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Points of View

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Phylogeny Reconstruction: The Role of Morphology

ROBERT W. SCOTLAND,[1] RICHARD G. OLMSTEAD,[2] AND JONATHAN R. BENNETT[3]

[1]*Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, U.K.; E-mail: robert.scotland@plant-sciences.ox.ac.uk*
[2]*Department of Botany, Campus Box 355325, University of Washington, Seattle, Washington 98195, USA; E-mail: olmstead@u.washington.edu*
[3]*Department of Biological Sciences, 105 Tucker Hall, University of Missouri–Columbia, Columbia, Missouri 65211, USA; E-mail: bennettjon@missouri.edu*

In this article we 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. The crucial difference between the two data sources relates to the number of potentially unambiguous characters available, their ease and speed of discovery, and their suitability for analysis using transformational models. We consider that the increased use of DNA sequence data, relative to morphology, for phylogeny reconstruction is inevitable and well founded, but that a crucial issue remains concerning the role of morphology in phylogeny reconstruction. We present the view that 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. This approach is preferable to compiling larger data matrices of increasingly ambiguous and problematic morphological characters.

We argue below that a main constraint of morphology-based phylogenetic inference concerns the limited number of unambiguous characters available for analysis in a transformational framework. This problem of a limited number of unambiguous characters is further compounded by obstacles to accurate homology assessment and character coding, which further reduce the number of characters available for analysis. We discuss and disagree with the view that more morphological data should be used in phylogeny reconstruction. Furthermore, we consider the claim that the greatest strength of morphological data—increased taxon sampling—to be mistaken. In the discussion that follows we use "phylogeny reconstruction" to refer to the computer-based algorithmic analyses routinely conducted in systematics today.

NUMBERS OF CHARACTERS

Accuracy and Support

Hillis (1987) cited the increased number of characters as the greatest advantage of molecular data. Increased numbers of characters have been shown to be crucial in relation to issues of accuracy (Hillis, 1987, 1996, 1998; Huelsenbeck and Hillis, 1993; Hillis et al., 1994a, 1994b; Lamboy, 1994; Cummings et al., 1995; Givnish and Sytsma, 1997b; Rosenberg and Kumar, 2001) and support (Felsenstein, 1985; Sanderson, 1995; Bremer et al., 1999) (Figs. 1a, 1b). Although the number of characters needed for accurate phylogeny reconstruction is difficult to estimate, the number of characters needed in simulation studies to recover accurate trees is an order of magnitude greater than that available from morphology (Lamboy, 1994; Hillis, 1996, 1998; Givnish and Sytsma, 1997a, 1997b). Whereas there are a few exceptionally large morphological matrices with many characters (e.g., Gauthier et al., 1989), morphological matrices have on average three characters per taxon (Sanderson and Donoghue, 1989). We reexamined the character/taxon ratio of 235 morphological studies currently held in Treebase (http://www.herbaria.harvard.edu/treebase/) and found 2.36 characters/taxon.

Figure 1a (adapted from Hillis, 1996, 1998) shows the relationship between accuracy and sequence length (number of informative characters) for a simulation study (Hillis, 1996, 1998). Whereas results of individual simulation studies need cautious interpretation (Lamboy, 1994; Wiens and Hillis, 1996), such studies have repeatedly demonstrated that increasing the number of characters generally increases accuracy (Nei et al., 1983; Kim and Burgman, 1988; Rohlf and Wooten, 1988; Huelsenbeck and Hillis, 1993; Charleston et al., 1994; Hillis et al., 1994a, 1994b; Hillis, 1996, 1998; Givnish and Sytsma, 1997a; Rosenberg and Kumar, 2001), with

