant Linear Coding (NLC). For a more complete treatment, including assessments of the strengths and drawbacks of the methods, see O’Grady and Deets (1987) and O’Grady et al. (in press).

In ABC every node on the tree is labeled. In Figure 18 there are four terminal taxa (A–D) and three internal nodes (E–G).



FIGURES 18–21.—Three ways of “mapping.” 18, Phylogeny with nodes labeled. 19, Tree constructed from ABC representation. 20, Tree constructed from RLC representation. 21, Tree constructed from NLC representation. (See Tables 3–5.)

TABLE 3.—ABC coding for Figure 18.

Taxa	Codes						
	A	B	C	D	E	F	G
A	1	0	0	0	0	0	1
B	0	1	0	0	0	1	1
C	0	0	1	0	1	1	1
D	0	0	0	1	1	1	1

TABLE 4.—RLC coding for Figure 18.

Taxa	Codes			
	A	B	C	D
A	2	1	1	1
B	1	3	2	2
C	1	2	4	3
D	1	2	3	4

TABLE 5.—NLC coding for Figure 18.

Taxa	Codes			
	A	B	C	D
A	1	0	0	1
B	0	1	0	2
C	0	0	1	3
D	0	0	0	4

The matrix values are determined by assigning a “1” code to every state lying along the minimum path between each taxon and the base of the tree. For example the minimum path for taxon D passes through D, E, F, and G, and each of those is coded as “1” for taxon D (see Table 3). The data matrix can be checked by using it to produce a tree (Figure 19), which indeed is identical to Figure 18, with each branch point supported by “characters.” In RLC each terminal branch on the tree becomes the terminal state in a linear transformation series constructed as the minimum path from the base of the tree. Every transformation series starts as a “1” state at the bottom node of the tree and changes at every nonterminal branch as it passes up the tree to the terminal state. For example, in RLC coding of Figure 18, taxon D has a code of “4” for D because there are three internodes between D and the base; it also shares three internodes with taxon C so C has a “3”; it shares two internodes with taxon B so it has a “2” for B; and it shares one internode with A so it has a “1” for A. The code for taxon D is, therefore, “1234.” Taxon B has a “1” for A because it shares one internode with A; it has a “3” for B because it shares three internodes with taxon B; and it has a “2” for C and a “2” for D because it shares two internodes with both. The code for taxon B is “1322” (Table 4). Figure 20 is the diagram produced from the RLC data matrix (Table 4).

NLC is similar to RLC in that each terminal branch on the tree becomes the terminal state in a linear transformation series construed as the minimum path. However, it differs in that only one of the terminal taxa goes all the way to the base of the tree. This is referred to as the major axis and it can involve any one of the terminal taxa. The other transformation series (minor axes) start from the point at which they branch off from the major axis. In Figure 18, if D is the major axis it would be the only taxon coded all the way up the tree, so D would have a “4.” Because A, B, and C are coded only from the point that they intersect with this axis, taxon D would have a “0” for all three of these and the code for taxon D would be “0004” (Table 5). Taxon B would have a “2” for D because it shares two internodes with taxon D and a “1” for B because it has one internode between taxon B and the point at which it intersects the main axis. The code for taxon B would be “0102”

(Table 5). Figure 21 is the tree resulting from Table 5. According to O'Grady and Deets (1987) the NLC method is more difficult to understand but eliminates the large data sets resulting from ABC and avoids the weighting of the RLC method. The ABC and the NLC give the same results, with the ABC being easier to use and the NLC being more economical.

Once a cladogram has been converted into a data matrix, it can be mapped (placed as characters) on an existing phylogeny (the existing phylogenetic pattern is maintained and data from the matrix are placed on it in the most parsimonious manner), or on an area or host cladogram, or it can be combined with data from other trees to produce a summary diagram. We will show applications of such analyses in studies involving questions on biogeography and coevolution.

An important consideration in interpreting the results of mapping phylogenies concerns homoplasies. Homoplasious occurrences can be interpreted either as similar but separately derived origins of a trait (parallelism) or as a single origin of the derived trait with a secondary appearance of the plesiomorphic condition (character loss or reversal). When heritable traits of organisms are used to construct phylogenetic trees, parallelisms sometimes can be distinguished from reversals by developmental studies. For example, all cases of pedomorphosis will appear on the phylogeny as character losses/reversals, but not all character losses are a result of pedomorphosis (see "Developmental Constraints," below). In other cases, a preference for parallel origins or losses can be made on empirical grounds using optimality measures like the F-ratio or the D-measure (Brooks, O'Grady, and Wiley, 1986). However, when phylogenies are mapped together, as in biogeographic or coevolutionary studies, parallelisms and losses imply different evolutionary stories. Parallelisms in such cases are instances of colonization or host-switching, dispersal from original environmental contexts to new environmental contexts. Reversals imply episodes of extinction or loss of ecological association. We believe that the most conservative approach to take in this regard is one of providing explanations based on what we observe directly as often as possible. Only when other additional data are available, or when more efficient mapping can be obtained by postulating occurrences for which we have no observations, should we involve such explanations. This means that in general we advocate interpretations of parallelisms over interpretations of losses (Figures 1 and 2) in all cases except when additional data are available or a more efficient mapping (i.e., a shorter tree) can be obtained by postulating reversals.

Cases for which unrestricted interpretations of extinctions are appropriate involve groups that are "numerical relicts" (Simpson, 1944), remnants of once more diverse groups. Brooks and Bandoni (1988) have outlined phylogenetic, biogeographic, and ecological conditions which should be satisfied before one postulates that a given group is a numerical relict. Of course, one is also free to provide solution trees based on the maximum and the minimum number of extinctions consistent with the shortest solution tree, and conclude that the

real story probably lies somewhere between the two extremes. In this regard, the different solution trees would be used in a manner similar to that of establishing confidence intervals.

To summarize this discussion of consensus and the mapping method: (1) strict consensus illustrates which portions of the various cladograms are identical; Adams consensus highlights the portions of different trees that are consistent with each other, but not necessarily identical. Having performed a consensus analysis, one cannot then recapture the initial trees nor in most circumstances can one provide explanations for the conflicting portions of the trees. (2) Mapping methods are designed to provide explanations for all portions of the different trees. However, there is often more than one possible explanation for portions of phylogenies that do not covary. Accordingly, the results of mapping analysis may be less clear than those of consensus analysis, even though they encompass more of the available observations.

Methods and Research Programs in Macroevolution

DEVELOPMENTAL CONSTRAINTS

This topic encompasses the study of biases in the production of phenotypes that are not directly attributable to natural selection (Maynard Smith et al., 1985). Such biases can range from traits that are invariant in all viable members of a species to nonhomogeneous frequencies of occurrence of phenotypes characteristic of simple Mendelian loci. At the microevolutionary level, generally unacknowledged acceptance of developmental constraints allows prediction of expected phenotypic frequencies for particular traits, encompassing simple Mendelian ratios (where either a 3:1 or 1:2:1 phenotypic bias is expected) to pleiotropic effects manifested in patterns of genetic variance/covariance. At the macroevolutionary level, developmental constraints are important sources of information about discontinuities in variation and about differences in magnitudes of phenotypic change during evolution (see e.g., Maynard Smith et al., 1985; Brooks and Wiley, 1986).

Attempts have been made to explain biased phenotypic frequency by extrapolating from within-species processes to macroevolutionary, i.e., among-species, patterns. These attempts involve questions of developmental constraints versus selection. One solution is to identify all invariant traits (among species) and conclude that they are due to developmental constraints. This does not address the possibility that their invariance is due to selection operating in the past. Or, one could look for selectionist explanations for the frequencies of each trait, and assume developmental constraints only for those for which selectionist explanations cannot be found. This approach is vulnerable to the problem of assuming that because something functions it has been produced by selection, providing a "selectionist" explanation for everything (for a discussion, see O'Grady, 1984, 1986). Charlesworth, Lande, and Slatkin (1982) have proposed that the influence of developmental constraints at the population biological level

can be documented by looking for correlations in genetic variance/covariance matrices. But even this advance does not address the questions of the origins of developmental constraints, either in particular or as a general phenomenon, or of possible macroevolutionary effects of such constraints. Microevolutionary explanations can only explain persistence (stasis) rather than origin and modification (diversification). At the microevolutionary level, developmental constraints tell us only that the range of variation upon which selection acts is not the full range of possibilities, all equally represented. They are part of the explanation for the arena in which selection operates.

As indicated above, there are two macroevolutionary questions that involve developmental constraints. The first is the question of discontinuous variation and the second is the question of differences in magnitudes of phenotypic change during evolution. These questions can be investigated fruitfully if phylogenies are available, because one can then estimate the meaning of "discontinuous" or "of great magnitude" with respect to closest phylogenetic relatives. Alberch et al. (1979) asserted that macroevolution is the relatively rapid attainment of significant morphological differences in evolving lineages. If some intermediate phenotypic states or combinations of states are unattainable due to developmental constraints, ascribing all discontinuities in variation to natural selection would overestimate the power of selection and would provide no reasons to consider other possible causal agents. References to a number of developmental studies that predict observed discontinuities without selection are given in Brooks and Wiley (1986, chapter 3; 1988). An accumulation of such effects could produce phenotypic differences among species that are quite marked.

Two major approaches to examining the question of magnitudes of phenotypic change during phylogenesis have been tried. The first involves proposing archetype ancestral phenotypes and the second involves comparing sister lineages in phylogenies. We will consider the second approach here. Systematists have recognized for a long time that sister species are not equally dissimilar to the ancestor. Hennig (1966) called this the "deviation rule": for any pair of descendant species, one will always resemble the ancestor more than the other. Traditional explanations for such states have stressed (1) differential adaptation under different selection regimes, and (2) founder effects. That is, dissimilar states are the result of different speciation modes. With the recent advent of interest in developmental constraints, we must now consider an additional possible contributing factor. The genetic and ontogenetic changes characteristic of a descendant population alone may even be sufficient to explain the perceived magnitude of phenotypic change in some cases.

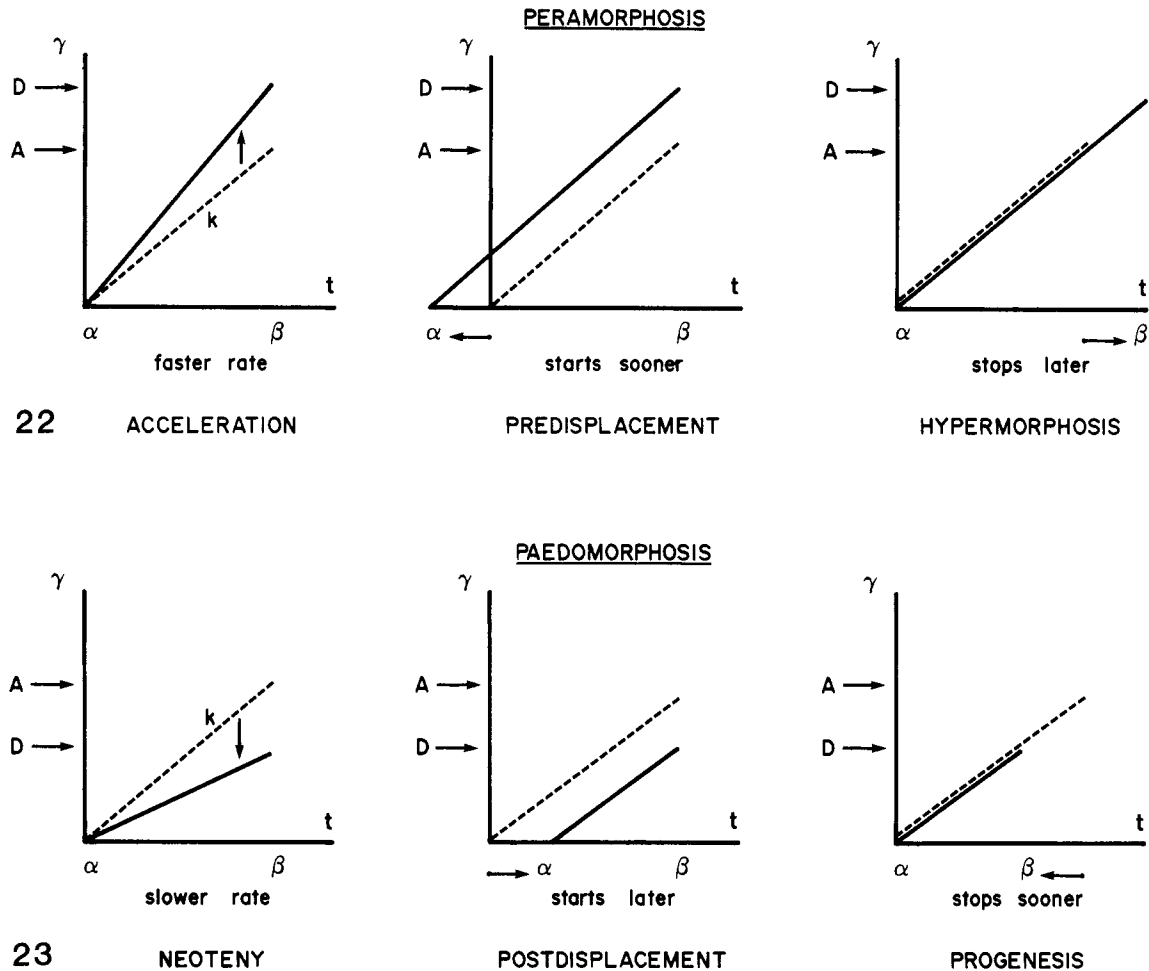
One major class of developmental constraints that has received recent attention is *heterochrony*. This is a general term denoting changes in timing of events during ontogeny. There are two reasons heterochrony is attractive to evolutionary biologists. The first is that genetic changes early in ontogeny

could have major phenotypic effects. This means that significant morphological differences could be achieved through relatively small genetic changes, and such genetic changes could be subject to effective selection (i.e., they could be relatively free of pleiotropic effects). Accepting this premise provides one way of reducing the concept of developmental constraints to standard microevolutionary processes and explanations. This also provides a mechanism whereby punctuated equilibrium could be explained as a wholly neo-Darwinian phenomenon (for recent attempts to provide such an explanatory reduction, see Charlesworth, Lande, and Slatkin, 1982; Stebbins and Ayala, 1984).

The second reason heterochrony is attractive to evolutionary biologists is that amplification of small differences in initial conditions producing markedly different endpoints is highly characteristic of nonequilibrium thermodynamic systems operating under a variety of kinetic constraints (Brooks and Wiley, 1986, 1988). If such processes characterize part of the production of phenotypic diversity in biology, evolution of such phenotypes would follow a "line of least resistance" determined by kinetic constraints, initial conditions (including phylogenetic history), and possible selective constraints. Robust evolutionary explanations would require partitioning out the relative contributions of each of these classes of causal agents rather than reducing phenotypic order to a single causal agent, such as selection or chemical kinetics.

We use the general description of classes of heterochronic changes proposed by Alberch et al. (1979). Their model assumes that an ancestral sequence can be construed as a trajectory characterized by a positive rate, "k." The trajectory has a direction in time determined by a starting point, α , and endpoint, β , and a degree of complexity (usually construed as size and/or shape change), γ . The trajectory has a positive slope appearing on a plane whose x-axis is time, with α and β indicated, and whose y-axis is complexity, denoted by values of γ . Thus, the trajectory is characterized by time-dependent (irreversible) increases in complexity, denoted by the rate "k."

Using this framework, heterochrony can be divided into two major classes, *peramorphosis* and *paedomorphosis*. *Peramorphosis* occurs when k increases, or when developmental timing (the difference between α and β) lengthens for a given γ ; *paedomorphosis* occurs when k decreases, or when developmental timing shortens for a given γ . There are three types of peramorphosis. If k increases, the process is termed *acceleration*; a portion of development has occurred more rapidly than in the ancestral condition. If α is displaced to the left, the length of time of development is increased by starting earlier; this is termed *pre-displacement*. If β is displaced right, the length of time of development is lengthened by continuing longer; this is termed *hyper-morphosis*. Also, there are three complementary types of paedomorphosis. If k decreases, the process is *neoteny*: a portion of ontogeny has proceeded slower than in the ancestral condition. Displacement of α to the right initiates a portion of ontogeny later than in the ancestral condition; this is termed *post-displacement*. Finally, *progenesis*



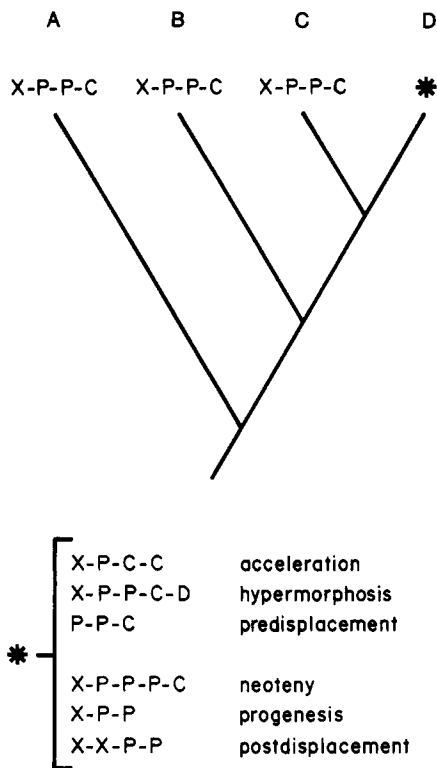
FIGURES 22–23.—Examples of the six categories of heterochronic changes. 22, The three types of changes representing peramorphosis, in that the descendant's morphology is more developed than that of the ancestor. 23, The three types of changes representing paedomorphosis, in that the descendant's morphology is less developed than that of the ancestor. Alterations in the rate of development (k), its time (t) of initiation (α), or its time of cessation (β) can produce changes in the morphology (γ) of the descendant (D), as compared to that of its ancestor (A). Dotted lines indicate ancestral "developmental trajectory"; solid lines indicate heterochronic derived trajectories. (Modified from O'Grady, 1987a, b.)

occurs when β is displaced left, terminating development earlier than in the ancestral condition. Figures 22 and 23 summarize these classes of effects.

Fink (1982) pointed out that Alberch et al. (1979) did not indicate how one might estimate the ancestral condition from which all assessments of heterochrony in evolution might be made. Fink further suggested that the outgroup criterion from phylogenetic systematics might provide an appropriate estimate of ancestral conditions in many cases, and provided examples of distributions of ontogenetic data on phylogenetic trees that correspond to the six forms of heterochrony listed above. Figure 24 shows a generalized view of the phylogeny-based observations that could lead to explanations of various forms of heterochrony in the evolution of characters.

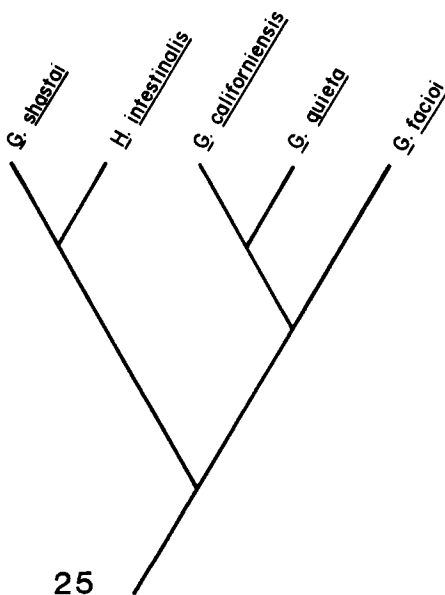
O'Grady (1987) used phylogenetic systematics and laboratory manipulations of development to apply Fink's (1982) formalism. The organisms used represent a monophyletic

group of digeneans (parasitic flukes) in the genus *Glythelmins*, inhabiting frogs and toads; Figure 25 is the phylogenetic tree for this group. One species, *G. intestinalis*, differs markedly from its sister species, *G. shastai*, and the rest of the members of its clade, by having an unusually attenuated hindbody (the portion of the body posterior to the ventral sucker, Figure 26). By raising *G. intestinalis* and one of its close relatives, *G. quieta*, under the same laboratory conditions, O'Grady was able to compare plesiomorphic and apomorphic developmental trajectories for the hindbody (Figure 27). According to the six categories established by Alberch et al. (Figure 24), the hindbody of *G. intestinalis* evolved by acceleration, a form of peramorphosis. O'Grady (1987) was able to confirm this through laboratory manipulations (raising *G. intestinalis* in an abnormal host, which retarded development) and produced specimens of *G. intestinalis* exhibiting the plesiomorphic hindbody condition. This amounts to experimentally produced



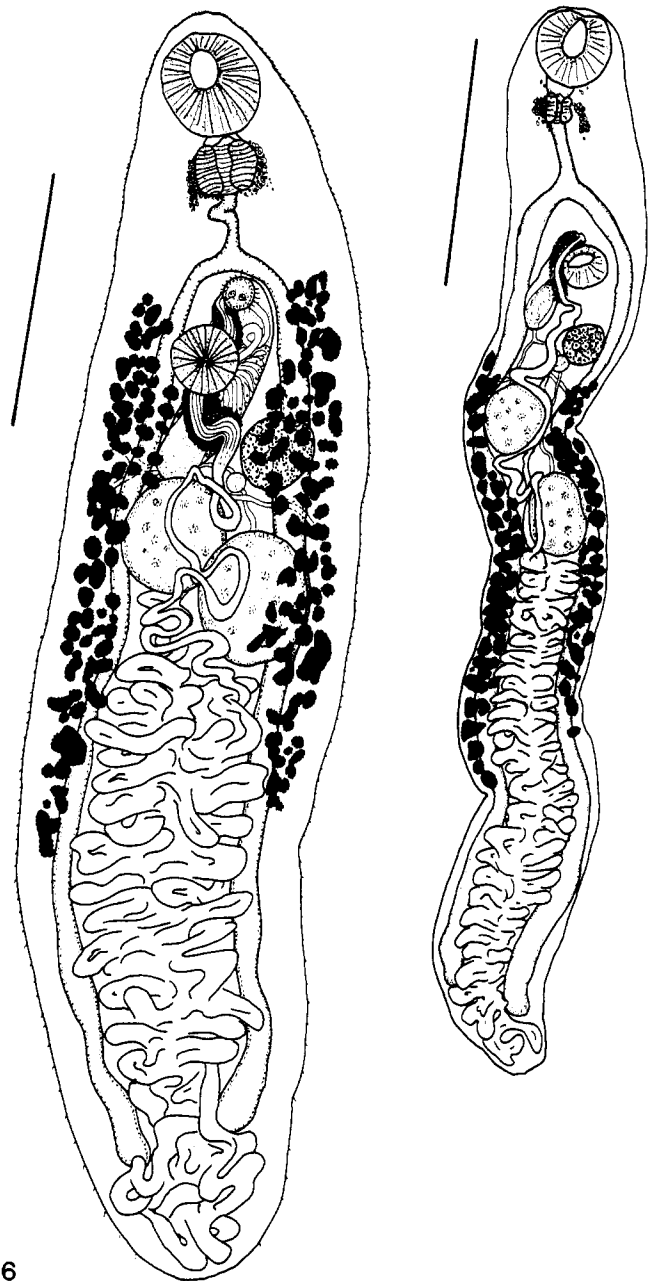
24

FIGURE 24.—Generalized view of phylogeny-based observations indicating evolution by means of six different modes of heterochrony. A, B, C exhibit plesiomorphic developmental trajectory beginning with initial state x developing into state p, finishing with state c. * = possible apomorphic conditions in D resulting from six different modes of heterochronic changes in evolution.



25

FIGURE 25.—Phylogenetic tree of a monophyletic group within the digenetic trematode genus *Glyphelmims* (parasitic flukes). This was the only tree produced.

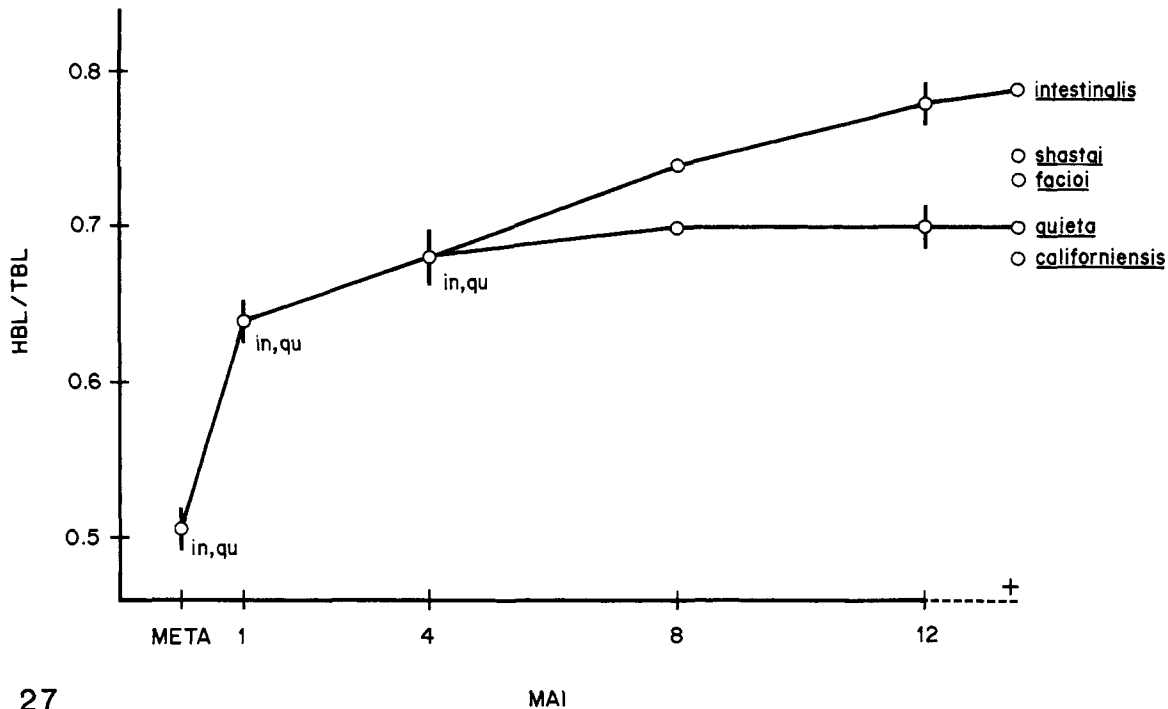


26

FIGURE 26.—Ventral view of two species of *Glyphelmims*. Left, *G. shastoi*, which has the plesiomorphic condition. Right, *G. intestinalis*, with a long hind body, which is the apomorphic condition. Scale bar = 1 mm.

neoteny, the form of paedomorphosis that is coupled with acceleration. Phylogenetic systematics allowed O'Grady to determine the plesiomorphic condition of the group. Likewise, Mooi (1987) used a phylogeny to determine plesiomorphic conditions in sand dollars and thereby identify progenesis and neoteny.

