

THE ROLE OF STRATIGRAPHIC AND MORPHOLOGIC DATA IN PHYLOGENY

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ABSTRACT—Some systematists have asserted that stratigraphy is not a "trustworthy guide" to the relative ancestry of taxa, and that phylogenetic inference should be based solely on comparative morphology. Yet in many groups phylogenetic analysis is seriously hampered without stratigraphic information. Most deep-sea microfossils, for example, lack a sufficient number of hierarchically nested sets of characters for cladistic analysis, and show frequent convergence and iterative evolution. The high quality deep-sea stratigraphic record is, instead, the major source of phylogenetic data for these groups.

The importance of morphology and stratigraphy in phylogeny reconstruction depends upon the relative quality of the stratigraphic and morphologic data for a given group. We feel that the assessment of the quality of these data in phylogenetic analysis requires probabilistic methods. Some of the factors that can be empirically analyzed to make the choice of methodology more objective and reduce the chance of error include frequency of character reversal and iterative evolution, geographic control, preservation quality, and probability of correct stratigraphic sequence.

INTRODUCTION

PALEONTOLOGISTS HAVE traditionally touted the importance of time and stratigraphy in phylogeny reconstruction. Limited by the loss of morphologic information inherent in preservation of fossils, paleontologists frequently "assert the inviolability of our own, extensive turf-time" (Gould and Eldredge, 1977, p. 120). Any number of paleontologists could be cited to document this belief, but a statement by a well-known stratigraphic paleontologist sums it up well:

"The fossil record . . . is better than many people realize and it is of fundamental importance for understanding phylogeny. If paleontology were synonymous with morphology, fossils would be far less valuable than they are today. However, paleontology is an historical science, and the stratigraphical attributes of fossils give them unique importance in the study of phylogeny" (Gingerich, 1979, p. 74).

Recently, however, the importance of time

and stratigraphy in phylogeny reconstruction has been challenged. Nelson (1969, p. 72) has stated that: "It is a general misconception that the problem of determining phyletic relationships among Recent animals can be directly approached only by the paleontologist. In reality, the paleontologist, even with a good fossil record, can contribute very little, if anything, to the solution of the problem. In fact, the paleontologist as a rule cannot do much in determining the relationships of his fossil species unless they are Recent relatives whose relationships are fairly well established."

Since ancestors can first occur later than their descendants, Patterson (1977, p. 625) has written that "stratigraphic sequence can never be a trustworthy guide to phylogeny, and paleontology must relinquish some of its claim to provide 'both the most direct and the most important data bearing on phylogeny.'" Colless (1967, 1969), Kluge (1971, p. 27), Schaeffer, Hecht, and Eldredge (1972) and others have also emphasized that time is neither essential, nor desirable, in phylogeny reconstruction.

Rebuttals from stratigraphic paleontologists (Bretsky, 1975, 1979; Campbell, 1975;

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Lehman, 1975; Harper, 1976) soon followed. The debate still rages today, as papers in a recent symposium demonstrate (Cracraft and Eldredge, 1979).

THE USES AND ABUSES OF STRATIGRAPHY

Why is there such a great schism over what would seem to be common ground among paleontologists? As Patterson (1977) has demonstrated, part of the problem has been vaguely formulated methodology, poorly examined or unstated assumptions, and unreasonable expectations for the fossil record. To a great extent, the controversy is also influenced by the nature of the material with which one deals. Stratigraphic phylogeny reconstruction still reigns supreme in groups with the better stratigraphic records—shelly invertebrates, microfossils, late Cenozoic mammals, and so on. It is no accident that cladistic procedures were first formulated by an entomologist and now find their most outspoken advocates among scientists who work with insects and other rarely fossilized invertebrates, fish, lower tetrapods, birds, and early mammals, all with relatively poor stratigraphic records.

Another factor influencing this divergence of opinion has been cases where stratigraphic ancientness and morphologic primitiveness are indeed uncorrelated, or where it was assumed that this correlation existed without further thought. Every paleontologist is familiar with examples where a form that is clearly very primitive in morphology appears in the fossil record long after its more specialized relative has come and gone. Exceptions to the "primitive equals ancient" rule should make every paleontologist more cautious. For example, the Paleozoic record of lower tetrapods, which is quite spotty until the Permian, shows a large number of Permian forms that are clearly primitive holdovers from the Carboniferous or earlier (Carroll, 1969). Most of these taxa (seymouriamorphs, limnoscelids, solenodonsaurids, diadectids, among others), as Colbert (1969, p. 111) noted, first appear "much too high in the geologic column to have been the ancestor of reptiles, yet in structure [are] almost exactly intermediate between amphibians and the reptiles. Thus *Seymouria* is a good example of a persistent structural ancestor; it shows how

paleontological grandfathers may live on with their descendants." This is but one example of the kind of anomalies that have made some workers wary of using stratigraphic data at all in phylogeny reconstruction.