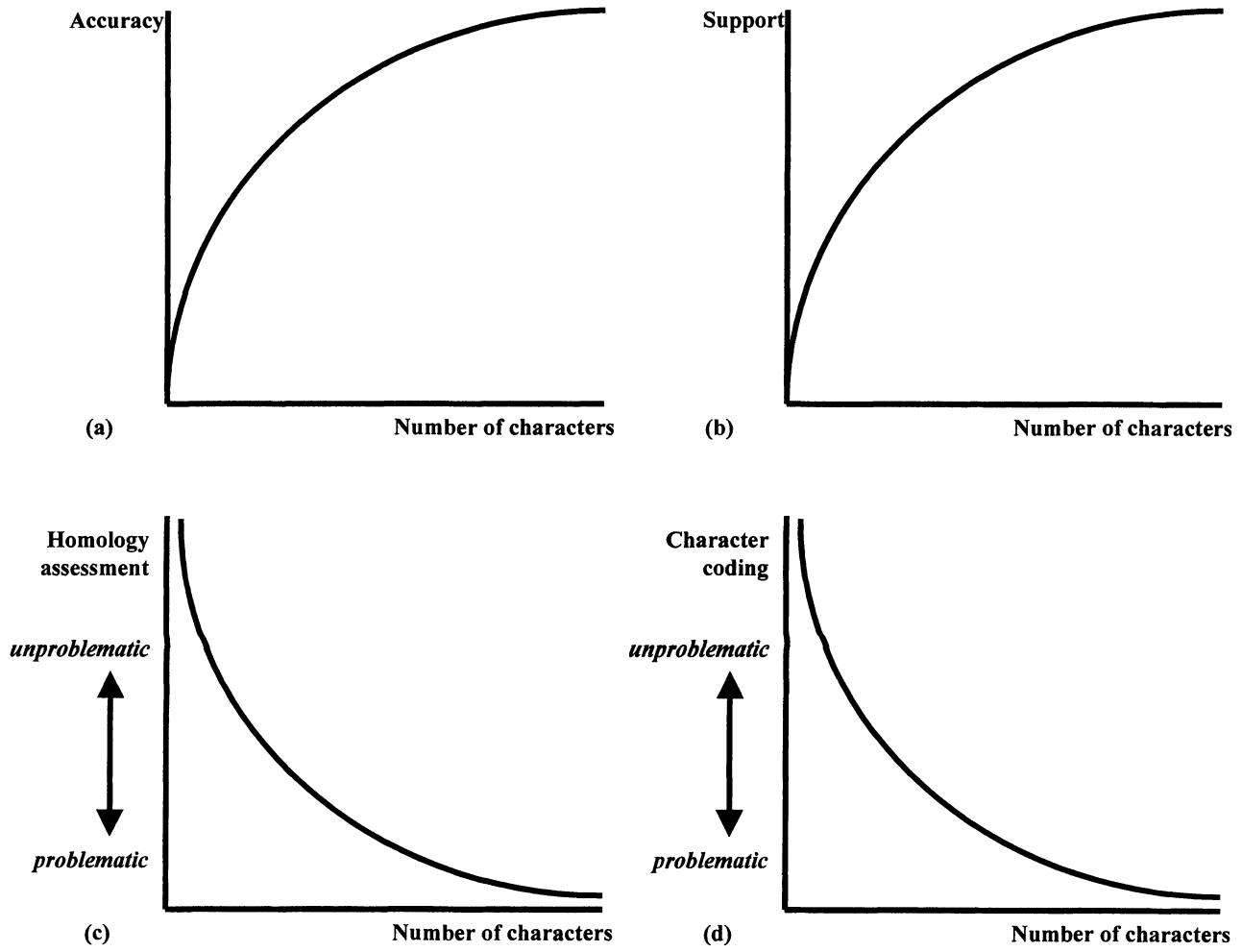

FIGURE 1. Possible relationship between an increase in the number of characters and features of the phylogeny. (a) Accuracy (Hillis, 1996, 1998). (b) Bootstrap support (Bremer et al., 1999). (c) Ease of homology assessment in morphological studies. (d) Character coding in morphological studies.

the proviso that increasing the number of characters for some tree models (e.g., the four taxon tree of Felsenstein, 1978) does not increase accuracy (Felsenstein, 1978; Huelsenbeck and Hillis, 1993).

Sanderson (1995) argued that the results of phylogenetic studies are of limited value unless some assessment of reliability for the various nodes of the tree has been made. Support measures such as bootstrap and jackknife have been widely discussed (Felsenstein, 1985; Hedges, 1992; Hillis and Bull, 1993; Kluge and Wolfe, 1993; Sanderson, 1995; Naylor and Brown, 1998) and are used as measures of support in most phylogenetic studies.

The interpretation of specific support measures is not straightforward (Hillis and Bull, 1993; Sanderson, 1995), although increased support values are preferable. However, the low character/taxon ratio in many morphological studies itself precludes high support values. Figure 1b (adapted from Bremer et al., 1999) shows that increased bootstrap percentages are positively correlated with the number of characters. The study of Bremer et al. (1999) demonstrated explicitly that the character/taxon ratio for morphological studies is such that bootstrap percentages are likely to be low.

