7 Cospeciation

There are a variety of ways in which phylogenetic trees can be used in studying the evolution of biological associations. Many of these applications involve investigating the degree of congruence between the history of one group and the history of the areas in which its members reside, or the histories of other groups with which it is ecologically associated. These comparisons, in turn, provide a way to distinguish among hypotheses concerning the observed species composition of the associations. For example, a species may occur in a certain geographic area because its ancestor lived in that area and the descendant evolved "*in situ*." You will recognize this as the result of vicariant speciation (allopatric speciation mode I). Alternatively, the species may have evolved elsewhere and dispersed into the area where it now resides, or it may have evolved as a result of dispersing into the area where it now resides (allopatric speciation mode II). In the first case we would expect the history of the species to coincide with (to be **congruent** with) the history of the area, whereas in the second case we would not. Similar reasoning can be applied to studies of interspecific associations regardless of their geographic context. Two or more species may be associated ecologically today because their ancestors were associated, or they (or their ancestors) may have evolved in association with other species and subsequently "switched allegiances." Such allegiance switching (or the common, but more restrictive, term "resource/host switching") in ecological associations is equivalent to dispersal in biogeographical associations. In the first case we would expect the histories of the taxa involved in the association to coincide with each other, whereas in the second case we would not expect to find such congruence. Taxa that show historical association either with geographical areas or with other taxa exhibit **cospeciation** patterns. Phylogenetic systematic methods can help to distinguish components of associations that are due to history (**association by descent**) from those that are due to dispersal or resource/host switching (**association by colonization**). Differentiating between these two components of any association in both geographical and ecological contexts will be the focus of this chapter.

Investigating the macroevolutionary components of ecological associations

requires some advanced applications of phylogenetic systematic methods. First, new terminology: Up to this point, we have equated "branching diagram" with **"phylogenetic tree."** In this chapter we will discuss methods for comparing the amount of ecological association between different clades throughout their evolutionary history. Such comparisons are summarized in branching diagrams derived by using the phylogenetic relationships of the taxa as "characters" and the ecological associations as "taxa." We will refer to these diagrams as **cladograms,** which literally means "branching diagram": that is, "area cladograms" when phylogenies are being compared with respect to common geographic distributions, or "host cladograms" when phylogenies are being compared with respect to common ecological associations. The term "phylogenetic tree" will be reserved for estimates of historical relationships among taxa based on characters intrinsic to the taxa. We realize that the term "cladogram" is commonly used synonymously with "phylogenetic tree"; however, we believe that it is important to distinguish between a genealogical reconstruction and an ecological reconstruction in evolutionary biology. We hope this distinction will be more helpful than confusing.

Cospeciation in a Geographic Context: How Did the Species Come to Be in the Same Geographical Area?

Basic Methodology

We will begin our discussion of this section with an example drawn from a group of rare flatworms, the Amphilinidea. Amphilinids, the sister group of the species-rich true tapeworms, are a small (eight known species) but widespread group of parasites that live in the body cavities of freshwater and estuarine ray-finned fishes and in one species of freshwater turtle.

1. The first step in the search for possible historical components in the association between the amphilinids and their geographical distributions is *the reconstruction of the phylogenetic relationships of the organisms.* Phylogenetic systematic analysis of the eight species of amphilinids, based on forty-six morphological characters, produced a single tree with a consistency index of 87.5% (Bandoni and Brooks 1987a). Figure 7.1 depicts these relationships for five of the eight species (we will include the other three later).

2. The next step is to *designate the areas in which the species occur as if they were taxa.* Geological evidence (e.g., Dietz and Holden 1966) is then used to produce an area cladogram showing the historical connections among the study areas (fig. 7.2).

3. We then prepare a list *placing the species* of amphilinid flatworms *with the areas in which they occur* (table 7.1).

4. The phylogenetic relationships of the five amphilinid species, previously

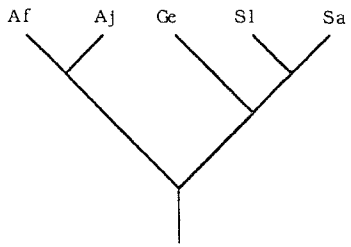

Fig. 7.1. Phylogenetic tree for five species of amphilinid flatworms. *Af = Amphilina foliacea; Aj = A. japonica; Ge = Gigantolina elongata; Sl = Schizochoerus liguloideus; Sa = S. africanus.*

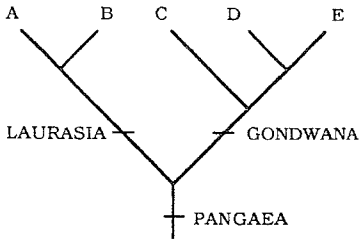

Fig. 7.2. Area cladogram for the major continents on this planet, based on historical geological data. *A* = Eurasia; *B* = North America; *C* = Australia; *D* = South America; *E* = Africa.

Table 7.1 List of geographical areas and species of amphilinid flatworms that inhabit them.

Area		Taxon	Taxon Name
A	Eurasia	1	*Amphilina foliacea*
B	North America	2	*Amphilina japonica*
C	Australia	3	*Gigantolina elongata*
D	South America	4	*Schizochoerus liguloideus*
E	Africa	5	*Schizochoerus africanus*

reconstructed using morphological data (fig. 7.1), can now be treated *as if they were a completely polarized multistate transformation series,* in which each taxon and each internal branch of the tree is numbered (fig. 7.3). The sequence of numbering is arbitrary, but each internal branch of the tree must have a number.

5. Each species of amphilinid now has a "code" that indicates both its identity *and* its common ancestry. For example, the code for *Amphilina japonica* is (2, 6, 9) and the code for *Schizochoerus africanus* is (5, 7, 8, 9).

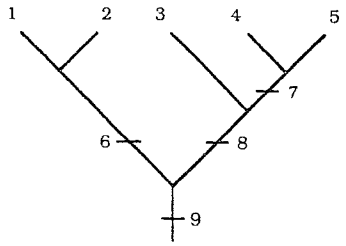

Fig. 7.3. Phylogenetic tree for five species of amphilinid flatworms, with internal branches numbered for cospeciation analysis. *1 = Amphilina foliacea; 2 = A. japonica; 3 = Gigantolina elongata; 4 = Schizochoerus liguloideus; 5 = S. africanus.*

Table 7.2 Matrix listing binary codes that represent the phylogenetic relationships among five species of amphilinid flatworms.

Taxon		Binary Code
1	*Amphilina foliacea*	100001001
2	*Amphilina japonica*	010001001
3	*Gigantolina elongata*	001000011
4	*Schizochoerus liguloideus*	000100111
5	*Schizochoerus africanus*	000010111

These codes, in turn, can be represented in a data matrix in which the presence of a number in the species code is listed as one and the absence of a number in the species code is listed as zero (table 7.2).

6. You should recognize this as an application of **additive binary coding** (see chapter 2). The phylogenetic relationships of the study group are now represented by the binary codes. This can be confirmed by performing a phylogenetic systematic analysis for species 1–5 using the binary codes from table 7.2 (fig. 7.4). If all is correct, this will reproduce the tree shown in figure 7.3.

7. Now we *replace the species names* in table 7.2 *with their geographic distributions* (table 7.3).

Table 7.3 Matrix listing binary codes indicating phylogenetic relationships among five species of amphilinid flatworms inhabiting five geographic areas.

Area	Binary Code
A Eurasia	100001001
B North America	010001001
C Australia	001000011
D South America	000100111
E Africa	000010111

8. Finally, we construct a new area cladogram based, this time, on the phylogenetic relationships of the species (fig. 7.5). This produces a "picture" of the historical involvement of areas in the evolution of the species.

In this example the area cladogram based upon geological evidence (fig. 7.2) and the area cladogram reconstructed from the phylogenetic relationships of the taxa occurring in each region (fig. 7.5) are identical. In addition, the consistency index for the area cladogram is 100%, indicating that all the speciation events postulated by the phylogenetic tree are congruent with the area cladogram. Therefore, we can hypothesize that the occurrence of the study species in the study areas is a result of a long history of association between amphilinids and the areas in which they now occur.

Dispersal of organisms is a common phenomenon in nature, so real data sets will generally show less than the 100% congruence depicted in the preceding example. Let us return to the amphilinids and complicate the picture somewhat by including the remaining three members of the group in the analysis.

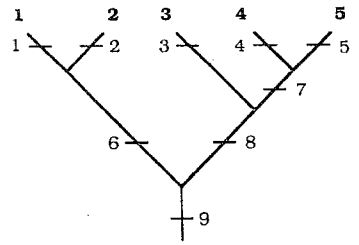

Fig. 7.4. Cladogram for five species of amphilinid flatworms, based on the additive binary matrix representing the phylogenetic tree for those species. *Numbers accompanying slash marks* indicate codes for species and their relationships from table 7.2.

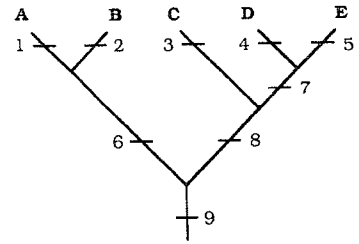

Fig. 7.5. Area cladogram for five areas, based on the phylogenetic relationships of five species of amphilinid flatworms that inhabit those areas. *A* = Eurasia; *B* = North America; *C* = Australia; *D* = South America; *E* = Africa. *Numbers accompanying slash marks* indicate codes for species and their relationships from table 7.2.

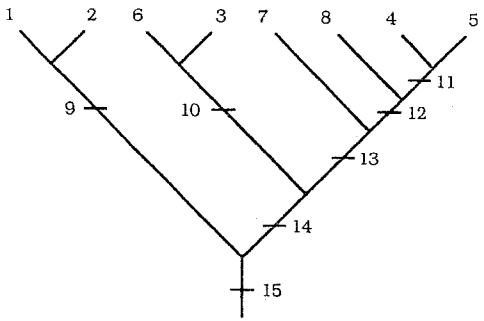

Fig. 7.6. Phylogenetic tree for eight species of amphilinid flatworms, with internal branches numbered for cospeciation analysis. *1 = Amphilina foliacea; 2 = A. japonica; 3 = Gigantolina elongata; 4 = Schizochoerus liguloideus; 5 = S. africanus; 6 = G. magna; 7 = S. paragonopora; 8 = S. janickii.*

1. The complete phylogenetic tree for the Amphilinidea is shown in figure 7.6, with internal branches numbered for additive binary coding. The "new" flatworms are *Gigantolina magna* (taxon 6), *Schizochoerus paragonopora* (taxon 7), and *S. janickii* (taxon 8).

2. The three additional species of amphilinids inhabit South America (*S. janickii*) and Indo-Malaysia (*G. magna* and *S. paragonopora*). Species codes (from fig. 7.6) are converted to binary codes and listed for each area in table 7.4 (when more than one species occurs in an area, the codes are combined—we will discuss this more fully later).

Table 7.4 Matrix listing binary codes for species of amphilinid flatworms inhabiting six geographic areas.

Area	Binary Code
A Eurasia	100000001000001
B North America	010000001000001
C Australia	001000000100011
D South America	000100010011111
E Africa	000010000011111
F Indo-Malaysia	000001100100111

3. The area cladogram reconstructed from that data matrix is depicted in figure 7.7.

The consistency index for this area cladogram is 93.75%. Note that "10" appears twice on the tree. This indicates that the common ancestor of species 3 and species 6 (taxon 10) occurred in both area C and area F. Its occurrence in area C coincides with the geological history of the areas, so we explain

this by saying that species 3 evolved in the same place (area C) as its ancestor (taxon 10). On the other hand, the occurrence of 10 in area F does not coincide with the geological history of the areas. We explain this by hypothesizing that at least some members of ancestor 10 dispersed to area F, where the population evolved into species 6. Hence, the occurrence of species 7 in area F is due to common history, whereas the occurence of species 6 in area F is due to dispersal of its ancestor into that area. If this is true, then what we have called area F is, from a historical perspective, two different areas for species 6 and 7.

