Morphology's Role in Phylogeny Reconstruction: Perspectives from Paleontology

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A recent article by Scotland et al. (2003; hereafter referred to as SEA) purporting to examine the value of morphological data in phylogeny reconstruction has been received critically by several systematists (Jenner, 2004; Wiens, 2004). As paleontologists—and in an area of systematics restricted solely to morphological data—we take exception to many of the arguments put forward by SEA and feel we may provide a unique perspective in the debate.

In their paper, SEA argued for a redefined role for morphology in phylogeny reconstruction, one in which “rigorous and critical anatomical studies of fewer morphological characters, in the context of molecular phylogenies, is a more fruitful approach to integrating the strengths of morphological data with those of sequence data” (p. 539). Such a statement is bold and therefore warrants a critical analysis, as it would effectively neuter the ability of morphological data to generate novel phylogenies. Though issues such as accuracy, support, character coding, and character conceptualization were discussed by SEA, in all cases these discussions resorted to a “too few characters” argument. As the authors characterized it, the “main constraint of morphology-based phylogenetic inference concerns the limited number of unambiguous characters available for analysis in a transformational framework” (p. 539). Additionally, the merits of increased taxon sampling in the context of morphological data were discussed by SEA, and found to be lacking.

Though several of the views presented by SEA are not novel (see Hedges and Sibley, 1994, and Hedges and Maxson, 1996), they provide the most detailed recent discussion of this position. We agree with many of the points made by SEA, especially the call for more critical and rigorous analysis of morphology; however, we draw different conclusions from the data. It is our goal to reexamine some of the arguments put forward by SEA, in order to illustrate that a much more optimistic conclusion exists regarding the current and future role of morphology in phylogeny reconstruction.

PHYLOGENETIC ACCURACY AND DATA SET SUPPORT

SEA (p. 539) describe the relationship between phylogenetic accuracy and number of characters with their Figure 1a (reproduced here as Fig. 1a), adapted from simulation studies of Hillis (1996, 1998). Simulation studies have generally demonstrated that increasing the number of characters in an analysis will lead to an increase in accuracy (Nei et al., 1983; Kim and Burgman, 1988; Rohlfs and Wooten, 1988; Huelsenbeck and Hillis, 1993; Charleston et al., 1994; Hillis et al., 1994a, 1994b; Hillis, 1996, 1998; Givnish and Sytsma, 1997; Rosenberg and Kumar, 2001). SEA (p. 541) refer to this relationship as evidence that the number of characters utilized in morphological analyses is less than the number that is “typically required to accurately reconstruct phylogenies in simulation studies.”

We take issue with SEA’s (p. 541) interpretation of Hillis’ (1996, 1998) results. The studies of Hillis (1996, 1998) were explicitly examining the number of characters that were required to accurately reconstruct a 228 taxon tree (Fig. 2), and were in no way intended to equate specific numbers of characters with specific levels of accuracy for any phylogenetic analysis, though they were intended to examine the possibility of accurately reconstructing large phylogenies. More importantly, the main point of Hillis’ (1996, 1998) simulation studies was that relatively few characters were required to accurately reconstruct a 228 taxon tree, given dense taxonomic sampling.

An equally critical point to bear in mind is that the “true” 228 taxon tree was originally inferred from 18S RNA by parsimony. This phylogeny and a specific model of nucleotide substitution (Kimura 2-parameter, alpha/beta = 2, gamma distribution of rate heterogeneity with shape parameter = 0.5; Hillis, 1998) were then used to generate artificial data sets, and the ability of parsimony (and neighbor-joining) to accurately estimate the phylogeny from these data sets was then measured. Given that this particular model of evolution is designed for molecular, not morphological, characters, and given that morphological characters (and more than likely molecular characters as well) probably do not evolve according to this specific model, it seems unwarranted to judge the quality of morphological data sets (in terms of numbers of characters needed to accurately reconstruct the true phylogeny) through a comparison with the results of Hillis’ (1996, 1998) simulation studies.

