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Systematic Biology is currently published by Society of Systematic Biologists.

On Applications of Geometric Morphometrics to Studies of Ontogeny and Phylogeny: A Reply to Rohlf

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Rohlf (1998) criticizes several papers by the assemblage of authors he labels Z&F (Bookstein, Fink, Lundrigan, Swiderski, and Zelditch). He objects to their choice of reference form and to their interpretation of variables, as well as to their use of partial warps in phylogenetic analyses, as done by Fink, Lundrigan, Swiderski, and Zelditch. In many cases, we agree with Rohlf's general statements about partial warps. Obviously we agree on the uncontroversial issues, such as the geometric meaning of the reference form, the definitions of the partial warps, and their dependence on a reference form. There is no room for disagreement on these purely mathematical issues. In other cases, we have made arguments similar to Rohlf's. We also have cautioned against interpreting partial warps as units of biologically process or anatomy or as based on a biological model (Zelditch et al., 1992, 1995; Fink and Zelditch, 1995). More generally, we have cautioned against interpreting any individual variables in those terms (Zelditch and Fink, 1996). Moreover, we too favor multivariate tests over univariate tests, if the multivariate test bears on the biological hypotheses. Certainly we oppose drawing a conclusion about the statistical significance of a change in overall shape from univariate tests. And we also agree that the basis for a shape space should be justified. We find many similarities between our arguments and Rohlf's. But we genuinely disagree with him on some issues, mainly those that arise in context of phylogenetic analysis.

Herein, we focus on systematic studies for several reasons. First, our systematic protocol is the one most accurately characterized by Rohlf and it is subject to the most serious criticism by him; that is the protocol ascribed to Z&F (Rohlf, 1998;146–157) and criticized for lacking the property of invariance to the selection of variables. That is a protocol for a phylogenetic study (Fink and Zelditch, 1995), and the rationale for using it is specific to a systematic study. Second, Rohlf says that the purpose of his note is to comment on applications of morphometrics in systematic biology, and that is our interest as well. Third, our genuine disagreements are largely confined to matters that arise in context of systematic studies. We do not seriously disagree on how to analyze ontogenetic allometry, but we do seriously disagree on methods appropriate for systematic studies. Before we begin to explain our disagreement, however, we need to mention one problem that could complicate our discussion of systematic issues: Our systematic studies are phylogenetic and address methodological issues unique to them. Most of Rohlf's comments do not concern phylogenetic studies. If we read his criticisms in the context of our studies, we may be taking them out of the context intended by him. But because our studies are the focus of his criticisms, we put his comments in context of our scientific questions, and interpret them as such.

Rohlf says that the issues dividing us are statistical and mathematical, not systematic: "It should also be clear that the present paper is concerned with general mathematical and statistical issues that have nothing to do with the phenetics/cladistics controversies because we are not concerned here with methods for creating classifications." He recommends several methods, some of which may not be intended for phylogenetic studies (e.g., principal components analysis, canonical variates analysis, or clustering based on Euclidean distances) and others that are explicitly intended for phylogenetic studies (maximum likelihood, squared-change parsimony). But we use morphometrics in character-based systematics and analyze the data by phylogenetic parsimony. Again, we agree on virtually all of the purely mathematical and statistical issues, but there is a major difference between the systematic methods we favor and those recommended by Rohlf. The disagreement on methods of analyzing systematic data is the primary issue.

We subdivide our response into three sections: (1) choice of reference form; (2) biological interpretation of variables in the context of systematic studies; and (3) phylogenetic parsimony. We single out phylogenetic parsimony as an issue in its own right, worthy of careful attention given its crucial role in phylogenetic systematics and Rohlf's objections to our use of it.

CHOICE OF REFERENCE FORM

There is no disagreement about the facts that the reference form is the tangent point and that it defines the partial warps. The disagreement is over criteria for selecting it. We use biological logic in choosing it; by biological logic, we mean that the reference form represents the biological starting point of a change. For example, Bookstein (1991) uses a normal face as a starting form in a craniofacial deformation; craniofacial deformities are viewed as biological as well as mathematical deformations of the normal face. Zelditch et al. (1992) use a neonate as the starting form in an ontogenetic study; normal growth is construed as a biological as well as a mathematical deformation of the neonate. Using similar logic in a historical context, Swiderski (1993) uses an average shape (calculated over several outgroups) as a starting form in his analysis of morphological evolution; Fink and Zelditch (1995) use an average of a sample of juveniles of one outgroup as the starting point in a phylogenetic analysis of ontogenetic transformations.

