Statistical evaluation of the clade ''Rhabdoweisiaceae''

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Abstract. Two previously published molecular analyses of the Dicranaceae and related families that supported as a taxonomic entity the clade ''Rhabdoweisiaceae'' as a segregate of the Dicranaceae s.lat. were subjected to a nine-step statistical analysis. The first study did not well support the Rhabdoweisiaceae but, in combination with the second, reliable support was obtained demonstrating that Rhabdoweisiaceae are both monophyletic and not merely a basal branch of the Dicranaceae. Although such molecular conclusions may guide taxonomy, there is no satisfactory morphological definition of the Rhabdoweisiaceae, and that uncertainty may lead to a paraphyletic classification of the Dicranaceae to include Rhabdoweisiaceae as simply one or more basal lineages.

Keywords. Mosses, Dicranaceae, Rhabdoweisiaceae, phylogenetic isolation, statistical reliability, paraphyly, multiple tests, phylogeny.

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Five studies, by Hedderson et al. (2004), La Farge et al. (2000, 2002), Stech (1999) and Tsubota et al. (2003) found, from molecular analyses of chloroplast DNA regions, evidence for the separation from the Dicranaceae of a clade represented by about 18 exemplars of species as the ''Rhabdoweisiaceae.'' The Rhabdoweisiaceae Limpr., long submerged in the Dicranaceae, are presently recognized, in part on the basis of these studies, in a recent influential classification of the mosses by Buck and Goffinet (2000), modified by Goffinet and Buck (2004). The family was re-described by Frahm (2000) based on the molecular work of Stech (1999). Concern about the utility of the Rhabdoweisiaceae has arisen in work on the bryophyte volumes of the Flora of North America project, and certain authors producing treatments for the Dicranaceae have opted not to recognize the Rhabdoweisiaceae. Were they justified? How shall we test the Dicranaceae as defined traditionally when challenged by molecular evidence?

Methods

Several concepts that are either new or unfamiliar to bryologists are represented here by abbreviations: **BA** is branch arrangement, at minimum a resolved 4-taxon tree, or when rooted simply three taxa, two of which are sister groups, and when well supported represents a conclusion of monophyly; **BCI** is binomial credible (or confidence) interval, for a 4-taxon data set, approximated by 1 minus the chance of random occurrence of the number of synapomorphies for the terminal two lineages out of the total synapomorphies shared by all three pairs of the three terminal lineages; **BP** is nonparametric bootstrap value; **BPP** is Bayesian posterior probability; **DI** is decay index or Bremer support; **FIR** is formula for implied reliability (see below); **PBA** is probability of branch arrangement, either the BPP or the BCI interpreted as a probability using translation tables from simulated 4-taxon data sets (see below).

A nine-step procedure, the ''operative transform,'' for evaluating the reliability of published

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molecular analyses (Zander 2007a) was applied, resulting in distinguishing high (0.95 and greater) probabilities of reconstructed BAs. Two quite separate problems are involved: (1) determining the reliability of the molecular phylogeny and (2) how to represent genealogy, morphology and any known evolutionary ecology in classification.

Step 1: Establish probabilities for all BAs in all published studies relevant to a BA of interest. Use BPPs directly or translate BPs and DIs into approximate probabilities as BCIs using translation tables (Zander 2004, 2006a). The BP-to-BCI tables were created from simulations with contrived four-taxon data sets as explained by Zander (2001). For Step 1, if there are many relevant cladograms, choose a single cladogram, usually the most complex or well supported, to work with; in this case that of La Farge et al. (2002). Translation of the BPs (all above 0.50) given by the authors to BCIs was done for all internodes of the La Farge et al. (2002) cladogram, and the BCIs were then accepted as approximate PBAs.

Step 2: Use Bayes' formula to combine published PBAs into a single posterior probability of branch arrangement (PBA) for each particular BA of interest. Two kinds of combination are possible, morphological (as a subjective prior) and molecular, and two molecular studies (involving empirical priors). Step 2 can be done immediately to deal with morphological priors, or even when two studies are available and the data are easily compared. Otherwise, the nine steps can be done recursively, as is done here with two molecular studies, when published cladograms are complex or simply rather different. Huelsenbeck and Ronquist (2001) and Huelsenbeck and Immenov (2002) have described making the posterior probability of one analysis the prior for the next (in empirical Bayesian analysis) by substituting the posterior probability of the previous study prior for a non-informative prior during the next analysis. The present simple method using Bayes' formula (Zander 2003b) advocated here is, however, nonparametric, and can be used without complex analysis.

