

Palaeontological data and identifying mass extinctions

Michael J. Benton

The fossil record is clearly incomplete, and that incompleteness may be ascribed to many factors: of the organisms themselves, of their habitats, of later changes within the lithifying rocks, and of the ways in which palaeontologists work^{1,2}. For example, soft-bodied organisms will be less well-preserved than those with hard parts. Similarly, organisms that fly or live in trees may be less well-preserved than those that lurk around ponds and rivers or live on the sea-bed. It might also be expected that larger organisms will be more preservable than smaller ones, because they can survive incarceration in fine- and coarse-grained sediments, and because they are easier to find. Broadly speaking, organisms preserved in older rocks are more liable to have been subducted, metamorphosed or eroded out of existence, than those in younger sediments. Human factors are also very important: our knowledge of the fossil record depends critically on the interest people have in particular groups, their geographic location and their ease of study.

It is often asserted that the fossil record is too incomplete for it to yield any useful macroevolutionary results. A lesser claim is, for example, that cladistic analyses of morphology which are intended to provide useful phylogenetic data should be based solely on living forms, since the fossils are not only incomplete morphologically, but they also represent an incomplete sample of all the extinct organisms that ever lived³⁻⁶. These ideas may be tested by relative and absolute measures. Relative measures involve comparisons of two or more parts of the fossil record in order to determine which is better in some defined way, and by how much. Such relative measures of the quality of the fossil record are frequently done by palaeontologists^{7,8} (see Box 1). Absolute measures of the quality of the fossil record, however, would attempt to set some external independent standard against which any parts of the fossil record might be assessed.

Absolute measures of fossil record quality

The absolute quality of the fossil record has been tested in three ways: (1) tests of how changes in palaeontological knowledge affect perceptions of macroevolutionary patterns; (2) tests of the correlation between branching patterns indicated by cladograms and dates of first appearance of clades based on the fossil record; and (3) tests of the goodness of fit of cladograms to different phases of palaeontological knowledge (in research time).

It is often assumed that mass extinctions may be read directly from the fossil record. However, recent work on the Cretaceous–Tertiary (K–T) boundary has shown the difficulty of doing this. For example, it is hard to tell whether the stratigraphic ranges of taxa are complete or not, and what the shape of an extinction really is. Range completeness may be assessed by (1) a statistical approach to the relative completeness of ranges of taxa, and (2) tests based on collecting effort near the ends of ranges. Tests carried out recently suggest that the record is good in parts and getting better. Hence, palaeontologists ought to be able to document the nature of extinction events ever more precisely.

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The first set of tests have suggested that, although fossil records change substantially through research time, the macroevolutionary conclusions alter relatively little. Maxwell and Benton⁹ compared the state of knowledge of the fossil record of tetrapods over the past 100 years, the time of the greatest rate of growth in palaeontological knowledge. The gross number of taxa increased as a result of new finds, but other aspects of the stratigraphic range lists (see Box 2 for definitions of this and other terms) changed in non-systematic and unpredictable ways. Revisions of stratigraphy, revisions of taxonomy at the alpha level, and broad-scale cladistic revisions of larger groups all affected the taxon range lists, but some ranges were shortened, some increased and

some remained unaltered. Some families and genera disappeared as a result of taxonomic revision and others appeared, so that there was no overall shift in the results. The main change that was detected in a comparison of a 1967 database¹⁰ and one from 20 years later⁸ was that familial durations of tetrapods had increased marginally (29.1% of families with unchanged range lengths, 44.8% with increased range lengths, 26.1% with decreased range lengths). Increased range lengths would be predicted by the simple rallying-cry that 'more palaeontological research means collecting more fossils', but the fact that more than one-quarter of the 515 families analysed showed decreased range lengths was more of a surprise. This was the result of cladistic redefinitions of families and the removal of suspect ancestral taxa, which lacked autapomorphies of the family, from the bottoms of ranges.