Biological logic is not the only possible criterion to use in choosing a reference, but any choice has implications that should be considered. When biological logic is used to choose a reference, the partial warps represent aspects of a deformation, both mathematical and biological, at progressively smaller spatial scales. That interpretation is specific to partial warps based on the biological starting point. Otherwise, the correspondence between the biological and mathematical deformation is lacking. Other criteria could be used to choose a reference, and under some conditions, other criteria might be appropriate. For example, if morphometric distance among shapes is the primary concern, it would be reasonable to use the consensus form as the reference because that would minimize the distortion of those distances. However, if distortion is a serious concern, perhaps because the range of shapes is extremely large, then the study may be beyond the limits of morphometric analysis.

We do not use a consensus form in our own studies because distances are not our primary concern and distortion is trivial; the range of shapes in our studies is generally small. For example, in our analysis of adults of six species of piranhas the maximal Procrustes distance is 0.200, which is smaller than the distance between neonatal and 30-day-old rats in the ontogenetic sample analyzed by Zelditch et al. (1992). Our studies are not unusual; as Rohlf says, linear approximations are usually good and the effects of different reference forms on distances are expected to be relatively minor. But the effects of different reference forms are not minor when it comes to studies of spatiotemporal integration.

In studies of spatiotemporal integration, we are interested in the spatial scale of change. Several studies by Z&F are specifically designed to analyze spatial integration (e.g., Zelditch et al., 1992; Swiderski, 1993; Zelditch and Fink, 1995; Fink and Zelditch, 1996). Zelditch et al. (1992) proposed a measure of spatial integration based on the ratio of summed squared loadings of partial warps at the highest spatial scales relative to more localized partial warps (although the summary ratio may be less interesting than the whole spectrum). Given that metric, it would not make sense to use a consensus form as a reference. Then the most localized departures away from the reference form would not correspond to the most localized components of the ontogenetic deformation. Losing information about spatially localized biological change is a high price to pay when it is precisely what we seek and the risk of distorted projections is trivial.

Although we defend the use of biological logic in choosing a reference, we do not claim that Z&F invariably chose the best possible reference in all their studies. Phylogenetic studies present a real problem because we cannot use the true biological starting point (the ancestor) unless it is represented in our samples. So we use outgroups instead. But most phylogenetic studies use multiple outgroups and only one can be used as the reference form. As a result, some choice among them must be made, or some method must be found to circumvent the need to choose. Fink and Zelditch (1995) chose the juvenile shape of one outgroup as reference, because the other outgroup has a derived juvenile shape. Swiderski (1993) takes a different approach, calculating an average of several outgroups because the uniquely derived features of individual outgroups might be given less weight by averaging. These are two different approaches and both raise questions. And there are other alternatives recommended in the literature, such as the hypothetical ancestor (Bookstein, 1996; Slice et al., 1996), but that is an impractical choice because that ancestor cannot be inferred until the end of the analysis.

The use of an outgroup as a reference form has been criticized by Bookstein (1996), even though he does not generally object to using biological logic when choosing a reference form. However, Bookstein's arguments actually seem to rule out using an outlier, not an outgroup. According to Bookstein, the outgroup reference will counterintuitively foreshorten Procrustes distances (Bookstein, 1996:145). That may be true of an outlier, but a properly chosen outgroup will not be that far distant from the other shapes in the study. Systematists do not typically choose outgroups that differ markedly from all ingroup taxa. Outgroups that are markedly different from all ingroup taxa create at least as many problems for phylogenetic inference as for morphometric analysis (Wiley, 1981).

In our view, biologists should choose a reference form in context of their biological questions. Sometimes the consensus form is a biologically plausible choice because the study might be concerned with variation around that form. Clearly the criteria for choosing a reference form in phylogenetic studies need further consideration; in general we favor biologically plausible candidates instead of ones justified by purely formal considerations.

