Schwarz, G. 1978. Estimating the dimension of a model. Ann. Stat. 6:461–465.
Semple, C., and M. Steel. 2003. Phylogenetics. Oxford University Press, Oxford.
Sober, E. 1988. Reconstructing the past—Parsimony, evolution, and inference. MIT Press, Cambridge, Massachusetts.
Sober, E. 2002. Reconstructing ancestral character states—A likelihood perspective on cladistic parsimony. The Monist 85:156–176.
Steel, M., and D. Penny. 2000. Parsimony, likelihood, and the role of models in molecular phylogenetics. Mol. Biol. Evol. 17:839–850.
Steel, M., and D. Penny. 2004. Two further links between *MP* and *ML* under the poisson model. Appl. Math. Lett. in press.
Swofford, D., G. Olsen, P. Paddell, and D. Hills. 1996. Phylogenetic inference. Pages 407–514 *in* Molecular systematics (D. Hillis, C. Moritz, and B. Mable, eds.). Sinauer, Sunderland, Massachusetts.
Tuffley, C., and Steel M. 1997. Links between maximum likelihood and maximum parsimony under a simple model of site substitution. Bull. Math. Biol. 59:581–607.

First submitted 29 July 2003; revisions returned 17 November 2003; final acceptance 4 January 2004
Associate Editor: Mike Steel

Syst. Biol. 53(4):653–661, 2004

ISSN: 1063-5157 print / 1076-836X online
DOI: 10.1080/10635150490472959

The Role of Morphological Data in Phylogeny Reconstruction

JOHN J. WIENS

Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794-5245, USA; E-mail: wiensj@life.bio.sunysb.edu

We live in the age of comparative genomics, and it may seem that there is not much point in reconstructing phylogenies using morphological data anymore. As more and more genes and genomes are being sequenced, the possibility that thousands or even millions of informative, independently evolving molecular characters can be brought to bear on a given phylogenetic problem is quickly becoming a reality (e.g., Rokas et al., 2003). Given the rate that new sequence data are being added, and the rate at which new innovations continue to accelerate this process, it seems possible that in the not-too-distant future we will be able to have a perfectly accurate and well-supported phylogeny of most living species on earth using molecular data alone. So why bother with morphology?

A recent paper by Scotland et al. (2003; SEA hereafter) offered a reappraisal of the role of morphology in phylogeny reconstruction. This is certainly an important and timely topic to discuss, and their main thesis is bold and controversial. They state that "We view any attempt to include more morphological data in phylogeny reconstruction as inherently problematic" (p. 545). Unfortunately, most of their arguments are based on unsupported speculation, and they fail to mention numerous studies that clearly contradict their conclusions. Given that many of their comments are written as responses to book chapters written by my collaborators and myself (e.g., Hillis and Wiens, 2000; Poe and Wiens, 2000; Wiens, 2000a), I feel obligated to elucidate some of these problems. Many of the issues raised are central to how systematics is done and will be conducted in the future. I will argue that, despite many undeniable advantages of molecular data, it is still absolutely necessary that we continue to collect additional morphological data for phylogenetic analysis, and continue to improve our methods for morphology-based phylogenetics. Note that Jenner (2004) has provided an independent rebuttal of the SEA paper, and he describes a large number of substantive criticisms which show only limited overlap with my own.

WHY WE STILL NEED TO COLLECT MORE MORPHOLOGICAL DATA

The Future

There are many reasons to continue to do morphological phylogenetics. But given the incredible rate of advances in molecular systematics, it may be useful to divide these reasons into those pertaining to the present and future. Those pertaining to the future may actually be the most relevant, because many present-day limitations of molecular phylogenetics seem likely to be overcome very soon. I will focus on the putative future first, and then deal with present-day issues.

The most compelling reason to continue to collect morphological data long into the future is to resolve the phylogenetic relationships of fossil taxa and their relationships to living taxa (e.g., Maddison, 1996; Hillis and Wiens, 2000; Jenner, 2004). The reconstructed Tree of Life must include fossil taxa. Considering all the species that have ever evolved, most are now extinct (>99% according to some estimates; Novacek and Wheeler, 1992), and many extinct groups were diverse, ecologically important, and very distinct from their closest living relatives. For now and the immediate future, the relationships of most fossil taxa can only be determined through phylogenetic analysis of morphological data (despite impressive molecular studies of very recent fossil taxa). Contrary to what SEA imply (p. 543), fossils are not merely important for their potential to help resolve relationships of living taxa, and Hillis and Wiens (2000) did not advocate thorough taxon sampling solely because of its potential benefits for phylogeny estimation.

Our understanding of the rate and timing of macroevolutionary processes in both living and fossil taxa also

requires phylogenetic information from fossils. Although methods are available that allow divergence dates for living taxa to be estimated with molecular data (e.g., Sanderson, 1997, 2002; Yoder and Yang, 2000; Thorne and Kishino, 2002), they still require external calibration. That calibration usually comes from fossil evidence, which requires correctly assigning fossils to groups of living taxa. Because older fossils are rarely identical or conspecific with living species, we cannot simply assign fossils to living groups based on overall similarity. We need to estimate a phylogeny for the fossil and living taxa, and this can only be done using morphological data.

Perhaps most importantly, given that the earth's biota has changed dramatically and repeatedly through time, understanding how the modern world became the way that it is requires studying fossils. When we look at a fossil the first thing we need to know is "what is it?," which really means "to what clade does it belong?" Again, this is a question that is best answered through phylogenetic analysis. Understanding evolutionary processes (e.g., character evolution) in fossil taxa also requires knowledge of their phylogenetic relationships, just as in living taxa (e.g., Gatesy and Dial, 1996).

SEA do mention fossils (p. 543), but mostly in the context of how their inclusion affects estimated relationships among living species. They question whether addition of fossil taxa can improve accuracy for phylogenetic studies focusing on living taxa, based on three points: (1) their belief that studies showing improved accuracy from increased taxon sampling used only large (>1000) numbers of characters, (2) a single example from seed plant phylogeny, and (3) the problem of missing data.

