TEMPORAL CONGRUENCE AND CLADISTIC ANALYSIS OF BIOGEOGRAPHY AND COSPECIATION

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Abstract.—Cladistic analysis of congruence between different area cladograms, and between parasite and host cladograms, is typically limited to comparing branching sequences only. Adding information on timing of the cladogenetic events can increase the power of the analysis. Instances where two cladograms have the same branching pattern but the relevant events occurred at different times can be distinguished from genuine congruence (cladistic and temporal agreement). Temporal information can also help resolve instances of apparent incongruence. As an example, I reanalyze data from Hafner and Nadler's (1988, Nature, 332:258-259; 1990, Syst. Zool., 39:192-204) elegant study of cospeciation between pocket gophers and their chewing lice. By combining both cladistic and temporal information, estimates can be made of relative roles of cospeciation, dispersal, and extinction in structuring the pattern of host-parasite association between the gophers and their lice. [Biogeography; bootstrap; chewing lice; cladistics; component analysis; congruence; cospeciation; molecular clock; pocket gophers; randomization tests; UPGMA.]

Questions of congruence are central to cladistic analysis. Congruence between different clades, for example between cladograms for a parasite taxon and its host or between area cladograms for two different taxa, is of special interest to parasitologists and biogeographers (Nelson and Platnick, 1981; Brooks, 1988). Attempts to investigate congruence between clades may be frustrated by ambiguities such as widespread taxa, redundant distributions, and sampling error (Nelson and Platnick, 1981; Nelson, 1984). For example, Platnick (1981) has shown how the apparent incongruence found by Rosen (1978) between area cladograms for the fishes *Xiphophorus* and *Heterandria* may be an artifact of how Rosen interpreted widespread taxa. Under another interpretation of widespread taxa, the two genera are in complete agreement on the relationships of the areas in which they co-occur.

Incongruence between clades may be due to a combination of sampling error and extinction. Consider the cladograms in Figure 1 for hypothetical parasites and their

host taxa. The two cladograms are incongruent. This incongruence might be an artifact. Figure 2 shows a reconciliation of the two cladograms obtained using the procedure described in Page (1990). This cladogram contains eight *items of error* (Nelson and Platnick, 1981); eight extra terms and components (Nelson, 1979) are required to reconcile the cladogram for the parasite with that of its host. These items of error could be due to the extinction of some parasites on some hosts or our failure to collect those parasites.

If we add sufficient extra components and terms we can reconcile the parasite cladogram with any host cladogram. How then might we refute the hypothesis that parasite and host have coevolved? If the fit between parasite and host trees is not significantly better than a tree drawn at random from the set of all possible host cladograms, then we could reject our hypothesis of cospeciation.

We could also predict, given the reconciled tree in Figure 2, that further collecting would recover the missing parasites from hosts a, b, c, and d, removing the incongruence. But these predictions have only heuristic value (Nelson and Platnick, 1981:412). Failure to collect the missing parasites does not refute the hypothesis,

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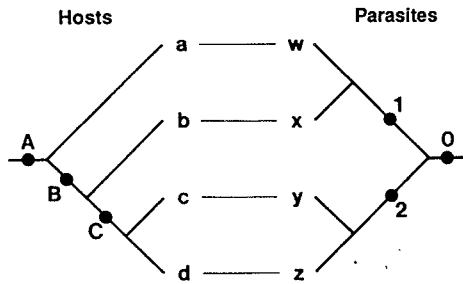
FIG. 1. Incongruent host and parasite cladograms.

for our search might not have been exhaustive enough or the parasites could simply be extinct.

Temporal Congruence

However, Figure 2 makes another set of predictions. If the components of the host and parasite cladograms represent cladogenetic events, then components 2 and C, and 1 and A, are predicted to be contemporaneous, and component 0 should be either contemporaneous with or predate component A. Figure 3 shows a host phylogeny consistent with the cladogram in Figure 1 and two parasite phylogenies, both consistent with the parasite cladogram in Figure 1 and hence incongruent with the host cladogram. The ages of all three cladogenetic events in the first parasite phylogeny (Fig. 3b) are consistent with the ages predicted from the reconciled tree. The second parasite phylogeny (Fig. 3c) agrees with the first prediction only, hence refuting the hypothesis of strict cospeciation.

These hypothetical examples show that deciding whether two cladograms (be they for parasite and host or for areas) are congruent may not always be straightforward (Nelson and Platnick, 1981; Nelson, 1984). Adding the dimension of time to our analysis enhances our ability to distinguish congruence from incongruence (see also Grande, 1985). The most detailed source of information on the timing of cladogenetic events is likely to be the "molecular clock."

This paper presents an empirical example of the utility of information on the timing of cladogenetic events in investigating
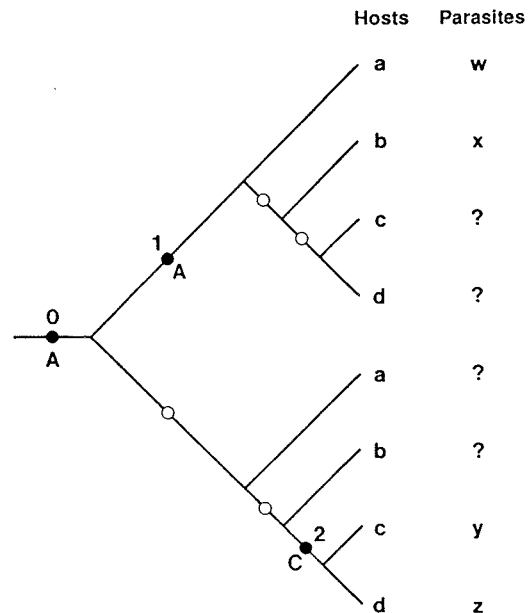

FIG. 2. Reconciliation between the incongruent host and parasite cladograms in Figure 1. The parasite cladogram is interpreted as a relict of a larger cladogram. Open circles and question marks represent the additional components and terms (items of error) necessary to reconcile the two cladograms.

the congruence between a pair of host-parasite cladograms, based on Hafner and Nadler's (1988, 1990) data. The hosts are 8 taxa of pocket gophers (belonging to the genera *Thomomys*, *Geomys*, and *Orthogeomys*); the parasites are 10 taxa of chewing lice (belonging to the genera *Thomomydoecus* and *Geomydoecus*). Hafner and Nadler (1988) identified six components (A, B, C, D, E, and F in Fig. 4) that were equivalent in the two groups. Components A, C, D, and E were considered to be contemporaneous and therefore due to cospeciation between gophers and lice. Two components (B and F) were not contemporaneous. Hafner and Nadler (1988) postulated three instances of parasite dispersal to explain the apparent incongruence between the two cladograms.

My analysis of Hafner and Nadler's (1988, 1990) data supports most of their conclusions and extends their analysis by showing that the apparent incongruence

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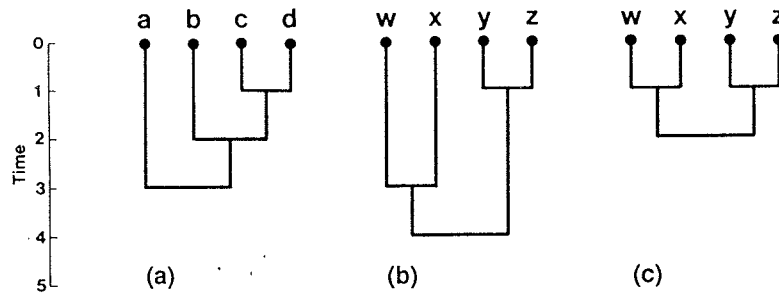most of their
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FIG. 3. (a) A host phylogeny consistent with the host cladogram in Figure 1 and (b, c) two parasite phylogenies consistent with the parasite cladogram in Figure 1. The ages of the cladogenetic events in parasite phylogeny (b) are all consistent with the reconciled cladogram in Figure 2, whereas only one of the events in parasite phylogeny (c) is consistent with the reconciled cladogram in Figure 2.

between the gophers of the genus *Orthogeomys* and their lice (Fig. 4) can be alternatively explained by postulating a combination of sampling error and extinction, without invoking dispersal. This explanation is supported by molecular clock estimates of the relative ages of the components in the two cladograms.
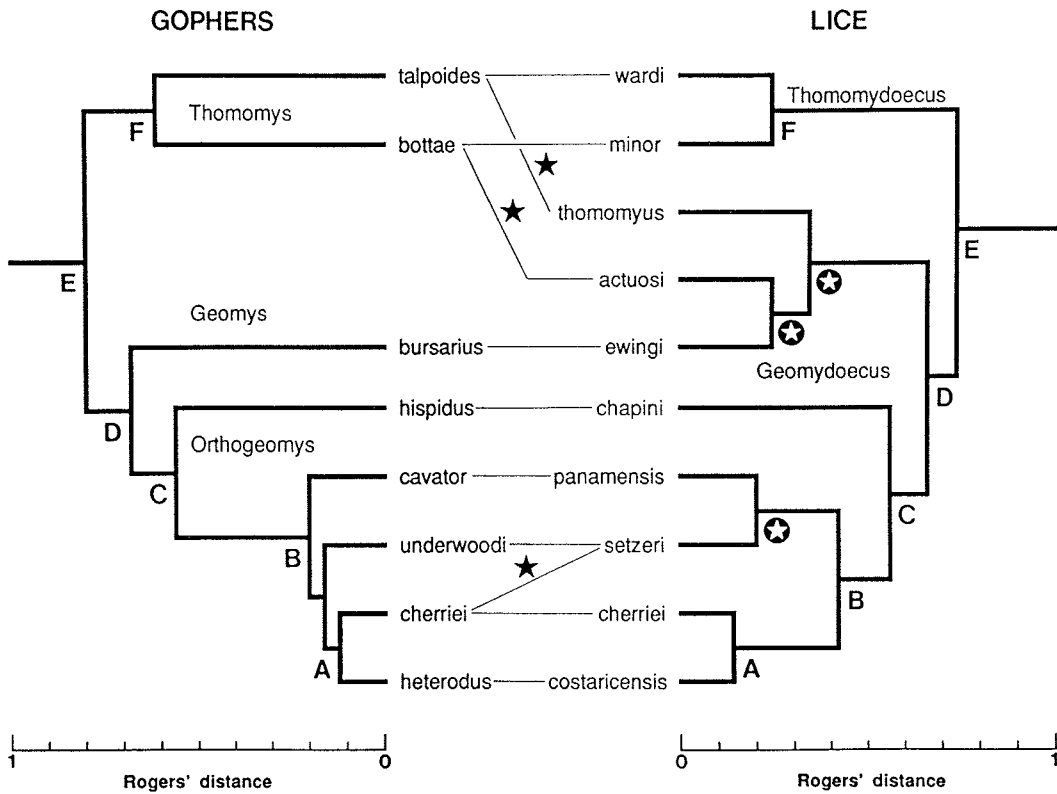

FIG. 4. Hafner and Nadler's (1988) interpretation of the parasite–host relationships between pocket gophers and their chewing lice. Parasite and host are connected by thin lines; stars mark hypothesized dispersal events. Components labeled by letters are shared by the host and parasite trees; components marked by encircled stars are unique to the parasite tree. (Redrawn from Hafner and Nadler [1988: their Fig. 2]. In that paper, the louse *Geomydoecus chapini* was incorrectly called *G. yucatanensis* [M. S. Hafner, pers. comm.].)

