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Partial Warps, Phylogeny and Ontogeny: A Reply to Adams and Rosenberg

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Adams and Rosenberg (1998) ask two questions prompted by our analyses of ontogenetic transformations (Fink and Zelditch, 1995). Both concern using partial warps to obtain characters for phylogenetic study. The first question arises from an issue left open by us: how to choose a reference form when there are multiple outgroups. As Adams and Rosenberg point out, we did not say how to select among equally reasonable choices. For good reason, Adams and Rosenberg ask if that choice affects the conclusion. The second question arises from an issue raised by both us and Rohlf (1998): whether the choice of basis (the coordinate system for the morphometric analysis) affects phylogenetic results. Adams and Rosenberg address this question in quite specific terms: whether rigid rotations affect phylogenetic conclusions.

Unfortunately, even though Adams and Rosenberg raise important and interesting questions, their studies are seriously flawed and permit no conclusions. One flaw is common to all their analyses: Adams and Rosenberg omit several necessary tests of independence. In particular, they do not examine their characters for anatomical overlap, nor check them for developmental correlations, nor compare characters with respect to modes of evolutionary change in ontogeny. In addition to that departure from our protocol, Adams and Rosenberg's conclusions are undermined by several problems discussed in more detail later: (1) They confound outgroups and reference forms, (2) they view the issue of choice of basis from a purely phenetic perspective, (3) their description of results is misleading, and (4) their interpretations are pervaded by conceptual confusion.

OUTGROUP/REFERENCE FORM

Adams and Rosenberg wish to know whether the choice of reference form, which is also an outgroup, affects the phylogenetic conclusions. So they conduct four analyses, changing *both* the outgroup *and* the reference form simultaneously! But we already know that outgroup choice can affect phylogenetic conclusions. To study the effects of reference form, outgroups should have been left constant and only the reference form varied. Due to their design, Adams and Rosenberg cannot isolate the effects of the reference form on phylogenetic conclusions because they cannot disentangle the anticipated effects of changing the outgroup from the possible effects of changing the reference form. Their analysis is thus severely flawed.

THE PHENETIC VIEW OF THE BASIS OF ANALYSIS

Adams and Rosenberg ask whether different bases can influence the phylogenetic conclusions. To address that question empirically, they must specify alternative bases and decide which among them are valid choices. Apparently, Adams and Rosenberg consider all rigid rotations to be equally valid choices. That perception is defended on the grounds that "Because the relative distances among taxa in tangent space are of interest, any orthogonal basis spanning tangent space is equally relevant to the study of shape" (171). But those relative distances are *not* of interest in phylogenetic studies; in the context of systematics, they are the subject of phenetic studies. The fact that rigid rotations do not alter phenetic distances is immaterial to deciding valid choices for a phylogenetic analysis. Before the equally valid choices can be specified, one must ask whether the particular rotations make sense from a phylogenetic perspective.

We have argued that some rigid rotations do not make sense from a phylogenetic perspective (Zelditch et al., 1995). We singled out principal component scores as one set of variables incompatible with phylogenetic reasoning. Yet, Adams and Rosenberg use those scores as one of their data sets, along with scores based on two QR decomposition rotations and a random rigid rotation. The phylogenetic justification for these choices is not self-evident and Adams and Rosenberg do not defend their choices. Thus, they seem to address the question: Do unjustified and potentially invalid bases affect phylogenetic conclusions? That question may be interesting but it is beside the point. The more relevant question is whether equally well-justified choices affect those conclusions. For example, when there are several outgroups and no means for deciding which should be the reference, any of them are equally well justified.

MISLEADING DESCRIPTION OF RESULTS

Adams and Rosenberg claim that their results reveal the dramatic effects of changing the reference form/outgroup or basis. But contrary to that statement, their results are reassuringly consistent. Of the eight data sets analyzed (four based on different reference forms/outgroups, and four based on different rotations of partial warps [one cladogram is shown twice]), four imply the ingroup topology ((ONT, OK)(GA, NY)), three imply (ONT (OK (GA, NY))), and one data set yields both topologies. In our view, those are not "dramatically different" results. The slight difference actually found could be due to data that do not strongly support one hypothesis relative to the other.