SEA question the benefits of increased taxon sampling in morphological studies, stating "less clear is the role of dense taxon sampling when there are fewer characters, as in morphological studies" (p. 542). Yet, contrary to what SEA imply, simulation studies have confirmed the benefits of increased taxon sampling for phylogenetic accuracy even when the number of characters is limited (e.g., 100 characters, Huelsenbeck, 1991 [cited but not mentioned by SEA]; Wiens, 1998b).

SEA also question the benefits of including fossil taxa for phylogenetic accuracy, based on a single example involving conflicts between morphological and molecular data in angiosperms (p. 543). The obvious counterexample (cited but not mentioned by SEA) is the morphological study of amniote relationships by Gauthier et al. (1988), in which lepidosaurs (tuataras, lizards, and snakes) are placed as basal within amniotes if certain fossil taxa are excluded. Numerous molecular studies confirm the traditional morphological hypothesis, showing that lepidosaurs are not basal (Meyer and Zardoya, 2003). Thus, the addition of fossil taxa seems to increase congruence between the molecular and morphological results in this case, suggesting that addition of fossil taxa is important for phylogenetic accuracy.

Finally, SEA suggest that the accuracy of phylogenetic analyses that include fossil taxa is limited by their "large amounts of missing data" (p. 543). Recent simulation studies suggest that the *amount* or proportion of missing data in incomplete taxa may be irrelevant to their accurate placement (i.e., taxa that are 90% incomplete with nearly 2,000 missing data cells each can be placed with perfect accuracy on a phylogeny; Wiens, 2003a), although a high *proportion* of missing data may limit their ability to change relationships among more complete taxa (Wiens, 2003b).

The Present

I have assumed a future in which the relationships of every living species are well established using molecular data. Although such a future seems likely (especially if rates of genome sequencing and species extinction both continue to accelerate), we are clearly not there yet. Given this, there are a number of compelling reasons to continue to reconstruct phylogenies using morphological data.

First, there are many taxa that are extant but may still be very difficult to include in molecular studies. For example, many reptile and amphibian species are known from a limited number of specimens, are preserved so as to make obtaining molecular data very difficult (i.e., formalin fixation), and may never be collected again (i.e., because of limited distributions, habitat destruction, and other factors). Given present technology, the only way that we may know anything about the relationships of these species is through phylogenetic analysis of morphology. A similar situation may exist in other taxa as well (e.g., insects and plants; Wilson, 1992; Donoghue and Alverson, 2000), and many species remain known from a single specimen that was collected decades ago. Nevertheless, such problems may be largely absent in other groups of organisms, and the technological barriers that presently limit obtaining significant DNA sequence data from some types of preserved specimens may soon be broken.

Second, until we reach the stage where all molecular phylogenies are reconstructed without error, it is still important to have rigorous, morphology-based phylogenies as a "reality check" for molecular results (e.g., Doyle, 1992; Hillis and Wiens, 2000; Jenner, 2004). There are many factors that may cause molecular analyses to reconstruct clades that are both incorrect and statistically well-supported, a possibility not considered by SEA. These factors include long-branch attraction (e.g., Felsenstein, 1978; Huelsenbeck, 1997), deviations between gene and species trees (e.g., Doyle, 1992; Maddison, 1997), and more mundane problems such as contamination and misidentification of specimens. Comparing molecular results to rigorous morphology-based phylogenies can help prevent us from being misled in these cases.

A real-world example illustrates this idea. Sites et al. (1996) presented a phylogeny for iguanid lizards based on mtDNA sequences from the ND4 gene, which conflicted with a tree based on morphology (de Queiroz, 1987). An important source of incongruence was the position of *Cyclura*. ND4 data placed *Cyclura* near the

base of the iguanid tree, whereas de Queiroz's data tentatively placed *Cyclura* with *Iguana*. A subsequent morphological study, using many additional characters, showed strong support for the *Cyclura* + *Iguana* clade (Hollingsworth, 1998). Analyses based on two additional mtDNA data sets gave conflicting results, with cytochrome *b* supporting the ND4 tree (Petren and Case, 1997), and ribosomal sequences (12S, 16S) supporting the *Cyclura* + *Iguana* clade (with *Sauromalus* potentially included as well; Rassmann, 1997). Further analysis and parametric simulations (Wiens and Hollingsworth, 2000) showed that the basal placement of *Cyclura* was likely an artifact of long-branch attraction in these two fast-evolving protein-coding genes, associated with an accelerated rate of change in these genes in *Cyclura* (a seemingly widespread problem in cytochrome *b* at higher levels of divergence; Meyer, 1994). There are several interesting lessons from this study: (1) the misleading results were concordant between two molecular data sets, and the combined analyses of all three molecular data sets was misled by long-branch attraction; (2) long-branch attraction can be problematic even in well-sampled groups of closely-related species, and use of maximum likelihood and multiple genes does not necessarily ensure estimating the correct topology under these conditions, and (3) analysis of the molecular data alone would seemingly have led to the wrong phylogenetic placement of *Cyclura*, and the problem was detected primarily because of discordance with a thorough phylogenetic analysis of the morphology.

Of course, problems in individual molecular data sets can also be detected by comparison to other, independently evolving molecular data sets. But there may be cases where all molecular data sets may give the wrong answer (e.g., sequencing a misidentified specimen for many different genes). Furthermore, a typical set of morphological characters should draw on information from many different unlinked genes (Doyle, 1992; Hillis and Wiens, 2000), whereas the characters in a given molecular data set are often linked and inherited as a single unit (i.e., nucleotide positions in a single gene).

