PARASITES, PHYLOGENY, AND COSPECIATION

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Running title: PHLYLOGENY AND COSPECIATION

Abstract—PAGE, R. D. M. 1993. Parasites, phylogeny, and cospeciation. *International Journal for Parasitology* 23:499-506. Host-parasite assemblages offer exciting possibilities for the comparative study of rates of speciation and evolution in different organisms. The basis for such studies must be a phylogenetic analysis of the host-parasite association. Some recent developments in this field are briefly reviewed and illustrated using phylogenies for pocket gophers and their chewing lice.

INDEX KEY WORDS: cladistics; congruence; cospeciation; phylogeny.

INTRODUCTION

THE primary goal of comparing the phylogeny of a host and its parasite is to document the history of their association. For each host-parasite association we want to be able to decide if that association is due to descent or dispersal (Brooks & McLennan, 1991). But more than this, host-parasite assemblages offer exciting possibilities for the comparative study of rates of speciation and evolution in different organisms (Hafner & Nadler, 1990). The basis for such studies must be a phylogenetic analysis of the host-parasite association.

This paper is a brief overview of some recent developments in applying phylogenetics to the study of cospeciation. I begin by reviewing some of the aspects of phylogeny that are relevant to the comparison of host and parasite phylogenies (note that I shall use the terms phylogeny and tree interchangeably throughout this paper). I then discuss some of the problems of comparing host and parasite phylogenies, with special reference to interpreting incongruence. Hafner & Nadler's (1988) recent study of cospeciation between pocket gophers and chewing lice is used to illustrate some of the points made.

This review is not intended to be comprehensive. Rather I seek to highlight some areas of recent activity and to provide some entry points into the literature. One goal of this paper is to show that phylogenies can be used to explore a number of questions in addition to resolving the origins of a particular host parasite association. One of the most exciting areas of cospeciation analysis concerns comparing the rate of evolution in host and parasites and the timing of host-parasite cospeciation (Hafner & Nadler, 1990; Page, 1990b, 1991). Another aim is to disabuse the reader of the notion that incongruence between host and parasite phylogenies must necessarily mean that one or more parasites have dispersed. The presence of multiple lineages of parasites on the same host can also give rise to incongruence (Page, in press). The expectation that the relationship between host and parasite phylogenies need be simple is naïve.

COMPARING HOST AND PARASITE PHYLOGENIES

A phylogeny of a group of organisms has several components. The most basic is recency of common ancestry — two taxa are more closely related to each other than either is to a third taxon. This aspect of phylogeny can be depicted using a cladogram (Fig. 1a). The lengths of the branches of a cladogram have no meaning, only the groups are meaningful. By making the branch lengths proportional to the amount of evolutionary change we have an additive or metric tree (Fig. 1b). The sum of the lengths of the branches between any two taxa on an additive tree represents the amount of evolutionary change that has taken place since those two taxa diverged. A special case of the additive tree is the dendrogram (Fig. 1c), in which all the terminal taxa are equidistant from the root of the tree.

Kinds of Comparison

When comparing host and parasite phylogenies the kinds of comparisons that are possible depends on the extent of our phylogenetic knowledge, which is mirrored in the kind of tree we use to represent that knowledge. The simplest comparison is between cladograms. Here we are asking whether or not hosts that are closely related harbor closely related parasites. However all tree building methods also provide some estimate of evolutionary change between taxa in the form of branch lengths. Hence we could also compare amounts of evolutionary change in the host and parasite clades by comparing lengths of the equivalent branches in the host and parasite phylogenies (that is, compare additive trees). This raises two problems. The first concerns identifying pairs of equivalent branches in the two trees, to which I shall return below. The second problem, raised in a different context by Lewontin (1984), is whether the characters used to estimate evolutionary change in the hosts and parasites are comparable. In morphological based studies this is likely to be a serious problem — for example, how does one rank changes in mammalian tooth enamel patterns with changes in setal formula in insects? Molecular data (especially nucleotide sequence

data) would seem to offer an attractive solution to this problem. In principle nucleotide sites are comparable across taxa. This is not to say that the rates of change, positional and transition/transversion biases need be the same in the hosts and parasites, but we do at least have a common unit of measurement.

Incongruence Between Host and Parasite Phylogenies

So far the implicit assumption has been that the host and parasite phylogenies are congruent (as in Fig. 1), that is, they have the same topology. Congruence is evidence that hosts and parasites have cospeciated, so that host and parasite are "associated by descent" (Brooks & McLennan, 1991;193). Conversely, incongruence is evidence for host switching, "association by colonisation" (Brooks & McLennan, 1991;193).

