

HOW COMPLETE DOES THE FOSSIL RECORD HAVE TO BE?

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ABSTRACT

No science is based on complete knowledge, so the incompleteness of the fossil record is not necessarily a serious limitation in using palaeontological data to test geological or biological hypotheses. Completeness and adequacy of data are measured against some prior requirement which, in turn, should determine sampling strategy. Adequacy is considered for single samples, for detecting patterns by comparing samples, and for comparisons with neontology. Adequacy of single samples can be determined by sample size or by "growth of knowledge" curves. When comparing samples, standard sample sizes have serious disadvantages. Pattern detection requires appropriate density of samples. In stratigraphy using standard intervals has disadvantages. Bed by bed sampling is often better, but one sample per bed is usually inadequate. In comparing morphological data from the fossil record with more extensive neontological data, what matters is not that extra data are available but whether or not they are necessary. Much neontological data is based on taxa identified morphologically anyway. Commonly problems with palaeontological data result as much from inadequate collection and recording as from inadequacies of the fossil record. We must be clear about our aims, and therefore what data are necessary, before data gathering begins.

Keywords: Fossil record, adequacy, completeness, sampling strategy.

RESUMEN

Ninguna ciencia se basa sobre un conocimiento total, por lo que la parcialidad del registro fósil no es necesariamente una limitación seria del uso de los datos paleontológicos para probar las hipótesis geológicas o biológicas. El que los datos sean completos y adecuados se mide respecto de requerimientos previos, que a su vez determinan la estrategia de muestreo. La idoneidad se considera para muestras determinadas, para la detección de tendencias y para comparaciones con la neontología. En el primer caso se determina por el tamaño de las muestras o por gráficos de "crecimiento del conocimiento". Cuando se comparan muestras, los contajes estandar presentan desventajas importantes. La detección de tendencias requiere una densidad adecuada de muestreo. En estratigrafía el uso de intervalos regulares tiene desventajas. El muestreo estrato por estrato es a menudo mejor, pero una sola muestra por estrato no suele ser suficiente. En la comparación morfológica de los fósiles con material neontológico, lo que importa no son los datos extra disponibles sino si son o no necesarios. La mayoría de los datos neontológicos provienen de taxones identificados, en cualquier caso, morfológicamente. En general, los problemas con los datos paleontológicos surgen tanto de las colecciones y muestreos inadecuados como de la parcialidad del registro fósil. Tenemos que tener clara cuál es nuestra intención y, en consecuencia, qué datos son necesarios antes de que comience la recogida de los mismos.

Palabras claves: Registro fósil, idoneidad, globalidad, estrategia de muestreo.

INTRODUCTION

The incompleteness of the fossil record is universally acknowledged and frequently cited as a serious drawback in using evidence from it to test any particular idea. In the last decade attempts have been made to develop and apply tests of completeness of the fossil (Paul, 1980, 1982; Dingus, 1984; McKinney, 1986a, b, c; Strauss & Sadler, 1989; Allmon, 1989; Marshall, 1990) and rock records (Schindel, 1980, 1982; Sadler, 1981; Sadler & Dingus, 1982; Retallack, 1984; Anders *et al.*, 1987). However, since no science is based on complete knowledge, it is legitimate to ask why the incompleteness of the fossil record should be so special. What matters is not that the fossil record is incomplete, but whether data incorporated in it are adequate to test theories. In this paper I wish first to consider definitions of completeness and then to discuss how complete the fossil record needs to be for its data to be

adequate. As will soon become apparent, adequacy depends on the definition of completeness that is chosen. This, in turn, usually depends on the hypothesis that is to be tested.

