HOMOPLASY EXCESS RATIOS: NEW INDICES FOR MEASURING LEVELS OF HOMOPLASY IN PHYLOGENETIC SYSTEMATICS AND A CRITIQUE OF THE CONSISTENCY INDEX

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Abstract.—Comparative systematic studies may use different sets of data or different sets of taxa to evaluate the quality of phylogenetic data and phylogenetic hypotheses based on levels of homoplasy as implied by the length of minimum length trees. For comparisons involving diverse arrays of characters and taxa, an appropriate index is required to permit comparisons. Examination of the number of steps per character (NSC) on minimum length trees for 28 data sets revealed a highly significant positive correlation between NSC and the number of taxa and, concomitantly, a highly significant negative correlation between the consistency index (CI) of Kluge and Farris (1969) and the number of taxa. Theoretical expectations from a study of the number of steps on random and minimum length trees (Archie and Felsenstein, 1989) agree with this finding. Computer simulations using randomly selected subsets of taxa and characters from the Drosophila data set of Throckmorton (1968) revealed a similar finding. The latter two studies also revealed a negative relationship between the CI and the number of characters in a study. These findings imply that the CI is not an appropriate index of homoplasy for comparative taxonomic studies. A new index, the homoplasy excess ratio (HER), is introduced that takes into account the expected increase in overall homoplasy levels with increasing numbers of taxa in systematic studies. The properties of HER are examined for the 28 data sets taken from the literature and, in conjunction with the simulations using the Drosophila data set, HER is shown to be more appropriate than CI in comparative taxonomic studies that wish to measure the average level of homoplasy in data sets involving different groups of taxa or different characters. Because HER is a computationally intensive statistic to calculate, two estimates are derived and examined. These estimates, the random expected homoplasy excess ratio (REHER) and the homoplasy excess ratio minimum (HERM), can be easily calculated from the formulas of Archie and Felsenstein (1989) and from intrinsic properties of the data matrix, respectively. HERM is shown to be a better estimator of HER and a linear regression equation is derived to estimate HER from HERM. [Comparative systematics; consistency index; homoplasy level; homoplasy excess ratio; optimality criteria; parsimony; phylogenetic systematics.]

Systematists and evolutionary biologists make comparisons and evaluations of the reliability of phylogenetic hypotheses and data in a diverse array of contexts. For phylogenetic hypotheses derived for the same group of organisms from different sets of data, it is useful to know which set of data provides more reliable information (implied because less homoplasy is exhibited) and which hypothesis of relationship is better supported. Numerous studies over the last 20 years have compared results from morphological data and biochemical or molecular data of a variety of different kinds (e.g., Smith and Koehn, 1971; Turner, 1974; King and Wilson, 1975; Johnson et al., 1976; Mickevich and Johnson, 1976; Maxson and Maxson, 1979; Miyamoto, 1981, 1983; Miyamoto et al., 1986; Seidel et al., 1986; Wyss et al., 1987; Good, 1987; Sullivan and Petersen, 1988; and Sites and Davis, 1989), while other investigators have compared different sets of morphological (including meristic, morphometric, adult, pupal, and larval), developmental, karyological, and biogeographic data (e.g., Mickevich, 1978; Schuh and Pulhemus, 1980; Fuiman, 1985; Kraus, 1988; and Sullivan and Peterson, 1988). In a similar way, when different groups of organisms are evalu-

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ated for the same or similar sets of characters, it is desirable to evaluate the properties or quality of the data for the different sets of taxa, either overlapping or completely distinct (e.g., Wyss et al., 1987). For each type of comparison, some method or index is necessary to evaluate and compare the data sets and phylogenetic hypotheses.

The most commonly used criterion for evaluating alternative phylogenetic hypotheses for a set of data is the total number of implied character state changes or steps present on a particular tree, i.e., the tree length (L). Either L or the number of extra steps, as proposed originally by Cain and Sokal (1965), is adequate for evaluating alternative trees using the Wagner parsimony criterion (Farris, 1970). L is an unbound statistic, however, varying proportionately with the number of characters and cannot be used directly in comparing the results of a parsimony analysis using different kinds of data or different sets of taxa. Kluge and Farris (1969) proposed using a measure called the consistency index (CI) as a “more general index of consistency . . . because it varies between fixed limits, and can be used on weighted and continuously coded data and to compare the fits of trees to different data sets” (p. 8). They defined CI as the ratio of the minimum number of steps required on a tree (when no homoplasy is present) to the observed number of steps on the estimated minimum-length tree. CI is monotonically related to the number of steps on arbitrary trees for a given data set but is standardized to be no greater than 1 (no homoplasy) and no less than 0. Kluge and Farris (1969) indicate that phylogenetic trees associated with a higher CI should be more reliable, powerful, and predictive (of improper character coding and weighting) than trees with lower CI values and, similarly, that data sets that yield trees with higher CI values should be more reliable. The reciprocal of the consistency index has seldom been used but is, perhaps, even easier to interpret as it is equivalent to the average number of steps per character (for binary characters) on a tree (Sokal [1985] called this H*).

The consistency index for a phylogenetic tree is easy to calculate, is intuitively appealing and as a result has been used extensively and assigned unusual importance in phylogenetic inference procedures using parsimony. The importance attributed to the CI in comparative studies is apparent from the following:

There are many not always clearly explicit criteria for evaluating the strength of a particular phylogenetic result. Criteria that address the strength of a hypothesis of character change or the diversity of traits sampled in various organisms may not be equally applied to anatomical, amino acid-sequence, or other kinds of data sets. A common, more quantitative, and more generally applicable means of judging the relative quality of data sets and their resultant cladograms is the consistency index (CI) [Wyss et al., 1987, p. 100].

Kraus (1988) made the following statement regarding the use of the consistency index in the comparison of morphological data sets: “Which of the two morphological data sets is best supported by the independent data may be determined by comparing the consistency indices of the independent data sets on those trees [derived from the two morphological data sets]. The cladogram . . . with the higher consistency index best fits the independent data set and, therefore, provides a better estimate of the phylogenetic relationships of the study group.” In another application of the CI, Mickevich (1978) found that taxonomic stability of classifications derived from different sets of data when compared across different groups of organisms could be positively correlated with the consistency index, used directly as a measure of the level of homoplasy in the data sets.

