

## THE RECOGNITION OF ANCESTORS

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The recognition of ancestors is problematic using cladistic logic alone because monophyletic groups (clades) are defined by shared derived characters (synapomorphies) which their ancestors *must* have lacked. Nevertheless, ancestors possess three key attributes. They belong within a larger, paraphyletic group. They will be morphologically most similar to their immediate descendants, and they evolved *before* any and all of their descendants. Recognition of ancestors requires both morphological and stratigraphic data and, in practice, the task is to reduce the size of the paraphyletic group within which the ancestor must lie. All ancestor–descendant relationships are phylogenetic hypotheses. Despite the legendary incompleteness of the fossil record, testing the validity of available data is far more difficult for character analysis than for stratigraphy.

KEY WORDS: Ancestors, phylogenetic hypotheses, morphology, fossil record.

### INTRODUCTION

There has been, and continues to be, considerable controversy in the literature concerning the recognition of ancestors. Cladistic analysis provides a formal, logical method of identifying the closest known relative of any taxon, but it does not allow definition of this relationship. A pair of most closely related species may be direct ancestor and direct descendant, or both could be daughter species of another ancestor. Farris (1976) and Hull (1979) have argued that ancestors cannot be recognized, whereas Bretsky (1979) took the opposite view and discussed the practical difficulties involved. In between, Fortey and Jefferies (1982), for example, offered a compromise view in which, in effect they accepted that ancestors could be recognized when the fossil record was good, but not when it was poor. Much of the argument has centred around the contribution of fossils, where there has been equal disagreement with, for example, Løvtrup (1977, p. 21) and Patterson (1981) denying entirely or largely the value of fossils, whereas Farris (1976) and Ax (1987) have argued that extinct and extant taxa should be treated identically in phylogenetic analysis, and therefore presumably that fossils do have some contribution to make. Detractors of the fossil record generally stress the completeness argument (see below). Finally, doubts have been expressed about the testability of phylogenetic hypotheses (of which ancestor descendant relationship form a subset). However, Harper (1976) suggested two simple tests which are valid, despite the criticisms of Platnick (1977) and Laws and Fastovsky (1987). Both are different aspects of what I would call the test of time. Do subsequently discovered taxa or additional characters not used in the original analysis invalidate, modify or leave unchanged the original hypothesis?

Given the controversy it is reasonable to question whether recognition of ancestors is worth the effort. Eldredge and Cracraft (1980) argued that it is impossible to recognize any evolutionary pattern in the absence of at least

hypotheses about ancestor-descendant relationships. How does one distinguish cladogenesis from anagenesis without some idea of which taxa are ancestors and which descendants? Even stasis, the absence of morphological change, cannot be recognized without accepting that older populations are genetically related (i.e. ancestral) to younger populations. Furthermore, ancestors undoubtedly existed and statistically it is a certainty that some at least have been preserved in the fossil record (Prothero and Lazarus, 1980). Therefore the search for them seems worthwhile. Laws and Fastovsky (1987) come closest to the ideas expressed here, but as far as I am aware, no-one has outlined a step by step method to recognize ancestors, which is the main purpose of this paper.

### *Terminology*

In this paper the phrases "direct ancestor" and "direct descendant" imply a species-to-species relationship analogous to that between parent and child. The unqualified term "ancestor" either implies a more distant relationship, analogous to grandparent, great grandparent, etc., or carries no specific implication about precise ancestral position. Also, following Engelmann and Wiley (1977), I agree that individuals and species are acceptable as ancestors but higher taxa are not. Nevertheless, in practice, recognizing ancestors often involves identifying a supraspecific taxon within which the ancestor must lie and then eliminating constituent species until (ideally) only one is left.

### PROPERTIES OF ANCESTORS

Ancestors have three primary properties. (1) They belong, together with all their descendants, within a larger clade. However, since descendants cannot possibly be their own ancestors, this leaves a paraphyletic group that will include the ancestor. This group is somewhat analogous to the "nodal-group" of Craske and Jefferies (1989). (2) Ancestors will be morphologically very similar to their direct descendants and (3) they must have evolved before the first appearance of any and all of their descendants.