There is simply no fixed relationship between character sampling and accuracy. Furthermore, most simulation studies have not examined number of characters and character/taxon ratios independently; i.e., these parameters tend to covary in most studies. The fact that character/taxon ratios may not accurately capture the ratio between number of taxa and possible variation is often overlooked as well. A more informative metric in this regard may be a character state/taxon ratio.
FIGURE 1. Possible relationship between an increase in the number of characters and features of the phylogeny. (a) Accuracy (Hillis, 1996, 1998). (b) Bootstrap support (bremer et al., 1999). (c) Ease of homology assessment in morphological studies. (d) Character coding in morphological studies. Text and figure reproduced as in Scotland et al. (2003: fig. 1).

would better deal with biases in data type (i.e., constraints on number of character states present in discrete morphological, nucleotide, amino acid, and quantitative morphological data).

CHARACTER CODING AND AMBIGUITY

Part of SEA’s (p. 541) argument focuses on the claim that the “number of unambiguously coded morphological characters for any study is finite (Fig. 1d) and less than the number typically required to accurately reconstruct phylogenies in simulation studies (Fig. 1a).” The authors defend this claim with a comparison of a figure depicting the relationship between accuracy and number of characters (Fig. 1a; Hillis, 1996, 1998), and another figure depicting the relationship between character coding and number of characters (Fig. 1d). Figure 1a appears misapplied. Though simulation studies may provide an idea of how many characters are required to reach an upper plateau of accuracy given specific evolutionary models (Hillis, 1996, 1998), no study has attempted to determine, or even examine, the “spectrum” of character ambiguity to which SEA refer. Figure 1d is uninformative, as it is based on no empirical data.

SEA state that there is no ambiguity in assigning character states to sequence data once the sequences have been aligned. Although true, this overlooks the potential for error in sequence alignment (Morrison and Ellis, 1997; Goldman, 1998). Additionally, Hillis and Wiens (2000:12) cite multiple sources of homology problems unique to molecular data, including gene duplication, horizontal transfer, and exon shuffling. SEA (p. 541) acknowledge but dismiss these as serious problems.

Though sources of ambiguity in morphological and molecular analyses are different, both can act to confound phylogenetic analysis (Hillis and Wiens, 2000). Unless it can be demonstrated that problems unique to the analysis of morphological data adversely affect more characters than do problems unique to the analysis of molecular data, claims such as those made by SEA reduce to assertions that morphological data sets typically

FIGURE 2. Performance of parsimony in estimating a 228-taxon tree plotted against sequence length. “Percent of tree correct” is based on the partition metric (Robinson and Foulds, 1981; Penny and Hendy, 1985). Text and figure are reproduced from Hillis (1998: fig. 2).
have fewer numbers of characters than DNA sequence data sets. Such arguments can by no means be used as justification for excluding morphological data from playing an independent role in phylogeny reconstruction.

**Character Conceptualization and Homology Assessment**

Character delineation and primary homology assessment of morphological data have traditionally been cited as inherently problematic due to their oftentimes subjective nature. In recent years, however, much progress has been made in terms of recognizing and ameliorating these biases and establishing a more rigorous framework for morphological character conceptualization (Wiens, 2000; Rieppel and Kearney, 2002; Wagner, 2001). Furthermore, many problems related to homology assessment are by no means unique to morphological data.

SEA (p. 541) refer to their graph (Fig. 1c) of the “relationship between homology assessment and number of morphological characters” to make three claims:

1. “There are few [morphological] characters that seem to be uncontroversial in relation to homology assessment” (p. 541).
2. These characters are typically “the first [morphological] characters to be included in a phylogenetic data set” (p. 541).
3. “Increasing the number of [morphological] characters increases the level of ambiguous or problematic characters” (p. 541).

We feel these claims oversimplify the problem of homology assessment in morphological data. As in other types of data, these problems are not distributed uniformly across phylogenetic studies and are more prevalent at particular hierarchical levels (i.e., levels where homologous structures have diverged greatly, or barely at all, in form from each other). Interestingly, these are often the hierarchical levels where homology assessment becomes more controversial for molecular data as well, albeit for different reasons. We believe that some of the most interesting questions in evolutionary biology exist at these particular levels, and (due in part to the specific problems they cause for various types of phylogenetic data) that the most fruitful approach for exploring these questions involves utilizing a variety of different phylogenetic data.