Phylogenetic analysis of cospeciation is based on this dichotomy between congruence and incongruence. Unfortunately the relationship between congruence/incongruence and cospeciation/colonisation is not necessarily straightforward. As Brooks & McLennan (1991) note

> "…theoretically at least, it is possible that the members of an associate group evolved as the result of sequential host switching that coincidentally mirrored the phylogenetic relationships of the hosts."

Hence congruence between host and parasite phylogenies need not be solely the result of cospeciation. Moreover, although Brooks and McLennan equate incongruence with parasite dispersal, this need not always be the case. Elsewhere (Page, 1990b; in press) I have argued that the presence of one or more lineages of parasites on the same hosts can, through either extinction or sampling error, give rise to incongruent host and parasite phylogenies. This problem is closely analogous to the distinction between orthologous and paralogous genes in molecular systematics (Fitch, 1970). For a fuller discussion of this problem see Page (in press).

Measuring Incongruence

Real host and parasite phylogenies typically contain parts that agree with each other and parts that do not; they are neither completely congruent nor completely incongruent. It would be desirable to be able to quantify the similarity between host and parasite trees. Such a measure could form the basis of a statistical test of whether the agreement between a host and a parasite phylogeny was greater than could be expected due to chance alone.

One method used to compare host and parasite phylogenies is "Brooks' Parsimony Analysis" (BPA). This method is described in some detail in Brooks & McLennan (1991) and I will not spend much space on it here. Rather I shall describe another method which emerged independently in molecular systematics (Goodman, Czelusniak, Romero-Herrera, & Matsuda, 1979) and biogeography (Nelson & Platnick, 1981). Recently the generality of this method has been recognised, and with it, the possibility that there may be a single problem of "historical association," be it between genes and organisms, organisms and other organisms, or organisms and areas (Doyle, 1992; Page in press). This method is in its infancy and a more detailed presentation will be given elsewhere. What follows is a brief sketch.

MAPS BETWEEN TREES

Consider the host and parasite cladograms in Figure 2. The two trees are incongruent in the sense that parasites 2 and 3 are monophyletic but their hosts are not. However, the two cladograms show some agreement in that parasites 2, 3, and 4 are monophyletic as are their hosts. How might we quantify this mixture of congruence and incongruence? One approach is to ask under what circumstances the two trees could actually be congruent. If the parasites 1-4 were relicts of a larger clade then the incongruence could be due to sampling error or extinction. Figure 3 shows the smallest such tree that could explain the incongruence between the two trees in Figure 2 (this tree is called a reconciled tree, see Page, 1990a). Parasites 2 and 3 could be relicts of a larger clade comprising three parasites, one of which (on host d) is either present but uncollected or it is extinct. Likewise, parasite 4 is the relict of a clade of three parasites, two of which are now unknown or extinct. The number of collection failures/extinctions required to reconcile the two trees is a measure of their agreement.

These hypotheses of collection failure or extinction are clearly ad hoc, but in principle they can be tested by looking for the missing parasites on the hosts. Furthermore, the reconciled tree (Fig. 3) makes additional predictions about the relative ages of speciation events in the host and parasite lineages. For example, the speciation of ancestral parasite 6 into parasites 4 and 7 is expected to predate the speciation of ancestral host f into hosts b and g, and parasite 7 is expected to be contemporaneous with host f. If we have information on speciation times in both host and parasite clades (for example from molecular clock data) then these predictions can be tested.

Constructing a reconciled tree requires making a map between the two trees. This map is also the basis for predictions about the relative ages of nodes in the host and parasite trees. Figure 4 shows the map between the two cladograms in Fig. 2. Each node in the parasite tree is mapped onto the node in the host tree whose

descendants include *all* the hosts of the parasite node and the fewest hosts of the other parasites (Page 1990a gives a more formal definition). Note that two parasite nodes (6 and 7) map onto the same host node (f). This implies that there were two sympatric parasite lineages present on host f before that host speciated, and neither of those lineages has completely survived to the present day. The first lineage is represented by parasites 2 and 3, the second by parasite 4.

Limitations

A limitation of the method described above is that it assumes that the host and parasites have in fact cospeciated. No horizontal transmission of parasites from one host to another is allowed. This restriction is unrealistic, but colonization events present difficulties for any tree-based method because trees implicitly assume vertical transmission (Sober, 1988). So far attempts to develop a method that combines both class of events have failed. Brooks Parsimony Analysis uses Wagner parsimony to fit parasite trees onto host trees and endeavors to incorporate both cospeciation (vertical transmission) and colonisation (horizontal transmission) events. However, this method can produce quite spurious results with, if interpreted at face value, would require the ancestors of a present day parasite to disperse every time the present day parasite disperses, or descendants of an ancestral parasite to go extinct even if their ancestor has gone extinct (and hence the descendant could not themselves have existed)(Page, 1990a)!