The first property allows prediction of some of the characteristics of potential ancestors and limits the size of any nodal group. For example, if birds are a true clade, the direct ancestors of all species of birds save one will be another bird, because only the very first species of bird to evolve could possibly have had a direct ancestor that was not another bird. The smallest nodal group will include just the direct ancestor, but since its recognition requires prior knowledge of the direct ancestor, in reality the task is one of narrowing down the possibilities, i.e. of reducing the size of the nodal group. For example no-one doubts the ancestors of the birds lay within the "reptiles".

The second property helps to eliminate many taxa on grounds of morphological distance. Within the "reptiles" there will be several nested sets of synapomorphies defining groups which are progressively smaller and some of whose members are progressively closer (both morphologically and phylogenetically) to the first bird. Again, although it may be argued that thorough character analysis will identify both the nodal group and the morphologically closest member of that group, in practice it is usually easier to recognize a taxon of supraspecific rank within which species that are candidates for direct ancestor can then be examined one by one.

(See the first example discussed below.) This is particularly true if the initial character analysis is applied to even some supraspecific taxa.

Finally, although ancestors may outlive their descendants, they cannot have evolved after their progeny. Thus some members of the nodal group may be eliminated on temporal grounds. No living "reptile" can possibly be ancestral to the birds unless it can be shown to have evolved before the first known bird.

So we have three steps in the recognition of ancestors. First recognize a group within which the ancestor must lie. Secondly eliminate species within it that are not morphologically close to the chosen species. Thirdly, reduce the choice further by eliminating those morphologically closest species which are not known to have evolved before the chosen species. To my mind the order of the last two steps is not particularly important.

## EXAMPLES

Here I use two fairly typical examples from the echinoderm fossil record to illustrate the technique. The first involves the Upper Cretaceous sea urchin genera *Hagenowia* and *Infulaster*, the second the Lower Jurassic crinoid genus *Isocrinus*.

