

# Testing the quality of the fossil record: Paleontological knowledge is improving

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## ABSTRACT

The value of the fossil record in giving a clear account of evolutionary history has been questioned because of its incompleteness. New evidence suggests, however, that this is not an overwhelming problem: a good match exists between sequences of lineage divergence as indicated by phylogenetic analysis (cladistic hypotheses of relation) and the order of appearance of groups in geologic time for 41 of 74 test-case cladograms of vertebrates. The relative completeness (ratio of known record to gap) of these test cases is highly variable, but there has been a clear improvement in paleontological knowledge (i.e., filling of the cladistically predicted gaps) over the past 25 years.

## INTRODUCTION

The fossil record of the history of life has been assumed generally to be incomplete. In the extreme, it might be asserted that the amount of data lost through incomplete preservation and sampling is so vast as to render the remaining fossil record virtually worthless. Debates about the value of the fossil record have been inconclusive, one side asserting blandly that paleontological data have little value, and the other denying the charge hotly. Recent tests (Gauthier et al., 1988; Norell and Novacek, 1992a, 1992b) have established, however, that the stratigraphic sequence of first appearances of fossil vertebrate groups frequently approximates cladogram branching order based upon character analysis alone. This result, based upon correlation of evidence from two independent sources, would be unexpected by those who view the fossil record as hopelessly incomplete.

In this paper, we analyze a large data set of vertebrate phylogenies and explore cases where the match between character analysis (cladistics) and the fossil record (stratigraphy) is good and contrast cases where the match is poor. Many reasons exist for poor matching, ranging from differences in preservability of the fossils and the overall age of the major branching points to less predictable effects such as the relative spacing in time of branch nodes. The absolute quality of these test-case cladograms is assessed further by comparing predicted gaps in the record with known taxon range. The resultant standardized measures of relative completeness are used to test whether paleontological knowledge has changed in a statistically detectable manner over the past 25 years.

## INCOMPLETENESS OF THE FOSSIL RECORD

The fossil record is incomplete and never will be perfect. Past debates have focused on

just how incomplete the record is, and some studies have addressed ways of testing stratigraphic aspects of that incompleteness (e.g., Paul, 1982, 1990; Maxwell and Benton, 1990; Strauss and Sadler, 1989; Marshall, 1990; Benton, 1994). Wider debates have considered whether useful macroevolutionary conclusions can be drawn from paleontological data. There have been three major areas of concern: does the fossil record indicate the true pattern of the diversification, and extinction, of life through time; can finer scale patterns of evolution be discerned from fossil sequences; are fossils of any value in reconstructing phylogenies, particularly using cladistic techniques?

The debate over the true pattern of the history of life began more than 20 years ago. Valentine (1969) asserted that his plots of the frequency of marine shelf taxa through time gave a reasonably accurate picture of the diversification of life in the sea, whereas Raup (1972) argued that much of the pattern could be explained by biases, that low levels of diversity in the early Paleozoic were not real but merely reflected how little was known of the fossil record in such ancient rocks. Raup (1972) made a case for a variety of systematic errors in the fossil record (exposed rock area, available rock volume, intensity of subsequent metamorphism and erosion, paleontological interest) that increased in magnitude with increasing geologic age. The case was settled in favor of Valentine's (1969) view by two empirical approaches: (1) Signor (1982, 1985) applied to the data corrections corresponding to the best estimates of Raup's (1972) systematic errors, yet the pattern of long-term diversification of life in the sea from low early Paleozoic levels was sustained; and (2) Sepkoski et al. (1981) compared graphs from five semi-independent data sets on the history of marine invertebrate life and found that the general pattern of diversity increase was identical in all cases. These demonstrations that the fossil

record was good enough for global-scale generalizations were not absolute tests of Raup's (1972) criticisms, however, but merely probabilistic arguments.