For the purpose of combining already analyzed data sets, likelihoods of all parameters have already been dealt with in the published study that one is analyzing, and the standard Bayesian conditioning simply requires that each factor in the formula be a likelihood for the same BA. Multiple studies can be combined: each posterior probability from using Bayes' formula with support values for a particular BA, from analysis of two studies, becomes then the prior likelihood for the next analysis using yet a different, third study. Because the result is conditioned on a particular BA, previously published contrary branch arrangements require estimation of support for the BA of interest from that given for the contrary BA. Subtracting the support for the contrary BA (or BAs) from unity is a generous way to do this. The uncertainty provided by support probabilities less than 0.50 must be included in the calculations, for instance as an estimated mean of 0.33 and 0.50. Support from morphological studies may be generalized under three levels: 0.95 if the BA is the same as the molecularly derived BA, 0.05 if contrary and the morphological evidence is fully supportive of that contrary BA, and 0.50 if the morphological result is equivocal. Here Dicranaceae s.str., following La Farge et al. (2002), are apparently a morphologically well-characterized group, at least after excision of the Rhabdoweisiaceae and a group equivalent to the Leucobryaceae, and here 0.95 is used as a morphological prior, though an alternative prior of 0.50 is also evaluated.

In the case of published papers on the Rhabdoweisiaceae, only chloroplast DNA sequences were used. The Hedderson et al. (2004) and Werner et al. (2004) studies used *rps*4, while La Farge et al. (2000) used *rps*4, *rbc*L and *trn*L-*trn*F span (ultimately ignoring *rbc*L because of little resolution), and La Farge et al. (2002) used *rps*4 and *trn*L-*trn*F. These were largely presented as total evidence, with combined data sets. Another study by Stech (1999) used *trn*L-*trn*F, the same sequences used by the La Farge et al. (2000, 2002) studies. An additional analysis, that of Tsubota et al. (2003), used *rbc*L alone (and different analytic software) and found genera of Rhabdoweisiaceae to be rather distant from the Dicranaceae; these data based on *rbc*L, a different sequence, are not subsumed by the La Farge et al. (2002) study, and cannot be ignored. The Tsubota et al. (2003) molecular information is here combined, in a Bayesian fashion, with the La Farge et al. (2002)

study not immediately but only after the latter analysis is subjected to the full operative transform for clarity and demonstration purposes.

Combining support values derived from approximately the same data would falsely increase the posterior probability, so together with the morphological prior only two studies, first the most complex and data-rich of the *rps*4 and *trn*L-*trn*F studies, being that of La Farge et al. (2002), and the Tsubota *rbc*L study are here relied on for support values for branch arrangements. Studies based on different loci are subjected to the full nine steps, then support values of BAs were combined using Bayes' formula. In any cases where contrary BAs are generated in different studies from essentially the same data, uncertainty contributed by different methods must be taken into account in another fashion, see Step 5.

Step 3: Partition the cladogram into phylogenetically isolated subclades, using pre-study concepts. This step formalizes the standard practice of focusing on only particular parts of a cladogram for evaluation, and provides exact measures of support. Steps three, four and seven deal with multiple test problems, in this instance when a set of BAs each with individual support must be true at once. Rather than deal with frequentist Bonferroni or sequential Bonferroni correction (Hochberg 1988; Holm 1979) or control of False Discovery Rate (Benjamini & Hochberg 1995), likelihoods are simply treated as contributing to a joint probability measure. Likelihoods (empiric measures of support) can be treated as probabilities (ideal, generalized expectation) if they are demonstrably non-null. Because BPs and BPPs greater than 0.50 are seldom obtained by random data under parametric bootstrap (Zander 2003a) they can justifiably be treated as probabilities (as PBAs after conversion to BCIs). For example, a set of two lineages each supported at 0.95 would have the probability of the product, or 0.90, of both being true at once; for a set of two lineages to be true (at the same time) at 0.95, both must average 0.975. There is only one relevant pre-study phylogenetic partition in the La Farge et al. (2002) and the Tsubota et al. (2003) cladograms, consisting of the Dicranaceae s.str. and the Rhabdoweisiaceae, plus any intermediate internodes.

Step 4: Preselect conclusions of monophyly to test, prioritized to break ties. There were only two conclusions of monophyly, those involving the Dicranaceae s.str. and Rhabdoweisiaceae, thus support values for each of the two lineages must average 0.975 for the statement "both lineages are monophyletic" to be true at sufficiently high reliability to contribute to a change in classification. Given that the Dicranaceae s.str. are the group from which the Rhabdoweisiaceae are isolated, if there were two support values of only 0.95, then we would choose the one for the Rhabdoweisiaceae and consider the one for the Dicranaceae s.str. as speculation as far as molecular data are concerned, though with Bayes' formula its accepted status on a morphological basis (with a subjective prior of 0.95) would allow any PBA from molecular data above 0.50 to be supportive (as increasing the posterior probability above 0.95).