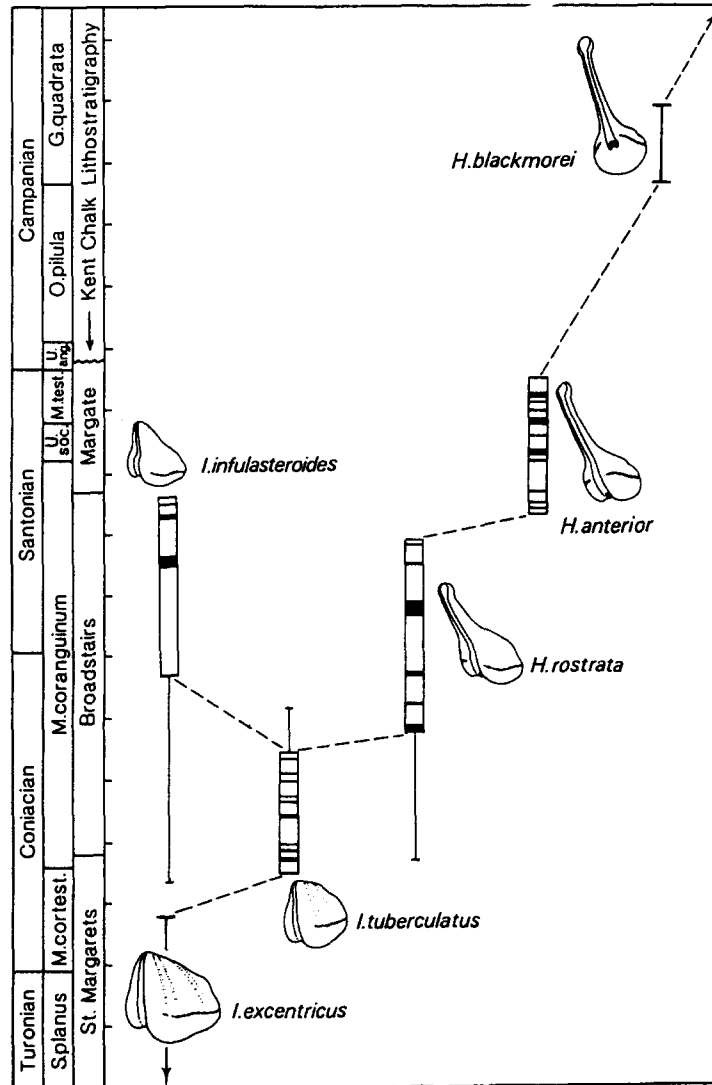
### *Hagenowia* and *Infulaster*

*Hagenowia* has a unique morphology. It is the giraffe of echinoids (Figure 1) with an elongate rostrum which bears a frontal groove and extends anteriorly from the globular main body of the test. The rostrum is composed of homologous plates in all four well characterized species and parsimony argues that this unique structure evolved only once. All species of *Hagenowia* have a unique, disjunct apical system with part at the tip of the rostrum and part at its base. Both these features confirm that *Hagenowia* is a truly monophyletic genus. Furthermore, all species of *Hagenowia* have an interrupted metasternal plastron and lack specialized respiratory tube feet. The plastron and ambulacral structure suggest that *Hagenowia* is descended from less derived holasterid echinoids. Thus the first step identifies the family Holasteridae as including the ancestor of *Hagenowia*.

Among known holasterid echinoids, the genus *Infulaster* is most closely similar to *Hagenowia*. It does not possess a true rostrum, but has a deeply incised frontal groove and the undivided apical disc lies at the apex of the test over the frontal surface (Figure 1). All species of *Infulaster* have a metasternal plastron which, in *I. infulasteroides*, is interrupted as it is in all species of *Hagenowia*. *Infulaster infulasteroides* also has elongate plates laterally in interambulacra 1 and 4. There is no detailed morphological information about *I. excentricus*, but clearly *I. infulasteroides* is closer to *Hagenowia* morphologically than *I. tuberculatus* is. The cladogram in Figure 2 can be derived from available morphological information (Gale and Smith, 1982; Smith, 1984).

Consideration of known stratigraphical ranges of the species concerned (Figure 1) casts doubt on one aspect of the cladogram derived from morphology alone, namely the relative order of appearance of *H. rostrata* and *I. infulasteroides*. Although such accurate stratigraphical data have so far only been recorded from the sections in Kent, nevertheless the best available information shows that *H. rostrata*, the oldest known and least apomorphic species of *Hagenowia*, occurs 9.5 m lower in the section than the first known specimen of *I. infulasteroides*. Taken at face value this would preclude *I. infulasteroides* as an ancestor of

*Hagenowia*. On stratigraphical grounds *I. excentricus* may also be excluded as the direct ancestor because not only does the top of its range terminate 26 m below the first known example of *Hagenowia*, but this interval includes the entire known stratigraphic range of *I. tuberculatus*. Thus morphological arguments suggest that *Infulaster* is the genus most closely related to *Hagenowia*, and that *I. infulasteroides* is the direct ancestor of *H. rostrata*. Stratigraphic information is consistent with *Infulaster* being ancestral to *Hagenowia*, but suggests *I.*



**Figure 1** General morphology, stratigraphic distribution and preferred phylogeny of British species of *Infulaster* and *Hagenowia*. Solid black, actual occurrences; white, gaps in known ranges. Thin lines below ranges of *I. infulasteroides* and *H. rostrata*, and above range of *I. tuberculatus*, 95% confidence intervals of first, and last occurrence, respectively. Scale in 10 m intervals, Data from Gale and Smith (1982) and Smith (1984); confidence intervals calculated using tables in Strauss and Sadler (1989).