We can test this possibility and further examine the question of ancestor 10's dispersal by recoding the data matrix in table 7.4, listing species 6 and species 7 in different subsections of area F (F_1 and F_2; table 7.5). When we

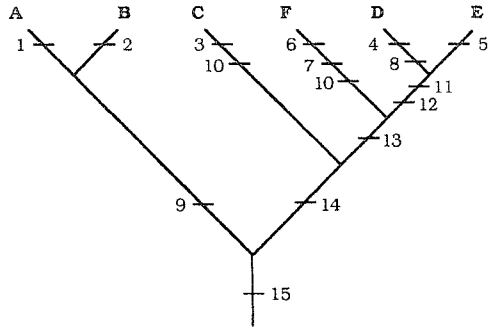

Fig. 7.7. Area cladogram based on phylogenetic relationships among eight species of amphilinid flatworms. *A* = Eurasia; *B* = North America; *C* = Australia; *D* = South America; *E* = Africa; *F* = Indo-Malaysia. "Characters," represented by numbers accompanying slash marks, are species. *1 = Amphilina foliacea; 2 = A. japonica; 3 = Gigantolina elongata; 4 = Schizochoerus liguloideus; 5 = S. africanus; 6 = G. magna; 7 = S. paragonopora; 8 = S. janickii.* Numbers *9–15* = ancestral species (see fig. 7.6).

Table 7.5 Matrix listing binary codes for species of amphilinid flatworms inhabiting six geographic areas.

Area[a]	Binary Code
A Eurasia	100000001000001
B North America	010000001000001
C Australia	001000000100011
D South America	000100010011111
E Africa	000010000011111
F_1 Indo-Malaysia	000001000100011
F_2 Indo-Malaysia	000000100000111

[a]Indo-Malaysia is listed once for species 6 (F_1) and once for species 7 (F_2).

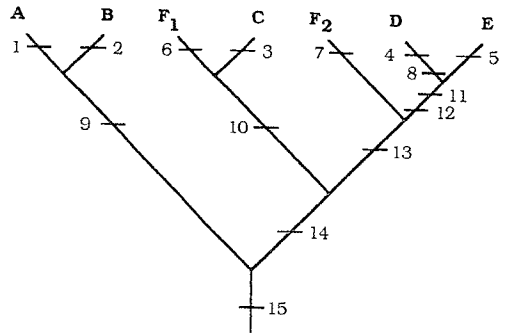

Fig. 7.8. Area cladogram based on phylogenetic relationships of eight species of amphilinid flatworms, listing Indo-Malaysia (*F*) as two separate areas. *A* = Eurasia; *B* = North America; *C* = Australia; *D* = South America; *E* = Africa.

perform a phylogenetic analysis using this new matrix, we obtain the area cladogram depicted in figure 7.8.

We now find areas F_1 and F_2 in different parts of the geographic cladogram, with F_1 connected to area C (Australia) and F_2 associated with areas D (South America) and E (Africa). The placement of F_2 is in accordance with the patterns of continental drift, but the placement of F_1 is not. The "misplacement" of area F_1, according to the original area cladogram based on geological evidence (fig. 7.2), strengthens our hypothesis that ancestor 10 did some dispersing (from Australia into Indo-Malaysia). The separation of F_1 and F_2 strengthens our suspicions that they are not the same areas historically, and this conclusion is reinforced by the observations that F_1 encompasses estuarine Indo-Malaysian habitats, while F_2 represents freshwater, nuclear Indian subcontinent habitat.

Special Applications

More than one member of the clade in the same area

The preceding example highlights some of the analytical problems that can occur when the patterns of species distribution include incidents of colonization. In the case of the amphilinids, this movement resulted in more than one member of the group occurring in the "same" area. When this happens, the binary code for the area is a composite of the codes from all the taxa in that area. For example, the codes for taxa 6 and 7 were combined to give a composite binary code for area F, while the codes for taxa 4 and 8 were combined to give a composite binary code for area D. This procedure is called "inclusive ORing" (Cressey, Collette, and Russo 1983). In this example, the patterns of dispersal did not override the historical patterns in the analysis, so

the resulting area cladogram coincided with the geological history of the areas. The dispersal episode appeared as a homoplasy, and the two speciation events within one area (producing species 4 and 8) appeared as an autapomorphy for the area. The ambiguity resulting from the occurrence of species 6 and 7 in Indo-Malaysia was resolved by assuming that "Indo-Malaysia" for species 6 was different from "Indo-Malaysia" for species 7. No ambiguity resulted from the "extra" speciation event in South America.

Dispersal in the Amphilinidea and the subsequent problems generated for researchers (although presumably not for the flatworms) demonstrated one kind of ambiguity that can arise from this procedure, and one way in which the source of the ambiguity could be discovered. A more serious analytical problem resulting from using the inclusive-ORing method can arise *when a large enough number of relatively derived taxa disperse into relatively primitive areas.*

1. Figure 7.9 depicts an area cladogram for hypothetical areas A–D based on geological evidence.

2. Figure 7.10 depicts the phylogenetic tree for hypothetical species 1–6, based on, say, morphological characters.

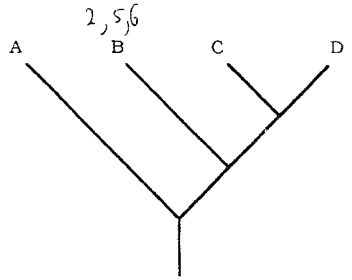

Fig. 7.9. Area cladogram for hypothetical areas A–D.

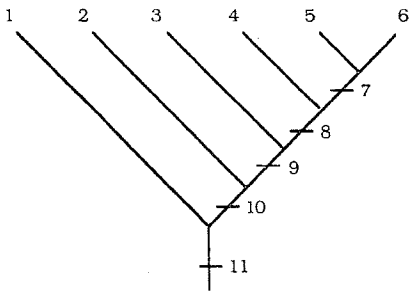

Fig. 7.10. Phylogenetic tree for hypothetical species 1–6, with internal branches numbered for cospeciation analysis.

Table 7.6 Matrix listing the geographic distribution of hypothetical species 1–6 among hypothetical areas A–D, along with the binary codes representing the phylogenetic relationships among species 1–6.

Area	Taxon	Binary Code
A	1	10000000001
B	2, 5, 6	01001111111
C	3	00100000111
D	4	00010001111

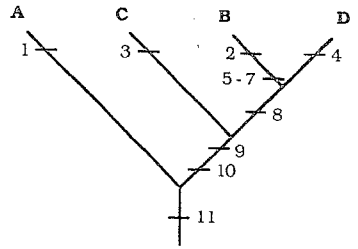

Fig. 7.11. Area cladogram for hypothetical areas A–D, based on phylogenetic relationships of hypothetical species 1–6.

3. The matrix depicting the geographic distributions of species 1–6 among areas A–D is shown in table 7.6.

4. The new area cladogram constructed from the binary codes is shown in figure 7.11. This cladogram has a consistency index of 100%; however, the positions of areas B and C are reversed. So, although we have perfect congruence between the relationships among the taxa and the **new** area cladogram, the new cladogram is not congruent with the area cladogram based on the geological history of the areas (fig. 7.9). This occurs because area B contains two highly derived members of the clade, species 5 and 6; therefore, area B is assigned a highly derived status when taxon codes are combined.

Since three species currently occur in area B, we will redo the analysis, treating area B as three areas, B_1 for taxon 2, B_2 for taxon 5, and B_3 for taxon 6.

1. This treatment produces a new data matrix (table 7.7).

2. Phylogenetic analysis of the new data matrix produces the area cladogram depicted in figure 7.12. According to the historical geological associations of the areas, B_1 is in the correct location on the new area cladogram, while areas B_2 and B_3 are misplaced. This leads us to hypothesize that the relatively derived taxa 5 and 6 are currently found in area B because their ancestor (species 7), which links areas B_2 and B_3, dispersed from area D into area B and subsequently speciated, producing species 5 and 6.

Table 7.7 Matrix listing the geographic distribution of hypothetical species 1–6 among hypothetical areas A–D, along with the binary codes representing the phylogenetic relationships among species 1–6.

Area[a]	Taxon	Binary Code
A	1	10000000001
B_1	2	01000000011
C	3	00100000111
D	4	00010001111
B_2	5	00001011111
B_3	6	00000111111

Note: [a]Area B is listed as three separate areas, one each for species 2, 5, and 6.

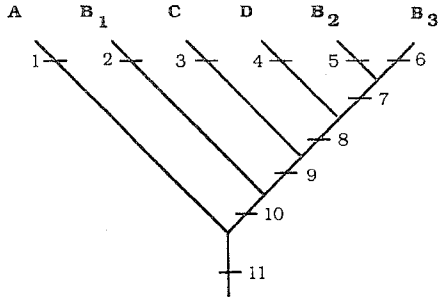

Fig. 7.12. Area cladogram for hypothetical areas A–D, based on phylogenetic relationships of hypothetical species 1–6 and treating area B as if it were three separate areas historically.

"Widespread taxa"

We now turn to the ambiguity that may result from the occurrence of a widespread taxon in the data set. *Species that occur in more than one of the areas being studied may occur there because they have dispersed from their area of origin into the other areas, or because they have failed to speciate in response to vicariance events.* Phylogenetic analysis will tend to treat widespread taxa as if their presence is plesiomorphic for all the areas inhabited. This may produce two types of ambiguity, relationships supported by the area cladogram that are inconsistent with the original estimates of phylogeny used as characters, and postulates of secondary loss (extinction) of the widespread taxon if it does not occur in all of the areas that are linked historically.

1. Figure 7.13 depicts our geologically based area cladogram for hypothetical areas A–D.

2. Figure 7.14 depicts a phylogenetic tree for hypothetical species 1–4 (not to be confused with hypothetical species 1–6 from the previous example).

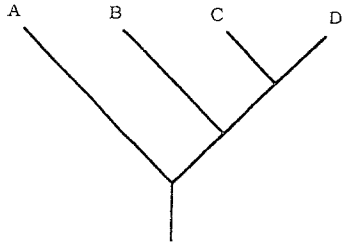

Fig. 7.13. Area cladogram for hypothetical areas A–D.

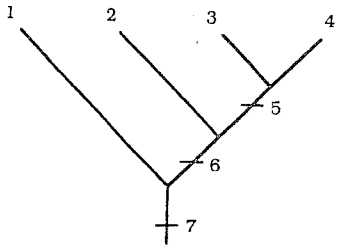

Fig. 7.14. Phylogenetic tree for hypothetical species 1–4, with internal branches numbered for cospeciation analysis.

Table 7.8 Matrix listing the geographic distribution of hypothetical species 1–4 among hypothetical areas A–D, along with the binary codes representing the phylogenetic relationships among species 1–4.

Area	Taxon	Binary Code
A	1	1000001
B	1, 2	1100011
C	1, 3	1010111
D	4	0001111

3. Table 7.8 lists the data matrix for the areas and the species (plus the codes for their phylogenetic relationships) that inhabit them.

4. Phylogenetic analysis of this data matrix produces the area cladogram depicted in figure 7.15. In this instance, the area cladogram derived from biological data is congruent with the area cladogram derived from geological data (fig. 7.13). Nevertheless, something is still amiss, because interpreting the absence of species 1 in area D as a reversal, or extinction event, in that area requires placing species 1 in a position ancestral to species 2, 3, and 4. This conflicts with the phylogenetic tree for the clade, which places species 1 as the sister group to the remaining taxa (fig. 7.14). Hence, while the most

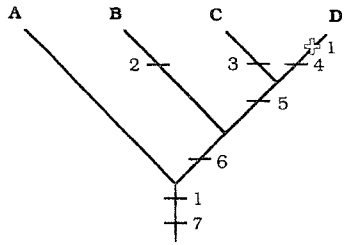

Fig. 7.15. Area cladogram for hypothetical areas A–D, based on phylogenetic relationships of hypothetical species 1–4. *Cross* = putative extinction of species 1 in area D.

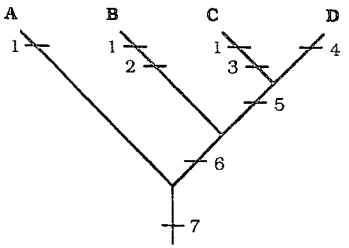

Fig. 7.16. Area cladogram for hypothetical areas A–D, based on phylogenetic relationships among hypothetical species 1–4 and using an optimization rule that allows no reversals. In this case, species 1 is hypothesized to have colonized areas B and C subsequent to its origin in area A.

parsimonious interpretation based on the occurrence of species in particular areas supports the postulate of extinction in area D, other evidence rules against it.

There are at least two general strategies available for dealing with this problem. The first is to perform a phylogenetic analysis using an optimization rule that allows no reversals. For the preceding example, this produces an area cladogram showing two episodes of colonization by taxon 1 (fig. 7.16). However, there might be cases in which extinction is a better explanation than colonization, so this option should be invoked with great care. This leads us to the second general strategy: expand the scope of a biogeographic study to include more than one group of species at a time.

