

The Reliability of Overall Convergence Relationships in Cladophenograms

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Abstract. A method for establishing reliability for implied shared ancestry between lineages distant on a cladogram is described. Exact binomial confidence interval calculation is used against a null of random and equal support for all three branch arrangements for any one internode. Across two or more concatenated internodes, reliability was evaluated by summing support for the optimal branches and for all three possible branch arrangements of nearest neighbor interchange at each internode. Significance of support was tested for the summed optimal lengths above an expected level of 1/3 of summed steps at any internode. An example is given with a morphological data set by superimposing a phenetic ordination over a cladogram. Four of seven apparent cases of convergence were reliable at a 0.95 confidence limit. Morphological data sets can, at this level of resolution, be used to infer reliable phylogenetic relationships. Keywords: confidence intervals, branch arrangements, significance, morphology

Introduction

Phylogenetic signal in cladograms is assumed when monophyletic taxa are selected for analysis. Strong overall nesting in cladograms is also demonstrable with a variety of statistical techniques, such as parametric bootstrapping with randomized data sets (Zander, 2003). The details of a cladogram are often arguable, however, especially branch arrangements based on morphological data for which reliability measures like the bootstrap are either not available or are not directly convertible into confidence limits.

Distances between lineages in a phylogram have been important in forensic medicine, where Metzker et al. (2002) found that a particular HIV lineage embedded within certain other HIV lineages demonstrated significant shared ancestry with those lineages, and in conservation biology, in which patristic distance is a

measure of relative evolutionary isolation of a gene pool (e.g., Zander, 1996). Patristic distance (the number of steps between two lineages summed across internodes) is not alone a good measure of branch arrangement reliability because the two alternative branch arrangements for any one internode may each have relatively large, contrary support.

There have been several methods proposed to evaluate support for internal branches of a parsimony tree (reviewed by Zander, 2001), but most of these require the abundance of data provided by molecular data sets. Using a modification of the Conditional Probability of Reconstruction measure as used by Zander (2001) for molecular data, it is possible to decisively evaluate the reliability of a single internode of a cladogram generated with a morphological data set.

In this paper, the lineages that are dealt with through nearest neighbor

interchange (NNI) are labeled A, B and C. Support in numbers of steps for each arrangement is labeled with letter names of the optimal terminal taxa, e.g. support for ((AB)C,D) is AB, for ((AC)B,D) is AC. By convention, A and B are the sister groups terminating the internode of the optimal tree, C is the basal branch (and D the outgroup in 4-taxon trees), thus the null is that support in numbers of steps A and B is equal to support for A and C, and for B and C; or $AB = AC = BC$, and all variation is random; thus the null arrangement is a star or unresolved tree, which is the longest possible tree, where all character states are autapomorphous, none shared by inferred ancestors. The alternative hypothesis is that one of the three possible arrangements has support larger than expected by chance alone, and is probably due to shared ancestry. Thus, if AB is significantly larger than $1/3$ of the sum $AB + AC + BC$, then that support may be assumed due to shared ancestry at a particular confidence interval, while all support for AC or BC is due to parallelism between these two pairs of taxa.

This estimation of significance is done here using VassarStat's (Lowry, 2003) exact BCI calculation, which treats the data as a Bernoulli trial. Although there are three possible arrangements, a BCI evaluation is justified. After a "best" tree is obtained, e.g. by maximum parsimony, the support in numbers of steps for each of the two alternative arrangements of lineages at any one internode must be assumed to be due to parallelism (random generation of synapomorphies from closely related lineages) and the two values may be added. As a theoretical example, if support for AB is 4 steps, and that for AC is 2 steps and for BC is 0 step, it does not matter if AC were, say, 1 step and BC were 1 step. The BCI confidence interval (BCI) is 1 minus the chance of the data as generated by chance alone with alternative steps pooled to make two categories. In the case of this example, 1 minus the chance of 4 or more successes out of 6 trials at $1/3$ probability yields a BCI of 0.90. A multinomial evaluation (SISA, 2003) of the ratio 4:2:0 produces a CI of

0.82 (the chance that, for instance, a three-sided die generating this data is loaded), and that of the ratio 4:1:1 produces a CI of 0.66; the differences are due to the spread of data, which is not relevant a posteriori.