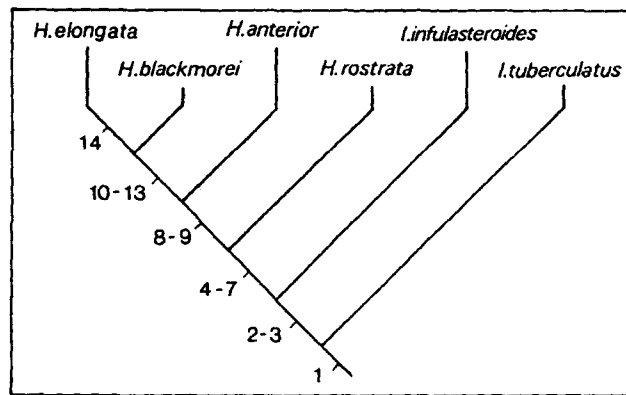
*tuberculatus* is the direct ancestor of *H. rostrata*. If the stratigraphical information is accepted, *I. infulasteroides* and *H. rostrata* are both daughter species of *I. tuberculatus* which is what Smith (1984) concluded.

### *Tests of Stratigraphic Data*

Most of the debate about the recognition of ancestors arises because those who put their faith in character analysis tend to ignore stratigraphy. They would interpret this as one of the supposedly common cases where an ancestor (*I. infulasteroides*) is preserved stratigraphically above its descendant (*H. rostrata*), due to the infamous incompleteness of the fossil record. So can the reliability of the stratigraphic information be tested?

The stratigraphic data on *Infulaster* and *Hagenowia*, although detailed and accurate, come from a small part of the geographic ranges of the two genera. It seems obvious that elsewhere *I. infulasteroides* may occur stratigraphically below *H. rostrata*. What are the chances that further collecting could extend down the stratigraphic range of *I. infulasteroides* while not affecting that of *H. rostrata*? Strauss and Sadler (1989) have developed a method of calculating confidence intervals on known ranges of fossils which depends primarily on the number of known fossil horizons (but see their paper for the underlying assumptions). The 95% confidence interval for the base of the range of *I. infulasteroides* extends below that for *H. rostrata*—indeed it runs to just below the base of the range of *I. tuberculatus* (Figure 1). Thus, in this case it would seem reasonable to accept the cladogram based on morphology, yet several points argue against this.

Although the first appearances of all species of *Infulaster* and *Hagenowia* are said to be stratigraphically slightly lower in Germany than in Britain, as far as is known, they still all appear in the same order. Certainly no-one has reported *I. infulasteroides* occurring below *H. rostrata*. Secondly, one can arrange the four well characterized species of *Hagenowia* in a morphological series from most



**Figure 2** Cladogram for species of *Infulaster* and *Hagenowia* derived from morphology alone. Numbers indicate shared derived characters as follows: 1, Apex anterior; 2, elongate plates laterally in interambulacra 1 and 4; 3, interrupted plastronal plating; 4, rostrum present; 5, interrupted apical disc; 6, loss of respiratory tube feet; 7, mouth antero-ventral at base of frontal groove; 8, plates of ambulacral columns IIa and IVb reduced in rostrum; 9, two genital plates; 10, plates of ambulacral columns IIa and IVb lost from rostrum; 11, reduced madreporic pores; 12, mouth anterior within frontal groove; 13, rostrum vertical; 14, only two madreporic pores. Data from Gale and Smith (1982) and Smith (1984).

plesiomorphic (*H. rostrata*) to most derived (*H. elongata*) and their stratigraphic occurrences are in exactly the same order. This is also true of both species of *Infulaster* for which morphological data are adequate. If this stratigraphic information is reliable, why are the relative appearances of *I. infulasteroides* and *H. rostrata* not? Thirdly the 9.5 m gap between the first known occurrences of *I. infulasteroides* and *H. rostrata* represents about 200,000 years (assuming there are no breaks in this part of the succession). Perhaps, more importantly, it represents 30 and 28%, respectively, of the total known stratigraphic ranges of *I. infulasteroides* and *H. rostrata*. (It is 46% of the total known range of *I. tuberculatus*!)

To summarize, direct ancestors can be recognized for one of three species of *Infulaster* and three of four species of *Hagenowia*. In addition, *I. excentricus* was probably directly ancestral to *I. tuberculatus*, while either *I. infulasteroides* or more likely *I. tuberculatus*, was the direct ancestor of *H. rostrata*.