MATERIALS AND METHODS

Overview

My analysis has two parts: (1) estimation of the phylogenies of the gophers and their lice and (2) comparison of those phylogenies. In comparing the gopher and louse phylogenies, I consider both cladistic and temporal information. Without a molecular clock, the comparison would be restricted to cladistic information only.

To estimate the gopher and louse phylogenies, I first constructed most parsimonious cladograms for both taxa. I then tested whether the molecular clock hypothesis was consistent with those cladograms. Having failed to refute the clock hypothesis for either group, I then used UPGMA clustering to estimate their phylogenies.

The cladistic aspect of the estimated gopher and louse phylogenies was compared using component analysis (Nelson and Platnick, 1981). From the resulting map between host and parasite phylogenies, I derived predictions about the relative ages of host and parasite speciation events. These predictions were then tested.

Data

Hafner and Nadler's (1988, 1990) data consisted of allele frequencies at 31 loci for 8 gopher taxa and allele frequencies at 14 loci for 10 louse taxa.

Parsimony

Swofford and Berlocher (1987) described a parsimony criterion for allele frequency data that avoids the problems associated with "presence/absence" coding (of either alleles or allele combinations). Their method has been implemented in the program FREQPARS (version 1.0, written by D. L. Swofford). FREQPARS uses linear programming to assign allele frequencies to the hypothetical ancestors. Because linear programming is computationally intensive, FREQPARS is restricted to either a simple heuristic search for a single tree or optimizing one or more user trees. It does not have the branch-swapping or branch-and-bound features of parsimony programs for discrete characters, such as PAUP (Swofford, 1985).

Swofford and Berlocher (1987:302) suggested using a manual "iterative refinement" approach to search for the most parsimonious tree(s). I have found that for small numbers of taxa with few polymorphisms, an effective search strategy is to (1) code the allele frequency data into discrete characters, (2) find the minimal- and near-minimal-length trees for the discrete data using a branch-and-bound search (Hendy and Penny, 1982), and then (3) input these trees into FREQPARS as user trees.

I used Swofford's (1985) program PAUP 2.4.1 to find minimal trees for the discrete data. Loci for which there were no polymorphic taxa (or for which the polymorphisms were due to unique alleles) were coded as unordered multistate characters with the alleles as character states (Mickevich and Mitter, 1981; Buth, 1984). PAUP's UNORDERED command optimizes multistate characters using Fitch's (1971) method, which produces results equivalent to linear programming (Swofford and Berlocher, 1987:324). Loci for which there were shared polymorphisms were coded using the independent alleles method (Mickevich and Mitter, 1981). This coding method preserves more of the information in the data than does coding different allele combinations as different states (e.g., Mickevich and Mitter, 1981). The resulting matrices are shown in Tables 1 and 2. Minimal- and near-minimal-length trees were found using PAUP's BANDB and BBSAVE commands.

Test for a Molecular Clock

The test for the clock makes use of two different types of trees. Ultrametric trees (also called dendrograms; Fig. 5c) impose the constraint that all terminal taxa be equidistant from the root of the tree. This is equivalent to hypothesizing a molecular clock. Additive trees (Fig. 5b) do not impose this constraint on the branch lengths of the tree. Given a cladogram constructed from the data by a method that does not assume a clock (e.g., a parsimony method), if there is a molecular clock then the branch

TABLE 1. Discrete coding of allele frequency data for pocket gophers.

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TABLE 1. Discrete coding of allele frequency data for pocket gophers.

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	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	33	34	35	36	37	38	39	40	41	42	43	44	45
talpoides	3	3	0	0	1	0	0	1	1	4	4	1	5	4	0	0	0	0	1	5	3	4	5	1	5	5	5	2	8	3	4	3	2	0	0	0	0	0	0	1	5	3	2	4	1
bottae	4	4	0	0	1	0	0	1	1	4	4	1	4	3	0	0	0	1	0	4	3	4	4	1	4	4	4	2	7	2	4	2	3	0	0	0	0	0	1	0	4	2	3	3	1
bursarius	5	1	0	1	0	0	0	1	1	3	3	1	3	2	0	0	1	0	0	3	2	3	4	3	3	3	3	1	6	1	3	1	2	0	0	0	0	1	0	0	3	1	1	1	1
hispidus	2	1	0	1	0	0	0	1	1	2	2	1	2	1	1	0	0	0	0	2	1	2	3	2	2	2	2	1	5	1	2	1	1	1	0	0	0	0	0	0	2	1	1	2	1
cavator	1	2	0	1	0	0	1	1	1	1	1	1	1	1	0	1	0	0	0	1	1	1	2	1	1	1	1	1	4	1	1	1	1	0	0	0	1	0	0	0	1	1	1	1	1
underwoodi	1	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	3	1	1	1	1	0	0	1	0	0	0	0	1	1	1	1	1
cherriei	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1
heterodus	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1

[a] Characters 3–7, 15–19, and 34–40 are presence or absence of an allele; all other characters represent a single locus. 1, Adh; 2, Sdh; 3, Ldh-1a; 4, Ldh-1b; 5, Ldh-1c; 6, Ldh-1d; 7, Ldh-1e; 8, Ldh-2; 9, Mdh-1; 10, Mdh-2; 11, Me; 12, Icd-1; 13, Icd-2; 14, Gdh; 15, G6pd-1a; 16, G6pd-1b; 17, G6pd-1c; 18, G6pd-1d; 19, G6pd-1e; 20, αGpd; 21, Sod-1; 22, Sod-2; 23, Got-1; 24, Got-2; 25, Ck-1; 26, Ck-2; 27, Ak; 28, Est-D; 29, Pep-A; 30, Pep-B; 31, Pep-C; 32, Lap; 33, Fum; 34, Acon-1a; 35, Acon-1b; 36, Acon-1c; 37, Acon-1d; 38, Acon-1e; 39, Acon-1f; 40, Acon-1g; 41, Acom-2; 42, Mpi; 43, Gpi; 44, Alb; 45, Hb.

lengths assigned to that tree by the ultrametric and the additive models should not be significantly different (Felsenstein, 1984). If the additive model is a significantly better fit, then the clock hypothesis can be rejected. Note that an ultrametric model cannot be a better fit than an additive model (Farris, 1979:495).

Branch lengths.—Branch lengths for the ultrametric and additive tree models were estimated by least-squares fit to a Manhattan distance matrix. The Manhattan distance D between two taxa A and B is given by

$$D(A, B) = \left(\frac{1}{2} \sum_{j=1}^{N} \sum_{i=1}^{M_j} |p_{ijA} - p_{ijB}| \right)/N, \quad (1)$$

where p_{ijA} and p_{ijB} are the frequencies of the ith allele at the jth locus in taxa A and B, respectively; M_j is the number of alleles at the jth locus; and N is the total number of loci.

For an ultrametric tree, the least-squares estimates of the heights of the components are given by

$$T = (B'B)^{-1}B'D, \quad (2)$$

where D is the column vector of $m = n(n-1)/2$ pairwise distances between the n populations, T is the column vector of at most $(n-1)$ component heights, and B is an $m \times (n-1)$ matrix in which $B_{ij} = 1$ if the jth component is the most recent common ancestor of the pair to taxa whose distance is D_i (Chakraborty, 1977). For an additive tree, T is the column vector of at most $(2n-3)$ branch lengths and B is an $m \times (2n-3)$ matrix in which $B_{ij} = 1$ if the jth branch is on the path between the pair of taxa whose distance is D_i (Cavalli-Sforza and Edwards, 1967; Farris, 1981).

If d_{ij} is the pairwise distance between the taxa i and j derived from the data, and p_{ij} is the pairwise distance between i and j implied by the additive (ultrametric) tree, then Equation 2 finds the branch lengths (component heights) that minimize

$$\Sigma_{1 \leq i < j \leq n}(d_{ij} - p_{ij})^2. \quad (3)$$

Statistical test.—If there is a molecular clock, then an ultrametric tree should be
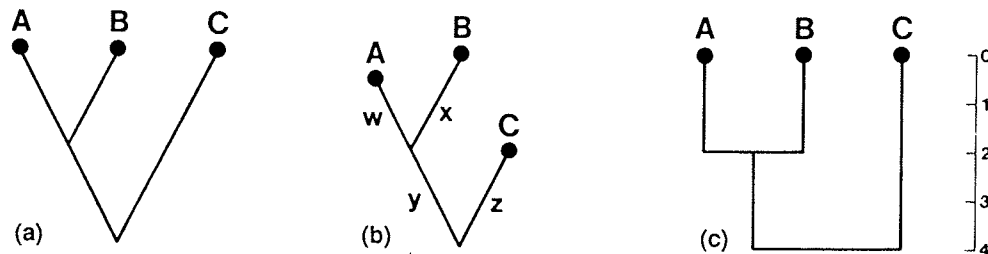
FIG. 5. The three kinds of trees referred to in this paper. (a) A cladogram. (b) An additive tree. (c) An ultrametric tree. All three trees share the same cladistic information: ((A, B), C). In addition the additive tree has branch length information (w, x, y, and z). If the tips of the tree are equidistant from the root (i.e., $w = x$ and $z = w + y$), then the additive tree is also an ultrametric tree. On an ultrametric tree, the distance of any tip to an ancestral component is the "height" of that component. For example, for tree (c), component AB has a height of 2 units and component ABC has a height of 4 units.

as good a fit to the data as the additive tree. To test this hypothesis, I used Smouse et al.'s (1986) extension to Mantel's test of matrix correspondence. Given two distance matrices (X_1, X_2) and a "response" matrix (Y), we can use the X matrices to predict the elements of Y. Smouse et al. described how to assess how much additional information is added by X_2, given that X_1 has already been included in the analysis. The test statistic is the increase in the coefficient of multiple determination (R^2) upon the addition of X_2.