Finally, it is important to note that we are very far from describing all the living species on earth, much less sequencing them. This issue is somewhat distinct from that of using morphology to build trees (the sole focus of the SEA paper, and most other morphology vs. molecules reviews), but is closely related and critically important (Maddison, 1996). Conservative estimates are that ~1.5 million species have been described and 5 to 10 million more await description (e.g., Wilson, 1992; May, 2000). With some exceptions, new species are generally discovered, delimited, and described using morphological data. Although species delimitation using morphological data is typically based on diagnostic characters rather than phylogenetic analysis, it can be, and perhaps should be, tree based (Baum and Donoghue, 1995; Wiens and Penkrot, 2002). In fact, the best methodology for delimiting species using morphological data remains entirely unresolved, and these different methods can give very different species limits for the same morphological data (Wiens and Penkrot, 2002). In the context of morphology-based taxonomy, phylogenetic analysis of morphological data is also critical for placing new species within a higher taxon, given the obvious shortcomings of using overall morphological similarity to classify species (e.g., Wiley, 1981).

Despite the many advantages of molecular data, it is absolutely critical that systematists continue to be trained in morphological systematics as well, particularly for poorly known groups (Hillis and Wiens, 2000). If students are trained exclusively in molecular techniques, the next generation of systematists may be incapable of identifying the species in their study groups, and phylogenetic progress in these groups may quickly "grind" to a halt. Quick and accurate identification of species in the field and laboratory based on morphological characters also is critical to many other areas of biology besides systematics (e.g., ecology, behavior, physiology; Maddison, 1996).

Why the SEA Approach is Problematic

The main thesis of the SEA paper is that morphological data are so intrinsically problematic that they should not be used to reconstruct phylogenies. Instead, SEA argue that "unambiguous" morphological characters should be merely mapped onto phylogenies established by molecular data to determine if they add further support to specific nodes. This approach will not succeed. The most unassailable advantage of morphological data is that it allows us to address the phylogeny of fossil taxa and their relationships to living taxa. Yet, their approach will not allow us to address the position of fossil taxa for which molecular data cannot be obtained (i.e., almost all of them). Similarly, the phylogenetic placement of any extant taxa known only from morphological data will remain unresolved. Further, morphological data will not provide rigorous independent corroboration for trees based on molecular data, because no new morphology-based trees will be reconstructed. In fact, it is unclear what meaningful purpose morphological data would serve under their approach.

The SEA approach assumes that, for a given analysis, having more morphological characters is not necessarily better. Their reasoning is basically as follows. (1) Our premolecular knowledge of phylogeny comes mostly from morphological classifications, not morphological phylogenetics. (2) The researchers who built these classifications found the best characters. (3) Any additional characters are likely to be problematic in terms of homology assessment and character coding. (4) Even though adding characters generally increases accuracy in simulation studies, adding characters in morphological phylogenetics will not, because the problematic nature of these characters (e.g., missing data, polymorphism, continuous variation, uncertain homology assessment) will outweigh their potential benefits. SEA are wrong about each of these points.

Morphology-Based Classification = Morphology-Based Phylogeny

Fundamental to the SEA approach is the assumption that prephylogenetic morphology-based classifications are largely equivalent to modern morphology-based phylogeny estimates, and make phylogenetic studies of morphology unnecessary. They (p. 543) took exception to my statement (Wiens, 2000a) that most of our knowledge of the Tree of Life is based on phylogenetic studies of morphological data. They claimed that most of our knowledge of phylogeny is based on classifications instead, but without any supporting evidence or citations. My statement was based largely on the observation that, in the 1980s and early 1990s, researchers undertook morphology-based phylogenetic analyses of many of the major groups of multi-cellular organisms, including plants (e.g., Mishler and Churchill, 1985; Doyle and Donoghue, 1986), animals (Brusca and Brusca, 1990), arthropods (Kristensen, 1981, 1991; Shultz, 1990), fish (Lauder and Liem, 1983), amphibians (Duellman and Trueb, 1986; Trueb and Cloutier, 1991), amniotes (Gauthier et al., 1988), mammals (Novacek, 1986), turtles (Gaffney and Meylan, 1988), birds (Cracraft, 1988), and squamates (Estes et al., 1988). These morphological studies, and many others at similar or lower taxonomic levels, revealed that many traditionally recognized higher-taxa are not monophyletic (e.g., Class Pisces, Class Reptilia). These studies also supported the monophyly of many traditionally recognized taxa. The important point is that the classifications of these major groups were tested with phylogenetic analyses of morphology, long before the current explosion of DNA sequence studies. Contrary to what SEA assert, not all classifications were handed down untested from pre-Hennigian days.

Adding Morphological Characters: All the Good Ones Are Taken

SEA claim (p. 541) that "...there are few characters that seem to be uncontroversial in relation to homology assessment. These characters typically are identified in traditional classifications and are the first characters to be included in a phylogenetic data set. Increasing the number of characters increases the level of ambiguous or problematic characters." There is no support for this claim. SEA do cite their own graphs showing the relationship between problematic homology assessment, problematic character coding, and number of characters (their Fig. 1). But these graphs lack any supporting data, and instead merely represent the unsupported opinion of the authors (see also Jenner, 2004). There is no a priori reason to assume that previous workers exhausted all the potentially useful characters. In fact, it may be more logical to assume that traditional workers primarily reported characters that supported their favored hypothesis, and not ones that they considered to be unimportant or misleading. My own experience in morphological phylogenetics (e.g., Wiens, 1993a, 1993b; Reeder and Wiens, 1996; Wiens and Reeder, 1997; Wiens and Penkrot, 2002; Stephens and Wiens, 2003; Wiens and Etheridge, 2003; Wiens et al., 2003) suggests that traditional workers did not report all of the potentially informative morphological characters, and they tended not to synthesize many different types of morphological characters in a single study. Thus, character lists in my own studies often credit many previous authors (but rarely a single author or set of authors) and contain characters not used by any of them. Furthermore, many types of morphological data may not have been