Regarding their second point, we suggest that the first characters included in any phylogenetic analysis are typically those that are easily accessed and that the researcher feels will give him/her the best estimate of the phylogeny. For a morphological analysis this may mean, as SEA (p. 541) suggest, characters that are relatively uncontroversial in regards to homology assessment. For an analysis of DNA sequence data this may mean characters from an appropriate gene, or characters from a region where alignment is relatively uncontroversial (i.e., a region that is uncontroversial in regards to homology assessment).

**Are Morphological Characters More Homoplastic?**

SEA (p. 542) argue that additional characters incorporated into a morphological analysis will generally be of limited value, whereas additional characters incorporated into an analysis of DNA sequence data will typically be of equal value. This assertion presumes a fixed, low number of characters that are actually phylogenetically informative in a morphological analysis, a claim that is prevalent throughout SEA and that is nowhere supported by actual evidence. Additional characters incorporated into a phylogenetic analysis, be they morphological or molecular, are just as likely to be homoplastic as the characters initially utilized (Sanderson and Donoghue, 1989; though see Hedges and Maxson, 1996; Sanderson and Donoghue, 1996; Givnish and Sytsma, 1997; and Baker et al., 1998, for claims that morphological or molecular data are more homoplastic in general), and any claim to the contrary must be backed up by empirical data.

One test of SEA’s assertion would be to identify recent phylogenetic analyses of morphological data for which references (author and year) are given for each character utilized (i.e., each analysis would effectively be a compilation of earlier analyses). Retention indices (R.I.) for the newer characters (from more recent studies) could be compared against the R.I.’s from older characters (included in the earliest studies). SEA’s hypothesis would predict that the R.I.’s of the newer characters would be significantly lower than those of the older characters. To our knowledge, no such comparison has been completed, and we suspect it would find no significant difference (see Wiens, 2004, for an empirical example demonstrating the absence of correlation between number of characters and levels of homoplasy).

There is a practical reason why new morphological characters might not have inferior homoplasy statistics, such as lower R.I.’s (C. Brochu, personal communication). In the case of many data sets incorporating new taxa, new characters are introduced to express a close relationship between the new form and another taxon or clade already in the data matrix. In cases such as this, most new characters would be expected to have higher R.I.’s. The distinction rests between new taxa that require a wholesale revisit of group relationships and those that represent another twig on the tree.

Hillis and Wiens (2000) discussed some of the problems caused by homoplastic characters in phylogenetic studies and aptly pointed out that homoplasy in the form of convergent evolution of characters is a problem faced equally by morphological data and molecular data (2000:11). The authors supported these claims by pointing to empirical studies (Cunningham et al., 1997; Bull et al., 1997) which conclusively demonstrated that selective convergence in molecular sequence data can confound phylogenetic analysis. We agree with Hillis and Wiens (2000:12) that phylogenetic error caused by convergence is probably “of little consequence (relative to sampling error, for instance), regardless of data type”
but feel it is relevant to the discussion to point out that phylogenetic analyses of both molecular and morphological data can suffer from these problems, and methods and practices exist for ameliorating these problems in both types of analyses. The argument that morphological data suffer from excessive homoplasy in the form of convergence is simply a straw man (Wiens et al., 2003).

A CRITICAL ROLE OF MORPHOLOGY (AND FOSSILS) REVISITED

Phylogeny Reconstruction of Extinct Taxa

Molecular data cannot reconstruct the phylogenetic relationships of extinct taxa, except for rare cases involving recently extinct forms (Cooper et al., 2001). Morphological data provide the only means to understand an extinct taxon’s evolutionary history. This is no trivial matter considering that nearly every species that has ever evolved is now extinct (Novacek and Wheeler, 1992). Fossil taxa, therefore, comprise the vast majority of the branches and twigs on the Tree of Life. The importance and relevance of phylogenetic hypotheses for these fossil taxa cannot be underestimated because our knowledge of the rates of morphological evolution and the acquisition of novel bauplans, the frequency of mass extinctions and the impact of global biodiversity crises, the calibration of molecular divergence estimates, as well as the origination of modern clades of taxa, all rely on data from these fossil phylogenies.

Considering the importance of fossil data, it is necessary to ask the question “Does SEA’s proposed role of morphology in systematics and phylogenetics allow for phylogeny reconstruction of fossil taxa?” The answer to this is “no.” With ambiguity and relevance of morphological characters determined from congruence with molecular phylogenies, phylogenetic hypotheses for groups with no living representatives (e.g., trilobites, blastoid echinoderms, pterosaurs, etc.) would of necessity remain unexplored because no molecular phylogeny can exist from which “unambiguous” morphological characters could be obtained.

