

## The imbalance of paleontological trees

Katherine G. Harcourt-Brown, Paul N. Pearson, and Mark Wilkinson

*Abstract.*—One of the most extensively studied aspects of phylogenetic tree shape is balance, which is the extent to which nodes divide a tree into clades of equal size. Several authors have stressed the importance of tree balance for understanding patterns of evolution. It has been remarked that paleontological studies commonly produce very unbalanced trees (also called pectinate cladograms or ‘‘Hennigian combs’’). This claim is tested here by comparing the balance of 50 paleontological trees and 50 neontological trees, all taken from the recent literature. Each tree was reanalyzed from the published data matrix to ensure its accuracy. The results confirm that paleontological trees tend to be more imbalanced than neontological trees.

That paleontological trees are more imbalanced has been represented as a shortcoming of fossil data sets, but here it is argued that this is the expected result. Even under a simple Markovian model in which all speciations and extinctions occur randomly and with equal probability in all parts of the tree, trees based on taxa from a single time period (e.g., the present day) are generally more balanced than trees based on all taxa that ever existed within the clade. Computer simulation is used to calculate the expected balance and standard deviation of trees for up to 40 terminal taxa over the entire history of a model clade. The balance is measured using Colless’s index,  $I_c$ , and the expected balance conforms well with published paleontological trees. The study underlines the difficulty of applying neontological tree statistics in paleontology.

*Katherine G. Harcourt-Brown and Paul N. Pearson.* Department of Earth Sciences, Wills Memorial Building, Queens Road, Bristol, BS8 1RJ, United Kingdom. E-mail: K.G.Harcourt-Brown@bristol.ac.uk and Paul.Pearson@bris.ac.uk

*Mark Wilkinson.* Department of Zoology, The Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom. E-mail: m.wilkinson@bris.ac.uk

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### Introduction

One of the central concerns of analytical paleobiology is to determine the nature of macroevolutionary processes and how these are reflected by the fossil record. Depictions of phylogenetic trees are an important part of this tradition. For example, Simpson (1953) suggested that nearly all paleontological phylogenies showed directional trends, and hypothesized evolutionary progression over time for most clades. However, early hypotheses were based on a phylogeny drawn entirely from the authors own experience. The advent of cladistics revolutionized taxonomy by providing a method of creating falsifiable hypotheses of relationships among taxa, containing information about branch lengths and character change. These trees contain more useful information than the schematic phylogenies used by earlier workers and are much more effective for studying evolution using tree shape.

Some of the first work on how cladogram

shape reflects evolution was carried out by paleontologists interested in whether random evolution could produce the patterns of diversification and extinction seen in the fossil record, without invoking any causal explanation. Raup et al. (1973) showed that a stochastic model can produce patterns of branching very similar to those observed in real phylogenies. Later, the shapes of real and random clades were compared, and it was suggested that patterns of diversification in real clades could be explained using a random model (Gould et al. 1977). Since then, however, few studies of tree shape have been carried out by paleontologists. Pearson (1998) recently suggested that processes such as iterative evolution and interspecies competition may leave their mark on the shape of stratophenetic phylogenies. Otherwise, the study of paleontological tree shape has been neglected.

Most phylogenies are based on cladistic analysis and sound arguments have been made to suggest that cladogram shape may reflect evolutionary processes (see Mooers

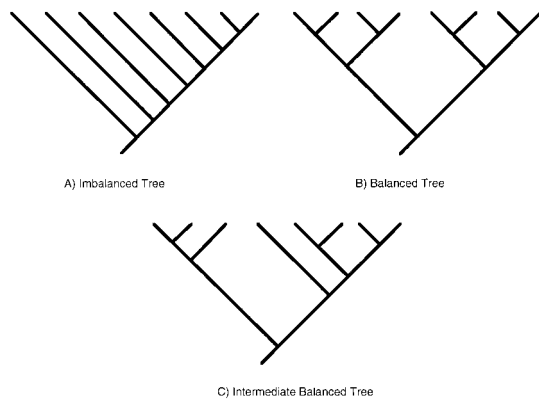


FIGURE 1. Different types of tree balance. Trees of intermediate balance are the most common. Totally balanced trees can occur only when there are even numbers of taxa.

and Heard 1997 for a review). A useful null hypothesis for the study of evolution is that all taxa in a clade have an equal chance of speciation or extinction. This is described as an Equal Rates Markov (ERM) model. Some evolutionary processes such as adaptive radiation or the development of a key innovation in a phylogeny might make a subclade radiate more rapidly than its sister group, so that over time the two clades become unequal in size. This inequality could be revealed when the shape of the actual tree is compared with the expected tree shape under an ERM model, indicating that there has been some variation in speciation or extinction rates during the clade's history.

This aspect of tree shape is reflected by the balance of the tree, or the extent to which internal nodes divide the tree into clades of equal size. In a totally balanced tree, every node divides the tree into clades with an equal number of terminal taxa. In a totally imbalanced tree, each node divides the tree into a pair of subclades, of which one includes only a single terminal taxon and the other includes all the remaining members of the clade. The balance of most phylogenetic trees is intermediate between these extremes (Fig. 1).

One of the first to discuss the balance of cladograms was Colless, who presented an index ( $I_c$ ) to measure it (Colless 1982; Heard 1992).

$$I_c = \frac{\sum_{\text{(all interior nodes)}} |TR - TL|}{(n - 1)(n - 2)/2} \quad (1)$$

where TR is the number of tips subtended by the right branch of a node, TL is the number of tips subtended by the left branch, and  $n$  is the total number of terminal taxa. The index gives a value between zero for a completely balanced tree and one for a completely imbalanced tree. Other indices measuring balance have also been proposed (see, e.g., Sackin 1972, Shao and Sokal 1990, Kirkpatrick and Slatkin 1993, and Rogers 1996). These indices are highly correlated with  $I_c$  (Shao and Sokal 1990; Rogers 1996) and are less easy to understand and apply, so  $I_c$  is used here.

Simberloff et al. (1981) proposed that patterns in the shape of trees could be tested by comparing a tree or group of trees against their expected balance under an ERM model. The model they used did not include extinction rates, possibly because it was initially introduced to test neontological trees (trees based on extant taxa alone). Effectively, a tree was grown by random branching with no extinction, and artificially terminated after a given number of branching events in order to simulate the clade at a given time slice (i.e., the present). For reasons discussed below, this is referred to as the ERM-TS (equal-rates Markov time slice) model here.

The expected value of  $I_c$  for trees of varying taxon numbers under this simple branching ERM-TS model was first calculated by Rogers (1994). Later, the expectation and standard deviation of  $I_c$  and other indices were computer simulated by Heard (1996) and mathematically derived by Rogers (1996). The expected value of  $I_c$  for different tree sizes, and two standard deviations above and below this expected value, are given as Figure 2. As numbers of terminal taxa increase, both the expected value of  $I_c$  and its standard deviation decrease. This is because under the ERM-TS, adding taxa to a tree will, on average, make it more balanced as the proportion of completely imbalanced topologies is much lower. This effect is shown in Figure 3. However, it is worth noting that the ERM-TS always produces fairly

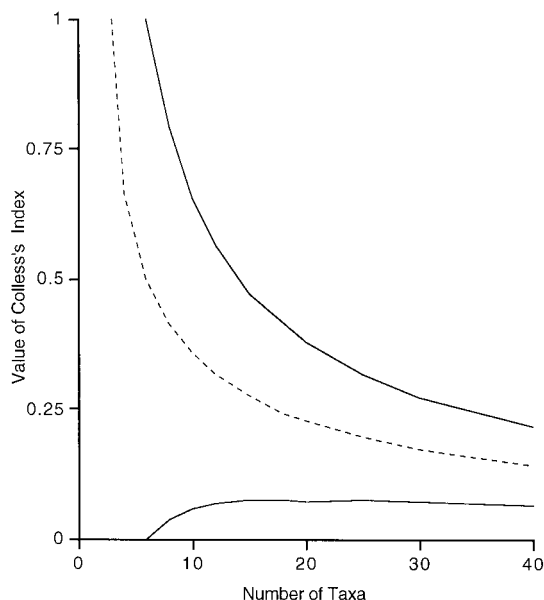


FIGURE 2. Expected values of Colless's index under the ERM-TS model (model of trees from a single time slice). The dashed line represents the expected value of Colless's Index, while the solid lines represent two standard deviations away from the expectation. Data taken from Rogers 1994.

imbalanced trees, especially for small numbers of taxa.