Multiple groups and "missing taxa"

The composition of species within particular biotas is not always similar among biotas. For example, species may be present in some areas and not in others because of different rates or degrees of dispersal. We have discussed methodological protocols for distinguishing species that have been *added to*

(dispersed into) an area from those that have evolved in situ. There are a number of reasons why certain clades might be *absent from* an area. In many cases, especially in the tropics, the observation of absence is simply an artifact of inadequate sampling. However, suppose we have sampled an area thoroughly and still can find no evidence of the species in question. The question now becomes, Are we dealing with a primitive absence of the species in this area or a secondary loss (extinction)? To answer this, we must examine more than one clade. Fortunately, the methods applied in a single clade analysis can be used to compare the degree of congruence between geographical history and phylogeny for more than one group at a time. In general, nothing will change: we will continue to treat areas as taxa and the phylogenetic tree for each clade as a separate transformation series, then perform a multicharacter phylogenetic analysis. Consider the hypothetical example of two clades inhabiting the same areas.

1. Figure 7.17 is the area cladogram based on geological evidence.
2. Table 7.9 lists the occurrence of species representing two hypothetical clades in the five areas.
3. Figure 7.18 depicts the phylogenetic trees for the clades containing the species 1–5 and species 10–14, with internal branches numbered for cospeciation analysis.

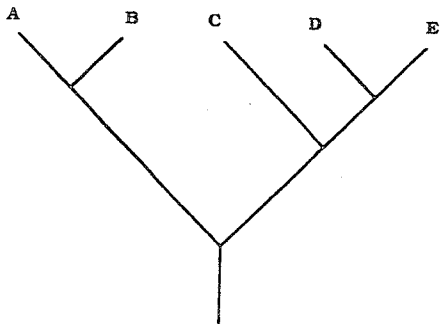

Fig. 7.17. Area cladogram for hypothetical areas A–E, based on geological evidence.

Table 7.9 Occurrence of species representing two hypothetical clades (1–5 and 10–14) in five hypothetical areas.

Area	Taxon 1	Taxon 2
A	1	10
B	2	11
C	3	12
D	4	13
E	5	14

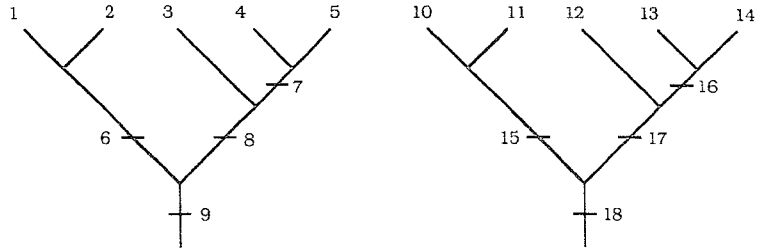

Fig. 7.18. Phylogenetic trees for the clades containing species 1–5 and species 10–14, with internal branches numbered for cospeciation analysis.

Table 7.10 Matrix listing binary codes for members of clades 1–5 and 10–14 inhabiting areas A–E.

Area	Binary Codes
A	1000010011000001001
B	0100010010100001001
C	0010000110010000011
D	0001001110001001111
E	0000101110000101111

4. Table 7.10 lists the binary codes for members of each clade for each area.
5. Figure 7.19 portrays the area cladogram that results from phylogenetic analysis of this data matrix.

In this hypothetical example, the consistency index for the area cladogram based on the covarying phylogenies of two different clades is 100%. The new area cladogram, in turn, is congruent with the geological history of the areas (fig. 7.17). Therefore, the evolutionary history of the clades represents an example of two co-occurring groups that have speciated in response to the same episodes of geological disruption of gene flow (allopatric speciation mode I). In the next example, two groups of species are not equally represented throughout the areas under investigation. Specifically, the members of one clade occur in five areas (A–E) and the members of the other clade occur in only four areas (A–D).

1. Figure 7.20 depicts the phylogenetic trees for the clades containing species 1–5 and species 10–13.
2. Table 7.11 lists the binary codes for the members of clades 1–5 and 10–13 in each area.
3. Two equally parsimonious area cladograms are produced based on phylogenetic analysis of the data matrix. One of these (fig. 7.21a) is congruent

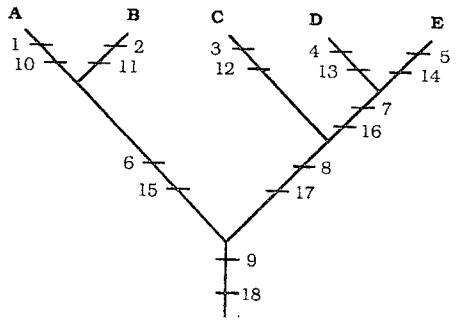

Fig. 7.19. Area cladogram for hypothetical areas A–E, based on phylogenetic relationships of species representing clades 1–5 and 10–14.

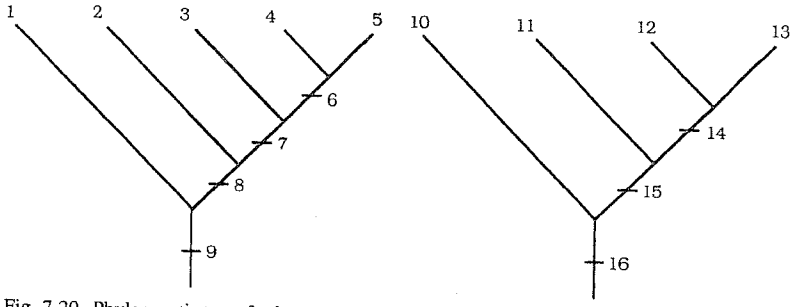

Fig. 7.20. Phylogenetic trees for hypothetical clades 1–5 and 10–13, with internal branches numbered for cospeciation analysis.

Table 7.11 Matrix listing hypothetical areas, the species that inhabit them, and the binary codes representing those species and their phylogenetic relationships.

Area	Taxon	Binary Code
A	1, 10	1000000011000001
B	2, 11	0100000110100011
C	3, 12	0010001110010111
D	4, 13	0001011110001111
E	5	0000111110000000

with the historical relationships among the areas, while the other (fig. 7.21b) places area E at the base of the cladogram rather than with area D. The reversals in characters 14–16 on the first area cladogram implies that clade 10–13 went extinct in area E. In contrast, the second area cladogram postulates three cases of parallel dispersal by ancestral taxa 8, 7, and 6, the latter producing species 5 in area E.

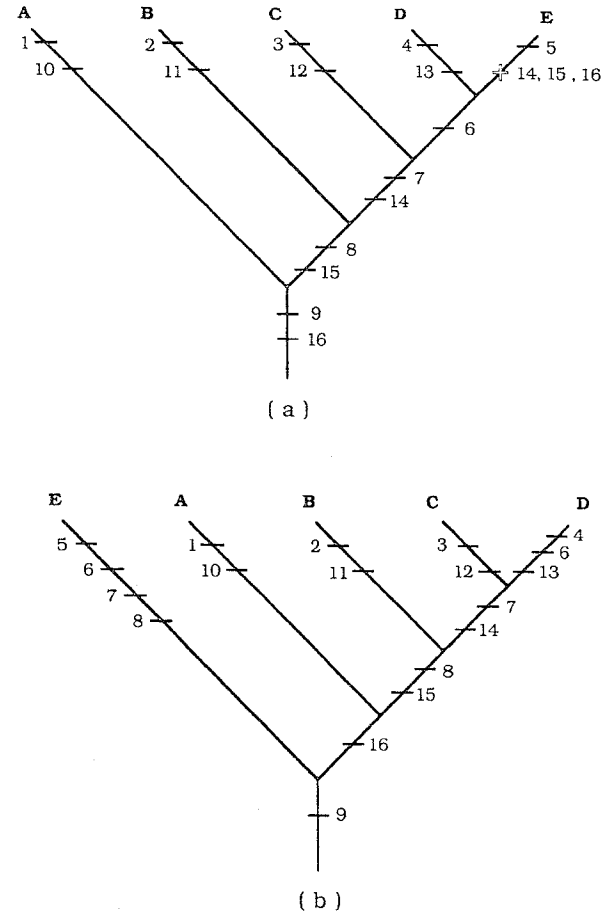

Fig. 7.21. Two equally parsimonious area cladograms based on phylogenetic relationships of members of clades 1–5 and 10–13.

Secondary loss (extinction) appears as a series of reversals in a phylogenetic analysis because taxa that are absent in an area are coded with a zero, which is equivalent to saying that they were primitively absent from the area. Wiley (1988a,b) suggested that absent taxa should be treated as missing data for the relevant area (fortunately, the newest computer programs for phylogenetic analysis have such an option). So, let us reanalyze the preceding example coding missing taxa with a question mark (?).

1. Table. 7.12 is the matrix produced by coding absent taxa as question marks.

Table 7.12 Matrix listing hypothetical areas, the species that inhabit them, and the binary codes representing those species and their phylogenetic relationships.

Area	Taxon	Binary Code[a]
A	1, 10	1000000011000001
B	2, 11	0100000110100011
C	3, 12	0010001110010111
D	4, 13	0001011110001111
E	5	0000111117777777

[a]? = taxa missing from an area.

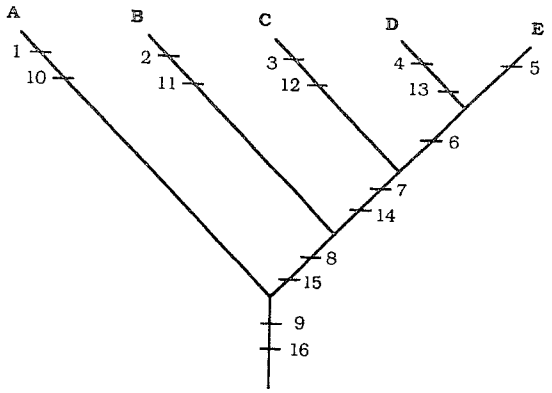

Fig. 7.22. Area cladogram for hypothetical areas A–E, based on phylogenetic analysis of clades 1–5 and 10–13 using "missing data" coding option (note absence of notation for clade 10–13 on branch connecting area E to the rest of the area cladogram).

2. Only one area cladogram, congruent with figure 7.21a, is produced by a phylogenetic analysis of this new data matrix (fig. 7.22). In this case, the absence of clade 10–13 from area E is not considered informative in constructing the area cladogram (i.e., relationships cannot be reconstructed from question marks, or *it is dangerous to group on the basis of character absence*). Note that there is no hypothesis concerning either the presence or absence of taxon 10–13 in area E. This is an important point to remember because some explanation must be offered a posteriori. For example, we might propose either that no members of taxon 10–13 ever inhabited area E or that some member of the clade reached it and then became extinct. The first proposal, in turn, implies that species 5 occurs in area E because of some form of allopatric speciation involving dispersal (allopatric speciation mode II). In the second case we would be postulating that species 5 occurs in area E because of vicariant speciation (allopatric speciation mode I).

A special case of this situation results in the creation of "pseudomissing taxa." Specifically, if you are working with multiple clades, one of which has two or more members occurring in the same area, duplicating the areas containing more than one clade member in the manner discussed above will produce areas with missing taxa. So, given that you now have multiple new areas, in which ones do you allocate the clades that have only single representatives in the area? The answer is straightforward: place them in the areas that contain other species with which they show historical congruence. *This is equivalent to invoking Hennig's auxiliary principle: assume homology unless forced by other data to abandon the assumption* (see chapter 2). *Note that if there is any biogeographic congruence among clades, it is necessary to invoke this assumption in order to find the congruence. Conversely, if there is no congruence, use of the principle will not force spurious congruence to result.* The next example demonstrates how this is done.

1. Figure 7.23 depicts the geographic distributions of the members of two clades (1–6 and 12–18) in six areas (A–F). Areas A, B, D, E, and F contain one member of each clade, while area C contains one member of clade 1–6 (species 3) and two members of clade 12–18 (species 14 and 18).