Even the phylogenies of fossil taxa with extant relatives would remain unresolved because not all taxa can simply be inserted into a molecular phylogeny. If these fossil taxa do not belong within the crown clade proper than they would optimize, given the available unambiguous morphological data, as a basal polytomy with all other extant members of that crown group. At this point, there would be no objective means of resolving their position among other stem members of the extant clade. Moreover, there is no reason to expect the extant members of a group would provide morphological homologies relevant to elucidating the phylogenies of their fossil relatives. Resolving the phylogenetic relationships within sauropod dinosaurs would be aided little by the discovery of morphological characters of unambiguous homology assessment in extant avian dinosaurs.

Morphology Bridges Extinct and Extant Taxa

Do cases exist where analysis of morphological data could be especially useful in elucidating the phylogeny of a group? As described by previous authors (Donoghue et al., 1989; Doyle, 1998; Smith, 1998; Wills et al., 1998), the most likely situation where morphological analyses may play an important role in phylogeny reconstruction would be when dealing with clades characterized by deep divergences and rapid radiations. Doyle (1998:456) states that this is “a situation in which molecular data are least likely to be reliable, because of the small number of molecular synapomorphies between nodes, the possibility that these were erased by later changes (multiple hits), and the related problem of long-branch attraction.” Several cases in which these problems may arise are in analyses of the higher-level relationships of annelids (Gauthier et al., 1988), seed plants (Doyle, 1998), echinoids and ophiuroids (Smith, 1998), arthropods (Wills et al., 1998), and metazoans (Rokas et al., 2003).

Rokas et al. (2003: fig. 6) clearly illustrated why the effects of homoplasy and substitutional saturation are particularly problematic for molecular analyses dealing with taxa characterized by deep divergences and rapid radiations. They related this problem to higher-level metazoan relationships by pointing to work conducted on 18S rDNA by Phillip et al. (1994), which demonstrates that splits in the metazoan tree separated by less than 40 million years cannot be confidently resolved. Recent simulation studies (Levinton et al., 2004) have confirmed the relationship between the ratio of radiation time/post-radiation time and accuracy of phylogenetic inference. Rokas et al. (2003) also aptly characterized more fundamental and philosophical problems relating to these situations (2003:355–356):

Phylogenetic reconstruction of deeply diverged taxa, such as the early branching metazoans, rests on the presence and availability of highly conserved genes that can be accurately identified as orthologs. Such strong conservation of amino acid sequences over long time periods can only be explained by invoking the action of strong purifying selection; in the absence of selection, genetic drift is expected to lead to wide divergence between orthologs, making them indiscernible after a few million generations (Gillespie 1991). Despite this realization, the assumption behind every phylogenetic analysis is that variation between sequences is neutral. Indeed, models of sequence evolution and phylogenetic reconstruction algorithms do not specifically take natural selection into account (Swofford et al. 1996).

The primary reason that morphological analyses may be capable of resolving the relationships of such groups is that morphological analyses can incorporate data from fossil taxa. Fossil taxa can preserve critical combinations of synapomorphy and plesiomorphy that can overturn hypotheses misled by homoplasy (Gauthier et al., 1988; Donoghue et al., 1989).

Although increased taxon sampling of extant organisms can also increase phylogenetic accuracy via these two means (in cases involving either the analysis of molecular or morphological data), fossil taxa are likely to be much more beneficial as divergence time of the group in question increases, and the time period within which
the group radiated decreases. Indeed, Kim (1996:363) concluded that “if taxa are added to counter inconsistency problems, the added taxa should have low rates of change and be close to the common ancestor of the clade” (see also Huelsenbeck, 1991; Poe and Swofford, 1999; and Poe, 2003).