To test for a clock, Y is the observed distance matrix, X_1 is the cophenetic matrix for the ultrametric tree, and X_2 is the cophenetic matrix for the additive tree. Adding X_2 should significantly increase the value of R^2 only if there are significant departures from the ultrametric model. The

significance of the increase in R^2 was evaluated by permuting Y 5,000 times, holding both X_1 and X_2 constant.

This test is a nonparametric analogue of Rohlf and Sokal's (1981) F-test for comparing additive and ultrametric trees, which has been used by Felsenstein (1984, 1986) to test for a molecular clock. The F-test is inappropriate in this situation because of the nonindependence of departures from the tree model (errors) (Farris, 1982, 1986; Felsenstein, 1988).

Phylogenetic Inference with a Clock

The phylogenies of the gophers and the lice were estimated using ultrametric trees (i.e., assuming a molecular clock) constructed from pairwise distance matrices. Estimates of genetic distance are subject to (sometimes considerable) uncertainty due

TABLE 2. Discrete coding of allele frequency data for chewing lice.

	Character[a]																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
wardi	1	3	2	8	4	2	2	4	0	0	0	1	0	1	0	1	4	2	1	7
minor	1	3	2	7	5	2	2	4	0	0	0	1	0	1	0	1	4	2	1	8
thomomyus	1	2	1	6	2	1	2	3	0	0	0	1	1	0	0	1	1	3	1	5
actuosi	1	2	4	5	1	1	2	3	0	0	0	1	0	1	1	1	1	3	1	6
ewingi	1	2	4	4	1	1	2	3	0	0	0	1	0	1	0	1	2	3	1	6
chapini	1	1	3	2	3	1	1	3	0	0	1	1	0	0	0	2	5	4	1	3
panamensis	1	2	3	3	3	1	1	2	0	1	1	0	0	0	0	1	4	1	1	4
setzeri	1	2	3	3	3	1	1	2	1	1	0	0	0	0	0	1	3	1	1	1
cherriei	1	2	3	2	3	1	1	1	0	1	0	0	0	0	0	1	1	1	2	2
costaricensis	1	2	3	1	3	1	1	1	0	1	0	1	0	0	0	1	1	1	2	2

[a] Characters 9–15 are the presence or absence of an allele; all other characters represent a single locus. 1, *Mdh*; 2, *Me*; 3, *Icd*; 4, *Xdh*; 5, *Sod-1*; 6, *Sod-2*; 7, *Ak*; 8, *Uae*; 9, *Est^a*; 10, *Est^b*; 11, *Est^c*; 12, *Est^d*; 13, *Est^e*; 14, *Est^f*; 15, *Est^g*; 16, *Pep-A*; 17, *Pep-C*; 18, *Ada*; 19, *Fum*; 20, *Gpi*.

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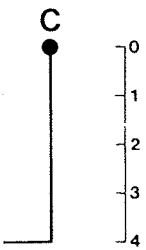
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2	3	1	6
5	4	1	3
4	1	1	4
3	1	1	1
1	1	2	2
1	1	2	2

3, Icd; 4, Xdh; 5, Sod-1; 6,
Gpi.

to sampling error (Mueller and Ayala, 1982), which affects both the topology of the tree and the heights of the clusters in the tree. Confidence intervals were placed on the estimates of both topology and cluster height using the bootstrap (Efron, 1982).

For each data set, I generated 1,000 bootstrap data sets by sampling loci (with replacement) from the original data (Felsenstein, 1985a; Sanderson, 1989). For each bootstrap sample, a Manhattan distance matrix, $D_i{}^*$, was constructed and an ultrametric tree computed. Finding ultrametric trees that minimize Expression 3 is an NP-complete problem (Day, 1987). Bootstrapping is computationally intensive, so I used the fast, heuristic method of UPGMA clustering, which is known to perform well (Farris, 1969). UPGMA trees were computed using a Pascal program I wrote that used a combinatorial algorithm based on priority queues (Belbin, 1984; Day and Edelsbrunner, 1984). This program could not search for equally well fitting trees (Hart, 1983), but would collapse zero-length branches to polytomies.

The majority-rule consensus tree (Margush and McMorris, 1981) for the 1,000 UPGMA trees constituted the bootstrap estimate of the topology of the phylogeny (Felsenstein, 1985a). The consensus trees were found using the *Consensus* command in my program COMPONENT (Page, 1989). Confidence intervals for the cluster heights in each consensus tree were computed using the percentile method (Efron, 1982). For each cluster, 1,000 bootstrap estimates of its height were computed by solving Equation 2 for the majority-rule consensus tree and each bootstrap matrix $D_i{}^*$. The central 95% of the distribution of cluster heights constituted the 95% confidence interval.

Component Analysis

Reconciling parasite and host cladograms.— The *Fit* command in my program COMPONENT was used to reconcile the parasite and host cladograms, under Nelson and Platnick's (1981) Assumptions 1 and 2 (see Page, 1990). The difference between the number of terms and components in the

reconciled tree and in the parasite tree is the number of items of error. The significance of the observed items of error was evaluated by reconciling the parasite tree with 1,000 randomly generated binary rooted trees with the same number of taxa as the host. The random trees were generated using a Markovian model (Harding, 1971; Savage, 1983).

Component mappings.— The reconciliation between parasite and host cladograms produces a mapping between the components in the parasite and host trees. If the mapping is unique (one parasite component maps onto one host component), then both components are expected to have the same height (the cladogenetic events they correspond to occurred at the same time). If the mapping is many to one (more than one parasite component maps onto the same host component), then more complicated relations might be expected. Component mappings were evaluated by comparing the bootstrap distributions of component heights for each parasite–host pair of components.

Statistical test.— If parasite and host have strictly cospeciated, then the heights of each pair of parasite–host components both estimate the date of the same speciation event. If we replace the parasites with the hosts that they infest, then we would expect to get an ultrametric tree identical to that for the hosts. Because of uninfested hosts, widespread parasites, and multiply infested hosts, simply substituting hosts for parasites will not always produce a tree with all members of the host clade represented only once. Such is the case with the lice in this study, so Nelson and Platnick's (1981) Assumption 2 was used to construct a host cladogram from the parasite cladogram using the algorithm described in Page (1988).

Lapointe and Legendre's (1990) double permutation test was used to test the null hypothesis that the ultrametric tree for the hosts derived from the parasite data was not significantly different from the actual host tree. Lapointe and Legendre's test uses a normalized version of Faith and Belbin's (1986) intermediate dissimilarity index

(NISI). Given two ultrametric trees and their respective cophenetic *similarity* matrices **A** and **B**, then the index is

$$\text{NISI} = 1 - \langle\{1 + [(\Sigma\Sigma\ |\mathbf{A}_{ij} - \mathbf{B}_{ij}| - \text{minimum}(\mathbf{A}_{ij},\ \mathbf{B}_{ij})) \div \text{MAX}]\}/2\rangle, \qquad (4)$$

where $\mathbf{A}_{ij}$ and $\mathbf{B}_{ij}$ are the cophenetic values of the ith and jth taxa in **A** and **B**, respectively, and

$$\text{MAX} = \text{maximum}[\Sigma\Sigma\ |\mathbf{A}_{ij} - \mathbf{B}_{ij}|, \Sigma\Sigma\ \text{minimum}(\mathbf{A}_{ij},\ \mathbf{B}_{ij})]. \qquad (5)$$

The significance of the statistic is evaluated by constructing pairs of random dendrograms with the same component heights as **A** and **B**. I constructed 5,000 such pairs using Lapointe and Legendre's CONSENSUSTAT algorithm.

RESULTS

Is There a Clock?

Gophers.—For the discrete data in Table 1, PAUP found a single minimal length tree of 92 steps, 9 trees of 93 steps, and 28 trees of 94 steps. When all 38 trees were optimized by FREQPARS, 5 trees had the shortest length of 173.92 steps. Hafner and Nadler's (1988) tree for the gophers was among the 38 trees and had a length of 174.32 steps.

Figure 6 shows one of the five best trees. Note that the branch lengths shown are only one of the possible most parsimonious reconstructions (Swofford and Berlocher, 1987; Swofford and Maddison, 1987). For example, the inequality of branch lengths between the sister taxa *Thomomys talpoides* and *T. bottae* can be removed or completely reversed in other equally parsimonious reconstructions (Fig. 7). Because of this ambiguity in assigning alleles to hypothetical ancestors, the unequal branch lengths in Figure 6 do not constitute evidence against the clock hypothesis.

Figure 8 shows the least-squares estimates of the branch lengths for the tree in Figure 6 and the distances in Table 3 under the additive tree model. The ultrametric
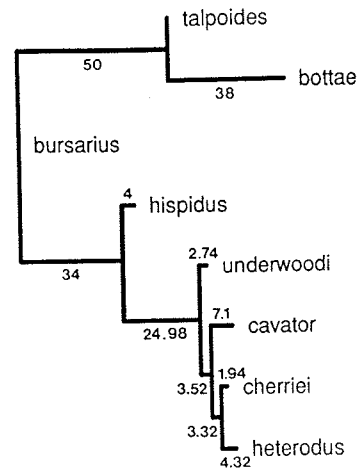
FIG. 6. One of the five equally parsimonious trees for the gophers (length = 173.92 steps). Branch lengths were computed using FREQPARS. The tree is arbitrarily rooted.

cophenetic matrix is a very good fit to the data ($R^2 = 0.9956$); addition of the additive cophenetic matrix does not significantly improve the fit (increase in $R^2 = 0.0022$, $P(H_0) = 0.8806$). Hence, the data are consistent with a molecular clock.