### *Isocrinus*

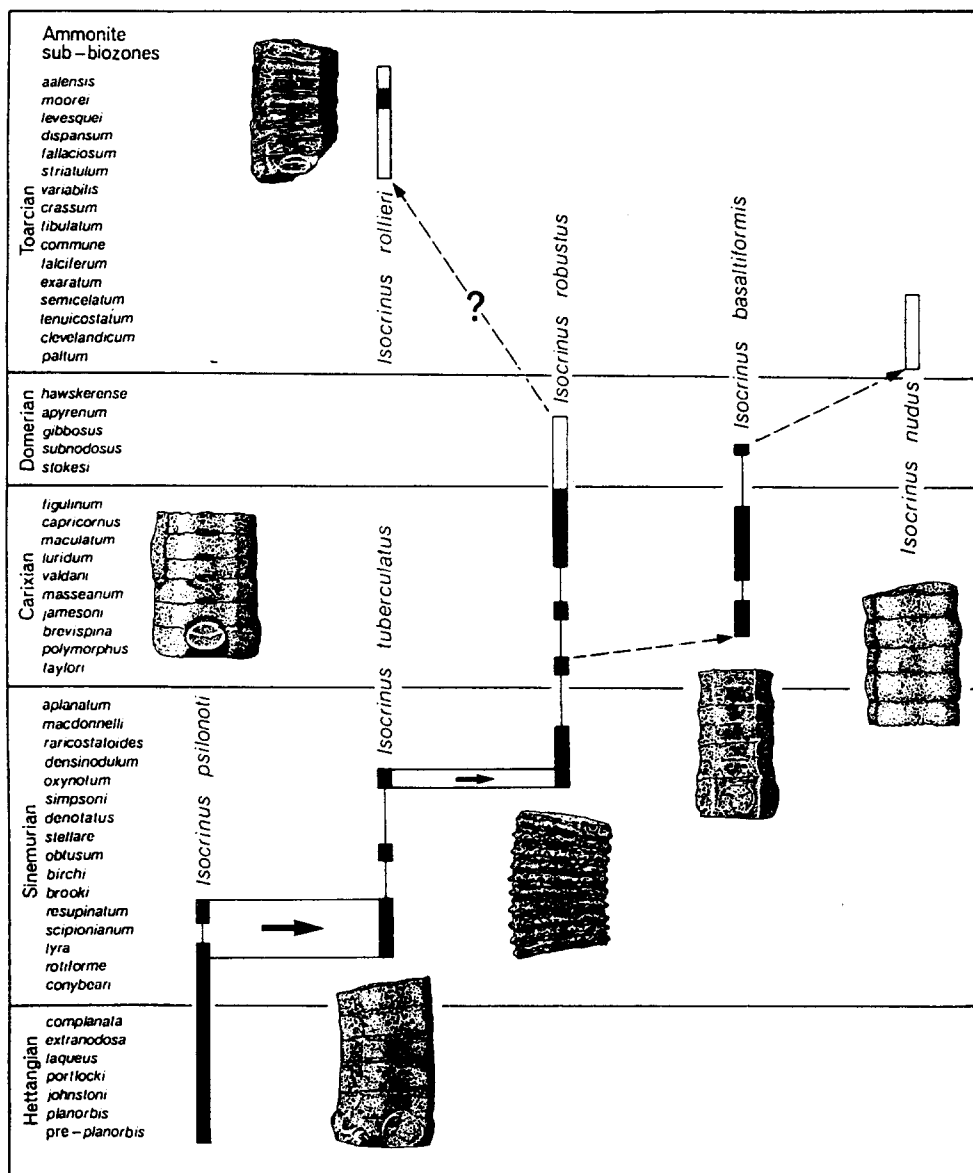
The stalked crinoid *Isocrinus* has a stem composed of pentagonal or pentastellate columnals, with larger nodal columnals bearing five cirri separated by a variable number of smaller internodals, and with articulating surfaces which bear crenulae in a petal-like arrangement (Simms, 1989). Petaloid articular surfaces are very distinctive and only found in some species of *Encrinus* and members of the families Pentacrinidae and Isocrinidae. This suggests petaloid articular surfaces are a synapomorphy defining a true clade. *Isocrinus* differs from *Encrinus* in details of the cup and arms and from pentacrinids in lacking prolongations of the basal plates of the cup and in having cirri with oval or rounded, rather than diamond-shaped, cross-sections. On morphological criteria, the family Isocrinidae can be identified as including the ancestor of *Isocrinus*.