The debate over modes of evolution, whether by phyletic gradualism (evolution within lineages, with speciation occurring as a byproduct) or by punctuated equilibria (little discernible lineage change, most evolution being concentrated in short-scale speciation events) also involved serious consideration of the quality of the fossil record (Eldredge and Gould, 1972; Gould and Eldredge, 1977; Gingerich, 1985). Early hopes that one pattern or the other (drifting lineages vs. largely static lines with abrupt punctuations) could be discerned in test-case fossil groups foundered on problems of interpreting morphological divergence and on the inability to find enough relatively complete fossil records for study (Sheldon, 1990). Even in the most complete sedimentary rock sequences, gaps on the order of  $10^5$  yr exist (Anders et al., 1987), and these are sufficient to cause problems in testing the shape of evolutionary trees.

The quality of the fossil record is also an issue in cladistics. It has been asserted that fossil taxa are much inferior to living taxa for the reconstruction of phylogeny, and that they should be ignored or accorded much lower value in branching pattern assessment (Nelson, 1969; Hennig, 1981; Patterson, 1981; Goodman, 1989). This view is based on the obvious fact that no fossil, however well preserved, can yield all of the soft-part, biochemical, ecological, and behavioral data that are available from living organisms. In practice, of course, the case is not as bad. For morphologic assessment, fossil and living taxa are often treated equally, and it is rare for taxonomists to have the luxury of a complete knowledge of any living taxon. Furthermore, fossil taxa can assist in resolving cladograms based solely upon modern taxa by offering unique character combinations, by indicating the presence of homologies, and by resolving character polarity (Gauthier et al., 1988; Donoghue et al., 1989; Novacek, 1992).

## PHYLOGENETIC AND STRATIGRAPHIC CORRELATION

In their tests of the match between the rank order of cladistic branching and stratigraphic appearance, Norell and Novacek