A recurring theme in comparative biology is the question of the relationship between the genotype and the phenotype. One way to approach this problem is to compare cladograms constructed from genotypic data (e.g., macromolecular, nucleic acid sequence) with those produced from phenotypic data (e.g.,



27

FIGURE 27.—Plesiomorphic and apomorphic developmental trajectories for the hindbody of two parasitic flukes. Values for the mean ratio (with means) of hindbody length to total body length (HBL/TBL) in specimens of the two species at metacercariae (META) and at 1, 4, 8, and 12 months after infection (MAI) in *Rana pretiosa*, for *Haplometrana intestinalis* (in), and in *Rana pipiens*, for *Glypthelmins quieta* (qu). The values for mature adults of other species of *Glypthelmins*, of unknown ages, are given at 12 + MAI. (Redrawn from O'Grady, 1987a, b.)

morphology, karyology). Hillis and Davis (1986) presented a summary phylogeny for North American ranid frogs based on information taken from allozyme, immunological distance, morphology, and rDNA data (see also Hillis, Frost, and Wright, 1983). Figures 28–31 are cladograms based on each type of data; Figure 32 is the summary tree. For these data, both Adams consensus and mapping methods yield Figure 32. Strict consensus analysis finds only two identical components in all four trees: (1) the clade containing “tarahumaræ group” and “palmipes group,” and (2) the clade formed by the “montezumæ group,” “areolata group,” “pipiens group,” and “berlandieri group.” These two components indicate instances in which evolutionary change occurred in all four data sets on the same internode. Figure 32 has 19 branches, 10 of which are characterized by phenotypic as well as some form of genotypic change. All morphological changes are correlated with some genotypic change but not all genotypic change is accompanied by phenotypic change. None of the four data sets conflicts with any of the others (except for a minor ambiguity in the immunological distance data), but neither does any of them alone produce the summary tree (Figure 32). Therefore, for the data examined, there is evidence of correlated genotypic and phenotypic change, and some evidence of genotypic change without phenotypic change.

HYBRIDIZATION

In an evolutionary sense, hybrids are organisms descended from parents with different lineages. As such, they fall outside of our normal idea of “inherited traits” in that characters from different lineages show up in the same individual. This movement of characters increases the “evolutionary noise” and makes the determination of phylogenies more difficult. There are three classes of hybrids. One can use the term hybrid to refer to offspring of parents from different demes or populations of the same species, but this is usually an accounting device used in studies of gene flow and need have no macroevolutionary connotations. There are two classes of interspecific hybrids—those that must be continually produced by interspecific matings and those that can persist on their own. Funk (1981, 1985) summarized various genetic combinations characteristic of hybrids. In some cases, the hybrid population consists of F1 generation organisms that are either infertile or which produce F2 offspring that are developmentally deficient. Such “hybrid swarms” must be replenished continually by reproduction between the two parental species. These populations are “evolutionary noise.”

In the second class of interspecific hybrids, some hybrids are capable of reproducing and persisting on their own. However, this ability to persist does not guarantee that they

will continue as independent evolutionary lineages. If the reproductive compatibility that allowed the parents to produce the hybrid in the first place does not disappear in the hybrid, it is possible that one or both of the parental species will assimilate the hybrid. Depending on how long the hybrid population persisted prior to such assimilation, one could construe this as a "reductive speciation event." If the hybrids are capable both of persisting on their own and of withstanding assimilation by either parent, they will be capable of persisting as distinct evolutionary species.

There are three phenotypic and ecological outcomes of speciation by hybridization. In the first case, the hybrids can segregate strongly with one parent (have most of the characteristics of one parent). When this happens, the hybrids are subject to the same selection regime as the parent. Since the parent species is already surviving in the environment, it is likely that the hybrids will survive as well. It is also possible, under such conditions, that interspecific competition will occur, since new genetic information has been added to the biota without enlarging the resource base used. In the second case, the hybrids may represent a mix of parental attributes, some of which may be intermediate in nature. Such hybrids are capable of surviving in a wider range of habitats than either parent, and should thus have a relatively good chance of survival. Although subject to a wider range of selection pressures, the flexibility of such hybrids should reduce the intensity of competition with either parent. Finally, the hybrids could represent a unique phenotypic and ecological system. In this case, survival should be more problematical, because the new combination must correspond to one allowed by the resource base available. However, such hybrids, if they survive, should face no competition from either parent. Thus, there are three pathways of survival open to species of hybrid origin. Each implies slightly different microevolutionary scenarios that can conceivably be tested, if one knows who the parental species were and the degree of phenotypic similarity between hybrids and parents. These can be assessed using phylogenetic systematic analysis.

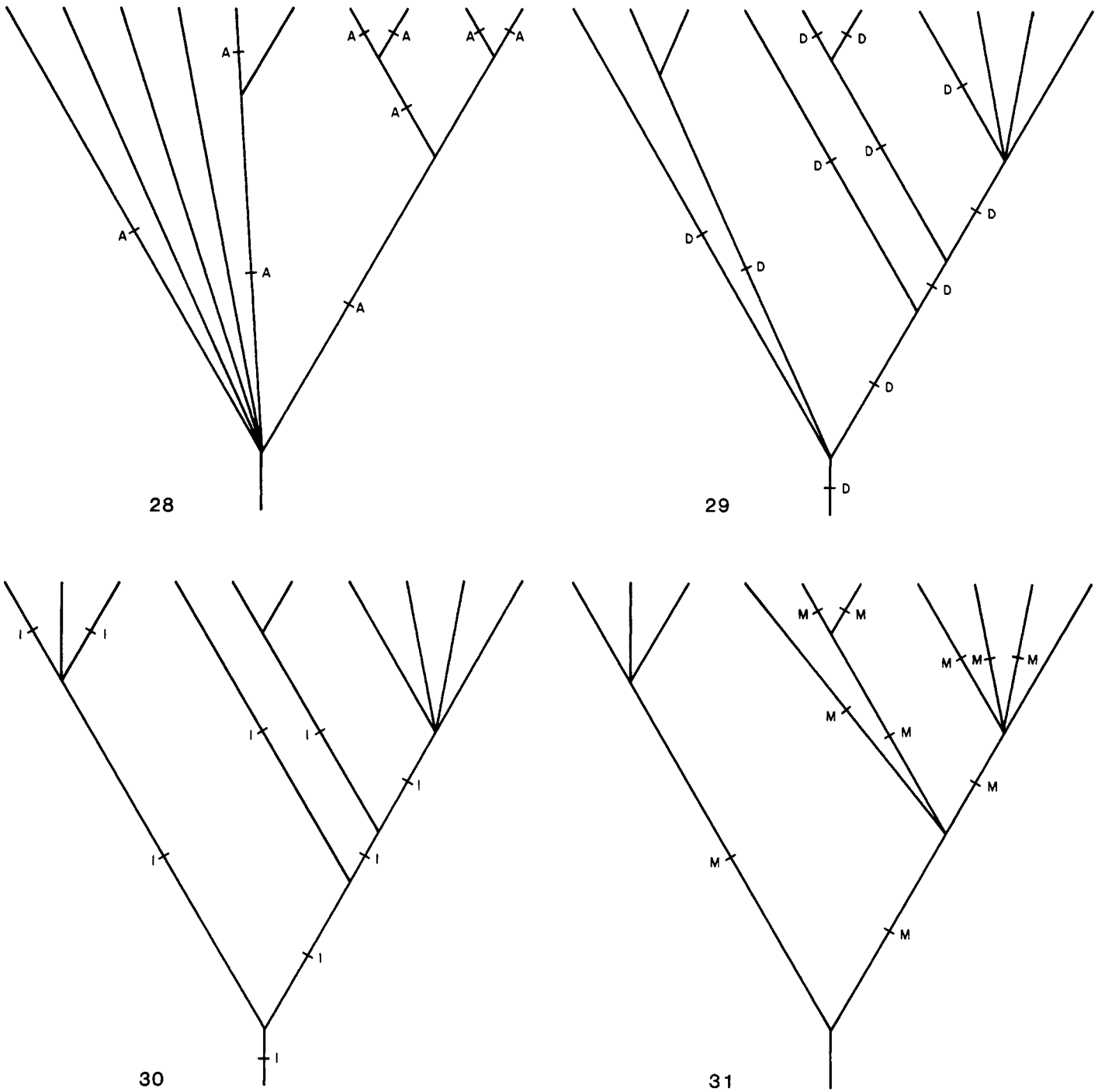
Over the years various methods have been suggested for identifying hybrids. Most involve the recognition of some intermediate character or combination of characters. However, recent publications using phylogenetic systematics (Humphries, 1983; Funk, 1985), show that hybrids can have characters of one parent, of both parents, or of neither parent.

It has been noted in the literature (Funk, 1985) that there is no reason to expect apomorphies from both parents to be expressed in the hybrid. Indeed, for this to be true, apomorphies would always have to be dominant over the corresponding plesiomorphy. For the sake of discussion, we will use a simple Mendelian example. If the apomorphy must be in the homozygous condition to be expressed, then all apomorphies not present in both of the parents will be in the heterozygous condition in the F1 and will not be expressed. In diploid hybrids the F2 would have a 1:2:1 and so on. Thus, some members of a hybrid would have apomorphies of the parents

and some would not. Indeed, any one organism would have the possibility of having any combination of the apomorphies of either parent. This condition is actually a good indication at the data gathering stage that the taxon under consideration is a diploid hybrid. Usually polyploid hybrids have the complete genome of both parents and so have the possibility of having all of the apomorphies of both parents. They usually express only a portion of the apomorphies possible to them because they inherit the genomes of both parents and so almost all characters are in the heterozygous condition. Hence, while they do not display all of the possible apomorphies, the ones they do express are usually more consistent from one individual to another than in diploid hybrids.

As well as displaying a bewilderingly inconsistent array of apomorphies, diploid hybrids tend to exhibit quantitative characters that are intermediate between the two parents. Because of these traits diploid hybrids are sometimes easier to identify at the data gathering stage than are polyploid hybrids. But whether diploid or polyploid hybrids exist in a data set, phylogenetic systematics can be useful in generating hypotheses of hybridization, which can then be investigated using independent data such as pollen fertility, karyotyping, or geographic distribution. Crossing experiments are useful in "recreating the hybrid" and for demonstrating that the putative parents are indeed capable of producing viable offspring. However, crossing data cannot be used to determine closeness of relationship (Rosen, 1975).

Funk (1985) presented many examples using cladograms to aid in the search for species of possible hybrid origin. A portion of one of those examples, a clade from the *Encelia* study, can be used to demonstrate the various techniques. The clade has ten taxa and 12 characters (Table 6). The PAUP computer program for phylogenetic analysis, written by David Swofford (Swofford and Maddison, 1987), produced 27 equally parsimonious cladograms, 15 of which were topologically different. Nearly all of the various branching patterns found in those cladograms can be represented in two cladograms (Figures 33 and 34). A strict consensus analysis produced Figure 35 and an Adams consensus tree is identical to Figure 34. Figure 36 is a summary diagram showing the various positions possible for these three taxa in all 27 cladograms. Figures 35 and 36 indicate that taxa ASP, CAL, and CAN are located in more than one place on the cladograms. In addition, LAC and CAN have characters that are intermediate in nature, and FAR is characterized by three reversals (Figures 33 and 34). Based on the cladograms there are five taxa that should be investigated as possible hybrids: ASP, CAL, CAN, FAR, and LAC. After examining the distribution and life history of these five taxa, three are supported as hybrids (ASP, CAN, and LAC). Examining the results of a phylogenetic analysis—both from the standpoint of character distribution and consensus tree construction—provides a method for indicating possible hybrids and their parents. Once a hypothesis of hybridization has been identified, it can be "tested" by information not used in the analysis. Some of the most useful types of information



FIGURES 28-31.—Four cladograms for ten groups of North American ranid frogs, each produced using a different type of data. 28, Allozyme data. 29, DNA data. 30, Immunological distance data. 31, Morphological data. A = apomorphic allozyme character, D = apomorphic DNA character, I = immunological distance data, and M = apomorphic morphological character. All taxon names follow the order found in Figure 32.

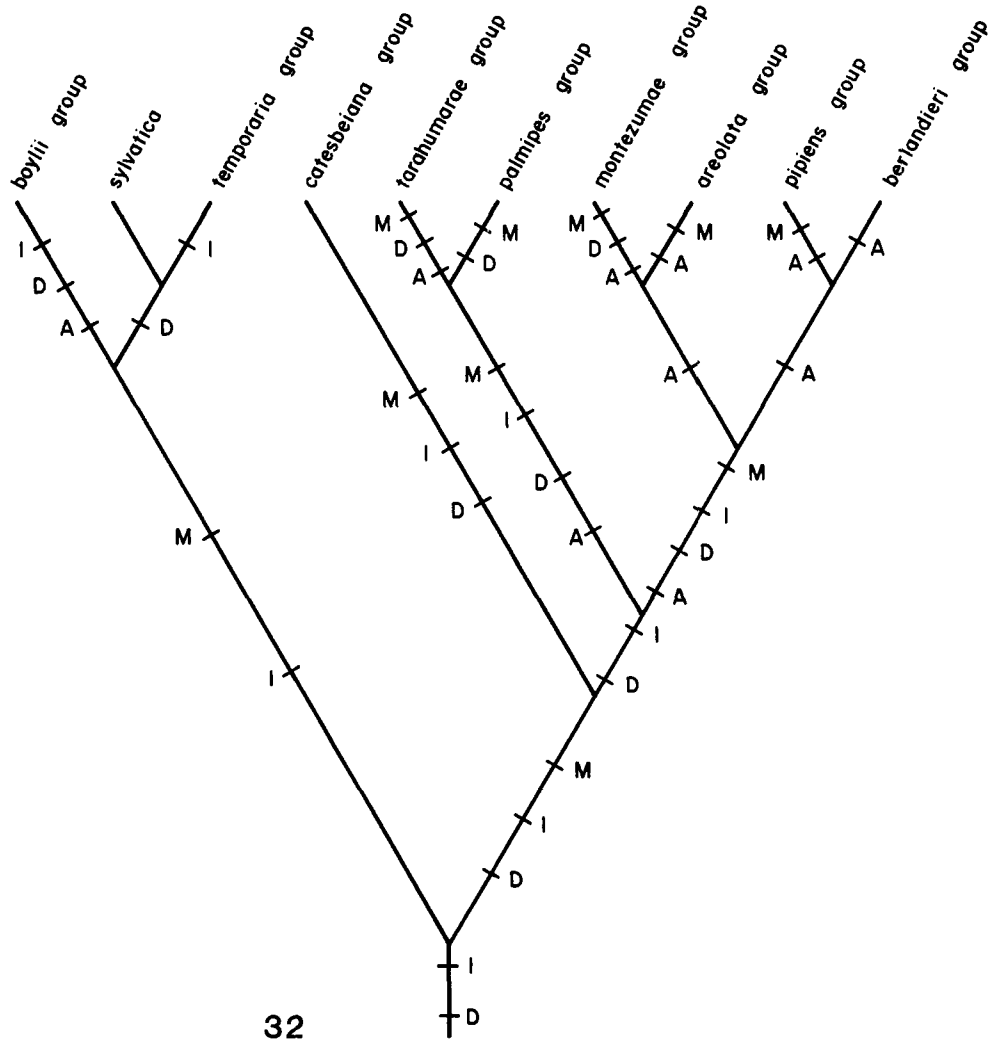


FIGURE 32.—Summary cladogram for 10 groups of North American ranid frogs (Figures 28–31). A = apomorphic allozyme character, D = apomorphic DNA character, I = immunological distance data, and M = apomorphic morphological character. (Redrawn from Hillis and Davis, 1986.)

are distribution, karyology, greenhouse hybridization studies, allozyme studies, pollen fertility, life history, and phenology studies.

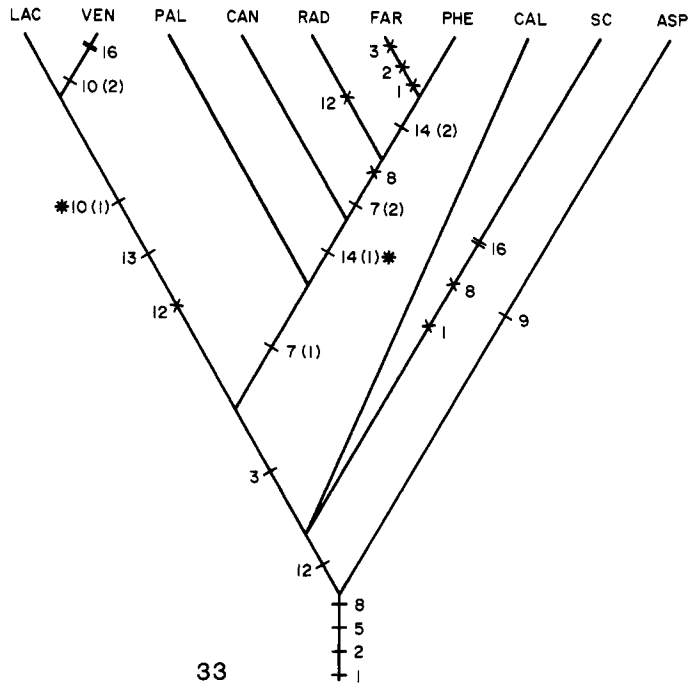
BIOGEOGRAPHY

With the advent of theories of an evolving geosphere, especially of plate tectonics and continental drift, biogeographic distributions have become an important source of information about the ages of evolutionary lineages, complementing data from paleontology and molecular biology. Paradoxically, this new knowledge has also led to controversy about evolutionary explanations for geographic distributions of related species.

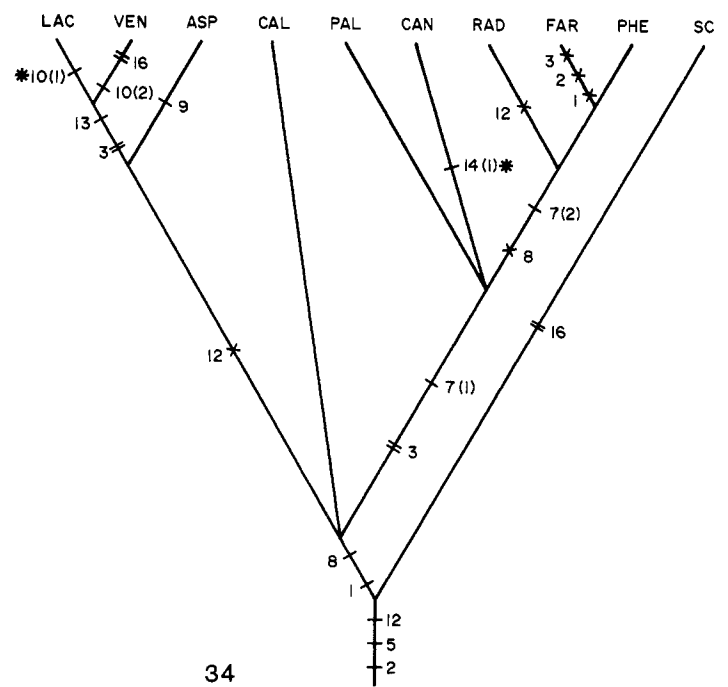
The general microevolutionary processes determining geographic distributions are reproduction and dispersal. At any point in time a species' distribution depends on the vagility of

its members. In the absence of constraints on range expansion, we would expect all species distributions to expand over time. That is, if a species originates as a small peripheral population, there should be a direct correlation between the age of the species and the area it occupies. Because abiotic (temperature, rain fall, etc.) and biotic (reproduction and vagility) factors exist, such "age and area" estimates have been criticized and rejected by most biogeographers. In fact, most species exist in relatively small ranges, while a few notable exceptions are widespread.

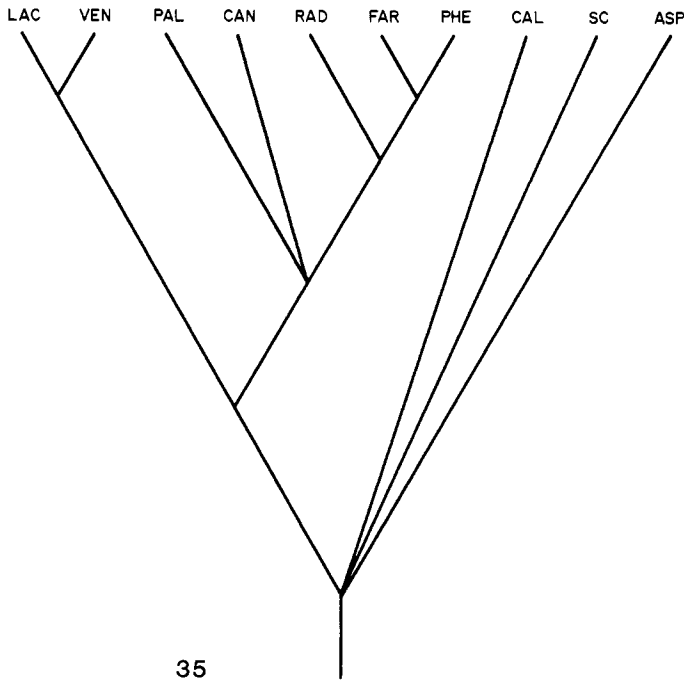
One common geographic distribution pattern is one in which the members of a given clade are allopatric or parapatric, and in which closest relatives occupy adjacent areas. If this pattern is the result of persistent microevolutionary processes, then dispersal into new areas accounts not only for the range occupied by the clade, but also for the particular pattern of occurrence of distinct species within the clade. The conven-



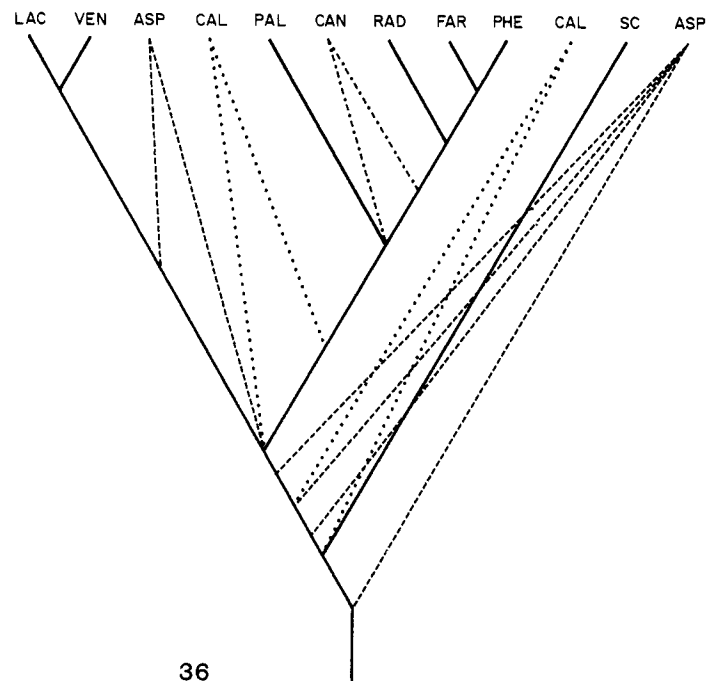
33



34



35



36

FIGURES 33–36.—Cladograms for a monophyletic group within the genus *Encelia*. 33 and 34, Two cladograms that maximize the differences found in the 15 equally parsimonious cladograms. 35, Strict consensus tree for Figures 33 and 34 (Adams consensus tree same as Figure 34). 36, Tree illustrating various positions for the four taxa that are found in more than one place on the 15 possible cladograms; dotted lines indicating multiple placement of terminal taxa. Taxon names are found in Table 6. * = intermediate characters.

tional explanation is that as an ancestral species disperses, it encounters new selection pressures and, in adapting to these pressures, it evolves into various descendant species, each characteristic of the particular environment found in a

particular area.