As can be derived from an examination of the recent systematic literature, phylogenetic hypotheses which exhibit lower values of the consistency index are given less credence than hypotheses with higher values, whether the comparison is made for the same set of organisms and different data sets or for different sets of organisms derived from either similar or qualitatively different data. Similarly, data from different sources (morphological measurements, developmental priority evaluations, electrophoretic allele frequencies, DNA or RNA sequences) which exhibit lower val-
ues of the consistency index on minimal length trees may be considered inferior because of the implied higher levels of homoplasy.

Considering the importance attributed to the consistency index in phylogenetic inference studies, one would expect this statistic to have been thoroughly evaluated for its properties in comparative studies. However, the consistency index has received essentially no such evaluation. Instead, perhaps because of its simplicity and intuitive appeal, it has been accepted with acclaim rather than scrutiny. In the present study, I present a critical evaluation of the behavior of the consistency index in response to the independent addition of both new taxa and new characters in phylogenetic analyses. As will be seen, a series of undesirable properties is exhibited by the consistency index to an extent that render it useless for comparative studies. I then introduce a new index, the homoplasy excess ratio (HER) as a measure of average homoplasy level in data sets. This index is sensitive to properties of the data array relevant to phylogenetic inference, exhibits none of the undesirable properties characteristic of the CI, and, as a result, is appropriate for the broad classes of comparison between data sets and phylogenetic hypotheses that are desired. Two additional indices which approximate HER are also introduced. Three other indices, the F-ratio (Farris, 1972), an information statistic (Brooks et al., 1986), and the percent incongruence (Mickevich and Farris, 1981) will also be discussed.

AN EMPIRICAL STUDY OF MORPHOLOGICAL DATA SETS

In the development of a randomization procedure for testing the null hypothesis that no phylogenetic information is present in a given set of data (Archie, 1989), I made the following empirical observation. For 28 data sets, I estimated the minimum-length tree using the program PAUP (version 2.4). A plot of the average number of steps per character from the trees calculated for each data set against the number of taxa (t) in each study (fig. 2A in Archie, 1989) showed a strong positive relationship between these two variables ($r = 0.885; P \ll 0.01$). A plot of the reciprocal of the number of steps per character, i.e., the consistency index of Kluge and Farris (1969), against number of taxa showed a strong negative correlation ($r = -0.853; P \ll 0.01$; fig. 3 in Archie, 1989).

Clearly, if the consistency index is inversely correlated with the number of taxa in this type of study regardless of the average level of homoplasy in the data, it is inappropriate for comparisons involving different numbers of taxa. A lower consistency index would not be an indicative measure of either the quality of the data or of the phylogenetic hypotheses generated from the data when different numbers of taxa are involved in particular comparative studies.

For the empirical studies examined by Archie (1989), however, one must ask whether in fact the results are due to a valid, and undesirable, relationship between the consistency index and the number of taxa in these studies or whether the result is simply a property of the data sets involved. Is there a greater amount of homoplasy, in some average sense, in the studies which contained more taxa? The data sets clearly exhibited a great variety of characteristics. Some of them were from plant groups while others were from animal groups. Some contained species within a genus and even populations within species while others contained distantly related species in multiple genera from families or even orders. Some were from studies in which characters were originally discretely coded into transformation series while others contained characters which were originally morphological measurements and had been coded into discrete form using generalized-gap coding (Archie, 1985). The range of numbers of taxa was large for most types of data sets. For example, the data sets contained studies of plants with from 8 to 34 taxa. Data sets for which generalized-gap coding was used contained from 5 to 32 taxa while data from discretely coded transition series contained from 8 to 44 taxa. None of the original data sets differed qualitatively from the pattern defined by the remaining sets.
There would seem to be little reason to suspect that a trend of increasing average homoplasy levels with increasing numbers of taxa should be observed based solely on the nature of the data.

THEORETICAL EXPECTATIONS

In a recent study, Archie and Felsenstein (1989) examined the expected number of steps per character on both minimum-length trees and random trees for phylogenetically random (or uninformative) data. Phylogenetically random data are data which contain no historical information on the phylogenetic relationships of a set of taxa. Such data can be created by assigning the states of characters at random with the probability that a particular taxon has either a 1, 0, or ? (i.e., ambiguous) state equal to 1/3 and with the states of all characters being assigned independently. A random tree is one created by randomly joining taxa and groups of taxa successively into a tree structure. They showed that the expected number of steps per character on random trees for these data was $2(t - 1)/9$, where $t$ is the number of taxa. For similarly defined, random binary $(0, 1)$ data it was shown that the expected number of steps per character was approximately $(3t - 2)/9$. The number of steps per character on minimum-length trees (versus random trees) for these same data was shown by computer simulation to approach the expected number of steps on the random trees as the number of characters in the studies increased.

Their findings indicated several things. First, for phylogenetically uninformative data there is a monotonically increasing, functional relationship between the number of taxa in a study and the number of steps per character on either random or minimum-length trees. Since the CI is exactly the reciprocal of the number of steps per character, for these data there is a direct, negative relationship between the consistency index and the number of taxa. While the relationship between the average number of steps/character and $t$ is strictly linear, the relationship between CI and $t$ is curvilinear because CI is restricted to lie between 0 and 1 while the number of steps per character is unbounded.

Second, the computer simulations carried out by Archie and Felsenstein (1989), which examined the relationship between the number of steps per character on minimum-length trees (for random data) and the number of characters, indicated a second predictable and undesirable relationship between the consistency index and an intrinsic property of data. For a constant number of taxa, they found that there is a distinct increase in the average number of steps per character on minimum-length trees as the number of characters used in an analysis increased. In addition, the magnitude of this empirically derived relationship was found to increase as the number of taxa increased. Figure 1, derived from the simulations of Archie and Felsenstein, shows this effect for both binary $(0, 1)$ and missing-value data $(0, 1, and ?)$. Again, since the consistency index is the reciprocal of the number of steps per character, there is expected to be a direct negative relationship between the CI and the number of characters present in a study—as the number of characters in a study increases, the average consistency index derived from minimum-length trees should decrease.