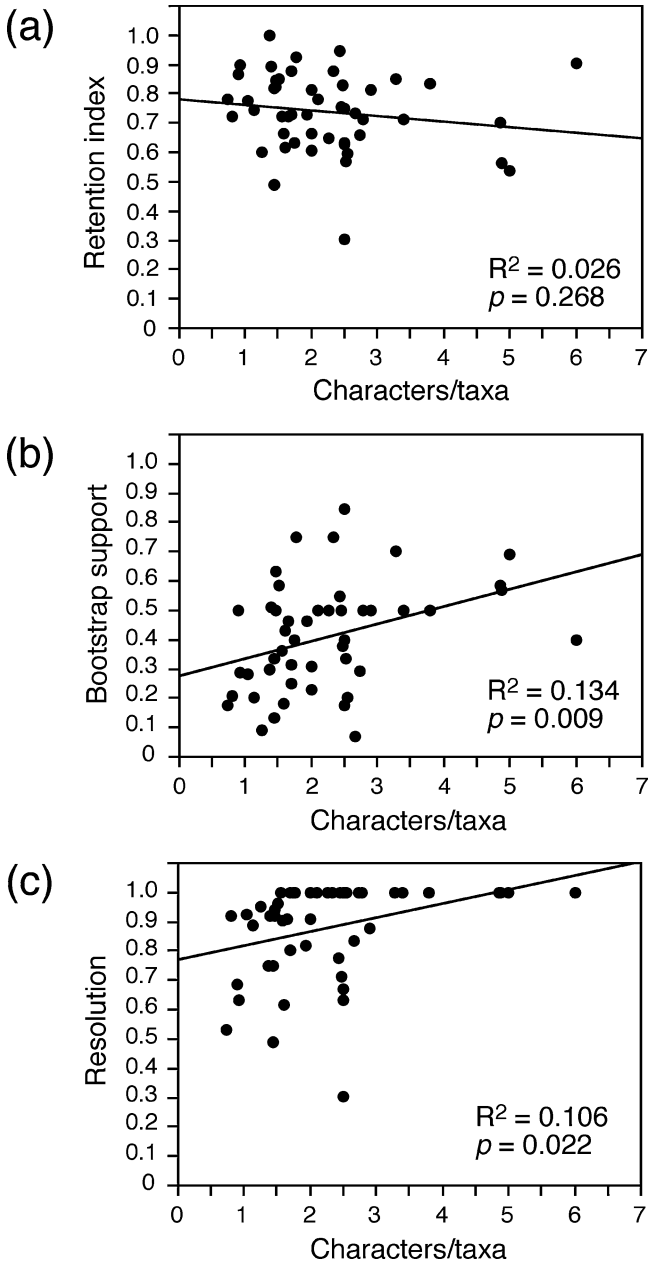

FIGURE 1. Relationships between levels of character sampling (number of characters/taxa) and (a) homoplasy (increasing values of the retention index indicate lower levels of homoplasy), (b) bootstrap support (proportion of clades with bootstrap values >50%), and (c) resolution (proportion of clades resolved in a strict consensus of the shortest trees), based on analyses of 49 morphological data sets for green plants (from data summarized in Sanderson and Donoghue, 1996).

available in older studies (e.g., characters from scanning electron microscopy).

Adding "Problematic" Types of Morphological Characters Will Not Increase Phylogenetic Accuracy

SEA assume that traditional researchers found the best morphological characters, and that characters added subsequently will not increase accuracy because they are somehow problematic or ambiguous. Nonetheless, SEA report the claim made by Poe and Wiens (2000) that there is no justification for excluding characters because of variation within terminal taxa, continuous and quantitative variation, unknown polarity, and assumed levels of homoplasy. SEA disagree with this claim.

What is fundamentally different between the views of SEA and Poe and Wiens (2000)? Clearly, SEA think that adding "ambiguous" characters will not increase phylogenetic accuracy, whereas Poe and Wiens (2000) think that they will. So who is right? In fact, SEA have no support for their statement; their single empirical example (see below) is entirely lacking data on the number of "ambiguous" characters. In contrast, the assertions of Poe and Wiens (2000) were based explicitly on numerous statistical, simulation, and congruence studies that showed that these types of so-called ambiguous characters do contain useful phylogenetic information (i.e., continuous and quantitative variation [Thiele, 1993, see also Wiens, 2001], polymorphic characters [Wiens, 1995, 1998a, 1998b, 1999, 2000b; Wiens and Servedio, 1997, 1998], characters with missing data [Wiens, 1998c]). Furthermore, many of these studies specifically addressed the question of whether accuracy was increased more by excluding these problematic characters or including them (Wiens and Servedio, 1997; Wiens, 1998a, 1998b, 1998c). The results showed that accuracy was increased more by including these problematic characters than excluding them. In other words, the benefits of increasing the number of characters outweighed the potential costs of including so-called problematic characters. Remarkably, SEA failed to mention any of these results, although they are discussed extensively in the paper by Poe and Wiens (2000) which they quote.

A Single Example Shows That More Characters will Not Increase Accuracy

SEA (p. 542) discuss an example which they believe shows that increasing the number of morphological characters does not increase phylogenetic accuracy. They compare four studies of seed plant phylogeny (Crane, 1985; Doyle and Donoghue, 1986; Nixon et al., 1994; Doyle, 1996). They claim that despite the generally increasing number of characters in these four studies over time (38, 62 103, 91, respectively) "all analyses lacked bootstrap support >50%" (p. 542). In fact, this claim is false. In the first three studies the authors performed no bootstrap analyses at all. Equating "no bootstrap analysis" with "lacking bootstrap support >50%" is rather misleading, to say the least. In the fourth study (Doyle, 1996), the author did perform bootstrap analysis, but contrary to the claim of SEA, 15 nodes have bootstrap support >50%, with 5 nodes >90% (Doyle's Fig. 5). Even if their claims were true (i.e., if they performed new bootstrap analyses of three of these data sets or if they intended something different by "all analyses lacked bootstrap support >50%"), SEA made no attempt to make these studies comparable in terms of number of taxa, incompleteness of fossil taxa, or other parameters. Finally, SEA provide no evidence to support their interpretation that the increasing number of characters failed to yield "better" results specifically because more "problematic" characters were being added.