An alternative explanation is that new species arise within the range of older species, and push them, or are pushed, into marginal habitats (see various papers in Nelson and Rosen,

TABLE 6.—Data matrix for one clade of *Encelia* (Compositae). ASP = *E. asperifolia* (S.F. Blake) Clark & Kyhas, CAL = *E. californica* Nuttall, CAN = *E. canescens* Cavanilles, FAR = *E. farinosa* Gray var. *farinosa*, LAC = *E. laciniata* Vasey, PAL = *E. palmeri* Vasey & Rose, PHE = *E. farinosa* var. *phenicodonta* I.M. Johnson, RAD = *E. radians* Brandegee, SC = undescribed taxon, VEN = *E. ventorum* Brandegee. * = character of intermediate nature. (See Figures 33–36.)

Taxa	Characters											
	1	2	3	5	7	8	9	10	12	13	14	16
ANC	0	0	0	1	0	0	0	0	0	0	0	0
ASP	1	1	0	1	0	1	1	0	0	0	0	0
CAL	1	1	0	1	0	1	0	0	1	0	0	0
CAN	1	1	1	1	1	1	0	0	1	0	1*	0
FAR	0	0	0	1	2	0	0	0	1	0	2	0
LAC	1	1	1	1	0	1	0	1*	0	1	0	0
PAL	1	1	1	1	1	1	0	0	1	0	0	0
PHE	1	1	1	1	2	0	0	0	1	0	2	0
RAD	1	1	1	1	2	0	0	0	0	0	0	0
SC	0	1	0	1	0	0	0	0	1	0	0	1
VEN	1	1	1	1	0	1	0	2	0	1	0	1

1981). Such “forced dispersal” results in the occurrence of relatively primitive members of a clade in marginal habitats.

Regardless of the particular scenario one adopts, previous explanations have relied on discerning the center of origin of a group to provide an explanation of the biogeographic history. That is, find the center of origin and connect the distributions of the members of a given group—this is the dispersal route. Darwin and Wallace seemed to view speciation as a sympatric phenomenon and yet viewed dispersal as evolutionarily important as well. Mayr (1942, 1963) forged a synthesis of speciation and biogeography by proposing that most speciation events took place in peripheral habitats occupied by small populations established by chance dispersal over geographic barriers.

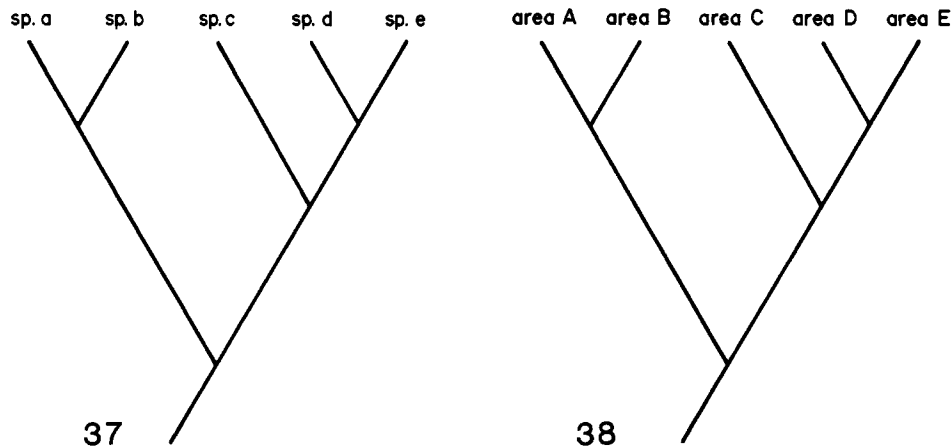
So long as geographic stasis is assumed, there appears to be a smooth reduction from macroevolutionary geographic patterns to microevolutionary ones. However, the advent of acceptable theories of mobile geology forces evolutionary biologists to consider a second possible interpretation for macroevolutionary biogeographic patterns. That is, despite the ongoing process of dispersal in all lineages in all generations, it is possible that some descendant species occur where they do and are distinct from the other members of their clade because the changing geography isolated them. In this case, dispersal explains how the ancestral population got into the area where the descendant occurs, but geological changes explain why the descendant population became isolated and subsequently speciated. Speciation could occur as a result of the isolation without directional selection from new environmental conditions. This is a possibility that cannot be deduced directly from microevolutionary processes in biology, although it is certainly not inconsistent with any of them. In addition,

if we are to allow the possibility of geological changes causing the isolation that led to speciation for one group, it is conceivable that a single geological episode could set the stage for speciation in a large number of co-occurring ancestral species. Thus, mobile geology inserts a macroevolutionary process into evolutionary theory. We now have more possible explanations, and the possibility that what explains one set of distributions may or may not explain another.

One assumes that a biogeographic pattern common to more than one group requires an explanation involving a process that can affect many lineages in a similar fashion. If the biogeographic pattern is a historical one, the general explanation should also be historical. The greatest constraint on this kind of research is a paucity of well-documented phylogenies. This has led some scientists to accuse systematists of culling their data, using only those few out of many phylogenies that showed the general patterns (Simberloff, Heck, McCoy, and Connor, 1981). These objections do not deny the reality of the patterns. They attempt to persuade other scientists that, although the patterns are real, given millions of phylogenies showing independent dispersal on a finite planet, some will be correlated by chance alone. Endler (1977) went even further, suggesting that the general patterns represent only common adaptive pathways by independent lineages. The conservative nature of ecological diversification in phylogeny contradicts this possibility.

Biogeographic studies using phylogenetic systematics have changed during the past twenty years. Hennig (1966) and Brundin (1966) plotted cladograms on distribution maps and produced explanations invoking dispersal routes (in “Speciation,” below, we will see that for certain modes of speciation, that is exactly what they represent). Following these publications, studies have concentrated on looking for associations between distributions and major tectonic changes. In many cases, the biogeographic analysis implied ages of origin and years of persistence in excess of fossil findings or of theoretical expectations. Paleontologists and traditionally minded ecologists and population biologists objected. This led to comparing the phylogenies of different groups of organisms having similar distributions (Croizat, Nelson, and Rosen, 1974; Rosen, 1975). This involved constructing *area cladograms*—cladograms of taxa (Figure 37) with their distributions in place of taxon names (Figure 38).

The null hypothesis in biogeography is that biogeographic patterns among clades or species should be due entirely to chance, that there is no pattern, and there should be no necessary underlying reason for distributional correlations, and the area of disjunction of the ancestral species cannot be determined by inspecting the ranges of its descendants. Therefore it is important to show first, which clades have unique distribution patterns and which have patterns exhibited by other clades. Initially studies concentrated on developing ways to highlight the redundant distributions. Cladograms for different groups of organisms were compared, and those species in each tree showing nonredundant distributions were



FIGURES 37–38.—The area cladogram. 37, For species a–e. 38, For letters A–E, indicating distribution and replacing the names of terminal taxa.

deleted, producing “reduced cladograms” showing those parts of the phylogenies of different groups that appeared to be the same (Rosen, 1975). This attempt to pinpoint the redundancies more closely unfortunately also fueled the suspicions of selective data culling raised by some ecologists. More recently, consensus tree methods have been employed in which the nonredundant portions of phylogenies are reduced to unresolved polytomies on consensus trees of the various areas involved in the study (Nelson and Platnick, 1981; Humphries and Parenti, 1986).

Another method of analysis involves treating cladograms as if they were multicharacter transformation series of the areas in which their members occur (Brooks, 1981). The assumption is that geographic distributions play a role in phylogenesis, and so any cladogram can be mapped onto a pattern of areas through time. Those portions of different clades that act as synapomorphies on a tree of areas have common evolutionary histories with respect to that pattern of areas. Those that show autapomorphic or homoplasious distributions on the tree of areas have unique histories, with autapomorphies indicating vicariant or peripheral isolates, allopatric speciation, or sympatric speciation, and homoplasies indicating secondary dispersal subsequent to speciation, or sympatric speciation.

All the above methods have some utility. Strict (Nelson) consensus trees are useful when looking for replicated areas of cladograms, and Adams consensus trees can be applied to questions of maximum resolution. Mapping gives a summary of all of the data. We will look at two different sets of data (fish and birds) to illustrate their utility.

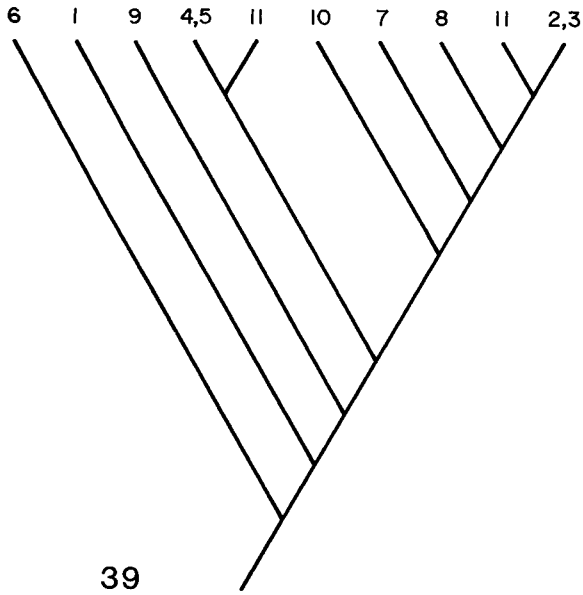
Possibly the most analyzed biogeographic data are Rosen’s on two genera of Central American fishes, *Heterandria* and *Xiphophorus* (Rosen, 1978, 1979). Figures 39 and 40 are the area cladograms for the clades of these genera found in Central America. The Adams consensus tree for the two area cladograms can be illustrated by either Figure 41 or by Figure 42, in which we have used the methods developed to recognize hybrids (see “Hybridization,” above) and have removed area

11 and placed it above the area cladogram. From studying Figure 42 and comparing it to Figures 39 and 40 it is obvious that the areas that are changing position are areas 6, 3, and 9. These areas may have been affected by dispersal.

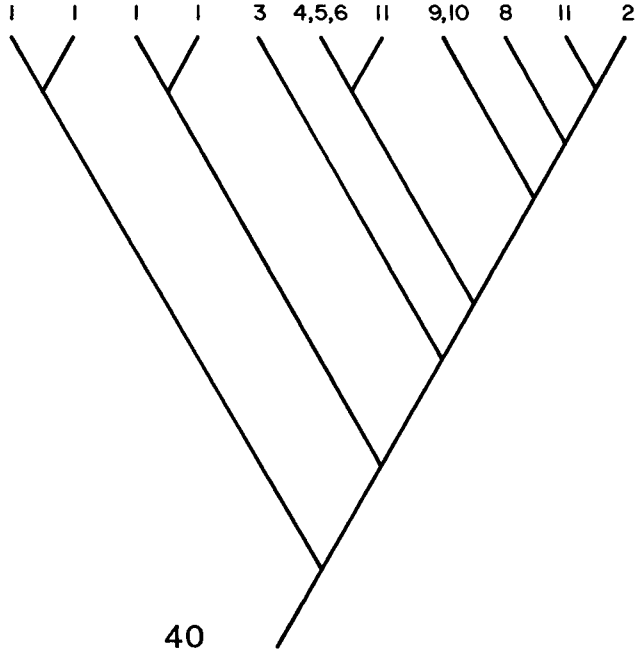
The bird data of Cracraft (1982) can also be analyzed by this method. Figures 43 (Wedgebills and Birds-of-Paradise have identical area cladograms) and 44 (Wrens) combine to form Figure 45 and this ACT combines with a third genus (Finches, Figure 46) to form the ACT in Figure 47. If one is willing to assume a hybrid origin for area 3 (dispersal act), Figure 48 is the best estimate of the relationships using Adams consensus.

The method developed by Rosen (1975) and Nelson and Platnick (1981) is similar to strict consensus or Nelson component analysis (see “Consensus Analysis,” above). It asks the question, “Given all of the area cladograms under consideration, what patterns of relationship are found in all of them?” It seeks to find redundant patterns because these are the patterns that provide the strongest evidence for vicariance. Areas that are not found on all of the area cladograms or that are in conflict are removed to produce a reduced area cladogram (for a justification of this procedure see Nelson and Platnick, 1981). Because the method for reducing Rosen’s two area cladograms to the redundant areas has been published several times (Rosen, 1978, 1979; Nelson and Platnick, 1981; Humphries and Parenti, 1986) we will not repeat it in its entirety here. Instead we will give the final reduction with Figure 49 (reduced area cladogram for *Heterandria*) and Figure 50 (reduced area cladogram for *Xiphophorus*) simplified to produce the summary reduced area cladogram shown in Figure 51, which gives the area relationships that are agreed on in both area cladograms. Figure 51 gives us the area relationships that may be a result of geographic separation by vicariance followed by speciation. Cracraft’s bird data do not lend themselves to this type of analysis because some of the area cladograms are mutually exclusive.

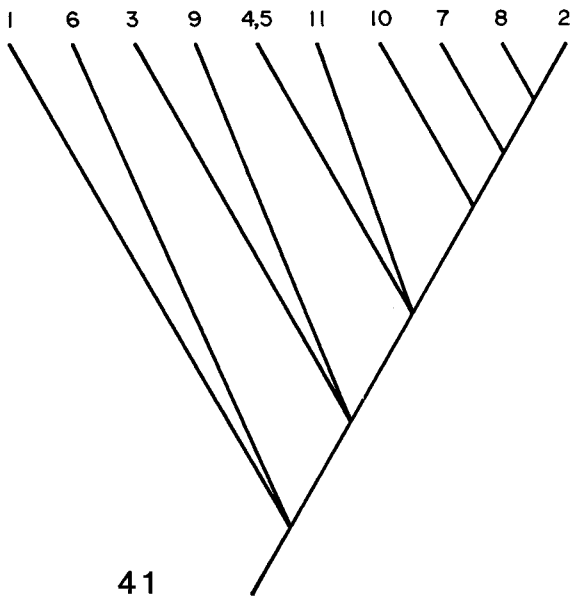
The third way of looking at nonidentical area cladograms is



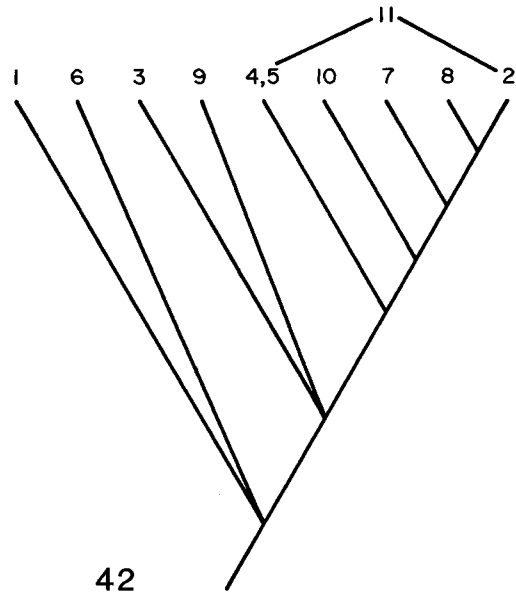
39



40



41



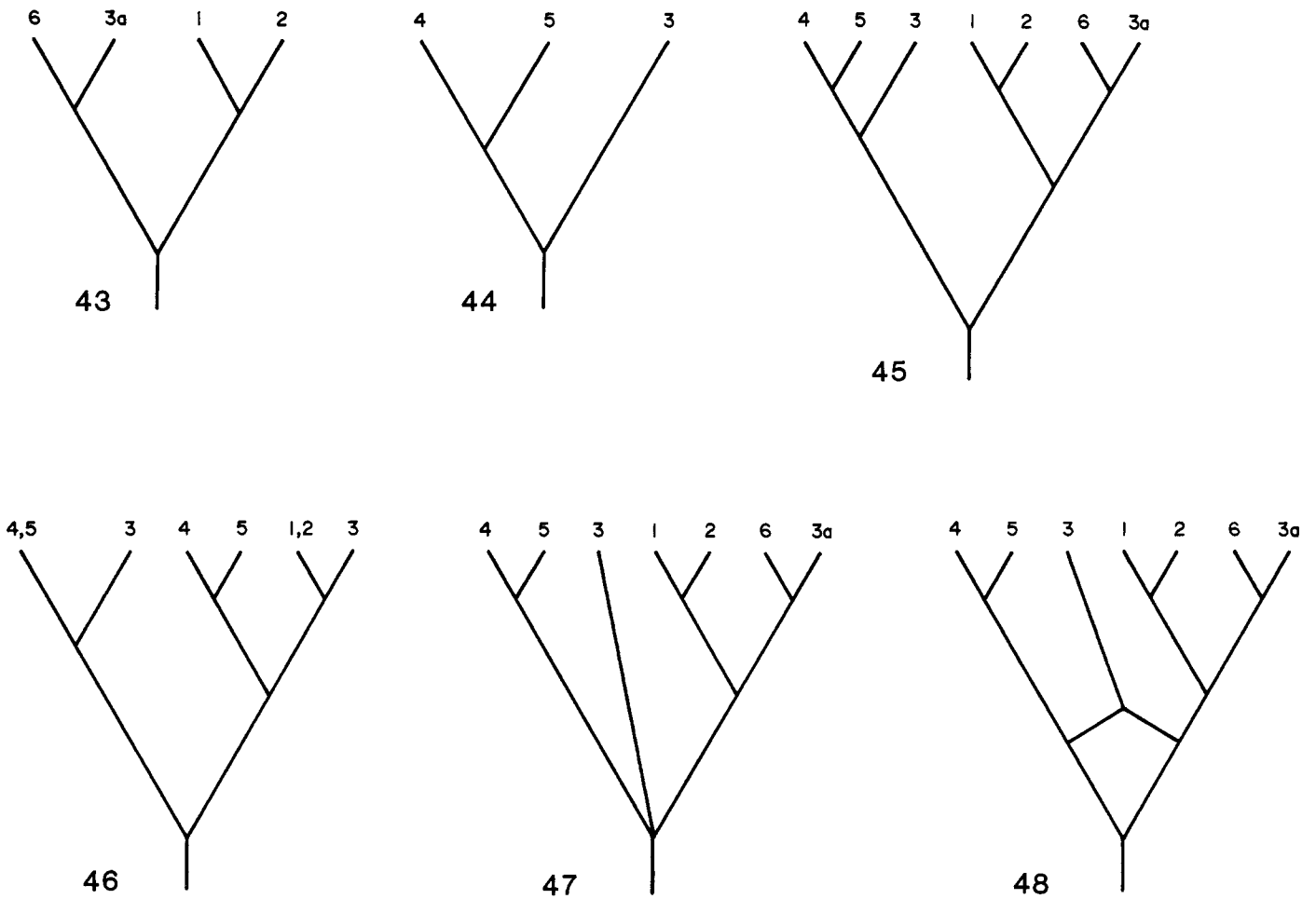
42

FIGURES 39-42.—Consensus analysis of fish data of Rosen. 39, Area cladogram for *Heterandria*. 40, Area cladogram for *Xiphophorus*. 41, Adams consensus tree. 42, Tree with area 11 treated as a hybrid area (dispersal act). Terminal taxa are geographic areas that reflect distribution of species.

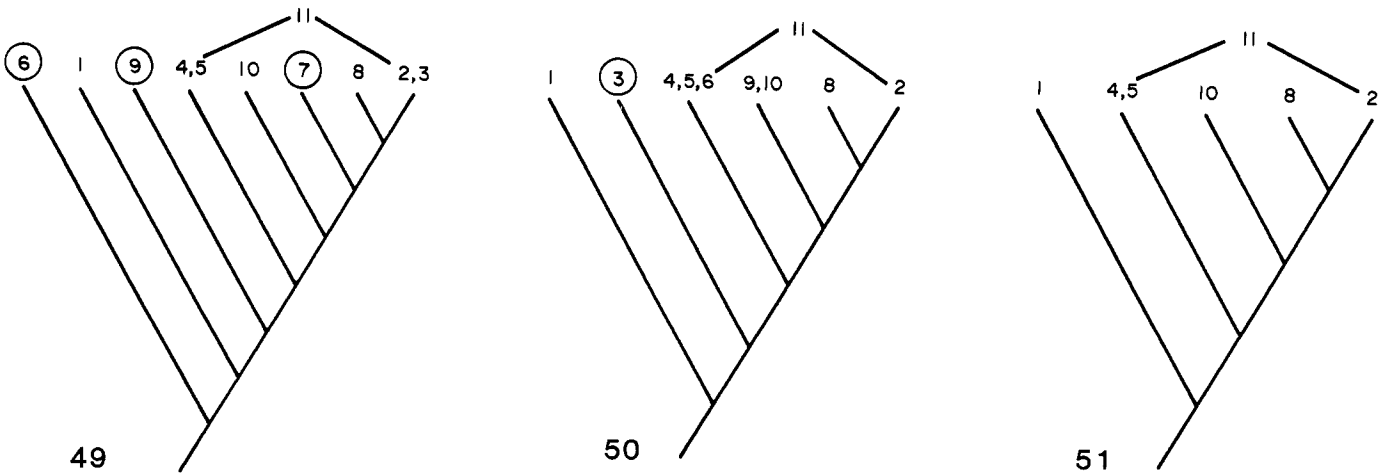
via mapping. Each tree can be coded as a multistate character (see "Character Coding," above) and the resulting diagram is a summary of all of the data. It differs from the two methods described above in that it gives weight to the number of times a pattern is repeated. For instance if five area cladograms imply that *a* and *b* are more closely related to each other than either was to *c* and one area cladogram implies that *b* and *c* were

more closely related to each other than either was to *a*, mapping analysis will link *a* and *b* together, suggesting that the single instance of close relation between *b* and *c* was due to dispersal. In both forms of consensus analysis, the result would be a trichotomy for *a*, *b*, and *c*.

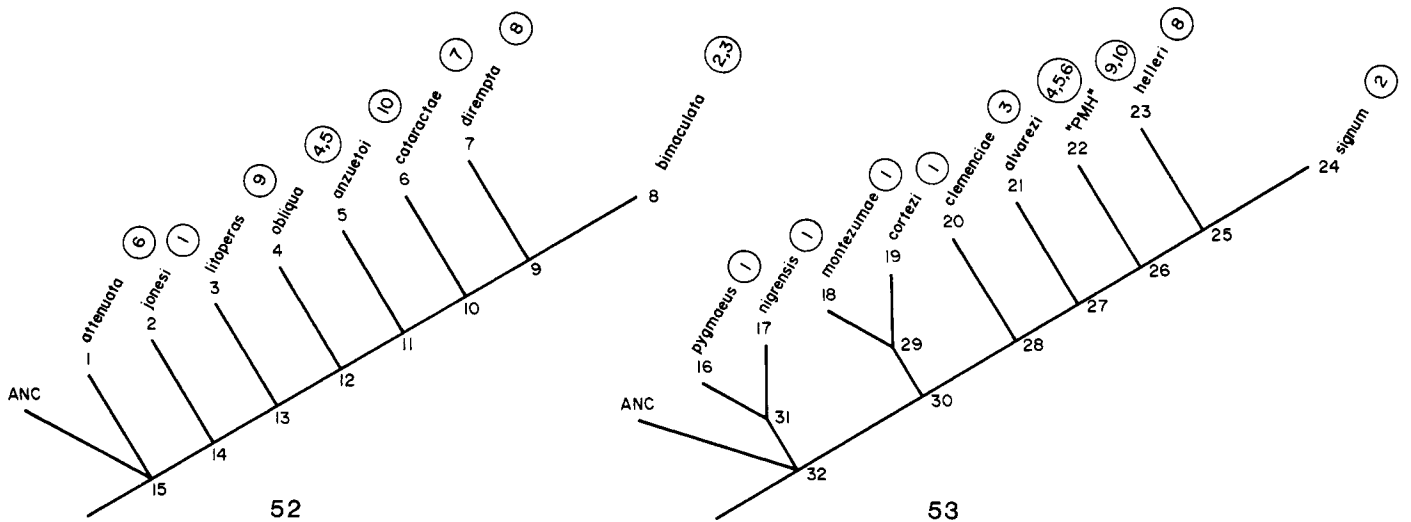
The procedure for coding the fish data is explained by examining Figures 52 and 53 in conjunction with Table 7 for



FIGURES 43-48.—Area cladograms for several groups of birds from Australia. 43, Area cladogram of Wedgebills; Birds-of-Paradise have an identical area cladogram. 44, Area cladogram of Wrens. 45, Adams consensus tree for Figures 43 and 44. 46, Area cladogram of Finches. 47, Adams consensus tree for Figures 45 and 46. 48, Consensus tree treating area 3 as a hybrid area (dispersal event). Terminal taxa are geographic areas that reflect distribution of species. (Data from Cracraft, 1982.)



FIGURES 49-51.—Area cladograms for *Heterandria* and *Xiphophorus*. 49, *Heterandria*. 50, *Xiphophorus*. 51, Summary diagram. Terminal taxa are geographic areas that reflect distribution of species; circled numbers indicate areas that, once removed, yield a reduced area cladogram. (Figures 49 and 50 redrawn from Rosen, 1978.)



FIGURES 52–53.—*Heterandria* and *Xiphophorus* cladograms with areas of occurrence listed above taxa and nodes labeled for ABC. Circled numbers refer to geographic areas representing species distribution. (See Table 7.)