Lice.—PAUP found six minimal trees of 47 steps and a further 51 trees of 48 steps for the data in Table 2. Twenty-one of these trees, including Hafner and Nadler's tree (Fig. 9), had the shortest length of 86.74 steps when optimized by FREQPARS. The ultrametric tree model is a good fit to the data ($R^2 = 0.9256$); the additive tree model (Fig. 10) does not significantly increase the fit (increase in $R^2 = 0.0591$, $P(H_0) = 0.1074$). Hence, the data (Table 4) are consistent with the molecular clock hypothesis.

Phylogenetic Estimates

The bootstrap estimates of the phylogenies of the gophers and their lice are shown in Figures 11–14. Tables 5 and 6 summarize the confidence limits for each component. Both trees are topologically identical to those found by Hafner and Nadler (1988: their Fig. 2; my Fig. 4).

Gophers.—All components in the gopher tree occurred in at least 70% of the bootstrap trees. The two main points of uncertainty are (1) the relationships of *Ortho-*

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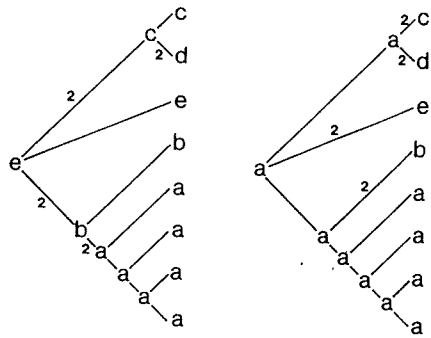majorit

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FIG. 7. Two equally parsimonious reconstructions for the gopher *Adh* locus for the tree in Figure 6. The locus contributes eight steps to the total length of the tree (173.92 steps). The distribution of these eight steps depends on the alleles assigned to the hypothetical ancestors. The reconstruction on the left is the one found by FREQPARS.

geomys hispidus (789 trees out of 1,000 supported the monophyly of *Orthogeomys*, 181 trees had *Geomys bursarius* more closely related to the other species of *Orthogeomys* than is *O. hispidus*, and 30 trees had *G. bursarius* and *O. hispidus* as sister taxa) and (2) the relationships between *O. cavator*, *O. underwoodi*, *O. cherriei*, and *O. heterodus*. The resolution of these four taxa shown by the majority-rule consensus tree was by far the
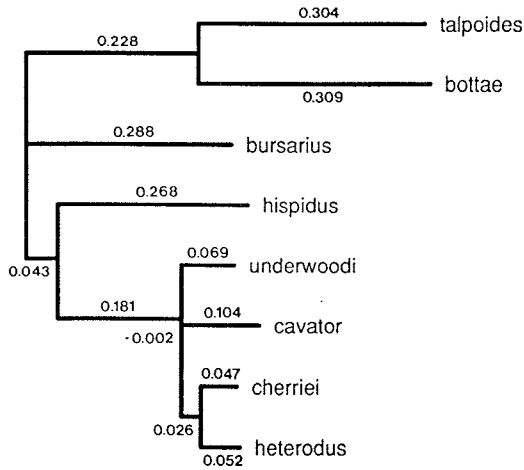
FIG. 8. Least-squares estimates of the branch lengths for the tree in Figure 6 and the distance matrix in Table 3, under the additive tree model. The tree is arbitrarily rooted.

best supported; the other resolutions were supported by between 1 and 116 trees.

Lice.—The estimate of the louse phylogeny is less certain than that for the gophers, reflecting the smaller number of characters available. The greatest uncertainty lies near the root of the tree. Just over half (520) of the bootstrap trees supported the monophyly of *Geomydoecus*, whereas 380 trees grouped *G. thomomyus*, *G. actuosi*, and *G. ewingi* with *Thomomydoecus*. The best supported components were among those linking the most recently diverged taxa (e.g., 1, 3, 7, and 8).

Rooting.—Ultrametric trees are, by definition, rooted trees. Although Hafner and Nadler's (1988) original data did not include outgroups, they have since reported that the rooting of both trees is supported by outgroups (Hafner and Nadler, 1990).

Component Analysis

Assumption 1.—Under Assumption 1, all occurrences of parasites on hosts are interpreted as being due to association by descent. Dispersal of parasites (host-switching) is not considered. Fifty-two items of error are needed to reconcile the estimates of the host and parasite phylogenies (Fig. 15; Table 7). Based on the distribution of items of error for 1,000 random trees (Fig. 16), the degree of fit between parasite and host cladograms is not significantly better than could be expected due to chance $(P(H_0) = 0.061)$.

Assumption 2.—Assumption 2 allows for the possibility that the multiple (redundant) occurrences of parasites on the same hosts might not all be equally informative of host relationships. Some of the redundant occurrences may be due to dispersal of parasites to new hosts. Nelson and Platnick (1981) distinguished between two different types of redundancy: redundant endemic taxa (e.g., *Geomydoecus thomomyus* and *G. actuosi*) and redundant widespread taxa (e.g., *G. setzeri*). For redundant endemics, all but one occurrence on a given host is ignored at a time. Four louse taxa have redundant distributions (*Thomomydoecus wardi*, *T. minor*, *Geomydoecus thomomyus*, and *G. actuosi*), so there are four different pos-
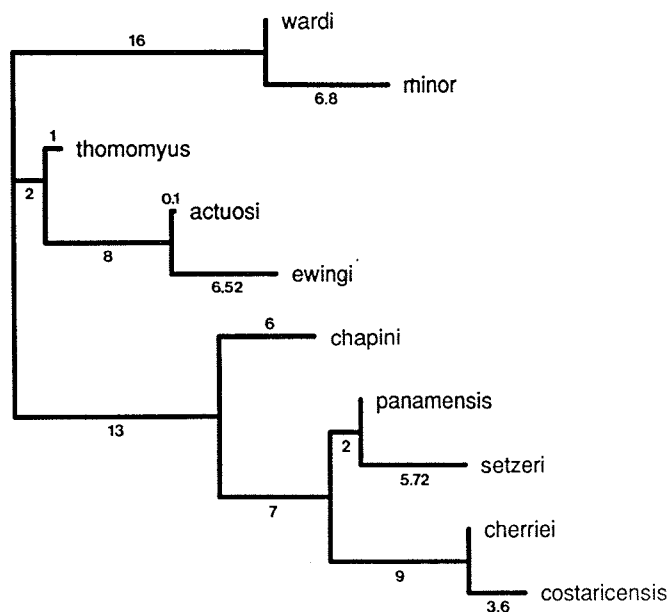
FIG. 9. One of the 21 equally parsimonious trees for the lice (length = 86.74 steps). Branch lengths were computed using FREQPARS. The tree is arbitrarily rooted.

FIG. 10. Least-lengths for the tree in Table 4, under arbitrarily rooted.

sible combinations of lice. For example, we might ignore the occurrences of *Geomydoecus thomomyus* and *G. actuosi* on *Thomomys talpoides* and *T. bottae*, respectively (Fig. 17). If a widespread parasite infests a host that also harbors an endemic parasite, then under Assumption 2, the occurrence of the widespread parasite is ignored. This rule is quite arbitrary, but increases the informativeness of the parasite cladogram.

One of the four different interpretations of the parasite cladogram under Assumption 2 (Fig. 18) had eight items of error ($P(H_0) = 0.001$; Fig. 19). The remaining three cladograms each had 40 items of error. The cladogram formed by deleting *Thomomy-*

doecus wardi and *T. minor* was not a significant fit ($P(H_0) = 0.112$); the other two were barely significant ($P(H_0) = 0.047$ and $P(H_0) = 0.048$).

Component mappings.—Under Assumption 1, four parasite components (0, 2, 3, and 4) map onto the host component A, implying that the common ancestor of the eight gophers sampled by Hafner and Nadler (1988, 1990) contained at least four different lineages of lice. Of the four components, 4 is predicted to be contemporaneous with A, whereas the other components are predicted to predate host component A (Fig. 15). All four predictions are falsified (Fig. 20a). Component 4 post-

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TABLE 3. Pairwise Manhattan distances between gopher taxa (taxon names are abbreviated to the first two letters of the specific epithet).

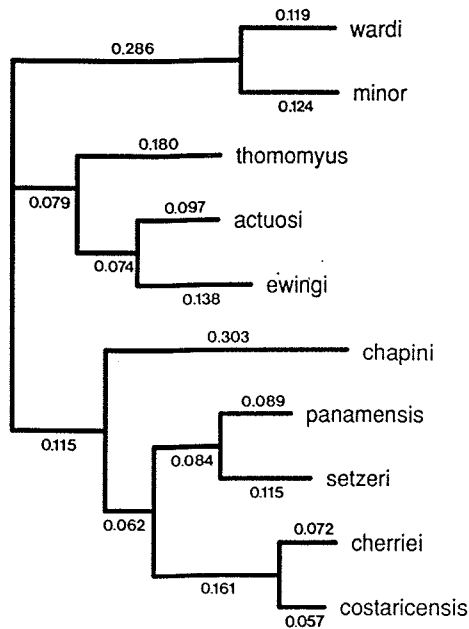|	ta	bo	bu	hi	ca	un	ch
bo	0.613						
bu	0.806	0.839					
hi	0.839	0.839	0.613				
ca	0.839	0.839	0.629	0.568			
un	0.839	0.839	0.564	0.512	0.183		
ch	0.841	0.841	0.569	0.504	0.191	0.133	
he	0.842	0.842	0.588	0.529	0.169	0.141	0.099

FIG. 10. Least-squares estimates of the branch lengths for the tree in Figure 8 and the distance matrix in Table 4, under the additive tree model. The tree is arbitrarily rooted.

FIG. 11. Majority-rule consensus tree for 1,000 bootstrap UPGMA trees for gophers.

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dates component A, whereas component 0 is approximately contemporaneous with it. Similarly, component 1 postdates its equivalent host component, B. These discrepancies might be due to different rates of evolution in the lice and pocket gophers, but the mappings between *Orthogeomys* and its lice suggest otherwise (see below).

Under the best fitting tree for Assumption 2 (Fig. 18), components 3 and 4 are ignored because *Geomydoecus thomomyus* and *G. actuosi* are assumed to have dispersed to their hosts, not evolved in situ. Component 0 is predicted to be contemporaneous with component A, and component 2 with component C. The data are consistent with both predictions (Fig. 20b).