Various studies have related patterns of tree balance observed in the literature to macroevolutionary hypotheses. Colless (1982) suggested that cladistic phylogenies tend to be more pectinate than expected and concluded that they may therefore be unreliable representations of phylogeny. The first work on published trees was by Savage (1983), who studied a data set of 1641 phylogenetic trees of four, five, and six taxa (cladograms, "phylograms" schematically representing phylogeny, and phenograms) and compared their balance with the ERM-TS expectation. He found that they fitted this model. Since then, other authors have studied balance patterns in published trees. For example, Guyer and Slowinski (1991) examined the balance of 240 five-taxon phylogenies and demonstrated a level of imbalance above that expected if speciation rates were equal across all lineages. This imbalance was consistent across different groups, and Guyer and Slowinski suggested that this imbalance showed that differences in rates of speciation and extinction were similar

even in different groups of organisms and that there may be large-scale evolutionary trends common to all groups. Later, they used a study of the balance of 30 large phylogenies (containing more than 100 species) to try to identify adaptive radiations. They suggested that adaptive radiation may be commonplace in the evolutionary history of most groups and recorded by high levels of imbalance at certain nodes in these trees (Guyer and Slowinski 1993). A review of other studies (Mooers and Heard 1997) illustrates how tree balance has become an important tool for studying macroevolution.

The ERM-TS null model used by authors studying patterns of balance is a model of net diversification and does not explicitly include rates of extinction (Mooers and Heard 1997). Real clades have a high probability of including extinct taxa in their history. Does this affect their balance? One possible answer to this question was given by Slowinski and Guyer (1989), who stated that "such taxa [extinct members of a clade], in a study of modern organisms, are 'invisible,'" and that as long as extinction rates are equal throughout the phylogeny, it is easy to show that a diversification-only ERM-TS model would still apply as a suitable null hypothesis. This has led many other authors to consider that "if extinction is random across lineages it does not affect tree balance and so a model of net diversification is sufficient [as a null hypothesis]" (Mooers and Heard 1997). However, we stress that this conclusion is relevant only to taxa from a single time slice (i.e., the modern), and below it is shown that the ERM-TS model is not applicable to trees where taxa have been selected from different time intervals, as is often the case in paleontological studies.

The imbalanced appearance of some paleontological phylogenies has led to discussion of whether the pattern is real or artifactual. Panchen noted the Hennigian comb shape of many paleontological cladograms and implied that it was an artifact by stating that "cladistic practice when dealing with taxa including fossils is only in practice distinguishable from those old-fashioned ancestor-descendant sequences of paleontologists which terminated in a single taxon by the more care-

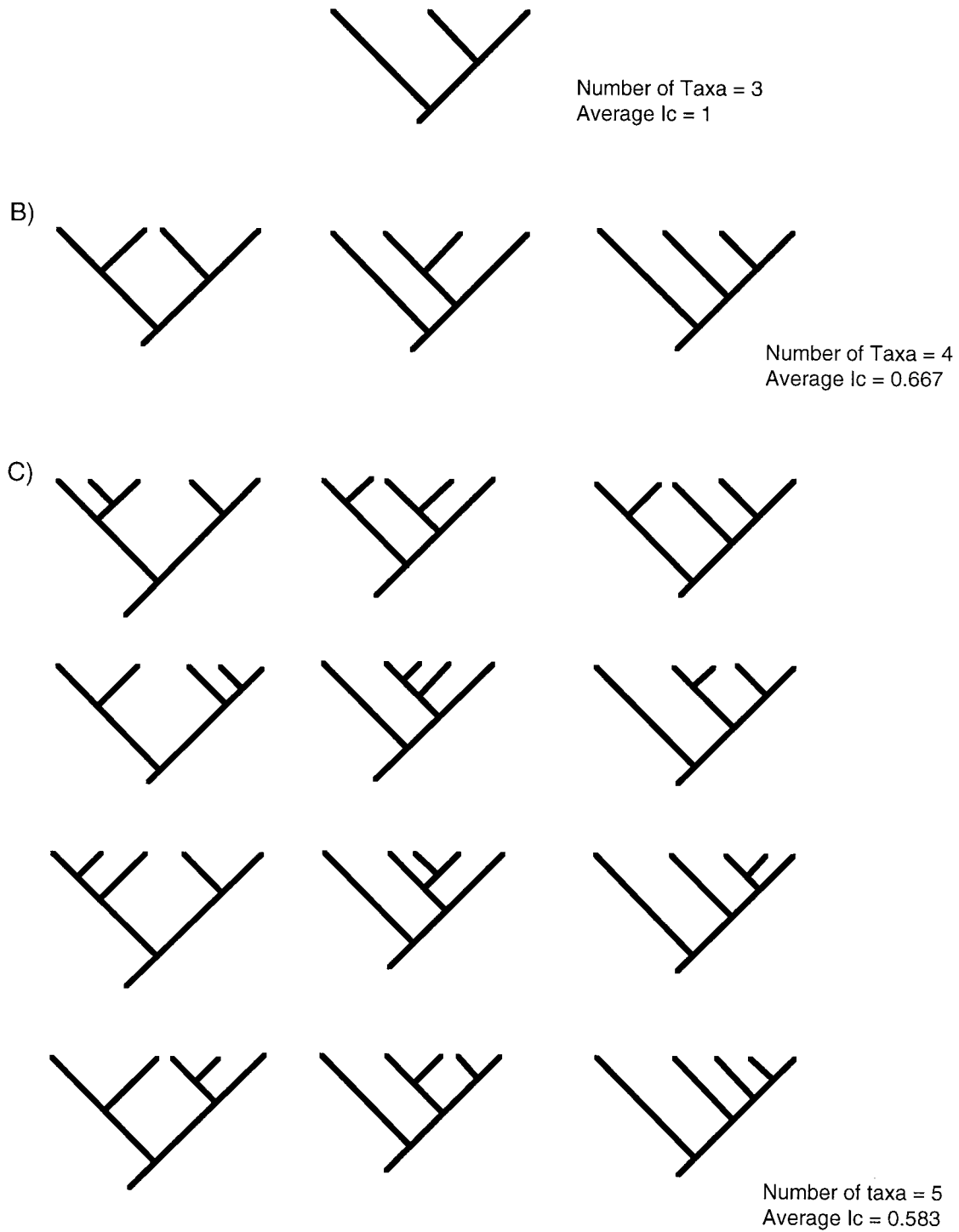


FIGURE 3. Expected value of Colless's index decreases with addition of taxa to a tree. A, For three-taxon trees there is only one, totally imbalanced topology. B, Splitting of the branches of the three taxon topology leads to these trees. The average (or expected) value of Colless's index is 0.667. C, Splitting of the branches of the four-taxon trees leads to these trees, with average Colless's index of 0.583. Addition of more taxa will lead to a further reduction in Colless's index.

ful specification of the fact that the members of the sequence have their own autapomorphies" (Panchen 1982: p. 322). Later, Panchen and Smithson (1987) stated that there was a convention among paleontologists of "always presenting their results as a Hennigian comb." This idea has also been noted in the tree shape literature by Shao and Sokal (1990), who commented that paleontologists often produce imbalanced trees. It has never been tested. Although some authors consider this pattern to be artifactual and caused by deliberate bias on the part of the researcher constructing the phylogeny, most paleontologists regard it as either an unconscious bias or a true reflection of paleontological phylogenies.

