CLADISTICS AND THE LAND PLANTS: A RESPONSE TO ROBINSON

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Cladistics and the land plants: a response to Robinson. Brittonia 37: 282-285. 1985. -- The reconstruction of phylogenetic relationships should be based not on belief but on an explicit and logical analysis of all available characters. Hennigian phylogenetic systematics (cladistics) provides a framework for evaluating putative homologies characterizing particular hierarchical levels, determining relationships of taxa sharing congruent patterns of homologies, and constructing a classification based on this information. Fossils can and should be included in the analysis if enough of the relevant characters are preserved; this is not currently possible for early land plants because of the fragmentary fossil record. To avoid circularity, adaptive and functional considerations should be addressed only after a phylogenetic hypothesis based on patterns of shared homologies is available.

We would like to thank Dr. Robinson (1985) for demonstrating that the charges listed in the conclusion to our first paper (Mishler & Churchill, 1984) were not directed entirely at straw men. His approach incorporates each of the aspects that we argued in the conclusion of our paper are characteristic of prevailing theories of systematics.

Dr. Robinson did not rebut these general arguments, nor did he question the homology of any of the 51 characters we used in our cladistic analysis. Instead he criticized those points of our analysis that support the old theory of the "antithetic" origin of the sporophyte generation in land plants. With admirable honesty, Dr. Robinson states that his rebuttal is based on his belief in an opposing theory, the "homologous" origin of alternation of generations in land plants.

We will refrain from polemics about opposing "beliefs," because we have no a priori feelings concerning the correctness of either theory and because we think such metaphysical considerations should be minimized in science. We are merely interested in a logical and explicit reconstruction of land plant phylogeny based on all available characters. If anything, one of us (B.D.M.) began the analysis with a bias towards the homologous theory (having been taught that view). We examined a number of cladistic hypotheses but none supported the homologous theory. In fact, it became clear that accepting the homologous theory led to very unparsimonious conclusions, requiring character transformations and hypothetical ancestors for which there was no evidence. We will address the substantive issues raised by Robinson seriatim.

First, however, we must correct Dr. Robinson's statement (first paragraph) about what our cladogram attempted to show. It (like all cladograms) simply summarized the hypothesized sister-group relationships of the major groups of extant land plants as evidenced by shared homologies (synapomorphies) at various levels. It, like all cladograms, did not imply that any extant group gave rise to another, only that extant groups shared a common ancestor at some point.

We must also correct Dr. Robinson's characterization of the debate over the antithetic versus the homologous theory. The issue has not been whether the genetics of the two generations are independent. As phases of the same life cycle the gametophyte and sporophyte share a common genotype. It has been demonstrated experimentally (see Smith, 1978 for a review) that one generation can be transformed to the other in mosses (through apogamy and apospory) without a change in ploidy level. At issue in the debate over the origin of alternation of
generations in land plants is solely the form of the immediate common ancestor of the group. Did this common ancestor have an isomorphic alternation of independent generations, or was it haplontic and oogamous with zygotic meiosis? That is the question. See Graham (1985) for a lucid treatment of this question and its likely answer.

Large phyletic gaps.—We discussed the problem of large phyletic gaps in our original paper (p. 418). We must reiterate the obvious here: one can only use available evidence. Currently unknown taxa and characters may modify our conclusions once they are discovered, but until then one has to do without. The parsimony method that cladists use does not assume that evolution is parsimonious. It is simply a methodological rule (common and necessary for all scientific inference) that ad hoc assumptions should be minimized.

Given Dr. Robinson’s comment that “such wide phyletic gaps cannot be bridged with confidence by any method of phyletic study,” it will be interesting to see what method he uses (belief, perhaps?) when as promised he publishes his own view.

Fossils.—Fossil taxa can and should be incorporated into a cladistic analysis if enough characters are available to allow reliable comparisons with extant taxa. Given the fragmentary nature of the Silurian and lower Devonian fossil record (reviewed by Taylor, 1982) it is currently impossible to find enough characters preserved to describe one fossil sufficiently to be included in a cladistic analysis of extant land plants at this level. Some progress is being made in using fossil taxa of seed plants in a cladistic analysis at a lower phylogenetic level (Crane, 1984, and pers. comm.), since these taxa are much more completely known.

We have recently prepared an elaboration (Mishler & Churchill, in press) of our 1984 paper. In this we present detailed preliminary cladograms of the green algae, liverworts, and the hornworts, present the most likely archetypes (i.e., hypothesized ancestral forms) for the major branch points, and discuss the fit of fossil evidence to these archetypes. For the present, fossils must be given little weight, but we argue there that known fossils fit our hypothesis well.

Contrary to Robinson’s claim, we were not biased against evolutionary reduction of the bryophytes. In fact, our hypothesis requires considerable reduction as will be noted below.

Transfer of characters between gametophyte and sporophyte.—Dr. Robinson is in error when he states that “the phloem cited for the mosses is in the gametophyte while that in the tracheophytes is in the sporophyte.” Reference to Hébant (1977) will show that hydroids and leptoids (xylem and phloem in our interpretation) are found in both the sporophyte and gametophyte of mosses. Scheirer (pers. comm.) pointed out that in a given moss species vascular tissue is always better developed in the sporophyte, if there is any difference in the expression of the tissue in the two generations. Furthermore, vascular tissue is occasionally expressed in polyploid gametophytes of the tracheophyte, Psilotum (Bold et al., 1980). We took sporophyte branching to be a synapomorphy of the tracheophytes because (with rare teratological exceptions) no extant bryophyte or charophyte produces a branched sporophyte.

Reductions of characters.—Contrary to Robinson, cladistic principles do not “bar the use of loss of characters as synapomorphies.” Hennig (1966, 1981) used “loss of a character” at various levels within the Insecta (see further discussion by Churchill et al., 1985; also Boudreaux, 1979). One of us (Mishler, in press) has used cladistic analysis to reconstruct phylogeny in the moss genus Tortula, a group in which character loss through neoteny appears to have been frequent. In Mishler and Churchill (In press) we used several “loss” characters as synapomorphies.