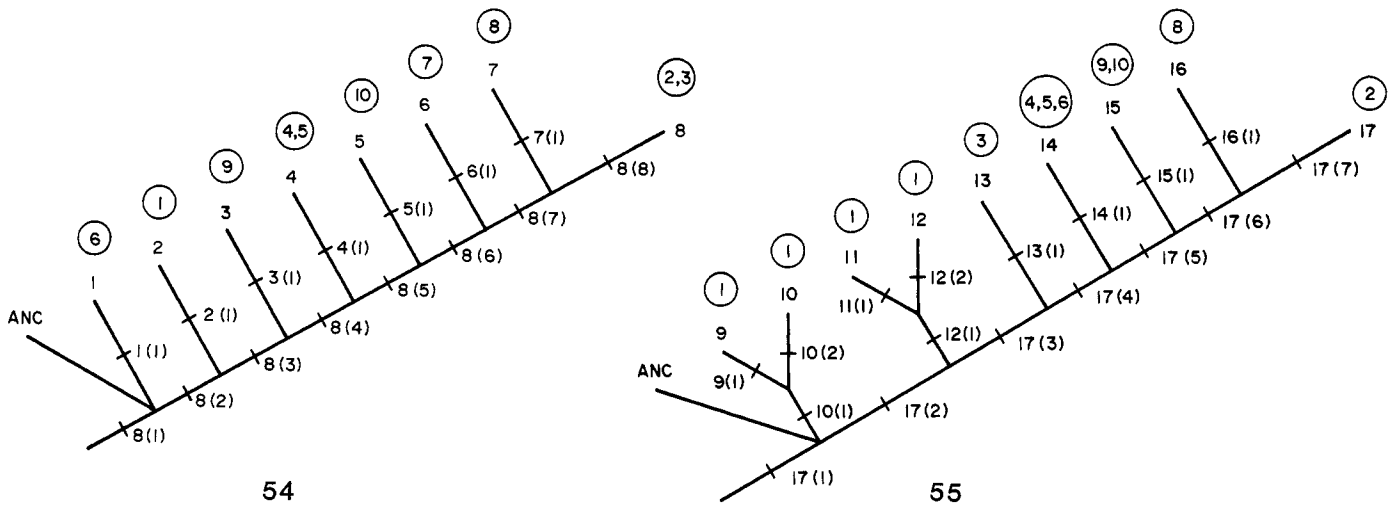
TABLE 7.—ABC matrix for the *Xiphophorus* and *Heterandria* data of Rosen (1979). “9” indicates the taxon is absent from the area. (See Figures 52 and 53.)

Areas	Codes																																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32				
ANC	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
ONE	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1		
TWO	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	1	0	1		
THREE	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	
FOUR	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	
FIVE	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	1	0	1	
SIX	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	1	0	1	
SEVEN	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	
EIGHT	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	0	1	0	1	
NINE	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	1	0	1	0	1	
TEN	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	0	1	0	1	0	1

the ABC and Figures 54 and 55 in conjunction with Table 8 for the NLC. The data were run using PAUP and the results using the two data matrices were the same. There are 10 equally parsimonious area cladograms (Figures 56–65), four of which (Figures 51, 53, 55, and 57) simply change the position of area 3. Close examination of the remaining six area cladograms shows where the taxa that were eliminated from the strict consensus may belong. Area 6 is either at the second node from the bottom or it is sister to the clade of 5 plus 4. Area 3 is either sister to 2 or sister to the clade of 2 plus 8. The most variable groupings are for 9 and 10, principally 9. Area 9 is found both below and above the clade of 4 plus 5. It is sister to 10 or sister to the clade of 4 plus 5. Areas 9 and 10 together can be above or below the clade of 4 plus 5 or sister to it. Species associated with the areas that are unstable on the

various area cladograms are prime candidates for hypotheses of dispersal. If we look at the distribution of characters (species) on the area cladograms we find that most are consistent but that several can be interpreted as either parallel evolution or loss. As suggested in “Comparative Methods,” above, we can interpret the parallel evolution as a result of dispersal and the loss as a result of extinction of the species in that area. With some, both hypotheses are equally likely. For example, *Heterandria bimaculata*, “character 8,” can be either independently gained in both area 2 and area 3 or it could have become extinct in area 8 (Figures 64 and 65). From such data, hypotheses of historical episodes of vicariance and dispersal can be generated.

The bird data were also coded using both ABC (Figures 66–69 and Table 9) and NLC (Figures 70–73 and Table 10).



FIGURES 54–55.—*Heterandria* and *Xiphophorus* cladograms with areas of occurrence listed above taxa and nodes labeled for NRL. Circled numbers refer to geographic areas representing species distribution. (See Table 8.)

TABLE 8.—NLC matrix for the *Xiphophorus* and *Heterandria* data of Rosen (1979). "9" indicates the taxon is absent from the area. (See Figures 54 and 55.)

Areas	Codes																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
ANCE	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
ONE	0	1	0	0	0	0	0	2	1	2	1	2	0	0	0	0	1
TWO	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	7
THREE	0	0	0	0	0	0	0	8	0	0	0	0	1	0	0	0	3
FOUR	0	0	0	1	0	0	0	4	0	0	0	0	0	1	0	0	4
FIVE	0	0	0	1	0	0	0	4	0	0	0	0	0	1	0	0	4
SIX	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	4
SEVEN	0	0	0	0	0	1	0	6	9	9	9	9	9	9	9	9	9
EIGHT	0	0	0	0	0	0	1	7	0	0	0	0	0	0	0	1	6
NINE	0	0	1	0	0	0	0	3	0	0	0	0	0	0	1	0	5
TEN	0	0	0	0	1	0	0	5	0	0	0	0	0	0	1	0	5

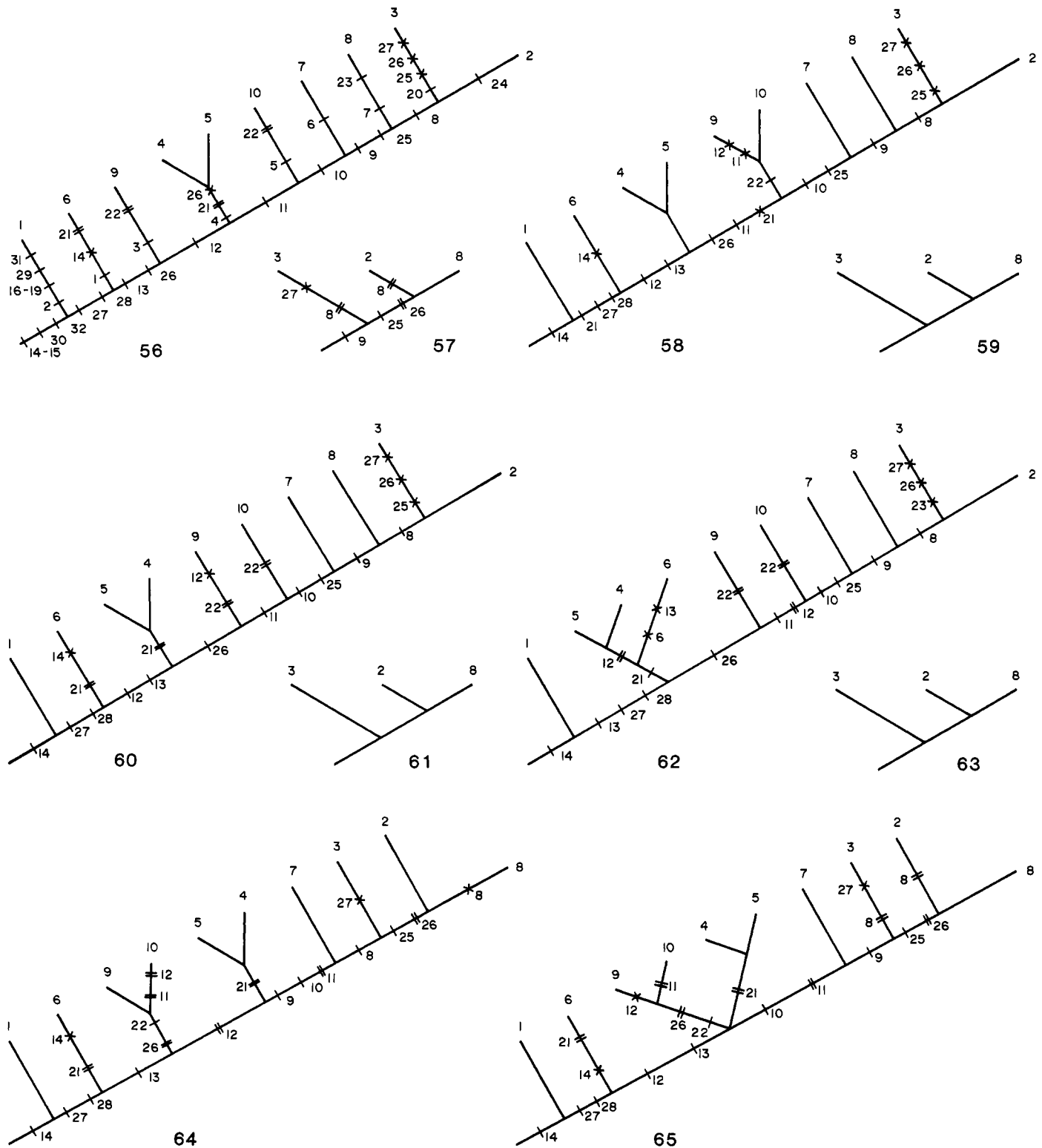
Figure 74 (constructed using NLC data matrix, Table 10) is the most parsimonious arrangement of the data for both ABC and NLC. It appears from the distribution of the data that areas 6 and 3a grouped together because they are missing 17(1) and 17(2) and that there is a link between area 3 and the clade of areas 1 and 2 because of the parallel occurrence of 17(3). One explanation for this area cladogram (Figure 74) is that there was a historical colonization (dispersal) event into area 3 by an ancestral species denoted by 17(3) and that some species have become extinct in areas 6 and 3a (perhaps due to a common event).

There is one facet of "mapping" that must be kept in mind: when a taxon is found in more than one area, the procedure is to score it as primitively present for both areas. This method called "inclusive ORing" (implicit in Brooks, 1981, and explicit in Cressy et al., 1983)—where presence in an area always has precedence over absence—will bias the outcome in some cases (O'Grady and Deets, 1987). For instance, if one

passes by three nodes to reach one of the areas in one cladogram and two nodes to reach the area in the other cladogram, the results will favor the location that has the three nodes because each node is counted as a character.

Phylogeneticists have used three methods in biogeographic analysis and each method is designed to ask a different question. Strict (Nelson) consensus analysis asks which portions of different cladograms exhibit identical distribution patterns. Adams consensus analysis asks which portions of phylogenies for different groups are consistent with a single geographic distribution pattern. Finally, mapping methods give a summary of all of the data with possible placements for the taxa that do not conform to a general pattern.

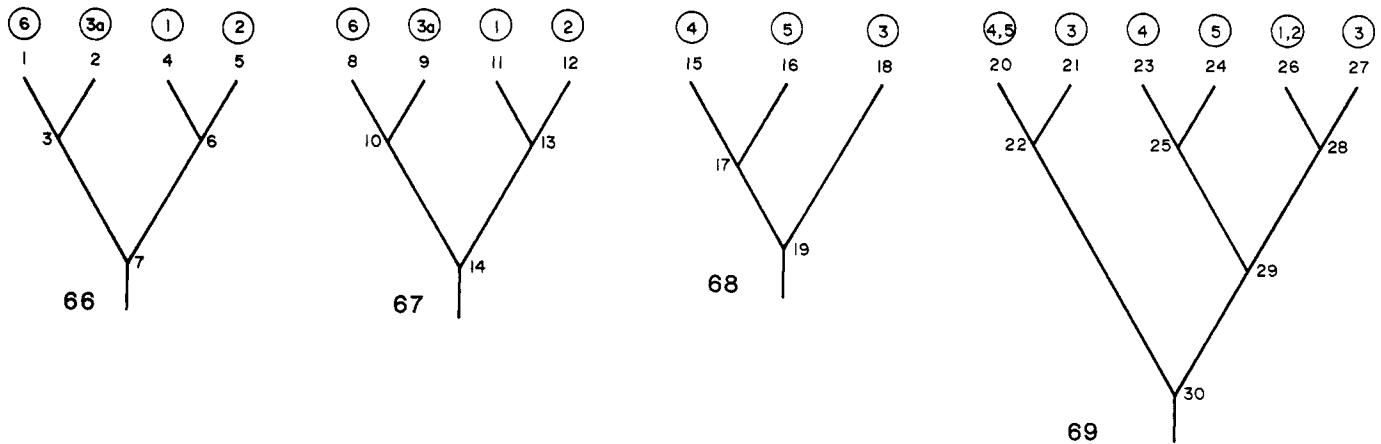
Biogeography has microevolutionary as well as macroevolutionary components. On microevolutionary scales, the phenomena of interest involve the local and regional movements of individual species. Even multispecies associations are considered to result from independent movements of the component species (MacArthur and Wilson, 1967). Macroevolutionary phenomena (historical biogeography) involve regional and global patterns of occurrence of different species. Associations of multiple species showing a single pattern are assumed to share common histories with respect to their geographic distributions. Wiley (1988) has recently stressed that historical biogeography encompasses two major research questions. First, do different clades exhibit speciation patterns that covary with respect to the same geographical distributions? And second, do the phylogenies of clades correspond to the geological history of the areas in which endemic species occur? If the answer to the second question is "yes," the answer to the first is also "yes." This does not necessarily mean that the converse is true. The relationship between geography and phylogeny is one of speciation events.



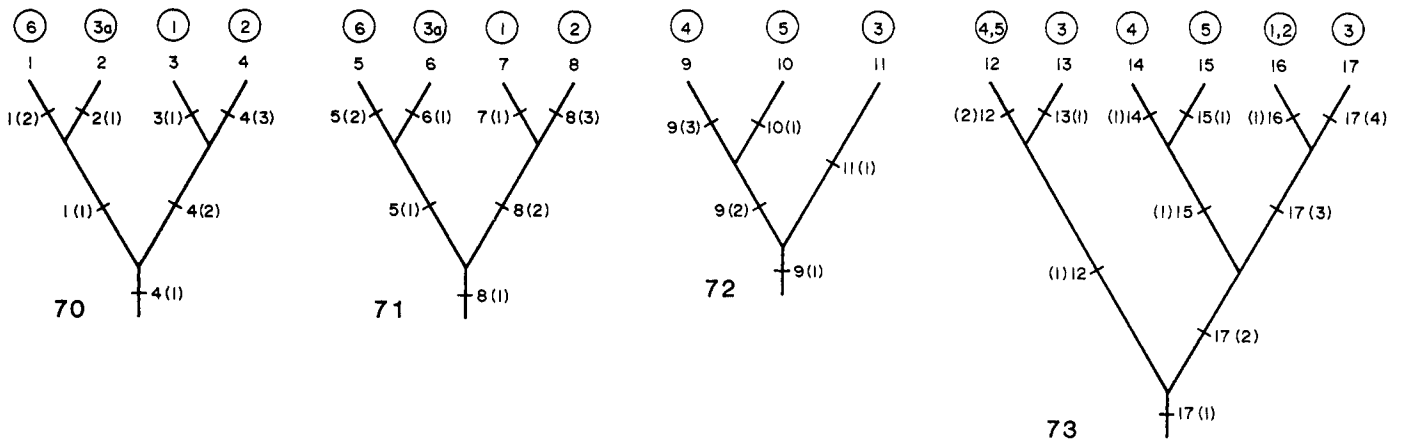
FIGURES 56-65.—Ten equally parsimonious area cladograms produced by “mapping” of distribution data of *Heterandria* and *Xiphophorus* phylogenies together as characters of their areas of occurrence. = indicates a possible dispersal event; x indicates a possible extinction event. Terminal taxa are geographic areas. Figures 57, 59, 61, and 63 differ from Figures 56, 58, 60, and 62, respectively, only in the placement of area 3.

TABLE 9.—ABC matrix of Cracraft's bird data (1986). "9" indicates the taxon is absent from the area. (See Figures 66–69.)

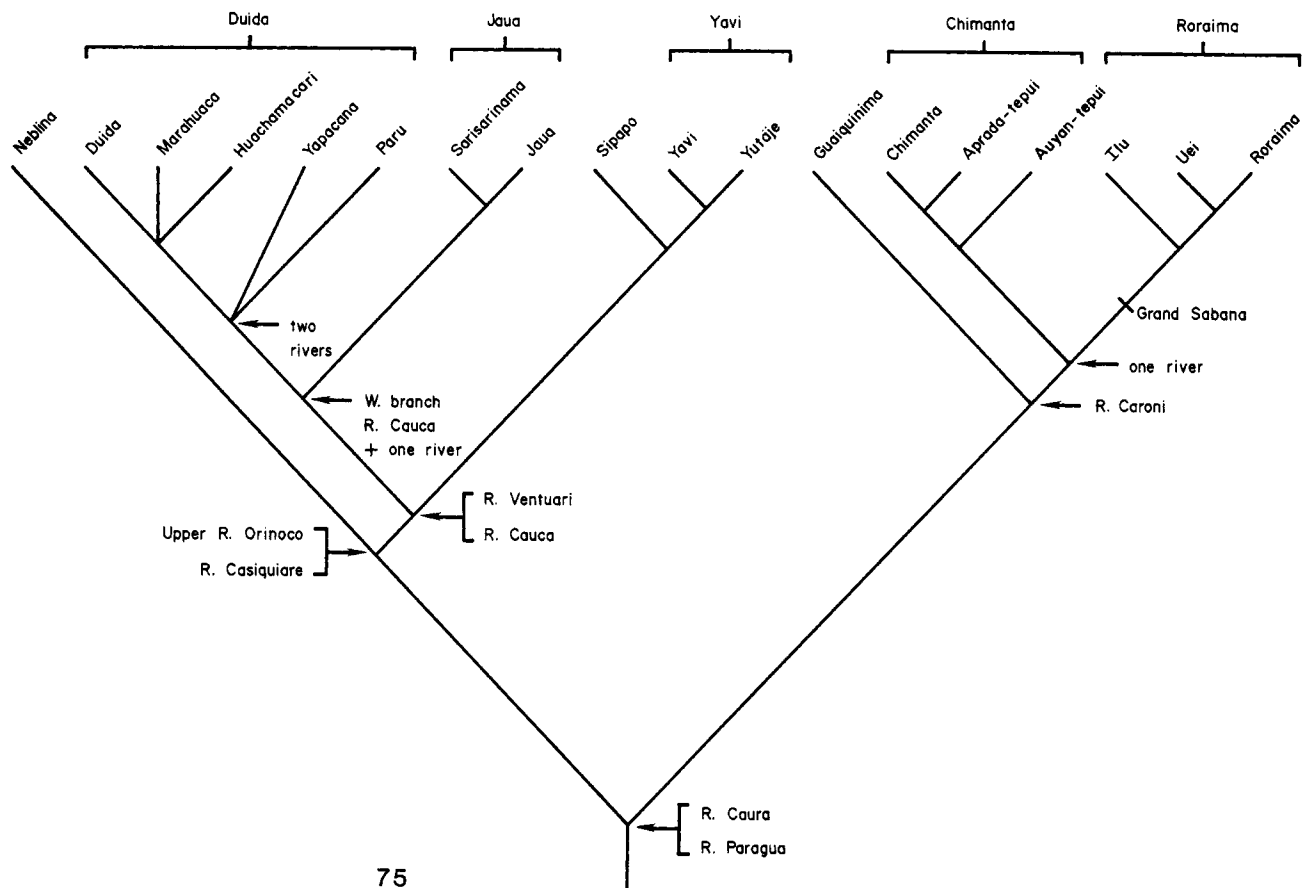
Areas	Codes																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
ANCE	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
ONE	0	0	0	1	0	1	1	0	0	0	1	0	1	1	9	9	9	9	9	0	0	0	0	0	0	0	1	0	1	1
TWO	0	0	0	0	1	1	1	0	0	0	0	1	1	1	9	9	9	9	9	0	0	0	0	0	0	1	0	1	1	
THREE	9	9	9	9	9	9	9	9	9	9	9	9	9	9	0	0	0	1	1	0	1	1	0	0	0	0	1	1	1	
THREA	0	1	1	0	0	0	1	0	1	1	0	0	0	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	
FOUR	9	9	9	9	9	9	9	9	9	9	9	9	9	9	1	0	1	0	1	0	0	0	1	0	1	0	0	0	1	
FIVE	9	9	9	9	9	9	9	9	9	9	9	9	9	9	0	1	1	0	1	0	0	0	1	1	0	0	0	1	1	
SIX	1	0	1	0	0	0	1	1	0	1	0	0	0	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	



FIGURES 66–69.—Australian bird cladograms with areas of occurrence listed above taxa and nodes labeled for ABC. 66, Wedgebills. 67, Birds-of-Paradise. 68, Wrens. 69, Finches. Terminal taxa are species, and numbers inside circles represent geographic areas that correspond to the species distribution. (See Table 9.)



FIGURES 70–73.—Australian bird cladograms with areas of occurrence listed above taxa and nodes labeled for NLC. 70, Wedgebills. 71, Birds-of-Paradise. 72, Wrens. 73, Finches. Terminal taxa are species, and numbers inside circles correspond to the geographic areas of those species distribution. (See Table 10.)



75

FIGURE 75.—Cladogram of the tepuis of Venezuela that have records of members of the flowering plant family Compositae, tribe Mutisieae. Labeled nodes refer to rivers that separate groups of tepuis. The groups of tepuis are named using the best known of the group, such as the Duida group, which refers to Duida, Marahuaca, and Huachamacari.

the physical separation of two relatively large populations of a single ancestral species and the attainment of lineage independence by each of these large populations. This will be reflected in biogeography in three ways: (1) the range of the ancestral species may be estimated by adding the ranges of the daughter species, (2) the geographic point of disjunction corresponds to the boundary between disjunct or contiguous daughter species, and (3) many clades inhabiting the same geographic area should show the same phylogenetic and biogeographic patterns.

An example of Model I is a group of plants found in the tepuis of the Guayana Highlands of the Venezuelan department of Bolivar and the Federal Territory Amazonas and adjoining areas. The tepuis are mountains that are part of the Guayana Shield, which was overlain by the Roraima Formation. This formation probably consisted of an extensive plateau that originally covered more than 2,000,000 square kilometers and that has since eroded away to leave these isolated, highly dissected, table mountains (= "tepui," singular). The tepuis often rise abruptly from the surrounding savanna or rainforest, and often have vertical cliffs exceeding 1000 meters and

sometimes reaching 2000 meters. Ecologically, the tepuis are very different from the hot tropical lowlands below, with summit climates that range from harsh and barren to cool and constantly moist. It has been estimated that there are approximately 2000 species of plants found on the summits with a 60%–95% endemism level (Maguire, 1970; Steyermark, 1986) for the larger tepuis.