Reliability in statistics has been defined as "morally certain" (J. Bernoulli in Newman, 1956) as opposed to "absolutely certain," and such confidence is now generally expressed as a confidence or credible interval with frequentists and Bayesians providing various fine distinctions between the two (Lewis, 2001). In this paper, reliability is couched in a rather Bayesian manner as that level of rejection of the null hypothesis of random generation of data at which one is then willing to act given the risk of being wrong--but see Bernardo & Smith (1994) for cautions on minimax thinking. That is, a reliable branch arrangement is one on which further analysis, such as biogeographic conclusions, will be based in spite of a strong antipathy to being wrong in one's science. Because phylogenetic estimation deals with reconstruction of single historical events, not the chance that a future or past series of like events can be estimated from a known series of like events, the analysis is philosophically Bayesian though the Bayes theorem may not be used. In sciences using statistics, the confidence intervals 0.95 or 0.99 are commonly accepted as minimal for reliability, and here the former is adopted.

The minimum level for a reliable reconstruction of a single internode at 0.95 BCI is a ratio of 3:3 of AB:(AB + AC + BC). This ratio would occur only 4% of the time if generated randomly. Since the null is a star, the chance that AB would be supported by 3 advanced states is $(1/3)^3$. Other levels of support possible but rare with morphological data sets would be 4:5, 5:7, 6:9, and 7:11, all of which would provide at least a 0.95 BCI.

Morphological data sets commonly do not have enough data relevant to any one internode to calculate the probability of AB not occurring by chance alone at a commonly accepted CI of 0.95 (Zander, 2003). That is, the support measure AB--the

number of steps supporting the lineage ((AB)C,D)--is usually not high enough in comparison with $AB + AC + BC$ to justify a judgment of confidence. Intuitively, however, two or more concatenated internodes may combine to provide such reliability; i.e., sister groups should be more reliably closely related to each other than to a third lineage when that third lineage is farther away in numbers of internodes on the cladogram. The aim of this paper is to generate a BCI that gauges the reliability of a hypothesis of shared ancestry of each of two pairs of four lineages separated by several contiguous internodes. The null hypothesis is that no internode exists (i.e. the data are not distinguishable from a random distribution) and the alternative hypothesis that there is one internode between the pairs of putative sister groups. This also obviates the multiple-test problem to which all lineages with reliability measures at each internode are vulnerable.

Calculated support for alternative branch arrangements of each of many concatenated internodes may be summed and compared. This is acceptable for several reasons. First, support contrary to the support for the optimal branch may be limited to that from NNI (i.e. support for the two immediate alternative branch arrangements for each internode) because once a "best" tree is decided on, the reliability of branch arrangements becomes a local problem. We are no longer searching for an optimal tree, we are evaluating the reliability of parts of that tree, and homoplasy in unrelated lineages (in the context of the cladogram) is not relevant. It is fail-safe because if support for the optimal branch arrangement is significantly higher than that for the two arrangements involving the phylogenetically closest taxa for that cladogram, then there is no point in involving more distantly related taxa in estimates of reliability. If the support for the optimal arrangement is not significantly different from the expected null, then the branch arrangement is no longer of interest. Though poorly supported arrangements may interfere with each other by exchanging

branches in slightly longer trees, this is also of no relevance to assessment of local reliability because a minimally acceptable BCI cannot be expected. Direct comparison of alternative branches when evaluating support has been largely ignored in the past by strict cladists, and this has been well demonstrated by Wilkinson et al. (2003).