Orthogeomys.—Figure 4 suggests that there are three points of disagreement between the phylogeny of *Orthogeomys* and its parasites: (1) component 7 (*G. panamensis* + *G. setzeri*) conflicts with the host tree; (2) *G. setzeri* infests both *O. underwoodi* and *O. cherriei*, which Hafner and Nadler (1988)

attributed to dispersal of *G. setzeri* onto *O. cherriei*; and (3) component 6 (Hafner and Nadler's component B) predates the equivalent host component.

Both Assumption 1 and Assumption 2 suggest an alternative interpretation that explains all three apparent contradictions. Parasite components 6 and 7 both map onto host component E, implying that two lineages of parasites infested the ancestor of the *cavator* group of gophers (*O. cavator, O. underwoodi, O. cherriei,* and *O. heterodus*). One lineage is represented by *Geomydoecus panamensis* and *G. setzeri,* and the other is rep-
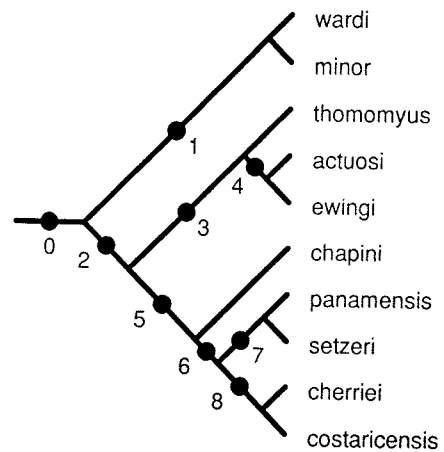

FIG. 12. Majority-rule consensus tree for 1,000 bootstrap UPGMA trees for lice.

TABLE 4. Pairwise Manhattan distances between louse taxa (taxon names are abbreviated to the first two letters of the specific epithet, except that *Geomydoecus chapini* = *ca*).

	wa	mi	th	ac	ew	ca	pa	se	ch
mi	0.243								
th	0.679	0.679							
ac	0.646	0.673	0.323						
ew	0.669	0.697	0.419	0.235					
ca	0.821	0.821	0.679	0.680	0.704				
pa	0.714	0.714	0.643	0.643	0.643	0.536			
se	0.786	0.786	0.643	0.643	0.643	0.571	0.204		
ch	0.857	0.857	0.643	0.643	0.714	0.571	0.393	0.419	
co	0.821	0.800	0.607	0.609	0.704	0.607	0.414	0.419	0.129

TABLE 5. Summary statistics for the bootstrap estimates of the phylogeny of the pocket gophers (Fig. 13). For each component, the table lists the frequency of that component in the 1,000 bootstrap trees (f_{boot}) and the mean ($\bar{x}$), variance (s^2), median (m), and 95% confidence interval (95% CI) for the 1,000 bootstrap estimates of the height of that component.

		Height			
Component	f_{boot}	$\bar{x}$	s^2	m	95% CI
A		0.838	0.00436	0.839	0.703–0.960
B	0.999	0.611	0.00794	0.613	0.452–0.774
C	1.000	0.592	0.00635	0.595	0.431–0.730
D	0.789	0.528	0.00678	0.529	0.365–0.689
E	0.999	0.181	0.00359	0.177	0.073–0.310
F	0.751	0.137	0.00229	0.132	0.052–0.242
G	0.725	0.098	0.00147	0.094	0.035–0.181

TABLE 6. Summary statistics for the bootstrap estimates of the phylogeny of the chewing lice (Fig. 14). For each component, the table lists the frequency of that component in the 1,000 bootstrap trees (f_{boot}) and the mean ($\bar{x}$), variance (s^2), median (m), and 95% confidence interval (95% CI) for the 1,000 bootstrap estimates of the height of that component.

		Height			
Component	f_{boot}	$\bar{x}$	s^2	m	95% CI
0		0.751	0.00826	0.751	0.561–0.921
1	1.000	0.240	0.01122	0.243	0.057–0.457
2	0.520	0.652	0.01034	0.653	0.451–0.842
3	0.975	0.368	0.01364	0.371	0.142–0.585
4	0.782	0.236	0.01125	0.227	0.060–0.470
5	0.619	0.572	0.01333	0.571	0.339–0.803
6	0.753	0.412	0.01577	0.411	0.197–0.661
7	0.954	0.209	0.01130	0.204	0.000–0.419
8	0.989	0.126	0.00713	0.129	0.000–0.314

resented by *G. cherriei* and *G. costaricensis*. Under the hypothesis of association by descent, *G. panamensis* and *G. setzeri* diverged at the same time as *O. cavator* diverged from the rest of the *cavator* group (Fig. 21). When *O. underwoodi* diverged from the ancestor of *O. cherriei* and *O. heterodus*, *G. setzeri* did not differentiate, hence its occurrence on *O. cherriei* can be explained by descent instead of dispersal. The predicted representative of this louse clade on *O. heterodus* has either gone extinct or is uncollected. The second louse clade is represented by *G. cherriei* and *G. costaricensis*, and has either

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	95% CI
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	2–0.774
	1–0.730
	5–0.689
	3–0.310
	2–0.242
	5–0.181

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	95% CI
	1–0.921
	7–0.457
	1–0.842
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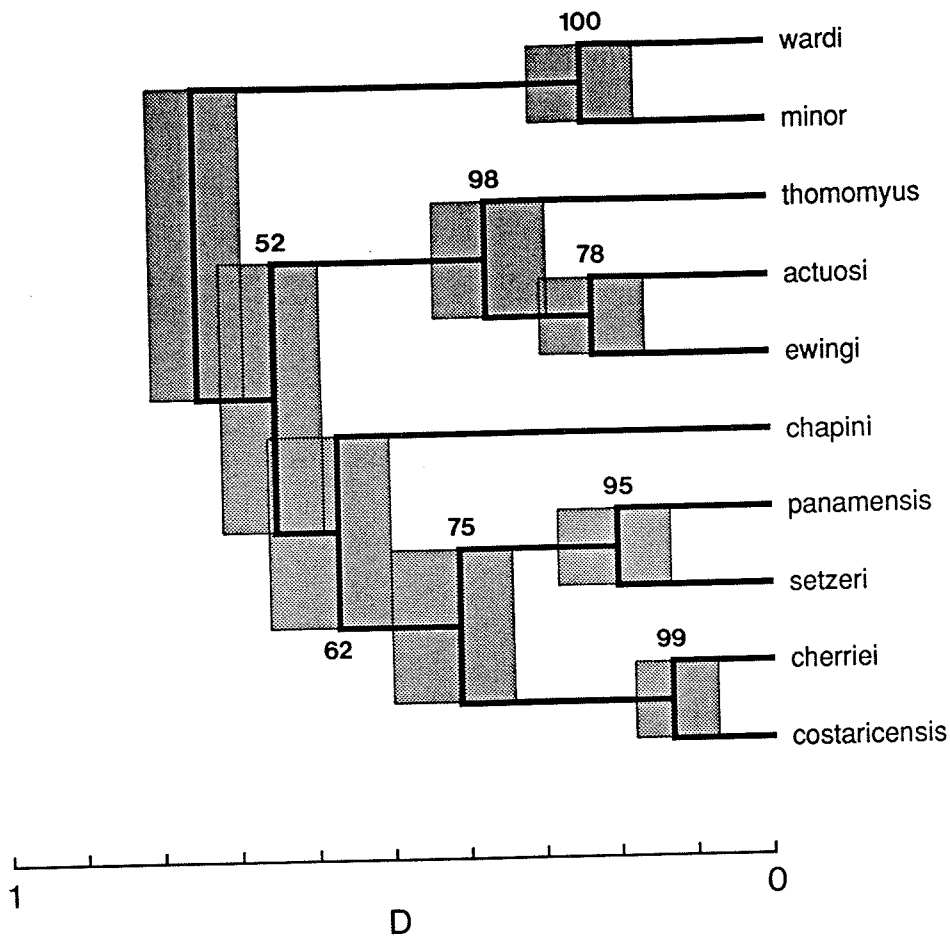resented by
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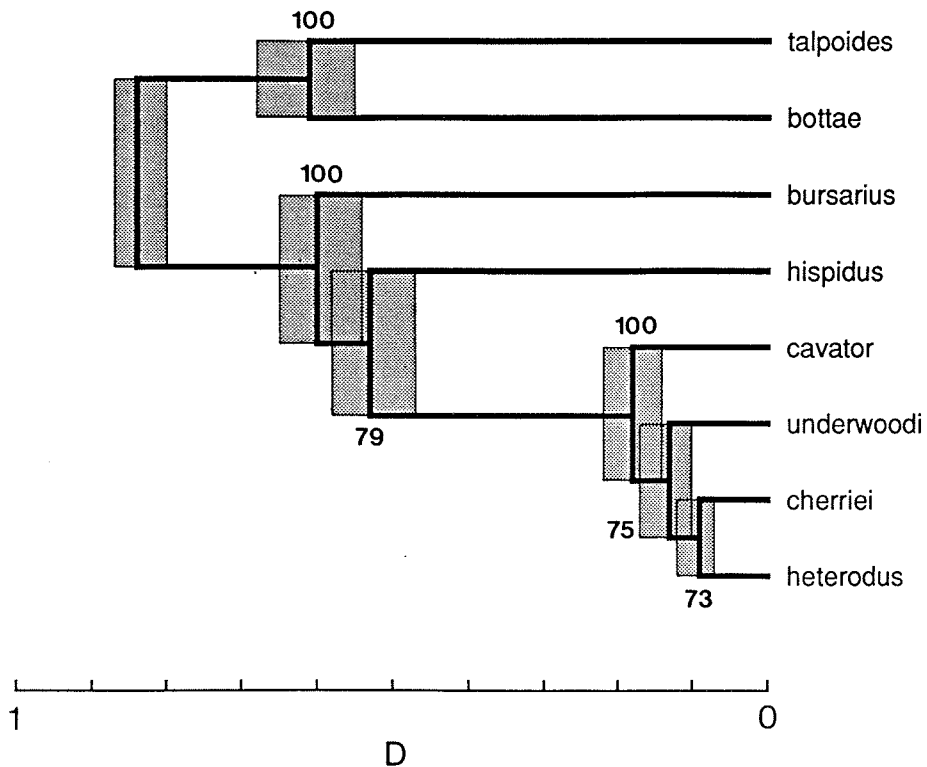
FIG. 13.   Bootstrap confidence intervals for the estimate of the gopher phylogeny. For each component the shaded rectangle encloses 50% of the distribution of the bootstrap estimates of that component's height, and the number records the percentage of bootstrap trees in which the corresponding component occurred (see also Table 5). Scale is in Manhattan distance units.

gone extinct or is uncollected from *O. cavator* and *O. underwoodi.*

This interpretation predicts that (1) parasite component 8 should be contemporaneous with host component G, (2) parasite component 7 should be contemporaneous with host component E, and (3) parasite component 6 should either predate host component E or be contemporaneous with it. Figure 22 shows that the distribution of the bootstrap estimates of the heights of components E and 7, and components G and 8, are almost coincident, whereas the distribution for component 6 is shifted to the right (earlier in time) of that for component E, as the interpretation predicts. However, for each pair of components, the estimates of the heights are not significantly different: (1) $t_{1,998} = 0.302$, $P(H_0) > 0.1$; (2) $t_{1,998} = 0.230$, $P(H_0) > 0.1$; and (3) $t_{1,998} = 1.662$, $P(H_0) >$

0.1. Although the height of neither component 6 nor component 7 is significantly different from the height of component E, the height of component 7 is clearly closer to that of component E than is that of component 6. Note that although the 95% confidence intervals for the heights of com-

TABLE 7.   Map between parasite and host components under Assumptions 1 and 2.