The Mutisieae (one tribe in the flowering plant family Compositae) has a high level of endemism on the tepuis. There are 13 genera containing 63 species (according to Steyermark, pers. comm., 1987), most of which are found only on or near the tepui summits. Figure 75 is a branching diagram constructed for all of the tepuis that have records of members of the Compositae growing on their summits. The positioning of the tepuis on this cladogram was based on the distance among the tepuis and the number and size of river systems separating them. Based on the assumption that all of the tepuis had a common origin and that the amount of time they have been isolated is reflected in the distance that separates them, we can use this branching diagram as an area cladogram. For the sake of this discussion we will refer to this area cladogram

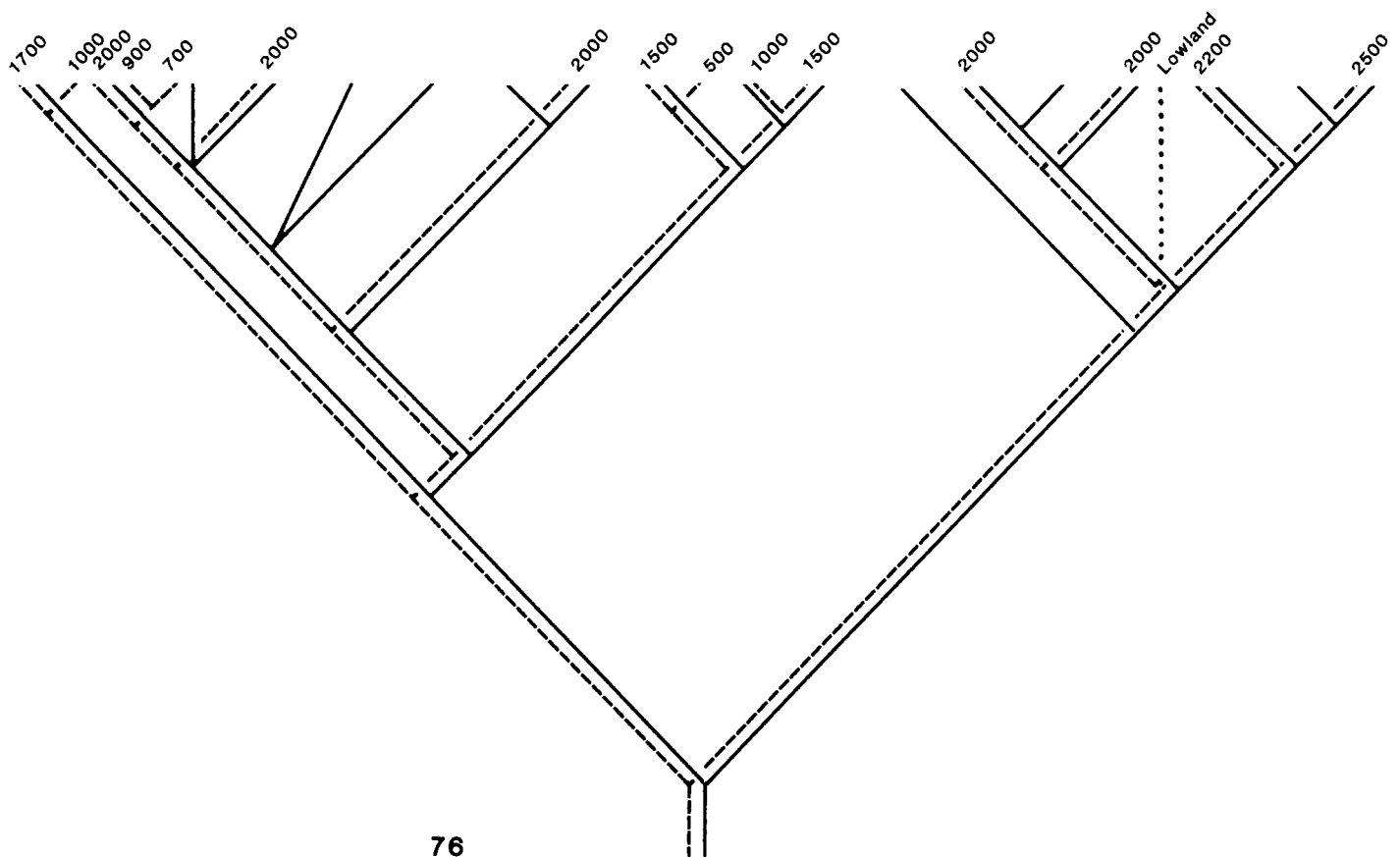


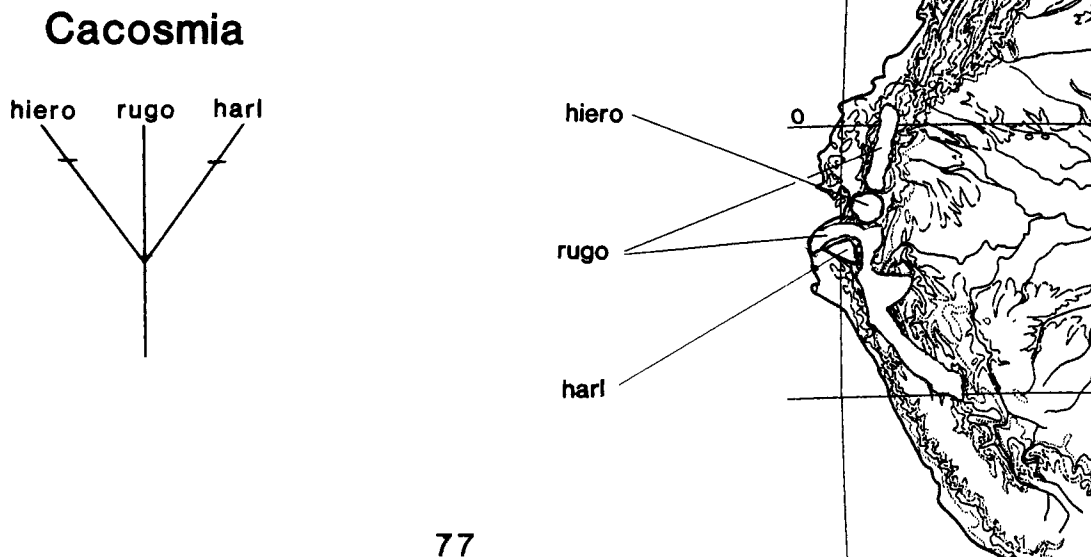
FIGURE 76.—Cladogram of the flowering plant genus *Stenopadus* (Asteraceae: Mutisieae) superimposed on the tepui cladogram (Figure 75). The tepui cladogram is represented by solid lines and the taxon cladogram by dashed lines with the elevations of the terminal taxa in place of their names. The position of one species of *Stenopadus* is uncertain and this is indicated with a dotted line.

as a "tepuí cladogram." Following the completion of the tepuí cladogram, the cladogram for each monophyletic group of plants (usually a genus) was constructed using characters based on morphology and anatomy. Each genus cladogram was then compared with the tepuí cladogram. One makes the assumption that if vicariance followed by allopatric speciation explains the occurrence of the endemic species in these summit tepuí groups, then the cladograms of the monophyletic groups should not conflict, or should be consistent, with the tepuí cladogram. The example from that ongoing study (Funk, in prep) which best exemplifies Model I is given here.

The cladogram for the genus *Stenopadus*, which has species on eleven of the tepuís, is compared with the tepuí cladogram in Figure 76. Optimization of the taxon cladogram shows that the ancestral species were distributed at high elevation. Even without mapping or consensus analysis, we think it is evident that the majority of speciation appears to support an interpretation of vicariance followed by allopatric speciation. However, several areas on Figure 76 suggest other explanations. On Duida there are three species: the one found at 2000 meters is sister to two species found further down the slopes at 900 and 700 meters. On Sipapo there are two species that

are most closely related, one at 1500 meters and one lower in elevation at 500 meters, and on Neblina there are sister species with elevations of 1700 and 1000 meters. These patterns are better explained by dispersal from the summits to lower elevations followed by allopatric speciation (see discussion under "Model II"). There is one species that cannot be placed at this point; it is found in the lowland areas around Roriamá and Chimanta. All six genera examined so far show similar results. Although the species of the monophyletic groups studied are not found on all of the same tepuís, the cladograms of the groups do not conflict with the tepuí cladogram. In addition, occasionally there appears to have been speciation resulting from dispersal into lower elevations or even, in one case, into the Venezuelan Andes. This is not unusual. A recent article by Huber (1988) points out that the tepuís were exposed to the same climatic changes as the Andes and that some groups do not have strong evidence of vicariance speciation.

ALLOPATRIC SPECIATION, MODEL II.—Model II, or *peripheral isolation*, supposes that a new species arises on the boundary of a larger central population. The parental species, which is primitive in morphology, must occupy the ancestral range. The isolate, exhibiting more derived morphology,



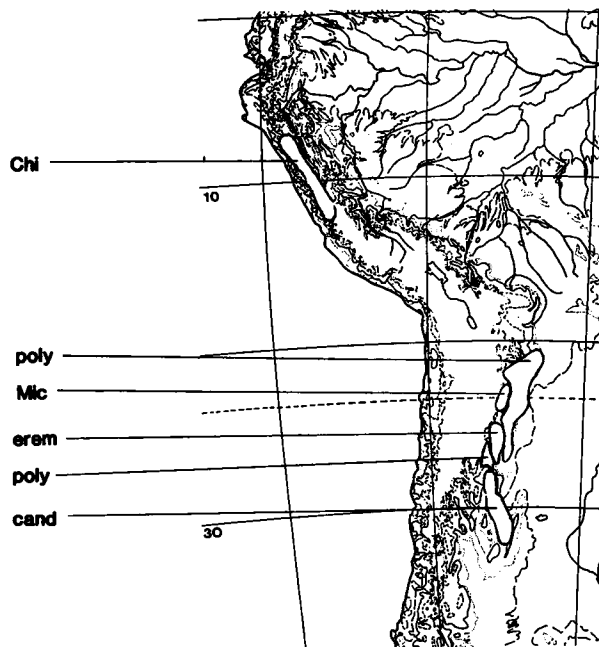
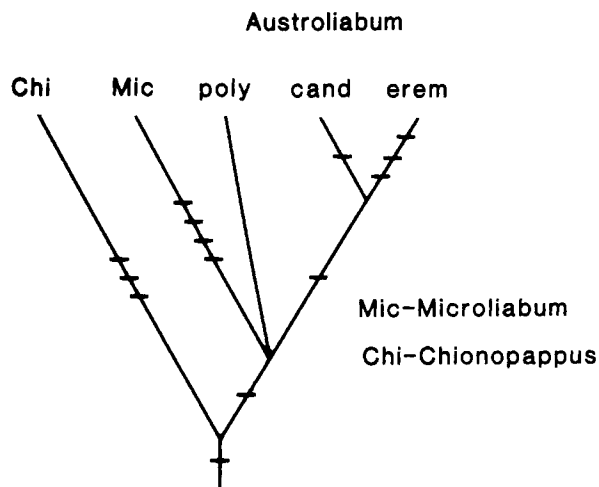
77

FIGURE 77.—Cladogram and distribution of the species of the flowering plant genus *Cacosmia* (Compositae: Liabeae). hiero = *C. hieronymi* H. Robinson, rugo = *C. rugosa* HBK, harl = *C. harlingii* Nordenstam.

occupies a new area peripheral to the ancestor. Other clades will not necessarily be expected to show similar biogeographic patterns because peripheral isolation is expected to occur in different ways in different species. However, under certain circumstances, such as dispersal and speciation along an island chain, there will be repeating patterns following *Hennig's*

Progression Rule (e.g., Brundin, 1966).

Hart (1985a, b) studied distribution patterns among species of *Lepechinia* sect. *Parviflorae* (Lamiaceae), a group of mid-to upper Andean weedy plants. The clade comprises both widespread and locally endemic species. In all cases the endemic species are more recently evolved (located further



78

FIGURE 78.—Cladogram and distribution of the species of the flowering plant genera *Microliabum* and *Austroliabum* (Compositae: Liabeae). The sister group is *Chionopappus*. poly = *A. polymnioides* (R.E. Fries) H. Robinson and Brettell, cand = *A. candidum* Grisebach) H. Robinson and Brettell, erem = *A. eremophilum* Cabrera.

along on the cladogram) than their widespread relatives. Hart was able to associate this pattern of apparent peripheral isolation speciation with climatic fluctuations in the inhabited areas during the Pleistocene. Data from the Compositae tribe Liabeae show similar results. Eight genera endemic to the Andes have been analyzed (Funk, in prep) and two of the simpler cladograms (Figures 77 and 78) show what we consider to be the classic pattern of speciation by peripheral isolation. The pattern is usually identified by a clade with most species in an unresolved polytomy with one member a wide ranging species without autapomorphies. The remainder of the species are isolated endemics with autapomorphies. In *Cacosmia* the three species are in a trichotomy with one, *C. rugosa*, being widespread and without apomorphies and the *C. harlingii* and *C. hieronymi* having restricted distributions and autapomorphies (Figure 77). Figure 78 is a cladogram for two genera, *Austroliabum* and the monotypic *Microliabum*, treated here as one group with four species (*Chionopappus* is the outgroup). Of the four species, one, *A. polymnioides* is widespread, lower in elevation and has no autapomorphies. The other three species are more restricted in distribution, higher in elevation, and have autapomorphies. Two of the species are more closely related to one another than they are to any of the other species. None of the cladograms constructed for this study have repeating patterns.

Other studies illustrating peripheral isolation are Lynch (1982), who provides complementary data involving toads (genus *Ceratophrys*) in eastern South America and Wiley (1981), who suggests that a number of the uniquely distributed species of *Heterandria* and *Xiphophorus* (discussed in "Biogeography," above) represent the products of speciation by peripheral isolation.

PARAPATRIC SPECIATION.—Parapatric speciation occurs when two populations of an ancestral species differentiate despite the fact that they maintain a small area of overlap throughout the speciation process. This will produce sister species that initially have parapatric distributions. Other clades are not expected to have the same pattern, so we do not expect to find repeating biogeographic patterns.

There is also the possibility that two populations of an ancestral species, having been separated, may differentiate to a degree allopatrically and then continue to develop lineage independence during a subsequent period of parapatry. This mode of speciation ("alloparapatric speciation") shares the biogeographic statements of Models I and II depending on the size of the isolated populations.

In using phylogenetic systematics to study speciation, repeating patterns are found in allopatric Models I and II, vicariance, and the progression rule, while in all other modes of speciation the phylogenetic pattern should be individualized for each clade.

HISTORICAL ECOLOGY

Historical ecology is the name of a research program in evolutionary ecology that uses phylogenetic trees to produce direct estimates of the origin and persistence of various aspects of ecological associations and diversity. It builds on phylogenetic studies of biogeography and speciation in an attempt to provide evolutionary explanations that take many different causal agents into account. The name was first proposed by Brooks (1985) because many evolutionary ecologists had objected to extending the term evolutionary ecology to studies involving phylogenetic trees. This pinpoints a problem to which we alluded in the introduction. One's choice of analytical methods depends on whether or not one allows for the possibility of among-species processes in explaining among-species patterns. Evolutionary ecology has developed as a discipline concerned with explanations based entirely in microevolutionary processes. If a unified view of evolutionary processes becomes widely accepted, the dichotomy between macroevolution and microevolution will largely disappear, and historical ecology will become that part of evolutionary ecology dealing with among-species phenomena.

Ricklefs (1987) referred to the "eclipse of history" in community ecology as having a profound negative influence on the field. He expressed hope that incorporation of historical (systematic and biogeographical) information, along with new methods of documenting statistical patterns, might "bring to ecology some of the resurgence enjoyed recently in the fields of systematics and biogeography" (Ricklefs, 1987:171). We think this is a readily achievable goal.

Ecological associations do not evolve in the same sense that we think species evolve; rather, they are "assembled." However, some of the "assembly rules" may be evolutionary. For instance, ecological associations (1) are spatially localized, although their boundaries are often fuzzy, (2) are comprised of particular species, although the species need not be endemic to the association, and (3) are characterized by particular ecological interactions among the member species. Each of these three aspects of ecological associations may have historical components; we have already examined this possibility with respect to geographic distributions. In this section, we will consider the question of macroevolutionary patterns and evolutionary processes with respect to species co-occurrence (coevolution) and to the evolutionary diversification of ecological and behavioral traits.

COEVOLUTION.—The critical question asked in macroevolutionary studies of biogeographic patterns is "Why do these species share the same real estate?" This does not presuppose that those species actually have anything to do with each other ecologically. However, in any ecosystem some species do interact, and in a variety of ways. In some cases the interactions are very general (zebras will eat a variety of plants, and lions will eat a variety of mammals). In other cases the interactions

are very specific and predictable, such as those of pollinators and plants, or of hosts and parasites. The proximal explanations for such regular associations is that one or more of any set of interacting species has very specific ecological life history traits that constrain the kinds of interactions possible.

The area of evolutionary ecology that deals with species having specific ecological relationships is coevolution (Futuyma and Slatkin, 1983). Like other areas of biology, coevolution has been construed in two different ways: one a within-species view, and the other an among-species view. The microevolutionary view stresses generation-length ecological phenomena that characterize and maintain such relationships. The macroevolutionary view attempts to estimate the conditions under which such relationships were established, and how long they have persisted. Phylogenetic analysis can aid studies of this macroevolutionary perspective that provides the historical context for ongoing coevolutionary dynamics.

There are two major inquiries to be addressed in a study of coevolution: (1) why do the species co-occur and (2) why do they interact the way they do? The microevolutionary explanations for co-occurrence of individuals of different species is parallel to the microevolutionary explanations for biogeographic co-occurrence. Dispersal of offspring forms the basis for the establishment of new associations characteristic of each generation. This form of dispersal is sometimes called host-switching. The diagnostic units of such associations are symbiotic species, just as the diagnostic units of geographic assemblages are sympatric species. The microevolutionary explanation for the traits that characterize particular associations is called *reciprocal adaptive response* (see Futuyma and Slatkin, 1983). It can often, but certainly not always, be shown that each species in an association constrains and is constrained by the other(s).

The macroevolutionary perspective begins by asking how long ecological associates have been associated. There can be either a historical or a nonhistorical answer in each case. The historical answer is that the ancestors of each species were themselves associated; the nonhistorical answer is that the symbionts differentiated evolutionarily in association with other species, and subsequently became associated by host-switching or colonization. The nonhistorical answer is thus a direct expansion of microevolutionary processes to explain macroevolutionary patterns. The historical explanation is analogous to historical explanations of biogeographic co-occurrence. And, just as the historical analysis of biogeographic patterns does not presuppose any particular ecological interactions, the analysis of coevolutionary patterns does not presuppose any particular reciprocal adaptive response. The development of phylogenetic protocols for examining coevolution has shown some degree of coevolution with the protocols for examining biogeography. In the late 1960s and 1970s some ecologists suggested that, in accordance with the MacArthur-Wilson model of island biogeography, "hosts" should be considered as "islands" and parasites or other symbionts as "colonizers." Beginning in the late 1970s phylogenies of

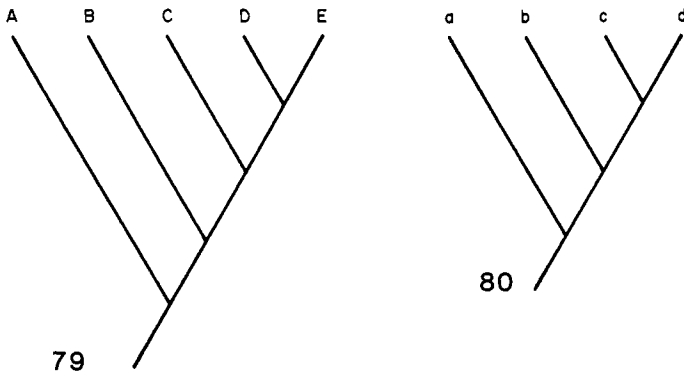
symbionts and their hosts were compared qualitatively with a view more towards long-term association than short-term colonization, just as comparisons of phylogenies for sympatric taxa were examined more with respect to patterns of continental drift than to dispersal on fixed geographical configurations (see references in Brooks, 1988).

First, we consider a hypothetical example: given a group of host species—Family X (five species), and their parasites, genus Z (four species)—one constructs a cladogram for each group (Figures 79 and 80). Then the host cladogram is used as a base and the parasite found in each species is written in above the host species (Figure 81). Now a transformation series can be constructed for the parasites based on the host cladogram. The ancestor to host species D and E is postulated to have been inhabited by the ancestor of parasite species d; the ancestor of host species CDE is postulated to have been inhabited by the ancestor of parasite species cd; the ancestor of host species BCDE is postulated to have been inhabited by the ancestor of parasite species bcd, and the ancestor of host species ABCD must have been infected by the ancestor of parasite species abcd. The transformation series for this is abcd–bcd–cd (Figure 82).

Next one examines the parasite cladogram (Figure 83; constructed using parasite characters) and forms another transformation series. According to the parasite cladogram, c and d shared an ancestor exclusive of the other parasite taxa; bcd shared an ancestor exclusive of the other parasite taxa, and abcd shared an ancestor exclusive of the other parasite taxa. This yields a transformation series of abcd–bcd–cd (Figure 84). The transformation series constructed from the host cladogram and the one constructed from the parasite cladogram are congruent and this gives complete support to the hypothesis of mutual descent.

The historical interaction of ecological associates has been likened to that of species and the areas that they inhabit, i.e., historical biogeography. In the case of parasites and their hosts one can view the host as a geographic area and the parasites as the biota in that area. The organisms in that area can either evolve with the area in response to some isolating event (vicariance) or they can disperse into new areas (dispersal) just as ecological associates can be assembled as the result either of mutual descent or of transfer from one ecological associate to another. Because of this similarity we can use all of the methods applied under "Biogeography," above, to handle problems such as missing data, widespread taxa, and congruence determination for studies in coevolution.

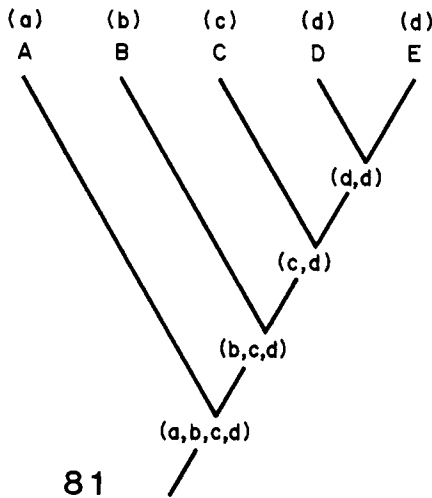
Comparing the phylogenies of ecological associates is the most commonly used method of assessing the extent to which mutual descent accounts for the history of groups of organisms. For example, phylogenies have been constructed for a group of figs (*Ficus*) and the wasps (*Agaonidae*) that inhabit their fruits (Ramirez, 1974a, b). When the two phylogenies are superimposed (Figure 85), the matching patterns indicate mutual descent. Note that the two cladograms are not identical, but are congruent (except for Area A, Figure 85). For instance,



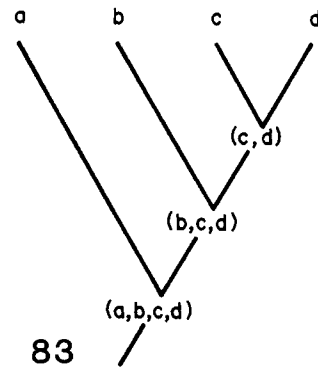
FIGURES 79–80.—Host/parasite cladograms. 79, Phylogeny of host. 80, Phylogeny of parasite.

there are several instances in which the same species of wasps is found in sister taxa of figs and one place (Area A, Figure 85) in which the same species of wasp is found in two figs that are not sister taxa. Area A (Figure 85) may be the result of host transfer.

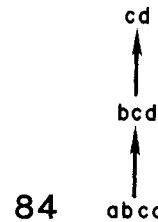
A second example of comparing phylogenies (Brooks and Glen, 1982; Mitter and Brooks, 1983) involves primates and a group of pinworms that parasitize them (*Enterobius*; Figure



FIGURES 81–82.—Parasite distribution and transformation series. 81, Parasite distribution mapped onto host cladogram. 82, Transformation series for parasite based on host cladogram. Upper case letters represent host species and lower case letters represent parasite species.



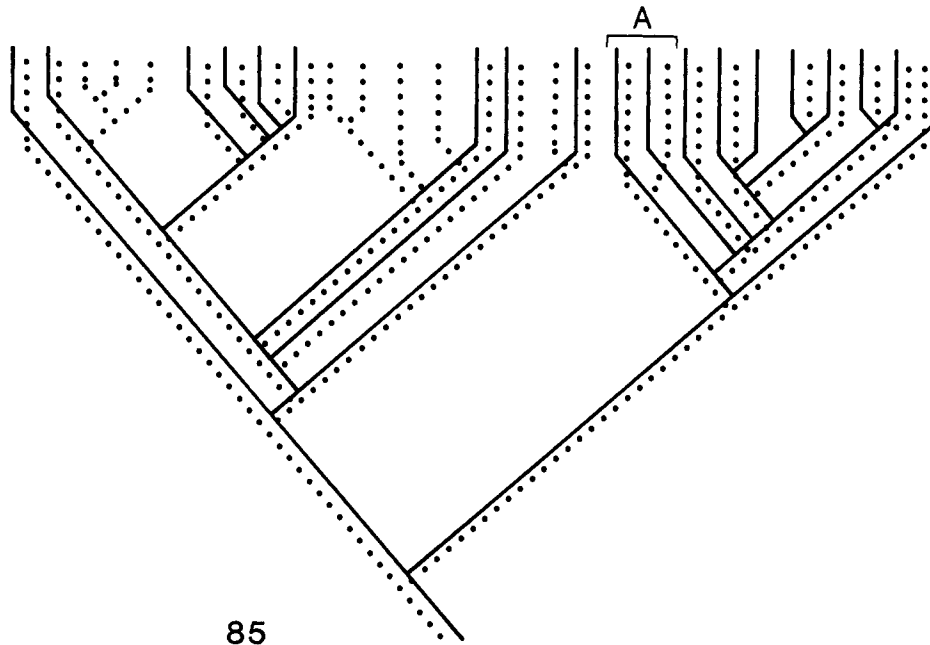
FIGURES 83–84.—Parasite phylogeny and corresponding transformation series. 83, Parasite phylogeny. 84, Transformation series for parasite based on parasite phylogeny. Lower case letters represent parasite species.



86). There is not complete congruence between the host and parasite cladograms, but there is, however, an overall similarity in the basic branching sequence. The indication is that mutual descent has played a role in establishing the general pattern but that host transfer (ecological associate transfer) has also taken place. This second example, in which both types of historical interaction appear to have had an effect, is more common, with complete congruence between the phylogenies of both ecological associates being rare. It seems logical that both mutual descent and host transfer have played important roles in establishing present day ecological interactions.