Box 1. Measuring relative completeness

A Simple Completeness Metric (SCM) may be assessed from a two-dimensional plot of fossil occurrence against time⁸. A grid is constructed where each cell represents a particular fossil taxon, during a defined interval of time. Actual fossil occurrences are recorded cell by cell. The completeness measure is based on assumed occurrences of taxa in the fossil record: a particular taxon may occur during intervals 1, 3 and 6, and it can be assumed to have occurred also within time intervals 2, 4 and 5 as well, since it is unlikely that the taxon died out and re-appeared several times. The SCM in this case, if all six time intervals are of equal duration, is 3/6 or 0.5, not a very complete record. Calculations for echinoderms⁷ show relatively complete fossil records at low levels of time resolution. Records are poorer for terrestrial vertebrates⁸, and they range from values below 50% completeness for lissamphibians and squamates to values over 90% for large mammals (all scaled to stratigraphic stages; duration c. 6 million years).

Box 2. Glossary

Autapomorphy: a derived character possessed by a single taxon.

MIG, Minimum Implied Gap: the stratigraphic interval between the oldest known fossil ascribed to a taxon and the minimum age of the node in the cladogram at which that taxon originated. MIGs occur when the sister taxon has an earlier apparent origin.

Principle of free rotation (in a cladogram): the observation that any part of a cladogram may be rotated about a node, without affecting the pattern of relationships indicated by the cladogram.

Range length: the known duration, in millions of years, of a taxon.

RCI, Relative Completeness Index: the ratio of MIGs to SRLs in a defined case study. Complete correspondence between the known fossil record and the implications of the cladogram leads to a sum of MIGs totalling zero, and a RCI value of 100%. Lower RCI values indicate cases of known missing fossils.

SCM, Simple Completeness Metric: the ratio of known gaps in a taxon stratigraphic range to times of recorded occurrence. Ranges up to 100% for a 'perfect' fossil record.

Sister taxon/group: the closest relative in a cladogram, having its origin from the same node as the taxon of interest.

SRL, Simple Range Length: the recorded range length of a fossil taxon, spanning from its first appearance to its disappearance.

Stratigraphic range lists: lists of fossil taxa with indications of their known occurrences in time.

However, Maxwell and Benton⁹ found that, although stratigraphic ranges of 70.9% of the tetrapod families had changed in a span of 20 years of research, the macroevolutionary conclusions derived from the databases altered little. The phases of diversification and of extinction remained the same (Fig. 1a). Rates of origination and extinction at particular times also remained in proportion. The main effect to be seen was an increase in overall diversity through much of the past 400 million years of tetrapod evolution, and slight sharpening of extinction events.

Sepkoski¹¹, in a similar study of the past ten years of change in his database of marine animals, found turnover in 50% of the data: families had been added and deleted; low-resolution stratigraphic data had been improved; and dates of apparent origination and extinction of families had been altered. However, despite these changes, plots of diversification remained nearly identical but for the fact that the 1992 curve lies 13% higher than the 1982 one (Fig. 1b). Furthermore, the identity and magnitudes of extinction events remained the same. The main changes were that family-range lengths tended to increase, with an approximately equal distribution of earlier originations

and later extinctions, and that mass extinctions became slightly sharper, with extinctions shifting closer to the boundaries. Hence, these tests have indicated two facts: (1) palaeontological knowledge is changing (advancing, one hopes) rapidly; (2) despite this change, broad-scale macroevolutionary patterns remain stable. If the fossil record were hopelessly incomplete, the patterns derived therefrom would probably change wildly as a result of new discoveries.