	Host	
Parasite	Assumption 1	Assumption 2
0	A	A
1	B	B
2	A	C
3	A	
4	A	
5	D	D
6	E	E
7	E	E
8	G	G

FIG. 14. Bootstrap confidence intervals for the estimate of the louse phylogeny. For each component the shaded rectangle encloses 50% of the distribution of the bootstrap estimates of that component's height, and the number records the percentage of bootstrap trees in which the corresponding component occurred (see also Table 6). Scale is in Manhattan distance units.

ponents 6 and 7 overlap, they are significantly different (in 958 of the 1,000 bootstrap trees the difference in height between components 6 and 7 is greater than zero). This is because confidence intervals on component heights in the same tree are not independent (Mueller and Ayala, 1982: 134).

Statistical test.—Two different cophenetic matrices were calculated for the parasites. The first matrix (Table 8) was computed from the best fitting tree under Assumption 2 (*G. thomomyus* and *G. actuosi* deleted; Figs. 16, 21a). The null hypothesis

that the cophenetic matrices for the gophers and their lice were not more similar than could be expected due to chance was rejected (NISI = 0.8581, $P(H_0) = 0.001$).

By ignoring the occurrence of *G. setzeri* on *O. cherriei*, Nelson and Platnick's (1981) rule for handling redundant widespread taxa results in incongruent parasite and host cladograms; their rule implies that *O. cavator* is the sister taxon of *O. underwoodi* (Fig. 23a). But the mapping described above shows that the two trees are not incongruent: the distribution of *G. setzeri* is consistent with the host tree. The parasite tree
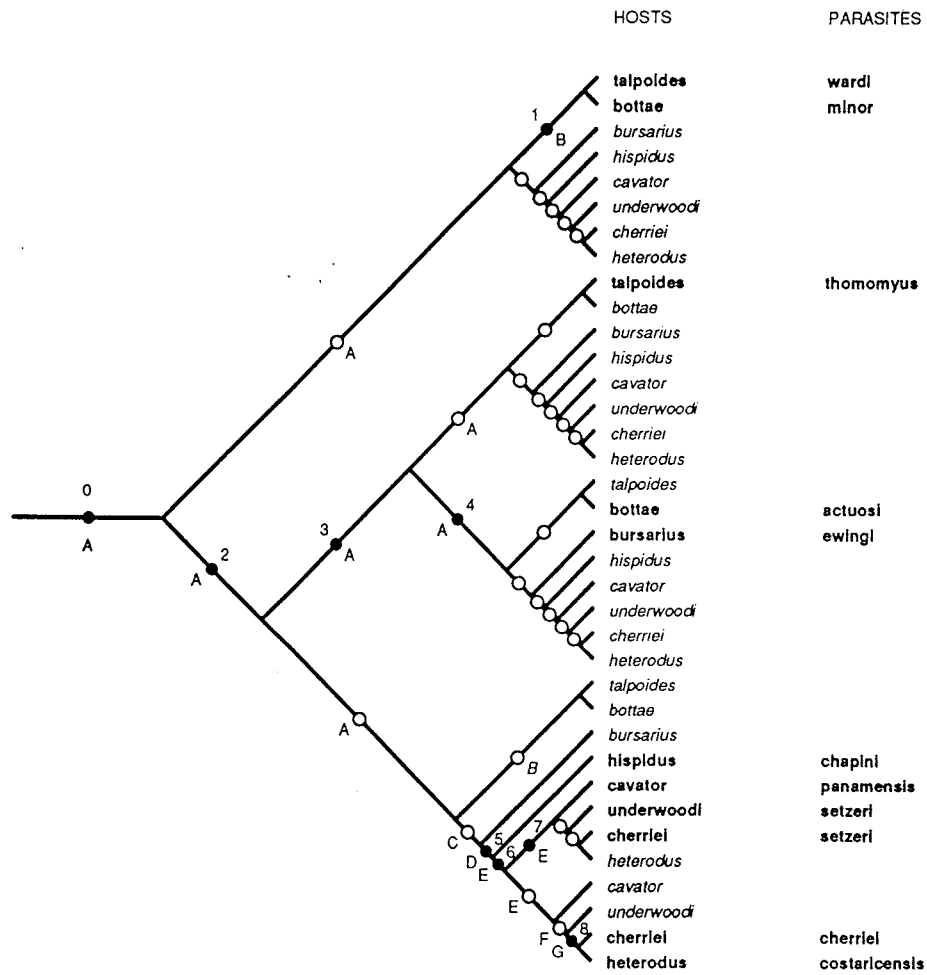
HOSTS   PARASITES

FIG. 15. Reconciliation between parasite (Fig. 12) and host (Fig. 11) cladograms under Assumption 1. The items of error are represented by open circles (components) and italicized taxon names (terms). Fifty-two items of error are needed to reconcile the two trees.

does not contain a component equivalent to host component F (Table 7), so I placed G. setzeri in a trichotomy with G. panamensis and G. cherriei + G. costaricensis and gave that trichotomy the height of parasite component 7. The resulting matrix (Table 9) is an even better fit to the host tree (NISI = 0.9088, $P(H_0)$ = 0.0002).

DISCUSSION

Limitations of the Analysis

The analysis presented here has several limitations. Perhaps the greatest is the un-certainty in the estimates of the host and parasite cladograms. This is particularly acute for the parasites. The variance of the bootstrap estimates of the component heights for the lice was up to five times greater than for the equivalent host components. Much of this difference is due to the smaller number of loci sampled (14 versus 31). A more precise estimate of the louse phylogeny must await the examination of further characters.

Although I have restricted my attention to uncertainty in component heights, there
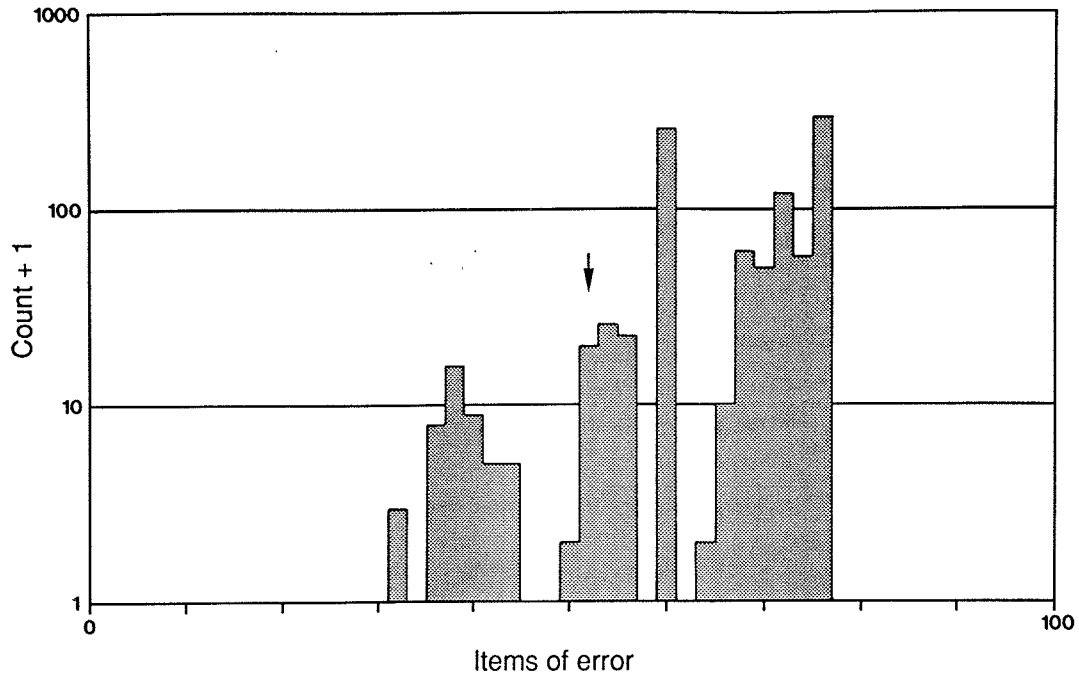
FIG. 16.   Distribution of items of error for 1,000 random trees for the eight gopher taxa when reconciled with the louse cladogram (Fig. 12) under Assumption 1. The observed value (52) is marked by an arrow and is not significantly smaller than could be expected to be due to chance $(P(H_0) = 0.061)$.
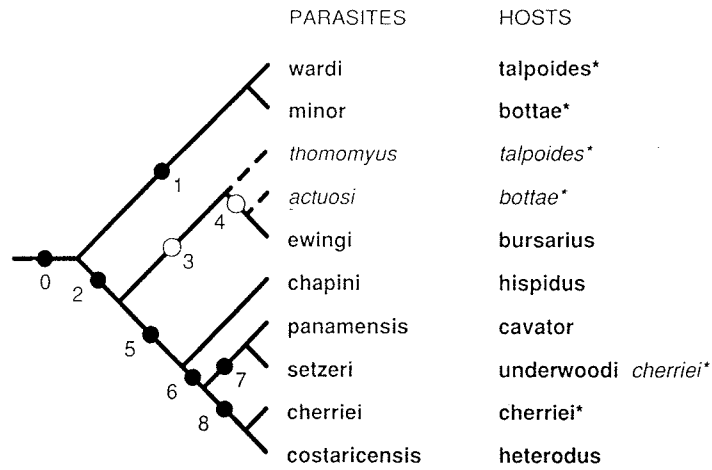
PARASITES	HOSTS
wardi	talpoides*
minor	bottae*
thomomyus	talpoides*
actuosi	bottae*
ewingi	bursarius
chapini	hispidus
panamensis	cavator
setzeri	underwoodi cherriei*
cherriei	cherriei*
costaricensis	heterodus

FIG. 17.   Distribution of hosts on the louse cladogram. Host occurrences labeled with an asterisk (*) are redundant. Under Assumption 2 the occurrence of Geomydoecus setzeri on Orthogeomys cherriei is ignored because O. cherriei has an endemic parasite (G. cherriei). There are four possible cladograms that can be generated from this cladogram, corresponding to the removal of a pair of parasites of Thomomyus talpoides and T. bottae. The cladogram with the best fit is formed by removing Geomydoecus thomomyus and G. actuosi (broken lines) and therefore components 3 and 4 (open circles). Removing those parasites is equivalent to postulating that they dispersed to their present hosts.