Even if SEA were right about every aspect of their example, a single example does not make a compelling case. Stacked against it are the many statistical, simulation, and congruence studies cited by Poe and Wiens (2000), which show the benefits of including more characters (even so-called problematic ones) in morphological phylogenetic studies. Furthermore, the previously mentioned studies of iguanid lizard phylogeny provide an interesting counterexample to that of SEA. de Queiroz (1987) generated a phylogeny of iguanid genera using ~95 morphological characters. His matrix was reanalyzed by Sites et al. (1996). When they reduced de Queiroz's matrix to the same taxa as their ND4 data (leaving ~58 parsimony-informative morphological characters), they found no support for placing *Iguana* with *Cyclura*. Hollingsworth (1998) increased the overall number of morphological characters to 142. Many of the added characters were polymorphic, a type of character considered "problematic" by SEA. Hollingsworth found the same generic-level phylogeny as de Queiroz, but resolved two polytomies in de Queiroz's tree. Reducing Hollingsworth's data set to (essentially) the same set of taxa analyzed by Sites et al. (1996) yields 84 parsimony-informative characters and very strong bootstrap support (95%) for the *Iguana* + *Cyclura* clade (Wiens and Hollingsworth, 2000). This example suggests that when the number of taxa is made comparable, increasing the number of morphological characters can increase resolution and bootstrap support, even if many of the added morphological characters are of types considered to be problematic by SEA.

TESTING THE ASSUMPTIONS OF THE SEA APPROACH

A key assumption of the SEA approach is that "increasing the number of characters increases the level of ambiguous or problematic characters" (p. 541). SEA provided no empirical or theoretical evidence to support this claim. Yet, this claim makes implicit predictions that can be readily tested. If increased numbers of morphological characters only lead to greater homoplasy and decreased accuracy, then phylogenetic analyses based on larger numbers of characters (relative to the number of taxa) should presumably show higher levels of homoplasy, lower levels of resolution, and lower levels of support (e.g., bootstrapping) than studies of morphologically similar organisms based on fewer characters.

Even a crude analysis shows that none of these predictions are supported. Sanderson and Donoghue (1996) summarized levels of homoplasy, resolution, and bootstrap support for 50 morphological data sets for green plants (i.e., organisms with comparable morphology), along with the number of taxa and characters for each data set. I performed simple regression analyses of the relationship between the character/taxon ratio and levels of homoplasy (retention index), resolution (proportion of resolved nodes in a strict consensus of the shortest trees from a parsimony analysis), and branch support (proportion of clades with bootstrap support >50%) for each data set (see Sanderson and Donoghue [1996] for details of how these measures were obtained). Given that "increasing the number of characters" presumably means that the number of taxa is held constant, I used the character/taxon ratio instead of the number of characters alone (and following SEA p. 540). One data set was a clear outlier in terms of the character/taxon ratio and was removed. The results (Fig. 1) do not support the claims of SEA. There is no significant relationship between the number of characters and levels of homoplasy, but there is a significant positive relationship between the relative number of characters and levels of resolution and bootstrap support. In many ways, these results are hardly surprising, and there are many problematic aspects to the analyses (e.g., studies of different groups are not directly comparable, autapomorphies were not removed, resolution and bootstrap support are related to accuracy but not strictly equivalent). However, the assumptions of SEA clearly are not supported, and they have provided no similar test or supporting data themselves.

A more fundamental assumption that is implicit in the SEA paper is the idea that morphological data are much more homoplasious than molecular data. If morphological data were found to have lesser or similar levels of homoplasy to DNA sequence data, then their claims for greater problems of homology assessment in morphological data would be refuted, or at least rendered irrelevant. This issue has been addressed in empirical surveys of independent phylogenetic analyses of molecular and morphological data (e.g., Sanderson and Donoghue, 1989, 1996; Givnish and Sytsma, 1997). The most recent studies show that morphological data may be (on average) slightly less homoplasious than DNA sequence data (Sanderson and Donoghue, 1996; based on the retention index in their Table 2) or slightly more (Givnish and Sytsma, 1997; based on the consistency index, their Fig. 2). Obviously, these studies do not support the assumption that morphological data show much greater levels of homoplasy than DNA sequence data (although this can depend on which genome, gene, or nucleotide position is being considered). Yet, these studies provide a somewhat indirect comparison because levels of homoplasy in different characters in different groups of organisms are typically being compared.

The strongest evidence that one type of data is more homoplasious than the other would come from comparing levels of homoplasy in morphological and molecular data sets obtained for the same taxa. Baker et al. (1998) found that the consistency index of morphological data was higher than that of molecular data in 26 of 31 studies with matched molecular/morphological taxon sampling, indicating lower levels of homoplasy in the morphological data. A paired sign test shows that this difference is highly significant ($P = 0.0002$). Thus, the empirical results that are most directly relevant to this issue strongly reject the fundamental assumption of the SEA approach (that morphological data are more homoplasious than molecular data), and show that the opposite pattern is actually more common.

Integrating Molecular and Morphological Data

SEA suggest that the best approach for integrating molecular and morphological data is to map a limited number of "unambiguous" morphological characters onto the molecular phylogeny. Yet it is unclear what this approach really tells us about the veracity of the molecular or morphological results. The typical outcome of this exercise seems easy to predict; some morphological characters will be concordant with the molecular tree and some will not (e.g., Fig. 2 of SEA). This is what we might also expect from mapping morphological characters onto a morphological tree, or molecular characters onto a molecular tree (i.e., some characters will be homoplastic, some will not). Without a relevant null hypothesis and an associated statistical test, their character mapping approach seems pointless.