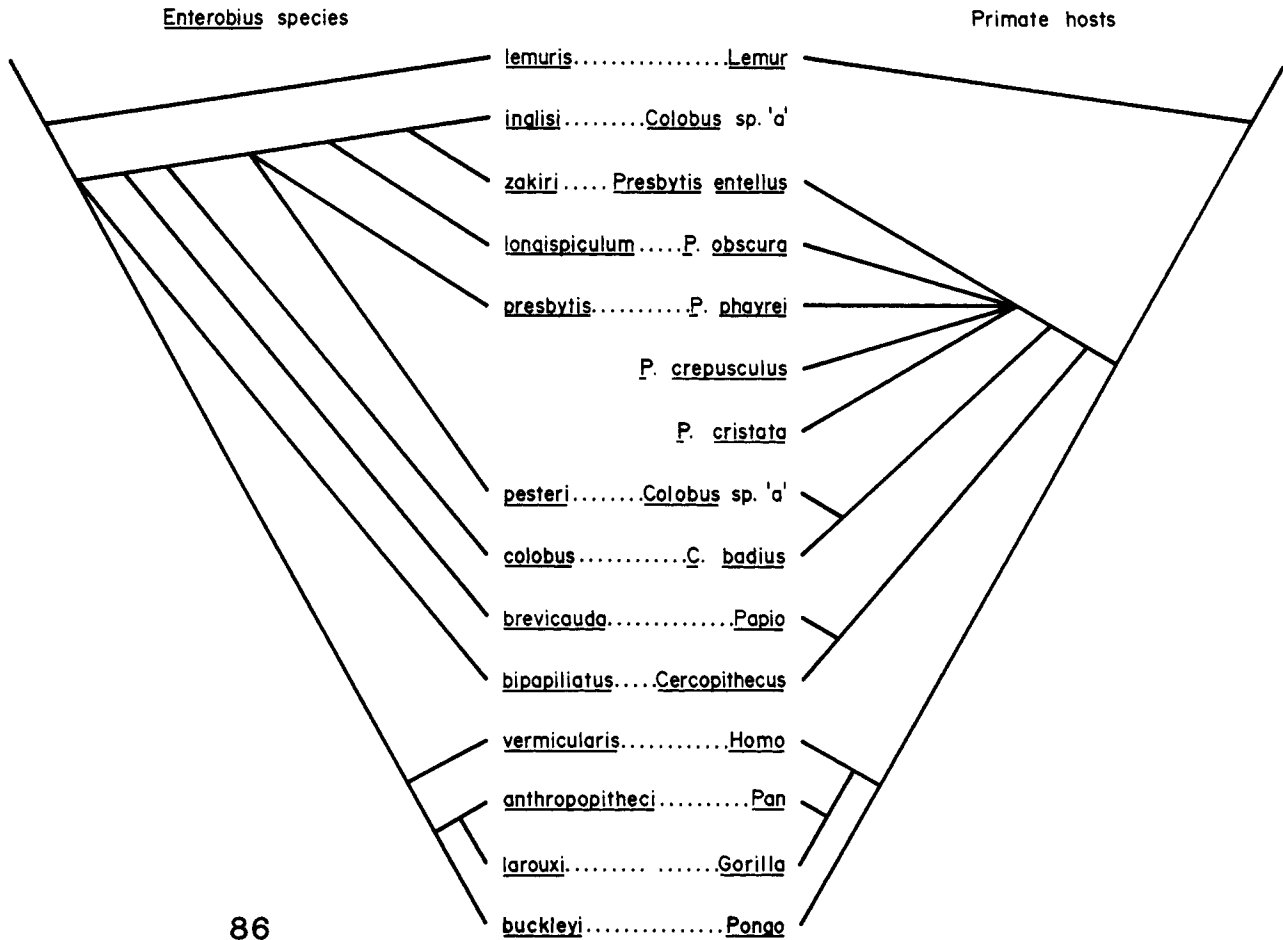
In another example, Hafner and Nadler (1988) compared branching patterns based on allozyme data of a group of rodents and their ectoparasites. The authors found a “high degree of concordance” in the diagrams, which they suggest is the result of cospeciation.

In an attempt to provide better estimates of which associations have historical bases and which do not, Brooks (1981) proposed that “hosts” could be used as taxa and “parasite” or “symbiont” phylogenies could be used as complex multistate characters of the hosts. If a host-group phylogeny is available, the symbiont phylogenies could be mapped onto the host phylogeny and an estimate made of which associations have historical bases and which do not. For example, Figure 87 depicts the relative phylogenetic relationships of four groups of vertebrates, and Figure 88 is a cladogram of four genera of closely related digenetic trematodes. Following the method of Brooks (1981), the parasite cladogram can be considered a character-state tree, or



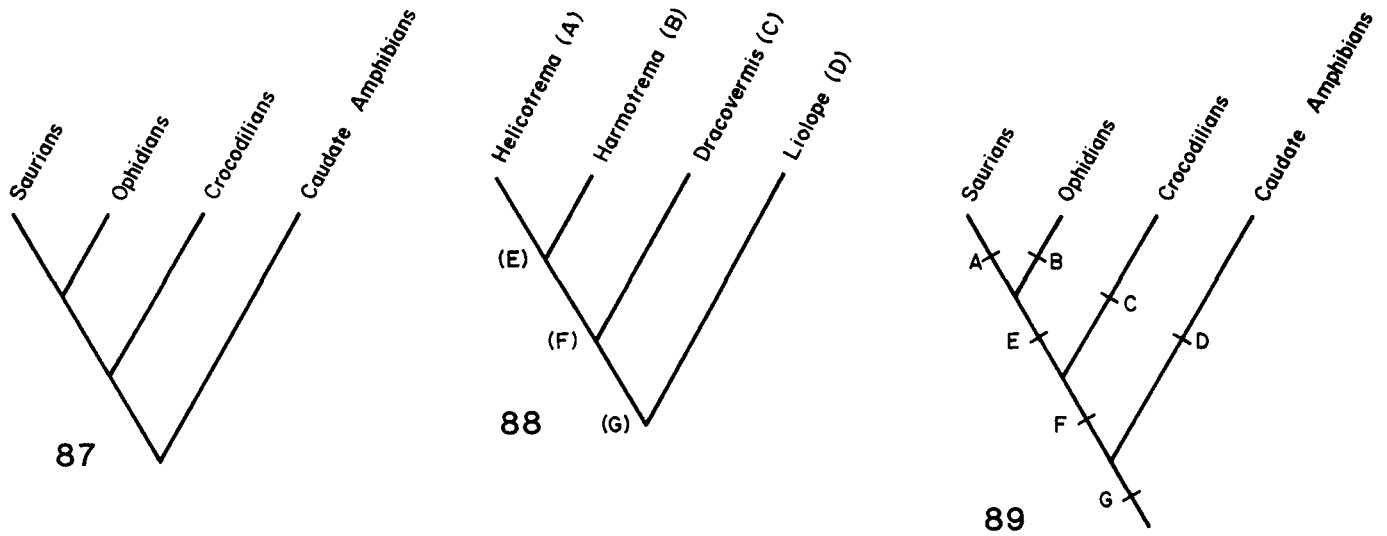
85

FIGURE 85.—Cladograms for figs (dotted lines) and fig wasps (solid lines) superimposed. Letter A marks the occurrence of the same species of wasp in two figs that are not sister taxa. (Redrawn from Ramirez, 1974.)



86

FIGURE 86.—Primate and pinworm phylogenies. (Redrawn and modified from Mitter and Brooks, 1983.)

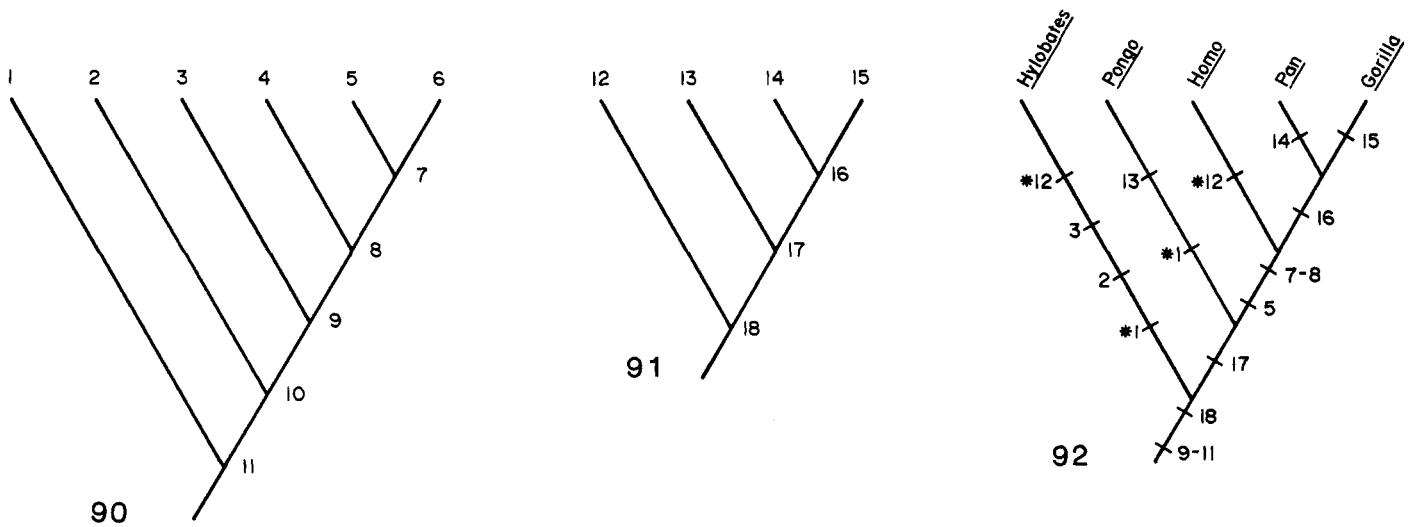


FIGURES 87-89.—Host parasite cladograms. 87, Phylogeny for four groups of vertebrates. 88, Phylogeny for four groups of digenetic trematodes. 89, Host relationships based on ABC mapping of Figures 87 and 88. (See Table 11.)

TABLE 11.—ABC matrix for the parasite phylogeny. (See Figures 87-89.)

Taxa	A	B	C	D	E	F	G
A	1	0	0	0	1	1	1
B	0	1	0	0	1	1	1
C	0	0	1	0	0	1	1
D	0	0	0	1	0	0	1
E	0	0	0	0	1	1	1
F	0	0	0	0	0	1	1
G	0	0	0	0	0	0	1

transformation series, of the host group, and can be converted into a matrix of binary codes (Table 11), out of which a cladogram of host relationships can be constructed (Figure 89). Points of agreement between host phylogeny and parasite-based host relationships support association by descent; points of disagreement represent episodes of colonization. Note the parallels between the documentation of historical and nonhistorical associations between species and the documentation of historical and nonhistorical geographic distributions. In the absence of a host phylogeny, the



FIGURES 90-92.—ABC for primate parasites. 90, Portion of the cladogram for *Enterobius*. 91, Portion of the cladogram for *Oesophagostomum* (*Conocheberia*). 92, Host phylogeny that results from mapping Figures 90 and 91 with respect to inhabited hosts. * = characters appearing more than once on the diagram (host-switching).

cladograms of more than one symbiont group could be used as characters, with hosts as taxa to provide a summary cladogram. In such cases, symbionts that act like homologies on the resultant tree indicate coevolutionary relationships and those that act like homoplasies indicate colonization events.

Figures 90 and 91 depict portions of the phylogenetic trees for *Enterobius* (pinworms) and *Oesophagostomum* (*Cono-beberia*) (hookworms) species inhabiting hominoid primates. Each cladogram is labeled according to its binary coding. Figure 92 shows the host cladogram that results from mapping the two trees together with respect to inhabited hosts. Note that two host transfers, one between *Hylobates* and *Homo* and one between *Hylobates* and *Pongo*, are postulated to have occurred. Thus, although neither parasite group shows strict mutual descent (i.e., *Homo* and its pinworm have different sister groups), the host tree based on these parasite data corresponds to the general pattern of primate phylogeny (Spuhler, 1988). For a more extensive analysis of parasite data pertaining to hominoid phylogeny, see Glen and Brooks (1985a, b).

Coevolution encompasses more than just mutual association; it also embodies concepts of mutual modification, or "reciprocal adaptation" between the members of any ecological association. "Hosts" evolve defense traits against attack by predators or parasites, which themselves evolve "counter-defense" traits. One theory is that many secondary plant products such as terpenes and flavonoids evolved as "defense" traits against insect predation. However, the compounds may be historical in nature—they may have coevolved with the plants. The only way to distinguish between these two alternatives is to employ a phylogeny. Sesquiterpene lactone data are available for 20 of the 30 taxa of the genus *Montanoa* (Seaman et al., in prep.; Table 12). The data can be handled in two ways. Using the method described by Seaman and Funk (1983) one can produce a phylogenetic tree for the group based on the biosynthetic pathways for various sesquiterpene lactones (Figure 93); each branching point in the phylogeny represents the origin of a possible "defense" trait. Comparing this chemical phylogeny with the cladogram produced from morphological data we find that there is little obvious concordance. Alternatively, the chemical characters can be mapped onto the morphology cladogram in order to judge their consistency with the phylogenetic hypothesis. Using the resulting cladogram of *Montanoa* (Figure 94) we can observe how well the possibility of a historical origin is supported by the data. Five of the chemical characters (A3, A5, A7, B1, B5) are completely consistent. Indeed, these characters resolve two trichotomies, provide an autapomorphy, and support the monophyly of a group. The remaining five characters show either homoplasy or loss. Characters A2 and B3 vary together as did A4 and B3. These four can be explained by a simple gain-loss phenomenon.

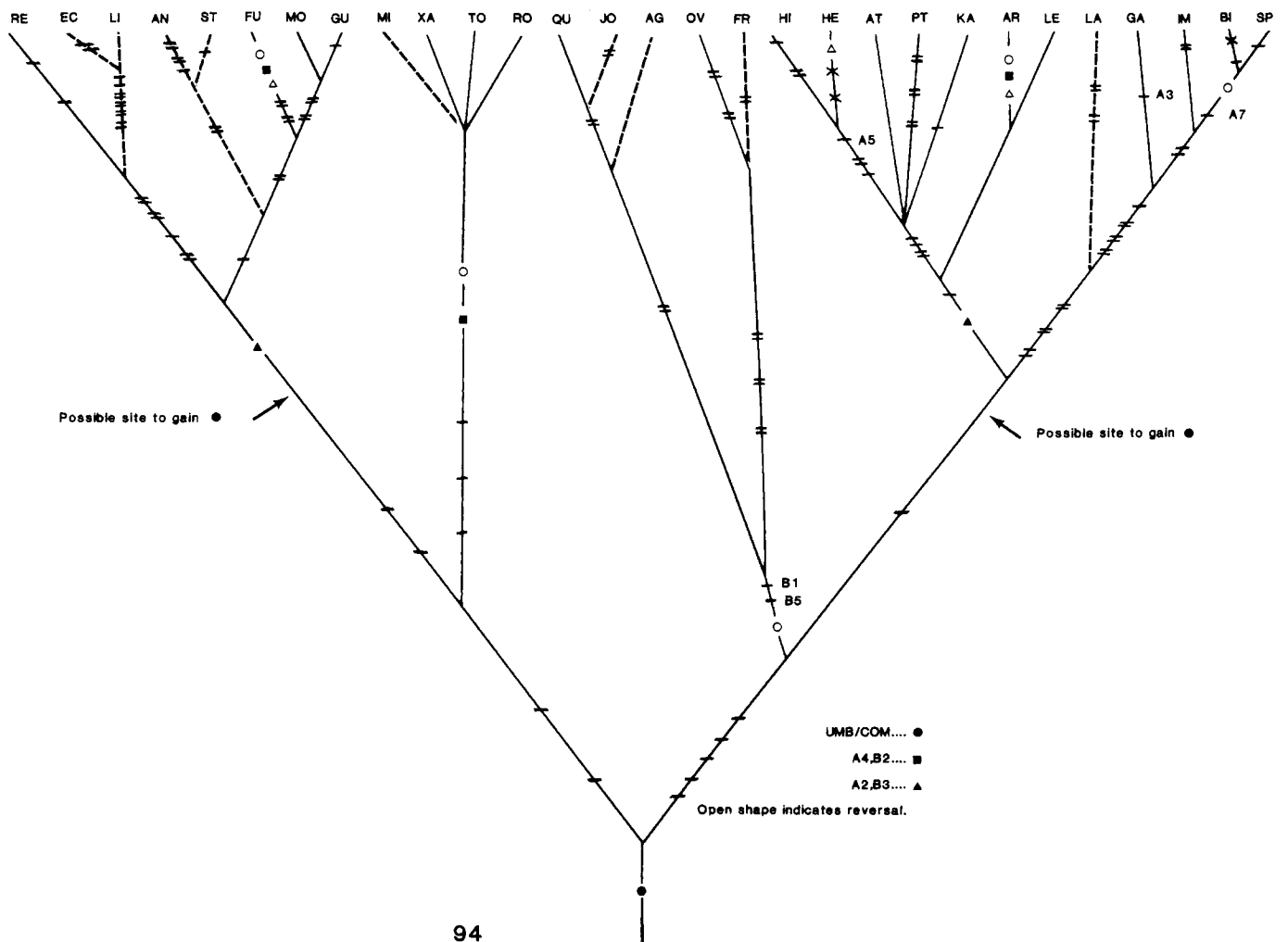
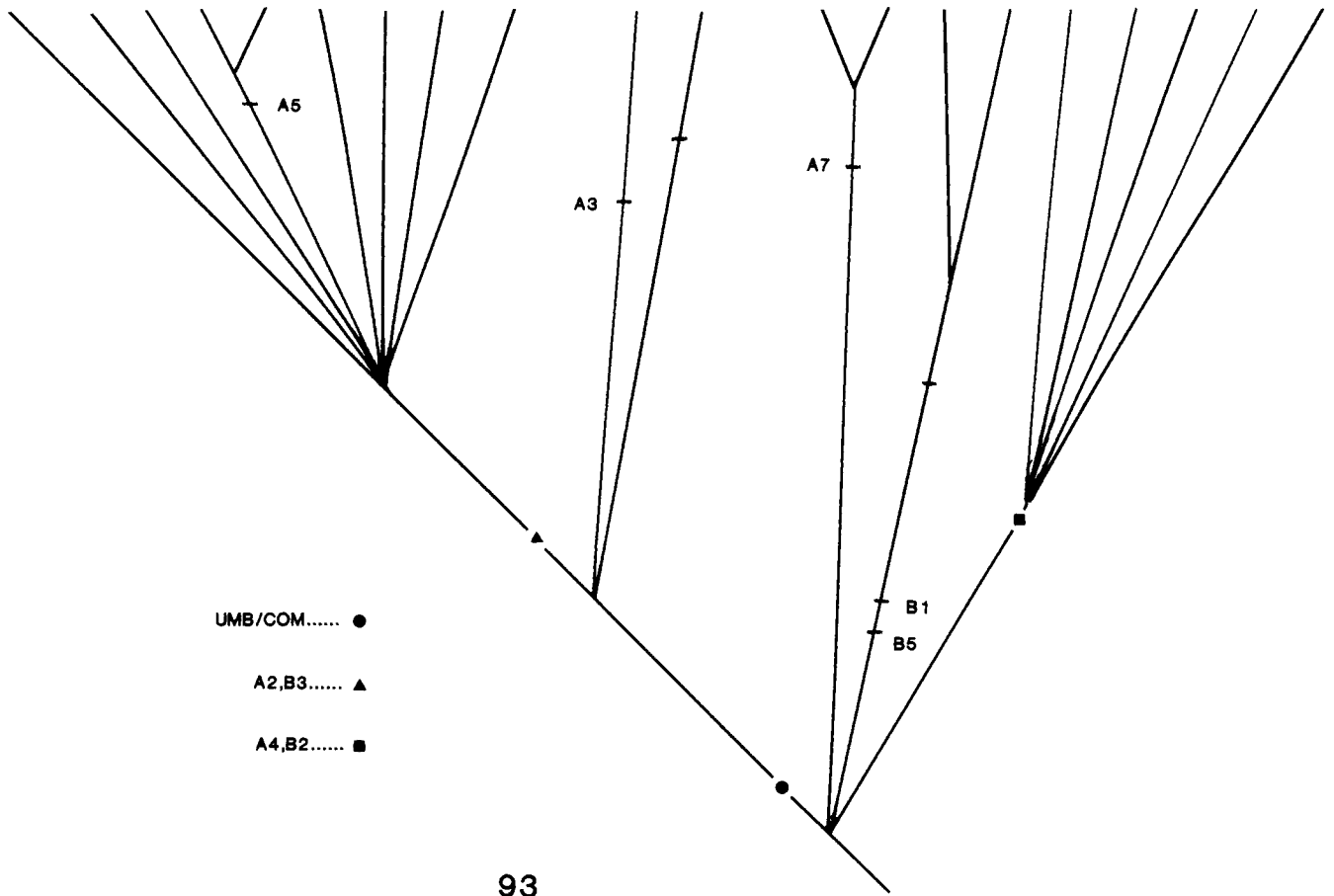
The most interesting character is the presence of two alternative pathways for the biosynthesis of sesquiterpene lactones, COM and UMB (UMB and COM favor oppositely

TABLE 12.—Data matrix for sesquiterpene lactones of 20 taxa of *Montanoa*. The 0 condition is regarded as plesiomorphic. The A and B in the characters do not indicate homology, A refers to skeletal changes and B to substitutional changes. The UMB is a regulatory change. (See Figures 93 and 94.)

Taxa	Characters									
	A2	A3	A4	A5	A7	B1	B2	B3	B5	UMB
OG	0	0	0	0	0	0	0	0	0	0
RE	1	0	0	0	0	0	0	1	0	1
FU	0	0	1	0	0	0	1	0	0	0
MO	1	0	0	0	0	0	0	1	0	1
GU	1	0	0	0	0	0	0	1	0	1
XA	0	0	1	0	0	0	1	0	0	0
TO	0	0	1	0	0	0	1	0	0	0
RO	0	0	1	0	0	0	1	0	0	0
QU	0	0	0	0	0	1	0	0	1	0
OV	0	0	0	0	0	1	0	0	1	0
HI	1	0	0	1	0	0	0	1	0	1
HE	0	0	0	1	0	0	0	0	0	1
AT	1	0	0	0	0	0	0	1	0	1
PT	1	0	0	0	0	0	0	1	0	1
KA	1	0	0	0	0	0	0	1	0	1
AR	0	0	1	0	0	0	1	0	0	1
LE	1	0	0	0	0	0	0	1	0	1
GA	0	1	0	0	0	0	0	0	0	1
IM	0	0	0	0	0	0	0	0	0	1
BI	0	0	0	0	1	0	0	0	0	0
SP	0	0	0	0	1	0	0	0	0	0

oriented introductions of hydroxyl groups at C-6). The presence of the UMB pathway in *Montanoa* is unique in the Compositae family. Previously it had been reported only from members of the Umbelliferae family. There are two ways to interpret this character on the *Montanoa* morphology cladogram. For one, the UMB is a synapomorphy of the entire genus followed by five random losses. The second alternative, which is one step shorter, has it gained twice and lost three times (Figure 94). The possibility that this unusual pathway occurred more than once is considered "not very likely" by the chemists involved in the study (Seaman et al., in prep.). Also, one wide-ranging COM species had two populations in Central America with UMB, which would seem to favor UMB being considered a synapomorphy for the entire genus. Regardless of which interpretation one accepts, the conclusion is that morphology-based phylogeny, combined with the data we have available, indicates that the presence of sesquiterpene lactones in *Montanoa* are consistent with a historical

FIGURES 93–94.—Cladogram of the members of the taxa of the genus *Montanoa* using sesquiterpene lactone data. 93, Cladogram based on sesquiterpene lactone data. 94, Cladogram based on morphology onto which the sesquiterpene lactone data has been mapped. Solid lines indicate taxa for which there are chemical data and dashed lines indicate taxa for which there are no chemical data. A dash represents a synapomorphy that shows no homoplasy or loss; solid circles, squares, and triangles indicate the gain of specific character(s); and open symbols indicate loss of that character(s). Taxon names can be found in Funk, 1982. (See Table 12.)



explanation only 37% or 38% of the time. So, in the majority of instances coevolution is not an acceptable explanation for the presence of specific sesquiterpene lactones. A study is now underway to investigate the possibility that, at least in parts of the cladogram, there may be a correlation between the chemistry, habitat, elevations, and other factors.

If phylogenetic trees for the other ecological associates, such as insect predators on plants, are mapped onto the "host" phylogeny, one could discern if the evolution of the "defense" traits coincided with any changes in association by descent or by colonization (the insect predators must belong to a clade). Furthermore, if there are postulated "counter-defense" traits that have evolved, mapping phylogenies together could show whether "defense" traits and "counter-defense" traits have evolved together or independently.

Phylogenetic systematics provides a way of differentiating between historically constrained characters and those independently acquired.

ECOLOGICAL AND BEHAVIORAL DIVERSIFICATION.—Salthe (1985) (see also Eldredge, 1985; Brooks and Wiley, 1988) has suggested that evolution results from the interaction of two biological hierarchies, each having its own characteristics in addition to the properties that emerge from the interactions. On the one hand, the *ecological hierarchy* is an economic system, manifested by patterns of energy flow in ecosystems. It is also the hierarchy of classes, such as trophic levels or herbivore-crop interactions. From the perspective of the ecological hierarchy the particular identities of the species involved does not matter. Any herbivore and any plant species will suffice to produce a herbivore-crop interaction. On the other hand, the *genealogical hierarchy* is an information-flow system, manifested by genealogical relationships and the phylogenetic hierarchy. It is the hierarchy of individuals. From this perspective, it does not matter what functional properties a given species possesses just so long as the members of the species can find sufficient resources to survive and reproduce.

Evolution does not make complete sense without taking both hierarchies into account. It takes energy to make and to maintain organisms, but each organism uses energy only in particular forms as determined by properties inherited from its parents.

If we adopt the two-hierarchy model as a working world-view, it is appropriate to ask questions about the genealogical context of ecological and behavioral traits or, to phrase it in an equivalent way, about the ecological context of genealogy. Are there macroevolutionary patterns indicating the way in which the two hierarchies have interacted in the past to produce the diversity we see today? There are a number of research programs amenable to this kind of analysis. The ecological life history and behavioral traits exhibited by species can be construed as "solutions" (or "strategies") to the problem of survival in the environment at hand. Using this reasoning, we would expect the different species in a clade that occupy similar habitats to show similar convergent ecological and behavioral traits. A phylogenetic tree can be used as a template

for comparisons to ask whether or not ecological and behavioral similarities among members of a clade are due to convergence or to inheritance from a common ancestor.