The decrease in consistency with increasing numbers of characters is a direct result of the fact that for even moderately large numbers of taxa ($t > 6$) the number of possible trees greatly exceeds the number of characters used in essentially any phylogenetic study. For example, if we had the total genome sequenced for a set of 20 primate species, we would have some $3 \times 10^9$ base pairs for each species (not all of which would be expected to vary between taxa). However, for 20 taxa there are $8.2 \times 10^{21}$ possible bifurcating trees (Felsenstein, 1978). Obviously we always use many fewer characters than that present in the primate genome and, practically, many systematic studies use no more than 100 characters although using current molecular sequence techniques we can expect investigators to begin to gather thousands of variable site data for a growing number of species. As long as there are many more
possible trees than characters in a study, it becomes possible to summarize phylogenetically random data or informative phylogenetic data with some randomness more effectively than expected from the formulas of Archie and Felsenstein. The proportional deviation in length of minimum-length trees from that expected for random trees and random data is large when few characters are examined, but the two lengths converge asymptotically as more characters are added. This phenomenon is analogous to that observed when fitting a polynomial regression curve to a limited number of data values for the independent variable. As the number of terms in the regression increases, the curve can be made to pass arbitrarily close to the data points.

For phylogenetically informative data that contain a random component (homoplasy), minimum-length trees can effectively summarize the character state distributions so the inferred number of steps on the minimum-length tree will be less than actually present in the data. As the number of characters increases, it becomes more and more difficult to summarize the conflicting information effectively.

Although the model used by Archie and Felsenstein (1989) for generating phylogenetically uninformative data does not seem general, in addition to being a baseline study for the examination of properties of data sets with other underlying character state distributions, a direct analogy can be made with models proposed for certain types of real data. For their model, a random number of character state changes was proposed to occur along all internal branches of a tree with equal probabilities of \(0 \rightarrow 1\) and \(1 \rightarrow 0\) (and possibly, \(0 \rightarrow ?\), \(? \rightarrow 0\), \(1 \rightarrow ?\) and \(? \rightarrow 1\)) transitions. Under this model the expected frequencies of character states among the terminal taxa are equal. For DNA sequence data, similar neutral models have often been proposed for the evolution of sequence differences (e.g., Jukes and Cantor, 1969). In such models, each site is subject to a small but positive probability of change (transition or transversion) along all branches in the true phylogeny with forward and backward mutations equally probable. Although the probabilities of transitions and transversions may not be equal in all of these sequence models, the expected effect on the relationship between the number of extant taxa in the study and the consistency index is the same: as the number of taxa present increases, the consistency index is expected to decrease proportionately.

**HOMOPLASY EXCESS RATIOS**

Motivated by apparently high levels of homoplasy in morphometric data sets, Archie (1989) examined a randomization pro-
procedure for 28 data sets to determine the distribution of the length of minimum-
length trees for phylogenetically random data that were otherwise comparable to the
original data sets. This distribution was derived by repeatedly randomly permuting
the character state assignments for all taxa within characters and then determining the
lengths of the minimum-length trees for the randomized data. For each data set the
randomization process was repeated 100 times and then the mean number of steps
and the mean number of steps per character on the randomized-data trees were
calculated. In a plot of the observed number of steps per character on ML trees and the
mean number of steps per character on the randomized-data trees against the
number of taxa for the 28 data sets (Fig. 2; reproduced from Archie, 1989) it can be
observed that certain points from the original data sets fall distinctly below the cor-
responding randomized-data tree means while the corresponding values for other
points are very close together.

The comparative relationship between the mean number of steps on the random-
ized-data trees and the observed number of steps on trees derived from the original
data can be used to derive a new statistic, the homoplasy excess ratio (HER), for com-
paring levels of homoplasy among phylogenetic studies. The number of steps per
character could also be used to make this comparison, but the derivation is simpler
using the absolute number of steps. The difference between the observed total number
of steps on the minimum-length tree (L) and the minimum possible number of
steps if there were no homoplasy (MINL) can be considered the homoplasy excess
[observed homoplasy excess] (HE = L − MINL) for a given data set and tree. For discrete
multistate data the minimum number of steps is the number of states in the data
matrix minus the number of characters. For binary data MINL is simply the number of
characters, N. The difference between the mean number of steps for the randomized-
data trees (MEANNS) and the minimum number of steps is the maximum homoplasy
excess (MHE = MEANNS − MINL) that

would be expected if there were no phylo-
genetic information in a data set.

The homoplasy excess ratio equals 1.0 minus the ratio of the observed homoplasy
excess (HE) to the maximum homoplasy ex-
cess (MHE).

\[
HER = 1.0 - \frac{HE}{MHE}
\]

\[
= 1.0 - \frac{(L - MINL)}{(MEANNS - MINL)}
\]

\[
= \frac{(MEANNS - L)}{(MEANNS - MINL)}
\]

By subtracting the ratio HE/MHE from 1.0, HER will be 1.0 when no homoplasy is
present in a given data set. As the number of steps on the observed minimum-length
tree approaches that for phylogenetically random data, HER will approach 0.0. For
completely random data, the expected value of HER is 0.0, although HER may take
on negative values due to sampling error, that is, the number of steps on the (single)
minimum-length tree may be greater than the mean number of steps on minimum-
length trees obtained from some arbitrary number of randomizations (of the already
random data) used to estimate the randomized-data mean tree length.
Table 1. Homoplasy excess ratio statistics for the 28 data sets listed in Table 1. Formulas for these statistics are described in the text.