Second, in my experience of testing a random data set generator (Zander, 1999), sets of random data will produce a most parsimonious cladogram that is almost always fully resolved, thus resolution alone is not a measure of reliability (Zander, 2003). Adding support pro and con concatenated branches on a cladogram of maximum parsimony generated from a randomized data set will soon generate significant support for AB because AB (where AB conventionally always labels the greatest support) is with randomized data arbitrarily and wrongly chosen as the (phylogenetically) loaded side of a (three-sided) coin. In an actual data set, however, the most parsimonious cladogram is already demonstrably more strongly nested than by chance alone, due to the shared ancestry found in the pre-selected taxa included in the study group. Therefore, the cladogram itself is the result of a priori phylogenetic loading. Also, a parametric bootstrap involving randomized data sets demonstrated that the data set used in the present study is well nested (Zander, 2003).

Third, one may object that evidence against the optimal arrangement is support for one of the two alternative arrangements, and these arrangements are not nested so support for them cannot be added. Calculations, inferences, or judgments, however, involving internodes that are not demonstrably reliable have no practical outcome, since the null hypothesis is that no internodes exist. Demonstrating that the data over two or more contiguous internodes on a most parsimonious cladogram do allow reliable recognition of shared ancestry of a pair of lineages in reference to a second pair simply means that at least one internode is quite sure between the two pairs.

Convergence is commonly defined as nonhomologous character states derived separately from character states that are themselves different, and parallel evolution is restricted to identical states derived independently each from the same ancestral character state. Usually homoplasy as discussed in the literature is that which is evident on the most parsimonious cladogram. Yet there is usually some homoplasy between the three branch arrangements generated by NNI, that is, some support for AC and BC (hidden alternative arrangements), here termed parallelism. Convergence in general refers to homoplastic character states duplicated at a distance in a cladogram. There is, however, a general convergence phenomenon involving many characters. Such overall convergence is a problem in many taxonomic groups such as the Pottiaceae (discussion by Zander, 1977, 1993: 13, 26), where certain phylogenetically distant taxa appear to have adapted similarly to a particular environment or are morphologically similar for no clear reason at all. The measurement of the degree of such convergence is possible with various forms of phenetic analysis, but phenotypic similarity may not reflect evolutionary relationship. A way to evaluate both evolutionary and phenetic relationships simultaneously is to combine a distance measure and a cladogram: a "cladophenogram" (Nickrent, 2003) or "phylogram" (Stuessy, 1990: 135), though the latter term is more commonly applied to cladograms with branch lengths that are proportional to support (evolutionary distance).

Zander's (1998) study of the 22 species of the moss genus *Didymodon* Hedwig (Pottiaceae) with 20 morphological characters (29 character states) demonstrated that certain species exhibited overall convergence in that they were distant in the cladogram but relatively close in the principal component analysis. This paper addresses the question: "Are these convergent relationships reliable?"

Materials and Methods

This paper is based on the morphological data set and analyses of Zander (1998) with 4% of the data scored as missing. In that study, a phyletic analysis combining cladistics, phenetics and patristics (see Stuessy, 1990) demonstrated convergence by combining a hypothetical evolutionary tree with a phenetic distance ordination. A cladistic analysis was done with the data set (Zander, 1998) of 20 morphological characters of 22 North American species of the genus *Didymodon* with *Barbula unguiculata* as outgroup. The parsimony software Hennig86 (Farris, 1988) was used to generate the most parsimonious tree or trees using the commands "mh*;bb*" for heuristic branch-swapping. The data were treated as non-additive (non-ordered) and equal weighting was used. Multiple runs using randomized addition sequences found no multiple islands (Maddison, 1991) of most-parsimonious trees. This work was replicated (Zander, 2001) with similar results with PAUP* (Swofford, 1998), and using the heuristic search, tree-bisection-reconnection (TBR) algorithm, unordered, steepest descent not in effect, ACCTRAN, MulTrees, and no weight. Three trees, differing only in placement of *D. nicholsonii* and *D. sinuosus*, were obtained, and an optimal tree (Fig. 1) was selected for analysis because it was closest to the UPGMA results (Zander, 1998). The internal branch lengths of the selected tree were calculated. User-defined tree formulae were used to exchange each of the sister branches terminating an internal branch of the fully resolved tree with the next most basal branch (no other variation was allowed as recalculation of optimal relationships is not the object of this study). These formulae were created by hand, though a program like TreeView (Page, 1996, 2001) would provide accurate constraint formulae after swapping a branch on a graphic of a complex tree. The lengths of these two new user-defined internal branches were obtained with PAUP* by simply searching again. Thus, three branch length values (number of steps) were determined, one for the optimal branch, and