DEFINITIONS OF COMPLETENESS

It may seem unnecessary to define what "complete" data are, but in practice completeness is measured against some predetermined aim (Paul, 1985, 1989b). For example, the data necessary to make a "complete" faunal list for a geological site (e.g. one identifiable fragment of each taxon) differ from those necessary to describe each fossil thoroughly (e.g. at least one "complete" specimen of each taxon), or to reconstruct the palaeoecology of the site (e.g. relative abundances of each taxon). Similarly, if we could make a "complete" faunal list of all the fossil species of sea urchins from

the Jurassic, for example, it would not necessarily be a "complete" list for each stage of the Jurassic. A species which originally lived in both the Callovian and Oxfordian might only be known from one of these stages. Indeed a unique specimen could be used to "complete" the faunal list for any stratigraphic interval from the bed in which it occurs, through the zone to the stage, period or even era during which that bed was deposited. Thus the way in which we collect and record data from the fossil record also affects the definition of "completeness". Failure to understand that "completeness" is relative to some predetermined aim, has led to examples of the incompleteness of the fossil record being accepted as fundamental limitations without question. The most commonly stated example is the astronomical chances against an individual being preserved in the fossil record (let alone surviving subsequent destruction by erosion, diagenesis or metamorphism to be discovered, recognized for what it is and thus to contribute to the science of palaeontology). But this undeniable fact matters only if it is important that a specified individual be known. For all the practical examples mentioned briefly above, a modest sample of the individuals that existed is quite adequate.

Of equal importance is the fact that seeking "complete" data is like seeking the holy grail. It can never be achieved, no matter which definition of "completeness" is used (Shaw, 1964; Paul 1982). So long as a single fossil remains in the rock it might add to our knowledge, thus rendering all previous knowledge "incomplete". In palaeontology we deal with samples. It is frequently not important that the fossil record preserves only a sample of past life, which itself may be small and of which we know a further minute subsample. The fundamental question is "how adequate is the known sample for our intended purposes?"

So we can never have "complete" data, but for most scientific purposes this does not matter. What we need are methods of determining the confidence with which we can accept data from the fossil record. For example, there are literally millions of Mesozoic and Tertiary fossils, but not one is a trilobite. Tomorrow we might find a living trilobite, but this is extremely unlikely. Even though the relatively recent discoveries of the living coelacanth *Latimeria* and the living monoplacophoran *Neopilina* demonstrate that this idea cannot be dismissed out of hand, most palaeontologists would agree that trilobites became extinct at the end of the Permian. Furthermore, every subsequent discovery of a post-Palaeozoic fossil tests this hypothesis. Indeed, there is overwhelming (but there can never be conclusive) evidence that trilobites are extinct. So we may be almost certain that trilobites are extinct, but we can be equally certain that by next year new species of trilobites will have been discovered and the known geographic and stratigraphic ranges of others extended. We can be more confident in our knowledge of the stratigraphic range of trilobites as a group than we can of our knowledge of the range of any particular trilobite species.

What constitutes adequate (i.e. sufficiently complete) data can be considered at three levels. First from a single site or geological horizon, then for comparisons between sites or horizons, and thirdly for comparisons

between palaeontological and neontological data. In all three cases "adequate" will still depend on some predetermined objective. Thus the same data may be perfectly adequate for one purpose and totally inadequate for another.

1) Data from a single site or horizon

Shaw (1964) considered this problem by asking the question "If a species is absent from a collection of fossils, what are the chances that it is present at the site but has been overlooked?" In other words, how large a sample do we need to be reasonably confident that a species is genuinely absent? Note again that we can never be certain a species is absent, because as long as one fossil remains in the rock it might be the one we are looking for. Shaw supposed that the fossil species was present but rare, say 1% of the preserved fauna. With random preservation and collection, the probability, p , that any one fossil found will be the desired species is: $p = 0.01$, and the probability, q , that it will be another species is: $q = 0.99$. This is because there are only two possible outcomes, either the fossil is the species sought or it isn't, and hence:

$$p + q = 1 \text{ (or 100 \%)} \quad (1)$$

With every additional fossil identified, the overall probability, Q , of not finding the species sought declines as:

$$Q = (q)^n \quad (2)$$

where n is the number of additional fossils identified.