The tree mapping method described above avoids these problems by allowing just vertical events. However, horizontal (colonization) events can still be incorporated into the analysis by simply deleting the parasites thought to have dispersed before mapping the two trees. An example of this procedure is given below.

A CASE STUDY: GOPHERS AND LICE

To illustrate some of the ideas presented above I shall use Hafner & Nadler's (1988) seminal study of cospeciation between pocket gophers and their chewing lice. The more than 400 species and subspecies of pocket gopher (Rodentia: Geomyidae) in North and Central America are host to 122 species and subspecies of parasitic lice (Mallophaga: Trichodectidae). In the opinion of Hellenthal & Price (1990:186):

> "Pocket gophers and their lice represent a unique opportunity for the study of host parasite relationships and cospeciation. No other arthropod-vertebrate association offers such a combination of great host diversity and availability coupled with the abundant and nearly universal presence of a diverse but related parasite fauna that has little or no impact on host survival."

Hafner & Nadler (1988) obtained allozyme frequency data from eight species of pocket gopher (representing four of the six recognised gopher genera) and their parasitic lice (a total of ten species from the two currently recognized genera, *Thomomydoecus* and *Geomydoecus*). The phylogenies they obtained are shown in Figure 5. For both the gophers and the lice the pattern of genetic divergence was "clock-like" so Hafner and Nadler used UPGMA to estimate the phylogenies. The trees found by UPGMA are also among the most parsimonious trees for the data (see also Page, 1990b).

Comparing the two trees Hafner and Nadler identified six putative instances of cospeciation between hosts and parasites, and three instances of dispersal of parasites from one host to another. The use of allozyme data for both hosts and parasites establishes a common scale for comparing amounts of divergence in the two lineages

(cf. Lewontin, 1984). This, together with the clock-like evolution in the two clades allowed Hafner and Nadler to compare not only the relative branching orders of the host and parasite cladograms (i.e., the cladistic aspect of the phylogenies), but also the estimated relative times of divergence for the hosts and their parasites.

Before discussing the gopher and lice data set further it is worth commenting on Brooks & McLennan's (1991:314-315) appraisal of this study (note that they erroneously refer to the lice as mites). Brooks and McLennan criticize Hafner & Nadler (1988) because

> "the allozyme data used to calculate the genetic distances between species were also used to construct the phylogenetic trees. Formulating evolutionary hypotheses about relationships between characters using a phylogenetic reconstruction based upon those characters introduces a degree of circularity, and thus weakens the resulting evolutionary hypothesis."

Hafner & Nadler (1988) were comparing estimates of genetic divergence between taxa based on the UPGMA dendrograms. These are part of the phylogenetic hypothesis as much as the tree topology itself, they were simply comparing two aspects of the one structure. There is no circularity. Brooks & McLennan (1991) also object to the use of "phenetic" methods of tree building because of the dependence on the molecular clock assumption. However, the validity of this assumption can be tested. Page (1990b) could find no evidence for significant departures from clock-like behavior for either the gopher or the lice data.

Is There Evidence for Cospeciation?

Figure 6 shows the reconciled tree for the gopher and lice trees shown in Fig. 5. The tree is large and requires a minimum of 10 parasite extinctions to reconcile the two trees. This seems excessive, and indeed Page (1990b) reports that the fit between the two trees is not significantly better than could be expected due to chance alone. Hence it seems that an hypothesis of complete cospeciation between gophers and their lice is untenable.

However, if we allow for two of the host switching events postulated by Hafner & Nadler (1988), namely those involving the lice *Geomydoecus actuosi* and *G. thomomyus*, by deleting those two parasites then the fit between the remaining lice and the gophers is much better (Fig. 7). There is still some incongruence, requiring the presence of two sympatric lice lineages to be postulated for the gophers in *Orthogeomys*, but this hypothesis correctly predicts that the genetic distance between *Geomydoecus panamensis* and *G. setzeri* should equal that between the gopher *O. cavator*and its sister taxa, and that the difference between the louse clade *G. panamensis* and *G. setzeri* and the clade *G. cherriei* and *G. costaricensis* should be greater than that between *O. cavator*and its sister taxa (see Page, 1990b).

Comparing the gopher and lice cladograms allows an assessment of how much cospeciation there has been between the two taxa. There are nine lice speciation events, of which two can be attributed to host switching involving the *Geomydoecus actuosi* and *G. thomomyus*, and one is a unique event in the lice that gave rise to the two sympatric lice clades on *Orthogeomys*. The remaining six louse speciations can be attributed to cospeciation with their gopher hosts.