The second test of the absolute quality of the fossil record, comparing the fit between cladograms and stratigraphic data, has also suggested that there is strong correspondence. The stratigraphic sequence of first occurrences of fossil vertebrate groups frequently matches the order of branching of cladograms based upon character analysis alone¹²⁻¹⁴. The justification for this kind of comparison is that phylogenetic trees compiled using cladistic methods are independent, or broadly independent, of stratigraphic information. The cladogram is produced solely from morphological, molecular and other character information which is processed by multivariate algorithms to produce a tree that maximizes informativeness, whether measured as parsimony or compatibility. One view^{5,15} holds that the procedure is wholly divorced from evolutionary and stratigraphic assumptions, while another^{12-14,16} states that the coding of characters, and determination of polarity, depends to some extent on broad evolutionary assumptions. Nevertheless, there is no direct input of stratigraphy into cladistics, and the two sources of data may be regarded as, at the very least, largely independent.

A technique for comparing clade rank data with age rank data (Box 3) has been developed¹²⁻¹⁴. In a small-scale study, Gauthier *et al.*¹² found that clade rank and age rank correlated. Norell and Novacek^{13,14}, using a larger sample, found that 18 of their 24 test cases (75%) gave statistically significant ($P < 0.05$) correlations of cladistic branching order and stratigraphic order. Best values were found for mammalian ungulate groups, which are believed qualitatively to have 'good' fossil records and relatively stable well-resolved cladograms. The six cases that failed (amniotes, Squamata, hadrosaurs 1, hadrosaurs 2, higher primates, artiodactyls) could not be simply explained.

Benton and Storrs¹⁷ have found less-convincing results from their study of 74 cladograms of vertebrates, only 41 (55%) of which showed statistically significant correlations

of clade order and age order at $P < 0.05$, and 25 (35%) at $P < 0.01$. The greater proportion of mismatches between clade rank and age rank in this latter study may be the result of including a wider range of cladograms in the test, some of which might not be as well resolved as those chosen by other authors. Nonetheless, all studies to date show that the majority of fossil records correspond to relevant cladograms in terms of their predictions of the order of appearance of groups. This suggests that the fossil record is not hopelessly bad, although the test gives no quantitative measure of quality.

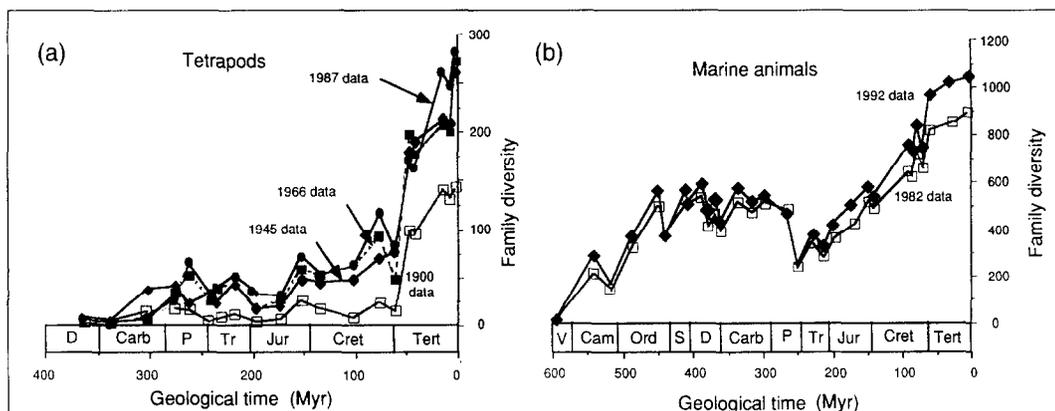


Fig. 1. Comparisons of the patterns of diversification of non-marine tetrapods (a), and marine animals (b), based on data-sets of different vintage. The diversity patterns are broadly similar, showing gradual increases in diversity through time, interrupted by various declines, corresponding to mass extinction events (late Cambrian, late Ordovician, late Devonian, end-Permian, late Triassic, end-Cretaceous and late Eocene). The main change, in both (a) and (b), is that overall diversity has increased. Abbreviations: V, Vendian; Cam, Cambrian; Ord, Ordovician; S, Silurian; D, Devonian; Carb, Carboniferous; P, Permian; Tr, Triassic; Jur, Jurassic; Cret, Cretaceous; Tert, Tertiary. Data obtained from Refs 9 and 11.