If there are phylogenetic constraints on ecological and behavioral diversification, closely related species may have the same ecological or behavioral traits regardless of the environment in which they find themselves. In addition, contemporaneous species may show ecological and behavioral traits that evolved in environments different from the ones in which they find themselves today. Two or more members of a clade may occur in different habitats and yet share common ecological life history traits. Alternatively, two or more members of a clade may occur in similar habitats and yet exhibit divergent ecological and behavioral traits. In these cases we recognize that there can be a degree of independence between the products of the genealogical hierarchy and the constraints of the environment. This is theoretically important if one assumes that phylogenetic change is driven by environmental changes that force ecological and behavioral changes, that in turn lead to morphological changes (e.g., see Mayr, 1963; Futuyma, 1979). Ecological and behavioral traits showing phylogenetic constraints lead us to think that ecological and behavioral change can be viewed as conservative elements in evolution, rather than as driving forces of it. And this begs the question of just what is the driving force of evolution if it is not ecological change.

Among-species questions in this regard can be investigated by considering just how closely phylogenesis in any clade is associated with changes in ecological or behavioral characteristics relevant to speciation. How closely does ecological and behavioral evolution match phylogenetic patterns? Can one obtain a robust cladogram by analyzing ecological and behavioral traits alone? Do such cladograms agree with phylogenies derived from morphological and biochemical data? How often do adaptive changes in structure and in function actually appear on the same branch of the phylogenetic tree? Are there ecological and behavioral traits that characterize species-rich clades? These questions can be examined by looking at individual cladograms.

By comparing the historical context of ecological and behavioral traits for several clades represented in ecological associations, it is possible to ask questions about the evolution of ecosystem structure. This is an important interface between the two hierarchies, because the range of energy-flow pathways in ecosystems is determined by the attributes of the component species; particular environmental effects at any time determine what subset of that range will actually be operating. Persistent ancestral ecological and behavioral traits represent instances in which the genealogical hierarchy has constrained the ecological hierarchy, and adaptive changes represent instances of the genealogical hierarchy responding to effects of the ecological hierarchy. Phylogenetic constraints will limit the way in which a species could adapt to changes in selection pressures (the "selection arena" again).

If a number of coevolving clades show ecological shifts at

the same points in history, it would be possible to find evidence of ecological reorganization and ask if it appeared to be episodic or stochastic. Such questions have been approached by Erwin (1985) for neontological data and by Boucot (1978, 1982, 1983) for paleontological data. For the latter, one might also want to see if such occurrences are correlated with episodic mass extinctions. If there are periodic mass extinctions, one would expect to find subsequent ecological reorganization. Boucot (1983) has suggested that such patterns occur in the fossil record, and are a major source of "punctuated" change in community structure.

Ross (1972a, b), who can be regarded as the modern father of historical ecology, suggested that for a variety of insect groups, ecological diversification is consistent with phylogenetic relationships but that it occurs infrequently. He suggested that approximately one in thirty speciation events is correlated with some form of ecological diversification.

Recently, a number of studies have been conducted to investigate just how consistent ecology and phylogeny really are. Andersen (1982) examined the Gerromorpha, a group of semiaquatic hemipteran insects. He demonstrated that ecological correlates of speciation could often be used as diagnostic traits at what he considered to be the generic level. This also indicates a high degree of phylogenetic concordance and conservatism in the evolution of ecological diversity. Roskam (1985) demonstrated parallel evolution of gall-inducers from mycetophages in sister taxa of a group of dipteran insects (Figure 95). Erwin (1985) proposed that a major part of the evolution of diversity in carabid beetle communities results from the irregular evolution of novel ecological traits in particular species, with subsequent geographic spread and speciation (through peripheral isolation) distributing carabids with new ecological traits in new communities. Erwin termed these periodic episodes of ecological diversification "taxon pulses." These neontological findings complement the paleontological findings of Boucot (1983) by indicating the conservative nature of ecological evolution. All of these studies show the utility of using phylogenies to study ecology.

Wanntorp (1983) examined the evolution of leaf retention and of deciduousness in oaks and beeches. Otto and Nilsson (1981, 1982) had proposed that leaf retention evolved from deciduousness as an adaptation to close the nutrient cycles of forest ecosystems over winter. Wanntorp demonstrated that leaf retention is the plesiomorphic condition in this group of trees, and that deciduousness was actually the trait that evolved secondarily. This renders the adaptive scenario untenable, and leads to questions about the evolution of deciduousness rather than about the evolution of leaf retention.

Several recent studies attest to an interest in phylogenetic constraints on reproductive modes or "strategies." Duellman (1985) found 29 reproductive modes among anuran amphibians (frogs and toads). He concluded that, although many reproductive modes have evolved independently in different clades, shared derived modes can be identified and can be shown to be congruent with the phylogenetic relationships of the

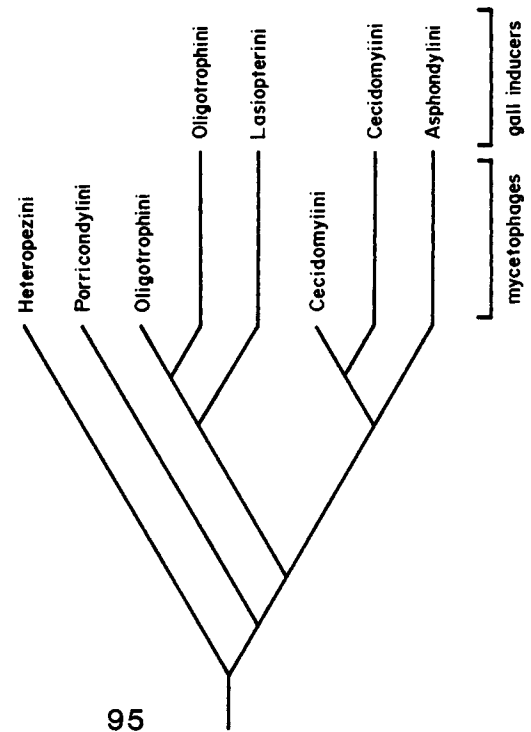


FIGURE 95.—Results of a study on gall-inducing diptera showing parallel evolution of gall-inducers from mycetophages. (Redrawn and modified from Roskam, 1985.)

members of the groups. Hart (1985b), in a study of dioecism in *Lepechinia* sect. *Parviflorae*, and Cox (in press), in a study of the Pandanaceae, also found a high degree of phylogenetic concordance and conservatism in the evolution of breeding systems in plants. Brooks, O'Grady, and Glen (1985) demonstrated phylogenetic congruence and conservation in the evolution of life cycles for digenetic trematodes.

Pearson et al. (1988) and Mooi et al. (in press) have used a branching diagram to examine the occurrence of benzaldehyde in tiger beetles. Both studies found that benzaldehyde does not correlate with ecology. In addition, Mooi et al. concluded that the presence of benzaldehyde is plesiomorphic for tiger beetles and that it is the "loss" of the production of the compound that has evolutionary significance. The point is not that everything is the result of phylogenetic constraints, but that the only way to distinguish among those that are the product of phylogenetic constraints and those that are not is to employ phylogenetic systematics.

Although many ecologists are beginning to recognize the significance of phylogenetic constraints, some comparative ethologists have expressed reservations about the existence or importance of phylogenetic constraints on behavior (Thornhill and Alcock, 1983; Vehrenkamp and Bradbury, 1984; Yokel, 1986). Others, such as Clutton-Brock and Harvey (1984) have doubted the utility of phylogenetic systematics (sensu Hennig

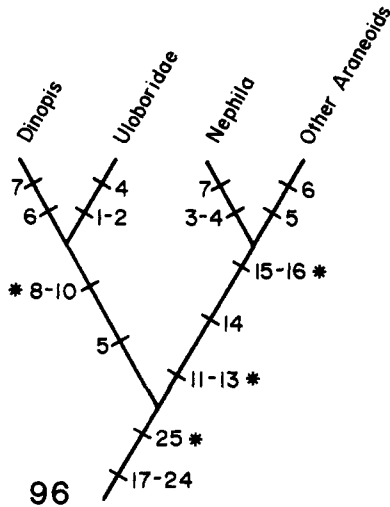


FIGURE 96.—Web-building behavior and morphology in araneoid spiders. * = morphological apomorphies; other characters refer to components of web-making behavior. (Redrawn and modified from Coddington, 1986.)

1966) for documenting such constraints. Both of these attitudes are currently being questioned. We have already mentioned Dobson's (1985) study of the run-jump behavior in Richardson's ground squirrels and in prairie dogs. In a more comprehensive

study, Coddington (1986) showed that it was possible to reconstruct the phylogeny of a group of spiders using a suite of characters derived from web-making behavior and morphology (Figure 96). His study has altered the basic premise of the phylogeny of araneoid spiders. McLennan et al. (1988) produced a phylogenetic tree for stickleback fishes (Gasterosteidae) using only behavioral characters (Figure 97) and found it to be consistent with phylogenies derived from morphology and karyology; in fact, the tree based on behavioral characters showed only three instances of homoplasy. They also showed how the tree could be used to assess relative contributions of inter-sexual selection, intra-sexual selection, and natural selection in true evolutionary diversification of certain behaviors (Figures 98–100). There appear to be macroevolutionary components in behavior, and when present these can be documented using phylogenetic systematics.

It seems that there are methodological resources available to explore a wide range of questions about phylogenetic constraints on the evolution of ecology and behavior. It also seems that the possibilities remain virtually unexplored. The few studies that have been done have found less adaptive change than necessary if we are to explain phylogenesis primarily in those terms (see Figure 101; also Brooks, 1985; Brooks and Wiley, 1986, 1988; Brooks, O'Grady, and Glen, 1985). These preliminary data indicate that we may have

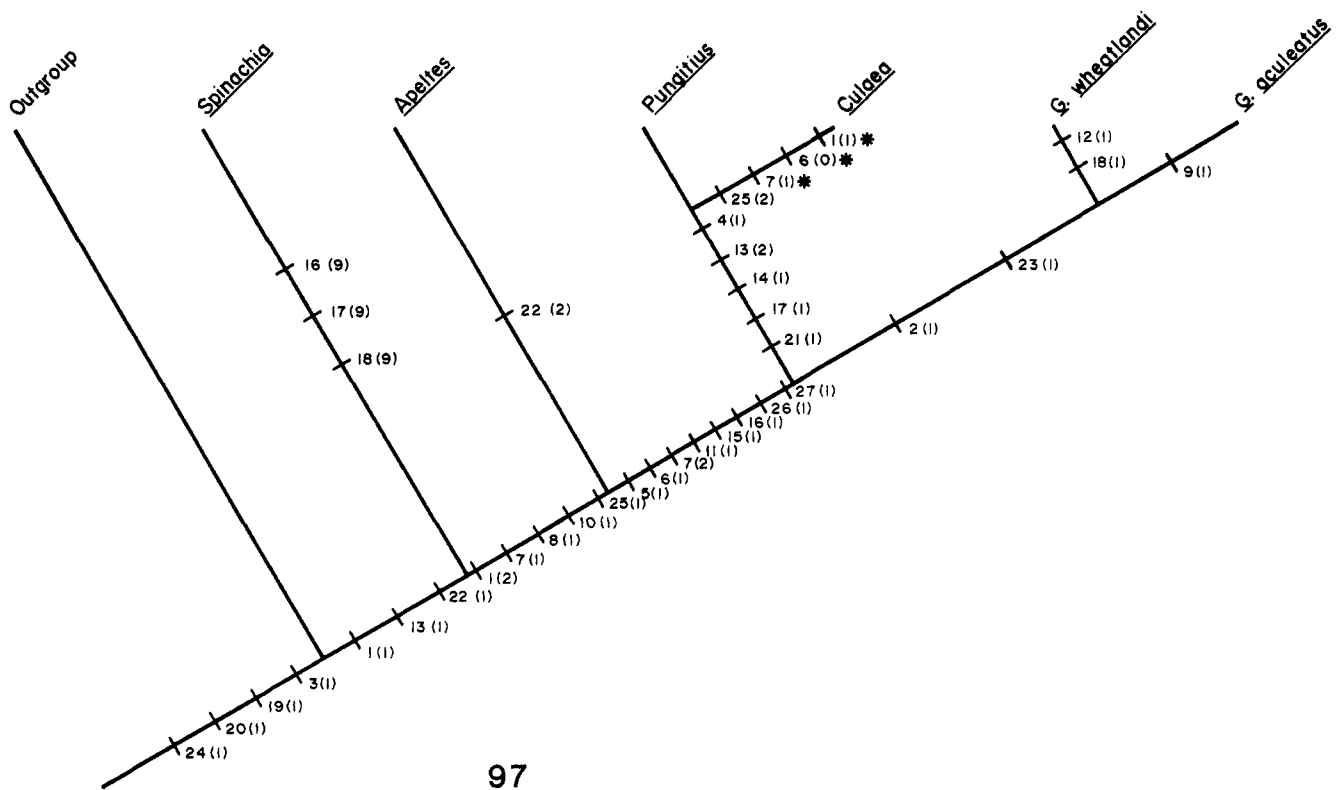
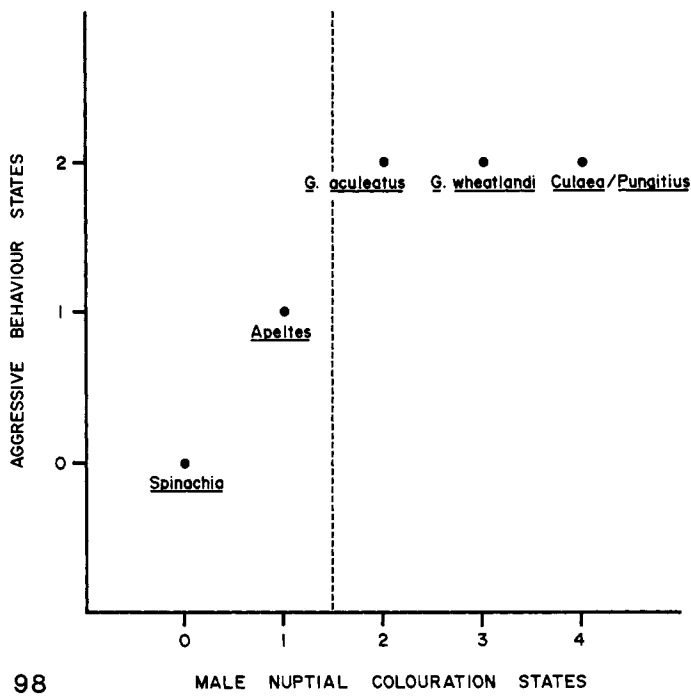
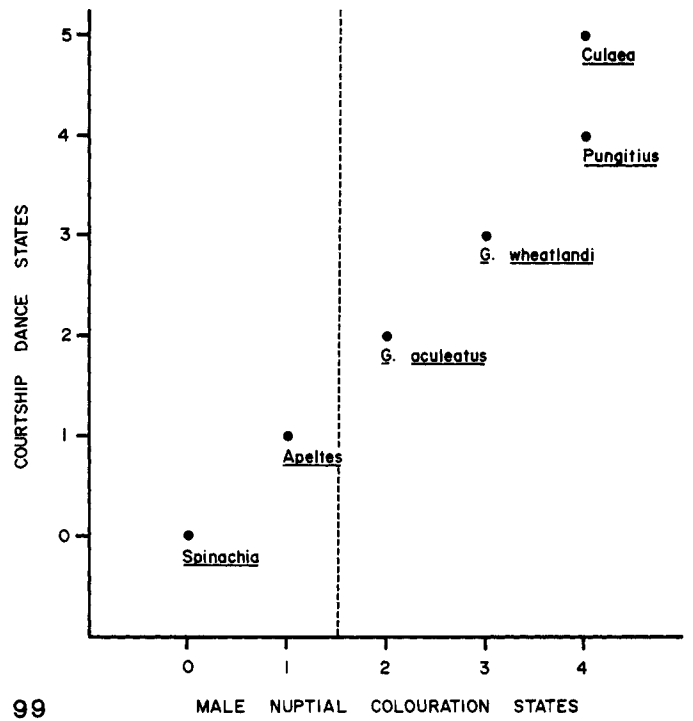


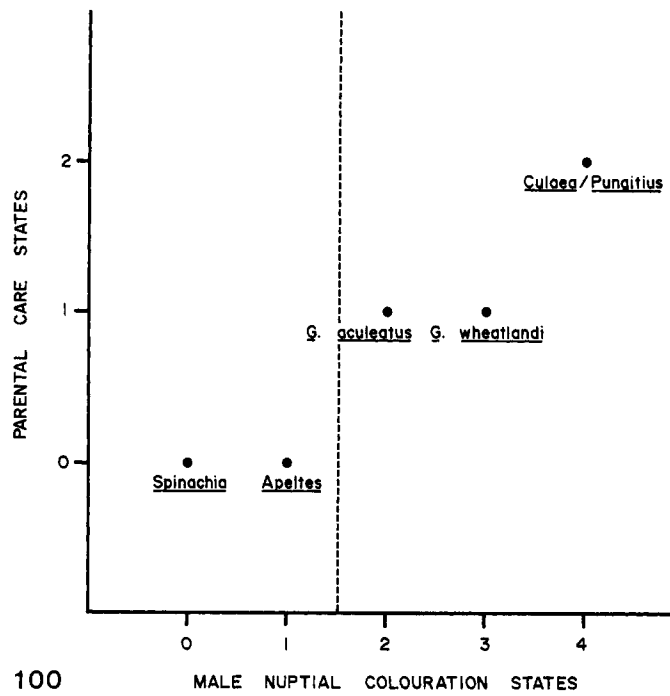
FIGURE 97.—Cladogram of gasterosteid fishes based on fish behavioral data. *** = reversals, numbers in parentheses indicate a character in a multicharacter transformation series. (Redrawn from McLennan, Brooks, and McPhail, 1988.)



98



99



100

FIGURES 98-100.—Plots of behavior during the phylogensis among gasterosteid fishes. 98, Changes in male-male aggressive behavior (intra-sexual selection). 99, Changes in courtship behavior (inter-sexual selection). 100, Changes in parental care behavior (natural selection). Taxa to the right of the dotted lines exhibit full-body coloration in males during the breeding cycle. The diversification of male coloration is weakly correlated with natural selection, and strongly correlated with inter-sexual selection. (From McLennan, Brooks, and McPhail, 1988.)

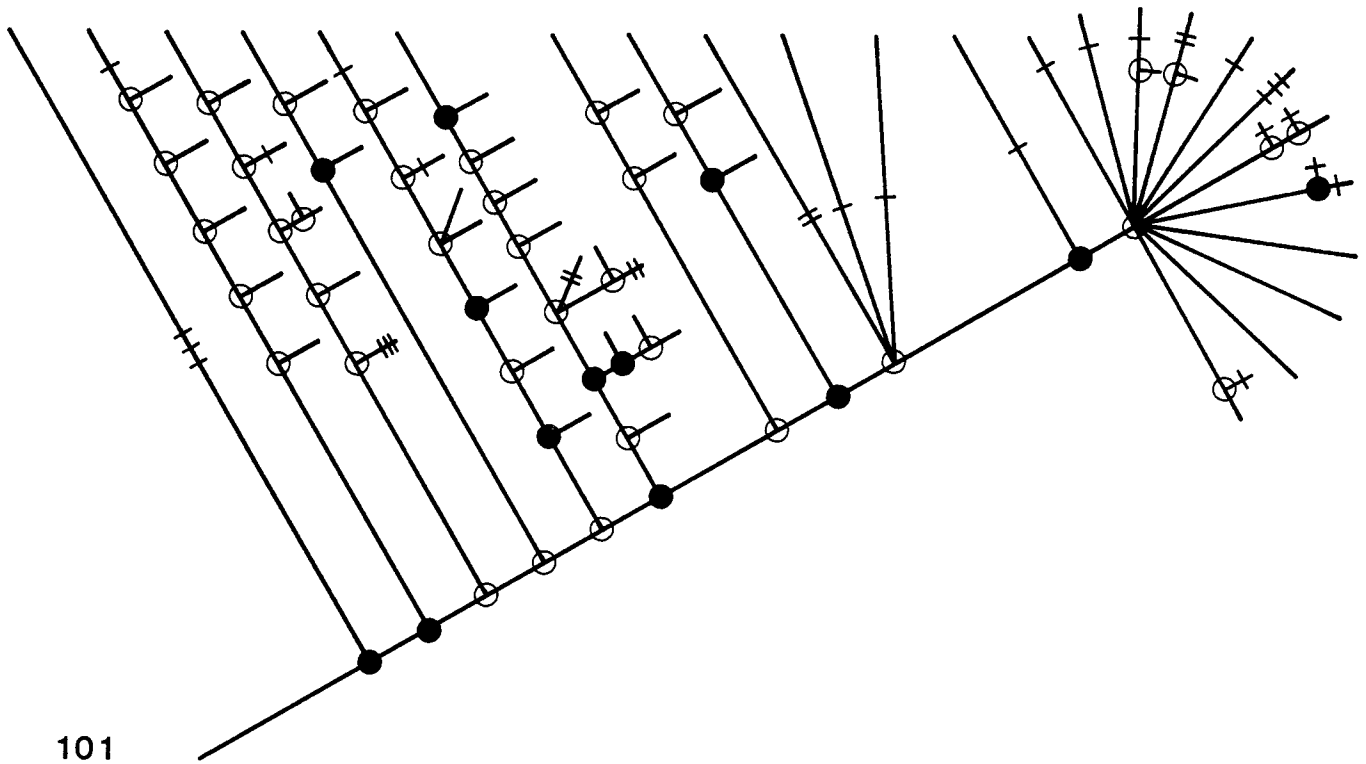


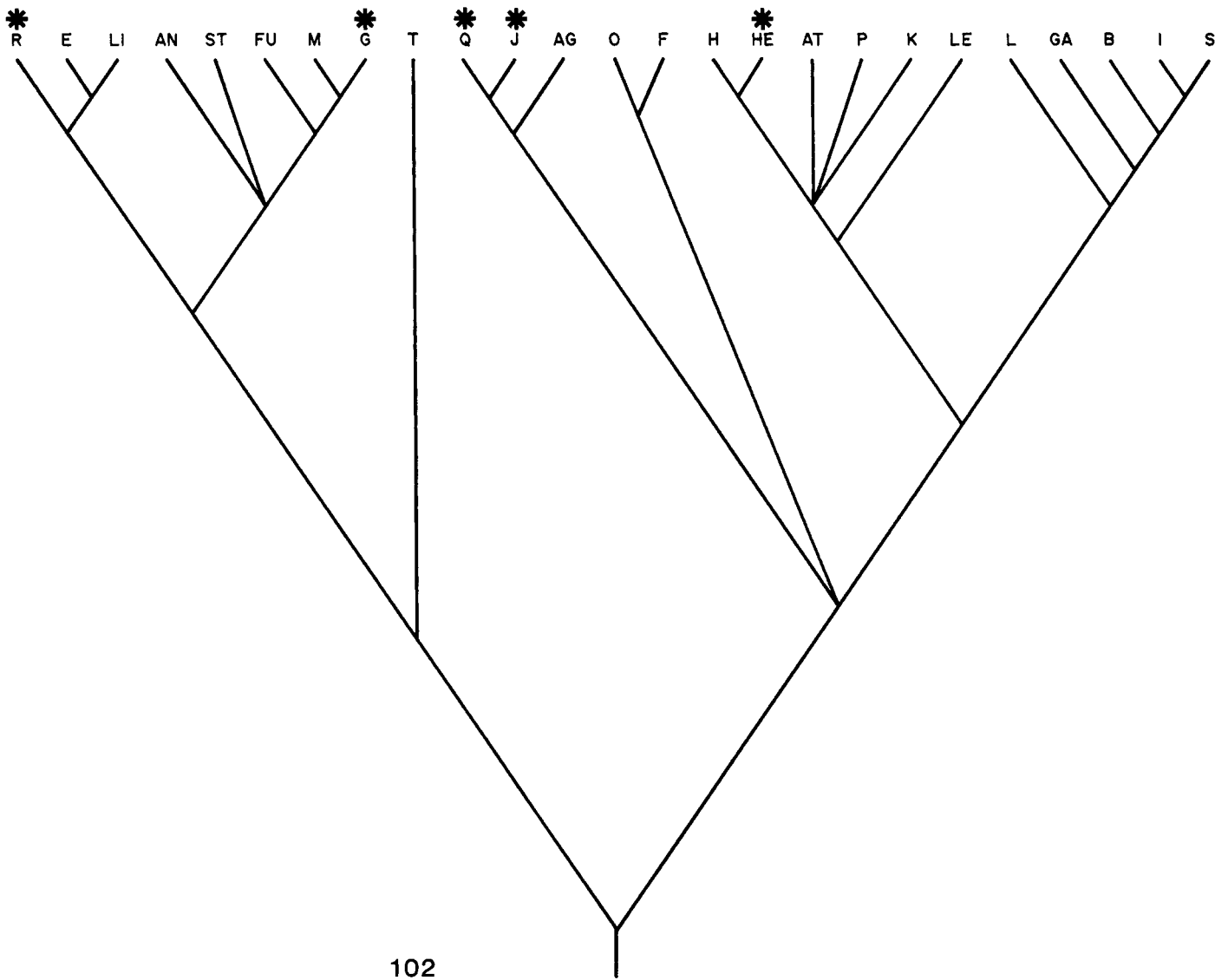
FIGURE 101.—Phylogenetic tree for families of digenetic trematodes. Solid circles represent nonterminal branches diagnosed by any of six categories of ecological change; slash marks indicate terminal branches diagnosed by any of six categories of ecological changes: changes in production of colonizing larvae; changes in first intermediate host type; changes in behavior of colonizing larvae; changes in second intermediate host type; changes in vertebrate host type; and changes in site of infection in vertebrate host. Over 60% of the branches on the tree are characterized by ecological conservatism. (Redrawn and modified from Brooks, O'Grady, and Glenn, 1985.)

overestimated the evidence supporting adaptively driven evolution. Whether or not adaptive changes have taken place, phylogenetic systematics offer us a method for studying it. If it can be shown that adaptive change is not involved, then evolutionary explanations must begin to include additional factors.