Even when q is very large, $(q)^n$ declines significantly as n increases. When Q declines below 0.05, we can be 95% confident that we have not overlooked the species in question. Shaw (1964, p. 109) and Paul (1982, p. 86) published tables of values of n , q , and Q , while Hay (1972, p. 259) figured an extremely wide-ranging graph of these values. Note that this relationship holds good for all species in the fauna, so that a formal definition of "adequate" can be given by selecting values for the proportion of the fauna desired (p), and the confidence level, Q . Q and p define the adequate sample size, n . For example, with 299 identified specimens one can be 95% certain of not having overlooked a species present as 1% of the fauna. This, I suspect, is why many micropalaeontologists make standard counts of 300 specimens from a sample.

Although it anticipates comparisons between samples, it is necessary to consider at this point the disadvantages of standard counts. There are three: 1) proportions of all taxa present are interdependent, so that changes in the abundance of one taxon inevitably affect apparent abundances of all other taxa; 2) they may be misleading, as for example when relative abundance increases but absolute abundance decreases; and 3) they completely obscure data on absolute abundance, changes in which are often extreme. The advantages of standard counts are first that they provide adequate and even sampling and second that differences introduced by sampling techniques can be overcome as, for example, when comparing counts of specimens from dissociated sediments with counts of specimens in thin sections. Here adequacy will depend heavily on the question

being investigated. Standard counts may well be preferable for stratigraphy, but they are certainly inadequate for palaeoecology (Paul, in press). They undoubtedly simplify comparisons of diversity, which are most easily done at a standard sample size (Raup, 1975). They may be essential to overcome unavoidable variation in sampling technique.

The interdependence of counts for all taxa present in the sample makes it extremely difficult, if not impossible, to distinguish "signal" (i.e. a genuine change in the abundance of a taxon) from "noise" (the passive response of one taxon to changes in abundance of another). This is most serious when the commonest species vary in abundance, but it is always present. Suppose, for example, that in one sample the commonest species is 70% of the count, then all the other taxa present can only contribute to the remaining 30%. If, in the next sample, the commonest species only constitutes 30% of the count, then the other species present will expand to complete the remaining 70%. If nothing else has changed they will more than double their relative abundance, whether or not they genuinely become more common. Furthermore, if a detection limit of

1% of the count is being used, species which were below this limit when they collectively constituted 30% of the count may well rise above the limit when they contribute to 70% of it. Thus the first sample will appear to be less diverse than the second, when in fact all that has happened is that the commonest species has become rarer. It is easy to produce beautiful patterns of variation through a series of samples for a species which does not vary in absolute abundance whatsoever (Fig. 1).

Another problem arises when, for example, there is a genuine change in diversity (number of species) between samples. In this case those taxa present in the less diverse samples will inevitably increase their relative abundance simply because there are fewer taxa to make up the standard count. If these species prefer warm water, for example, it would be extremely tempting to interpret the change as being due to an increase in water temperature. However, if the decrease in diversity was accompanied by a decrease in absolute abundance, a common occurrence, the warm water taxa will in fact have become rarer, which would suggest a decrease in water temperature.

Finally, significant changes in palaeoenvironments are often accompanied by quite drastic shifts in absolute abundance of taxa. I have personally recorded ten-fold changes in absolute abundance of non-marine molluscs through an archaeological site (Paul, 1987), a Tertiary limestone succession (Paul, 1989a) and of foraminifera through a single Cenomanian chalk/marl rhythm (Paul, in press). Few taxa will have such large changes in relative abundance, and standard counts only record relative abundance.

Since standard counts may be inappropriate, an alternative approach is to consider "growth of knowledge" curves. The theory behind these curves is easy to understand but developing adequate statistical tests is by no means as simple. Any palaeontologist knows that when collecting fossils one soon discovers the common species, but it takes longer (larger samples) to detect the rarities. Durham (1966) presented some impressive examples of how large samples increase faunal lists. Plots of diversity (number of taxa) against sample size