The third test of the absolute quality of the fossil record has been to compare palaeontological knowledge at different points in research time. Benton and Storrs compared the goodness of fit of all 74 cladograms in their test sample both to a comprehensive sample of palaeontological knowledge in 1993 (Ref. 18), and to a similar compilation from 1967 (Ref. 10). Two measures of fossil record quality were used: (1) the correlation of clade rank and age rank, measured using the Spearman rank correlation statistic (with quality of correlation assessed at confidence levels of $P < 0.05$ and $P < 0.01$); and (2) the Relative Completeness Index (RCI) of all test cladograms when plotted as phylogenies against a geological time scale [measured as the proportion of Minimum Implied Gaps (MIGs), indicated by branching points of pairs of sister groups, to Simple Range Lengths (SRLs), based on total range lengths represented by fossils]. The results (Fig. 2) showed improvements in the goodness of fit of palaeontological and cladistic data between 1967 and 1993. Of the 71 cladograms that could be compared directly, we found that 46 showed an increase in the RCI, one remained constant and 26 showed a reduction. This indicates a statistically significant (Chi-square test, $P < 0.05$) increase in the quality of the known fossil records of their fit to the control cladograms. However, there was no evidence for change in the degree of correlation of clade rank and age rank data when the 1967 and 1993 datasets were compared for all 71 comparable cladograms: 43 of the 71 comparisons showed no change of state, while 28 changed, but the changes were equally balanced, with 14 'improvements' (i.e. negative to positive correlation; insignificant to significant correlation, at values of $P < 0.05$ or 0.01; correlation at $P < 0.05$ to correlation at $P < 0.01$) and 14 deteriorations.

Hence, the three tests just outlined have shown that knowledge of the fossil record is changing at a great rate, but that most of the macroevolutionary conclusions based on that record are relatively stable to non-systematic changes. Also, there is a surprisingly good fit between fossil data and cladistic data on the order of origin of groups, and that the relative gap content of the fossil record is diminishing through research time.

Stratigraphic ranges and extinction boundaries

Stratigraphic range charts, in which the distribution of fossil taxa is indicated by solid bars plotted against a time scale, are commonly used in seeking to determine the patterns of extinction during particular time intervals. Commonly, however, what is plotted as a solid bar spanning some interval of time may be a summation of rather scattered fossil occurrences. At one extreme, the span of time indicated by the solid bar may be packed with fossil representatives of the taxon in question. At the other extreme, there may only be two fossil occurrences, the first and the last, and nothing in between. Intuitively, one must have more confidence in the correctness of the terminal points of the first example and very little confidence in the latter example.

Strauss and Sadler¹⁹ modelled this concept mathematically (Box 4), arguing that confidence intervals can be calculated for the terminal points by assessing the probability that a certain number of unobserved records may exist beyond those points. This technique of estimating potential ranges is simple to calculate, and may be applied to all levels of taxonomic and stratigraphic division. However, the formula depends critically on the assumption that fossil finds are scattered randomly through the re-

Box 3. Node order and ghost ranges

Techniques used in the comparison of the branching order of cladograms and stratigraphic branching order, illustrated by an example involving ten taxa (A-I), each of which is monophyletic. The initial cladogram (a) has to be standardized so that the order of branching may be compared with the sequence of occurrence of fossils in geological time. Cladistic rank is determined by counting the sequence of primary nodes in the cladogram; nodes are numbered from one (basal node) upwards to the ultimate node. As this method cannot cope with complex cladograms comprising several subclades (a), such cladograms are converted to a hierarchy of nodes along a single branch (b). This is accomplished by collapsing each subordinate clade to a single polytomous node originating at the main stem; each such lineage is assessed equally and given equal cladistic rank. In cases where subordinate clades are large, the convention is adopted that the source cladogram is collapsed so as to maximize node number (using the principle of free rotation).