**Taxon Sampling and the Importance of Fossils**

Aside from reconstructing relationships of fossil taxa, utilizing morphological data for phylogenetic analyses offers a considerable advantage in its ability to increase taxon sampling. This advantage is often best employed through the addition of fossil taxa, which may possess unique combinations of characters not present in extant taxa (Gauthier et al., 1988; Donoghue et al., 1989). Several empirical studies of widely disparate taxa have shown that the addition of fossil taxa can impact tree topology (Gauthier et al., 1988; Donoghue et al., 1989; Smith, 1998; Wills et al., 1998). SEA comment on these possible advantages, stating that: “morphological data from fossil taxa can increase taxon sampling in a way not possible for sequence data,” but dismiss them on relatively unsubstantiated grounds (p. 543):

> Although it can be demonstrated that adding taxa with unique combinations of characters can alter a topology (Doyle and Donoghue, 1987; Smith, 1994, 1998) and sometimes give slightly increased levels of support (Lecointre et al., 1993; Baker et al., 1998; Smith, 1998), this is not the same as increasing the accuracy of a given estimate. It is unclear whether breaking up long branches by dense taxon sampling (Gauthier et al., 1988; Graybeal, 1998) using morphological data on the basis of reduced cost or specimen accessibility (Hillis and Wiens, 2000) will lead to a more accurate assessment of phylogeny... given that these data will suffer from problems discussed above (Figs. 1c, 1d) plus the additional problem of large amounts of missing data.

The first part of this argument presumes an objective means of assessing phylogenetic accuracy (not support) for empirical data. This assumes knowledge of evolutionary history unattainable by researchers. Throughout their paper, SEA appear to proxy true phylogenetic accuracy through comparison with currently accepted molecular analyses. We caution against such a practice under these circumstances for the simple reason that most phylogeny estimates are typically accepted as being accurate because of their comprehensiveness and high levels of support. It would seem logically flawed to utilize levels of support to consider one estimate of phylogeny as “accurate,” but then divorce support and accuracy in order to dismiss another estimate of phylogeny, as SEA appear to do in the above statement.

SEA (p. 543) question the beneficial effect of dense sampling in the context of fossils, considering that “in the context of recent molecular analyses (Mathews and Donoghue, 1999; Qiu et al., 1999; Soltis et al., 1999; Barkman et al., 2000; Bowie et al., 2000; Chaw et al., 2000; Graham and Olmstead, 2000), earlier studies based on morphological data and dense sampling of fossils (Crane, 1985; Doyle and Donoghue, 1986, 1987, 1992; Loconte and Stevenson, 1990; Nixon et al., 1994) have now been recognized as being inaccurate estimates of phylogeny.” SEA do not point out that earlier studies of amniote relationships based on morphological data and dense sampling of fossil taxa (Gauthier et al., 1988; Donoghue et al., 1989) were initially contradicted (Hedges et al., 1990), but ultimately validated (Hedges, 1994), by phylogenetic analysis of molecular data. Furthermore, early molecular estimates of seed plant phylogeny, although consistent in rejecting the “anthophyte hypothesis,” still differed significantly in topology from each other (Doyle, 1998).

As far as accurate phylogeny reconstruction is concerned, the value of including morphological data (in the form of fossil or extant taxa) is indeed difficult, if not impossible, to determine a priori. We are in agreement with SEA that more studies, utilizing both simulation and empirical data, should be conducted to specifically address and examine these conditions. However, the current lack of these studies is not sufficient grounds for utterly dismissing the possibility that the addition of fossil taxa can result in more accurate phylogeny reconstruction. Also, given that increased taxon sampling within a monophyletic group increases the accuracy of reconstructing that clade’s phylogeny (Rannala et al., 1998), we suggest fossil taxa may be critical for accurate phylogeny reconstruction of crown groups with few extant members (Smith, 1998). We recommend the advice of Gauthier et al. (1988:105): “While fossils may be important in phylogenetic inference only under certain conditions, there is no compelling reason to prejudge their contribution. We urge systematists to evaluate fairly all of the available evidence.”