The arguments that follow with regard to character coding and homology assessment are also displayed in diagrammatic form in Figures 1c and 1d, which are presented alongside Figures 1a, and 1b because the relationships among accuracy, support, character coding, and homology assessment partly explain why there are too few morphological characters to provide confidence in any given estimate of phylogeny.

Character Coding

Problems associated with character coding in systematics have been widely discussed (e.g., Jardine, 1969; Archie, 1985; Pimental and Riggins, 1987; Bryant, 1989; Pogue and Mikevich, 1990; Nelson, 1994; Pleijel, 1995; Wilkinson, 1995; Brower and Schawaroch, 1996; Hawkins et al., 1997; Scotland and Pennington, 2000). In a recent survey of morphological cladistic data matrices for different plant groups, Hawkins (2000) categorized nine different coding strategies for translating

observations into discrete numerical codes for morphological cladistic analyses. These coding regimes affect the outcome of phylogenetic analyses (Pleijel, 1995; Wilkinson, 1995; Hawkins et al., 1997; Forey and Kitching, 2000) and therefore add a level of subjectivity and interpretation to any phylogeny estimate. The difficulty in choosing an appropriate coding strategy in terms of homology assessment is illustrated even for simple characters. For example, the data first discussed by Maddison (1993) relevant to the context of inapplicable data (no tails, red tails, blue tails) have been widely discussed in the context of coding (Hawkins et al., 1997; Lee and Bryant, 1999; Strong and Lipscomb, 1999) and viewed as one, two, or three separate characters.

Whereas some morphological characters are binary and discrete and therefore relatively straightforward to code, others are less clear (Stevens, 1991). This is especially true for continuous (measurement) data where large sample sizes are needed to obtain good estimates of means and variances that can be used to help develop binary or multistate codes (Archie, 1985). A spectrum exists from unambiguously coded characters at one extreme to much more problematic characters at the other. The exact ratio of unambiguously to ambiguously coded characters is group specific (e.g., vertebrates with bony skeletons and determinant growth patterns probably have more characters that are easily coded than do plants), but this type of problem is a feature of all morphological matrices. Therefore, 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).

For aligned sequence data, there is no ambiguity in assigning character states, although stretches of sequence may be problematic when they include missing data, polymorphisms, and indels. Such areas of ambiguity can be excluded, and the number of characters may still remain relatively large. Excluding ambiguity from a morphological data set typically will leave very few characters.

In conclusion, problems surrounding character coding of morphological data reduce the number of unambiguous morphological characters for analysis.

Character Conceptualization

Problems associated with homology assessment of morphological data also have been widely noted (Pimental and Riggins, 1987; Stevens, 1991; Thiele, 1993; Gift and Stevens, 1997; Givnish and Sytsma, 1997b; Patterson and Johnson, 1997; Scotland and Pennington, 2000; Wiens, 2000). In the context of morphological data and phylogeny reconstruction, the problem is one of character definition. Although morphological and molecular data are similar in that criteria of topological correspondence (Remane, 1952; Rieppel, 1988) are used to assess primary homology (de Pinna, 1991), morphological character definitions nonetheless engender a great deal of disagreement. Therefore, as Smith (1994: 34) noted, "different workers will perceive and define characters in different ways." These differences in character concepts introduce a further level of ambiguity into phylogenetic analyses of morphological data. Although similar problems of homology assessment exist for molecular data relative to issues such as alignment (Mindell, 1991; Baum et al., 1994; Goldman, 1998; Simmons and Ochoterena, 2000), the crucial issue for morphology is that the already small number of morphological characters is further compromised by ambiguous homology assessment.

Figure 1c outlines the relationship between homology assessment and number of morphological characters, and shows 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. For example, recent molecular analyses of seed plants (Bowe et al., 2000; Chaw et al., 2000) have overturned the "anthophyte hypothesis" that concerns the closest relatives of flowering plants. Inaccurate homology assessment (Doyle, 1996, 1998) is one explanation for why the anthophyte hypothesis, which was erected on the basis of morphological analyses (Crane, 1985; Doyle and Donoghue, 1986, 1992; Loconte and Stevenson, 1990, Nixon et al., 1994), may be wrong.