Comparing Rates of Evolution

Difference in amounts of evolutionary divergence between a given pair of host and parasite taxa may reflect either different rates of evolution, different divergence times, or a combination of both. Without some way of estimating divergence times it is difficult to distinguish between differences in rate and differences in timing.

However, if there is a molecular clock in both taxa the rate of evolution in host and parasites will be constant (although the two rates can be different) our task is much simpler. We can ask two questions: (1) is the rate of molecular evolution the same in the two taxa, and (2) is there any delay in the response of parasites to a host speciation event.

Hafner & Nadler (1990) outlined a simple method for addressing these questions that involves plotting genetic divergence between pairs of parasites against genetic divergence between the pairs of corresponding hosts. However, I have argued (Page, 1991) that this approach is flawed, and that we should be comparing dendrograms for the gopher and lice taxa, specifically dendrograms containing just those hosts and parasites that are thought to have cospeciated. Host switching events are not relevant to this problem. Also irrelevant are parasite speciations that produce sympatric host lineages.

Figure 8 shows the dendrograms for the gophers and lice after all non-cospeciation events have been removed. By definition the trees have the same topology, but note that the estimates of the genetic divergence (and hence the time of speciation) in the two taxa differ (compare nodes B and 1). By plotting the divergence of the six pairs of nodes against each other (Fig. 9) we can explore the relationship between genetic divergence in the hosts and parasites by drawing a line through the data. The slope of the line reflects the relative rate of evolution in the two groups (Hafner & Nadler, 1990). A slope of 1 indicates both taxa area evolving at the same rate. A non-zero intercept indicates that speciation in the parasites is not synchronous with their hosts.

For the gophers and lice the correlation in genetic divergence is high (r = 0.818) and the slope of the line is nearly 1, suggesting that the two clades are evolving at the same rate. This is an interesting result, given the differences in population size and generation time in gophers and lice. However, the analysis is not quite straightforward. The data points in Fig. 9 are not independent, and the degree of independence is a function of the underlying tree topology. The more unbalanced or

asymmetrical the shape of the tree the greater the possibility of observing a high correlation between the genetic divergences due to chance alone (see Page, 1991). For these two trees the probability of getting a correlation of 0.818 or higher is 0.55.

Tree shape affects our ability to distinguish between correlation between host and parasite divergence due to a causal relationship and correlation that is simply an artifact of tree shape. The more balanced the tree the easier it is to distinguish between these two sources of correlation. This fact could be used to guide sampling strategies for host and parasite taxa if the broad outlines of either the host or parasite cladogram are known. For the gopher and lice example discused here, sampling additional gophers and their lice from *Thomomys*, *Geomys*, *Pappogeomys*, and *Zygogeomys* (see Honeycutt & Williams, 1982: fig 2) would help balance the host cladogram and hence enable a more sensitive test of hypotheses concerning the timing of gopher and louse speciation events.

PROSPECTS

The explosion of nucleic acid sequence data promises further exciting developments in the phylogenetic analysis of host-parasite assemblages. The acquisition of numerous large, independent data sets will allow additional testing of phylogenetic hypotheses, the prerequisite for phylogenetic analysis of host-parasite associations. Sequence data also allows the use of a common scale of divergence (nucleotide substitutions), avoiding the problems of comparing different character systems (cf. Lewontin, 1984). Of course, phylogenetic analysis of sequence data is not without its own problems (see for example the papers in Miyamoto & Cracraft, 1991).

Parasitology stands to gain greatly from phylogenetic studies of host-parasite assemblages. The most informative studies will be those with carefully thought out sampling strategies and extensive, comparable character data. Hafner & Nadler's (1988) study illustrates what can be achieved with modest data but a careful design. The gopher-lice system will repay further study (e.g., Sudman & Hafner, 1992).

Another system that looks attractive is the sea bird-lice assemblage being studied by Paterson, Gray, & Wallis (in press; see also Timmermann, 1965).

Unsolved Problems

The following problems are "unsolved" in the sense that either the problem has yet to be adequately tackled, or the proposed solutions are the subject of some controversy. This list is not intended to be comprehensive, nor are the problems listed unique to this field, rather, it is intended as a guide to where some of the problems lie.

(1) How much faith can we place in our estimates of phylogeny? Is it possible to place confidence limits on these estimates? (Felsenstein, 1985; Sanderson, 1989)

(2) Is it possible to combine both vertical and horizontal transmission in one procedure for comparing host and parasite phylogenies, without leading to biological absurdities?

(3) Is the rate of molecular evolution ever sufficiently clock-like to enable us to estimate times of divergence, either relative or absolute?

(4) How do we compare rates of evolution and timing of cospeciation in the absence of a molecular clock? (See Page, 1991 for when there is a clock.)