A typical case in which the issues surrounding paleontological tree balance have been discussed is that of the stem-group mammals. Gee (1992: p. 529) proposed that the imbalanced phylogeny of therapsids and mammals was due to "the capacity of the human mind to pick patterns from apparently random information" and that the shape of this phylogeny suggests gradualistic evolution from therapsids to crown-group mammals. In this case, the imbalance of the phylogeny is not deliberate but is still caused by human bias. In reply, Ahlberg (1993: p. 596) stated that "cladistic analyses of several major vertebrate groups have revealed stem lineages carrying sequentially arranged sister taxa below the crown group," and in his opinion, these are true reflections of the phylogeny.

Resolving such issues is clearly important for macroevolutionary studies. If paleontological trees are more imbalanced than neontological trees, there are implications for studying tree balance and evolution. If paleontological tree imbalance is artifactual, it suggests that trees based on paleontological data should be excluded from studies of balance, and possibly from studies of phylogenetic evolution in general. Conversely, if the difference in the balance of paleontological and neontological trees is real, then it may be of relevance to evolutionary theory. For example, Pearson (1998) demonstrated statistically significant asymmetry in various stratophenetic trees, and suggested that this asymmetry was due to newly evolved species being more spe-

ciation prone and less extinction prone than their more plesiomorphic sister taxa ("co-existing ancestor"). Factors such as this could lead to significant levels of imbalance in paleontological phylogenies, as speciation or extinction rates are not constant across all lineages within a tree.

### **Are Paleontological Trees More Imbalanced Than Neontological Trees?**

Our first objective is to test the claim (Shao and Sokal 1990) that paleontological trees are more imbalanced than neontological trees. Fifty paleontological trees and 50 neontological trees were taken from the literature for use in this test. Data sets were found by systematically examining selected journals and books in reverse chronological order for phylogenetic studies, and then determining whether they satisfied the seven criteria below relating to the degree of resolution, amount and type of data, repeatability of the analysis, and numbers of trees. The Appendix shows the authors of each data set, the year and journal or book in which they were published, the balance of the resulting tree, and the taxa on which the phylogeny was based. If they were paleontological data sets, it also shows the stratigraphic range covered by the phylogeny.

*1. Degree of Resolution.*—Only binary (fully resolved) trees were used. This was for two reasons: because the distributions of measures of tree balance are best understood for binary trees (following work by Rogers [1994, 1996] and Heard [1992, 1996]) and because Colless's index of balance cannot be calculated accurately for trees containing polytomies (Heard 1992).

*2. Number of Terminal Taxa.*—Only trees that include seven or more terminal taxa (excluding outgroups) were used. Rogers (1994, 1996) has shown that for fewer than seven taxa the standard deviation for Colless's index of tree balance is so high that any value could be expected for a tree under most types of model. As the number of taxa increases, the standard deviation of Colless's index and its expected value decreases, because there is an increase in the possible number of topologies of the tree. This has the effect of making it inappropriate to directly compare balance indices between

trees of different sizes. In this study, trees were not directly compared against each other, but instead compared with the expected balance distribution calculated by Rogers (1994).

3. *Type of Taxa*.—Mooers et al. (1995) showed that tree balance is not affected by the taxonomic level at which a tree is sampled, as long as the rank is consistent throughout the tree. For example, it does not matter whether four taxa are phyla or species; the same possible set of branching relationships among the taxa exists. Perhaps counterintuitively, we believe it does not even matter if the taxa are mixed rank, provided one does not know in advance the phylogenetic relationships among taxa. For example, a four-taxon tree consisting of two families and two species has the same possible topologies with the same probabilities as a four-taxon tree of species only. However, previous studies of tree balance have avoided using trees containing terminal taxa of mixed rank (e.g., Heard 1992; Guyer and Slowinski 1991) and we have followed this precedent. Trees were used only if they included terminal taxa that are of the same rank, or if they could be converted into such trees by considering clades of terminal taxa of lower rank as single branches of the same rank as the other terminal taxa. Trees with a few lower-rank taxa were considered by interpreting the lower-rank taxa as exemplars of higher taxa.

4. *Number of Characters*.—Trees were included only if they are based on data that include more characters than taxa. The effect of this criterion is twofold. First, because a binary tree for  $n$  terminal taxa includes  $n - 1$  internal nodes, the criterion enhances the prospect of there being sufficient character data to support a fully resolved tree. Second, all other things being equal, the accuracy of the tree should be correlated with the ratio of numbers of characters to numbers of terminal taxa.

5. *Type of Characters*.—Trees were not included if they were based on macromolecular sequence data. Macromolecular sequence data are generally not available for paleontological studies and our aim has been to render the paleontological and neontological trees as comparable as possible. As a result, most of the characters used are morphological, but some

data sets based on extant groups contain limited amounts of behavioral characters.

6. *Repeatability*.—Only trees that could be recovered by reanalysis of the published data (using PAUP 3.1.1 [Swofford 1993]) were used. Original results may not be repeatable for a variety of reasons, including errors in the published data. Where the possibility of such errors could not be discounted, the study was excluded.

7. *Number of Trees*.—Trees were used only if parsimony analysis of the data set generated fewer than 100 most parsimonious trees (MPTs). Where there were multiple MPTs, in lieu of any more sophisticated patterns of balance among the MPTs, the first MPT output by PAUP was used. Although trees are stored in a nonrandom order in PAUP, this is unlikely to affect the balance patterns seen in phylogenetically informative data sets (D. L. Swofford personal communication 1999). There is not necessarily an inverse correlation between the number of MPTs and their accuracy, but it might be expected that as the number of MPTs increases, so does the extent to which choice of a representative tree mimics simply choosing a tree and associated balance at random. Using matrices that support fewer than 100 MPTs should help to minimize this problem.

If a data set met the above criteria, the balance of the resulting tree was determined using Colless's index (Colless 1982; Heard 1992) (eq. 1). The balances of our samples of paleontological and neontological trees are summarized in Figure 4. The data for any given sample size is too small to allow statistical testing of the results, but for most tree sizes the paleontological trees are more imbalanced on average than the neontological trees. A chi-squared test of the results (observed partitioning for paleontological trees is 12 groups more imbalanced than neontological trees of the same size and 2 less imbalanced; expected partitioning 7 and 7) gives a probability of 0.0075, so results are significant at a 0.05 level.

It has been shown by various authors that as data quality decreases, cladograms become more imbalanced (Mooers et al. 1995; Colless 1996; Heard and Mooers 1996; Huelsenbeck and Kirkpatrick 1996). To evaluate the possibility that poor data quality was responsible

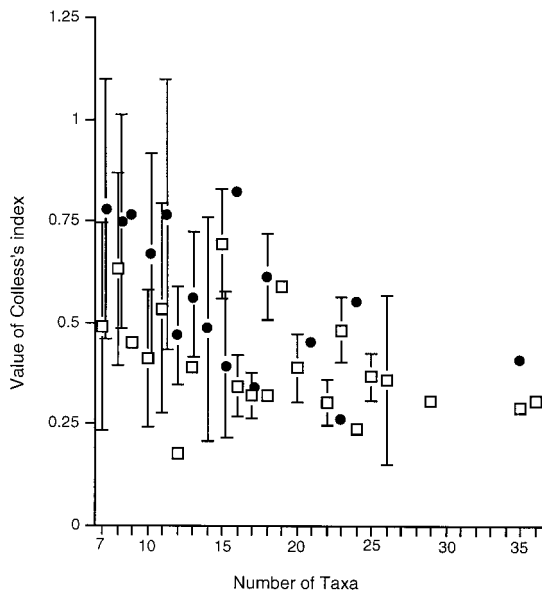


FIGURE 4. Comparison of average balances for cladograms based on neontological and paleontological data. Paleontological data are represented by filled circles and neontological data are represented by empty squares. The error bars represent one standard deviation from the average for each taxon size. Points with no error bars represent classes with data from only one cladogram. For most sizes, the paleontological trees are on average more imbalanced than the neontological trees.