*Isocrinus* is represented by six species in the Lower Jurassic of western Europe (Simms, 1989). They can be characterized by their crowns and stems. The ornament of the latera and shape of isolated columnals are usually enough to identify any of them. *Infulaster psilonoti* has smooth latera, *I. tuberculatus* has granular latera, while *I. robustus* has highly ornamented latera with a continuous median keel. *Infulaster basaltiformis* has weakly to strongly granular columnals sometimes with a weak keel that is discontinuous over the interradial, which, unlike those of the previous three species, are angular not rounded. *Infulaster rollieri* has smooth latera, like those of *I. psilonoti*, but with only 7–8 internodals compared with 13–23 in the latter species. Finally, *I. nudus* has very large columnals which have smooth latera with inflated radial. In this case there is no obvious outgroup to indicate which are primitive and which derived character states, there are fewer characters and reversals occur. However, on morphological grounds *I. psilonoti* is least closely related to *I. robustus*.

The known stratigraphical distribution of all six species of *Isocrinus* is shown in Figure 3. Taking both morphological and stratigraphic information into account for the first four species, suggests that *I. psilonoti* was directly ancestral to *I. tuberculatus* which was, in turn, directly ancestral to *I. robustus* and probably *I. basaltiformis* as well. In the first two transitions there is remarkable confirmation from both morphology and stratigraphy. Morphologically intermediate forms occur, but only at the precise stratigraphic levels where two species coexist. Thus mixed populations with smooth, weakly granular and granular articular surfaces occur in the *lyra* and *resupinatum* subzones of the Sinemurian, where *I. psilonoti* and *I.*

*tuberculatus* coexist. Similarly, mixed samples of granular and keeled columnals occur in the *oxynotum* subzone which is the only interval in which *I. tuberculatus* and *I. robustus* coexist (Simms, 1989).

These stratigraphic data can be tested against a null hypothesis of randomness.



**Figure 3** Stem morphology, stratigraphic distribution and inferred phylogeny of west European species of *Isocrinus*. Solid black, occurrences accurate to subzone; white, gaps or ranges known only to zonal level. Arrows within boxes indicate occurrences of morphological intermediates. Query between *I. robustus* and *I. rollieri* is because stratigraphic gap is too large to accept direct descendence. Data from Simms (1989).

For example, if we regard the *I. psilonoti* to *I. tuberculatus* transition as consisting of three populations of smooth, granular and mixed columnals, the probability of the observed pattern of distribution arising by chance is vanishingly small. Consider just the probability that the mixed populations represent chance discoveries. They occur in just two subzones in a total range (for both species) of 19 subzones. Under the null hypothesis of random distribution and chance discovery there is a 1 in 19 chance of discovering a mixed population in any one subzone and a 1 in 361 chance of discovering two mixed populations specifically in the *lyra* and *resupinatum* subzones. This alone is sufficient to reject the null hypothesis, but that these two subzones should coincide exactly with the interval of overlap between the known ranges of *I. psilonoti* (which ranges through 12 subzones) and *I. tuberculatus* (which ranges through 10 subzones) strengthens the case against the null hypothesis immeasurably.