DRAWBACKS OF A PURELY MORPHOLOGICAL ANALYSIS

Does it follow then that stratigraphy is useless in phylogeny reconstruction? Is pure morphology sans stratigraphy always a "trustworthy guide" to phylogenetic analysis? We would like to suggest the contrary. Stratigraphic information gives us insight into phenomena that would not be recognized in a purely morphological analysis. Many fossil groups are prone to homoplasy and frequent iterative evolution. Ammonites (Kennedy, 1977), bryozoans (Schopf, 1977; Blake, 1980), trilobites (Kaufmann, 1933, 1935; Simpson, 1953, p. 248), bivalves (Newell and Boyd, 1975), graptolites (Bulman, 1933; Rickards, 1977) and brachiopods (Williams, 1953; Williams and Hurst, 1977) are but a few of the groups with well-studied examples. Newell and Boyd (1975, p. 61) concluded that "parallel trends constitute the general, not unusual, phenomena inherent in the evolutionary process. Sister groups necessarily are genetically similar and are likely to display similar adaptive responses to similar environmental pressure. Hence, although similar morphologic trends may suggest genetic alliance, 'identical' structures within these trends may originate long after the fission of sister groups." Without clear evidence from the stratigraphic record that earlier homeomorphs became extinct before the evolution of later ones, one would erroneously assume that the two taxa are far more closely related than they actually are.

A PROBABILISTIC APPROACH

Thus it appears that neither stratigraphy nor morphology are infallible guides to phylogeny reconstruction. The usefulness of each depends upon the relative quality of the stratigraphic and morphologic data of the group in question. In some groups, a purely morphological approach is futile, or at least leads to erroneous conclusions. In groups without a fossil record, stratigraphy is irrel-

evant. Most examples fall somewhere between these extremes.

How do we decide which source of phylogenetic information has greater weight in these intermediate cases? In the past, this decision has been almost entirely subjective. A worker familiar with a particular fossil group generally places more emphasis on data that his experience tells him is more trustworthy. We need to make this decision more objective so that one can better justify one's choice of approach in a given case. In this paper, we can only point out some approaches to this problem. Rigorously quantified solutions will require much further effort, and are not attempted here.

It is our aim to assess the relative probabilities of 'correctness' of alternative phylogenetic trees. Each tree implies a unique cladogram. Given three alternative trees (Figure 1A) and their associated cladograms (Figure 1B), we estimate the likelihood of each by comparing our observations to the predictions that each tree makes for the stratigraphic and morphologic data. In each case we try to estimate objectively the probability that the tree is correct. We estimate 'probability of correctness' by comparing the observed degree of fit of the tree to either stratigraphic or morphologic data, weighting this with our understanding of the reliability of the data itself. Because both the stratigraphic and morphologic evaluations have been reduced to a roughly equivalent variable (probability), the two values can be combined to produce a joint estimate of the likelihood of a particular hypothesis.

RELIABILITY OF MORPHOLOGIC DATA

Let us frame our discussion around the hypothetical set of three possible three-taxon phylogenetic trees in Figure 1A. These trees represent three of several possible trees which could be constructed within the framework of a higher-level taxonomic hypothesis. Each tree makes the morphologic prediction that derived character states will be distributed in a particular arrangement of nested sets. For example, if hypothesis 1 is correct (B and C are more closely related to each other than either is to A), B and C will share derived character states not found in A. Real examples, of course, are much more complex than

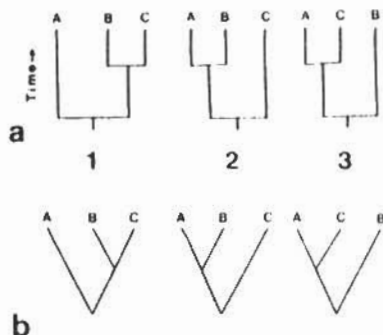


FIGURE 1—A, Three of the many possible three-taxon phylogenetic trees. B, The same hypotheses expressed as cladograms.