When the data provide almost equal support for two (or more) alternative hypotheses, redefinition of individual variables (by changing the reference form or basis) could easily tilt the balance of evidence from one poorly-supported result to another. It seems premature to attribute their results to mathematical artifacts when they have not checked other explanations for their results. Unfortunately, we cannot check whether their characters are independent, nor assess the support for their cladograms. This is particularly important because the evidence favoring one hypothesis could consist of a single character, counted twice. Had they provided the necessary information, this explanation could be pursued. Since the authors did not describe the characters, we cannot check them for anatomical overlap; nor can we check them for developmental correlations (those correlations are not given). Neither can we estimate the support for the cladograms, nor evaluate their relative support (the analyses are published without accompanying data matrices or character support indices).

In our view, their data may well be equivocal. The taxa are nominally conspecific host races. Adams and Funk (1997) argued that they are actually cryptic species, distinguishable by statistical tests of shape. But statistical differences among average adult shapes (or intercepts) do not ensure that ontogenetic transformations of shape exhibit an unequivocal phylogenetic structure.

PERVASIVE CONCEPTUAL CONFUSIONS

Adams and Rosenberg exhibit considerable confusion on many points, none of which affect their conclusions but all of which betray misunderstanding of our methods (in particular) or of phylogenetic analyses (in general). For example, they seem to believe that our protocol prohibits an adequate representation of ontogeny because we use the outgroup juvenile shape as a reference form. Certainly that choice has consequences, but it does not lead to misrepresentative ontogenetic transformations. It means only that the reference form is not the actual biological starting point for each ontogenetic series. That is taken into account in our ontogenetic analyses. Adams and Rosenberg also suggest that our analyses face problems atypical of phylogenetic studies because we cannot "desensitize" our characters to the variation among outgroups, even though we can use multiple outgroups (only one serves as the reference form). But the variation can be taken into account by use of multiple outgroups. The role of the starting form is a different issue. In any case, diversity of juvenile shape (or of ontogeny) does not affect standard phylogenetic procedures for coding or polarizing characters. It means only that we cannot designate one shape or ontogeny as "ancestral."

Adams and Rosenberg also demonstrate confusion when they cite Naylor's (1996) results as a challenge to ours. Naylor's protocol departs substantially from ours, which is hardly surprising because he was not informed about our protocol. His interpretation was based on informal communications with us, not on the final, published version. Moreover, our methods require studies of variation and ontogeny, but Naylor's imaginary "taxa" have neither. In the absence of our protocol, Naylor was forced to devise a method of coding that could be applied to a single shape representing each "taxon" and to forego testing character independence. By construing Naylor's study (and his interpretations of findings) as comparable to ours, Adams and Rosenberg betray considerable confusion about our methods and interpretations.

CONCLUSIONS

The questions raised by Adams and Rosenberg are important and should be addressed. Unfortunately, their analyses do not address those questions, being severely flawed in several ways. Contrary to their assertions, they do not demonstrate any consequences specific to changing the reference form, and they do not show that equally valid alternative bases yield dramatically different conclusions. Instead, they show that different outgroups and phylogenetically unjustified variables can produce consistent (if possibly equivocal) results. Perhaps the shape data of *Neochlamisus bebbianae* do not evince a hierarchical, phylogenetic structure. Perhaps shape data, by themselves, cannot resolve what phylogenetic structure exists. Neither Adams and Rosenberg, nor we, can explain their results until they complete their analyses of character independence, redesign their study so that outgroups are not varied along with the reference form, justify their bases in phylogenetic terms, and actually assess the character support for their alternative cladograms.

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