(5) What are appropriate null hypotheses for testing hypotheses of cospeciation? (Hafner & Nadler, 1990; Page, 1990a, b)

(6) What are the effects of tree topology on estimates of amounts of evolution? (Sanderson, 1990)

Acknowledgements — I am indebted to Allen Rodrigo for inviting me to the "Phylogenetics and Parasitology: Methods and Applications" symposium at the Joint Conference of the New Zealand and Australian Societies for Parasitology, and for his efforts in obtaining funds for my trip. I also thank the New Zealand and Australian Societies for Parasitology for their generous grant enabling me to attend the symposium. My research is funded by a Research Fellowship from the Natural History Museum, London.

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Legend to figures

FIG 1. Three kinds of phylogenetic trees for hosts and parasites: (a) cladograms, (b) additive trees, (c) dendrograms. Cladograms allow just a comparison of recency of common ancestry, additive trees also permit comparisons of amounts of evolutionary change, while dendrograms allow comparisons of relative timing of speciation (see text).

FIG 2. Incongruent host and parasite cladograms. Note that parasites 2 and 3 are monophyletic but their hosts (b and c) are paraphyletic.

FIG 3. The reconciled tree explaining the incongruence between the host and parasite trees in Figure 2. Nodes in the tree that are shaded represent parts of the parasite tree that are missing due to either collection failure or extinction, so that the four extant parasites 1-4 are regarded as relicts of a larger clade (see text).

FIG 4. The map between the host and parasite trees in Figure 2 used to construct the reconciled tree. Each node in the parasite cladogram is mapped onto the corresponding node in the host cladogram. A duplication is required at node f because two nodes in the parasite tree (6 and 7) both map onto node f in the host tree.

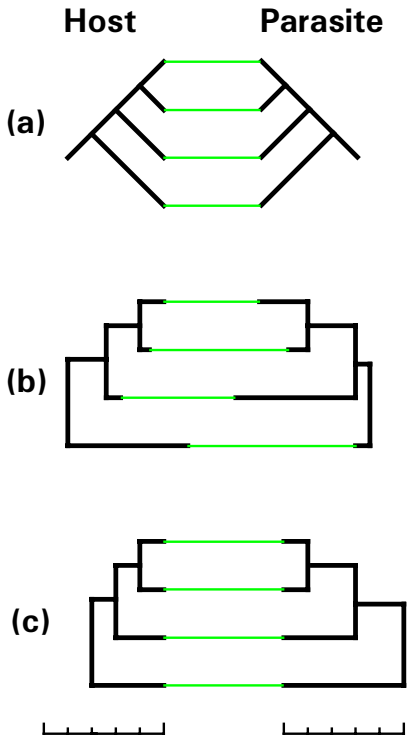
FIG 5. Phylogeny of eight species of pocket gophers and their parasitic lice, based on UPGMA clustering of allozyme frequency data (after Hafner & Nadler, 1988: fig. 2). The nodes in the host and parasite trees labeled A-F represent the cospeciation events proposed by Hafner and Nadler.

FIG 6. Reconciled tree for the gopher and lice phylogenies shown in Figure 5, allowing no host switching. Solid branches lead to extant lice, hollow branches represent missing or extinct parasites, and the four circles represent "duplications" of the parasite lineages. The two solid circles are duplications due to incongruence between host and parasite trees, the two open circles are duplications required because of the overlap in the host ranges of the descendants of that node. Note the large amount of missing or extinct parasites that must be postulated in order to reconcile the two trees.

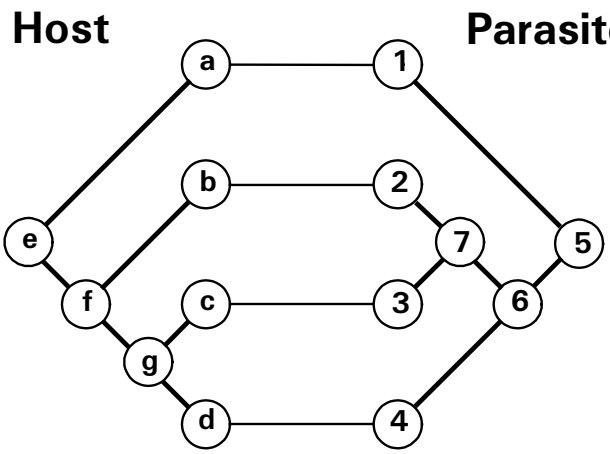
FIG 7. Reconciled tree for gopher and lice phylogenies after allowing for two host switching events involving G*eomydoecus actuosi* and *G. thomomyus*. Compare with Fig. 7.