<table>
<thead>
<tr>
<th>Data set</th>
<th>Minimum tree length total steps</th>
<th>Consistency Index (CI)</th>
<th>Minimum no. steps per character</th>
<th>Mean steps per character for randomized data</th>
<th>Homoplasy excess ratio (HER)</th>
<th>Homoplasy excess ratio maximum (HERM)</th>
<th>Random expected homoplasy excess ratio (REHER)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Anacyclus</td>
<td>68</td>
<td>0.809</td>
<td>1.236</td>
<td>1.56</td>
<td>0.5793</td>
<td>0.7593</td>
<td>0.8880</td>
</tr>
<tr>
<td>2. Angiosperms</td>
<td>287</td>
<td>0.213</td>
<td>4.705</td>
<td>5.84</td>
<td>0.2349</td>
<td>0.5272</td>
<td>0.6336</td>
</tr>
<tr>
<td>3. P. boylii</td>
<td>110</td>
<td>0.755</td>
<td>1.325</td>
<td>1.77</td>
<td>0.5755</td>
<td>0.7188</td>
<td>0.7748</td>
</tr>
<tr>
<td>4. Chloris</td>
<td>39</td>
<td>0.513</td>
<td>1.950</td>
<td>2.38</td>
<td>0.3091</td>
<td>0.6545</td>
<td>0.7242</td>
</tr>
<tr>
<td>5. Cnemidophorus</td>
<td>325</td>
<td>0.323</td>
<td>3.095</td>
<td>4.43</td>
<td>0.3897</td>
<td>0.5857</td>
<td>0.7306</td>
</tr>
<tr>
<td>6. Corellas</td>
<td>38</td>
<td>0.947</td>
<td>1.056</td>
<td>1.59</td>
<td>0.9052</td>
<td>0.8444</td>
<td>0.9615</td>
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<tr>
<td>7. Dasyuridae</td>
<td>204</td>
<td>0.230</td>
<td>4.340</td>
<td>6.40</td>
<td>0.3819</td>
<td>0.6609</td>
<td>0.7081</td>
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<tr>
<td>8. Dipodomys</td>
<td>89</td>
<td>0.884</td>
<td>1.712</td>
<td>2.09</td>
<td>0.3474</td>
<td>0.6146</td>
<td>0.7438</td>
</tr>
<tr>
<td>9. Drosophila-1</td>
<td>370</td>
<td>0.300</td>
<td>3.217</td>
<td>5.68</td>
<td>0.5260</td>
<td>0.6739</td>
<td>0.8117</td>
</tr>
<tr>
<td>10. Drosophila-2</td>
<td>139</td>
<td>0.827</td>
<td>1.209</td>
<td>2.10</td>
<td>0.8110</td>
<td>0.8689</td>
<td>0.9329</td>
</tr>
<tr>
<td>11. Equus</td>
<td>26</td>
<td>0.808</td>
<td>1.238</td>
<td>1.67</td>
<td>0.6429</td>
<td>0.8276</td>
<td>0.8872</td>
</tr>
<tr>
<td>12. Gerygone</td>
<td>95</td>
<td>0.421</td>
<td>2.375</td>
<td>2.93</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>13. Heliconia</td>
<td>47</td>
<td>0.702</td>
<td>1.424</td>
<td>2.35</td>
<td>0.6847</td>
<td>0.8654</td>
<td>0.9342</td>
</tr>
<tr>
<td>14. Leptodactylidae</td>
<td>359</td>
<td>0.222</td>
<td>4.944</td>
<td>6.14</td>
<td>0.3102</td>
<td>0.5873</td>
<td>0.7364</td>
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<tr>
<td>15. Leptodonomorpha</td>
<td>74</td>
<td>0.851</td>
<td>1.175</td>
<td>1.77</td>
<td>0.7727</td>
<td>0.8778</td>
<td>0.9173</td>
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<tr>
<td>16. Menidia</td>
<td>79</td>
<td>0.785</td>
<td>1.274</td>
<td>2.51</td>
<td>0.8190</td>
<td>0.8859</td>
<td>0.9333</td>
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<tr>
<td>17. Microteiidae</td>
<td>59</td>
<td>0.441</td>
<td>2.269</td>
<td>2.61</td>
<td>0.2162</td>
<td>0.6207</td>
<td>0.7803</td>
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<tr>
<td>18. Myobatrachidae</td>
<td>158</td>
<td>0.354</td>
<td>2.821</td>
<td>4.65</td>
<td>0.5007</td>
<td>0.6918</td>
<td>0.7174</td>
</tr>
<tr>
<td>19. Ophedrydys</td>
<td>71</td>
<td>0.676</td>
<td>1.479</td>
<td>1.87</td>
<td>0.4498</td>
<td>0.6349</td>
<td>0.6683</td>
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<tr>
<td>20. Orthopteroid</td>
<td>180</td>
<td>0.511</td>
<td>1.957</td>
<td>2.56</td>
<td>0.3880</td>
<td>0.5926</td>
<td>0.6925</td>
</tr>
<tr>
<td>21. Percina-1</td>
<td>356</td>
<td>0.399</td>
<td>2.507</td>
<td>3.28</td>
<td>0.3385</td>
<td>0.6651</td>
<td>0.8404</td>
</tr>
<tr>
<td>22. Percina-2</td>
<td>72</td>
<td>0.903</td>
<td>1.108</td>
<td>3.12</td>
<td>0.9491</td>
<td>0.9671</td>
<td>0.9715</td>
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<tr>
<td>23. Podarctis</td>
<td>779</td>
<td>0.282</td>
<td>3.541</td>
<td>5.34</td>
<td>0.4140</td>
<td>0.5633</td>
<td>0.7211</td>
</tr>
<tr>
<td>24. Pomocentridae</td>
<td>61</td>
<td>0.672</td>
<td>1.488</td>
<td>2.98</td>
<td>0.7540</td>
<td>0.7872</td>
<td>0.8979</td>
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<tr>
<td>25. Pygopodidae</td>
<td>236</td>
<td>0.589</td>
<td>1.698</td>
<td>4.44</td>
<td>0.7969</td>
<td>0.8582</td>
<td>0.8858</td>
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<td>26. Saimandridae</td>
<td>104</td>
<td>0.596</td>
<td>1.677</td>
<td>2.30</td>
<td>0.4776</td>
<td>0.6957</td>
<td>0.8033</td>
</tr>
<tr>
<td>27. Tamias</td>
<td>90</td>
<td>0.589</td>
<td>1.698</td>
<td>2.08</td>
<td>0.3565</td>
<td>0.5795</td>
<td>0.7144</td>
</tr>
<tr>
<td>28. Uma</td>
<td>51</td>
<td>0.863</td>
<td>1.159</td>
<td>1.39</td>
<td>0.5930</td>
<td>0.7308</td>
<td>0.6420</td>
</tr>
</tbody>
</table>

Note: Statistics were not calculated for the Gerygone data set as it consisted of multistate data.