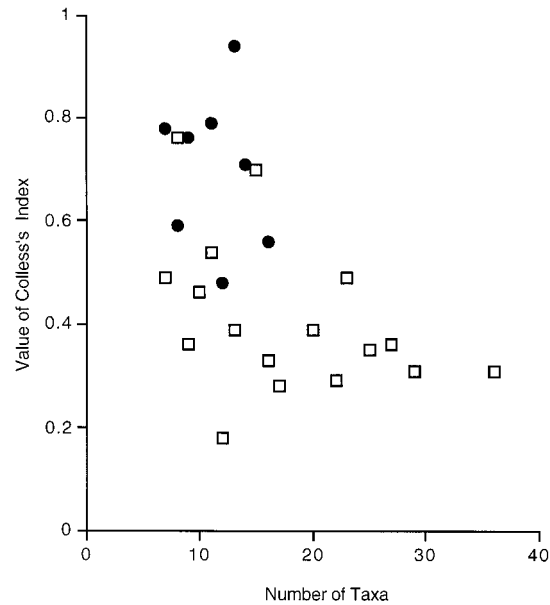


FIGURE 5. Comparison of average balances for cladograms based on a pruned data set of neontological and paleontological data. The data set was pruned to make the neontological and paleontological data more equivalent in quality. Filled circles represent paleontological data and empty squares represent neontological data. The paleontological data appear more imbalanced than the neontological data.

for the difference in balance distribution of paleontological and neontological trees, the data sets were pruned until they were equivalent in quality. This was done by

1. removing all data sets producing more than 5 MPTs;
2. removing data sets with more than 10% missing data;
3. removing data sets where the retention index (R.I.) of the trees was less than 0.6.

Although these steps reduce the number, and therefore the power, of comparisons, they also reduce the likelihood that the difference in balance between paleontological and neontological trees is due to differences in data quality. Phylogenies included in the pruned data set are marked by asterisks in the Appendix.

A comparison between the balances of the pruned data sets shows that the paleontological trees are still on average more imbalanced than the neontological trees (Fig. 5). The data set is now too small for statistical testing, even

with a chi-squared test, but out of seven comparisons the paleontological phylogenies were more imbalanced on six occasions. We conclude that no obvious link between Ic and data quality can be discerned in the trees studied.

### Models of Tree Balance

Before presenting the results, it is necessary to discuss various models of tree balance that may act as null hypotheses for our study. The ERM-TS model has limitations, which are addressed, and a new Markovian null model is introduced. The new model applies to extinct clades and is called the ERM-TI (equal-rates Markov time-inclusive) model. A third model to be discussed is the proportional-to-distinguishable arrangements (PDA) model, which can be applied as a null hypothesis for trees constructed by parsimony using random data (Colless 1996).

*The Equal-Rates Markov Time Slice (ERM-TS) Model.*—The most commonly used null model is the ERM-TS model, where all branches have an equal chance of splitting at any time (Fig.

3). The ERM-TS model does not explicitly accommodate extinction, because a pattern of diversification without extinction is considered to be an appropriate null model (Slowinski and Guyer 1989; Mooers and Heard 1997). However, Slowinski and Guyer (1989) suggested this only for trees where all terminal taxa are contemporaneous. Their premise was that as long as extinction has occurred at an equal rate on all branches leading to the terminals, it is unlikely that one branch will have significantly more surviving taxa on it than another. We contend that this model is not usually appropriate for paleontological phylogenies, because these may contain taxa that did not coexist. Rather than reconstructing a tree from a single time plane, the paleontologist effectively samples a growing tree through some or all of its history. This leads to imbalance in the phylogeny, for reasons explored in Figure 6. The figure shows the two members of a clade alive at T1. At T2, one taxon goes extinct, while the other speciates. This leads to imbalance in the tree in the following way: if a taxon goes extinct, the survival and speciation of its sister taxon will promote asymmetry. This is true of all nodes on a time-transgressive tree and will lead to considerable imbalance within the clade. The earlier (more basal) the extinction, the more pronounced the asymmetry will be. Extinct taxa are more likely to occur in a basal position on the cladogram than later forms, as their sister taxon has continued to diversify. This pattern leads to a greater degree of imbalance than expected under an ERM-TS model and explains why paleontological trees are more imbalanced than neontological trees.

*The Equal Rates Markov Time-Inclusive (ERM-TI) Model.*—The hypothesis that trees based on all taxa that ever existed would be more imbalanced than trees based on contemporaneous taxa was tested by computer simulation. The program begins with a single taxon that has a small but equal probability of speciation or extinction. In 50% of cases this single taxon eventually becomes extinct without branching and the clade is terminated, but in 50% of cases it branches, giving a clade of two species, each of which has the same probability of splitting or extinction as does the initial

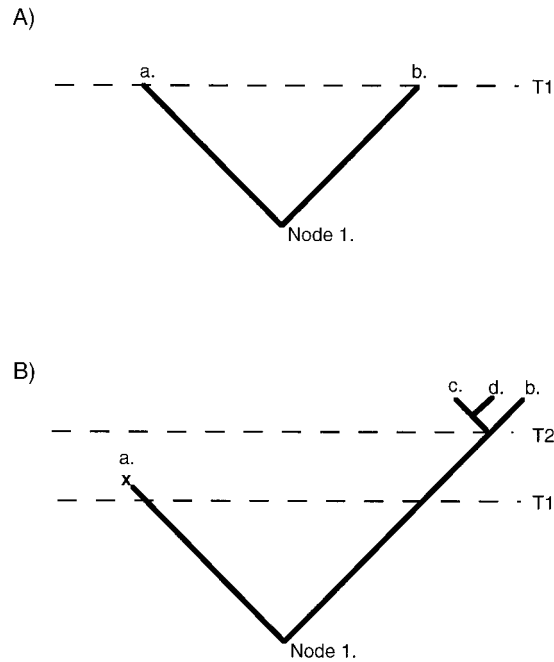


FIGURE 6. Diagram showing how extinction can lead to imbalance in a tree. A, Two taxa, a and b, which coexist at T1 and are sister groups. At time T1 node 1 is completely balanced. B, Later in time, taxon a has become extinct, while taxon b has speciated at time T2. This creates imbalance at node 1. If any taxa belonging to the same clade as b speciate—for example, if taxon c gives rise to taxon d as shown—this will further increase the imbalance at node 1. As taxon a is extinct, it has no chance of speciating and so this node can only become more imbalanced over time. This pattern is the same for all nodes in a tree and is the reason the random extinction causes imbalance in a time-transgressive tree. Most paleontological phylogenies are time transgressive and could be expected to be more imbalanced for this reason.

branch. The probability of speciation and extinction are both arbitrarily set at 0.01, so for most iterations each taxon remains unchanged. The tree is grown in this way until it terminates by extinction of all taxa. It was not determined for clades of more than 40 taxa, so trees of this size were not analyzed.

The program was used to grow 1000 trees of every size from 3 to 40 taxa, and the standard deviation and mean of each size class were calculated (Table 1). The results of this simulation are compared with the ERM-TS model in Figure 7. Note that there is some stochastic fluctuation in the program, meaning that our values of the standard deviation and expected value of  $I_c$  under the ERM-TI model



TABLE 1. Mean values and standard deviation of  $I_c$  for trees of up to 40 taxa, generated by computer simulation. The program grew trees using a small but equal chance of speciation and extinction (1%), and then the mean value and standard deviation of  $I_c$  were calculated for each size of tree.