BIOLOGICAL INTERPRETATION

According to Rohlf, the most fundamental problem with the studies by Z&F is that they interpret the partial warps as biologically meaningful rather than as a priori variables whose definition does not reflect covariance patterns in the data. He says that Z&F interpret (and statistically test) each partial warp separately, and he goes on to criticize what he perceives to be the reasoning used by Zelditch et al. (1992). He objects to the methods ascribed to us because the deformations corresponding to partial warps are just functions of the reference form, are only fortuitously aligned with biologically meaningful structures, and several partial warps taken together are required to yield a complete description of a morphological difference (such as presented in his example). Rohlf also crit-

icizes our statistical analyses as being univariate. Moreover, he recommends some specific alternatives to the methods we use, among them conventional multivariate methods such as principal components analysis (PCA) or canonical variates analysis (CVA) or, in the context of evolutionary studies, squared-change parsimony or maximum likelihood.

We have several responses to Rohlf's criticisms. First, we do not actually interpret individual partial warps in biological terms. Rohlf's representation of the reasoning used by Zelditch et al. (1992) is not consistent with the way we interpret partial warps. Second, Rohlf's view of "biologically meaningful" apparently is different from ours. This is particularly clear in the context of his artificial example. That example may be useful for illustrating some problems that can arise when using partial warps, but those problems are not directly linked to our sense of biologically meaningful, which is grounded in homology and phylogenetic inference. Third, Rohlf apparently overlooks our phylogenetic analyses of correlation and our multivariate statistical analyses. In addition, he takes our bivariate or univariate analyses out of the context of specific scientific questions that could not be answered by a multivariate statistical analysis (e.g., questions that could not be answered by testing the hypothesis that overall shape is isometric). Most important, Rohlf does not consider the issue of biological interpretation in the context of the search for characters, but it is only in that context that we draw conclusions from individual partial warps.

Rohlf seems to imply that we read too much biological reality into individual partial warps, interpreting them as if they correspond to units of anatomy or biological process. But we do not read them in that way. We do not believe that the partial warps dissect organisms into individual units of structure, function, or history, and we do not believe that any variables should be interpreted in isolation. For example, we strongly object to comparative ontogenetic studies that infer heterochrony .from changes in ontogenetic rates or timings of individual variables (Zelditch and Fink, 1996). Any attempt to relate shape variables to biological processes requires a full consideration of all variables correlated with that process. Rohlf seems to accuse us of doing precisely what we explicitly oppose. Perhaps he reads our detailed and often lengthy descriptions of individual partial warps as biological interpretations; perhaps he conflates our approach with Naylor's (1996) quite different protocol, as Rohlf claims that Naylor's results reveal problematic aspects of our methods.

We have said, at length, why we find partial warps useful tools in studies of spatial integration (Zelditch et al., 1992; Swiderski, 1993; Zelditch and Fink, 1995), supplementing Bookstein's (1991) arguments to that effect. We have also said why we find them useful in the search for characters (Fink and Zelditch, 1995; Zelditch et al., 1995). Moreover, we (Zelditch et al., 1995) have explained why we consider principal components and canonical variates to be inappropriate tools in the search for characters (but we do not dismiss those methods in all contexts). Herein we are concerned specifically with systematic applications of partial warps so we focus on the search for characters. In that context, conventional multivariate methods like PCA or CVA are not useful. For example, canonical variates analysis can supply meaningful variables in answer to the question: What is the dimension of greatest phenetic dissimilarity among samples relative to within-sample variance? But that answer is not meaningful in the light of our questions. Our questions concern the phylogenetic relationships among taxa and the evolutionary modifications of organismal features, and we consider variables meaningful if they diagnose taxa or describe evolutionary novelties. In that context (as well as in the context of studies of spatiotemporal integration) we find partial warps both useful and interesting.

Rohlf's artificial example may seem to challenge any justification for partial warps, in any context. His example is helpful in some respects because it may make certain abstract points intuitively accessi-

ble. But it does not represent the reasoning we have used in any of our studies so it cannot reveal flaws in that reasoning. Given Rohlf's example, we would interpret it exactly as he does (except that we would not consider the change simple or highly integrated). But, unlike our systematic studies, the problem of historical inference does not arise in Rohlf's example. He has a priori knowledge that the three partial warps describe a single change, a situation strikingly different from that of empirical studies that do not have that information at the outset. It may be that multiple historical changes account for the observed net difference between two taxa. Consequently, we cannot say which combinations of partial warps describe a single evolutionary change until we have inferred the cladogram and examined the distribution of partial warps on it. Rohlf's example fails to capture the reasoning required in those situations. It also fails to capture the reasoning used in ontogenetic studies of spatial integration, for several reasons, but most importantly because Zelditch et al. (1992) base their interpretations on the full set of partial warp scores (not on individual variables). For these reasons, Rohlf's example is not instructive about our methods, nor does it provide a useful guide for criticizing our interpretations.