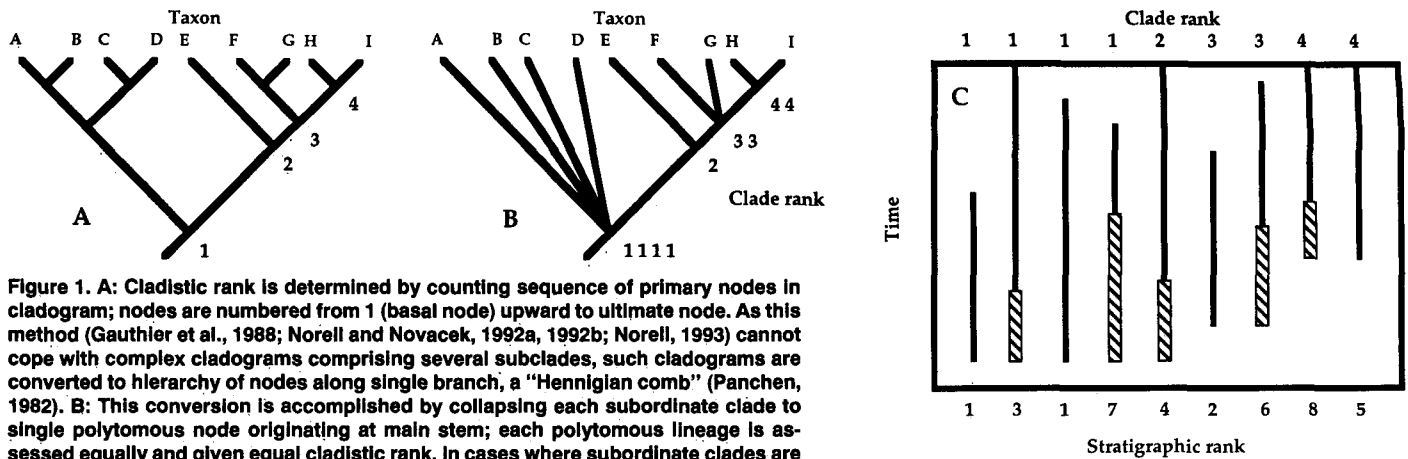


Figure 1. A: Cladistic rank is determined by counting sequence of primary nodes in cladogram; nodes are numbered from 1 (basal node) upward to ultimate node. As this method (Gauthier et al., 1988; Norell and Novacek, 1992a, 1992b; Norell, 1993) cannot cope with complex cladograms comprising several subclades, such cladograms are converted to hierarchy of nodes along single branch, a "Hennigian comb" (Panchen, 1982). B: This conversion is accomplished by collapsing each subordinate clade to single polytomous node originating at main stem; each polytomous lineage is assessed equally and given equal cladistic rank. In cases where subordinate clades are large, we have adopted convention that source cladogram is collapsed so as to maximize node number (using principle of free rotation). In four cases, alternate cladograms of different taxa produced from large data sets were tested separately. Stratigraphic sequence of clade appearance is assessed from earliest known fossil representative of sister groups. C: Minimum implied gap (MIG, diagonal rule) is difference between age of first representative of lineage and that of its sister, as oldest known fossils of sister groups are infrequently of same age. MIG is minimum estimate of stratigraphic gap, as true age of lineage divergence may lie well before oldest known fossil. Potential for MIGs is increased by presence of unresolved nodes.

(1992a) found that 18 of 24 test cases (75%) gave statistically significant ( $P < 0.05$ ) correlations, using the technique of Spearman rank-order correlation (SRC). Mammal-like reptiles, and certain higher mammals, believed qualitatively to have "good" fossil records and relatively stable, well-resolved cladograms, gave the best values. Six failed cases (amniotes, Squamata, hadrosaurs 1 and 2, higher primates, artiodactyls) could not be simply explained. In a slightly larger test (Norell and Novacek, 1992b), 24 of 33 test cases (73%) gave statistically significant ( $P < 0.05$ ) correlations. The additional failed cases were hadrosaurs 3, Squamata 2, and euryapsids.

We analyzed 74 vertebrate cladograms, using the same test, to assess more fully the correlation between cladistic rank and stratigraphic appearance (Fig. 1). Of these, only 41 (55%) showed statistically significant correlations at  $P < 0.05$ , and 25 (35%) at  $P < 0.01$ , when 1993 stratigraphic data are used (Benton, 1993a). Of the samples showing no correlation, five were negatively correlated. Our findings show a greater proportion of cladogram-stratigraphy mismatch than the previous studies (Norell and Novacek, 1992a, 1992b), possibly because we have sampled a wider array of available (and potentially less well resolved) cladograms. Where we reanalyzed Norell and Novacek's (1992a, 1992b) examples, our results agreed, excepting the case of Theropoda (Benton, 1990), which no longer yielded a significant ( $P < 0.05$ ) correlation.

SRC, the statistical technique used by Norell and Novacek (1992a, 1992b), and by us, to assess matches of cladistic and stratigraphic data is not an ideal approach. The first problem is that the branching events

within a cladogram are not independent but are constrained in sequence by the preceding nodes, and hence a time-series statistical approach might be appropriate. (This will be investigated in future papers.) In addition, the SRC approach provides a good, but imperfect, first-approximation test, because it simply orders times of origin and takes no account of the amount of time involved. Thus, correlation values may be high where dates of origin are well spaced temporally, such as in examples that span much of the Phanerozoic. Correlation is more likely to be insignificant, however, in cases where originations were more nearly synchronous, perhaps all being compressed within a 5 m.y. span. In the former case, enormous gaps would be required to place the points of group origins out of sequence, whereas in the latter, small gaps in the fossil record or minor errors in dating could introduce serious mismatch.