2. Table 7.13 is the binary data matrix, using inclusive ORing, for the areas.

3. Phylogenetic analysis of the data matrix produced one area cladogram

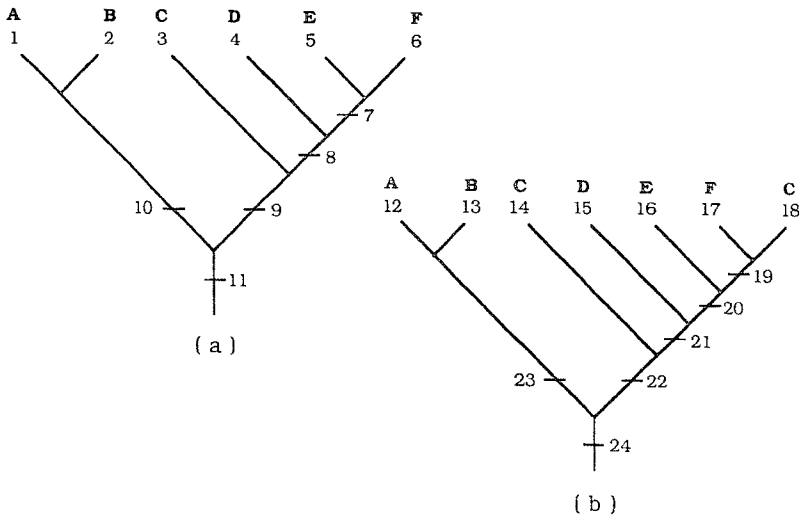

Fig. 7.23. Phylogenetic trees for members of two clades (1–6 and 12–18), with internal branches numbered for cospeciation analysis and with geographic distributions (in areas A–F) listed above species numbers.

Table 7.13 Matrix listing hypothetical areas, the species that inhabit them, and the binary codes representing those species and their phylogenetic relationships.

Area	Taxon	Binary Code		
A	1, 12	1000000001	1100000000	0011
B	2, 13	0100000001	1010000000	0011
C	3, 14, 18	0010000010	1001000111	1101
D	4, 15	0001000110	1000100000	1101
E	5, 16	0000101110	1000010001	1101
F	6, 17	0000011110	1000001011	1101

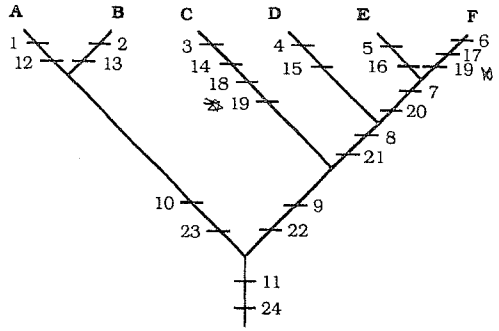

Fig. 7.24. Area cladogram for six hypothetical areas, based on phylogenetic relationships of two clades (1–6 and 12–18). Note that taxon 19 (ancestor of species 17 and 18) occurs twice, once in area F and once in area C.

with a consistency index of 96% (fig. 7.24). Note that taxon 19, the ancestor of species 17 and 18, occurs twice, and that area C has two representatives of clade 12–18 (species 14 and 18).

4. As a consequence of the dual occurrence of clade 12–18 in area C, we recode, listing area C twice, C_1 for species 14 and C_2 for species 18. However, should we put the codes for species 3 with area C_1 or with area C_2? In this case, we place species 3 with species 14 in the same area (C_1) because those two species are phylogenetically congruent with respect to their geographic distributions. Species 18 (more accurately, its ancestor 19) is associated with the incongruent portions of the area cladogram, so we place species 18 in an area by itself (C_2) and list "missing taxa" codes for clade 1–6 in area C_2. In this case, the "missing taxa" are created by our splitting area C into two different areas. Table 7.14 is the binary matrix reflecting this recoding.

5. Phylogenetic analysis of this data matrix produces one area cladogram with a consistency index of 100% (fig. 7.25).

6. Note that we still must provide an a posteriori explanation for the fact

Table 7.14 Matrix listing hypothetical areas, the species that inhabit them, and the binary codes representing those species and their phylogenetic relationships.

Area[a]	Taxon	Binary Code[b]		
A	1, 12	1000000001	1100000000	0011
B	2, 13	0100000001	1010000000	0011
C_1	3, 14	0010000010	1001000000	0101
C_2	18	??????????	?000000111	1101
D	4, 15	0001000110	1000100000	1101
E	5, 16	0000101110	1000010001	1101
F	6, 17	0000011110	1000001011	1101

[a]Area C is split in two.
[b]? = taxa missing from an area.

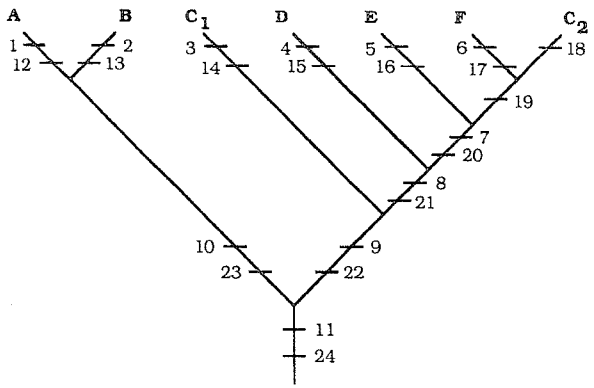

Fig. 7.25. Area cladogram for six hypothetical areas, based on phylogenetic relationships of two clades (1–6 and 12–18), with area C coded as two different areas. Note absence of clade 1–6 from area C_2.

that area C_2 has no representative of clade 1–6. There are two general possibilities; first, that species 18 results from an episode of allopatric speciation mode II in which clade 1–6 did not participate, and second, that there was once a member of clade 1–6 (which would have been the sister species of 6) in area C_2, which has become extinct. If the secondary extinction hypothesis is correct, we may be dealing with allopatric speciation mode I or mode II (refer to chapter 4 for what to do in such cases).

Case Studies

North American freshwater fishes: pre- or post-Pleistocene origins?

Our first example involves the North American freshwater fish fauna. This fauna, containing many localized (endemic) species, is extremely diverse.

their parasites) arrived in neotropical freshwater habitats no later than the mid-Miocene, we must reevaluate our ideas about the source of those marine ancestors. The geography of South America prior to the mid-Miocene differed in three significant ways from what we see today: Africa and South America were joined (i.e., there was no Atlantic Ocean at the mouth of the Amazon), the Andes began sweeping upwards from the south in the early Cretaceous and moving northward, and the Amazon River flowed into the Pacific Ocean until the mid-Miocene, when it was blocked by Andean orogeny, becoming an inland sea and eventually opening to the Atlantic Ocean. *This leads us to the startling conclusion that if potamotrygonids are a relatively old component of neotropical freshwater diversity east of the Andes,* ***they must have come from the Pacific Ocean, which is west of the Andes!***

Now if we enlarge the spatial scale of this study to include the geographic distribution of the marine relatives of the parasites inhabiting potamotrygonids, we find additional support for the hypothesis that these stingrays and their parasites originated from marine ancestors that were isolated in South America from the Pacific Ocean by the Andean orogeny. The closest relatives of the parasites inhabiting potamotrygonids occur in Pacific marine stingrays (fig. 7.36). A similar origin has been suggested for Amazonian freshwater anchovies (Nelson 1984) and possibly for neotropical freshwater needlefish (Collette 1982). In addition, each of the parasite species inhabiting potamotrygonids requires a mollusc or arthropod intermediate host, so it seems likely that mollusc and arthropod species derived from marine ancestors also moved into neotropical freshwater habitats along with the ancestor of the potamotrygonids. As a consequence, we now recognize the possibility that *a sizeable component of current neotropical freshwater diversity might be derived from Pacific marine ancestors.*

Overall then, the current data base indicates that potamotrygonids and their parasites (1) are older (no later than mid-Miocene rather than Pliocene), (2) came from a different source (moved into the Amazon River from the Pacific rather than the Atlantic Ocean), and (3) have been affected more strongly by phylogenetic influences (i.e., allopatric speciation mode I) on their diversification and distribution, than previously thought. These findings could not have been achieved without phylogenetic analysis and historical biogeography.

Comments on Historical Biogeographic Studies

Choice of spatial scale greatly influences the type of questions asked and the analytical methods used in ecological biogeography (Brown and Gibson 1984). Advocates of macroecology (Brown and Maurer 1989) have suggested

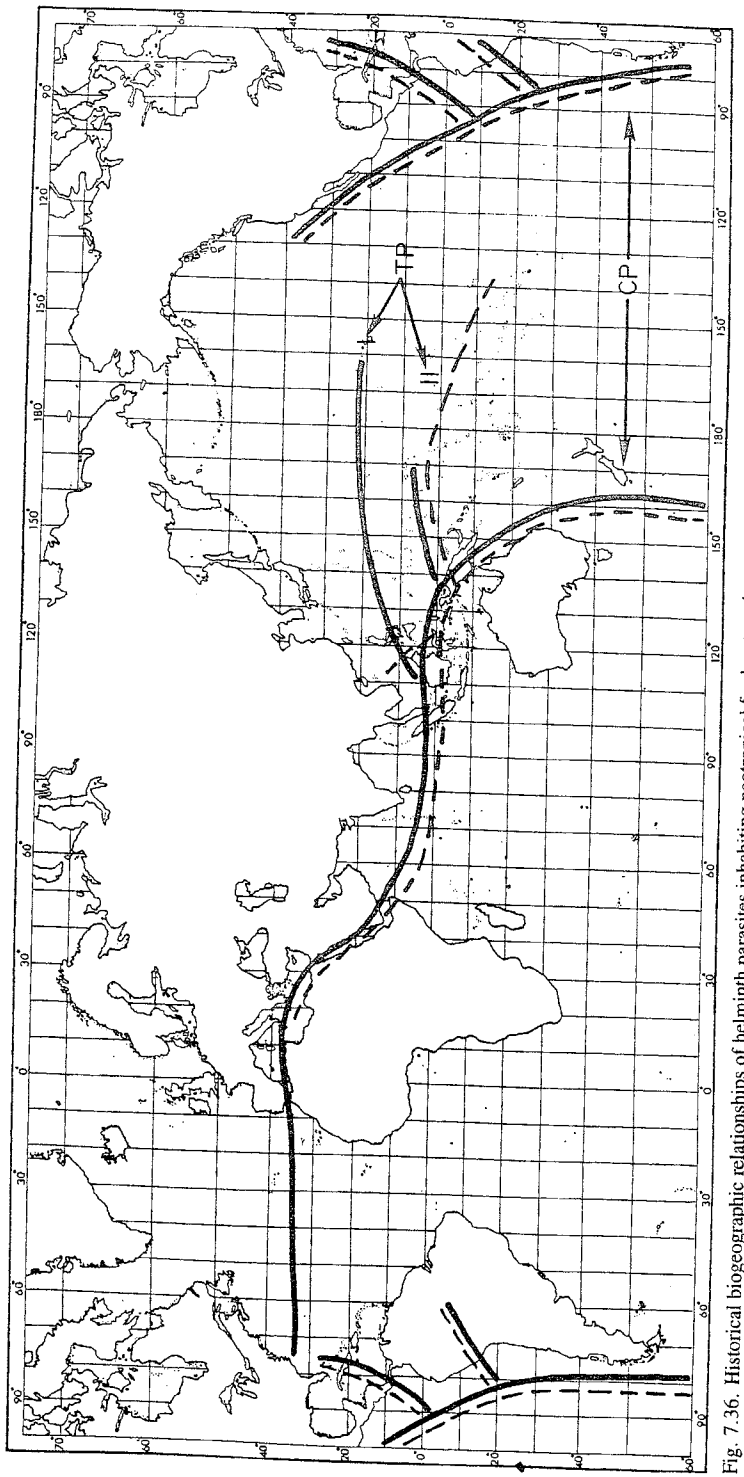

Fig. 7.36. Historical biogeographic relationships of helminth parasites inhabiting neotropical freshwater stingrays and their closest relatives, based on phylogenetic trees for species groups in the tapeworm genera *Acanthobothrium*, *Eutetrarhynchus*, and *Rhinebothrium* (*solid lines*) and in the roundworm genus *Echinocephalus* (*dotted lines*). Note both circum-Pacific and trans-Pacific distribution patterns, with species most closely related to those occurring in freshwater stingrays being part of the circum-Pacific pattern. (Redrawn and modified from Brooks 1988b and from Brooks and Deardorff 1988.)

that researchers studying ecological associations should search for regular patterns of distribution and abundance by expanding the spatial scale of their studies. Brooks (1988b) recently suggested that the degree and form of phylogenetic influence in historical biogeography may also be influenced by the spatial scale chosen. Specifically, the larger the spatial scale chosen for study, (1) the more likely we are to find evidence of replicated allopatric speciation events (allopatric speciation mode I), (2) the greater the phylogenetic effects on the diversity examined, (3) the older the origins of the biotas studied, and (4) the more complicated the historical explanations for the biotic composition. The stingray example illustrates the importance that spatial scale may have on historical biogeographic explanations.