This issue of character conceptualization is fundamentally related to the role of models of transformation in phylogenetic analysis. Models of evolution that describe character state changes are used either implicitly or explicitly in methods of phylogenetic analysis (Yang et al., 1994; Swofford et al., 1996; Posada and Crandall, 2001). Even parsimony, viewed by some as being model-free, assumes a basic model of character state transformation (Farris, 1973; Humphries and Chappill, 1988; Nelson, 1996; Carine and Scotland, 1999; Steel and Penny, 2000).

For molecular data, explicit models of nucleotide substitution are well documented, from the simple model of Jukes and Cantor (1969) to more complex and arguably more realistic models incorporating additional parameters (e.g., Kimura, 1980; Felsenstein, 1981; Hasegawa et al., 1985; Kishino and Hasegawa, 1989; Rodríguez et al., 1990; Yang, 1993, 1996). Homology propositions at the level of the nucleotide rest on our understanding that one nucleotide may be substituted by another. There is no ambiguity that the unit of comparison is the nucleotide and that adenine, guanine, cytosine, and thymine represent different versions of the same entity. Even though the exact processes underlying nucleotide substitution are more complex than the simple models used in phylogenetic reconstruction (Miramontes et al., 1995), character conceptualization is rendered more straightforward for molecular sequence data than for morphological data, where there is little agreement as to what constitutes the unit of comparison between organisms (see two recent multiauthor books edited by Scotland and Pennington, 2000, and Wagner, 2001).

In contrast, our understanding of the processes underlying morphological evolution is much poorer. Fundamental to this are the problems encountered in accurately proposing character state transformations, as outlined above in relation to character and character state delimitation. Our current inability to incorporate models of morphological evolution into phylogeny reconstruction methods restricts the range of techniques available for analyses of matrices containing morphological data (though see Lewis, 2001, for an alternative perspective on modeling morphology).

Problems of homology assessment are not restricted to morphology and also occur for molecular data (e.g., Mindell, 1991; Hickson et al., 2000). However, given that there are unambiguously aligned sequences at virtually all phylogenetic levels and that the delimitation of characters and character states in these situations is relatively unproblematic, DNA sequence data at least offer the unique potential of scoring large numbers of unambiguous characters and character states.

More Morphological Characters or Fewer?

Poe and Wiens (2000) discussed character selection in the context of morphological studies. In a survey of 512 morphological studies, they found that only 20% contained explicit criteria for character selection and exclusion. They also discussed explicit selection and exclusion criteria, i.e., variation within terminal taxa, missing data, continuous and quantitative variation, unknown polarity, and levels of homoplasy, and stated that most criteria for excluding characters were unjustified. Furthermore, they reached the conclusion that "much more [morphological] variation could be included in phylogenetic analyses than is used presently" (Poe and Wiens, 2000:33–34). The effect of increasing the number of morphological characters for a given phylogenetic problem is illustrated by comparing the increase in the number of characters used in four phylogenetic analyses of seed plants between 1985 and 1994 (Table 1) (Crane, 1985; Doyle and Donoghue, 1986; Nixon et al., 1994; Doyle, 1996). Whereas these analyses differed in detail, the main findings were generally in agreement with those of Crane (1985): Gnetales are the closest extant relatives of angiosperms (i.e., all were congruent with the anthophyte hypothesis). In these analyses, a two- to threefold increase in the number of characters did not alter the original phylogeny estimate. One explanation for the increase in the number of characters used in studies from 1985 to 1994 is that the authors were attempting to estimate phylogeny and therefore a simple increase in the number of characters was viewed as desirable in terms of support and accuracy. Nevertheless, all analyses lacked bootstrap support >50%, and very different alternative topologies were only slightly less parsimonious. The increase in the number of characters made no significant difference to the results that have now been shown to be incongruent with phylogenetic analysis of DNA data (Doyle and Endress, 2000). One interpretation of this is that the accumulation of more characters for morphological analyses generally adds characters of limited value, whereas molecular analyses at least have the potential to add characters of more or less equal value to well beyond the size of data sets typically used today. This is not to claim that simply increasing the amount of sequence data is always in itself enough to solve a particular phylogenetic problem (Naylor and Brown, 1998). The quality of the data is of primary importance. For morphological studies comprising a relatively high number of characters, both character coding and character conceptualization become increasingly important variables that may have a negative impact on a study as more characters are added (Fig. 1).

TABLE 1. Number of morphological characters in four phylogenetic analyses of seed plants, 1985–1996.