this; phylogenetic hypotheses with character conflicts are the rule, rather than the exception. A number of sophisticated methods are available for maximizing the likelihood of a particular hypothesis (Duncan et al., 1980; Felsenstein, 1979; Harper, 1979). Some of these methods also give a measure of the relative "improbability" of the hypothesis in terms of the number of character conflicts invoked by the most parsimonious solution. The number of conflicts or parallelisms, scaled to the number of characters used in the analysis, could be used as an index of probability of a given hypothesis on purely morphological grounds. The more parallelisms we must invoke for a given number of characters, the less likely the hypothesis. This is but one of several possible ways to estimate reliability from the observed 'imperfections' in the morphologic data.

The number of character conflicts in a particular hypothesis provides only a minimum estimate of the unreliability of the morphologic data. A cladogram with no conflicts may prove completely erroneous when the number of convergent characters overwhelms the number of truly derived characters. When parallelism is very common and the number of characters is limited, a purely morphological approach can be futile, as Felsenstein (1978) has demonstrated. To estimate more accurately the likelihood of an hypothesis, we

must consider the frequency of parallelism in the group as a whole. Parallelism may not be apparent from individual taxonomic studies. The true frequency of parallelism and convergence is often only appreciated from broad taxonomic surveys.

THE RELIABILITY OF STRATIGRAPHIC DATA

A probabilistic approach can be applied to stratigraphic data as well. Each of the hypotheses in Figure 1 implies a temporal sequence of the origin of the taxa. Hypothesis 1 implies that taxa B and C appeared after taxon A, whereas hypothesis 2 implies that C appeared before A and B, and so on. If the stratigraphic record were everywhere perfect, testing these hypotheses would be a simple matter of examining the stratigraphic distribution of the taxa. Since the stratigraphic record varies in quality from group to group, we must find a way to assess the quality of the stratigraphic data in a given case.

To do this, we can assess the probability of the implied sequence of events from our observed stratigraphic sequences, and then weight this probability by our confidence in the completeness of the stratigraphic data in a given case. We do not offer a comprehensive numerical model here which integrates all these factors. This will require much further work. Instead, we discuss some of the data on which such a model may be objectively based.

The first step in our analysis is to estimate the probability of an hypothetical sequence based on our observed stratigraphic sequence. Such probability assessment has a long history in the biostratigraphic literature. Perhaps the most appropriate method would be one similar to the probabilistic biostratigraphy of Hay (1972, 1974; Hay and Southam, 1978. For a recent review and discussion, see Harper, 1981). Quantitative measures of probability can be formulated by these techniques so that sequences that are found everywhere in the same order in numerous sections give a probability value at or near one. Increasing percentages of sequences disagreeing with the most common arrangement decrease this probability.

Objective methods of weighting our estimates due to the limitations of preservation and geographic control are also possible. The probability that a local sample contains all

taxa of interest originally present in the area is essentially equivalent to the fraction of the original local taxonomic diversity preserved in the fossil sample. Analysis of preservation is the province of the rapidly burgeoning field of taphonomy, which continues to generate more refined estimates of preservation probability for given taxa in given environments.

To estimate the reliability of stratigraphic data obtained in a restricted locality, it is useful to weight the data according to the probability that the geographic spread of the sample localities covers at least part of the geographic range of all likely ancestors and descendants in a particular phylogenetic hypothesis. Obviously, in widespread groups, those taxa with numerous localized species are more difficult to sample than taxa whose species display little geographic restriction. Yet it is not always necessary to sample all geographic diversity in order to sample all likely taxa of phylogenetic interest. For many groups, limits on dispersal substantially limit the likelihood of two geographically distant taxa having any direct interaction (Scheltema, 1977), phylogenetic or otherwise. Vacant geographic niches in groups with limited abilities to disperse are usually filled by members of the group living in adjacent regions, not by taxa living on the other side of the globe. Newly formed or recently depleted environments (whether natural or man-made) are usually repopulated by taxa from adjacent regions.

In a few groups, proximity is of lesser importance. The mammals, for example, are notorious for their ability to disperse great distances or even displace the local inhabitants. For most groups, however, proximity seems to be a primary consideration, and this limits our need for worldwide geographic control. Two reasons can be given. Local taxa are more apt to be ecologically suited to a nearby region, since habitats are not arranged haphazardly over the earth but vary clinally. Secondly, where ecology is less important than 'getting there first', local taxa have the advantage in this respect, too.