A better approach to integrating molecular and morphological data may be to (1) perform separate analyses to identify areas of strongly supported incongruence between data sets (i.e., areas where combined analysis might be expected to fail; de Queiroz et al., 1995; Huelsenbeck et al., 1996); (2) perform a combined analysis; and (3) consider regions of the comined-data tree that are strongly contested by different data sets to be ambiguously resolved until the source of error is identified, or (if the source is unknown) a majority of independent data sets clearly supports one hypothesis over another. This approach may be advantageous relative to unilateral separate or combined analysis, or even relative to those approaches that focus on testing for overall congruence between data sets to decide whether they are generally "combinable" or not (e.g., Bull et al., 1993; Farris et al., 1995). The reason is simple. For any phylogenetic problem with more than four taxa, trees from different data sets may contain a mixture of concordant, weakly discordant, and strongly discordant clades. Thus, combined analysis and separate analysis may each be favored in different parts of the same tree, almost guaranteeing that both approaches will be suboptimal in some part of the tree if applied globally to a complex phylogeny (Wiens, 1998d). The approach outlined above (see Wiens and Reeder, 1997; Wiens, 1998d) utilizes the results from combined analysis in those parts of the tree where combined analysis should succeed (i.e., no or weakly supported incongruence) and should treat the combined-data results as ambiguous in those sections of the tree

where combined analysis might be expected to fail (i.e., strongly supported incongruence).

SEA state that they consider combined analysis as "another possible solution" (p. 545). However, none of the approaches that they advocate allows for trees to be reconstructed from the morphological data alone. Thus, there is no opportunity for morphological data to help identify potential problems in the molecular results or to provide real corroboration for molecular phylogenies in the form of a rigorous independent phylogenetic analysis.

Improving Morphological Phylogenetics

The main premise underlying the SEA paper is that morphological phylogenetics is so problematic that trees should no longer be reconstructed using morphological data. Although I would readily agree that there are serious problems in the current practice of morphological phylogenetics, we are not as helpless in the face of these problems as suggested by SEA. For example, many of the ambiguities in character analysis that they lament (p. 541) may be solved by simply treating morphological characters as continuous quantitative traits (Felsenstein, 1988; Wiens, 2001). Furthermore, several approaches can be used to address the accuracy of different methods for selecting, coding, and analyzing morphological characters, including simulations and congruence studies (i.e., comparing how well different methods of analyzing morphological data recover clades that are strongly supported by independent, nonmorphological data sets; Wiens 1998a). My own work on methods for coding polymorphic morphological characters suggests that these different approaches for testing phylogenetic accuracy can give highly concordant results (Wiens, 1999, 2000b). I think that the 21st century should be an exciting time for morphological phylogenetics as well as molecular phylogenetics, as new methods for collecting and analyzing morphological data are developed (e.g., high-resolution computed tomography scanning; Rowe et al., 1997; new likelihood/Bayesian methods for morphological data; Lewis, 2001) and the performance of morphology-based methods can be more readily tested using the wealth of new molecular data. In contrast, SEA basically advocate giving up on using morphological data to reconstruct phylogenies.

Conclusions

The wealth of new molecular data raises the question: what should be the role of morphological data in phylogeny reconstruction? SEA have suggested that morphological data should not be used to build trees and new morphological data should not be included in phylogeny reconstruction. I have argued that their approach is built on a series of mistaken premises, and is bound to fail. Most importantly, their approach ignores fossil taxa, and they do not consider the importance of morphology in comprehensive sampling of living taxa, in alpha taxonomy, and in identifying problematic molecular results. Although there are many areas where morphological phylogenetics can be improved, the best solution to these problems is not to simply give up on using morphological data to build trees. Instead, many of these problems may be solved through more explicit methodology, development and application of new methods, and rigorous testing of these methods using simulations and congruence studies.

Acknowledgments

For many helpful comments on the manuscript, I thank Tim Collins, Alan de Queiroz, Michael Donoghue, Tag Engstrom, R. Geeta, Lucinda McDade, Steve Poe, Chris Simon, Patrick Stephens, Dan Stoebel, and Chris Wolfe. My research was supported by NSF grant DEB-0129142.

References

Baker, R. H., X. Yu, and R. DeSalle. 1998. Assessing the relative contribution of molecular and morphological characters in simultaneous analysis trees. Mol. Phylogenet. Evol. 9:427–436.

Baum, D. A., and M. J. Donoghue. 1995. Choosing among alternative "phylogenetic" species concepts. Syst. Bot. 20:560–573.

Brusca, R. C., and G. J. Brusca. 1990. Invertebrates. Sinauer Associates, Inc., Sunderland, Massachusetts.

Cracraft, J. 1988. The major clades of birds. Pages 333–355 *in* The phylogeny and classification of the tetrapods (M. J. Benton, ed.). Systematics Assoc. Special Vol. No. 35A, Clarendon Press, Oxford, United Kingdom.

Crane, P. R. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. Ann. Mo. Bot. Gard. 72:716–793.

de Queiroz, K. 1987. Phylogenetic systematics of iguanine lizards. A comparative osteological study. Univ. Calif. Publ. Zool. 118:1–203.

de Queiroz, A., M. J. Donoghue, and J. Kim. 1995. Separate versus combined analysis of phylogenetic evidence. Annu. Rev. Ecol. Syst. 26:657–681.

Donoghue, M. J., and W. S. Alverson. 2000. A new age of discovery. Ann. Missouri Bot. Gard. 87:110-126.

Doyle, J. A. 1996. Seed plant phylogeny and the relationships of Gnetales. Int. J. Plant Sci. 157 (suppl.):S3–S39.

Doyle, J. A., and M. J. Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. Bot. Rev. 52:321–431.

Doyle, J. J. 1992. Gene trees and species trees: Molecular systematics as one-character taxonomy. Syst. Bot. 17:144–163.

Duellman, W. E., and L. Trueb. 1986. Biology of amphibians. Johns Hopkins University Press, Baltimore.