Number of terminal taxa	Mean value of $I_c$	Standard deviation of $I_c$
3	1.0	0
4	0.803	0.39793134
5	0.7161667	0.30743931
6	0.7038	0.28214388
7	0.64139996	0.25548258
8	0.62295245	0.23601889
9	0.59196436	0.21782074
10	0.58336115	0.21355333
11	0.56868889	0.19642461
12	0.55387273	0.19146717
13	0.52472727	0.18455829
14	0.52447436	0.18510409
15	0.51897803	0.17433498
16	0.50872379	0.17149291
17	0.48800834	0.1612854
18	0.48225001	0.15802332
19	0.47137256	0.15648359
20	0.45709358	0.15119905
21	0.46928421	0.15437887
22	0.45283334	0.1489757
23	0.45035055	0.14724093
24	0.43763241	0.14027671
25	0.42673551	0.13288832
26	0.42373332	0.12735564
27	0.42484923	0.1291076
28	0.41462092	0.13183864
29	0.41615077	0.12801321
30	0.40800739	0.12856949
31	0.40469197	0.12543821
32	0.40607312	0.12474006
33	0.39675202	0.12712863
34	0.3919943	0.12156038
35	0.39048485	0.1188567
36	0.38739664	0.11795968
37	0.38374605	0.11792014
38	0.37708105	0.11738887
39	0.37147939	0.11775314
40	0.36934819	0.11725125

are not exact, although they are precise enough to show a clear pattern.

Our simulation shows two main results:

1. The mean value for  $I_c$  is always greater under the ERM-TI model than the ERM-TS model, except for the case of  $n = 3$ , where all trees must be entirely imbalanced under both models.
2. The standard deviation is considerably larger under the ERM-TI model, meaning that the expected values of imbalance for trees under this model have a much greater scatter. Strongly pectinate clades with high

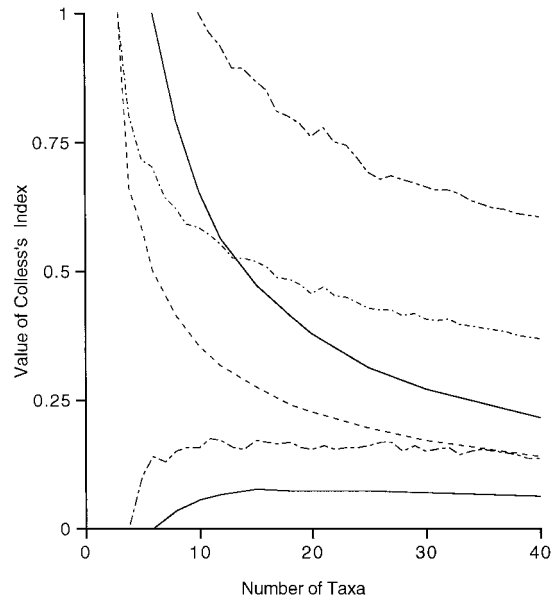


FIGURE 7. Comparison of distributions under the ERM-TS model (trees from a single time slice) and the ERM-TI model (trees from all taxa ever to have existed in a clade). The ERM-TS model is represented by a dashed line for the expected value and by solid lines for two standard deviations away from it. Data for this model were derived from Rogers 1994. The ERM-TI model is represented by a dotted and dashed line for the expected value and by a short- and long-dashed line for two standard deviations from the expected value. Values of the ERM-TI model were derived from the computer program described in the text. For all tree sizes (apart from three-taxon trees, which have only one topology under any model) the ERM-TI model produces significantly higher levels of imbalance than the ERM-TS model. It also has a larger standard deviation.

values of  $I_c$  ( $I_c > 0.75$ ) are common for clades of up to  $n = 20$ .

*The Proportional-to-Distinguishable Arrangements (PDA) Model.*—A third model that should be considered was devised by Rosen (1978) and Simberloff et al. (1981), under which all labeled trees are equally likely. It has been called the equal probability (EP) model (Colless 1996; Rogers 1996); however, to avoid confusion with the very different equi-probable types (EPT) model in which all unlabeled topologies are equally likely (Simberloff et al. 1981), here it is called the proportional-to-distinguishable arrangements (PDA) model (Simberloff et al. 1981; Savage 1983; Mooers and Heard 1997). The model is equivalent to picking at random from all possible trees (Mooers and Heard 1997). It is not immediate-

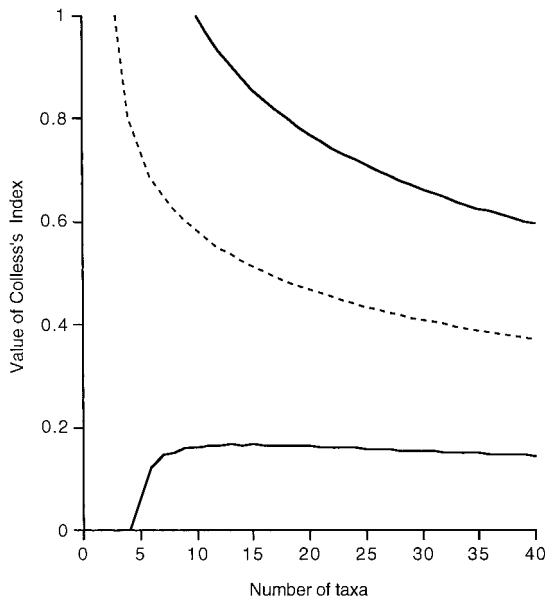


FIGURE 8. Expected values of Colless's index under the PDA model. The dashed line represents the expected value while the solid lines represent two standard deviations away from the expectation. Data taken from Rogers 1994.

ly obvious that any evolutionary process could produce such an expectation, but the PDA has been considered useful as a proxy for "poor data" in a cladogram (e.g., Colless 1996). If poor-quality data lead to recovery of more imbalanced cladograms (Mooers et al. 1995; Colless 1996; Heard and Mooers 1996; Huelsenbeck and Kirkpatrick 1996) and paleontological phylogenies are based on poorer-quality data than neontological phylogenies, paleontological trees would be, on average, more imbalanced, so the PDA model also needs to be considered as an appropriate model for paleontological tree shape.

The mean and standard deviation of the PDA model have been calculated by Rogers (1996) and are presented here as Figure 8. The PDA model produces much more imbalanced values of  $I_c$  than the ERM-TS model, and the distribution of the PDA model is close to the output of the seemingly very different ERM-TI model discussed above. We conjecture that the ERM-TI model and the PDA model may be mathematically equivalent, although the reasons for this are not apparent. The PDA model does not include any evolutionary information, such as splitting or extinction rates,

whereas the ERM-TI model does. However, the similarity of the two models means that we cannot reject the hypothesis that imbalance of paleontological trees results from use of poorer quality data simply by examining the balance distribution of paleontological cladograms.

#### Comparing Real Data with the Models

It is too simplistic to claim that the ERM-TS model should be applied to neontological studies whereas the ERM-TI model should be applied to paleontological phylogenies. For one thing, some paleontological studies use fossils from a single time slice (e.g., bedding plane assemblages) and in these cases the ERM-TS model is more appropriate. Most of the fossil studies will include taxa from a range of ages, but not the entire time interval of the clade to which they belong. Assuming that these fossil studies include taxa selected in a nonrandom way (e.g., by preservational biases being stronger in certain parts of the fossil record), then they would be expected to show a balance intermediate between the ERM-TS and ERM-TI models. Random selection of fossil taxa would not affect the balance, under the same principles described by Mooers (1995) for tree completeness in neontological groups. Also, many paleontological data sets include extant taxa, and so might be expected to be slightly more balanced than under the ERM-TI model. There are cases in neontological work where the ERM-TI model may be more appropriate, such as in viral phylogenies (see below). Nevertheless, the two models are a useful guide of expected tree balance under a variety of circumstances.

Figure 9 compares the distribution of data points from the neontological and paleontological data sets with both the ERM-TS and ERM-TI models.