The HER values calculated for the data sets of Archie (1989) can be used to identify data sets that show substantially more or less deviation from randomness (Table 1). For example, the Percina-2 data set has an excess ratio of \((202.5 - 72)/(202.5 - 65) = 0.9491\), that is, the observed homoplasy excess is only 5.09% of that possible for completely random data. In contrast, the homoplasy excess ratio for the Microteiidae data set is only 0.2162; the observed excess homoplasy is nearly 80% of that possible for random data. Twelve other data sets exhibit HERS of less than 0.50 although only one other has an HER less than 0.25.

**Approximations of HER**

Calculating the homoplasy excess ratio statistic for some data sets requires a substantial amount of computer time because a large number of randomizations of the original data set, followed by calculation of the corresponding minimum-length trees, must be carried out. Although no sensitivity analyses have been carried out on the variance of the number of steps on randomized data trees or on HER, at least 100 repetitions of the randomization procedure are recommended. For data sets with 20–25 or fewer taxa this may be a reasonable procedure, but with 30 or more taxa, computer time may be excessive and it is desirable to have an approximate formula for HER that is easy to calculate. Two related approximations to this statistic can easily be calculated using either the expected number of steps per character for phylogenetically random data on minimum-length trees (ENS), as derived by Archie and Felsenstein (1989), or the maximum possible number of steps on any tree for the observed data (MAXNS).
The first of these approximations to HER, the \textit{random expected homoplasy excess ratio} (REHER), is calculated using the expected number of steps for phylogenetically random data (ENS\_N) in place of the mean number of steps for randomized data.

\[ \text{REHER} = \frac{(\text{ENS}\_N - L)}{(\text{ENS}\_N - \text{MINL})} \]  

(3)

For binary data, ENS = (3t - 2)/9, (approximately) and N is the number of characters. Although this statistic is simple to calculate, it has the disadvantage of being relatively insensitive to changes in structure of the data matrix (discussed below).

A second approximation to HER, the \textit{homoplasy excess ratio maximum} (HERM), uses the maximum number of steps possible on any phylogenetic tree for the observed data array (MAXNS) to standardize the observed homoplasy excess (HE) for the data set.

\[ \text{HERM} = \frac{(\text{MAXNS} - L)}{(\text{MAXNS} - \text{MINL})} \]  

(4)

The maximum possible number of steps (MAXNS) for the ith binary character on any undirected tree optimized to be of minimum-length can be calculated directly from the character data as MAXNS\_i = \text{min}(N_i \cdot t - N_i) where N_i is the observed number of 1 states for a binary character across taxa and t is the number of taxa. The maximum number of steps possible on any tree for all characters (MAXNS) is then the sum of the MAXNS\_i. MAXNS\_i is expected always to exceed the mean number of steps estimated for randomized data (even if the data are phylogenetically random) as, generally, no bifurcating tree will be able to require the maximum number of steps possible for each character alone when the characters are combined into a single data set. The random expected homoplasy excess ratio and homoplasy excess ratio maximum statistics were calculated for the 28 data sets in this study (Table 1) and are plotted in Figure 3 against HER.

The HERM statistic appears to be a more appropriate statistic for practical studies than REHER. The expected number of steps per character for random data on random trees is a constant for a given number of taxa. As a result, in studies involving the same number of taxa but different sets of characters ENS would be uncorrelated with the observed average number of steps per character obtained by the randomization process described earlier, that is, it is not dependent on the particular characteristics of a data set. On the other hand, the sum of the maximum number of steps (MAXNS) is expected to be highly correlated with the observed average number of steps obtained through randomization when the number of taxa is held constant. The observed range of variation in the maximum number of steps per character for data sets with the same numbers of taxa can be quite large (Table 1). For example, for the two data sets in the present study with 23 taxa, the mean maximum number of steps per character is 4.15 and 6.91. The ENS for both data sets, based on the number of taxa alone, is 7.44.

Across studies involving different numbers of taxa, the homoplasy excess ratio maximum (HERM) is expected to be more highly correlated with HER than is REHER. For the 28 data sets in the current study, product-moment correlations between these variables are \( r_{\text{HER, HERM}} = 0.947 \) and \( r_{\text{HER, REHER}} = 0.8111 \) \((n = 27; \text{Fig. 3})\), respectively. The correlation between the maximum number of steps with the mean
number of steps on the randomized-data trees was 0.991.

For a given set of data, HER and HERM are perfectly rank correlated with the number of steps on arbitrary phylogenetic trees as well as with CI. This can be easily deduced by examining the formulae for HER or HERM. For a given data set, the mean and maximum number of steps on minimum-length trees and the number of characters is constant. The only factor in the formulae that varies and affects either HER, HERM, or CI is the number of steps on a particular tree. HER or HERM are therefore appropriate summary statistics to use in evaluating specific trees for a single data set.

Across data sets, it is reasonable to expect that HER will have some correlation with CI. For a given number of taxa, t, as CI decreases, HER will in general decrease although this will vary from data set to data set. For the 28 data sets of Table 1, HER has a correlation of 0.497 (P < 0.01) with the CI for the same data sets (Fig. 4a). For these same data sets, the correlation between HER and t is somewhat lower (r = −0.416; 0.05 > P > 0.01; n = 27; Fig. 4b). This correlation is considerably less than that between the CI and t (r = 0.853; P ≪ 0.01; N = 28). In Figure 4b it can be seen that the correlation of HER and t is influenced considerably by data sets which have particularly high HER values and small numbers of taxa. Six of the eight highest values are from studies which were originally discretely coded characters with some collected specifically for phylogenetic analysis. Such studies might be expected to have high HER and CI values, although Figure 4a shows that this is not invariably true. For the data sets with large numbers of taxa, the average levels of homoplasy corrected for characteristics of the data sets and the numbers of taxa do appear to be unusually low. However, there are also data sets among the 28 that have small numbers of taxa and unusually high levels of homoplasy (low HER). It is these data sets that were not effectively identified by the CI. For studies with 20 or fewer taxa the lowest CI value was 0.511 while the lowest HER value was 0.309.