Author	No. characters
Crane, 1985	38
Doyle and Donoghue, 1986	62
Nixon et al., 1994	103
Doyle, 1996	91

Whereas the optimistic view of Poe and Wiens (2000) is contrary to those expressed here, we are in agreement with those and other authors (Pimental and Riggins, 1987; Stevens, 1991; Thiele, 1993; Patterson and Johnson, 1997; Hawkins, 2000) regarding the importance of explicit criteria for character selection. The justification and discussion of character selection is the problematic or ambiguous aspect of using morphological data for phylogeny reconstruction.

Taxon Sampling

Hillis and Wiens (2000) stated that dense taxon sampling is the greatest advantage of morphological data, citing recent simulation studies demonstrating the importance of taxon sampling for accurate phylogeny estimates (Hillis, 1996, 1998; Graybeal, 1998). An important point here is that the above papers (Hillis, 1996, 1998; Graybeal, 1998) demonstrated, in the context of simulation studies, that increased taxon sampling is important for phylogenetic accuracy in the context of analyses with large numbers of characters. Less clear is the role of dense taxon sampling when there are fewer characters, as in morphological studies. For example, in one simulation study, Graybeal (1998) demonstrated that under some conditions phylogenetic accuracy was improved as the number of taxa increased, but not when more characters were added. The exception occurred in the smallest matrix (eight taxa, 1,000 characters), in which a decline in accuracy with increasing numbers of taxa was observed. Other authors (Kim, 1996; Poe, 1998; Rosenberg and Kumar, 2001; Hillis et al., 2003) have claimed that the relationship between accuracy and taxon sampling is complex and that for some clades and tree models an increase in the number of characters or choosing characters with an overall low rate of change is more important than increased taxon sampling.

Smith (1998:440) discussed several examples of increasing taxon sampling in the context of fossil taxa and concluded that "the addition of fossil taxa to a primary matrix has a similar beneficial effect as adding more characters." Smith (1998) cited the contributions of Doyle and Donoghue (1987) and Donoghue et al. (1989) for first pointing out the beneficial effect of dense sampling in the context of fossils. Doyle and Donoghue (1987) argued that increased sampling of fossil taxa was crucial for an accurate understanding of phylogeny and character evolution. However, in the context of recent molecular analyses (Mathews and Donoghue, 1999; Qiu et al., 1999; Soltis et al., 1999; Barkman et al., 2000; Bowe 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 (Doyle and Endress, 2000). Therefore, 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. Morphological data from fossil taxa can increase taxon sampling in a way not possible for sequence data, and therefore these data can potentially provide unique character combinations and information on polarity and can alter ideas on character evolution, rooting, and homology assessment (Patterson, 1981; Doyle and Donoghue, 1987; Gauthier et al., 1988; Huelsenbeck, 1991; Smith, 1994, 1998; Benton, 1998). What remains unclear is whether this potential is realized in the context of accurate phylogeny reconstruction, given that these data will suffer from problems discussed above (Figs. 1c, 1d) plus the additional problem of large amounts of missing data.

Another important issue relative to increased taxon sampling, in the context of morphological data, relates to the potential decreased number of unambiguous characters as more taxa are added to a study. Carine and Scotland (2002) constructed a matrix of 32 morphological characters for 66 taxa of *Strobilanthes*. Moylan et al. (unpubl.) extended this study to include a further 22 taxa, for a total of 88 taxa. In the matrix of Moylan et al. (unpubl.), the number of characters in the matrix reduced from 32 to 12 because characters that were discrete in the Carine and Scotland (2002) matrix were no longer discrete when additional taxa were added.