The known stratigraphic distribution (Simple Range Length, SRL) of the nine taxa is plotted [indicated by solid lines in (c)] and minimum implied gaps [MIGs, indicated by cross-hatching in (c)], or 'ghost ranges'¹³ are estimated. The MIG is the difference between the age of the first representative of a lineage and that of its sister, as the oldest known fossils of sister groups are infrequently of the same age. The MIG is a minimum estimate of stratigraphic gap, as the true age of lineage divergence may lie well before the oldest known fossil. The figures are used to calculate the Relative Completeness Index (RCI) of the fossil record in question, according to the formula:

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

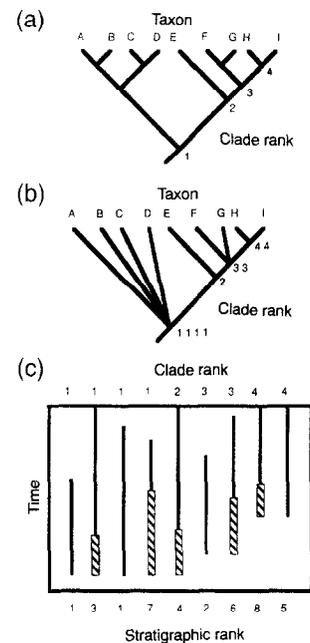


Diagram courtesy of G.W. Storrs.

corded range, and not bunched at one end or the other²⁰⁻²². Excessive zeal in collecting at one horizon, a horizon which exhibits exceptional preservation, misidentified specimens, or sedimentary truncation events can clearly render the calculation of confidence intervals invalid.

Ward²³ has shown that more collecting extends the ranges towards a particular cut-off point. After two seasons of collecting ammonites in the Late Cretaceous sediments of Zumaya, northern Spain, he found a pattern (Fig. 3) of apparent gradual disappearance of 16 species through the last 200 metres of sediments below the K-T boundary. The first species to disappear did so 160 metres below the boundary, and the last reached about 15 metres below. After further collecting (up to 1989) the picture changed: all ranges were expanded, both at the top and bottom, and one species virtually reached the K-T boundary. Seven species came within 40 metres of the K-T boundary, compared to only three in the 1986 data. A further increase in collecting effort, indicated by composite ranges for

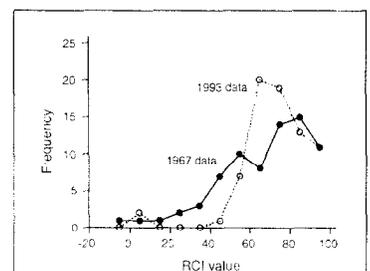
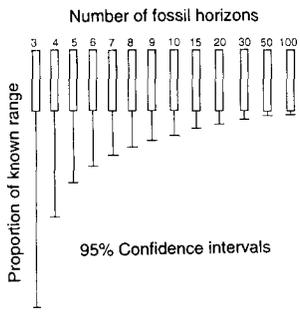


Fig. 2. Relative improvement in fossil record quality from 1967 (Ref. 10) to 1993 (Ref. 18). During these 26 years, gaps in the record were filled, and there is a clear shift in the distribution of RCI (Relative Completeness Index) values to the right from 1967 to 1993, indicating improvement in palaeontological knowledge (significant shift at $P < 0.05$; t test and non-parametric signs and Wilcoxon signed ranks tests).