HOSTS   PARASITES

talpoides   wardi
bottae   minor
bursarius   ewingi
hispidus   chapini
cavator   panamensis
underwoodi   setzeri
cherriei   (setzeri)
heterodus
cavator
underwoodi
cherriei   cherriei
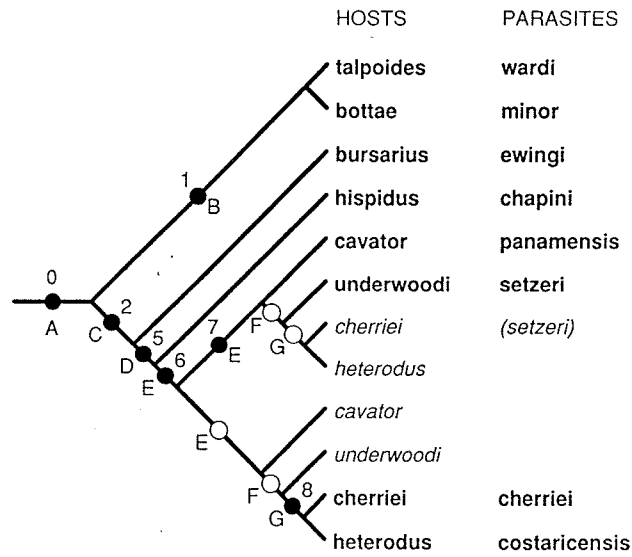heterodus   costaricensis

FIG. 18.   The best reconciliation between parasite (Fig. 12) and host (Fig. 11) cladograms under Assumption 2. The items of error are represented by open circles (components) and italicized taxon names (terms). Eight items of error are required to reconcile the two trees. The occurrence of *Geomydoecus setzeri* on *Orthogeomys cherriei* was removed by the algorithm for Assumption 2, but the reconciled tree shows that this occurrence can be explained by descent.
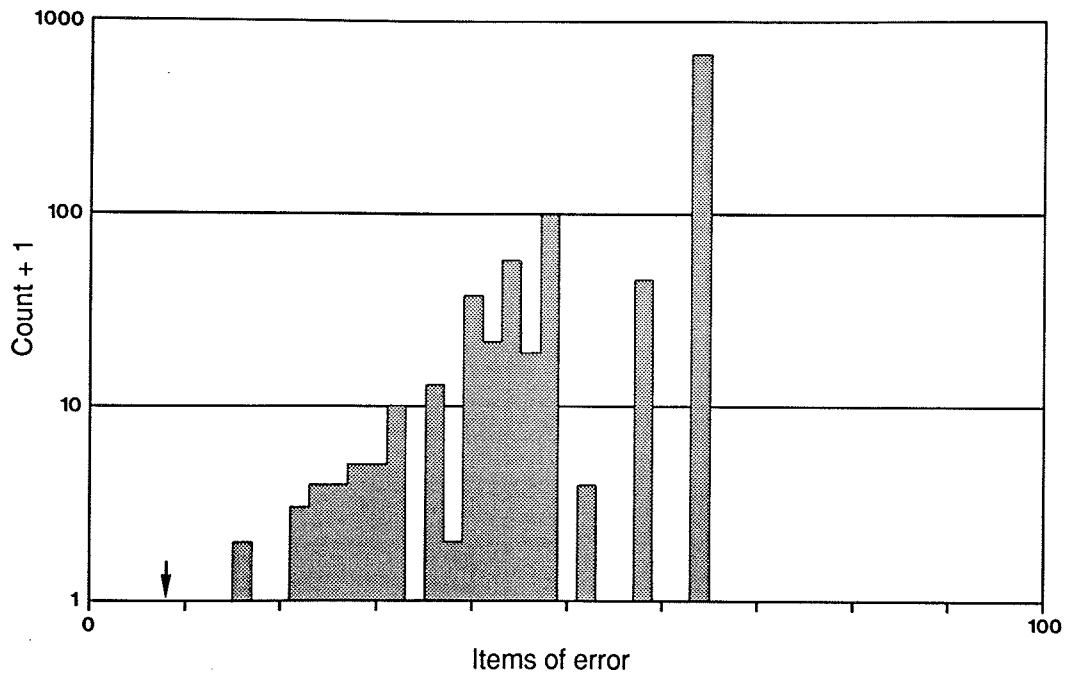
FIG. 19.   Distribution of items of error for 1,000 random trees for the eight gopher taxa when reconciled with the louse cladogram (Fig. 16) under Assumption 2. The observed value (eight) is marked by an arrow and is significantly smaller than could be expected to be due to chance $(P(H_0) = 0.001)$.
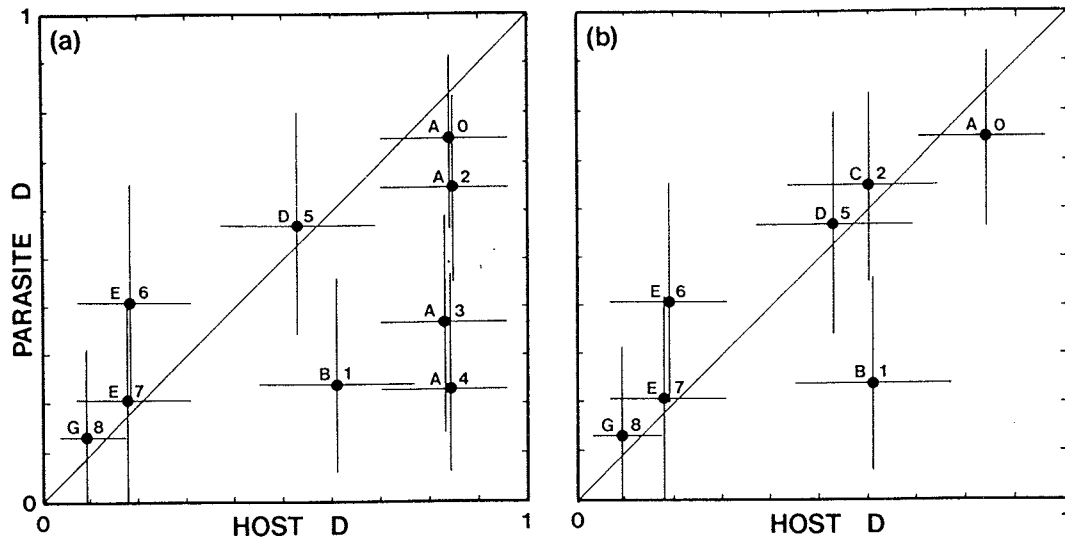
FIG. 20. Plot of heights for pairs of host (gopher) and parasite (louse) components under (a) Assumption 1 and (b) Assumption 2. Each point is the median of 1,000 bootstrap estimates; the horizontal and vertical lines are the 95% confidence intervals for gophers and lice, respectively (see Tables 5, 6). Scales are in Manhattan distance units.

is uncertainty in the topology as well. Mappings between other pairs of bootstrap trees could be explored. Sanderson (1989) has described a method for delimiting confidence sets of trees from the set of bootstrap trees.

The molecular clock hypothesis is central to tests of temporal congruence. Comparing branch lengths for additive and ultrametric trees is not an unbiased test of the clock hypothesis because current methods of assigning branch lengths to these trees are biased toward uniformity of rates

(Fitch and Smith, 1982). A better test for the clock is clearly needed (see Felsenstein's [1988] discussion of other tests). Furthermore, although the clock hypothesis may hold overall, local variations may distort estimates of the ages of particular events, resulting in false conclusions. A more sophisticated analysis would allow for such local variations in the clock (e.g., Hasegawa et al., 1989).