FIG 8. Dendrogram for the six cospeciation events between the pocket gophers and lice implied by Fig. 7. Scale is in Manhattan distance units. (After Page, 1991: fig. 3)

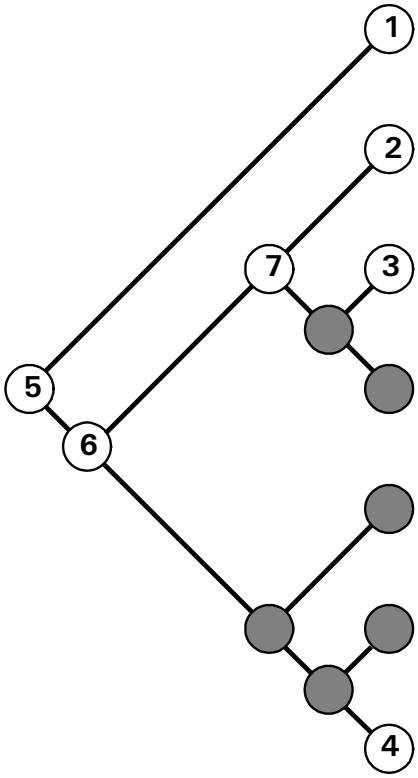
FIG 9. Bivariate plot of cluster heights for the six pairs of cospeciation events in the gopher and louse dendrograms in Figure 8. Scale is in Manhattan distance units. (After Page, 1991: fig. 4)