Even in groups where local derivation of taxa is less important, it is possible to detect invasion events by other criteria and thus temper our phylogenetic considerations. Many examples of wholesale invasion from distant environments are known in the fossil

record. The great South American-North American interchange in the mid-Pliocene is one example. Similar phenomena of ecological invasion have been seen in historical times. On several occasions man has introduced taxa from one continent to another with dramatic results. The introduction of rabbits (Troughton, 1941, p. 260) and prickly pear cacti (Dodd, 1940) to Australia are infamous examples. Two features of fossil data sets may be used as indicators of wholesale migrational events. Synchronous turnover in several groups at any one locality would suggest that a substantial biogeographic change has occurred. Similarly, synchronous change in several adjacent environments would suggest the same phenomenon.

For many groups, then, it is possible to devise workable field sampling strategies which offer: 1) a reasonable assurance of geographic comprehensiveness in the absence of major biogeographic events, and 2) the ability to detect these events. Factors which must be taken into account include the range sizes and dispersal characteristics of the group, as well as modern large-scale distributions (clinal or heterogeneous). Whatever the geographic configuration, it is also necessary to demonstrate that the relative temporal order can be accurately determined between regions. The stratigraphic methodology necessary to do this is well developed and need not be discussed here.

Thus, by combining measures of observed variability in stratigraphic order in local environments with objectively based estimates of the completeness of the data base, it is possible to derive a reasonably non-subjective estimate of stratigraphic reliability.

AN EXAMPLE

The utility of the approach discussed above can be demonstrated by an example. The deep-sea microplankton have unusually excellent fossil records. Unlike the sequences on continents, deep-sea microfossil sequences allow us to study geographic variation, and to trace fossil populations in the world ocean back through time. Because geographic control is unusually complete, and the degree of preservation can be objectively estimated (Prothero and Lazarus, 1980), deep-sea sequences need not be subject to the uncertainties of geographic variation and

preservation common in the land record. Stratigraphic correlation can be made with considerable confidence, since, in addition to the biostratigraphy of several unrelated groups, deep-sea microfossil sequences have magnetic stratigraphy, isotope stratigraphy, and several other means of correlation available. In such cases it is indeed possible to follow morphologic change back through time and "read the patterns of descent revealed by fossils, like the genealogist tracing family history in written records" (Patterson, 1977, p. 620). Such an approach also reveals the pitfalls of purely morphologic analyses.

Consider the following two sets of planktonic Foraminifera. Set 1 consists of *Schackoina cushmani* and *Hantkenina alabamensis*; Set 2 consists of *Hedbergella*, *Gumbeltrina*, *Woodringina*, and the biserial heterohelics. These Foraminifera are of late Cretaceous and Paleogene age. Sediments containing well preserved planktonic Foraminifera from this interval of geologic time are quite common, and have been studied for many years in both land sections and in sediment cores throughout the world ocean. A list of the character states used to differentiate these taxa is given in Table 1. As can be seen from Figure 2, no character conflicts arise when *S. cushmani* and *H. alabamensis* are considered to be more closely related to each other than either is to any of the other taxa. Stratigraphic information, on the other hand, gives a very different picture of relationships. Dozens of well preserved late Cretaceous and Paleogene sections around the world show that *S. cushmani* is restricted to the late Cretaceous (Masters, 1977), and that *H. alabamensis* is no older than Eocene (Berggren, 1977; Smit, 1977). In between these two intervals lies the Cretaceous-Tertiary boundary, at which all planktonic Foraminifera except the taxa in Set 2 became extinct (Cifelli, 1969; Boersma, 1978; Boersma, pers. commun.). Some or all of the taxa in this extremely low diversity fauna consequently must have been ancestral to all subsequent Cenozoic forms, including *H. alabamensis*. Our most parsimonious hypothesis, completely without character conflicts, is falsified by our understanding of the stratigraphic data.

This example clearly demonstrates the need to consider additional ways of detecting unreliability in morphologic data. It is clear why

TABLE 1.—Distribution of character states in the foraminiferal taxa shown in Figure 2. Data after Ellis et al., 1968; Töpelich and Tappan, 1964, and Olsson, 1964. The primitive state for each character occurs in *Giumbelitina*, as established by outgroup comparison and ontogenetic data.