two values corresponding to the lengths of the two alternative branches obtained by NNI. This was done for each internal branch.

A standardized principal component analysis (PCA, Sneath & Sokol, 1973; Kovach, 1995) was performed with the same morphological data set to show similarities in two-dimensional ordination. There was no variation in results with different data orderings. Axes 1 and 3 were chosen to avoid the distortion of the unusually high score for propagulum type on axis 2. Axes 1 and 3 reflected 45% of the variation, unrotated to preserve the usual multiple-variable representation of Axis 1. Plots of axes 1 and 2, and 2 and 3, supported the convergences seen in 1 and 3.

The PCA plot and the cladogram were combined into a cladophenogram. Pairs of phylogenetically distant taxa that were relatively near each other on the PCA plot were evaluated against the null hypothesis, which stated that these lineages were unresolved and any internodes between them were generated randomly at a probability of 1/3. This was done through exact BCI analysis of support pro and con of NNI branch arrangements of each internode as summed across the several internodes between the taxa of interest.

Results

One of the three most parsimonious phylogenetic trees of 22 species of *Didymodon* (outgroup *Barbula unguiculata*) from the study by Zander (1998) was selected as most like the results of UPGMA analysis (Fig. 1). Tree length is 63 steps, consistency index is 0.44. The bold-faced capital letters correspond to the same species in the cladophenogram (Fig. 2). Numbers above the internodes are ratios of the steps supporting the optimal branch to the sum of the steps supporting the optimal branch and the two possible alternative branch arrangements though NNI, that is, AB:(AB + AC + BC).

An overlay of the principal components analysis and the evolutionary tree (the terminal taxa are represented by single capital letters, see Fig. 1 and below) is

presented in Fig. 2. The stars are placed between pairs of phylogenetically distant taxa that appear phenetically similar. Overall convergence was initially apparent for the seven species pairs labeled with letters (Figs. 1 and 2): A (*Didymodon anserinocapitatus*) and R (*D. sinuosus*); B (*D. asperifolius*) and T (*D. tophaceus*); E (*D. fallax*) and K (*D. michiganensis*); G (*D. giganteus*) and M (*D. nicholsonii*); I (*D. leskeoides*) and V (*D. vinealis*); D (*D. brachyphyllus*) and N (*D. nigrescens*); L (*D. nevadensis*) and P (*D. revolutus*).

Zander (2001) reported AB, AC and BC support values for the internodes in this cladogram (Fig. 1). Following the rationale above, total support pro and con for each of the sets of contiguous internodes between the pairs of taxa above was calculated: support ΣAB for the internodes of the optimal branch arrangement was added and compared to the support $\Sigma(AB + AC + BC)$ through exact BCI calculation (Lowry, 2003). This calculates the chance that this number of tosses of a phylogenetically loaded three-sided coin would produce ΣAB by chance alone, and when subtracted from unity is in effect the BCI or the chance that these data are not to be expected by chance alone. A high CI would signal a good chance that one true internode exists between the pairs of taxa.

Results (Table 1) of this study measure the reliability of the previous work. Of the seven apparently convergent pairs of species, four pairs had reliable (0.95 or greater CI) separation by at least one internode, and overall convergence between distantly related species in the genus *Didymodon* (widely recognized as one of the most taxonomically difficult of the mosses) was demonstrated with confidence.