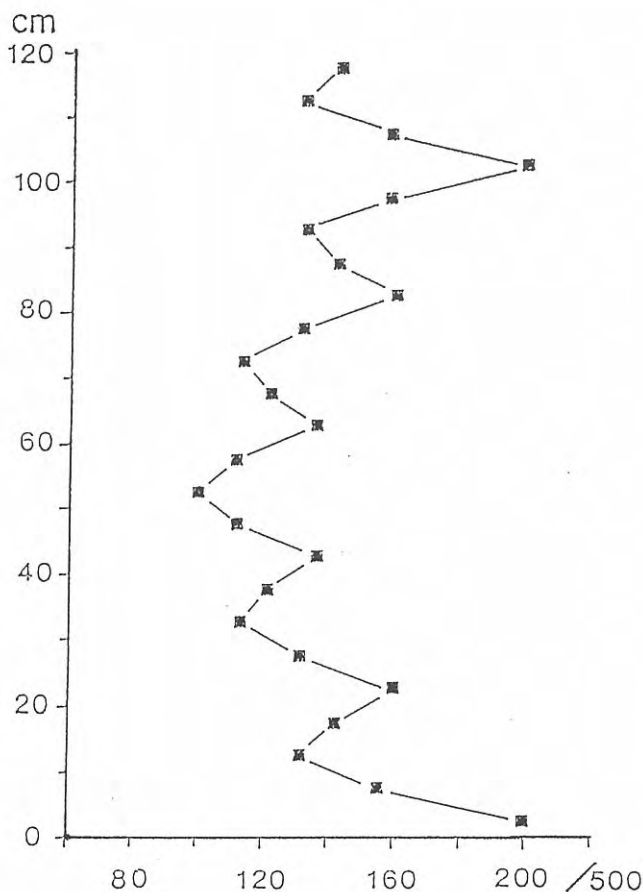


Figure 1. Artificial cyclic pattern in apparent abundance of one taxon generating by using fixed counts of 500 specimens and varying relative abundances of two other taxa at different periodicities. The pattern is pure echo. By definition this taxon did not vary in absolute abundance (specimens per cc of sediment, or per metre square of sea floor) whatsoever.

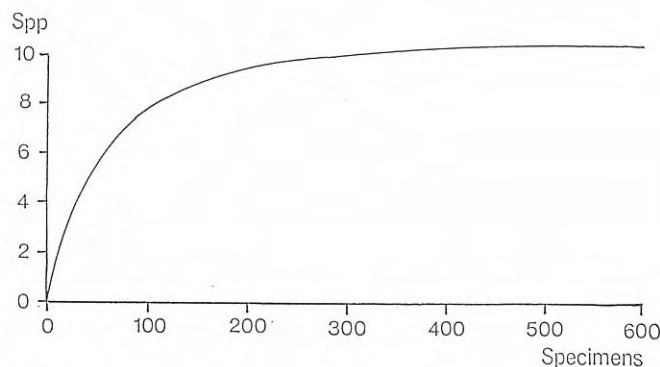


Figure 2. A "growth of knowledge" curve. As the number of specimens increases so does the number of species (spp), but at a progressively decreasing rate. At this site, stopping collecting at 50 specimens (for example) would yield an inadequate sample of the fauna present, whereas collecting more than 3-400 specimens would add little to knowledge of the site.

(number of specimens) resemble Figure 2. The curve is initially steep, but gradually becomes more nearly parallel to the x axis. Clearly to stop collecting while still on the steep part of the curve would give an inadequate sample of the taxa present, but to continue collecting long after the nearly horizontal part of the curve has been reached would add little or no new information. Theoretically, to stop collecting at the same point on the curve for any sample would allow equivalent comparison of samples irrespective of either their diversity or their abundance. Plant ecologists developed this concept (as the species/area curve) in the 1930s (e.g. Cain, 1938). However, to use species/area curves the shape of the curve has to be known beforehand. This is reasonable for modern grassland or forest, for example, where repeated counting has established the general shape of the curve, but not for most palaeontological samples.

Nevertheless, a technique can be used which yields approximately equally thorough treatment of all samples, irrespective of their diversity or population structure. If every time a new taxon is added to the faunal list a count is made of the total number of specimens so far identified, this can be used to define a new target sample size. For example, if doubling the number of specimens does not add a new species to the faunal list, one could conclude that the population was adequately known and no more specimens need be identified. Clearly such a strategy cannot always be taken literally, otherwise if the first two specimens identified were of

the same species one would stop collecting. Personally I always identify 20 specimens and then set an initial target at the first new species added thereafter (giving a minimum count of 40 specimens). Computer simulations of the technique using a random number generator suggest that one can be 95% certain the species detected will collectively represent more than 90% of the fauna. Increasing the starting point (i.e. to 25 or 30 specimens) increases the proportion. Such a technique takes account of variations in diversity and population structure, but it requires a thorough knowledge of the fauna. Whilst the odd unknown specimen can be allowed for, it is not possible to go back and identify difficult taxa after the count has been made. The technique cannot be applied by novices, nor at present can confidence intervals be put on the actual sample size at which counting stops.