The Role of Morphology in Systematics

Although the extent of congruence between morphological and molecular phylogenetic analyses has not been quantified, some researchers anticipated a high level of congruence between molecules and morphology (e.g., Hillis, 1987; Sanderson and Donoghue, 1989; Sytsma, 1990; Donoghue and Sanderson, 1992; Hillis and Wiens, 2000), whereas others were less optimistic or sceptical (e.g., Patterson et al., 1993; Lamboy, 1994; Hedges and Maxon,1996; Givnish and Sytsma, 1997a, 1997b; Baker et al., 1998). We suspect that the optimism of congruence between morphology and molecules in plants is well placed simply because many taxa long recognized on the basis of morphology have been supported using molecular data and that this is widely appreciated (Hillis, 1987; Sanderson and Donoghue 1989; Sytsma, 1990; Donoghue and Sanderson, 1992; Patterson et al., 1993; Hillis and Wiens, 2000). Less clear is the extent to which phylogenetic analyses of morphological data have increased our understanding of phylogeny. In this context, we strongly disagree with the claim that "most of our knowledge of the Tree of Life, both at lower and higher taxonomic levels, is based on *phylogenetic studies* [emphasis added] of morphological data" (Wiens, 2000:ix), even though we do consider that most of our knowledge of phylogeny based on our knowledge of morphology is broadly accurate. In other words, most of our current knowledge of phylogeny still stems from classifications (Platnick, 1979), which are in turn based on morphology. Much of what we know (or think we know) about phylogeny derives from morphology indirectly through the interpretation of many generations of taxonomists who developed the concepts of groups, which they recognized in classifications, due to the coincidence of some morphological similarities being synapomorphies. However, this does not endorse the statement of wiens above, because this knowledge preceded Hennig (1966) and any of the "phylogenetic studies" in the sense that Wiens used the term. We disagree that morphology offers any hope for the future to resolve phylogeny at lower or higher taxonomic levels. In other words, just because there are enough morphological synapomorphies for careful observers to recognize many monophyletic groups over the years in traditional taxonomic studies, further dissection of morphology by present or future scientists may still not be able to resolve the full branch structure of the tree of life. Molecular phylogenetics holds several orders of magnitude more hope for that end, even though an honest observer would have to agree that even whole genomes for all species will probably not yield a fully resolved, highly confident tree.

The time scale over which morphology has been applied to the problem of classification is important when evaluating the role of morphology in phylogeny reconstruction. Not only have classifications been refined over a long period of time, but they have usually comprised only a limited subset of nodes at the three main ranks of species, genus, and family. Therefore, it seems uncontroversial to claim that morphological data have been responsible over a long period of time for what we have learned about many taxa that are an accurate part of phylogeny. The fact that classifications based on morphology can be congruent with modern notions of monophyly is a