Discussion

With the paucity of data in morphological data sets, bootstrapping and jackknifing produce sparse results. Although the decay index (Bremer, 1988, 1994) is commonly used with morphological data, it has been criticized by, e.g., Giribet (2003), Oxelman et al. (1999), and Yee (2000), especially in

that the actual length of the branch is needed to give meaning to this measure. In the local sense it means that the optimal branch is n steps longer than the next alternative branch arrangement, and does not take into account that there are three possible branch arrangements for any one internode. This definition, of course, discounts branch collapse with incremental relaxation of parsimony caused by homoplasy in distant areas of the tree that would lower the decay index, and it perhaps might be better called a "local decay index" (Zander, in press). Thus, a local decay index of 3 for an optimal branch 5 steps in length may mean in the worst case that there are two alternative branches each with support of 2 steps. The chance, then, of 5 steps occurring by chance alone out of 9 steps with a null hypothesis of random generation of steps at 1/3 probability is 0.15, which is not generally considered statistically significant. The ambiguity of the decay index as usually implemented and its sensitivity to relationships elsewhere in the cladogram make it a poor measure of local branch arrangement reliability.

Consider the analogy of a loaded three-sided coin, where strong or weak support for the optimal branch arrangement (against support for each of the other two possible arrangements) is equivalent to strong or weak loading on one side of the coin. The results of flipping a weakly loaded coin is not different when they are summed (e.g. 20 tails, 15 heads, 14 third-side) from those of switching back and forth between a strongly loaded coin and a fair (random) coin (you still get 20 tails, 15 heads, 14 third-side). One might tell when a fair or weakly loaded coin was occasionally inserted in a series of flips by analysis of the data from short runs of flips (e.g. the portions of the cladogram connecting stars, as shown in Fig. 2). Analysis of the summed support pro and con the optimal arrangement across particular numbers of contiguous internodes can give a measure of either the degree of phylogenetic loading of one evolutionary coin, or the insertion of randomized data among data giving a strong signal (2 or more coins). However, if the

BCI is low, then the null hypothesis cannot be rejected at the selected confidence limit. Because such data can be combined, this method is especially valuable for morphological data that seldom provide sufficient information for statistical analysis of the reliability of individual branch arrangements.

Upweighting in parsimony analysis will increase the CI as calculated here. For instance, consider a AB:(AB + AC + BC) ratio of 4:6. If all characters were not weighted, then at 1/3 probability the CI would be 0.90, but if half of the characters in the data set were weighted double, and the weighted and unweighted characters were evenly distributed among taxa, the ratio would be (4+2):(6+3) or 6:9, with a CI of 0.96. The BCI is calculated on the differences between the absolute values of AB and AB + AC + BC, at probability 1/3. An increase in CI is justified in two cases. First, if weighting refers to combined independent evolutionary events (where a weight of 2 really means two synapomorphies when this character state is shared). Second, if the character state is less expected; for instance, an AB:(AB + AC + BC) ratio of 1:1 involving 1 synapomorphy at weight 1 yields an alpha (chance of occurrence by chance alone) of 0.33, but at weight 2 would have the same alpha as the ratio 2:2 with weight 1, or 0.11. When weighting merely means "more important" or some other simple qualifier, then weighting interferes with reliability estimations, and perhaps the data set needs reevaluation or partitioning. Weighting all character states at one is indeed weighting, but it is fail-safe in providing a minimum BCI, which, if high, is less likely to be ambiguous.