One of those additional factors is developmental constraints. Brooks, O'Grady, and Glen (1985) examined the phylogenetic relationships of all digenetic trematodes at the familial level. Previous efforts to study the phylogeny of these parasitic worms concentrated on data from a larval stage (the *cercaria*) that develops in mollusks and spends some time swimming freely before infecting a host, or from the adult stage that resides in a vertebrate, generally in the intestine. Some workers felt that the cercarial stage would be less "adaptively plastic" and would therefore provide better estimates of phylogeny; others felt that the adult stage would be less plastic. Both sides of the argument agreed that different phylogenetic relationships would be supported by each data set. Because each stage develops in a different environment, it was felt that each would be subjected to different selective pressures. Brooks, O'Grady, and Glen showed that when the data were analyzed phylogenetically, both cercarial and adult characters agreed on the

same phylogeny, and that neither developmental stage showed more plasticity than the other. The cercarial and adult data resolved approximately 75% of the familial relationships, and more than 50% of all branches were diagnosed by both cercarial and adult changes (the c.i. for a cladogram with all characters is 74%). This indicates strong phylogenetic components of developmental constraints (Figure 101). Presumably cercarial and adult stages are as well adapted as possible, in a microevolutionary sense, given the macroevolutionary constraints provided by their developmental programs.

The Compositae genus *Montanoa* Cervantes offers an additional example of how one can study adaptation (Funk, 1982). *Montanoa* has 30 taxa, 25 of which are shrubs or vines and five of which are trees of approximately 30 meters in height. The trees all have daisy-like flowers, grow in cloud forests in higher elevations than the rest of the taxa, and three that have been examined chromosomally are high-level polyploids (Funk and Raven, 1980; Funk, 1982). One species grows in each of the following areas: Guerrero, Mexico; Chiapas, Mexico, and northern Guatemala; Costa Rica; Venezuela and Colombia; and the Santa Marta Mountains, Colombia. All five species have a number of similar morphological and anatomical characters that allow them to



102

FIGURE 102.—Cladogram of *Montanoa* showing conservative nature of the evolution of habitat. * = species that are polyploid trees; remaining species are diploid shrubs. (Redrawn and modified from Funk, 1982.)

survive in cloud forests. None of the trees has been found at lower elevations. They are members of four different clades in the genus (Figure 102, the two taxa from South America are sister taxa), their sister species being shrubs living allopatrically at lower elevations. One could speculate that in these four clades natural selection has “selected” those characters that allow these species to be better adapted to cloud forest environments. However, an understanding of developmental constraints leads us to a more interesting conclusion. Among composites, it is not uncommon for polyploids to be larger than diploids; perhaps, being trees rather than shrubs may be simply a developmental consequence of high ploidy level. Composites, especially woody polyploids, conduct water less efficiently than some other plants, so it is likely that tree forms of composites can survive only in habitats, like cloud forests, where they are continuously moist. Conversely, greenhouse

experiments (Funk, pers. observ.) indicate that the shrub-like species of *Montanoa* cannot survive under conditions of high moisture. Hence, the developmental constraints on size, moisture requirements, and moisture tolerance indicate that polyploids of *Montanoa* produced too far from a cloud forest to disperse into high moisture zones for germination will have difficulty surviving. Likewise, diploid seeds that disperse into a cloud forest will have difficulty surviving. The evolution of tree-like species of *Montanoa* four times indicates a certain degree of developmental plasticity in polyploid production (something common among composites in general), while the strict habitat segregation (altitudinal and moisture-level) between trees and shrubs in the genus indicates developmental constraints rather than any possible competitive interactions as the originator of the characteristics.

These examples are not meant to indicate that all characters

are the result of developmental constraints. Rather, they emphasize that the use of phylogenetic systematics can enhance and direct studies in ecology and behavior.

Concluding Statement

As stated at the outset, a major reason for pursuing macroevolutionary research is to try to determine if there are any macroevolutionary processes. Thus far, there appear to be two classes of them: (1) those affecting many lineages simultaneously and in the same way, and (2) those affecting particular lineages but operating on time scales longer than those appropriate for microevolutionary processes (i.e., longer than the duration of any one species), so their evolutionary effects are not apparent in the record of each speciation event. None of these processes is a sufficient explanation for evolutionary diversification, nor can they be deduced from microevolutionary considerations. For these reasons, we eschew any attempts to reduce evolutionary explanations to either macro- or microevolutionary processes. We opt for a hierarchy of causal agents, each operating on a different time scale and each contributing something to the evolved diversity we study.

Macroevolutionary processes affecting many lineages simultaneously are responsible for at least some correlated speciation events and for correlated extinctions. The correlated speciation

events are those due to the effects of isolation by mobile geological elements. Cracraft (1982, 1985b) has suggested that the extent to which speciation events are tied to geologically mediated isolation is the extent to which geological evolution will act as a rate-limiting factor, a macroevolutionary constraint, on evolution. Likewise, the extent to which extinctions in different groups are correlated and are due to terrestrial or extraterrestrial perturbations of a periodic nature is the extent to which those perturbations affect the rate of extinction.

Macroevolutionary processes affecting particular lineages comprise phylogenetic constraints. Phylogenetic constraints can be seen both in structural and in functional diversification. They affect evolution in two ways. First, they limit the extent to which, and the manner in which, species can adapt to different selection regimes. Second, the constrained portions act as conservative "filters" on changing portions, eliminating variants that might be seen as functional individual units but which do not integrate with the whole organism well enough to allow viability. In both senses, they establish the arena, or context, of evolutionary change. Changes in the genealogical hierarchy are slow; changes in the ecological hierarchy are fast. The interplay of the two hierarchies produces a strong self-organizing and adaptive evolutionary imperative in biological systems.

Literature Cited

- Adams, E.N.
1972. Consensus Techniques and the Comparison of Taxonomic Trees. *Systematic Zoology*, 21:390-397.
- Alberch P., S.J. Gould, G.F. Oster, and D.B. Wake
1979. Size and Shape in Ontogeny and Phylogeny. *Paleobiology*, 5:296-315.
- Alcock, J.
1984. *Animal Behavior: An Evolutionary Approach*. Sunderland, Massachusetts: Sinauer Associates.
- Andersen, N.M.
1982. The Semi-aquatic Bugs (Hemiptera, Gerromorpha): Phylogeny, Adaptations, Biogeography, and Classification. *Entomograph*, 3:1-455. Klampenborg, Denmark: Scandinavian Science Press.
- Boucot, A.J.
1978. Community Evolution and Rates of Cladogenesis. In M. K. Hecht, W.C. Steere, and B. Wallace, editors, *Evolutionary Biology*, 11:545-655. New York: Plenum.
1982. *Paleobiologic Evidence of Behavioral Evolution and Co-Evolution*. Corvallis, Oregon: by the author.
1983. Does Evolution Take Place in an Ecological Vacuum? *Journal of Paleontology*, 37:1-30.
- Brooks, D.R.
1981. Hennig's Parasitological Method: A Proposed Solution. *Systematic Zoology*, 30:229-249.
1985. Historical Ecology: A New Approach to Studying the Evolution of Ecological Associations. *Annals of the Missouri Botanical Garden*, 72:660-680.
1988. Macroevolutionary Comparisons of Host and Parasite Phylogenies. *Annual Review of Ecology and Systematics*, 19:235-259.
- Brooks, D.R., and S.M. Bandoni
1988. Coevolution and Relicts. *Systematic Zoology*, 37:19-33.
- Brooks, D.R., and D.R. Glen
1982. Pinworms and Primates: A Case Study in Coevolution. *Proceedings of the Helminthological Society of Washington*, 49:76-85.
- Brooks, D.R., R.T. O'Grady, and D.R. Glen
1985. Phylogenetic Analysis of the *Digenea* (Platyhelminthes: Cercaria) with Comments on their Adaptive Radiation. *Canadian Journal of Zoology*, 63:411-443.
- Brooks, D.R., R.T. O'Grady, and E.O. Wiley
1986. A Measure of the Information Content of Phylogenetic Trees, and Its Use as an Optimality Criterion. *Systematic Zoology*, 35:571-581.
- Brooks, D.R., and E.O. Wiley
1986. *Evolution as Entropy*. Chicago: University of Chicago Press.
1988. *Evolution as Entropy*. 2nd edition. Chicago: University of Chicago Press.
- Brundin, L.
1966. Transantarctic Relationships and Their Significance, as Evidenced by Chironomid Midges. *Kungliga Svenska Vetenskapsakademien Handlingar (f)*, 11:1-472.
- Charlesworth, B., R. Lande, and M. Slatkin
1982. A Neo-Darwinian Commentary on Macroevolution. *Evolution*, 36:474-498.
- Clutton-Brock, T.H., and P.H. Harvey
1984. Comparative Approaches to Investigating Adaptation. In J.R. Krebs and N.B. Davies, editors, *Behavioural Ecology: An Evolutionary Approach*. 2nd edition, pages 7-29. Sunderland, Massachusetts: Sinauer Associates.
- Coddington, J.A.
1986. Orb Webs in "Non Orb Weaving" Ogre-faced Spiders (Araneae: Dinopidae): A Question of Genealogy. *Cladistics*, 2:53-67.
- Cox, P.A.
In press. Breeding Systems and the Evolution of Pandanaceae. *Annals of the Missouri Botanical Garden*.
- Cracraft, J.
1982. Geographic Differentiation, Cladistics and Vicariance Biogeography: Reconstructing the Tempo and Mode of Evolution. *American Zoologist*, 22:411-424.
1985a. Species Selection, Macroevolutionary Analysis, and the "Hierarchical Theory" of Evolution. *Systematic Zoology*, 34:222-229.
1985b. Biological Diversification and Its Causes. *Annals of the Missouri Botanical Garden*, 72:794-822.
1986. Origin and Evolution of Continental Biotas: Speciation and Historical Congruence within the Australian Avifauna. *Evolution*, 40:977-996.
- Cressey, R.F., B. Collette, and J. Russo
1983. Copepods and Scombrid Fishes: A Study in Host-parasite Relationships. *Fishery Bulletin*, 81:227-265.
- Croizat, L., G. Nelson, and D.E. Rosen
1974. Centers of Origin and Related Concepts. *Systematic Zoology*, 23:265-287.
- Dobson, F.S.
1985. The Use of Phylogeny in Behavior and Ecology. *Evolution*, 39:1384-1388.
- Dobzhansky, T.
1937. *Genetics and the Origin of Species*. New York: Columbia University Press.
- Duellman, W.E.
1985. Reproductive Modes in Anuran Amphibians: Phylogenetic Significance of Adaptive Strategies. *South African Journal of Science*, 81:174-178.
- Eldredge, N.
1985. *The Unfinished Synthesis*. New York: Columbia University Press.
- Eldredge, N., and J. Cracraft
1980. *Phylogenetic Patterns and the Evolutionary Process: Method and Theory in Comparative Biology*. New York: Columbia University Press.
- Endler, J.A.
1977. *Geographic Variation, Speciation, and Clines*. Princeton: Princeton University Press.
- Erwin, T.
1985. The Taxon Pulse: A General Pattern of Lineage Radiation and Extinction among Carabid Beetles. In G.E. Ball, editor, *Taxonomy, Phylogeny and Zoogeography of Beetles and Ants*, pages 437-472. Dordrecht: W. Junk.
- Farris, J.S.
1974. Formal Definitions of Paraphyly and Polyphyly. *Systematic Zoology*, 23:548-554.
1983. The Logical Basis of Phylogenetic Analysis. In N.I. Platnick and V.A. Funk, editors, *Advances in Cladistics: Proceedings of the Second Meeting of the Willi Hennig Society*, pages 1-36. New York: New York Botanical Garden.
- Fink, W.L.
1982. The Conceptual Relationship between Ontogeny and Phylogeny. *Paleobiology*, 8:254-264.

- Funk, V.A.
 1981. Special Concerns in Estimating Plant Phylogenies. In V.A. Funk and D.R. Brooks, editors, *Advances in Cladistics: Proceedings of the First Meeting of the Willi Hennig Society*, pages 73–86. New York: New York Botanical Garden.
 1982. Systematics of *Montanoa* (Asteraceae: Heliantheae). *Memoirs of the New York Botanical Garden*, 36:1–135.
 1984. Cladistics and Generic Concepts in the Compositae. *Taxon*, 34:72–80.
 1985. Phylogenetic Patterns and Hybridization. *Annals of the Missouri Botanical Garden*, 72:681–715.
 In prep. Modes of Speciation in High Elevation South American Sunflowers (Asteraceae).
- Funk, V.A., and P.H. Raven
 1980. Polyploidy in *Montanoa* Cerv. (Compositae, Heliantheae). *Taxon*, 29:417–419.
- Futuyma, D.J.
 1979. *Evolutionary Biology*. Sunderland, Massachusetts: Sinauer Associates.
- Futuyma, D., and M. Slatkin
 1983. *Coevolution*. Sunderland, Massachusetts: Sinauer Associates.
- Glen, D.R., and D.R. Brooks
 1985a. Phylogenetic Relationships of Some Strongylate Nematodes of Primates. *Proceedings of the Helminthological Society of Washington*, 52:227–236.
 1985b. Parasitological Evidence Pertaining to the Phylogeny of the Hominoid Primates. *Biological Journal of the Linnean Society*, 27:331–354.
- Goldschmidt, R.B.
 1940. *The Material Basis of Evolution*. New Haven: Yale University Press.
- Hafner, M.S., and S.A. Nadler
 1988. Phylogenetic Trees Support the Coevolution of Parasites and Their Hosts. *Nature*, 332:258–259.
- Hart, J.A.
 1985a. Peripheral Isolation and the Origin of Diversity in *Lepechinia* sect. *Parviflorae* (Lamiaceae). *Systematic Botany*, 10:134–146.
 1985b. Evolution of Dioecism in *Lepechinia* Willd. Sect. *Parviflorae* (Lamiaceae). *Systematic Botany*, 10:147–154.
- Hennig, W.
 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin: Deutscher Zentralverlag.
 1966. *Phylogenetic Systematics*. Urbana: University of Illinois Press.
- Hillis, D.M., and S.K. Davis
 1986. Evolution of Ribosomal DNA: Fifty Million Years of Recorded History in the Frog Genus *Rana*. *Evolution*, 40:1275–1288.
- Hillis, D.M., J.S. Frost, and D.A. Wright
 1983. Phylogeny and Biogeography of the *Rana pipiens* Complex: A Biochemical Evaluation. *Systematic Zoology*, 32:132–143.
- Huber, O.
 1988. Guayana Highlands versus Guayana Lowlands, a Reappraisal. *Taxon*, 37:595–614.
- Humphries, C.J.
 1983. Primary Data in Hybrid Analysis. In N.I. Platnick and V.A. Funk, editors, *Advances in Cladistics: Proceedings of the Second Meeting of the Willi Hennig Society*, pages 89–104. New York: Columbia University Press.
- Humphries, C.J., and V.A. Funk
 1984. Cladistic Methodology. In V.H. Heywood and D.M. Moore, editors, *Current Concepts in Plant Taxonomy*, pages 323–362. London: Academic Press.
- Humphries, C.J., and L. Parenti
 1986. *Cladistic Biogeography*. London: Academic Press.
- Lauder, G.V.
 1982. Historical Biology and the Problem of Design. *Journal of Theoretical Biology*, 97:57–68.
- Lynch, J.D.
 1982. Relationships of the Frogs of the Genus *Ceratophrys* (Leptodactylidae) and Their Bearing on Hypotheses of Pleistocene Forest Refugia in South America and Punctuated Equilibria. *Systematic Zoology*, 31:166–179.
- MacArthur, R.H., and E.O. Wilson
 1967. *The Theory of Island Biogeography*. Princeton: Princeton University Press.
- Maguire, B.
 1970. On the Flora of the Guayana Highland. *Biotropica*, 2:85–100.
- Maynard Smith, J., R. Burian, S. Kauffman, P. Alberch, J. Campbell, B. Goodwin, R. Lande, D. Raup, and L. Wolpert
 1985. Developmental Constraints and Evolution: A Perspective from the Mountain Lake Conference on Development and Evolution. *Quarterly Review of Biology*, 60:265–287.
- Mayr, E.
 1942. *Systematics and the Origin of Species*. New York: Columbia University Press.
 1963. *Animal Species and Evolution*. Cambridge, Massachusetts: Harvard University Press.
- McLennan, D., D.R. Brooks, and J.D. McPhail
 1988. The Benefits of Communication between Comparative Ethology and Phylogenetic Systematics: A Case Study Using Gasterosteid Fishes. *Canadian Journal of Zoology*, 66:2177–2190.
- Mitter, C., and D.R. Brooks
 1983. Phylogenetic Aspects of Coevolution. In D.J. Futuyma and M. Slatkin, editors, *Coevolution*, pages 65–98. Sunderland, Massachusetts: Sinauer Associates.
- Miyamoto, M.M.
 1983. Frogs of the *Eleutherodactylus rugulosus* Group: A Cladistic Study of Allozyme, Morphological and Karyological Data. *Systematic Zoology*, 32:109–124.
- Mooi, R.J.
 1987. Analysis of the Sand Dollars (Clypeasteroidea: Scutellina) and the Interpretation of Heterochronic Phenomena. Doctoral dissertation, University of Toronto, Toronto, Canada.
- Mooi, R., P.F. Cannell, V.A. Funk, P.M. Mabee, R.T. O'Grady, and C.K. Starr
 In press. Historical Perspectives, Ecology, and Tiger Beetles: An Alternative Discussion. *Systematic Zoology*.
- Nelson, G.
 1979. Cladistic Analysis and Synthesis: Principles and Definitions, with a Historical Note on Adanson's *Familles des Plantes* (1763–1767). *Systematic Zoology*, 28:1–21.
 1983. Reticulation in Cladograms. In N.I. Platnick and V.A. Funk, editors, *Advances in Cladistics: Proceedings of the Second Meeting of the Willi Hennig Society*, pages 105–111. New York: Columbia University Press.
- Nelson, G., and N.I. Platnick
 1981. *Systematics and Biogeography: Cladistics and Vicariance*. New York: Columbia University Press.
- Nelson, G., and D.E. Rosen
 1981. *Vicariance Biogeography: A Critique*. New York: Columbia University Press.
- O'Grady, R.T.
 1984. Evolutionary Theory and Teleology. *Journal of Theoretical Biology*, 107:563–578.
 1986. Historical Processes, Evolutionary Explanations, and Problems with Teleology. *Canadian Journal of Zoology*, 64:1010–1020.
 1987. Phylogenetic Systematics and the Evolutionary History of Some Intestinal Flatworm Parasites (Trematoda: Digenea: Plagiiorchioidea) of Anurans. Doctoral dissertation, University of British Columbia, Vancouver, British Columbia, Canada.
- O'Grady, R.T., and G.B. Deets
 1987. Coding Multistate Characters, with Special Reference to the Use of Parasites as Characters of their Hosts. *Systematic Zoology*, 36:268–279.

- O'Grady, R.T., G.B. Deets, and G. Benz
In press. Additional Observations on Nonredundant Linear Coding. *Systematic Zoology*.
- Oosterbroek, P.
1987. More Appropriate Definitions of Paraphyly and Polyphyly, with a Comment on the Farris 1974 Model. *Systematic Zoology*, 36:103-108.
- Otto, C., and L.M. Nilsson
1981. Why do Beech and Oak Trees Retain Leaves until Spring? *Oikos*, 37:387-390.
1982. Reply to Dunberg's Comments. *Oikos*, 39:278.
- Pearson, D.L., M.S. Blum, T.H. Jones, E. Gonda, and B.R. White
1988. Historical Perspective and the Interpretation of Ecological Patterns: Defensive Compounds of Tiger Beetles. *American Naturalist*, 132:404-414.
- Platnick, N.I.
1977a. Paraphyletic and Polyphyletic Groups. *Systematic Zoology*, 26:195-200.
1977b. Parallelism in Phylogeny Reconstruction. *Systematic Zoology* 26:93-96.
1979. Philosophy and the Transformation of Cladistics. *Systematic Zoology*, 28:537-546.
- Ramirez B., William
1974a. Coevolution of *Ficus* and Agaonidae. *Annals of the Missouri Botanical Garden*, 61:770-780.
1974b. Host Specificity in *Ficus* and Agaonidae. Doctoral dissertation, University of Kansas, Lawrence Kansas.
- Remane, A.
1956. *Die Grundlagen des natürlischen Systems der vergleichenden Anatomie und Phylogenetik*. Volume 2. Leipzig: Geest und Portig K. G.
- Ricklefs, R.E.
1987. Community Diversity: Relative Roles of Local and Regional Processes. *Science*, 235:167-171.
- Rosen, D.E.
1975. A Vicariance Model of Caribbean Biogeography. *Systematic Zoology*, 24:431-464.
1978. Vicariant Patterns and Historical Explanation in Biogeography. *Systematic Zoology*, 27:159-188.
1979. Fishes from the Uplands and Intermontane Basins of Guatemala: Revisionary Studies and Comparative Biogeography. *Bulletin of the American Museum of Natural History*, 162:267-376.
1985. Geological Hierarchies and Biogeographic Congruence in the Caribbean. *Annals of the Missouri Botanical Garden*, 72:636-659.
- Roskam, J.C.
1985. Evolutionary Patterns in Gall Midge-host Plant Associations (Diptera, Cecidomyiidae). *Tijdschrift voor Entomologie*, 128:193-312.
- Ross, H.H.
1972a. An Uncertainty Principle in Ecological Evolution. In R.T. Allen and F.C. James, editors, A Symposium on Ecosystematics. *University of Arkansas Museum, Occasional Paper*, 4:133-160. Fayetteville, Arkansas.
1972b. The Origin of Species Diversity in Ecological Communities. *Taxon*, 21:253-259.
- Salthe, S.N.
1985. *Evolving Hierarchical Systems: Their Structure and Representation*. New York: Columbia University Press.
- Seaman, F.C., and V.A. Funk
1983. Cladistic Analysis of Complex Natural Products: Developing Transformation Series from Sesquiterpene Lactone Data. *Taxon*, 32:1-27.
Seaman, F.C., V.A. Funk, N.H. Fischer, and T.J. Mabry
In prep. Biochemical Systematic Analysis of Terpenoid Variation in *Montanoa* (Asteraceae).
- Simberloff, D., K.L. Heck, E.D. McCoy, and E.F. Connor
1981. There Have Been No Statistical Tests of Cladistic Biogeographical Hypotheses. In G. Nelson and D.E. Rosen, editors, *Vicariance Biogeography: A Critique*, pages 40-63. New York: Columbia University Press.
- Simpson, G.G.
1944. *Tempo and Mode in Evolution*. New York: Columbia University Press.
- Spuhler, J.N.
1988. Evolution of Mitochondrial DNA in Monkeys, Apes, and Humans. *Yearbook of Physical Anthropology*, 31:15-48.
- Stebbins, G.L., and F.J. Ayala
1984. Is a New Evolutionary Synthesis Necessary? *Science*, 213:967-971.
- Steyermark, J.
1986. Speciation and Endemism in the Flora of the Venezuelan Tepuis. In F. Vuilleumier and M. Monasterio, editors, *High Altitude Tropical Biogeography*, pages 317-373. New York: Oxford University Press.
- Swofford, D., and W. Maddison
1987. Reconstructing Ancestral Character States under Wagner Parsimony. *Mathematical Biosciences*, 87:199-229.
- Thornhill, R., and J. Alcock
1983. *The Evolution of Insect Mating Systems*. Cambridge, Massachusetts: Harvard University Press.
- Vehrenkamp, S.L., and J.W. Bradbury
1984. Mating Systems and Ecology. In J.R. Krebs and N.B. Davies, editors, *Behavioural Ecology: An Evolutionary Approach*. 2nd edition, pages 251-278. Sunderland, Massachusetts: Sinauer Associates.
- Wanntorp, H.-E.
1983. Historical Constraints in Adaptation Theory: Traits and Non-traits. *Oikos*, 41:151-160.
- Wiley, E.O.
1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. New York: Wiley-Interscience.
1988. Vicariance Biogeography. *Annual Review of Systematics and Ecology*, 19:513-542.
- Wiley, E.O., and R.L. Mayden
1985. Species and Speciation in Phylogenetic Systematics, with Examples from the North American Fish Fauna. *Annals of the Missouri Botanical Garden*, 72:596-635.
- Yokel, D.A.
1986. Monogamy and Brood Parasitism: An Unlikely Pair. *Animal Behaviour*, 34:1348-1358.