EXPERIMENTAL ANALYSIS

Although there was no apparent bias among the 28 data sets in types of data analyzed or in levels of diversification correlated with t that would be expected to produce the high correlation between numbers of taxa and numbers of steps per character (or CI), I wanted to know whether the effects of 1) decreasing consistency index with an increasing number of taxa (t) and 2) decreasing consistency index with an increasing number of characters (N), could be seen within a single data set where levels of homoplasy would be essentially constant. Such a study would avoid the compounding effects produced by the admitted heterogeneity among the data sets examined earlier. This study would also find any undesirable dependencies between general properties of data sets and HER or, in this case, HERM. For this analysis I chose the data set of Throckmorton
which contains 39 species and 60 qualitative binary and multistate characters. The multistate characters from this data set were recoded using additive binary coding to produce a total of 115 characters. The overall consistency index and homoplasy excess ratios for the minimum-length tree estimated using PAUP for this data set were CI = 0.300 and HER = 0.526. I chose this data set because it had been collected for the purpose of phylogenetic analysis and because it had a high diversity of taxa and characters. The low overall consistency index for the complete data set indicated that, if the relationships between the CI and increasing numbers of taxa and characters were to be found, they would be apparent in this data set. Under the expectation of no relationship between these two variables and the CI, consistently low values of the CI should be found for all combinations of taxa and characters. Similarly, constant levels of HER should also be found across combinations of t and N.

SIMULATION METHODS

For the Drosophila data set I performed the following sampling experiment. I created subsamples of the data by randomly sampling both taxa and characters without replacement from the original data set. Initially I selected random samples of 6, 12, 18, 24, 30, or 36 taxa. Once the taxa were chosen, I created random subsets of the characters containing 20, 40, 60, 80, and 100 characters. In all cases only characters which exhibited variability among the reduced set of taxa were chosen. For each of 10 samples of the specified numbers of taxa, 10 separate random character sets containing the specified number of characters were selected. Thus, for six combinations of numbers of taxa and five combinations of numbers of characters (30 combinations in all) a total of 10 \times 10 \times 30 or 3,000 data sets could potentially have been generated. However, in forming the randomly selected characters for a given subset of taxa, I enforced the requirement that at least 10 more variable characters be available than the number of characters to be selected for the specific taxa in the new data set in order to ensure sufficient variability between the data sets. When this was not the case for a given subset of taxa, a new subset was selected. For sets of six randomly selected taxa, there were rarely more than 80 variable characters and therefore only data sets containing 20, 40, and 60 characters could be created. For 12, 18, 24 and 30 taxa, there were seldom more than 100 variable characters so data sets containing 100 characters could not be created. As a result, only 2,400 data sets were created for analysis.

For each of the data sets based on random subsets of taxa and characters, I first determined the maximum number of steps possible on any minimum-length tree (MAXNS) by examining the character array. I then submitted the data sets to PAUP (version 2.4) to obtain estimates of the minimum-length trees using the options: MULPARS, HOLD = 10, SWAP = GLOBAL, MAXTREES = 100. Using these options the heuristic algorithms of PAUP search a large number of possible trees for the given data. Although one hopes that the analysis procedure will obtain the shortest length tree for the given data, it is generally acknowledged that in some cases the trees may not be of minimum length. All parsimony packages are subject to this criticism except where all possible trees can be examined or where the branch and bound algorithm of Hendy and Penny (1982) can be used for small numbers of taxa.

For each minimum-length tree estimate for each data set I recorded the number of steps on the tree and Kluge and Farris' consistency index. I then calculated the homoplasy excess ratio maximum (HERM) using equation 4. The true homoplasy excess ratio (HER) was not determined for these data as this process would have required an additional excessive amount of computer time. Total computer time for the present simulation was about one week using an ACER 1100/16 microcomputer based on an Intel 80386 microprocessor (16 MHz). I calculated the mean CI, HERM, and maximum number of steps per character for each set of randomly selected taxa for the 10 replicate character sets. From these data
I then calculated the correlation between the mean maximum number of steps and the mean CI and HERM values.

**SIMULATION RESULTS**

The results from the simulations are shown in Table 2 and Figures 5 and 6. The relationship between CI and HERM and the number of taxa and number of characters in the simulations is plotted in Figures 5 and 6. Figure 5a shows a precipitous and monotonic decrease in the mean CI as the number of taxa is increased. Figure 5b shows the moderate but also monotonic decrease in the CI for increasing numbers of characters when the numbers of taxa are held constant (except for the case with six taxa which has highly variable results). In contrast to these results, there is an increasing relationship between the mean HERM and the number of taxa (Fig. 6a). There is a moderate, decreasing relationship between HERM and the number of characters (Fig. 6b) that is of the same magnitude as the decrease seen in Figure 5b for the CI.

The maximum number of steps per character (MAXNSC = MAXNS/N) is an intrinsic property of each data set and it is of interest to know how each of the two indices responds to changes in this property (Table 2c, d). For 6 and 12 taxa, there was a large amount of scatter in the individual index values for each subset of taxa and each replicate sample of characters. This is indicative of the diverse array of taxa and characters present in the complete
TABLE 2. Simulation results for the consistency index and homoplasy excess ratio maximum produced by varying the numbers of taxa and characters for the *Drosophila* data set of Throckmorton (1968).