Estes, R., K. de Queiroz, and J. A. Gauthier. 1988. Phylogenetic relationships within Squamata. Pages 119–281 *in* Phylogenetic relationships of the lizard families (R. Estes and G. K. Pregill, eds.). Stanford University Press, Stanford, California.

Farris, J. S., M. Kallersjo, A. G. Kluge, and C. Bult. 1995. Testing significance of incongruence. Cladistics 10:315–319.

Felsenstein, J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. Syst. Zool. 27:401–410.

Felsenstein, J. 1988. Phylogenies and quantitative characters. Ann. Rev. Ecol. Syst. 19:445–471.

Gaffney, E. S., and P. A. Meylan. 1988. A phylogeny of turtles. Pages 157–219 *in* The phylogeny and classification of the tetrapods, Vol. 1 (M. J. Benton, ed.). Clarendon Press, Oxford.

Gatesy, S. M., and K. P. Dial. 1996. Locomotor modules and the evolution of avian flight. Evolution 50:331–340.

Gauthier, J., A. G. Kluge, and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. Cladistics 4:105–209.

Givnish, T. J., and K. J. Sytsma. 1997. Homoplasy in molecular and morphological data: The likelihood of correct phylogenetic inference. Pages 55–101 *in* Molecular evolution and adaptive radiation (T. J. Givnish and K. J. Sytsma, eds.). Cambridge University Press, New York.

Hillis, D. M., and J. J. Wiens. 2000. Molecules versus morphology in systematics: Conflicts, artifacts, and misconceptions. Pages 1–19 *in*