Recent discussions of the literature and methods employed in historical biogeography (Wiley 1988a,b; Cracraft 1988; Noonan 1988) have warned against approaches that eliminate or minimize the effects of any evolutionary process a priori. After all, although "corroboration" and "refutation" are part of the scientific process, the attraction of that process lies beyond hypothesis testing in the realm of discovery. Based on the preceding examples, it is evident that there are historical components in the current distributions of many groups of species. It is also evident that evolutionary independence in terms of dispersal and speciation can be manifested within a single historical sequence of area relationships. Not surprisingly then, the geographical distribution patterns of species and clades have apparently been molded by the evolutionary interactions among a variety of historical and nonhistorical processes. We hope we have demonstrated that the methodology presented herein is sensitive to these diverse influences.

For those of you with a taste for more-complicated examples there are numerous studies available: for example, North and Central American coleopteran insects (Whitehead 1972, 1976; Noonan 1988; Liebherr 1988); neotropical leptodactylid frogs (Lynch 1975); a variety of fish groups to examine Caribbean biogeography (Rosen 1975); fossil and recent gars (Wiley 1976); African caddisflies (Morse 1977); Central American poeciliid fishes (Rosen 1979; see also Zandee and Roos 1987; Funk and Brooks 1990); neotropical microteiid lizards (Presch 1980); the southern beeches (*Nothofagus*: Humphries 1981); cyprinodontiform fishes worldwide (Parenti 1981); fishes, frogs, turtles, birds, insects, plants, and marsupials to examine the relationships of biotas on North America, South America, Europe, Australia, and New Zealand (Patterson 1981); Australian birds (Cracraft 1982a, 1983a, 1986); elements of the Central American herpetofauna (Savage 1982); neotropical gymnopthalmid lizards (Hillis 1985); xantusiid lizards (Crother, Miyamoto, and Presch 1986); Indo-Pacific cicadoid insects (Duffels 1986); the high Andean herpetofauna (Lynch 1986); members of *Eucalyptus* (Ladiges and Humphries 1986; Ladiges, Humphries, and Brooker 1987); Indo-Pacific

mirid (Heteroptera) insects (Schuh and Stonedahl 1986); harpacticoid copepods associated with hermit crabs (Ho 1988); some cyprinid fishes from West Africa (Howes and Teugels 1989); lunulate sand dollars (*Mellita* spp.: Harold and Telford 1990). There are also other examples, many cited in Wiley (1988b) and some presented in other parts of this book. This list is by no means exhaustive, but it is a good starting point!

Cospeciation among Ecological Associates: How Did These Particular Species Come to Be Associated with One Another?

In the preceding sections we discussed a variety of methods used to differentiate between historical and nonhistorical components in *the distribution patterns of extant organisms* (cospeciation with respect to geography). In this section we will explore the historical (cospeciation) and nonhistorical (departures from cospeciation) components in *the patterns of ecological associations of organisms*. We will begin with studies based on a variety of different groups, each of which exhibits a different type of ecological association. These examples will highlight two important points: the methods of historical analysis for ecological associations parallel the methods of historical biogeographic analysis (only here we use hosts rather than areas as "taxa"), and these methods are not constrained by particular types of associations. We will then turn our attention to four groups of flatworms parasitizing vertebrates. These examples, drawn from members of the monophyletic subclass called the Cercomeromorphae, are presented to demonstrate that it is possible to assess macroevolutionary patterns of cospeciation among members of large clades.

Sharks and rays with copepods up their noses

Deets (1987) presented a phylogenetic systematic study of a monophyletic group of seven species of copepods that attach themselves with their large, prehensile second antennae to the nasal lamellae of a variety of sharks and stingrays. His study produced a single phylogenetic tree for the genus *Kroeyerina* plus *Prokroyeria meridionalis* (the sister species to *Kroeyerina* + *Kroyeria*), based on ninety-one characters with a consistency index of 92.86% (fig. 7.37).

1. Table 7.20 is the data matrix produced when the binary codes for the parasite species are listed with their associated hosts.
2. Phylogenetic analysis of the hosts based on the phylogenetic tree for the copepod parasites (using the binary codes listed in table 7.20) produces a single host cladogram with a consistency index of 100% (fig. 7.38).

So far everything should look familiar. Instead of using the phylogenetic relationships of organisms to reconstruct the historical relationships of geographical areas (new area cladogram), we are using the phylogenetic relationships of one group of organisms to reconstruct the historical relationships of another group of organisms (new "associate" or "host" cladogram). In this way, we get a picture of the histories of particular ecological associations. However, we are missing a critical piece of information in this example, a phylogenetic tree for the hosts, the equivalent of an area cladogram based on geological evidence. This is an important component of an ecological association study. Although the consistency index for the host cladogram is 100%, the relationships of the hosts indicated by the parasite data do not necessarily reflect the "actual" host phylogeny. The position of the ratfish *Callorhinchus callorhynchus* in figure 7.38 agrees with the hypothesis that chimaeroids are the sister group of the elasmobranchs (sharks and rays). Likewise, *Mobula*,

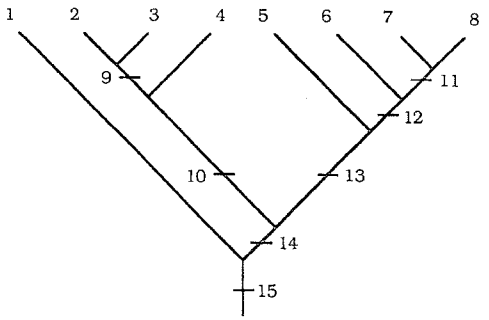

Fig. 7.37. Phylogenetic tree for parasitic copepods *Prokroyeria meridionalis* and seven species of *Kroeyerina*, coded for cospeciation analysis. *1* = *P. meridionalis; 2* = *K. mobulae; 3* = *K. nasuta; 4* = *K. deborahae; 5* = *K. elongata; 6* = *K. scottorum; 7* = *K. cortezensis; 8* = *K. benzorum.*

Table 7.20 Matrix listing chondrichthyan hosts and binary codes for the phylogenetic relationships of the copepods *Prokroyeria meridionalis* and species of *Kroeyerina*.

Host	Parasite	Binary Code
Callorhinchus callorhynchus	1	100000000000001
Mobula japonica	2	010000001100011
Mobula lucasana	2	010000001100011
Dasyatis centroura	3	001000001100011
Rhinobatus productus	4	000100000100011
Prionace glauca	5	000010000000111
Galeocerdo cuvier	5	000010000000111
Sphyrna lewini	6	000001000001111
Sphyrna zygaena	6	000001000001111
Carcharhinus falciformis	7	000000100011111
Isurus oxyrhynchus	8	000000010011111
Alopias vulpinus	8	000000010011111

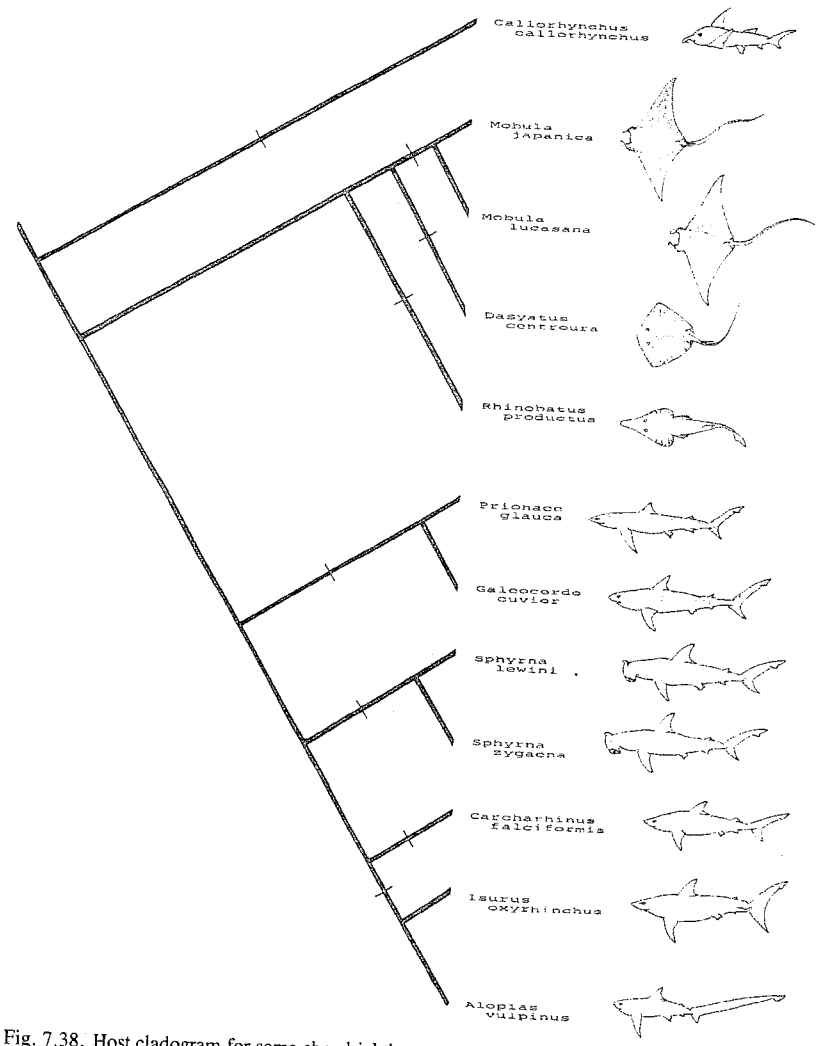

Fig. 7.38. Host cladogram for some chondrichthyan groups, based on phylogenetic relationships of parasitic copepods *Prokroyeria meridionalis* and species of *Kroeyerina*. (From Deets 1987.)

Dasyatis and *Rhinobatus* are "rays," and their relative relationships in figure 7.38 also agree with current estimates of elasmobranch phylogeny. The other hosts are all "lamnoid" (*Prionace, Galeocerdo,* and *Sphyrna*) and "carcharhinoid" (*Carcharhinus, Isurus,* and *Alopias*) sharks. Each of those groups is considered monophyletic on the basis of current taxonomy, but the parasite data support a paraphyletic status for the "lamnoids." In the absence of a

phylogenetic tree for the hosts, or phylogenetic trees for other parasites inhabiting the same elasmobranchs, we are left with some inconclusive portions of this study. Remember, the ultimate goal in cospeciation studies is to delineate the historical and nonhistorical components of biological association and distribution patterns. This can only be accomplished by comparing the new host (area) cladogram with the "actual" historical relationships of the hosts (areas).

Monkeys and mites

O'Connor (1988) presented a phylogenetic systematic analysis of seven species of psoroptid mites (subfamily Cebalginae), whose members inhabit the hair follicles and fur of New World monkeys. His phylogenetic tree for six genera was based on seventeen characters and had a consistency index of 100% (fig. 7.39).

1. Table 7.21 is the data matrix produced when the binary codes for the parasite species are listed with their associated hosts.

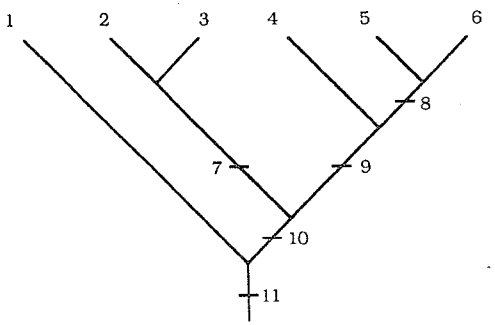

Fig. 7.39. Phylogenetic tree for six genera of cebalgine mites inhabiting New World monkeys, coded for cospeciation analysis. *1 = Procebalges; 2 = Schizopodalges; 3 = Alouattalges; 4 = Cebalgoides; 5 = Cebalges; 6 = Fonsecalges.*

Table 7.21 Matrix listing New World monkeys and binary codes for the phylogenetic relationships of the cebalgine mites.

Host	Mite	Binary Code
Pithecia	1	10000000001
Lagothrix	2	01000010011
Alouatta	3	00100010011
Sanguinus	4	00010000111
Cebus	4, 5	00011001111
Saimiri	6	00000101111
Callithrix	6	00000101111

figure 7.42a as the host cladogram for this cospeciation study. The consistency index is less than 100% (88.9%), due to two postulated cases of host switching, one between *Hylobates* and *Pongo* (hookworm taxon 1: *Oesophagostomum (C.) blanchardi*) and the other between *Hylobates* and *Homo* (pinworm taxon 12, the ubiquitous *Enterobius vermicularis*). It appears, then, that these nematodes ape the phylogeny of their hosts quite closely.

Historical Congruence: "Real" or Fortuitous?