A recent paper by Scotland et al. (2003) asserted that the role of morphology is limited in phylogenetic analysis because "the number of characters needed for accurate phylogeny reconstruction is an order of magnitude greater than that available from morphology" The authors also point out that in addition to being few, morphological characters have

ambiguous homology assessment, and that simply adding additional morphological characters is problematic because "much of the useful morphological diversity has already been scrutinized." Generally, the authors promote the idea that morphology provides "anchor points" as determined by congruence studies, and molecular studies then contribute reliable details of phylogeny. The present study demonstrates, on the other hand, that morphological characters can provide reliable phylogenetic analyses. The use of a BCI allows homology and parallelisms to be distinguished, and new reliable characters identified without reference to molecular analyses. Molecular studies are commonly accepted as better supported than morphological, but calculations of measures of internode reliability in such studies, though generally based on more characters, are isolated from many factors that may affect reliability, including the potential of incorrect results caused by sample error, sequence misalignment, wrong models, recombination, differential lineage sorting, etc. The CI implied by a reliability measure (e.g. corrected BP, Bayesian posterior probability, or BCI--see Zander, in press) and the estimated probabilities of all factors to generate a different answer from that same data set need to be multiplied to yield a composite CI, yet estimates of the probability of all factors that may affect reliability are seldom given in molecular analyses, even in Bayesian studies. Because there are only five percentage points available for error when the target CI is 0.95, "well supported" molecularly determined branch arrangements may not, in some cases, be much more reliable than those determined with morphological data (Zander, 2003).

In summary, the results of this study (Table 1) indicate that after an optimal cladogram is established involving judicious selection of an outgroup and maximum parsimony analysis, the resulting phylogenetic separation of similar taxa that are potentially subject to overall

convergence can be evaluated as to reliability.

Acknowledgements and a Caution

I appreciate the support of the Missouri Botanical Garden. Anonymous reviewers helped clarify the ideas expressed here.

This paper was written long ago, before the present posting on the Res Botanical Web page, but is interesting as an exercise for certain methodologies. One may be cautioned that preadaptation of morphological traits and subsequent selection of these during speciation may result in several morphological traits fixed as a unit, for instance a number of traits enhancing survival in aridity, thus when parsimoniously choosing between two branch arrangements, say (AB)C and (AC)B, comparing numbers of shared traits of AB and AC may not be a trustworthy, probabilistic guide to choosing which branch arrangement is the result of shared ancestry and which is then necessarily convergent, e.g. independently selected for arid habitats (February 14, 2008). This paper has not been published in hardcopy.

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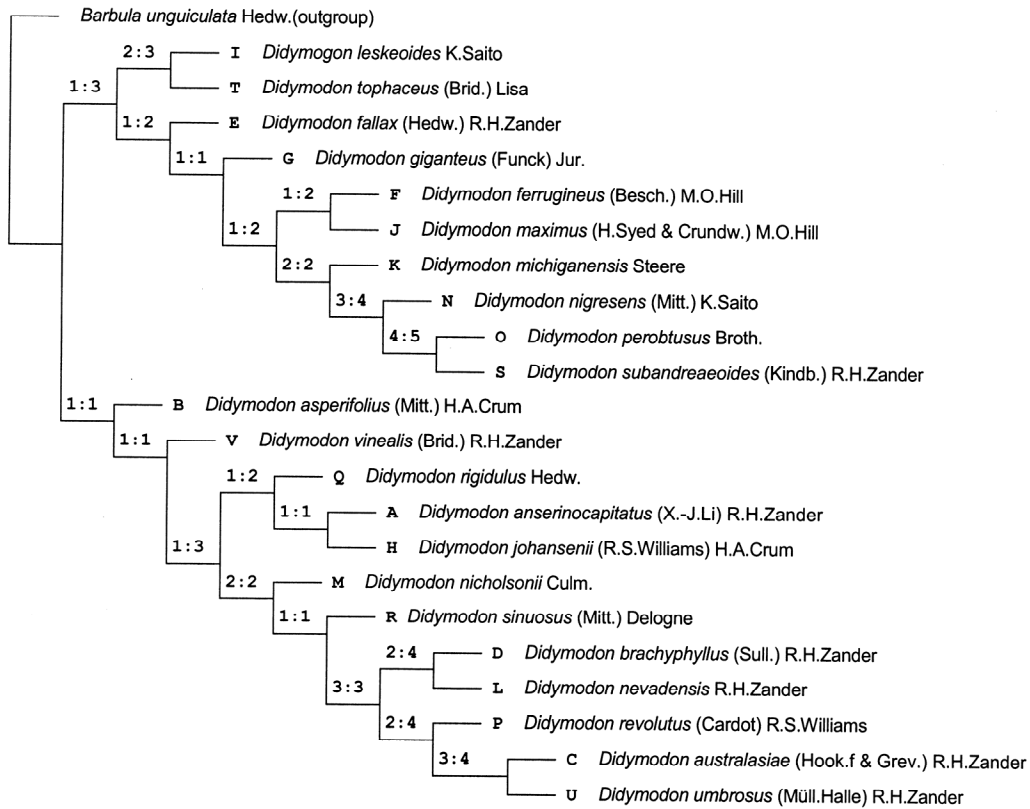