<table>
<thead>
<tr>
<th>Number of characters</th>
<th>Number of taxa</th>
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<tbody>
<tr>
<td></td>
<td>6</td>
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<tr>
<td>a) Mean consistency index</td>
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<tr>
<td>20</td>
<td>0.826</td>
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<tr>
<td>40</td>
<td>0.771</td>
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<tr>
<td>60</td>
<td>0.795</td>
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<td>80</td>
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<td>100</td>
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<tr>
<td>b) Mean homoplasy excess ratio maximum</td>
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<tr>
<td>6</td>
<td>0.658</td>
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<tr>
<td>12</td>
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<td>18</td>
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<td>30</td>
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<td>36</td>
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<tr>
<td>c) Correlation of consistency index with maximum number of steps per character</td>
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<td>80</td>
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<tr>
<td>100</td>
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<tr>
<td>d) Correlation of homoplasy excess ratio maximum with maximum number of steps per character</td>
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<td>36</td>
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<tr>
<td>20</td>
<td>0.125</td>
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<td>—</td>
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<td>80</td>
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<tr>
<td>100</td>
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</tbody>
</table>

As the number of taxa increased, the range of HER and CI values for each replicate decreased. There was no consistent pattern in the correlation between CI and the mean MAXNSC with increasing numbers of characters or taxa. For most combinations of N and t, HERM is positively correlated with the mean MAXNSC, although when t is large and N is small, HERM and mean MAXNSC are negatively correlated. Even when the correlation between the variables is high, the slopes (Model I regression) of the relationships of both CI and HERM with MAXNSC are, in general, quite small and the average slope decreases with increasing numbers of taxa. These relationships require additional investigation as in some cases quite distinct patterns of correlation are exhibited within different subsets of taxa across randomly sampled character sets versus the pattern seen between sets of taxa. It is not entirely apparent what relationship should be expected between an index of homoplasy and this property of data sets as it has not previously been examined. As the average homoplasy levels in the data sets are constant, there should be essentially no relationship between the number of steps on a tree and the maximum number of steps determined from data sets. This is essentially what was found here (Fig. 7). In addition, the mean MAXNSC determined from data sets was not correlated with the number of characters, verifying the effect of the averaging process in making the character sets equivalent.

**DISCUSSION**

Whenever comparative evaluations are made to determine the confidence that investigators should put in particular phy-
logenetic hypotheses or phylogenetic data, an index that is appropriately sensitive to variation in properties of the data relevant to phylogenetic inference is required. The consistency index of Kluge and Farris (1969) has, until now, been used predominately for these classes of comparison. However, as has been shown here, the CI is unsuited and misleading for this purpose. First, the CI was found to be overly sensitive to certain, obvious properties of data sets. The CI fails to adjust for the expected (and observed) increases in absolute homoplasy levels (versus average homoplasy levels) as the number of taxa in a study is increased. Second, the CI was found to be insensitive to the summarizing abilities of minimum-length trees and the algorithms used in their construction, that is, the ability of minimum-length trees to summarize randomness (homoplasy) in phylogenetic data due to the fact that number of possible bifurcating trees drastically outnumbers the characters in a study. This effect is manifested in the decrease in the CI as the number of characters is increased. The consequences of the unsuitability of the CI are apparent even when the overall average level of homoplasy remained approximately constant as was the case when homoplasy levels were averaged over repeated random samplings from the same character pool. Although the observed par-

tial correlation between the CI and numbers of characters for the 28 data sets (holding the number of taxa constant) was essentially 0.0 (Archie, 1989), the empirically derived dependence of these two statistics observed by Archie and Felsenstein (1989) and in the present study with the Drosophila data set cannot be ignored. This dependence may influence the level of the CI and would be particularly important in cases where new characters are added to a previous data set.

In contrast to the consistency index, the homoplasy excess ratio (HER) appropriately evaluates total observed homoplasy, and is adjusted 1) for the total homoplasy increase expected as the number of taxa increases, 2) for the distribution of states among taxa, and 3) for the ability of minimum-length trees to summarize random data. Presumably, low values of HER may be seen either because homoplasy levels are high or because, although homoplasy levels are not excessive, there is simply little phylogenetic information in the data set. In the latter case, more informative data need to be gathered. HER statistics appear to be appropriate measures for comparative analyses between data sets for the same group of organisms or for comparisons of the overall quality of diverse sources of data between different groups of taxa. Lower average values of HER statistics indicate that there is less useful (i.e., more conflicting) information for phylogenetic analysis than in other types of data for which a comparison is being made. For example, different sources of molecular data are hypothesized, based on particular models for rate and type of character change, to be useful at different levels of diversification (Hillis, 1987; Simon, 1988). However, different sources of molecular data (e.g., nuclear or mitochondrial DNA or ribosomal RNA sequences) as well as different sequences within particular regions can be expected to have different total amounts of information for different groups of organisms. Studies which involve comparisons of various molecular systems and morphological or other character systems can be expected to become
more frequent in systematics. In many cases, these studies may be from only partially or nonoverlapping sets of taxa. For example, Wyss et al. (1987) examined phylogenetic hypotheses for eutherian mammals derived from four different enzyme systems and three separate morphological studies. In these data sets t varied from 12 to 27 while N varied from 17 to 104. The highest CI values (0.72, 0.82) had the fewest taxa while the lowest CI values had both a large number of taxa (t = 21) and the largest number of characters (N = 104). In such studies, the CI is clearly an inappropriate statistic for comparison due to its direct dependency on properties of the data unrelated to the usefulness of the data for phylogenetic inference. HER can be expected to measure average homoplasy levels appropriately to permit meaningful comparisons.

Although data sets that show low values of the consistency index invariably exhibit low homoplasy excess ratios, data sets with the lowest HER values do not necessarily have the lowest consistency. In fact, CI is apparently unable to identify data sets with high homoplasy levels, as compared to the maximum achievable values for the data. This is particularly apparent when there are small numbers of taxa in a study.