Incongruence between a "host cladogram" (reconstructed from the associate's phylogenetic relationships) and the hosts' phylogenetic tree (reconstructed from host characters) is attributed to colonization events by the associate species. Now, is the reverse situation, congruence between the "host cladogram" and host phylogenetic tree, always an indication of cospeciation? The preliminary answer to this question is no, because, theoretically at least, it is possible that the members of an associate group evolved as a result of sequential host switching that coincidentally mirrored the phylogenetic relationships of the hosts (see chapter 8). In such a case we would find congruence between host and associate phylogenies that was not indicative of a historical association between the groups. This is an important consideration because it clouds the distinction between historical and nonhistorical influences on the evolution of ecological associations. In recent years, there has been some concern on the part of parasite ecologists (e.g., Holmes and Price 1980) that patterns of congruence between host and parasite phylogenies might not always imply cospeciation. Specifically, if we find a situation in which the phylogenetic relationships of a group of parasites are congruent with the relative phylogenetic relationships of their hosts, but the hosts that are actually inhabited represent only a small portion of the members of the host clade(s), how do we know that it is not simply a fortuitous outcome of host switching?

Brooks and Bandoni (1988) proposed a research protocol for distinguishing ecological associations that represent relictual episodes of cospeciation from those that had been assembled by sequences of host switching that fortuitously mirrored host phylogenetic relationships. They proposed that the first step out of the maze is the recognition that the associations are less diverse than expected. This is accomplished by asking two questions: Are the associations depauperate with respect to associations exhibited by sister groups? Is the depauperate group old enough to have achieved a relictual status? Notice that this is simply another application of Mayden's (1985) criteria for studying species diversity within clades (see chapter 4). The methods of historical biogeography are well suited to investigating the second question.

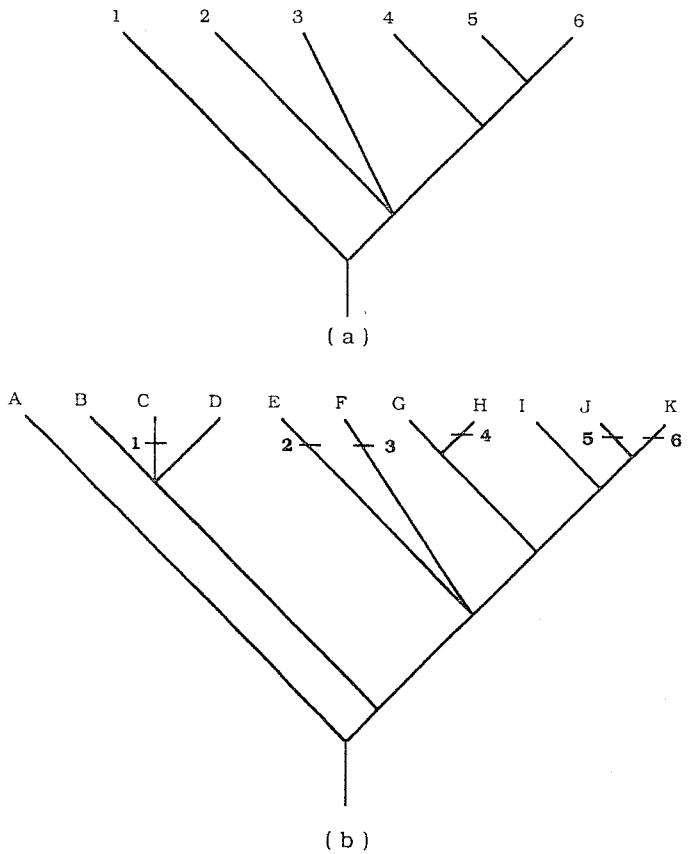

Fig. 7.43. Phylogenetic trees for the digenean family Liolopidae and its vertebrate hosts. (*a*) Liolopid genera: *1* = *Liolope copulans; 2* = *Moreauia; 3* = *L. dollfusi; 4* = *Dracovermis; 5* = *Harmotrema; 6* = *Helicotrema*. (*b*) Eleven major groups of tetrapod vertebrates hosting liolopids: *A* = Sarcopterygii (lungfishes, coelacanths); *B* = Anura (frogs); *C* = Caudata (salamanders); *D* = Gymnophiona (caecilians); *E* = Mammalia (mammals); *F* = Chelonia (turtles); *G* = Aves (birds); *H* = Crocodilia (crocodilians); *I* = Rhynchocephalia (tuatara); *J* = Ophidia (snakes); *K* = Sauria (lizards). *B–D* = Amphibia; *E–K* = Amniota; *F–K* = Reptilomorpha; *G* + *H* = Archosauria; *J* + *K* = Squamata.

Numerical relicts

Let us consider the Liolopidae, a trematode family, comprising fewer than fifteen species allocated to five genera, inhabiting the intestines of a variety of tetrapod vertebrates (fig. 7.43). Mapping the phylogeny of the trematodes onto the phylogeny of the hosts reveals complete congruence between these two markers of evolutionary history, but closer examination of the distribution patterns casts some doubts on our original interpretation. Five of the eleven major groups of tetrapods do not host liolopids, and the vast majority of species within the inhabited tetrapod groups are also not associated with liolopids. It is therefore tempting to explain the phylogenetic "fit" as a coincidence and invoke sequential host switching. However, it is possible that the congruence reflects a long-standing association in which one or more members are relictual groups. Is there a way out of this maze?

The liolopids are much less diverse than their sister group, the strigeoid digeneans (comprising the families Cyathocotylidae + Proterodiplostomatidae + Strigeidae), and exhibit biogeographic patterns coinciding with the breakup of Pangaea (fig. 7.44). Hence, it would appear that the liolopids are a very old and very depauperate group. Biological data support the ancient picture painted by the geographical distribution patterns. Liolopids are generally associated with a wide range of archaic vertebrate hosts, including cryptobranchid salamanders, sideneck turtles, the duck-billed platypus, crocodilians, and iguanid lizards. It appears that all the evidence collected to date implies that they are relicts of some sort. According to Simpson's (1944) definitions (see chapter 4), the liolopids are either **numerical relicts,** the few remaining survivors of a group that was once more diverse, or **phylogenetic relicts,** "living fossil" species that originated a long time ago and have never become very diverse. In chapter 5 we discovered that ecological and behavioral diversification tend to be phylogenetically conservative. Given this, it may be possible to distinguish numerical relictual associations from phylogenetic relictual associations, based on the degree of ecological diversification among the associations. Since liolopids inhabit freshwater, estuarine, and terrestrial hosts, indicating a fair amount of diversification in life cycle characters, we suggest that current associations represent the survivors of a group of associations that were once more diverse; that is, the liolopids are numerical relicts.

Phylogenetic relicts

There are two types of phylogenetic relicts in ecological associations. The first type involves cases in which neither of the associated groups ever became very diverse. The gyrocotylid flatworms are prime candidates for this category. They are ecologically conservative, being restricted as adults entirely to the spiral intestines of chimaeroid fishes, which are themselves phylogenetic relicts. Like their hosts, the gyrocotylids are less species-rich than their sister group (in this case the amphilinideans + the tapeworms). In the second case one of the associates becomes highly diverse while the other does not. For example, the amphilinidean flatworms are much less diverse than their sister group, the true tapeworms, and also exhibit a high degree of ecological uni-

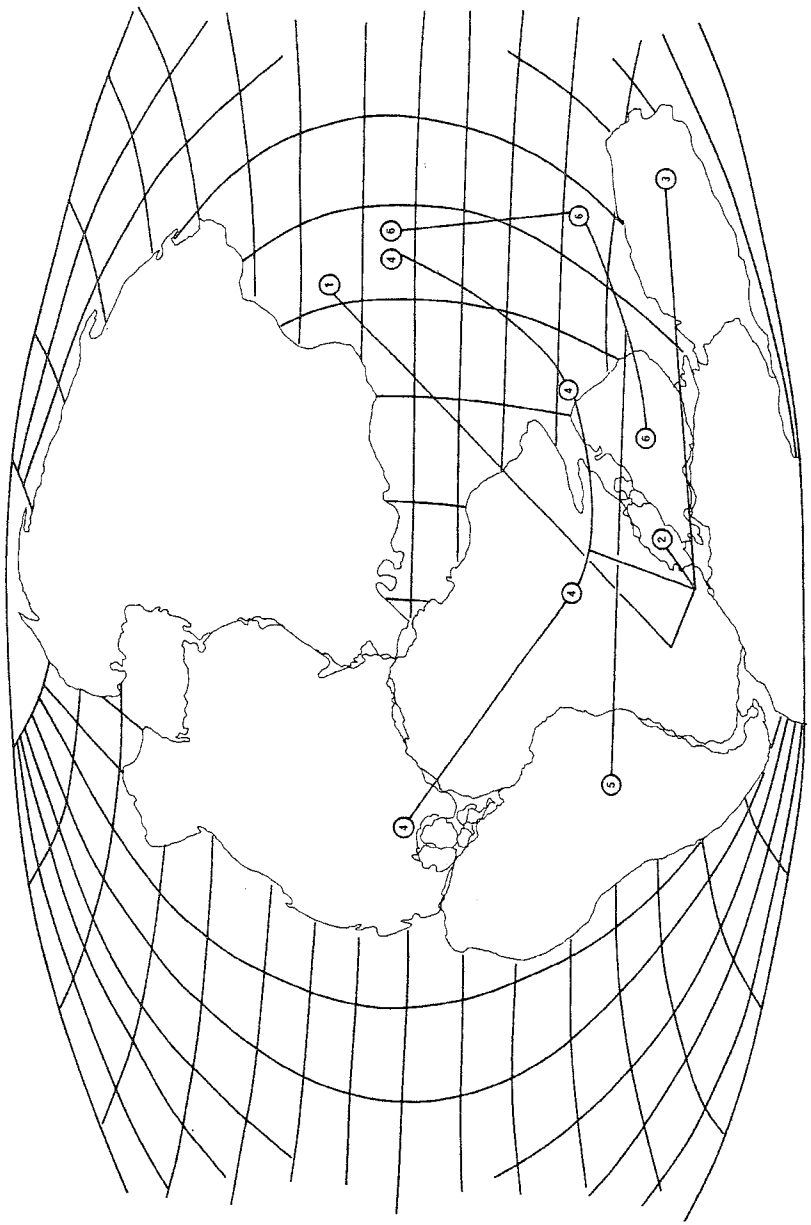

Fig. 7.44. Map depicting continental configurations prior to the breakup of Pangaea beginning in the early Cretaceous, showing distribution of liolopid digeneans connected by their phylogenetic relationships. *1 = Liolope copulans; 2 = Moreauia; 3 = L. dollfusi; 4 = Dracovermis; 5 = Harmotrema; 6 = Helicotrema.* (From Brooks and Bandoni 1988.)

formity. They all occur as adults in the body cavity of their hosts, and six of the eight known species inhabit freshwater ray-finned fishes. We have shown biogeographic evidence of their antiquity (see the beginning of this chapter), and we will show a high degree of congruence between amphilinidean phylogeny and the relative phylogenetic relationships of their hosts (see the next section). Amphilinids differ from gyrocotylids because they do not inhabit hosts that are themselves phylogenetic relicts; therefore, they are an example of a group that failed to become as diverse as the other member of its association.

Spurious congruence due to host switching

Entepherus laminipes is a parasitic copepod species inhabiting the branchial filters of mantid stingrays, including the manta ray (*Manta birostris*), the spinetail mobula (*Mobula japonica*), the *vacatilla* (*Mobula tarapacana*), the smoothtail mobula (*Mobula thurstoni*), and the devilfish (*Mobula hypostoma*) from the Sea of Cortez, as well as *Mobula rochebrunei* from Madagascar. It is the sister species of four other genera: *Leutkenia,* occurring on louvars, epipelagic teleostean fishes of the genus *Luvarus;* and *Philorthagoriscus, Orthagoriscola,* and *Cecrops,* all of which inhabit the ocean sunfish (*Mola mola*).

Phylogenetic systematic analysis (Benz and Deets 1988) of the family Cecropidae, based on forty characters, produced a single phylogenetic tree with a consistency index of 90.9% (fig. 7.45).

1. Table 7.23 is the data matrix produced when the binary codes for the parasite species are listed with their associated hosts.