Character	<i>Shack- orna cushmani</i>	<i>Hant- kenma alabam- ensis</i>	<i>Heilberg- ella</i>	<i>Gumbe- littia</i>	<i>Wood- ringina</i>	Other biserial hetero- helical
Number chambers per whorl	4+	4+	4+	3	2-3	2
Spire height: H = high; L = low trochospiral; P = planospiral	P	P	L	H	H	H
Chamber shape: G = globular, E = ellipsoidal	E	E	G	G	G	G
Aperture shape: A = arched, T = elongate	A	E	A	A	A	A
Planar tubulospines: (+) = present, (-) = absent	-	+	-	-	-	-
Non planar secondary spines	+	-	-	-	-	-

purely morphologic methods failed in this example when we consider the frequency of character homoplasy in the group as a whole, and not just the parsimony of the hypothesis.

Morphology is anything but a reliable guide to phylogeny in planktonic Foraminifera. For

practically any character, iterative evolution (Figure 3) has occurred at least once, and often several times (Cifelli, 1969; Frerichs, 1971; Steineck and Fleisher, 1978). Homoplasy is so complete in many characters that they are treated as "biocharacters" with their own independent stratigraphic ranges (Steineck and Fleisher, 1978; Hart, 1980). Taxa are merely convenient names for successive body forms which reoccupy the morphospace of each biocharacter (see especially Hart, 1980, fig. 1). Some biocharacters have as many as ten independent derivations; at least ten biocharacters have appeared independently more than once (Steineck and Fleisher, 1978, Table 1). Characters such as these can hardly be

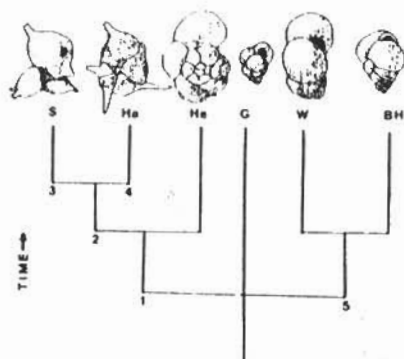


FIGURE 2.—Phylogenetic tree of selected foraminiferal taxa (see text). Taxa abbreviated as follows: G, *Giumbelitina*; H, *Hantkenina alabamensis*; He, *Heilbergella*; W, *Woodringina*; BH, other biserial heterohelical (example shown is *Chilogumbelina*); S, *Shackorna cushmani*. Drawings not to scale. Character states at nodes (see Table 1) are: 1) increase to four or more chambered whorl, low trochospiral test; 2) planospiral test; ellipsoidal chambers; planar tubulospines; 3) non-planar secondary tubulospines; 4) elongate aperture; 5) reduction to two chambers per whorl, biserial elongation.

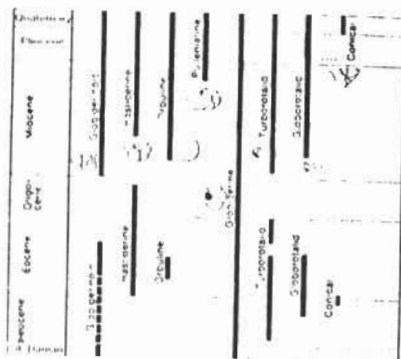


FIGURE 3.—Iterative evolution in Cenozoic planktonic Foraminifera (after Cifelli, 1969).

considered useful synapomorphies, since they are clearly not uniquely derived characters. As Steineck and Fleisher (1978, p. 624) pointed out, "comparative anatomy alone cannot discriminate between convergent and true derived similarity." Given these circumstances, morphologic analysis in the Foraminifera should emphasize methods that are sensitive to detecting and analyzing iterative evolution and homeomorphy. Concepts such as character complexes and bioseries may be more useful in this regard, since they recognize and make explicit use of the covariation of characters.

DISCUSSION

Our ability to analyze stratigraphic reliability in phylogenetic research varies significantly from group to group. Prothero and Lazarus (1980) reviewed the significant factors for other deep-sea planktonic groups. Stratigraphic sequences in multiple well-preserved deep-sea sections from the same oceanic region are quite consistent, due to the nature of oceanic sedimentation. For many groups, preservation is essentially complete. Although the total number of biogeographic regions is small, most major open ocean water masses should be considered adjacent, in the sense of the discussion above, due to the phenomenon of low-latitude submergence (Casey, 1977). The integrity of the stratigraphic data for these groups is readily determined and is generally excellent, so long as adequate geographic control is included. In many cases continuous transitions between ancestral and descendant forms can be traced, obviating the necessity for more elaborate analyses of stratigraphic uncertainty.