The use of distance methods in phylogenetic inference is controversial (Farris, 1981, 1985, 1986; Felsenstein, 1984, 1986).
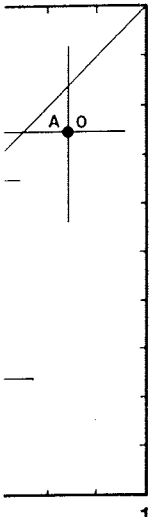
TABLE 8. Pairwise Manhattan cophenetic similarity matrix between pocket gopher taxa based on allele frequencies in gophers (upper right triangle) and allele frequencies in parasitic lice (lower left triangle). Values for the lice were computed for the tree in Figure 23a.

	ta	bo	bu	hi	ca	un	ch	he
ta	1.000	0.387	0.163	0.163	0.163	0.163	0.163	0.163
bo	0.757	1.000	0.163	0.163	0.163	0.163	0.163	0.163
bu	0.221	0.221	1.000	0.407	0.407	0.407	0.407	0.407
hi	0.221	0.221	0.318	1.000	0.472	0.472	0.472	0.472
ca	0.221	0.221	0.318	0.429	1.000	0.819	0.819	0.819
un	0.221	0.221	0.318	0.429	0.796	1.000	0.863	0.863
ch	0.221	0.221	0.318	0.429	0.589	0.589	1.000	0.901
he	0.221	0.221	0.318	0.429	0.589	0.589	0.871	1.000

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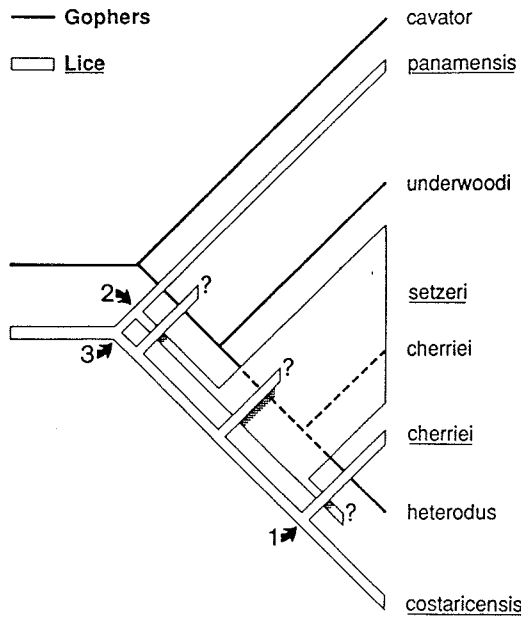| he |
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| 0.163 |
| 0.163 |
| 0.407 |
| 0.472 |
| 0.819 |
| 0.863 |
| 0.901 |
| 1.000 |

FIG. 21.   A hypothesis explaining apparent incon-
gruence between *Orthogeomys* gophers and their par-
asitic lice. Two clades of lice are postulated to have
infested the ancestor of the *O. cavator* group. The first
clade (the ancestor of *Geomydoecus panamensis* and *G.
setzeri*) differentiated with *O. cavator*, but did not dif-
ferentiate when *O. underwoodi* split from the ancestor
of *O. cherriei* and *O. heterodus*. As a result, *G. setzeri*
infests both *O. underwoodi* and *O. cherriei*. The first
clade is either extinct or uncollected on *O. heterodus*.
The second clade (the ancestor of *G. cherriei* and *G.
costaricensis*) is either extinct or uncollected on *O. ca-
vator* and *O. underwoodi*. The three predictions about
the relative ages of speciation events in the gophers
and the lice are numbered 1-3 (see text).

Because I have modeled phylogeny as an
ultrametric tree, I have used a distance
method to estimate component heights. For
both the gophers and the lice, the esti-
mated phylogenies are among the most
parsimonious (or nearly most parsimoni-
ous) trees for the data, hence little or no
explanatory power has been sacrificed by
using distances.

Indeed, with a molecular clock, both
autapomorphies and invariant characters
become informative. The number of aut-
apomorphies a taxon possesses is expected
to be proportional to the time since that
taxon diverged from its sister taxon. In-
variant characters do not discriminate be-
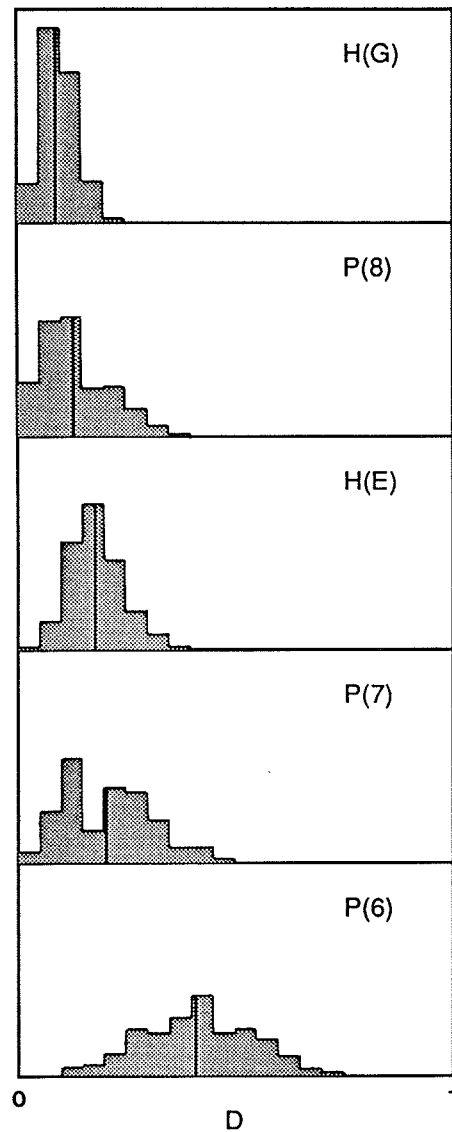tween topologies, but do provide infor-

FIG. 22.   Frequency distributions of the bootstrap
estimates of component heights for host (H) com-
ponents E and G and parasite (P) components 6, 7,
and 8. The vertical line is the median. The model in
Figure 21 predicts that pairs of components G and 8,
and E and 7, should be contemporaneous (predictions
1 and 2, respectively), whereas component 6 should
predate component E (prediction 3). The data are con-
sistent with these predictions. Scale is in Manhattan
distance units.

mation on time of divergence. It is in this
sense that "phenetic" techniques such as
UPGMA use information disregarded by
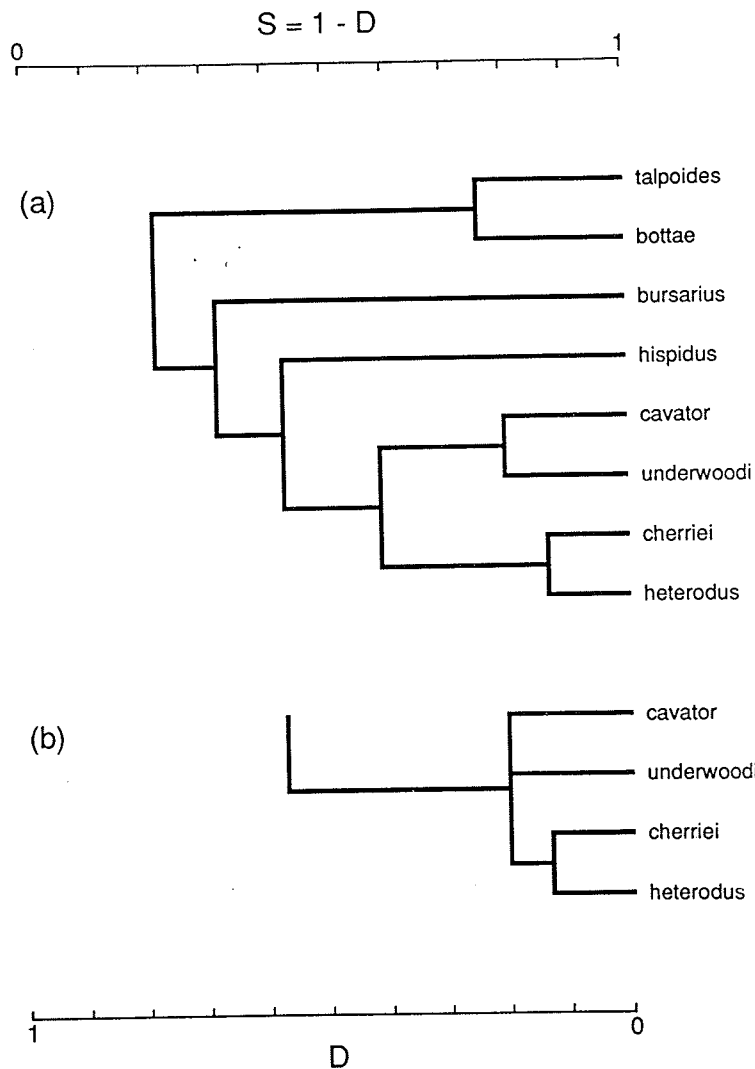parsimony methods (Cornish-Bowden,

$$S = 1 - D$$

FIG. 23. (a) Ultrametric tree for gophers derived from the parasite phylogeny under Assumption 2 (Table 8). (b) Modification of tree based on results of component mapping (Table 9).

1983; Felsenstein, 1985b). Of course, if the underlying assumption of uniformity of rates is violated, then UPGMA is not appropriate for phylogenetic inference (e.g., Kim and Burgman, 1988).

Temporal Congruence

Information on the timing of cladogenetic events permits more detailed tests of hypotheses of cospeciation than is possible with only cladistic information (the branching sequence of a cladogram). Hafner and Nadler (1988:259) pointed out that although the *Thomomys–Thomomydoecus* association is cladistically congruent (components B and 1), speciation in the parasitic lice postdates that in the host gophers (Figs. 4, 18). This they termed pseudo-cospeciation. Estimates of the number of instances of cospeciation based solely on cladistic congruence could be inflated by cases of pseudo-cospeciation.

TABLE 9. Modified pairwise Manhattan similarity matrix between gopher taxa based on ultrametric tree for lice, calculated from the tree in Figure 23b.

	ca	un	ch	he
un	0.796			
ch	0.796	0.796		
he	0.796	0.796	0.871	

Temporal information may also help resolve instances of cladistic incongruence, as I have suggested here for four species of *Orthogeomys* and their lice. In this instance Hafner and Nadler (1988) underestimated the number of cospeciation events. They postulated that *Geomydoecus setzeri* dispersed to *O. cherriei*, whereas my analysis shows that the distribution of *G. setzeri* can be explained without invoking dispersal.

Hafner and Nadler (1990) have since outlined a linear regression approach to comparing rates of evolution in host and parasite lineages. We can use a similar approach to characterize each speciation event in the history of a parasite lineage (Fig. 20b). For the 10 lice there have been nine speciation events. Two of these events (components 3 and 4 in Fig. 12) were accompanied by transfer to new hosts (in both cases from *Geomys bursarius* to a species of *Thomomys*), five were cospeciations (represented by components 0, 2, 5, 7, and 8), and one was a pseudo-cospeciation (component 1). The remaining event (component 6) was a speciation of the lice independently of their hosts, resulting in two lineages of lice infesting the same lineage of hosts. If this interpretation is correct, then there may have been up to three additional speciation events (accompanied by up to three extinction events), corresponding to the missing parasites of *Orthogeomys* (Fig. 21).

Nelson and Platnick's (1981) approach to reconciling parasite cladograms with host cladograms is just one possible method for determining the component relations between cladograms. Other possibilities include finding the largest subtree (Finden and Gordon, 1985) of hosts for which both parasite and host agree. This

method may be more appropriate if dispersal has played a major role in structuring the distribution of the parasites. By combining tree comparison methods, temporal information, and randomization tests, a rigorous approach to testing hypotheses of cospeciation (and, by analogy, vicariance) can be developed.

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