Step 5: Impose a penalty for unaccounted assumptions. There are at least 100 assumptions (Zander 2005) common in the literature that are involved in phylogenetic analysis and contribute uncertainty not reflected in support values for branch arrangements as generated by analytic software. Chief among these are possible changes in BAs or PBAs due to reasonable alternative sequence alignments and different but reasonable outgroups. Although Redelings and Suchard (2005) have made a major advance in dealing with the alignment problem albeit with considerable computational limitations, many difficulties remain, and we must still deal with the older literature short of redoing the studies. An across-the-board penalty of 1% on all support values is justified, although *ad hoc*, in the following manner: if only 10 of the 100+ assumptions were relevant to any particular BA of interest, and each assumption was wrong and thus changed the BA or support value of the BA only one in 1000 times, 10 $\times$ 0.001 yields 0.01, or a minimum of fully 0.20 of the 0.05 window of reliability. The only other alternatives to this procedure are either throwing out the study as too speculative, or basing classification (or biogeography or other contingent research) on speculation not easily distinguished from well-founded theory. After using the BP-to-BCI tables for conversion to PBAs, the 0.01 penalty was made.

Step 6: Support values may be increased to 0.95 or more by combining lower values with the Formula for Implied Reliability (FIR). This formula is based on the well-known, simple probabilistic calculation that the chance of one thing happening out of two or more is given by multiplying the chances each will *not* happen, then subtract the product from one. We can thus calculate an implied PBA as the chance of one BA correct out of several concatenated BAs. This is, from concatenated BAs i through j and defining probabilities of BAs being correct as P_{ij}:

$$P_{\text{one correct BA}} = 1 - \left((1 - P_i)(1 - P_{i+1}) \ldots (1 - P_j)\right)$$

For instance, consider two concatenated internodes, each at 0.80 probability. The chance one BA is correct is one minus the quantity 0.20×0.20, or 0.96, and that then is the support for the distance between the end members. Increasing distance between BAs on a cladogram, of course, implies greater reliability that they are separately integral. The position of the intermediate lineage(s) is equivocal and can be collapsed toward the root of the tree. The FIR is used both to determine the number of reliable nodes between a distal subclade and a node towards the root, or between two subclades. PBAs of internodes cannot be reused for separate calculations because determination of monophyly in respect to the root is not especially relevant, rather monophyly in respect to nearby clades is important. The question to ask is: If only one of the two or more nodes used for FIR calculation is correct, will that support at least a one node distance between two subclades of interest?

The FIR was used to combine separately concatenated internal support for the Dicranaceae s.str. and for the Rhabdoweisiaceae from the La Farge et al. (2002) cladogram, and later the Tsubota et al. (2003) cladogram, to see if one or more internodes at 0.95 implied PBA or greater can be reached. The FIR analysis can be done with an unrooted cladogram to see if two lineages are distinct from each other, then with a rooted cladogram to see if two lineages are distinct in respect to the root of the cladogram, but in no case can two support values be used twice in the same calculation.

Step 7: Correct for multiple tests. After corrections and consolidation of all BAs into only those BAs with support of 0.95 or greater between the Dicranaceae s.str. and Rhabdoweisiaceae, the reliability of the two putative lineages can be evaluated as prepared for in Steps two and three. Step 7 judges whether two lineages are reciprocally monophyletic at 0.95 or greater probability. Step 8 tells whether two lineages are not just sister groups. Both are similar but separate multiple test problems.

Step 8: Distinguish taxonomically independent lineages from mere basal branches in a molecular context. With molecular data alone, to distinguish a lineage from being simply a basal branch (and therefore to support a new name), we need a distance of at least two reliable internodes with one or more morphologically well-characterized intermediate lineages (minimally a sister group to the terminal lineage). This is because a sister group cannot stand alone taxonomically with only molecular support at the present level of knowledge (even a unique synapomorphic trait or set of traits is not particularly acceptable among taxonomists today without morphological support). The two reliable lineages (i.e., the monophyletic terminal group and the internode below it) must be true at the same time (i.e., as a set), and so the product of their molecularly based support values should reach 0.95. Thus, high support for reciprocal monophyly for both lineages from molecular data alone is *a priori* insufficient to distinguish a lineage nomenclaturally as a new taxon rather than a basal branch.

Step 9: Check for contravention of Dollo's Rule against reëvolution of complex traits. This step requires consideration of evolutionary reticulation. There are many examples of complex deep homologies reëxpressed higher in a phylogenetic tree, as reviewed by Zander (2006b) who demonstrated that *Timmiella*, though isolated near the base of the Werner et al. (2004) cladogram, could not be morphologically separated from the Pottiaceae because of possession of the characteristic twisted peristome and a host of pleisiomorphic traits. The Pottiaceae s.str. were considered an evolutionary Lazarus taxon, with the peristome arising several times in the family but not elsewhere in families intermediate between the Pottiaceae s.str. and *Timmiella*. As no such massive discontinuity in homology is evident between the Dicranaceae s.str.

and the Rhabdoweisiaceae, this step was satisfied as inapplicable, but see discussion of paraphyly below.