In summary, it is essential to consider the nature of the data required to test the hypothesis being investigated **before** any data are gathered. Practical considerations may force one to use a less than ideal technique, as for example when different preparation techniques mean that samples cannot be taken in an identical fashion and are therefore not comparable. Wherever possible, the most appropriate technique should be used. If in doubt, publish the raw counts. Then others who want percentages or diversity at standard sample sizes, etc., can derive these from the published data. It is not usually possible to do things the other way round.

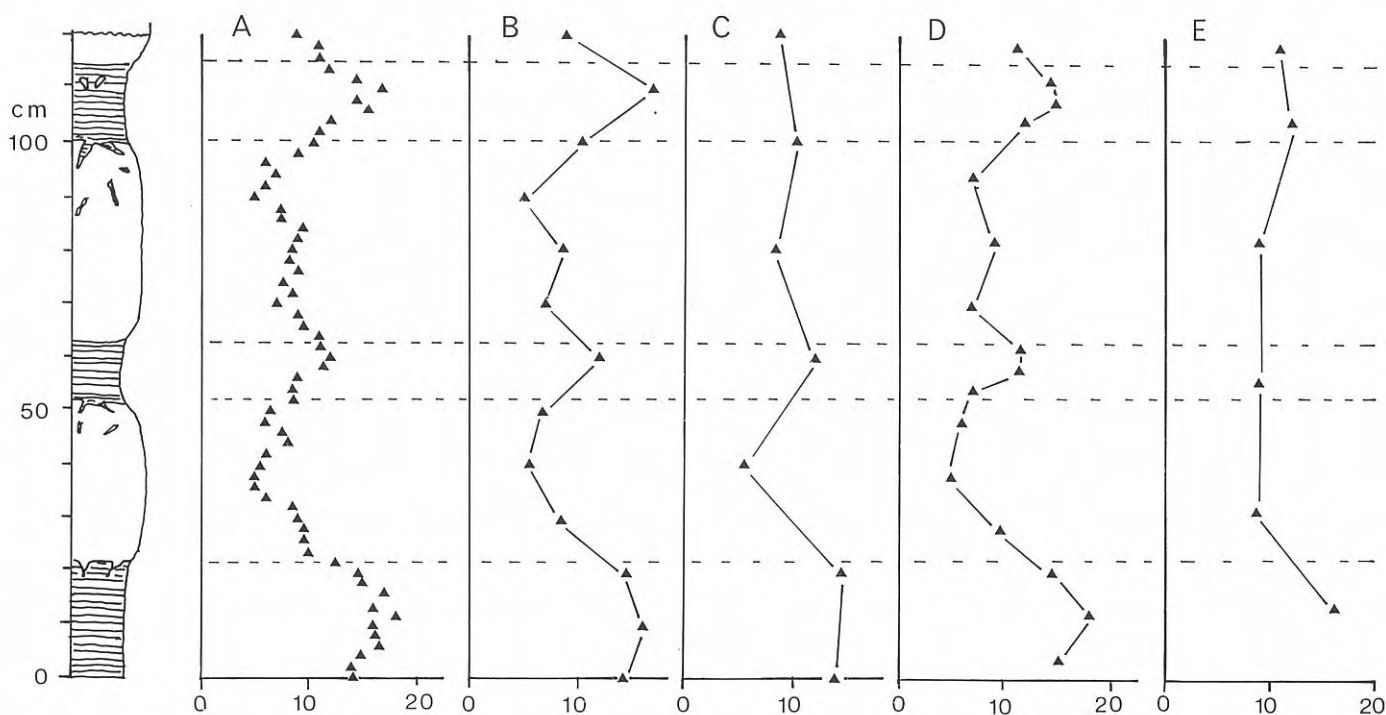


Figure 3. Effects of sampling intensity and sampling strategy. A, The "complete" pattern. Samples at 2 cm intervals. B & C, Sampling at fixed intervals of 10 and 20 cm, respectively. Using 10 cm intervals (the thickness of the thinnest bed) gives a reasonable pattern, largely because in the upper two marls samples fall near the tops of the beds and yield high values. Sampling at 20 cm intervals gives a poorer pattern and completely misses the upper marl. D & E, sampling bed by bed rather than at standard intervals. D, with three samples per bed, yields a good pattern. E, with one sample per bed, completely obscures the pattern. Original data are percentage insoluble residue values from Cenomanian chalk/marl rhythms near Folkestone, Kent (Ditchfield, 1990).

2) Comparisons between sites or horizons

Many applications of the fossil record involve building up patterns of occurrence from different localities or horizons. Palaeobiogeography and biostratigraphy are obvious examples. All the requirements of adequate sampling at one site apply to each site or horizon, but an additional consideration concerns the number of sites necessary to reveal a pattern adequately. Once again, a "complete" pattern cannot be obtained, because so long as there is one site remaining unsampled it might alter the pattern. Nevertheless, it is usually possible to predict both the intensity of sampling and the size of the unit to be sampled, that are necessary to reveal a pattern adequately. Both will depend on the objective of the sampling programme and therefore generally applicable limits cannot be defined. It is also essential to understand the problem being investigated beforehand, so that samples come from the target population and not a mixture of populations. Quadrats in grassland reveal nothing about woodland herbs or invertebrates, no matter how thoroughly sampled.