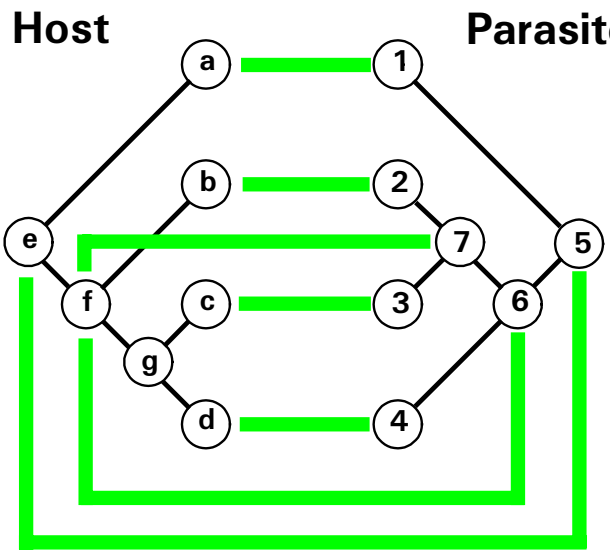
R. D. M. Page Figure 1



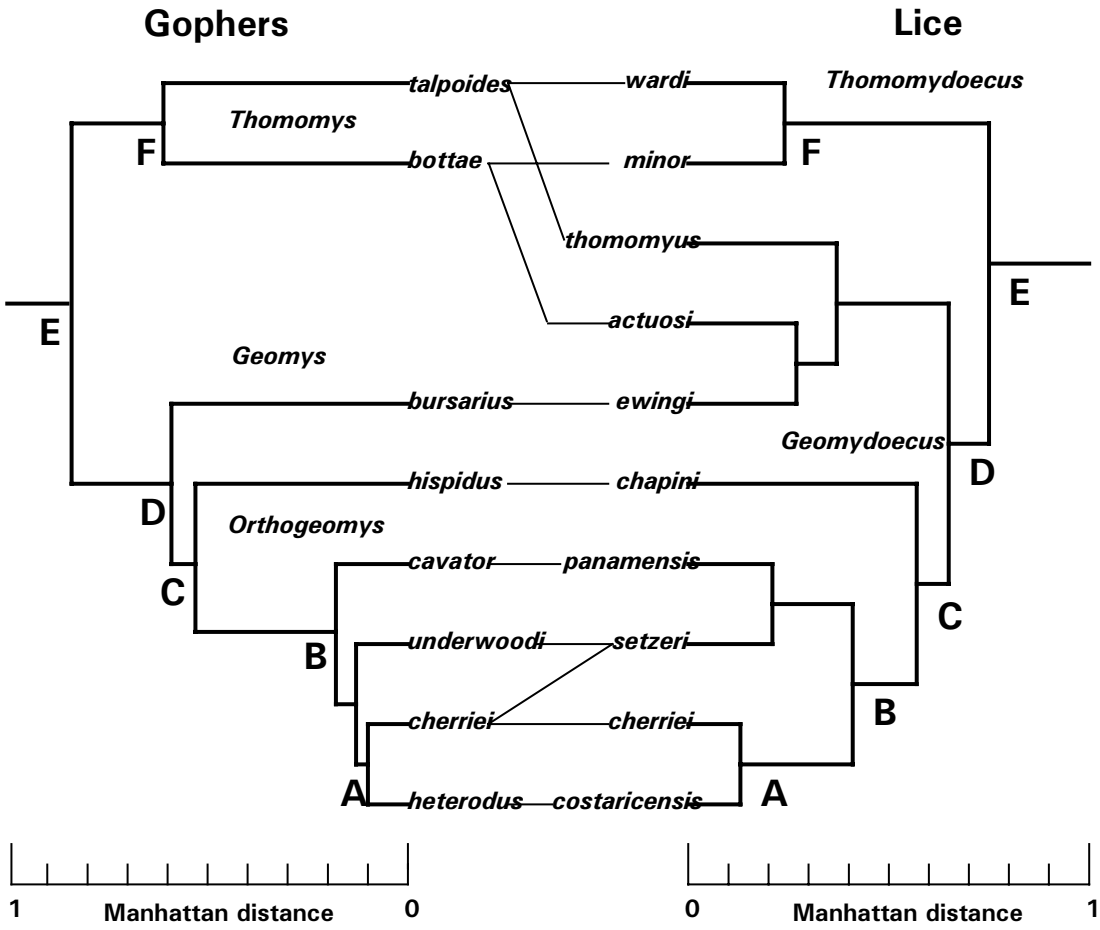
R. D. M. Page Figure 2



R. D. M. Page Figure 3



R. D. M. Page Figure 4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ewingi
Geomydoecus
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hispidus
chapini
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cavator
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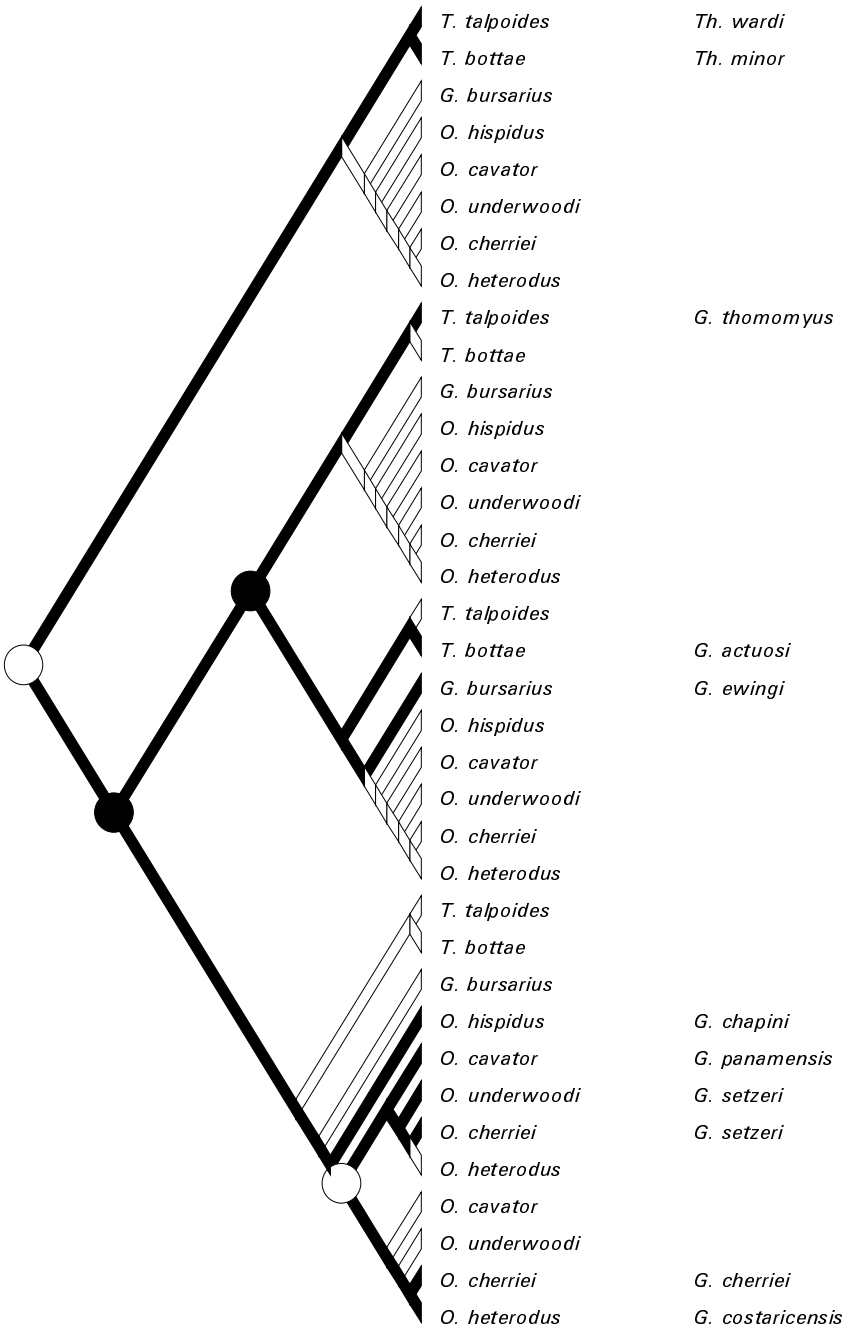
Fig. 5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O. heterodus
O. cavator
O. underwoodi
O. cherriei
O. heterodus
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Th. minor
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G. setzeri
G. setzeri
G. cherriei
G. costaricensis