The neontological data fit the ERM-TS model very badly; 19 out of 50 data points fall more than two standard deviations away from the expected value and all of these are more imbalanced than expected. Only eight cladograms gave a value that was less imbalanced than the mean expectation and these fell well within two standard deviations. These results show that trees based on data taken from ex-

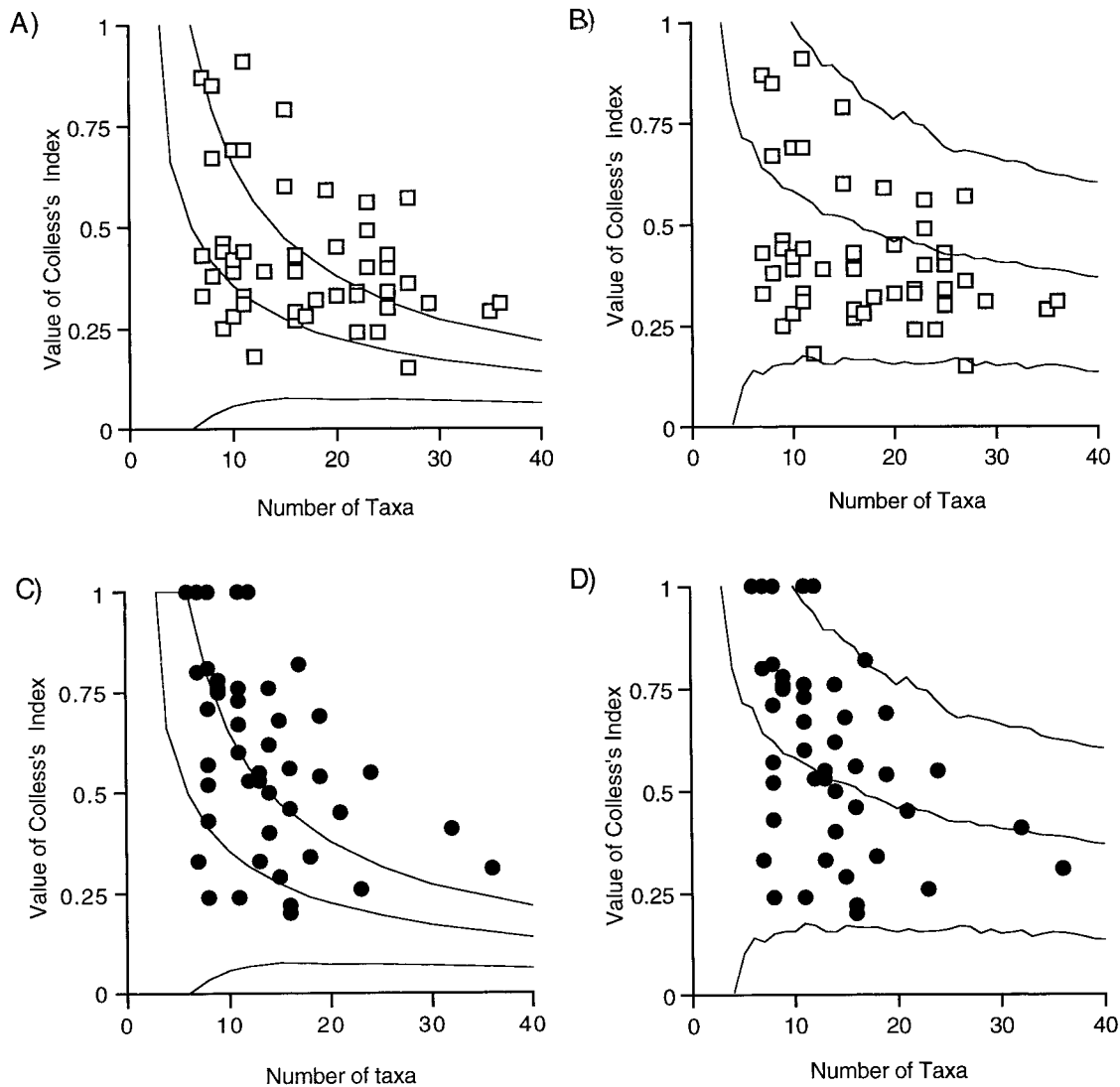


FIGURE 9. Comparison of the neontological and paleontological data sets with both the ERM-TS and the ERM-TI models. A, A comparison of the neontological data (represented by empty squares) with the ERM-TS model. The data fit this model badly. Nineteen out of 50 points are more imbalanced than two standard deviations away from the mean. B, A comparison of the neontological data with the ERM-TI model. All 50 points fall within two standard deviations of the mean, but only twelve are more imbalanced than the expected value. C, A comparison of the paleontological data sets with the ERM-TS model. Only sixteen out of 50 points fall within two standard deviations of the expected value under this model. D, A comparison of the paleontological data sets with the ERM-TI model. All but two points fall within two standard deviations of the expected value. Of the 50 data sets, 26 fall above the expected line and 24 fall below it.

tant taxa are more imbalanced than would be expected under a model of growth where diversification rates are equal across all lineages. This result is in accord with most other studies (Guyer and Slowinski 1991, 1993; Heard 1992; Mooers 1995), and it seems to be well established that the ERM-TS model underestimates tree balance in estimated phylogenies.

This pattern may be caused by evolutionary factors, such as adaptive radiation (e.g., Guyer and Slowinski 1993; Kirkpatrick and Slatkin 1993) or by problems with reconstructing phylogenies using poor data (e.g., Mooers et al. 1995; Colless 1996; Heard and Mooers 1996; Huelsenbeck and Kirkpatrick 1996).

Comparing the neontological data with the

ERM-TI model gives a much better fit. Twelve points fall above the expected value and 38 fall below, so the fit of the data to the expected values is not good. However, all the points fall within two standard deviations of the expected, but given the wide range of values that two standard deviations covers, perhaps this is not too surprising.

Factors that cause imbalance in neontological trees also affect paleontological trees. However, the balance distribution of paleontological cladograms fits their null model, the ERM-TI model, extremely well. Only two data points are more than two standard deviations away from the average value, and roughly half the points fall above the average line and half fall below it. This means that the ERM-TI model cannot be rejected for paleontological trees. All things being equal, it might be expected that the paleontological cladograms should be more imbalanced than the expectation, as the neontological phylogenies are for the ERM-TS model. There are several possible reasons that this is not the case. First, as discussed above, it is much easier for paleontological phylogenies to show a good fit to the ERM-TI model, owing to the much wider range of balances this model predicts. Second, many of the paleontological phylogenies contain either some extant groups or are concentrated on a single time plane with a few representatives from other stratigraphic levels. In these cases, the expected balance would be somewhere between the two null models. These trees may therefore make the overall distribution more balanced than expected. Third, Kim (1993) showed that true imbalanced trees are harder to recover than balanced ones, which may have the effect of artificially lowering the balance distribution of the paleontological trees.

The ERM-TS model is easily rejected by the paleontological data. Only 16 paleontological data points fall within the two standard deviation range, and all the other points are more imbalanced than expected.

### Discussion

Our simulations of tree growth and balance, and our examination of published phylogenies raise several issues:

1. *Interpretation of Studies of Balance.*—The number of paleontological trees that have been included in a particular data set is a factor that needs to be considered when looking at patterns of balance. A data set that contains only trees based on neontological data would be expected to be more balanced on average than a data set containing trees based on paleontological data. Data sets that combine paleontological and neontological trees will not be as informative about balance patterns because the expectation of balance for the two classes of data is different.

2. *The Balance of Paleontological Cladograms.*—This study demonstrates that paleontological cladograms should not be expected to be very symmetrical. In fact, entirely comb-shaped cladograms are not unusual for trees of up to 12 taxa. Cladograms of this topology should not necessarily be viewed with suspicion, or considered to be an unlikely representation of phylogeny.