It is in the context of character-based systematics that we examine partial warps separately. Rohlf objects to this because the variables are defined a priori and do not reflect the covariance patterns in the data, but that is precisely why we find them useful. Partial warps are a function of physical distances among homologous landmarks on one form, not of morphometric distances among specimens. Partial warps are defined before empirical patterns are analyzed, and they are defined in terms of locations of landmarks in one particular form. As such, they are a function of an organism, not of a variance–covariance matrix. These are desirable properties for phylogenetic analysis because the variables do not change when specimens are added or deleted from the study, as would be the

case for variables that reflect dimensions of dissimilarity within a particular sample (e.g., PCA). In addition, partial warps are phylogenetically comparable, by virtue of the homology of the landmarks. This allows us to propose hypotheses of homology for shape variables when taxa share those features. Other variables meet our criteria, such as shape coordinates (Bookstein, 1991), and we therefore accept their legitimacy in phylogenetic studies. Components of phenetic dissimilarity might be useful in other contexts, but they do not meet the criteria for use in phylogenetic studies. Our emphasis on homology and our interpretation of "biological meaning" in terms of homology make partial warps interesting to us. Those arguments justify the use of partial warps in phylogenetic studies, although those arguments do not mean that any given set of partial warps will supply a uniquely justified basis.

Even though we can use partial warps in our search for characters, partial warps cannot be equated to phylogenetic characters. That is because characters are not axes of a morphometric space; rather, they are independent evolutionary novelties. Of course the word character has many definitions, but studies that use phylogenetic parsimony should use a conception of character consistent with that method. Phylogenetic parsimony minimizes the number of individual novelties required by the data, so the word character should be defined in those terms. If character is defined as evolutionary novelty, no observation (morphometric or otherwise) can be considered a character a priori. In our studies, we allow for the possibility that each partial warp might describe a separate shape difference that is a character, but no observed shape difference is automatically inferred to be a character. We reassess the individuality of the proposed characters once we have a cladogram inferred from all our data. Then we can ask whether each separately described shape difference is an independent character or, instead, is a component of a character. To make that determination, we examine the distributions of all the shape differences on

the tree, first seeking common patterns in their distributions and then analyzing all those optimized to a single node for anatomical overlap, developmental correlations, and similar modes of evolutionary change. Should they appear to be intrinsically correlated (rather than correlated due to a common history) we interpret the combination of shape differences as representing a single character, recode it as such, and reanalyze the data matrix.

Rohlf apparently overlooks our analyses of phylogenetic correlations as well as our multivariate analyses of ontogenetic allometry when he criticizes our studies for being univariate. In studies of ontogenetic allometry we use the recommended (Bookstein, 1991) biometric procedures for testing the statistical significance of overall ontogenetic shape change (Zelditch and Fink, 1995). In one case (Zelditch et al., 1992) we did not test the null hypothesis of overall shape isometry because the idea that mammalian skulls are invariant in shape from birth to sexual maturity is dubious on biological grounds and our data did not suggest otherwise. In several cases we are interested in hypotheses other than the allometry of overall shape, and we thus test the hypotheses of interest, such as the significance of change at each spatial scale (Zelditch et al., 1992), or the separate significance of each partial warp and of the changes aligned with organismal body axes (Zelditch et al., 1992; Zelditch and Fink, 1995). Other analyses do not use statistical tests at all (Swiderski, 1993; Zelditch et al., 1993), although one uses multivariate analysis, PCA (Zelditch et al., 1993). In our phylogenetic analysis of ontogeny (Fink and Zelditch, 1995) we do not test the hypothesis of ontogenetically isometric body shape species by species, although the results are implied by our other tests. Although we do use multivariate analyses, when appropriate to the biological hypothesis, we cannot use conventional biometric analyses in our phylogenetic studies. In particular, conventional biometric methods for estimating correlations are not appropriate in phylogenetic studies. We instead estimate phylogenetic correlations

from the distributions of characters on a tree, as explained earlier.