Other indices have occasionally been used in the literature as measures of agreement between characters and trees or to measure the quality of different sets of characters. The F-ratio (Farris, 1972) and the D information measure (Brooks et al., 1986) were introduced to measure agreement between characters and trees, while Mickevich and Farris (1981) introduced the percent incongruence statistic for the comparison of levels of homoplasy in data sets. Brooks et al. (1986) outlined a series of objections to the use of D and the F-ratio statistics as well as the CI. Neither D nor F are monotonic with the number of steps on trees (unlike CI or HER) and cannot be used to choose between alternative trees that may differ in length. Both D and F also depend on the arbitrary reconstruction algorithm used to generate hypothetical character states for ancestors on trees. D, F, and CI were shown to vary due to the addition of autapomorphic characters and D and F were shown to vary due to the addition of taxa. The F-ratio can be shown to be a very redundant measure of homoplasy since the same character state change may be counted repeatedly along internal tree branches. In addition, Brooks et al. (1986) showed that D depends on the rooting of the tree, which may not be well defined, rather than on the topology of the tree. As a result of these criticisms, neither D nor F appears to be an appropriate measure of homoplasy for comparative purposes.

The percent incongruence statistics of Mickevich and Farris (1981) appear potentially useful for measuring comparative homoplasy levels but have not been investigated extensively. However, these statistics depend on the total length of the trees derived from two (or more) data sets and the tree derived from a combined data set, as does the CI, rather than solely on the number of extra steps. It does not depend at all on the character state distributions within each data set, as used to calculate HER statistics. As a result, the percent incongruence statistics will likely be directly dependent on the number of taxa and characters in a study rather than properties of the data relevant to phylogeny estimation, i.e., average homoplasy levels.

In the results from the simulations with the Drosophila data set, HERM exhibited an increase as the numbers of taxa, t, increased (Fig. 6a). This, in fact, is an expected and desirable property given the simulation paradigm used here. Since samples were chosen at random from the same and limited data set, in data sets with small numbers of taxa, most or all of the taxa will be distantly related. In these data sets we expect a relatively large amount of homoplasy when averaged across characters. However, as more and more taxa are included in the data sets, some of those selected will be very closely related and similar in character state values to other taxa in the data set. Less homoplasy is expected between these closely related pairs than between randomly selected pairs when few
pairs are chosen. As a result, although the mean maximum number of steps possible on any tree will increase on average as more taxa are added, since some taxa are closely related to others, the length of the minimum-length tree derived from the data set will not increase proportionately. We therefore expect a decrease in the average level of homoplasy in data sets containing more taxa which have been randomly selected from the limited pool of taxa as reflected in the increase in HERM in the simulation results. In contrast, in spite of this expected decrease in average homoplasy level, the CI was seen to decrease systematically and precipitously (indicating an increase in homoplasy level) as the number of taxa was increased (Fig. 5a).

The increase in HERM with t may be stronger than apparent from Figure 6a. As the number of taxa increases, phylogenetic data analysis procedures cannot guarantee that shortest length trees are found. In an unknown number of cases, the minimum-length tree will not be found. This will bias the HERM statistic downward. In spite of this, in the simulations with the Dro sophila data set, the predictable increases in HERM with numbers of taxa were seen.

The observed decreasing relationship between HERM and the number of characters, N (Fig. 6b), at first seems anomalous. Such a relationship was found to be an undesirable property of CI and is an equally undesirable property of HERM. However, a similar relationship should not be seen between N and HERM. Unlike values of HERM and CI, the value of HER depends on the relationship between N and tree length in the randomized data in a manner equivalent to the relationship between N and tree length for the original data as identified by Archie and Felsenstein (1989). The lack of independence of these two factors is the reason for the observed increase in CI with N. This phenomenon requires further investigation, however.

As an index of average level of homoplasy for comparisons between studies, HER (calculated from the mean length of the randomized data trees) may be too intensive computationally to be calculated routinely in phylogenetic inference computer packages. HERM is easily calculated from a given set of data and is essentially as appropriate an index for the comparison of homoplasy levels as HER. However, as expected and observed for the 27 data sets examined here, HERM consistently overestimates HER. Since the correlation between the two indices is high for these diverse data sets ($r = 0.947$), a Model 1 predictive regression equation derived from the 27 data sets can be used to estimate HER from HERM. This equation derived from Figure 4 is as follows:

$$HER = -0.600 + 1.581 \times HERM$$

The equation effectively predicts that HER will be essentially 1.0 (actually 0.981) when HERM is 1.0, as appropriate. The standard error of the regression slope is 0.0139 and the 95% confidence limit of the slope includes 1.6. This value of the slope parameter identically predicts an HER value of 1.0 when HERM is 1.0. When HER is predicted to be 0.0 (its lower limit), HERM will be approximately 0.38. This latter statistic is interesting as it indicates the degree that the potential maximum amount of homoplasy in a set of data (used to calculate HERM) differs from that which is present in phylogenetically random data (used to calculate HER). The standard errors of the parameter estimates of this equation are very small and can be expected to be reduced further by adding new data sets to the 27 currently analyzed. However, as the correlation between the two indices is high, the equation is not expected to change dramatically as new data sets are added.

It may eventually be appropriate to add additional terms to the prediction of HER from HERM. These will include the number of characters in the study and an index of the character state distributions for the taxa. However, the estimation of appropriate parameter values associated with the number of characters will require the incorporation of substantially more data sets and the accuracy gained by the addition of a new term to the predictive equation will not be great. In cases with 25 or fewer taxa,
it is reasonably convenient to carry out the randomization procedure to estimate HER directly from the data, at least for publication purposes, and the correlation observed in Figure 6b can be ignored. The relationship between HER or CI and the distribution of states among the characters (MAXNS) is still poorly understood and a detailed examination of additional data sets, similar to that performed here with the Drosophila data set, or simulations with probability distributions different from those examined by Archie and Felsenstein (1989), will be required.

HER (or its estimate, HERM) appears to be a sensitive and useful indicator of the confidence that an investigator should have in a cladogram based on parsimony since appropriate, intrinsic properties of the data array are incorporated. Low values of HER (or HERM) indicate that the data differ little from phylogenetically uninformative data either because a large average amount of homoplasy is present in the data or because there is simply little information in the data set at all. When extremely low values of HER are observed, a statistical test is available (Archie, 1989) to evaluate whether the data, in fact, do differ significantly from phylogenetic randomness. In contrast, high values of HER indicate that on average the data differ substantially from random and that a significant amount of information is available for constructing phylogenetic hypotheses.

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