The expected distributions of balance under an ERM-TI model suggest paleontological phylogenies may not be as sensitive to variations in speciation and extinction rates as neontological phylogenies. The range of balances generated by the ERM-TI model is so great that it is unlikely that any tree will fall outside two standard deviations of the expected value, even if significant evolutionary processes that affect tree shape have occurred. Tree shape might therefore be of little in identifying macroevolutionary patterns from the fossil record.

3. *Viral Phylogenies, and Other Fast-Evolving Laboratory Organisms.*—Not all neontological studies contain taxa from the same time interval. Phylogenies of modern, fast-evolving genomes of, for example, bacteria and viruses may be time transgressive in the same sense that paleontological trees are. Important examples can be found in the human immunodeficiency virus (HIV) and influenza phylogenies. For example, HIV phylogenies constructed for viruses taken from a single infected individual over timescales of several years may contain viral strains ancestral to later variants (Holmes et al. 1992), and may also contain strains that have since become extinct in the host. Phylogenies for influenza

have been constructed for strains that have evolved and become extinct over the last 100 years (Webster et al. 1995). Viral phylogenies of this type include extinct taxa and so the ERM-TI model would be useful as a null hypothesis in a study of their balance.

4. *Position of Fossil Taxa on Cladograms and Macroevolutionary Hypotheses.*—The effects of time and extinction on tree shape mean that over long periods of time, the earliest forms are likely to become extinct, while later forms may continue to diversify. The later forms will necessarily be more derived than earlier ones simply because of the random extinction of one of a pair of sister clades at the earliest nodes of a tree (Fig. 5). This makes paleontological phylogenies fundamentally different from time-slice phylogenies, where no prediction can be made about the position of the more-derived taxa. This fact has been underappreciated and has led paleontologists to speculate about macroevolutionary trends that may cause this pattern.

One consequence of such speculation is that imbalanced paleontological phylogenies may show a pattern that is then interpreted as an evolutionarily progressive sequence. The evolution of birds is an example. The bird phylogeny appears very imbalanced, with *Archaeopteryx* as the most basal taxon and Neornithes (modern birds) as the most derived. Padian and Chiappe (1998) have used this cladogram to suggest a gradual evolution of modern birds from more basal groups in a progressive way by acquisition of derived characters. However, only nine groups are portrayed on the cladogram. Under the ERM-TI model, which is appropriate in this case as the groups portrayed cover a stratigraphic range from the Late Jurassic to the recent, a totally imbalanced tree of nine taxa is within two standard deviations of the expected imbalance, so this topology is not unusual and cannot be attributed to variation in speciation and/or extinction rates. Benton (1987) suggests that the notion of evolutionary progress derived from these imbalanced phylogenies has led to the development of macroevolutionary hypotheses such as key innovation and competitive replacement. An imbalanced, step-series cladogram gives the impression

that the later clade has some feature that caused it to radiate and become more diverse than its sister clade (the key innovation hypothesis), or that the more derived clade drove its more primitive sister group to extinction (competitive replacement). The cladogram shape therefore may give an illusion of directed evolutionary progress, but it is possible that drawing this conclusion may be overinterpretation of a pattern that can be explained by the effects of random extinction on the shape of a phylogeny including fossils. To fully test evolutionary hypotheses such as these, information such as character distribution patterns on the tree (Pearson 1999) may be more useful than considering tree balance alone.

### Summary

1. Under a model of equal rates of speciation and extinction, phylogenies of taxa from a single time slice can be expected to be more balanced than phylogenies of all members of a group that have ever lived. This might explain why paleontological phylogenies, which are usually time transgressive, often appear more imbalanced than neontological phylogenies.

2. The ERM-TI model provides an explanation for these imbalanced paleontological trees without invoking an evolutionary hypothesis or assuming that they are inaccurate representations of the true phylogeny.

3. The ERM-TS model and the ERM-TI model provide the two end-member null hypotheses for trees of a mixture of extinct and extant taxa. As such, they provide useful guidelines about the expected balance of most types of phylogeny under a model of equal rates of evolution.

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## Appendix

Information about data sets used in the analysis. Abbreviations: Ic = value of Colless's index; Am. Mus. Nov. = American Museum Novitates; Bull. AMNH = Bulletin of the American Museum of Natural History; Herp. = Herpetologica; JVP = Journal of Vertebrate Paleontology; Mal. = Malacologica; Pal. = Palaeontology; Sys. Biol. = Systematic Biology; ZJLS = Zoological Journal of the Linnean Society; Liz. Phyl. = *Phylogenetic relationships of the lizard family*, Estes and Pregill, eds. Stanford University Press, Stanford, Calif.; Mamm. Phyl. = *Mammal phylogeny*, Vols. 1, 2, Szalay, Novacek, and McKenna, eds., Springer, Berlin; Paleon. = paleontological data set; Neon. = neontological data set. Data sets marked with an asterisk (\*) were also used in the second analysis, where data sets were pruned until they were of equivalent quality.

Author	Ic	Place of publ.	No. of char.	No. of taxa (excl. out-groups)	Type of data set	Stratigraphic coverage	Taxa used	Year of publ.
Rougier et al.	0.69	Am. Mus. Nov.	51	19	Paleon.	Ter-Rec	Mammaliaforms	1996
Macovicky	0.76	Am. Mus. Nov.	95	11	Paleon.	Cret	Theropods	1998
MacPhee et al.	0.22	Am. Mus. Nov.	32	16	Paleon.	Ter-Rec	Monkeys	1995
Gaffney*	0.56	Bull. AMNH	40	16	Paleon.	Cret-Plio	Turtles	1996
MacPhee	0.29	Bull. AMNH	30	15	Paleon.	Quat	Eutherians	1994
Gaffney et al.	0.62	Cladistics	39	14	Paleon.	Trias-Rec	Turtles	1991
Yates	0.67	JVP	68	11	Paleon.	Trias	Temnospondyls	1999
Froehlich	0.31	JVP	125	36	Paleon.	Eoc	Perissodactyls	1999
Heckert and Lucas	0.43	JVP	60	8	Paleon.	Trias	Aetosaurus	1999
Wilson and Li*	0.55	JVP	54	13	Paleon.	Eoc	Fish	1999
Baez and Pugener*	0.33	JVP	48	13	Paleon.	Cret-Rec	Frogs	1998
Steppan and Pardini	0.34	JVP	45	18	Paleon.	Plei-Rec	Muroids	1998
Reisz et al.*	0.76	JVP	31	9	Paleon.	Perm-Carb	Synapsids	1998
Zhang	0.26	JVP	67	23	Paleon.	Cret-Rec	Fish	1998
Hooks	1	JVP	27	8	Paleon.	Cret	Turtles	1998
Wilson and Sereno*	1	JVP	109	11	Paleon.	Trias-Cret	Sauropods	1998
Head*	1	JVP	20	8	Paleon.	Cret	Hadrosaurids	1998
Wang et al.*	0.81	JVP	20	8	Paleon.	Trias-Cret	Holotherians	1998
Sues	0.8	JVP	47	7	Paleon.	Jur-Cret	Theropods	1997
Jalil	0.82	JVP	71	17	Paleon.	Perm-Trias	Proclertiforms	1997
Geraads	1	JVP	22	8	Paleon.	Ter	Nimravids	1997
Gower and Sennikov	0.24	JVP	35	8	Paleon.	Trias	Archosaurs	1997
Wu et al.	0.41	JVP	128	32	Paleon.	Jur-Cret	Protosuchians	1997
Novas	1	JVP	75	7	Paleon.	Jur-Cret	Theropods	1997
Li and Wilson*	0.24	JVP	28	11	Paleon.	Ter-Rec	Fish	1996
Reynoso	0.76	JVP	42	14	Paleon.	Trias-Rec	Sphenodonts	1996

Appendix. Continued.