The methods discussed above may be applied to many other groups as well. In mammals, for example, the preservation factor is becoming much better understood as mammalian taphonomy advances (Behrensmeier and Hill, 1980; Shipman, 1982). In a Pleistocene site, Wolff (1975) found that only 55% of the original live mammalian community was collected by bulk sampling and screen-washing. Surface collecting, a far more common procedure, yielded only 36% of the original live community, biased toward larger taxa. Thus, the odds that any one member of the original live community has been sam-

pled by normal techniques is in the order of 0.3-0.6 for this example.

Geographic reliability is more difficult to estimate. Mammals have geographic ranges that tend to be quite small relative to those of planktonic microfossils [in the order of 10^2 - 10^6 square km or less (Anderson, 1977)], as opposed to water masses whose areas range from 10^7 - 10^9 square km]. However, since there is a linear relationship between body size and minimum geographic range in mammals (Brown, 1981 fig. 2), it is possible to estimate how much area must be sampled before one approaches a reasonable approximation of the total original geographic range of a fossil mammal. Usually, however, we find that mammals have many unsampled geographic ranges relative to the number of areas which typically are sampled at a given stratigraphic level for the Cenozoic land record. In addition, terrestrial environments are more heterogeneous than the open ocean by orders of magnitude. The dispersal abilities of some mammals make almost worldwide geographic control necessary. As a result, geographic uncertainties will probably make stratigraphically-based phylogeny reconstruction unreliable in most mammalian groups. A possible exception might be some Plio-Pleistocene mammals, which are relatively abundant at many stratigraphic levels in many areas of each continent (Kurten and Anderson, 1980; Sylvester-Bradley, 1977).

Finally, the reliability of stratigraphic sequence is a problem that is seldom addressed in vertebrate paleontology. This may be due to the fact that there are few examples in the vertebrate fossil record of multiple parallel sections with good stratigraphic data for each specimen. However, Prothero (1982) has known that techniques commonly used in invertebrate biostratigraphy are effective in fossil mammal sequences as well. Excessive reliance on the character polarity shown by a single sequence can lead to the problems. For example, Schankler (1980, 1981) has shown that some of the stratigraphic patterns documented by Gingerich (1979) for the northern Bighorn Basin of Wyoming do not hold for the central Bighorn Basin, only 50 km to the south. A single local stratigraphic sequence is not in itself sufficient to justify the use of stratigraphic superposition as a means of determining morphocline polarity. Too

many variables are present that could give a completely erroneous picture.

There is undoubtedly a considerable body of literature available to estimate stratigraphic reliability in many shelly macroinvertebrates. Our lack of familiarity with this literature prevents us from giving an example, but we hope that we have stimulated other workers to do so for their own groups.

CONCLUSION

The controversy over the importance of stratigraphic and morphologic data in phylogeny reconstruction has too long been the domain of dogmatism. In this paper, we do not arbitrarily champion the superiority of either stratigraphic or morphologic data. Instead, we point out the fallacy of doing so, for in many cases stratigraphic and morphologic data are sufficiently imperfect that it is not immediately clear which is more reliable.

In many groups, both sources of data may be so incomplete that attempts to reconstruct phylogeny would be pointless. But phylogenetic analysis is not the only interesting problem in paleontology or comparative biology. If the quality of the data in some groups does not allow us to reconstruct phylogeny, then there are many other worthwhile avenues of research (for example, functional analysis, biogeography, development, changes in diversity through time, among other problems) that might be profitably pursued.

In groups where both morphologic and stratigraphic data are relevant to testing phylogenetic hypotheses, each source of data must be assessed for its relative importance. We have suggested, and demonstrated by example, some methods by which this assessment can be made more objective. It would be very convenient if, as in physics, taphonomic processes were so well understood that explicit equations and precise numbers could be routinely set down. Although this is not yet the case, we are still not justified in ignoring the problem. Morphologic systematics has recently made considerable progress in developing methods to analyze and cope with the imperfections of morphologic data. Stratigraphically-based taxonomy can be advanced similarly by considering the sources of error in geologic data, and the means by which we detect them. Even without quan-

titative expressions, explicitly stated reasons for accepting or rejecting particular types of data are preferable to the uncritical, subjective assessments and dogmatic assertions that presently plague us.

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