Consider first the size of the unit to be sampled. This will usually be determined by the size of the taxa being sampled and on the area/volume they are likely to occupy. For example, identifying all plants within a metre square quadrat might well give an adequate idea of the species present in a grassland or meadow, but counting the trees in a hectare might be necessary to get the same level of precision for a forest. Equally a cc of chalk will contain a superabundance of coccoliths, but few foraminifera and no sea urchins or brachiopods.

As to intensity of sampling, this will depend on the size of the units which make up the pattern. For example, in biogeography to reveal the pattern of distribution of a woodland flower might require at least one sample site every hectare if the woods cover only a few hectares as is typical of southern England, but one site per 10 or 50 km square might be adequate if extensive forests covering thousands of square km survive, as for example in northern Europe or Canada. An integral part of most modern biogeographic sampling is the use of standard units of area, e.g. all data are recorded per hectare or per square km, usually based on national or international grid systems (e.g. Kerney, 1976a, Kerney & Cameron, 1979). In these cases numbers of sample sites usually vary but unit area is standardized. In biostratigraphy, standard sampling intervals are frequently used, e.g. one sample from 5 cm thickness every metre up the section. In this case not only is the interval standardized, but the number of samples too. Since even in one section stratigraphic units vary significantly, not only in thickness but also in the time they represent, I personally think that standard sampling intervals should be avoided. A single sample may be enough to characterize a bed, but it will not be enough to reveal a pattern of change within a bed, nor from one bed to the next. Thus in stratigraphy I think that sampling interval should be determined by bed (or unit) thickness, not absolute intervals, and if a pattern is to be revealed an absolute minimum of three samples per bed (lower, middle and upper) is required to determine if changes between beds are sharp or gradual, symmetrical or asymmetrical, etc. (Fig. 3).