Phylogenetic analysis of morphological data (J. J. Wiens, ed.). Smithsonian Institution Press, Washington, DC.
Hollingsworth, B. D. 1998. The systematics of chuckwallas (*Sauromalus*) with a phylogenetic analysis of other iguanid lizards. Herpetol. Monogr. 12:38–191.
Huelsenbeck, J. P. 1991. When are fossils better than extant taxa in phylogenetic analysis? Syst. Zool. 40:458–469.
Huelsenbeck, J. P. 1997. Is the Felsenstein Zone a fly trap? Syst. Biol. 46:69–74.
Huelsenbeck, J. P., J. J. Bull, and C. W. Cunningham. 1996. Combining data in phylogenetic analysis. Trends Ecol. Evol. 11:152–158.
Jenner, R. A. 2004. Accepting partnership by submission? Morphological phylogenetics in a molecular millennium. Syst. Biol. 53:333–342.
Kristensen, N. P. 1981. Phylogeny of insect orders. Annu. Rev. Entomol. 26:135–157.
Kristensen, N. P. 1991. Phylogeny of extant hexapods. Pages 125–140 *in* The insects of Australia. Cornell University Press, Ithaca, New York.
Lauder, G. V., and K. F. Liem. 1983. The evolution and interrelationships of actinopterygian fishes. Bull. Mus. Comp. Zool. 150:95–197.
Lewis, P. O. 2001. A likelihood approach to inferring phylogeny from discrete morphological characters. Syst. Biol. 50:913–925.
Maddison, W. P. 1996. Molecular approaches and the growth of phylogenetic biology. Pages 47–63 *in* Molecular zoology: Advances, strategies, and protocols (J. D. Ferraris and S. R. Palumbi, eds.). Wiley-Liss, New York.
Maddison, W. P. 1997. Gene trees in species trees. Syst. Biol. 46:523–536.
May, R. M. 2000. The dimensions of life on earth. Pages 30–45 *in* Nature and human society: The quest for a sustainable world (P. R. Raven and T. Williams, eds.). National Academy of Sciences Press, Washington, DC.
Meyer, A. 1994. Shortcomings of the cytochrome *b* gene as a molecular marker. Trends Ecol. Evol. 9:278–280.
Meyer, A., and R. Zardoya. 2003. Recent advances in the (molecular) phylogeny of vertebrates. Annu. Rev. Ecol. Evol. Syst. 34:311–338.
Mishler, B. D., and S. P. Churchill. 1985. Transition to a land flora: Phylogenetic relationships of the green algae and bryophytes. Cladistics 1:305–328.
Nixon, K. C., W. L. Crepet, D. Stevenson, and E. M. Friis. 1994. A reevaluation of seed plant phylogeny. Ann. Mo. Bot. Gard. 81:484–533.
Novacek, M. J. 1986. The skull of lepticid insectivorans and the higher-level classification of eutherian mammals. Bull. Am. Mus. Nat. Hist. 183:1–112.
Novacek, M. J., and Q. D. Wheeler. 1992. Extinct taxa—accounting for 99.9990 . . . % of the earth's biota. Pages 1–16 *in* Extinction and phylogeny (M. J. Novacek and Q. D. Wheeler, eds.). Columbia University Press, New York.
Petren, K., and T. J. Case. 1997. A phylogenetic analysis of body size evolution and biogeography in chuckwallas (*Sauromalus*) and other iguanines. Evolution 51:206–219.
Poe, S., and J. J. Wiens. 2000. Character selection and the methodology of morphological phylogenetics. Pages 20–36 *in* Phylogenetic analysis of morphological data. (J. J. Wiens, ed.). Smithsonian Institution Press, Washington, DC.
Rassmann, K. 1997. Evolutionary age of the Galápagos iguanas predates the age of the present Galápagos islands. Mol. Phylogenet. Evol. 7:158–172.
Reeder, T. W., and J. J. Wiens. 1996. Evolution of the lizard family Phrynosomatidae as inferred from diverse types of data. Herpetol. Mon. 10:43–84.
Rokas, A., B. L. Williams, N. King, and S. B. Carroll. 2003. Genome-scale approaches to resolving incongruence in molecular phylogenies. Nature 425:798-804.
Rowe, T., J. Kappelman, W. D. Carlson, R. A. Ketcham, and C. Denison. 1997. High-resolution computed tomography: A breakthrough technology for Earth scientists. Geotimes 42:23–27.
Sanderson, M. J. 1997. A nonparametric approach to estimating divergence times in the absence of rate constancy. Mol. Biol. Evol. 14:1218–1231.
Sanderson, M. J. 2002. Estimating absolute rates of molecular evolution and divergence times: A penalized likelihood approach. Mol. Biol. Evol. 19:101–109.
Sanderson, M. J., and M. J. Donoghue. 1989. Patterns of variation in levels of homoplasy. Evolution 43:1781–1795.
Sanderson, M. J., and M. J. Donoghue. 1996. The relationship between homoplasy and confidence in a phylogenetic tree. Pages 67–89 *in* Homoplasy. The recurrence of similarity in evolution (M. J. Sanderson and L. Hufford, eds.). Academic Press, San Diego, California.
Shultz, J. W. 1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics 6:1–38.
Scotland, R. W., R. G. Olmstead, and J. R. Bennett. 2003. Phylogeny reconstruction: The role of morphology. Syst. Biol. 52:539–548.
Sites, J. W., Jr., S. K. Davis, T. Guerra, J. B. Iverson, and H. L. Snell. 1996. Character congruence and phylogenetic signal in molecular and morphological data sets: A case study in the living iguanas (Squamata: Iguanidae). Mol. Biol. Evol. 13:1087–1105.
Stephens, P. R., and J. J. Wiens. 2003. Ecological diversification and phylogeny of emydid turtles. Biol. J. Linn. Soc. 79:577–610.
Thiele, K. 1993. The holy grail of the perfect character: The cladistic treatment of morphometric data. Cladistics 9:275–304.
Thorne, J. L., and H. Kishino. 2002. Divergence time and evolutionary rate estimation with multilocus data. Syst. Biol. 51:689–702.
Trueb, L., and R. Cloutier. 1991. A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). Pages 223–313 *in* Origins of the higher groups of tetrapods-Controversy and consensus (H.-P. Schultze and L. Trueb, eds.). Comstock Publishing Associates, Ithaca, New York.
Wiens, J. J. 1993a. Phylogenetic systematics of the tree lizards (genus *Urosaurus*). Herpetologica 49:399–420.
Wiens, J. J. 1993b. Phylogenetic relationships of phrynosomatid lizards and monophyly of the *Sceloporus* group. Copeia 1993:287–299.
Wiens, J. J. 1995. Polymorphic characters in phylogenetic systematics. Syst. Biol. 44:482–500.
Wiens, J. J. 1998a. Testing phylogenetic methods with tree-congruence: Phylogenetic analysis of polymorphic morphological characters in phrynosomatid lizards. Syst. Biol. 47:427–444.
Wiens, J. J. 1998b. The accuracy of methods for coding and sampling higher-level taxa for phylogenetic analysis: A simulation study. Syst. Biol. 47:381–397.
Wiens, J. J. 1998c. Does adding characters with missing data increase or decrease phylogenetic accuracy? Syst. Biol. 47:625–640.
Wiens, J. J. 1998d. Combining data sets with different phylogenetic histories. Syst. Biol. 47:568–581.
Wiens, J. J. 1999. Polymorphism in systematics and comparative biology. Ann. Rev. Ecol. Syst. 30:327–362.
Wiens, J. J. 2000a. Preface. Pages ix–x *in* Phylogenetic analysis of morphological data (J. J. Wiens, ed.). Smithsonian Institution Press, Washington, DC.
Wiens, J. J. 2000b. Coding morphological variation for phylogenetic analysis: Polymorphism and interspecific variation in higher taxa. Pages 115–145 *in* Phylogenetic analysis of morphological data (J. J. Wiens, ed.). Smithsonian Institution Press, Washington, DC.
Wiens, J. J. 2001. Character analysis in morphological phylogenetics: Problems and solutions. Syst. Biol. 50:688–699.
Wiens, J. J. 2003a. Incomplete taxa, incomplete characters, and phylogenetic accuracy: What is the missing data problem? J. Vert. Paleontol. 23:297–310.
Wiens, J. J. 2003b. Missing data, incomplete taxa, and phylogenetic accuracy. Syst. Biol. 52:528–538.
Wiens, J. J., P. T. Chippindale, and D. M. Hillis. 2003. When are phylogenetic analyses misled by convergence? A case study in Texas cave salamanders. Syst. Biol. 52:501–514.
Wiens, J. J., and R. E. Etheridge. 2003. Phylogenetic relationships of hoplocercid lizards: Coding and combining meristic, morphometric, and polymorphic data using step matrices. Herpetologica 59:375–398.
Wiens, J. J., and B. D. Hollingsworth. 2000. War of the iguanas: Conflicting molecular and morphological phylogenies and long-branch attraction in iguanid lizards. Syst. Biol. 49:143–159.

Wiens, J. J., and T. L. Penkrot. 2002. Delimiting species based on DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). Syst. Biol. 51:69–91.
Wiens, J. J., and T. W. Reeder. 1997. Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. Herpetol. Mon. 11:1–101.
Wiens, J. J., and M. R. Servedio. 1997. Accuracy of phylogenetic analysis including and excluding polymorphic characters. Syst. Biol. 46:332–345.
Wiens, J. J., and M. R. Servedio. 1998. Phylogenetic analysis and intraspecific variation: Performance of parsimony, likelihood, and distance methods. Syst. Biol. 47:228–253.
Wiley, E. O. 1981. Phylogenetics. The theory and practice of phylogenetic systematics. John Wiley and Sons, New York.
Wilson, E. O. 1992. The diversity of life. Harvard University Press, Cambridge, Massachusetts.
Yoder, A. D., and Z. Yang. 2000. Estimation of primate speciation dates using local molecular clocks. Mol. Biol. Evol. 17:1081–1090.

First submitted 1 December 2003; reviews returned 8 February 2004; final acceptance 7 March 2004
Associate Editor: Tim Collins