We acknowledge that our protocols merit criticism; additional and improved tests of character independence are especially necessary. But finding flaws in our current protocols would not lead us to reject phylogenetic methods of analysis. Finding flaws would lead us to modify the protocols or, if the problems prove intractable, to look elsewhere for characters. We would not turn to the methods that Rohlf recommends such as the one exemplified by his own analysis, a UPGMA phenogram of generalized morphometric distances (Rohlf et al., 1996). Phenetic methods do not address our scientific questions. Nor would we use model-based methods of inference unless the models are relevant to morphological evolution and are well supported empirically.

PARSIMONY

Rohlf's criticisms of coding and phylogenetic parsimony occupy relatively little space in his critique, but they are obviously significant for phylogenetic systematists. Thus, we single them out and consider them in the general context of phylogenetic studies. Rohlf seems to oppose the practice of coding continuously valued variables and the use of phylogenetic parsimony (a term for conventional, i.e., Manhattan distance-based parsimony, as distinct from other methods, also called parsimony, that are based on different principles, models, and metrics, e.g., squared-change parsimony). Rohlf criticizes coding and phylogenetic parsimony on the grounds that these basic elements of a phylogenetic analysis fail to take into account the continuity of the measurement scale and the need for rotation-invariant results. Sensitivity to rotation could imply that conclusions are essentially arbitrary, that is, artifacts of a particular set of variables chosen by an investigator. Although distances between shapes are unaffected by rigid rotations of the morphometric space, the variables are changed by such rotations, and therefore the conclusions based on them also could be affected by rotation. Because coding and phylogenetic parsimony

do not respect morphometric distances, they can be sensitive to the choice of variables. Consequently, phylogenetic conclusions may be sensitive to the particular ways that a multidimensional space is subdivided into characters. Rohlf suggests using methods such as maximum likelihood (Felsenstein, 1981) or squared-change parsimony (Maddison, 1991), which are invariant to the selection of variables, unlike phylogenetic parsimony.

We share Rohlf's concern about the sensitivity of results to arbitrary choices. This is undeniably an important issue. But we see it as a general issue, not one peculiar to partial warps, nor even to quantitative data. To the extent that coding and phylogenetic parsimony are ruled by the continuity of the underlying measurement scale, or the multidimensionality of the data, or the inability to justify one particular basis as the only legitimate one, the arguments are very general. Data used by systematists, including qualitative shape data, behavior, and color pattern, are no more inherently discrete nor one-dimensional nor uniquely justified than morphometric data. The difference between qualitative and quantitative data may be only semantic (Stevens, 1987, 1991). Many qualitatively described traits could also be measured using a scale that is continuously valued (infinitely divisible). Multidimensionality also is an attribute of most systematic data. In addition, we can rarely justify a particular basis of comparison as uniquely best. Thus, some details of Rohlf's arguments may be specific to particular morphometric variables, but important and general implications follow from them.

No one doubts that judgment and some degree of arbitrariness enter into any subdivision of an organism into characters, a point well known to morphologists. Different investigators, handed the same specimens, may subdivide them into different characters. We rarely can know, a priori, that the features we describe as separate traits are indeed individual evolutionary novelties. Individuality and evolutionary novelties are matters of phylogenetic infer-

ence, not raw observation. There is a certain degree of judgment and arbitrariness in any character-based study. But our judgments are based on principles of comparative biology and systematics.

Arbitrariness and sensitivity to rotation are not the crucial issues in this debate. The real difference between our approach to systematics and Rohlf's is the difference between using Manhattan distances to represent hypotheses of novelty and using morphometric distances between observed shapes. As Farris (1983) showed, phylogenetic parsimony can be formalized as minimizing Manhattan distances (number of steps). Farris also showed that Manhattan distances are the only distances that can be interpreted in terms of the quantity minimized by phylogenetic parsimony. Coding puts the observation of morphological differences (qualitative or quantitative) in terms appropriate for parsimony analysis, representing each hypothesis of novelty as a step of one unit (Swiderski et al., 1998). Thus Manhattan distances lie at the core of phylogenetic systematics and we cannot simply replace this metric by another, such as a Euclidean distance (even though Euclidean distances are insensitive to rotation and appropriate for measuring distances among shapes in the tangent space). Euclidean distances have an undeniable role in morphometric studies and we use them in our ontogenetic studies. But replacing the Manhattan distance in systematics by any another metric would require that the new metric be justified in terms of systematic principles.