3) Comparison between palaeontological and neontological data

Another truism about the incompleteness of the fossil record is that almost all data which it preserves concern morphology, and usually only skeletal morphology at that. Neontology (the study of living organisms) offers so much more information, from soft anatomy, through physiology and behaviour, to embryology and molecular biology, especially nucleic acid sequencing. This has led Løvtrup (1977), for example, to argue that the discovery of new fossils has no impact on classification. No-one can dispute that neontology offers more information than palaeontology, despite the burgeoning science of organic geochemistry. Once again, however, the fundamental point is not that these data are available, but whether or not they are necessary. Bretsky (1979), for example, classified some living and fossil lucinid bivalves on shell morphology alone. If her classification works, all additional data become redundant, at least for this purpose. The impact of additional data will depend on the hypothesis that is being investigated. The recognition of species is perhaps the most basic question in palaeontology, so it is reasonable to ask "how good a proxy for the recognition of biospecies is skeletal morphology?" The answer will depend on which major taxon is involved. I suspect skeletal morphology is a good proxy for echinoderms and vertebrates, but poor for worm tubes and hopeless for entirely soft bodied organisms such as jellyfish.

The idea can be tested, however, by investigating how often newly available data cause revisions of species concepts or classification. Or, alternatively, by assigning species within a major taxon to the best modern classification and investigating how much of the diversity and classification can be recognized using skeletal morphology alone. For example, of 21 species-level taxa described in Reid's (1986) very detailed study of the tropical snail genus *Littoraria*, only two cannot be recognized unequivocally on shell characters (pp. 80-82); and of 37 species-level taxa considered valid, only four are new (pp. 72-3). Since most of these were described last century on shell morphology alone, this suggests a similar proportion can only be recognized with the additional "neontological" data. A third general test would be to assume that sibling species are too similar to be distinguishable as fossils and estimate the proportion of sibling species in a major taxon. Among British non-marine molluscs with external shells (Kerney 1976b, Waldén 1976) there are perhaps 15 pairs of sibling species (about 15% of the total fauna) and about as many again which would pose problems of identification to the uninitiated (a total of 30%). However, of these, all but the succineids (5 species) can be identified on shells alone. There are about 30 species (15%) of slugs with internal shells that can only be identified to genus at best. On both counts, this suggests that at worst 80% of the species (i.e. excluding all slugs and succineids) can be identified on shell morphology alone. Again it must be emphasized that the problem is not that examples exist of taxa, such as the succineids, which cannot be identified on skeletal morphology alone, but how common they are. Among molluscs it would

seem that skeletal morphology alone enables identification in the majority of species.

One final point concerning these additional neontological data. In many cases, and I suspect especially with molecular biology, researchers are not good field biologists in addition to their skills in their chosen specializations. They neither collect nor identify their own material, but rely on someone else. And you can guess what characters the identifier uses most often to recognize living taxa; their morphology. To be sure, it is more likely to include soft anatomy rarely preserved in the fossil record, but for well skeletized groups, such as molluscs, shells alone are frequently all that is in fact used. It is, therefore, legitimate to question how much of the additional data that neontology offers is truly independent of skeletal morphology. There is no doubt that a much more complete picture can be drawn of a living species than a fossil species, using behavioural, physiological, developmental and molecular information in addition to classical morphology. However, if the prime aim is simply to recognize the species and name it accurately, how much of this elaborate picture is actually necessary? How many taxa can only be identified using nucleic acid sequences?

CONCLUSIONS

Although estimates of the completeness of the rock and fossil record have an intrinsic interest in their own right, they tend to concentrate attention on what is missing rather than on using the data that are available to best advantage. No other science is based on complete data so the really significant test is whether or not available palaeontological data are adequate for some specified purpose. The same data may well be adequate for one purpose yet totally inadequate for another. Adequacy is related to some predetermined aim and may involve three levels of application: adequacy of a single sample, adequacy of sampling strategy; and adequacy compared with neontological data. Simple tests can be developed to estimate adequacy in all three cases. Clearly, valid tests of palaeontological hypotheses require examples from the fossil record that are adequate for those tests (e.g. large enough samples, dense enough sample spacing, or preservation of adequate biological information). If information on annual changes is required, for example, collect fossils from a varved sequence.

Too often inadequacies are our own rather than those of the record itself. For example, Shaw (1971) and Paul (1985) have documented how inadequately stratigraphic data are recorded in standard descriptions of fossils. Such poor documentation encourages belief in the inadequacy of the fossil record and becomes a self-fulfilling prophecy. Data cannot be useful if they are not available. Since we all accept that the fossil record is incomplete, surely it behoves us to record the data that are available as thoroughly as possible?

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