2. Phylogenetic analysis of the data matrix produced a host cladogram with a consistency index of 100%. The host cladogram (fig. 7.46) depicts the

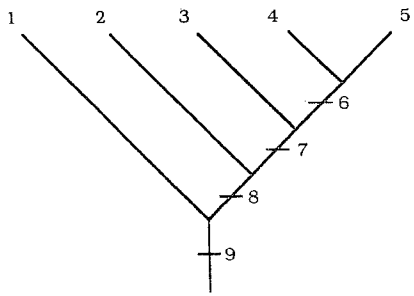

Fig. 7.45. Phylogenetic tree for five genera of parasitic copepods, representing the family Cecropidae, inhabiting mesopelagic fish, with internal branches numbered for cospeciation analysis. *1 = Entepherus; 2 = Luetkenia; 3 = Philorthagoriscus; 4 = Orthagoriscola; 5 = Cecrops.*

Table 7.23 Matrix listing hosts for members of the copepod family Cecropidae and the binary codes indicating the phylogenetic relationships of the parasites.

Hosts	Parasite	Binary Code
Mobula	1	100000001
Luvarus	2	010000011
Mola mola	3, 4, 5	001111111

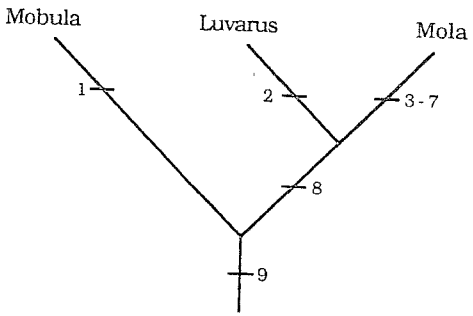

Fig. 7.46. Host cladogram based on phylogenetic relationships of parasitic copepods of the family Cecropidae.

elasmobranch hosts (*Mobula* spp.) as the sister groups of the louvar and the ocean sunfish. This is congruent with the relative phylogenetic relationships of the hosts. However, among the vast numbers of elasmobranchs and teleosts, only these three taxa are known to host these copepods. Additionally, the hosts that are inhabited are epipelagic organisms. This is an independently derived trait within each of the host groups. We believe, therefore, that the current host-parasite associations result from a series of host-switching events.

Do Related Groups Show Similar or Different Proportions of Cospeciation and Host Switching?

Once we have established a solid phylogenetic data base for single-clade associations, we can expand our evolutionary perspective to cospeciation patterns among related groups of organisms. This information will allow us to ask whether members of monophyletic groups within a larger clade have all been influenced to the same degree by the interaction between historical (cospeciation) and nonhistorical (host-switching) factors, or whether each group represents a unique evolutionary outcome of this interaction. Such investigations are already underway for the Cercomeromorphae, the group of parasitic platyhelminths containing the Eucestoda, or true tapeworms; their sister

group the Amphilinidea; the Gyrocotylidea, which is the sister group of the Eucestoda plus Amphilinidea; and the Monogenea, which is the sister group of the other three taxa (Brooks, O'Grady, and Glen 1985b; Brooks 1989a,b; fig. 7.47).

Monogeneans and catfish

The monogeneans are among the smallest, most host-specific, and most diverse groups of parasitic flatworms. They enjoy the dubious distinction of being an extremely well studied parasitic group, not because of their inherent beauty as living organisms, but because of their negative impact on commercial fisheries projects. Monogeneans exhibit direct development and have generation times much shorter than those of their vertebrate hosts; hence, it is possible for a single individual to establish a viable deme, and produce colonizing offspring, while residing on one host. Additionally, these flatworms are easily transferred between hosts; all that is required is that the hosts come into contact with each other from time to time. Based on these life cycle characteristics, then, the evolutionary diversification of this group has traditionally been consigned to the realm of sympatric speciation via widespread host switching.

Members of the genus *Ligictaluridus* (five species) inhabit the gills of a variety of ictalurid catfish hosts in North America. Klassen and Beverly-Burton (1987) presented a phylogenetic systematic analysis of *Ligictaluridus,* based on ten characters, that produced a single tree with a consistency index of 100% (fig. 7.48).

1. Table 7.24 is the data matrix produced when the binary codes for the parasite species are listed with their associated hosts.

2. Phylogenetic analysis of the data matrix produced one host cladogram with a consistency index of 100% (fig. 7.49). The perfect fit of the data to the cladogram is due to the marked host specificity of the parasites. However,

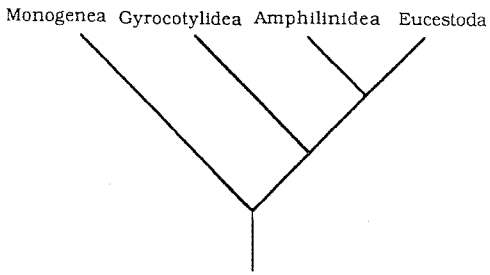

Fig. 7.47. Phylogenetic tree for the four major groups of parasitic flatworms composing the Cercomeromorphae.

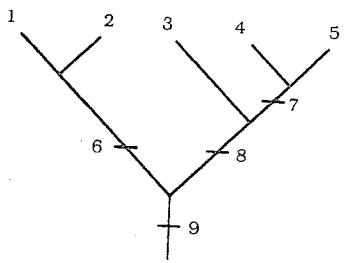

Fig. 7.48. Phylogenetic tree for five species of *Ligictaluridus*, with internal branches numbered for cospeciation analysis. *1 = L. pricei; 2 = L. monticellii; 3 = L. posthon; 4 = L. floridanus; 5 = L. mirabilis.*

Table 7.24 Matrix listing ictalurid catfish hosts (by subgenus) and the binary codes for the phylogenetic relationships of species of the monogenean genus *Ligictaluridus*.

Host	Parasite	Binary Code
Ictalurus (Ameiurus)	1, 2	110001001
Ictalurus (Ictalurus)	4, 5	000110111
Noturus (Noturus)	3	001000011
Noturus (Schilbeodes)	1	100001001

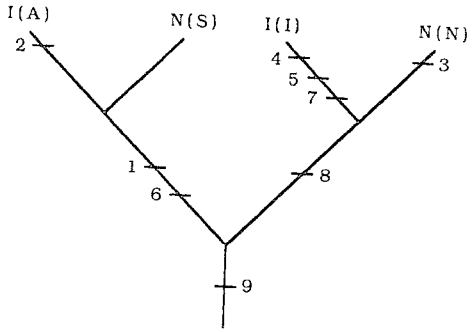

Fig. 7.49. Host cladogram for four subgenera of ictalurid catfish, based on the phylogenetic relationships of five species of the monogenean genus *Ligictaluridus* that parasitize them. *I(I) = Ictalurus (Ictalurus); I(A) = I. (Ameiurus); N(N) = Noturus (Noturus); N(S) = N. (Schilbeodes).*

pronounced host specificity does not guarantee phylogenetic congruence, as evidenced by the fact that the host cladogram mixes *Ictalurus* and *Ameiurus* with *Noturus* and *Schilbeodes* in a way that does not correspond to current hypotheses of relationships.

3. When the parasite phylogeny data are mapped onto either of two phylogenetic hypotheses for the ictalurid taxa (fig. 7.50) the "fit" between the

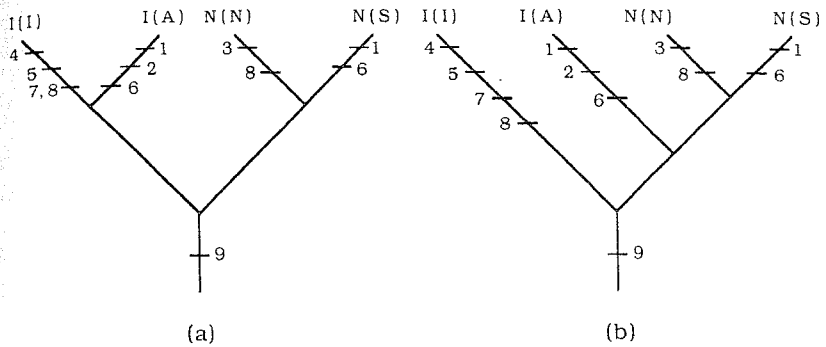

Fig. 7.50. Phylogenetic trees for four ictalurid catfish taxa. *I(I) = Ictalurus (Ictalurus); I(A) = I. (Ameiurus); N(N) = Noturus (Noturus); N(S) = N. (Schilbeodes).* (*a*) Phylogenetic tree redrawn from Taylor 1969. (*b*) Phylogenetic tree redrawn from Lundberg 1970.

parasite data and the host phylogeny is reduced to 75%. A number of host-switching scenarios may be postulated to explain the given host-parasite relationships.

Now, reexamine table 7.24. Notice that the bullheads, *Ameiurus*, and the channel catfish, *Ictalurus*, are associated with more than one species of parasite. This situation is analogous to the problem arising in biogeography when more than one member of the same clade occurs in one area (see table 7.6).

1. So, paralleling the biogeographical resolution to the problem, let us recode *Ictalurus* and *Ameiurus* as separate taxa for each parasite species (table 7.25).

2. Phylogenetic analysis of this matrix produces one tree with a consistency index of 100% (fig. 7.51).

This new host cladogram supports the following explanation. The common ancestor of *Ligictaluridus* (species 9) parasitized the common ancestor of *Ictalurus*. The separation of the two major clades within *Ligictaluridus* is

Table 7.25 Matrix listing ictalurid catfish taxa and the binary codes for the members of the monogenean genus *Ligictaluridus* that inhabit them, with each host group listed separately for each occurrence of a member of the parasite group.

Host	Parasite	Binary Code
Ictalurus (Ameiurus)	1	100001001
Ictalurus (Ameiurus)	2	010001001
Ictalurus (Ictalurus)	4	000100111
Ictalurus (Ictalurus)	5	000010111
Noturus (Noturus)	3	001000011
Noturus (Schilbeodes)	1	100001001

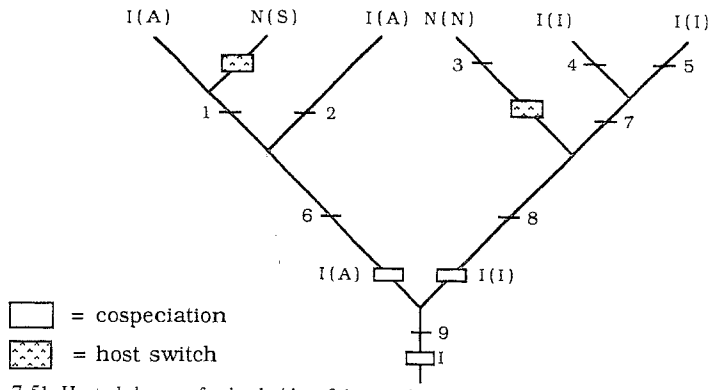

Fig. 7.51. Host cladogram for ictalurid catfish taxa, based on *Ligictaluridus* phylogenetic relationships and listing each host group separately for each occurrence of a member of the parasite group. *I(I) = Ictalurus (Ictalurus); I(A) = I. (Ameiurus); N(N) = Noturus (Noturus); N(S) = N. (Schilbeodes).*

congruent with the divergence of the channel cats and the bullheads from their common ancestor. These associations were maintained through the speciation events producing *L. pricei and L. monticellii* (associated with bullheads) and *L. floridanus and L. mirabilis* (associated with channel cats). The occurrence of *L. pricei* on the madtom *Noturus* (*Schilbeodes*) and of *L. posthon* on the stone catfish *Noturus* (*Noturus*) represent two incidents of host switching. Thus, the majority of the evolutionary divergence of *Ligictaluridus* occurred in association with the ancestral host group. Interestingly, ecological evidence can shed some light on one of the proposed host switches. Both bullheads and madtoms prefer shallow-water, muddy-bottomed, heavily vegetated habitats (Klassen and Beverly-Burton 1987). If these fishes also occur together, then the transfer of *L. pricei* between these unrelated hosts is relatively easy to envision. The transfer of some members of ancestor 8 from a channel cat to a stone cat and subsequent speciation of *L. posthon* in association with a stone cat is more problematical. The fishes do not overlap in their ecological preferences today, stone cats living on the bottom of rapidly flowing deep streams and rivers, while channel cats are members of the pelagic community in rivers and lakes. Further data are required to explain this anomalous example.

Gyrocotylids and ratfish

The gyrocotylideans are a small group of parasitic flatworms, often resembling pieces of sea lettuce, that live as adults only in the spiral intestines of chimaeroid fishes (ratfish). Very little is known of their biology or natural

This example demonstrates another shortcoming of combining species codes when more than one species inhabits the same hosts. This should sound familiar. It is equivalent to the problems encountered when two or more members of the same clade inhabit the same area (see figs. 7.9–7.12).

1. We recode, listing each species separately (table 7.29).

Table 7.29 Matrix listing larid and alcid bird hosts and binary codes for the phylogenetic relationships of species of the tapeworm genus *Alcataenia*.