Another problem with the SRC statistic in the present case is that there is a correlation between SRC values and the size of the tested cladograms. For the 1993 data, a plot of SRC values against  $n$  (number of terminal taxa in cladogram) gives a straight-line relation of  $y = 0.338 + 0.024x$  ( $r = 0.257$ ;  $P < 0.05$ ). (For 1967 fossil record data, the straight line is  $y = 0.245 + 0.031x$ ;  $r = 0.293$ ;  $P < 0.02$ .) The SRC measure may depend on cladogram size (as indicated by  $n$ ), and thus cannot be a perfect test of the fit of stratigraphic and cladistic data on branching points, unless cladogram size were standardized to permit direct comparisons. Because of these two problems with the SRC method, another technique is required to assess the scale of differences between predicted origination times and the relative

amounts of missing data in particular fossil records.

#### RELATIVE COMPLETENESS OF FOSSIL RECORDS

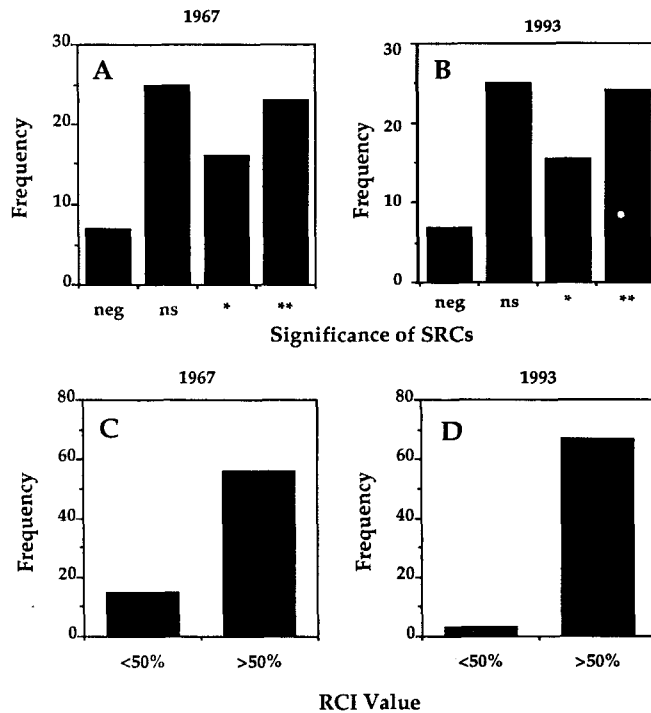
The quality of individual fossil records was assessed by calculating minimum implied gaps (MIGs) for each cladogram (Fig. 1) (Norell and Novacek, 1992a, 1992b; Weishampel and Heinrich, 1992; Norell, 1993; Storrs, 1993; Benton, 1994). MIGs may be measured and summed for any phylogenetic tree (a cladogram plotted against known stratigraphic taxon ranges) giving total MIG value. This is best cited as a measure of relative completeness of the tree, because the quality of any particular fossil record will depend upon the numbers of taxa involved and their known stratigraphic ranges.

A relative completeness index (RCI) was calculated for each case with the purpose of comparing the amount of gap in a particular fossil record (assessed as MIG) to the part of the record represented by fossils:

$$RCI = \left(1 - \frac{\sum (MIG)}{\sum (SRL)}\right) \times 100\%$$

where SRL is the simple range length for each taxon (the time between first and last known appearance) (Storrs, 1993). RCI, being a measure of total inherent gap (based upon a predictive phylogeny) to known lineage duration based upon fossil appearances, theoretically may vary from a negative value, where the amount of expected gap exceeds the sum total of proven stratigraphic range lengths, to 100%, where no gaps are evident. Examples of total gap being greater than total known record appear

**Figure 2.** Change in paleontological knowledge documented by using Harland et al. (1967) and Benton (1993a). A, B: Spearman rank coefficients (SRCs) for 1967 vs. 1993 data show no evidence of improvement (neg—negatively correlated; ns—positively correlated but not significantly so; asterisk—positively correlated at significance  $P < 0.05$ ; double asterisk—positively correlated at  $P < 0.01$ ). C, D: Between 1967 and 1993, however, more cladograms show better than 50% RCI fit to fossil record, an increase from 57 to 69. This shows clear evidence of improvement in paleontological knowledge.



to be rare for analyses involving numerous taxa. In the present study, no negative RCI values were obtained using the 1993 stratigraphic data set (Benton, 1993a). When an older set of range dates (Harland et al., 1967) was used, a single negative value was found ( $-0.53$  for Actinopterygii).