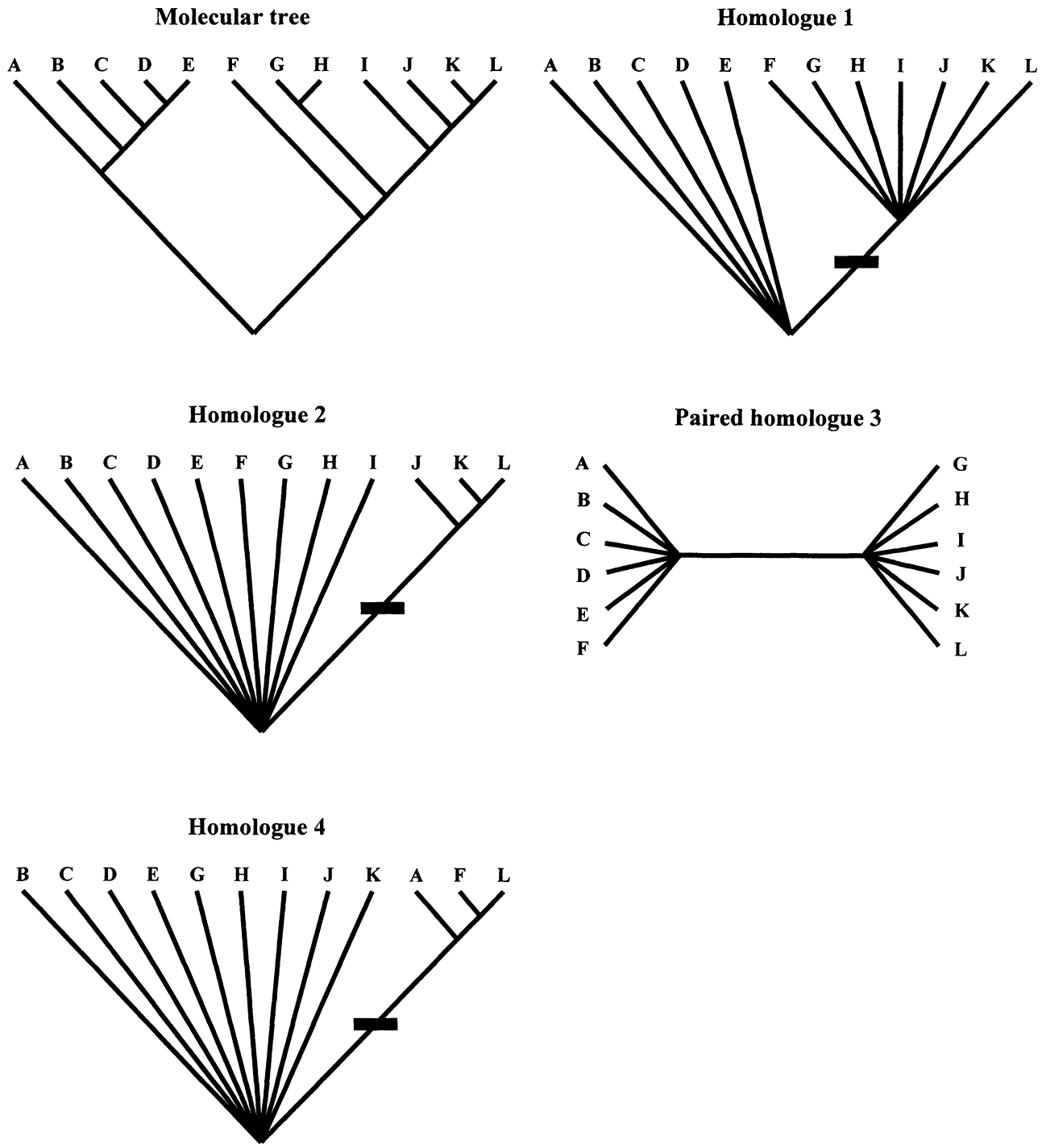

FIGURE 2. Trees of four morphological homologues, three rooted and one unrooted, in comparison to a molecular tree to illustrate the approach of examining each morphological homologue for congruence with all others and with relevant nodes on the molecular tree. In this straightforward example, homologue 4 and the A–F component of paired homologue 3 are incongruent with the molecular tree, whereas homologue 1, homologue 2, and G–L from paired homologue 3 are congruent with the molecular phylogeny.

consequence of the fact that evolutionary novelty (which is polarized) and morphological distinctness (which is unpolarized) can be the same. Given this historically important role for morphology, a continued role for morphology in phylogeny reconstruction seems a reasonable expectation. The question remains however as to the best way to optimize the role of morphology in relation to phylogeny reconstruction.

It is our view that the recognition of taxa on the basis of morphological data has occurred largely in those parts of phylogeny in which there are morphological characters that fully diagnose taxa, i.e., taxic homologues sensu Patterson (1982), which are equivalent to synapomorphies sensu Hennig (1966). For example, nucleic acids, paired appendages, vertebral column, mammary glands, integumented megasporangia (seeds), and carpels are taxic homologues at the level of all orgnisms, gnathostomes, vertebrates, mammals, seed plants, and angiosperms, respectively. Patterson (1982) characterized his taxic homology approach by stating that discovering a homology was equivalent to discovering a taxon. However, there remain several obstacles to simply equating readily identifiable diagnostic characters with synapomorphy. First, readily identified homologues may diagnose nonmonophyletic groups (as with plesiomorphies). Second, even when the number of putative taxic homologues is reduced to very few by stringent character selection, they may conflict in the groups they define.

A solution to the lack of morphological data accepts that morphological data are most appropriately used for phylogeny reconstruction when hypotheses of homology are clear and unambiguous in terms of anatomy. There are many hierarchical levels where appropriate morphological data are lacking. This approach acknowledges that there are too few unproblematic morphological characters to construct accurate or robust phylogenies and that time, effort, and expertise is more productively spent exploring anatomy and morphology for fewer characters that may be used in the framework of reciprocal illumination and congruence in relation to molecular phylogenies (Patterson, 1982; Miyamoto and Fitch, 1995; Kellogg, 2000; Scotland and Vollesen, 2000). This approach examines each morphological homologue for congruence with a relevant node on a molecular tree on the basis that morphological characters can be diagnostic for nodes on molecular trees and that taxonomic congruence provides evidence of accuracy (Hillis, 1996; Miyamoto and Fitch, 1995). This approach is akin to Patterson's (1982) congruence test, since each homologue can be tested for congruence with each other and for congruence with each node on a molecular phylogeny (Fig. 2). As a phylogeny, the molecular tree would provide the most accurate estimate for all taxa in the phylogeny, whereas morphological data provide evidence for a more limited number of monophyletic taxa that can be examined for congruence with each other and with the molecular phylogeny. As in the congruence approach discussed by Patterson (1982), incongruent data are not incorporated into the phylogenetic hypothesis but remain as nonhomologies to be explained in the light of the phylogeny.