Host[a]	Parasite	Binary Code
Laridae	1	100000000000001
Laridae	2	010000000000011
Fratercula	3	001000000000011
Cerorhinca	4	000100000000111
Aethia	5	000010000001111
Uria aalge (1)	6	000001000011111
Uria lomvia (1)	6	000001000011111
Uria aalge (2)	7	000000100011111
Uria lomvia (2)	7	000000100011111
Uria aalge (3)	8	000000010111111
Uria lomvia (3)	8	000000010111111
Cepphus carbo	9	000000001111111
Cepphus columba	9	000000001111111
Cepphus grylle	9	000000001111111

[a]Each host is listed separately for each parasite species that inhabits it.

2. Phylogenetic analysis of this new data matrix produces one cladogram, also with a consistency index of 100% (fig. 7.60), which gives us a better picture of the possible history of cospeciation between *Alcataenia* and alcids. Note that despite marked host specificity, there may have been as many as five host-switching events during the evolutionary elaboration of the tapeworm-alcid association. As previously discussed, one or both of the occurrences of the older tapeworm species in the older alcids may be the result of a host switch from larids to alcids (species 3 and 13). If, as Strauch suggested, *Cerorhinca* is the sister group of *Fratercula*, then the presence of *Alcataenia fraterculae* may represent a host switch and subsequent speciation by a population of ancestor 13 in *Cerorhinca*. And finally, the paraphyletic status of *A. armillaris*, *A. longicervica*, and *A. meinertzhageni* is highlighted by the separation of *Uria* into three groups; however, only two of the three associations between *Alcataenia* and *Uria* need be explained by host switching.

Comments on Cospeciation in an Ecological Context

It is evident from the studies presented in this section that historical components can be found in a variety of specialized ecological associations. It is

also evident that considerable evolutionary independence, in terms of host switching, can be manifested within a single historical sequence of host relationships. When ecological associations are examined at the level of the Cercomeromorphae clade, cospeciation and host switching each account for about half of the observed patterns. However, the degree of cospeciation varies considerably among closely related groups within members of this clade, as does the importance of host switching. For example, the influence of history is (1) strong in the association between amphilinids and fish and turtles (two host switches in fifteen speciation events, or 86.7% cospeciation); (2) strong in the association between monogeneans and catfish (two host switches in nine speciation events, 77.8% cospeciation); (3) moderate in the association between *Alcataenia* tapeworms and alcid birds (five host switches in fifteen speciation events, 66% cospeciation); and (4) weak in the association between gyrocotylids and ratfish (about 50% cospeciation). The picture is even more complicated when we examine the taeniids, highly host-specific tapeworms that inhabit a variety of carnivores, including mustelids, canids, and felids. A phylogenetic systematic analysis of fifteen taeniid species reported virtually no congruence between host and parasite phylogenies (Moore and Brooks 1987). This study was based on nineteen characters and produced

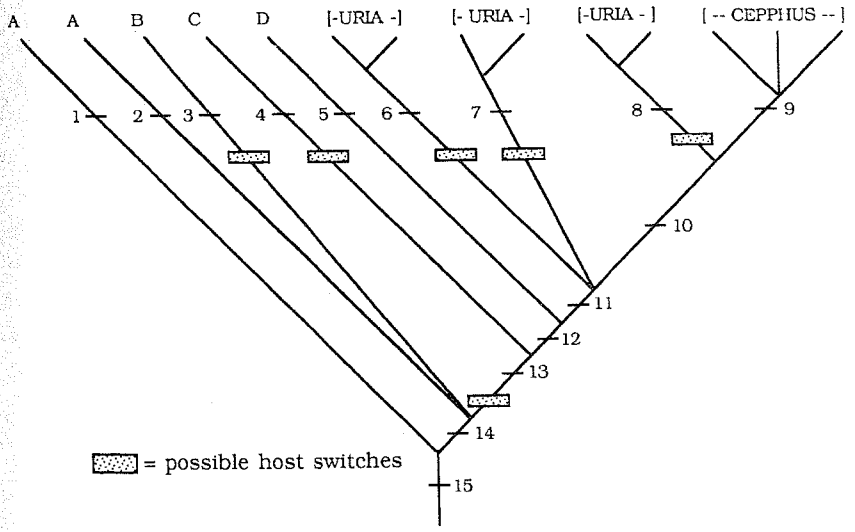

Fig. 7.60. Host cladogram for larid and alcid birds, based on phylogenetic relationships of members of the tapeworm genus *Alcataenia*, with each host group listed separately for each species of *Alcataenia* that inhabits it. Birds: *A* = Laridae; *B* = *Fratercula*; *C* = *Cerorhinca*; *D* = *Aethia*. Tapeworms: *1* = *Alcataenia larina pacifica*; *2* = *A. l. larina*; *3* = *A. fraterculae*; *4* = *A. cerorhincae*; *5* = *A. pygmaeus*; *6* = *A. armillaris*; *7* = *A. longicervica*; *8* = *A. meinertzhageni*; *9* = *A. campylacantha*.

four different trees, each with a consistency index of 38%. However, because of the paucity of characters and the ambiguity of the results (multiple trees with a low consistency index), we are not particularly confident that the results represent a robust phylogenetic hypothesis for the group. In addition, the fifteen species analyzed represent only a fraction of all the taeniids. Therefore, we are not certain how much of the disagreement between host and parasite phylogenies is due to rampant host switching and how much is due to a poorly resolved parasite phylogeny.

Interestingly, the relative contributions of cospeciation and host switching also show considerable variation within groups. As discussed above, the associations between monogeneans in the genus *Ligictaluridus* and their catfish hosts are tightly constrained by history. Boeger and Kritsky (1989) discovered a different pattern in their investigations of the twelve monogenean genera making up the family Hexabothriidae whose members inhabit ratfish, sharks, and rays. They used ninety-two characters to produce a single phylogenetic tree with a consistency index of 81.2%. They then compared the fit of the parasite phylogeny with three phylogenetic hypotheses of elasmobranch relationships discussed by Compagno (1977). The fit of the hexabothriid genera to the various host phylogenies ranged from 32.7 to 45.7%, suggesting widespread host switching among ancestral groups. Klassen and Beverly-Burton (1988) examined the phylogenetic relationships of yet another group of monogeneans, with the imposing description "ancyrocephalids with articulating haptoral bars," inhabiting the gills of the centrarchid fishes *Micropterus* (basses) and *Lepomis* (sunfishes). The phylogenetic relationships of parasite species inhabiting basses and those of the hosts were virtually identical, whereas there was no discernible phylogenetic association between sunfish species and their monogeneans. Klassen and Beverly-Burton discussed the widespread hybridization that occurs among species of *Lepomis*, in contrast to *Micropterus*, and suggested that this facilitated the numerous host transfers that apparently occurred during the evolutionary diversification of these parasites. This may be a prime example of extensive diversification in a group resulting from repeated sympatric speciation by means of host switching.

We began this section by asking whether members of monophyletic groups within a larger clade have all been influenced to the same degree by the interaction between historical (cospeciation) and nonhistorical (host-switching) factors, or whether each group represents a unique evolutionary outcome of this interaction. The data at hand support the latter explanation; however, until we have a larger and more comprehensive data base, we cannot draw any generalizations about the relative importance of historical and nonhistorical influences on the evolution of close ecological associations. At the moment, there are very few detailed studies of large groups once we move outside the parasitic flatworms and arthropods, and even there the coverage is pretty thin.

Brooks (1988a) recently reviewed the literature and methods employed in past studies comparing host and parasite phylogenies. For those who wish to pursue this research program further, other studies are listed in table 7.30.

Table 7.30 Studies of cospeciation in an ecological context, using phylogenetic systematics listed by associate group, with host groups and references following.

Protists

Coccidians in cricetid rodents (Reduker, Duszynski, and Yates 1987)

Helminths

Platyhelminths: Digeneans in vertebrates (Brooks 1979a; Brooks and Macdonald 1986); tetrapods (Brooks and Overstreet 1978); anurans (Brooks 1977); crocodilians (Brooks 1980b, 1981); North American freshwater turtles (Platt 1988; Macdonald and Brooks 1989). **Aspidobothreans** in vertebrates (Brooks, Bandoni, Macdonald, and O'Grady 1989). **Monogenea** on elasmobranchs (Boeger and Kritsky 1989); North American catfish (Klassen and Beverly-Burton 1987); North American centrarchid fishes (Klassen and Beverly-Burton 1988). **Gyrocotylidea** in chimaeroid fishes (Bandoni and Brooks 1987a). **Amphilinidea** in vertebrates (Bandoni and Brooks 1987b). **Eucestoda** in tetrapods (Brooks 1978); neotropical catfish (Brooks and Rasmussen 1984); carnivore mammals (Moore and Brooks 1987); alcid birds (Hoberg 1986).

Nematoda: oxyurids in Old World primates (Brooks and Glen 1982); **strongyloids** in Old World primates (Glen and Brooks 1985); **trichostrongyloids** in North American ruminants (Lichtenfels and Pilitt 1983); **metastrongyloids** in North American cervids (Platt 1984).

Digeneans + nematodes in crocodilians (Brooks and O'Grady 1989). **Digeneans + eucestodes + nematodes** in hominoid primates (the great apes; Glen and Brooks 1986). **Digeneans + eucestodes + monogeneans + nematodes** in neotropical freshwater stingrays (Brooks, Thorson, and Mayes 1981).

Arthropods

Chelicerata: mites on primates (O'Connor 1984); cormorant birds (O'Connor 1985); New World primates (O'Connor 1988).

Mandibulata: Crustacea: pinnotherid crabs on echinoderms (Griffith 1987); **copepods** on marine teleosts (Ho and Do 1985); pelagic marine fishes (Benz and Deets 1988); scomberomorph marine fishes (Cressey, Collette, and Russo 1983; Collette and Russo 1985); elasmobranchs (Deets 1987; Deets and Ho 1988; Dojiri and Deets 1988). **Insecta: dipterans** on various plants (Roskam 1985); **agaonid wasps** on figs (Ramirez 1974); **beetles** on termites (Jacobson, Kistner, and Pasteels 1986); **lice** on carnivore mammals (Kim 1985); **fleas** on neotropical mammals (Linardi 1984); **variety of groups** on *Nothofagus* (Humphries, Cox, and Neilson 1986).

Summary

Cospeciation studies are important because they allow us to estimate the ages of biotas and to reconstruct the historical sequence by which they have been assembled. This, in turn, sets the stage for historical ecological studies of coevolution and of community evolution, which we will discuss in

chapter 8. One basic theme underlying this and subsequent chapters is that spatial and resource allocation are important components of community evolution. Spatial allocation patterns are revealed by studies of cospeciation in a geographical context (historical biogeography), whereas resource allocation patterns are revealed by studies of cospeciation in an ecological context. As a consequence, historical ecologists investigating both aspects of cospeciation will uncover the extent to which phylogenetic influences have shaped these components of community and biotic structure.

For this reason, it is important to emphasize two generalities that emerge from this chapter. First, we have presented a single methodological approach for documenting patterns of both spatial and resource allocation (the latter in terms of co-occurring species). Wiley (1988a) has termed this approach BPA, for *Brooks parsimony analysis*, because it was first outlined for use in studies of host-parasite associations (resource allocation) by Brooks (1981) and extended to studies of biogeography (spatial allocation) by Brooks (1985). As we have noted above, BPA has required substantial modification, most recently by Wiley (1988a,b) and Brooks (1990), from the original formulation. As a result of this modification, BPA is now robust enough to be used as a general analytical tool for documenting macroevolutionary patterns of spatial and resource allocation. However, beware of the assumptions that it is either a "perfect" method (something not yet produced by scientists) or the best possible formulation. Both Page (1987, 1988) and Simberloff (1987, 1988) have called for statistical tests of cospeciation hypotheses (see the discussion in chapter 6). Since these tests are designed to examine a different set of questions (degrees of congruence among phylogenetic trees) than those addressed by BPA (pinpointing particular instances of incongruence), the development of and interaction between both methodologies will add depth to our evolutionary explanations.

The second generalization that emerges from this chapter is that this modified version of BPA is sensitive to a variety of evolutionary influences (see, for example, the study of Amazonian birds by Cracraft and Prum 1988). This is an encouraging result, for it frees us of concerns that BPA might be a reductionist approach that attempts to force data to conform to an "all cospeciation" model. In fact, the results of the numerous studies presented in this book imply that entire clades do not generally evolve as a result of a single speciation mode. We therefore do not expect all members of an association to conform to a single cospeciation scenario, but rather to represent the unique interaction of historical (vicariance/cospeciation) and nonhistorical (dispersal/resource-switching) events.