In our 74 analyses, individual RCIs for the 1993 data set ranged from  $<10\%$  (poor fossil record) to  $>90\%$  (excellent record). Lowest values were for two cladograms of Crocodylomorpha (RCI  $<10\%$ ), followed by Primates and Theropoda (RCI =  $40\%$ – $50\%$ ), Chalicotheriinae, Chalicotherioidea, Equidae, Ornithopoda, Proboscidea, and two cladograms of Testudines (RCI =  $50\%$ – $60\%$ ). Of these 11 records with low relative completeness, eight nonetheless show good correlation of stratigraphic and clade rank ( $P < 0.01$ ). There is no single explanation for these poor records: the groups include diverse diapsids and turtles, and time scales range from 50 to 220 m.y.

The comparisons are sensitive to the magnitudes of time scales used and the relative ages of lineage origins. If all else is equal, best values may be obtained for comparisons of ancient high-category groups, where the known stratigraphic range is bound to exceed the MIG by a great deal. Hence, for comparisons of the major groups of fishes, tetrapods, amniotes, or diapsids, the SRLs are so large (hundreds of millions of years) that they swamp the MIGs, even if the latter are themselves large. The Tertiary mammal groups which have low RCI values show the opposite combination of time-scale properties: short SRLs, because the groups arose

geologically recently, and hence relatively large MIGs. Further, the category level at which the analysis is presented may be crucial since durations (SRLs) of species and genera are shorter than those of families or orders. Thus, some of the perissodactyl and proboscidean groups have “good” fossil records by any qualitative assessment, but they lose out in the RCI measure because the analyses are presented at the level of the genus or species (hence giving low SRLs), and these durations approach the stratigraphic acuity of some of the fossil records.

High-quality records are more readily explained. The best (RCI  $>90\%$ ), when 1993 data are used, are based on very long time scales and high-level taxa (Amniota 1, Amphibia 1, Archosauria;  $>250$  m.y.) (Gnathostomata [two], Sarcopterygii [four];  $>400$  m.y.). The record for Sauropterygia (RCI =  $94.4\%$ ) spans 180 m.y. Long time scales and high-level groupings mean that many SRLs are large and may greatly exceed some very large gaps, thus artificially enhancing apparent completeness. Another high-quality record (Perissodactyla; RCI =  $97.6\%$ ) is based on a much shorter span (60 m.y.), implying a genuinely excellent fossil record with negligible gaps. Only one of the 11 highest quality records (Archosauria), however, yielded a significant ( $P < 0.05$ ) rank correlation. Another 13 groups in the RCI range of  $80\%$ – $90\%$  show fewer long time scales (six) and more (nine) statistically significant rank correlations ( $P < 0.05$ ), a trend continued in the  $70\%$ – $80\%$  range (12 and 10 out of 19, respectively).

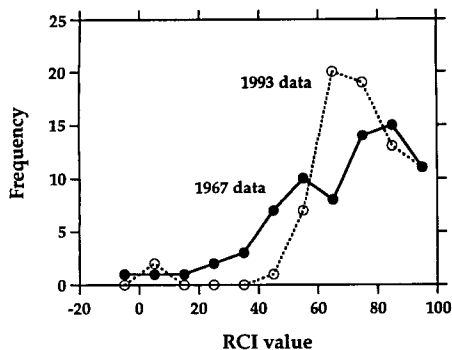
## TESTING CHANGES IN PALEONTOLOGICAL KNOWLEDGE

Why do so many cladograms (33 out of 74) not reveal statistically significant ( $P < 0.05$ ) correlations of clade and age rank? Mismatches may result from a poor fossil record (i.e., one preserving only a relatively small proportion of the organisms in question) or inadequate phylogenetic analysis (where branch nodes are false because of incorrect taxon pairing). In addition, many of the mismatches may be the result of imbalance between the mean durations of low-category taxa (e.g., species or genera) and the maximum stratigraphic acuity possible, as discussed above. Here, we test the effects of changes in paleontological knowledge over the past 26 years, and consider whether there has been an improvement in some, or all, cases.