Methods that do not use Manhattan distances, such as those recommended by Rohlf, may seem free of the problems posed by sensitivity to rotation and the conclusions, for that reason, may seem less arbitrary than ours. But sensitivity to rotation is not the only source of arbitrariness and it may not be the most important one. Phenograms are arbitrary with respect to phylogenetic history (even though they may fortuitously correspond to cladograms), and model-based methods yield arbitrary results unless the process models are biologically justified. The problems

posed by potentially arbitrary choices (of variables, clustering algorithms, models) are neither easy to circumvent nor peculiar to morphometric data. Arbitrariness cannot be eliminated from systematic studies by replacing phylogenetic parsimony with methods insensitive to the choice of the variables.

At present, there is no evidence that phylogenetic results are fatally compromised by sensitivity to rotation. In our analyses, we have obtained the same results from shape coordinates and partial warps, so our conclusions have not depended on the choice of variables. Adams and Rosenberg (1998) claim to show that conflicting results can be obtained from different variables (describing the same shapes) but their analyses and conclusions are questionable, for reasons we discuss in our response to their paper (Zelditch and Fink, 1998). Naylor's (1996) results, although sometimes cited as showing the problems with our methods, do not bear on our method because Naylor used a different one. Nor do Bookstein's (1994) arguments challenge our argument; we would not dispute Bookstein's geometric arguments but we do question the systematic implications inferred from them.

The delimitation of characters is usually difficult, and character-based systematics is always based on characters. Although the questions raised by morphometric data may seem peculiar to those data, they are nevertheless general. Many of these questions are already familiar to systematists, albeit in other terms. And yet, even though we rarely can say that our basis of comparison is the uniquely justified one, we do not normally use methods that are invariant to the selection of characters. We do not normally resolve the problems posed by character-based systematics by turning to phenetics or unsupported evolutionary models. We see no reason to invoke special rules for morphometric data.

Conclusions

In our response to Rohlf, we have focused on systematic issues because we agree with most of his other points and those agreements are reflected in our publications. We do not defend the notion that partial warps typically correspond to units of morphology or modules of a biological process because they need not; we have made that point repeatedly (e.g., Zelditch et al., 1992; Swiderski, 1993; Fink and Zelditch, 1995). We do not defend interpreting individual variables in terms of individual biological processes because we argue that they should not be interpreted in those terms (Zelditch and Fink, 1996). We do not defend testing multivariate hypotheses by series of univariate tests because we consider that procedure to be indefensible. We do not dispute any of Rohlf's purely mathematical arguments, such as the fact that partial warps depend on the choice of reference form, or that a given set of partial warps is simply one suite of variables for analyzing shapes in the tangent space. There is no room for disagreement on those points. Our substantial agreement with Rohlf on these points may be obscured by our emphasis on disagreements, but those disagreements deserve emphasis because they are genuine and those issues matter to systematists.

Like other choices we make in systematics, the use of partial warps must be justified. That requires a rationale for a particular reference form (because it determines the partial warps), a rationale for using partial warps rather than another set of variables (e.g., shape coordinates), and a rationale for using individual partial warps rather than linear combinations of them (e.g., principal components). Our justifications for our variables are based on homology and comparative biology, but that does not restrict us to partial warps, because other variables, like shape coordinates, also can be justified in those terms. We prefer partial warps over shape coordinates because shape coordinates (like superimposition techniques) are unable to visualize spatial correlations over the landmarks (Bookstein, 1996).

The focus of our disagreement with Rohlf is the use of phylogenetic systematics to analyze the evolution of shape features described by the partial warps. This

may seem a minor point because Rohlf does not devote much space to it, but it is at the heart of our evolutionary studies. The methods we use, phylogenetic parsimony analysis of shape differences coded as discrete states, depend on Manhattan distances, and these distances are sensitive to rotation. So, although the disagreement may seem to be about mathematics, in reality it is entirely about systematic methods. Our justifications, both for partial warps and for phylogenetic parsimony, are consistent with general principles of phylogenetic systematics. Methods insensitive to characters are not consistent with those principles.

ACKNOWLEDGMENT

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