Fig. 6

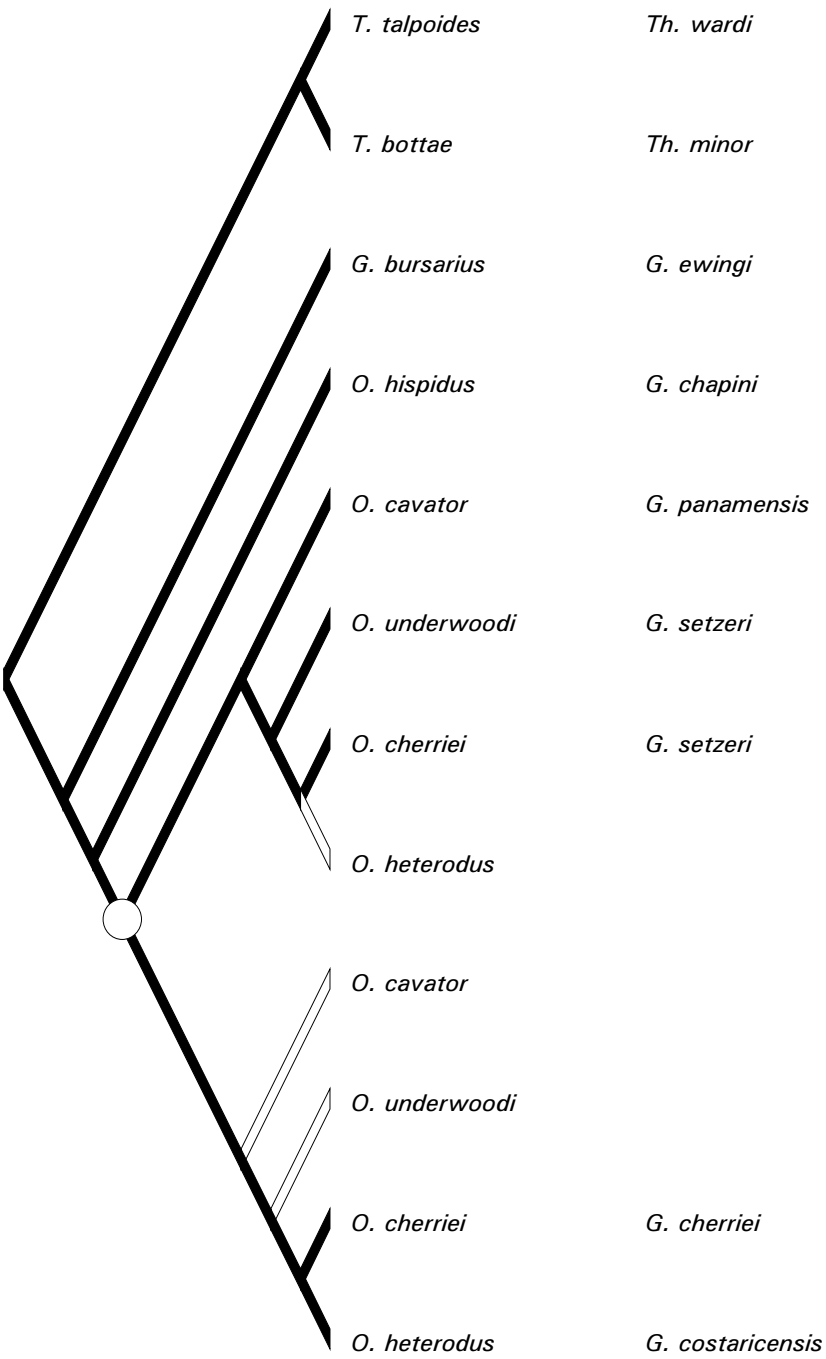
T. talpoides
Th. wardi
T. bottae
Th. minor
G. bursarius
G. ewingi
O. hispidus
G. chapini
O. cavator
G. panamensis
O. underwoodi
G. setzeri
O. cherriei
G. setzeri
O. heterodus
O. cavator
O. underwoodi
O. cherriei
G. cherriei
O. heterodus
G. costaricensis

Fig.7