To test the effect of improving fossil records on clade and age rank correlation, two snapshots of paleontological knowledge, in 1967 (Harland et al., 1967) and in 1993 (Benton, 1993a) were selected for comparison (Fig. 2). Our sample of 74 phylogenetic hypotheses was assessed, after cladistic standardization, for relative completeness and rank correlation using these alternative data bases. Of the 71 cladograms (or adaptations of same) that could be compared directly, SRCs for 1967 vs. 1993 data show no evidence of improvement (Fig. 2, A and B): 43 of the 71 comparisons (61%) showed no change of value category. Of the 28 values (39%) that did change, 14 could be regarded as improvements in the fit of clade rank to stratigraphic age over research time (i.e., negative to positive correlation; insignificant to significant correlation, at values of  $P < 0.05$  or  $0.01$ ; and correlation from  $P < 0.05$  to  $P < 0.01$ ) and 14 others as deteriorations (category reversals). Thus, changes in the fit of cladistic to paleontological data occurred in 39% of cases between 1967 and 1993, but improvements precisely matched deteriorations.

The results for comparison of RCIs between 1967 and 1993, however, show clear evidence of improvement. Of the 73 comparable records, 46 (63%) showed an increased RCI over the past 26 years, one (1%) remained constant, and 26 (36%) were reduced. This indicates a statistically significant (chi square,  $P < 0.05$ ) increase in the quality of known fossil records from the sample relative to each control cladogram. Tested another way (Fig. 2, C and D), there has been a significant (chi square,  $P < 0.01$ ) decrease in the number of test cladograms and/or records with RCIs of  $<50\%$  between 1967 and 1993 (from 15 to 3).

In more detail (Fig. 3), there is a clear shift in RCI values when the 1967 and 1993 data



**Figure 3. Relative improvement in fossil record quality as determined from Harland et al. (1967) and Benton (1993a). There is clear shift of distribution of RCI (relative completeness index) values to right from 1967 to 1993, indicating improvement in paleontological knowledge.**

are compared. The means (67.856, 72.289) differ significantly ( $P = 0.045$ ), according to a Student's *t* test. Nonparametric tests, perhaps more appropriate here, confirm the distinct improvement in completeness of the fossil record from 1967 to 1993. A sign test (comparison of increases and decreases in pairs of values between the two data sets) indicates significant difference ( $P = 0.025$ ). The rather more subtle Wilcoxon signed ranks test (which takes into account the amount of difference between pairs of values) also indicates significant difference between the two data sets ( $P = 0.026$ ).

This is the first semi-independent test of whether the state of paleontological knowledge has changed over research time. Knowledge of the paleontological record between 1967 and 1993 has seemingly improved over the past 26 years, an apparent vindication of the labors of paleontologists, morphologists, and stratigraphers during that time. Previous studies (Maxwell and Benton, 1990; Benton, 1993b; Sepkoski, 1993) indicate that, whereas over 50% of data-base records for the stratigraphic ranges of fossil taxa have changed in the past several decades, macroevolutionary conclusions drawn from them, such as measures of rates of diversification and the timing of mass extinctions, have not altered significantly. Only increases in the presumed magnitudes of certain mass-extinction events, and decreases in their durations, have changed in a major way. The present study suggests an absolute improvement in paleontological knowledge and is therefore justification for increased confidence in the conclusions of statistical studies of paleontological databases.

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