Box 4. Confidence intervals on stratigraphic ranges



Strauss and Sadler¹⁹ presented a technique of calculating confidence intervals for the ends of stratigraphic ranges. This technique was based on the intuitive assumption that recorded total ranges will tend to be more accurate the more closely packed the fossils are within the known range. In other words, if fossils are found every millimetre through a section, the palaeontologist will have high confidence that the origin and extinction of the taxon are accurately placed in the geological record. At the other extreme, if

there are only two fossil specimens of a species known, spaced many metres or many millions of years apart, the known range can be stated as the line joining those two records. However, confidence intervals on both end points would then be huge, since fossils are so rare. The confidence intervals on end points of a range, expressed as a fraction of that range (α), are calculated according to:

$$\alpha = (1 - C_1)^{-1/(H-1)} - 1$$

where C_1 is the confidence level and H is the number of known fossiliferous horizons¹⁸⁻²¹. At the extreme, where only the terminal points of a range are represented by two fossils, the 95% confidence intervals are more than ten times the observed range ($C_1 = 19$). As the number of fossil horizons sampled increases, the confidence interval declines (see diagram). Even with six point occurrences of fossils through the range, the predicted range extensions must equal the observed range, at the 95% confidence level. With more than six records, the error bars diminish (but never quite disappear) reaching negligible values for intensely sampled ranges (e.g. $C_1 = 0.03$ when $H = 100$). Diagram redrawn, with permission, from Ref. 20.

the whole basin up to 1989, showed that six of the ammonite species reached the K-T boundary, and ten entered the last 40 metres. More collecting will extend stratigraphic ranges. Sepkoski¹¹ also found this phenomenon at a much larger scale, global distributions of family ranges measured at stage level, in his comparison of 1982 and 1992 databases: the 1992 data showed a shift of extinctions closer to recognized mass extinction boundaries, when compared to the 1982 data.

The next step in this study will be to quantify collecting effort throughout the process of establishing a range chart. The reason is that, simplistically, one might read from Ward's²³ study that the extinction pattern of ammonites is becoming more catastrophic with greater collecting effort. It might be predicted that, sooner or later, the evidence will confirm a catastrophic extinction event, with all 18 species of ammonite dying out exactly at the K-T boundary, instead of a gradualistic extinction, with only one or two reaching the boundary. The test has to focus on whether specimens are equally abundant throughout their ranges, or there was a severe tailing-off in abundance towards the top of the range. Diversity of species, or other taxa, is regularly shown on palaeontological range charts, but abundance rarely is. Hence, even if vast efforts of collecting did eventually extend all 18 ammonite ranges right to the K-T boundary, these species might have been very rare in the final years of the Cretaceous, and this would be evidence for a gradualistic extinction. If, however, they remained equally abundant right to the end, then it would be true to postulate a catastrophic extinction.

Collecting effort

In ecology, as in palaeontology, it is rarely possible to collect or observe all specimens or individuals. Hence, species richness has to be assessed from a sample of the total population. Most communities sampled by ecologists display a log-normal pattern of species abundance²⁴⁻²⁶, in which a small number of species is represented by

many individuals and there is a long tail of rare species. As sample size increases, more and more of the true curve is revealed, but only truly gigantic sample sizes are likely to reveal figures close to the true species richness^{27,28}. Similar principles apply in cases of palaeontological sampling, where the majority of species available to be sampled are rare and only likely to be encountered as a result of gargantuan collecting efforts. Koch²⁹⁻³¹ reports studies based on samples of 1000-95 000 fossil mollusc specimens.

In field ecology, sampled species richness is related to the amount of collecting effort that has been expended^{32,33}. The 'collector's curve'³⁴, plotting cumulative sampled species richness against 'effort', is generally convex-up, showing an initial rapid rise in sampled species richness, and a levelling-off as the curve approaches the actual species richness of the community in an asymptotic manner. The first specimens collected may all represent new species records, but subsequent specimens are likely to duplicate previous finds. The rate of discovery of new species eventually tails off, and the effort required to find each additional species becomes progressively greater.