We do not see the solution presented here as an exclusive solution to the problem. However, our own experience in gathering morphological data (e.g., Olmstead, 1989; Carine and Scotland, 1998, 2000, 2002; Scotland and Vollesen, 2000; Moylan et al., 2002, unpubl.; Bennett and Scotland, 2003; Wood and Scotland, 2003; Wood et al., 2003) has led us to the conclusion that building morphological matrices for groups at all levels is not only problematic in terms of homology assessment and coding but is unrealistic in terms of the time scale necessary to complete the anatomy and sampling of morphological data with any degree of rigor.

Another approach to the role of morphology in phylogeny reconstruction, exemplified by Poe and Wiens (2000), is to argue that morphological data are good indicators of phylogeny. Thus, more morphological data than are used at present should be used either in separate morphological analyses or in combined analyses with molecular data. In this context, we view the recent example concerning anthophytes and seed plant phylogeny (Nandi et al., 1998) as a salutary lesson concerning the role of morphology in phylogeny reconstruction. We view any attempt to include more morphological data in phylogeny reconstruction as inherently problematic.

Another possible solution accepts a limited role for morphological data in phylogeny reconstruction. With this approach, those characters that are unproblematic in terms of homology assessment and character coding are selected are analyzed simultaneously with molecular data to provide a combined estimate of phylogeny. Any number of additional morphological characters may increase accuracy or explanatory power, but in the context of a stringently selected morphological data set the increase in character number will always be relatively low. We see little to argue with concerning this approach, although it does not automatically provide an independent role for morphological data in the context of accuracy and diagnosability.

Conclusions

Morphological data are responsible for what we know about much of the phylogeny of life. Over the last 2,000 years, regardless of methodological shortfalls, hierarchical classifications have been constructed on the basis of morphology and it seems that these classifications reflect and are congruent with many accurate nodes of phylogeny. These classifications, although limited in resolution, provide a framework of diagnostic monophyletic anchor points around which DNA sequence analyses can provide corroboration, resolution, support, and accuracy for those parts of phylogeny for which appropriate morphological data is lacking. 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. Therefore, in contrast to the view that "much more [morphological] variation could be included in phylogenetic analyses than is used presently" (Poe and Wiens, 2000:33–34), we take the view that rigorous and critical anatomical studies of fewer morphological characters in the context of a molecular phylogeny is the way that integrated studies will and should develop.

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Fishes and Birds: Gondwana Life Rafts Reconsidered

JOHN C. BRIGGS[1]

Zoological Collections, Georgia Museum of Natural History, University of Georgia, Athens, Georgia 30602, USA; E-mail: johnc.briggs@verizon.net

> . . . that grand subject, that almost keystone of the laws of creation, geographical distribution. (Charles Darwin, in a letter to J. D. Hooker, 1845)

Recent research on phylogenetic relationships at the molecular level has attributed the present circumglobal distributions of four groups of vertebrate animals to the Mesozoic fractionation of Gondwana (or Gondwanaland), the southern part of the ancient supercontinent Pangaea that existed from the mid-Triassic to the early Cretaceous, about 220 to 110 million years ago (MYA). These conclusions, based primarily on the analysis of mitochondrial DNA (mtDNA), are important because in all four cases a much later evolution and dispersal had previously been recognized.

APLOCHEILOID FISHES

The suborder Aplocheiloidei comprises a group of freshwater and euryhaline fishes that is divided in two families, the New World Rivulidae and the Old World Aplocheilidae. The mtDNA of both families was analyzed by Murphy and Collier (1997), who constructed a phylogeny that was then fitted to an area cladogram. The cladogram indicated significant divisions between six different parts of the globe: West Africa, East Africa, South America, Indo-Malayasia, Madagascar/Seychelles, and North America. Previously, Murphy and Collier (1996) had found a significant division between the revulid fishes of Central America and the Greater Antilles. In their conclusion, the authors' stated that their cladogram divisions were completely congruent with the historical breakup of Gondwana.

Except for the West Africa–East Africa division, the separations in the cladogram of Murphy and Collier (1997) represent contemporary oceanic barriers. The African puzzle was solved by hypothesizing an epicontinental sea that had extended through Africa southward from the Tethys Sea. The authors gave no reason for postulating a Mesozoic dispersal aboard tectonic plates, but in so doing they did follow two of their predecessors.

The classic systematic work on the order Cyprinodontiformes, that includes the Aplocheiloidei, was published

[1]Present address: 82-651 Skyview Lane, Indio, California 92201, USA.