## DISCUSSION

### (A) *Certainties, Probabilities and Possibilities*

Ancestor–descendant relationships, such as discussed above, are just one subset of phylogenetic hypotheses, and recent authors have stressed that to be scientific these hypotheses must be testable (e.g. Hull, 1967; Harper, 1976; Engelmann and Wiley, 1977; Szalay, 1977; Platnick, 1977; Patterson, 1981; Laws and Fastovsky, 1987; Archie, 1989; Bryant, 1989). However, these authors differ as to whether or not character analysis alone (i.e. cladograms), or combined with ancestor–descendant hypotheses (i.e. trees) or with stratigraphic data constitute testable hypotheses. Laws and Fastovsky (1987), following Hull (1967) distinguish “universal generalities” from “tendency statements”, the latter being commonly, but not universally, true. Furthermore, they argue that only universal generalities are falsifiable, because a single contrary observation negates their universality, whereas a single (or several) contrary observations do not invalidate a tendency statement. Indeed they may be “the exceptions that prove the rule”. However, Harper (1976) has proposed two valid tests of all phylogenetic hypotheses. Any phylogenetic hypothesis, including ancestor–descendant relationships can be falsified by discoveries of additional taxa or characters not available when the hypothesis was formulated.

In science there are no certainties. We can never prove that any hypothesis is true, merely that it has not been disproved so far. Thus, I believe universal generalities are merely tendency statements that have yet to be recognized as such. Possibilities can be equally misleading. So long as a single taxon, character or character state remains to be evaluated, it *might* modify a phylogenetic hypothesis. Even with complete knowledge, re-evaluation would still not necessarily cease. Indeed the biggest revolution in evolutionary biology came about not by the discovery of new facts, but by the adoption of Hennig’s methods of analysis. Possibilities must always be evaluated for this likelihood. Thus Novack and Norrell (1982, Figure 1) illustrate a hypothetical tree in which one fossil existed for 50 Ma before it became preserved. While this is clearly possible, one must ask how typical of the fossil record it is. Pigs might fly but personally I do not have insurance against the possibility of one crashing into my greenhouse. A robust hypothesis that has been tested many times is less likely to be modified by new observations than one which has only been tested once. In effect, science evaluates

probabilities; it does not deal in certainties, nor should it be mesmerized by possibilities.

(B) *The Validity of Stratigraphic Data*

To me a double standard is used in evaluating the contribution of fossils or stratigraphy to evolutionary theory, exemplified by one anonymous reviewer who claimed that “stratigraphic order [provides] a ‘rule of thumb’ for recognizing ancestor–descendant relationships” whereas “character analysis provides hypotheses of relationship”. I cannot for the life of me see why evolutionary hypotheses based on stratigraphic data, or fossils in general, are *a priori* inferior, less scientific, or less testable than those based on character analysis, nor could Szalay (1977). This double standard manifests itself in two principal ways; demanding certainties and stressing possibilities. If both types of argument are applied to other evidence, e.g. character analysis, they can be shown to be equally valid (or invalid). For example, the same reviewer stressed that one can only ever disprove ancestor status, but this is true of all science. One can only ever disprove apomorphic status. Nevertheless, if I identify an ancestor or a cladist an apomorphy, and after 100 years, numerous discoveries of new taxa, new characters and new character states, both are still acceptable surely they are equally well founded?

Another example is completeness of data. Patterson (1981, p. 208) has argued “If specific hypotheses of ancestry are to be justified, . . . additional assumptions or criteria must be used (e.g. the fossil record is complete . . .)” and “The additional assumption inherent in this [the stratophentic method] is that the fossil record is complete: there are no unsampled taxa”. This is just one example where the incompleteness of the fossil record is highlighted. Yet no science is based on complete knowledge. Shaw (1964) and Paul (1982, 1985) have stressed that total stratigraphic range or complete fossil faunal lists are unknowable, because so long as a single fossil remains in the rock it *might* add to knowledge. But this is equally true of character analysis. So long as a single living specimen, remains unstudied it *might* reveal a new DNA sequence or protein or morphological character state, and thereby alter some phylogenetic hypothesis. These possibilities are testable by sampling theory and the test of time. We can put confidence intervals on stratigraphic ranges (Strauss and Sadler, 1989; Marshall, 1990) and on the chances of overlooking a fossil when collecting (Shaw, 1964; Paul, 1982, 1985). It is not as easy to do this for sampling character states (see below), although Archie (1989) and Bryant (1989) have made a start, nor on character weighting (but see Cheetham and Hayek, 1988).