Author	Ic	Place of publ.	No. of char.	No. of taxa (excl. out-groups)	Type of data set	Stratigraphic coverage	Taxa used	Year of publ.
Coria and Salgado*	1	JVP	40	6	Paleon.	Cret	Iguanodontians	1996
Steppan*	0.57	JVP	27	8	Paleon.	Plei-Rec	Rodents	1996
Meylan	0.5	JVP	35	14	Paleon.	Cret-Rec	Turtles	1996
Wu	0.54	JVP	46	19	Paleon.	Jur-Rec	Eusuchians	1996
Sues et al.*	0.53	JVP	34	13	Paleon.	Trias-Rec	Sphenodontians	1994
Chiappe and Calvo*	1	JVP	73	8	Paleon.	Jur-Rec	Birds	1994
Wu and Chatterjee	0.73	JVP	65	11	Paleon.	Jur-Rec	Dinosaurs	1993
Novas	1	JVP	51	8	Paleon.	Trias	Sphenosuchians	1993
Sereno	0.52	JVP	36	8	Paleon.	Trias-Jur	Basal archosaurs	1991
Fischer and Tassy	0.68	Mamm. Phyl.	77	15	Paleon.	Ter-Rec	Proboscoid clade	1993
Beard*	0.71	Mamm. Phyl.	29	8	Paleon.	Ter-Rec	Primate morphs	1993
Cifelli	0.2	Mamm. Phyl.	51	16	Paleon.	Ter-Rec	Ungulates	1993
Williams	0.46	Pal.	39	16	Paleon.	Cam-Perm	Brachiopods	1998
Ruta*	1	Pal.	38	12	Paleon.	Ord-Dev	Mitirates	1997
Prado and Alberdi*	0.4	Pal.	20	14	Paleon.	Mio-Rec	Horses	1996
Janvier	0.45	Pal.	89	21	Paleon.	Cam-Rec	Vertebrates	1996
DeBraga and Reisz*	0.78	Pal.	50	9	Paleon.	Carb-Perm	Diapsids	1995
Dilkes*	0.75	Pal.	28	9	Paleon.	Trias	Rhynchosaurs	1995
Dodick and Modesto*	0.71	Pal.	39	8	Paleon.	Perm	Captochinids	1995
Alroy*	0.56	Sys. Biol.	55	16	Paleon.	Mio-Plio	Horses	1995
Schultze	0.33	Sys. Biol.	213	7	Paleon.	Dev-Rec	Sarcopterygians	1994
Lee	0.55	ZJLS	128	24	Paleon.	Perm	Pareiasaurs	1997
Ericson	0.6	ZJLS	51	11	Paleon.	Paleo-Rec	Birds	1997
Laurin and Reisz*	0.53	ZJLS	124	12	Paleon.	Perm-Rec	Amniotes	1995
Rozen*	0.33	Am. Mus. Nov.	27	22	Neon.	n/a	Bees	1996
Morrone*	0.69	Am. Mus. Nov.	20	10	Neon.	n/a	Weevils	1995
Roig-Juñent*	0.24	Am. Mus. Nov.	41	22	Neon.	n/a	Beetles	1995
Gould	0.36	Am. Mus. Nov.	103	27	Neon.	n/a	Hedgehogs	1995
Morrone*	0.28	Am. Mus. Nov.	32	17	Neon.	n/a	Weevils	1994
Simmons and Geisler	0.43	Bull. AMNH	207	25	Neon.	n/a	Bats	1998
Yeates	0.44	Bull. AMNH	22	9	Neon.	n/a	Bombyllids	1994
Pleijel and Dahlgren	0.32	Cladistics	42	18	Neon.	n/a	Annelids	1998
Cigliano et al.*	0.29	Cladistics	29	16	Neon.	n/a	Grasshoppers	1996
Hausdorf	0.38	Cladistics	14	8	Neon.	n/a	Gastropods	1995
Carlson*	0.28	Cladistics	112	10	Neon.	n/a	Brachiopods	1995
Wheeler et al.*	0.44	Cladistics	100	11	Neon.	n/a	Arthropods	1993



Appendix. Continued.

Author	Ic	Place of publ.	No. of char.	No. of taxa (excl. out-groups)	Type of data set	Stratigraphic coverage	Taxa used	Year of publ.
Ladige et al.*	0.4	Cladistics	36	25	Neon.	n/a	Eucalypts	1992
Vane-Wright et al.	0.39	Cladistics	100	10	Neon.	n/a	Butterflies	1992
Schultz*	0.33	Cladistics	64	11	Neon.	n/a	Arachnids	1990
Sundberg*	0.79	Cladistics	38	15	Neon.	n/a	Plectonemertids	1989
Albert and Fink*	0.43	Copeia	35	7	Neon.	n/a	Fish	1996
Mayden and Kuhajda*	0.42	Copeia	51	10	Neon.	n/a	Fish	1996
Wilkinson and Nussbaum*	0.6	Copeia	47	15	Neon.	n/a	Caecilians	1996
Guisu and Winterbottom*	0.85	Copeia	46	8	Neon.	n/a	Fish	1993
Wiens*	0.67	Copeia	45	8	Neon.	n/a	Fish	1993
Harold*	0.33	Copeia	64	7	Neon.	n/a	Lizards	1993
Greer	0.28	Herp.	42	10	Neon.	n/a	Lizards	1997
Burke*	0.69	Herp.	38	11	Neon.	n/a	Turtles	1996
Hinx*	0.31	Herp.	32	11	Neon.	n/a	Turtles	1996
Mikkelsen	0.59	Mal.	47	19	Neon.	n/a	Cephalaspids	1996
Wyss and Flynn*	0.45	Mamm. Phyl.	63	20	Neon.	n/a	Carnivores	1993
Wible and Hopson*	0.91	Mamm. Phyl.	37	11	Neon.	n/a	Mammals	1993
Whiting et al.*	0.34	Sys. Biol.	176	25	Neon.	n/a	Strepsipterans	1997
Shaffer et al.*	0.31	Sys. Biol.	115	29	Neon.	n/a	Turtles	1997
Brochu*	0.43	Sys. Biol.	164	16	Neon.	n/a	Crocodylians	1997
Livezey*	0.31	Sys. Biol.	165	36	Neon.	n/a	Anseriforms	1996
Lafay et al.*	0.33	Sys. Biol.	43	7	Neon.	n/a	Asteroids	1995
Lydeard	0.24	Sys. Biol.	55	24	Neon.	n/a	Fish	1995
Titus and Larson*	0.33	Sys. Biol.	44	20	Neon.	n/a	Salamanders	1995
Eernisse	0.4	Sys. Biol.	141	23	Neon.	n/a	Metazoans	1992
Wilson and Keable*	0.46	ZJLS	75	9	Neon.	n/a	Isopods	1999
Nygren*	0.18	ZJLS	44	12	Neon.	n/a	Polychaetes	1999
Reynolds*	0.25	ZJLS	34	9	Neon.	n/a	Mollusks	1999
Gosliner and Johnson*	0.49	ZJLS	37	23	Neon.	n/a	Nudibranchs	1999
Hallermann	0.34	ZJLS	144	22	Neon.	n/a	Squamates	1998
Miller*	0.3	ZJLS	85	25	Neon.	n/a	Moths	1996
Oosterbroek and Courtney*	0.15	ZJLS	98	27	Neon.	n/a	Dipterans	1995
Smith et al.*	0.57	ZJLS	43	27	Neon.	n/a	Ophiroids	1995
McHugh	0.29	ZJLS	22	35	Neon.	n/a	Polychaetes	1995
Kluge*	0.39	ZJLS	75	13	Neon.	n/a	Snakes	1993
Pleijel	0.39	ZJLS	23	16	Neon.	n/a	Polychaetes	1993
Bryant et al.	0.56	ZJLS	46	23	Neon.	n/a	Mustelids	1993
Presch*	0.27	Liz. Phyl.	91	16	Neon.	n/a	Lizards	1988
Grismer*	0.87	Liz. Phyl.	75	7	Neon.	n/a	Lizards	1988