SEA (p. 543) also claim one drawback of increased taxon sampling to be “the potential decreased number of unambiguous characters as more taxa are added to a study,” citing a decrease in the number of unambiguous morphological characters observed as more taxa were added to a phylogenetic analysis of *Strobilanthes*. Specifically, the original number of 32 discrete morphological characters coded for 66 taxa in an analysis by Carine and Scotland (2002) was reduced to 12 characters upon the addition of 22 taxa by Moylan et al. (unpublished). This example does not, as SEA (p. 543) suggest, demonstrate that adding taxa to a study may reduce the number of *unambiguous* characters. The 20 *ambiguous* characters were already present in the initial analysis, but were not recognized as such. This example instead demonstrates how increased taxon sampling can improve a data set by improving character conceptualization and knowledge of the range of variation. Moreover, the 20 characters were not ambiguous due to poor homology assessment, but because they were no longer discrete (SEA, p. 543). Though we do not presume to judge the character selection methodology employed by Carine and Scotland (2002) and Moylan et al. (unpublished), it is worth note that a growing body of work has been directed at utilizing quantitative and continuous data in phylogeny reconstruction (Swiderski et al., 1998; Polly, 2001; Wiens, 2001; MacLeod and Forey, 2002; Polly, 2003a, 2003b). A priori dismissal of these characters ignores their potential as phylogenetically informative data and artificially reduces the scope of variation that morphological data can
offer to systematics. This example furthermore serves as a caution to all researchers to be careful in character selection and conjectures of primary homology (Rieppel and Kearney, 2002), as well as taxon sampling (Hillis, 1998).

Closing Points

But morphology is a much more complex subject than it at first appears (Darwin, 1872:584).

Charles Darwin wrote these words in reference to a paper by the eminent zoologist E. Ray Lankester, in which several important terms in evolutionary biology were coined, including the still-used homoplasy and homoplastic (Lankester, 1870:39). Lankester distinguished homoplastic structures from homogenous structures by defining homology in terms of reference to a common ancestor (Lankester, 1870:36), whereas homoplasy would comprise “all cases of close resemblance of form which are not traceable to homogeneity, all details of agreement not homogenous, in structures which are broadly homogenous, as well as in structures having no genetic affinity” (Lankester, 1870:41). It was in this way that Lankester parsed out homoplasy from a broader set of “cases which have all been equally ranked by naturalists as homologous” (Darwin, 1872:584) and made substantially clearer the primacy of common ancestry in characterizing homology.

In the years since Darwin’s and Lankester’s statements even more progress has been made to this end, and a methodologically rigorous framework now exists in systematics that allows homology and homoplasy to be distinguished from each other in a relatively clear and scientifically testable manner. We view Darwin’s lament of morphology’s complexity not as a cry of despair, but as a source of elation, an intrinsic benefit of morphology and a spur to action and continued research. It is precisely the complexity of morphology that allows us to dissect underlying patterns of relationship, which is in part why we take particular issue with SEA’s (p. 545) final claim that: “One reason why morphology is being superseded by DNA data for phylogenetic studies is because much of the useful morphological diversity has already been scrutinized.” Even a cursory review of many current morphological- and phylogenetic-based research programs and journals would reveal that a great deal of the useful morphological diversity of the earth’s biota, present and past, has not been scrutinized. To deny this, and instead make the blanket statement implied by SEA that we are “all out of morphology,” would be to deny the impact of new specimens (recent and fossil), new methods and technology (CT scanning, electron microscopy, histological methods, staining/preparation methods), and, perhaps most importantly, the impact of new researchers.

In their paper, SEA attempted to “explore the paradox of why morphological data are currently utilized less for phylogeny reconstruction than are DNA sequence data, whereas most of what we know about phylogeny stems from classifications founded on morphological data” (p. 539). SEA argue that the current prevalence of molecular studies is due to inherent problems in the analysis of morphological data. In contrast, we view this shift as a logical step towards utilizing and exploring the historically untapped phylogenetic information content of molecular data. However, it is worrisome if this shift is done at the expense and dismissal of further morphological scrutiny and revision (Hillis and Wiens, 2000).

We agree with SEA (pp. 545, 542) that a goal of current phylogenetic analyses of morphological data should be more “rigorous and critical anatomical studies” of morphological characters, as well as “explicit criteria for character selection” (see also Rieppel and Kearney, 2002; Poe and Wiens, 2000). However, we do not find relegating morphology to a subservient position is the means to achieve this. We maintain that the majority of phylogenetically informative morphological diversity has not been scrutinized, in addition to pointing out that a great deal of morphological diversity needs to be rescrutinized. Many thorough, critical, and novel phylogenetic studies of morphological data await and will be crucial in reconstructing the phylogeny of the earth’s biota.

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