The completeness of the fossil record is an example of overstressing possibilities. For different reasons Bretsky (1979, Figure 2) and Fortey and Jefferies (1982, Figure 3) have presented hypothetical phylogenetic trees in which only a small proportion of the taxa are known. Clearly this possibility cannot be discounted. However, recent estimates suggest that similarly small percentages (5–10%) of living soil microbes, or fungi are known, while some estimates of total numbers of living species imply that only 10% have been named, let alone studied adequately. The point of this is not to stress the inadequacy of neontological knowledge, but to point out that what we do not know about living or fossil taxa, does not invalidate what we do know. However, it may enable us to evaluate current ideas in the future. Known species may be organized into cladograms or phylogenetic trees and these hypotheses tested by future discoveries.

Completeness of data is irrelevant to the formulation of specific ancestor-descendant hypotheses, but may become crucial to their testing.

(C) *Parsimony*

Another apparent area of double standard is the use of parsimony. It is greatly stressed in the construction of cladograms, but apparently abandoned where fossils are concerned. Thus, for example, Ax (1987), who argues (correctly in my view) that fossils should be treated no differently from living taxa, nevertheless uses a diagram (Figure 6.5, p. 207) to illustrate how to incorporate fossils into a cladogram. The diagram involves of 1:1 ratio of hypothetical ancestral species to known fossil species, which is scarcely parsimonious. The most parsimonious interpretation of the phylogenetic relationships of the four well characterized species of *Hagenowia* (using morphological and stratigraphic data) is that they all lie within a single anagenetic clade. Why should this most parsimonious hypothesis be rejected in favour of any other?

Two final points. First stratigraphic data are open to a variety of tests as to their validity. Both the reliability of known ranges and their precise pattern can be tested (Strauss and Sadler, 1989; Shaw, 1964; Paul, 1982, 1985; Marshall, 1990). While it is true that cladograms and trees can also be tested by parsimony and compatibility, the characters chosen cannot be, yet they are absolutely crucial to the resulting cladogram or tree. There is at present no acceptable test that the right characters, or enough of them, have been selected, nor that those chosen have been correctly weighted. See, for example, the three different cladograms for the living classes of echinoderms derived by Raff *et al.* (1988), Smiley (1988), and Smith (1988). The discrepancies are largely due to Raff *et al.* putting more emphasis on molecular biological characters, Smiley stressing developmental characters and Smith including data from the fossil record. Not surprisingly cladograms with different data bases are likely to differ. As yet there is no objective way of deciding which author has the best data. Indeed, the greatest challenge facing evolutionary biologists at present is to develop tests for the adequacy of character data bases.

Second, Gould (1980) and Lazarus and Prothero (1984), among others, maintain that there are numerous cases in the fossil record where ancestors are preserved stratigraphically above (i.e. later than) their descendants. Apparently there is no difficulty whatsoever in recognizing ancestors when their recognition can be used to reinforce our beliefs about the inadequacies of the fossil record! If the order of species in the fossil record is too unreliable for us to recognize ancestors, there can be no known cases of ancestors preserved after their descendants.

Cladistics is an excellent first step in phylogenetic analysis, but it is only the first step. Phylogenetic trees contain more information than cladograms (Szalay, 1977) precisely because they depict suggested ancestor-descendant relationships. Many phylogenetic trees are compatible with the same cladogram (22 for a three taxon cladogram according to Platnick, 1977). Alternative trees can be tested against known stratigraphic data (Paul, 1985; Cheetham and Hayek, 1988). Not to attempt to recognize ancestors is like trying to trace one's family history while denying that anyone had a recognizable parent! To me this seems defeatist, especially when the task is by no means as hopeless as some would argue. Can't is spelt TRY.

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