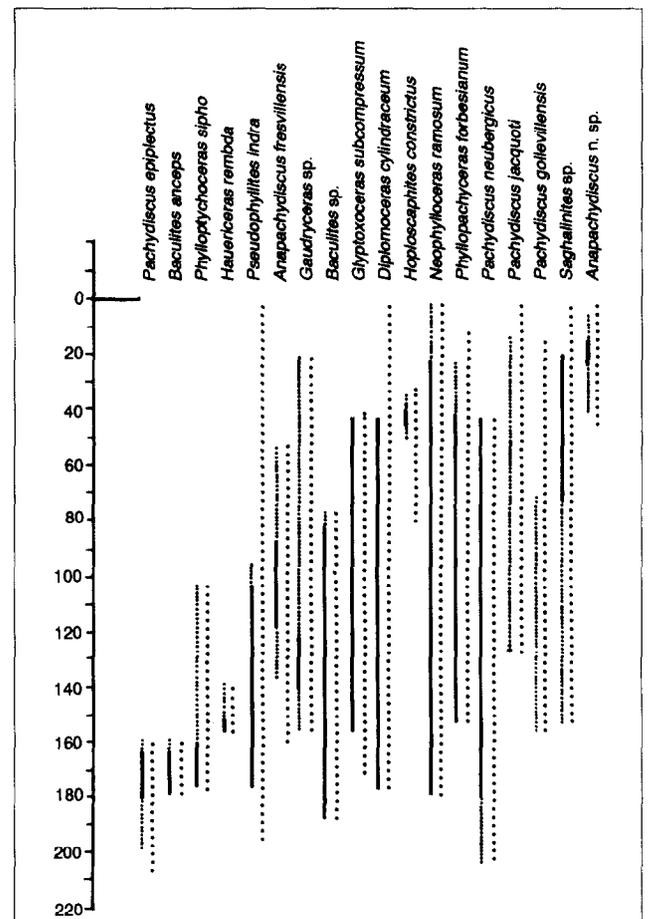


Fig. 3. Ammonite species ranges from the Late Cretaceous of the Zumaya section in northern Spain, showing the results of two seasons of field sampling (1986), the results of a further three seasons of sampling at the same section (1989), and the basinwide distribution of fossils. Increased collecting effort has yielded longer stratigraphic ranges for all species of ammonites. Solid lines indicate stratigraphic ranges of ammonite species determined by collecting up to 1986 at the Zumaya locality only; dense dotted lines show range extensions as a result of further collecting up to 1989; light dotted lines show composite ranges for all species based on the Zumaya locality, and others in the vicinity, up to 1989. The scale to the left is represented by the stratigraphic column which is measured in metres, with the K-T boundary at zero. Redrawn, with permission, from Ref. 23.

There are problems in application and in interpretation of the collector's curve. One problem is to identify the point at which the collector's curve becomes asymptotic, and then to use this information to calculate the actual species richness. Further, the nature of the curve depends on the pattern of species abundance distribution, the spatial distribution of specimens, and the distribution of sampling points. In cases where the last two factors cannot be guaranteed to be random, other approaches, such as capture-recapture methods^{35,36}, may be used, and these have also been applied in palaeontological examples^{37,38}.

Measures of 'effort' in field ecology include numbers of specimens examined, numbers of quadrats thrown, and search time expended. In geological applications, collecting effort can be quantified in various ways: (1) number of specimens found on repeated traverses of the outcrop, if the sequence of sediments is relatively uniform, and specimens are rare; (2) search time, when specimens are abundant throughout the section; (3) volume of sediment collected at fixed intervals up a section, where fossils are common, but sediment types are highly variable in potential ease of collecting; and (4) fixed-area searches, where all specimens are recovered from a randomly selected fixed area of outcrop.

In using calculations of relative abundance to supplement basic diversity plots of fossil taxon ranges, more data are made available for qualitative and quantitative assessments of the fates of the taxa. In particular, the nature of the decline of a group before an event horizon may be more fully documented. It may also be possible to use relative abundance data through the known stratigraphic range of a fossil taxon to supplement the straightforward calculations of confidence intervals¹⁹⁻²². Determining the completeness of the fossil record is of crucial importance to palaeobiologists, and new techniques will put macro-evolutionary studies on a firmer, quantitative footing.

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