FIG. 1. One of three of the most parsimonious trees for 22 species of *Didymodon* (outgroup *Barbula unguiculata*). Tree length is 63 steps, consistency index is 0.44. The bold-faced capital letters refer to species in the phylogram of Fig. 2. Numbers above the internodes are support levels AB:(AB + AC + BC).

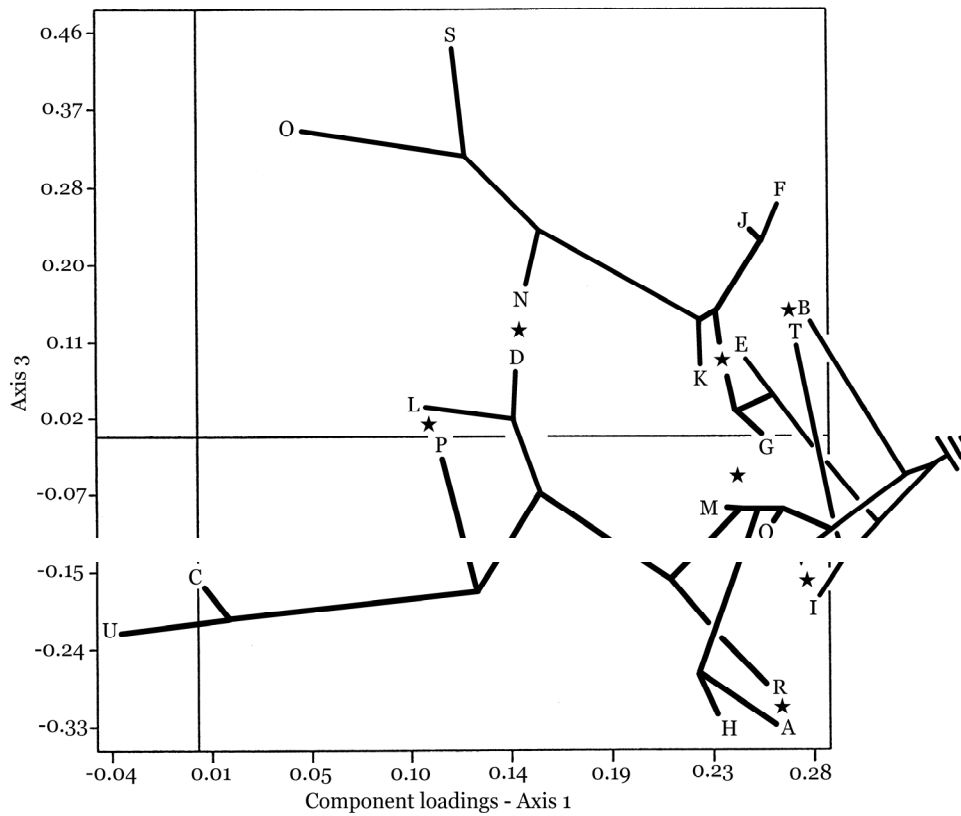


FIG. 2. Cladophenogram of the principal components analysis and the evolutionary tree (Fig. 1). The stars are placed between each of seven pairs of phylogenetically distant taxa that appear phenetically similar and therefore overall convergent. Some lines are broken to allow insertion of other lines and of symbols.