Recursion with a second published analysis using different data. The La Farge et al. (2002) study was fully analyzed (**Figs. 1**, **2**) for demonstration purposes. The Tsubota et al. (2003) study was fairly complex, warranting its own, later analysis (**Fig. 3**). The questions asked the second round were: (1) can the probabilities of branch arrangements be increased by support from the Tsubota et al. (2003) study using the Bayes' formula of Step 2, (2) what new branch arrangements developed through the FIR in Step 6 may be supported (or contradicted) by that second study; and (3) are the conclusions different? The new analysis focused on the same branch arrangements (those between Dicranaceae and Rhabdoweisiaceae), and thus already addressed Steps three, four, and seven. As with the first study, the analysis of Tsubota et al. (2003) sought to find intermediate lineages demonstrating that Rhabdoweisiaceae, as represented by molecular exemplars, are not just a basal branch of the Dicranaceae, and evaluated support for their reciprocal monophyly.

Results

The La Farge et al. (2002) cladogram. The La Farge et al. (2002) cladogram was fully transformed through the nine steps, resulting in **Fig. 1**, which presents the single partition of interest (labeled as 0.96 PBA) and includes correction for multiple tests, and **Fig. 2,** the original cladogram fully transformed into one with only branches having support (particularly from Step 7) of probability 0.95 or greater, but without correction for multiple tests (the chance of all of these high BAs being true at once in the full cladogram is the product, or 0.51). The relevant support values that can be used as non-null factors in calculating the PBAs from the original published cladogram (see **Fig. 1**) are as follows: Dicranidae supported with 15 steps at 0.91 BP = 0.96 BCI, minus 0.01 penalty for unaccounted assumptions = 0.95 PBA. Under the same calculation and penalty, the two more distal BPs of 0.64 (5 steps) and 0.58 (5 steps) yield 0.68 and 0.62 PBA, respectively. The Dicranaceae s.str. of 0.78 BP (15 steps) = 0.86 PBA. The Rhabdoweisiaceae of 0.62 BP (5 steps) = 0.71 PBA. The Dicranaceae s.str. are here taken to be morphologically well characterized but the Rhabdoweisiaceae are not (see discussion below); we can thus assign the somewhat arbitrary subjective Bayesian priors of 0.99 and 0.50, respectively, with Bayes' formula yielding PBAs of 0.99+ and 0.71. We can now combine support values with FIR to yield reliable (i.e., 0.95+ PBA) BAs.

With a morphology prior of 0.99 (Step 2), the Dicranaceae s.str. form a reliable group at 0.99+ PBA rooted at Dicranidae; with 0.50, the PBA is 0.98 (combining 0.86, 0.62, and 0.68), for the latter see **Fig. 2**. It cannot be rooted any higher in the tree because the two nodes between, of 0.62 and 0.68 PBA, yield only 0.86 chance that there is one additional reliable BA proximal to the Dicranaceae s.str. in the tree. Even without using Bayes' formula and the subjective priors, the Dicranaceae s.str. could be rooted at the node marked 0.64 BP (= 0.68 PBA), but then that node would have to be collapsed to the base of the Dicranidae tree, anyway, since the node with 0.68 PBA is not reliable and it is the only node with a BP value more proximal to the base.

Considering the clade of Rhabdoweisiaceae as presented by La Farge et al. (2002), only a single internode at 0.96 PBA is possible when the original cladogram, viewed as unrooted, is analyzed with FIR (**Fig. 1**). Between the Rhabdoweisiaceae and Dicranaceae s.str. the original cladogram (viewed as unrooted) showed only two internodes with BPs greater than 0.50 linking the two groups, translating to PBAs of 0.71 and 0.86. With FIR calculation, the two internodes are probabilistically equivalent to a single internode of 0.96 PBA, and the exemplars in the two groups are well distinguished if all other taxa are ignored.

There is, however, no strong support from La Farge et al. (2002) for distinction of the Rhabdoweisiaceae from being a sister group basal to the Dicranaceae s.str. If the set of the Rhabdoweisiaceae and Dicranaceae s.str. are rooted, one or the other must split into several branches. With respect to the Dicranidae root (**Fig. 2**), the Dicranaceae s.str. are split into two reliable lineages (labeled "Dicranaceae") with two genera (labeled "D") occurring elsewhere, while the Rhabdoweisiaceae are also in part reliable but two genera (including *Rhabdoweisia* itself, labeled "R")

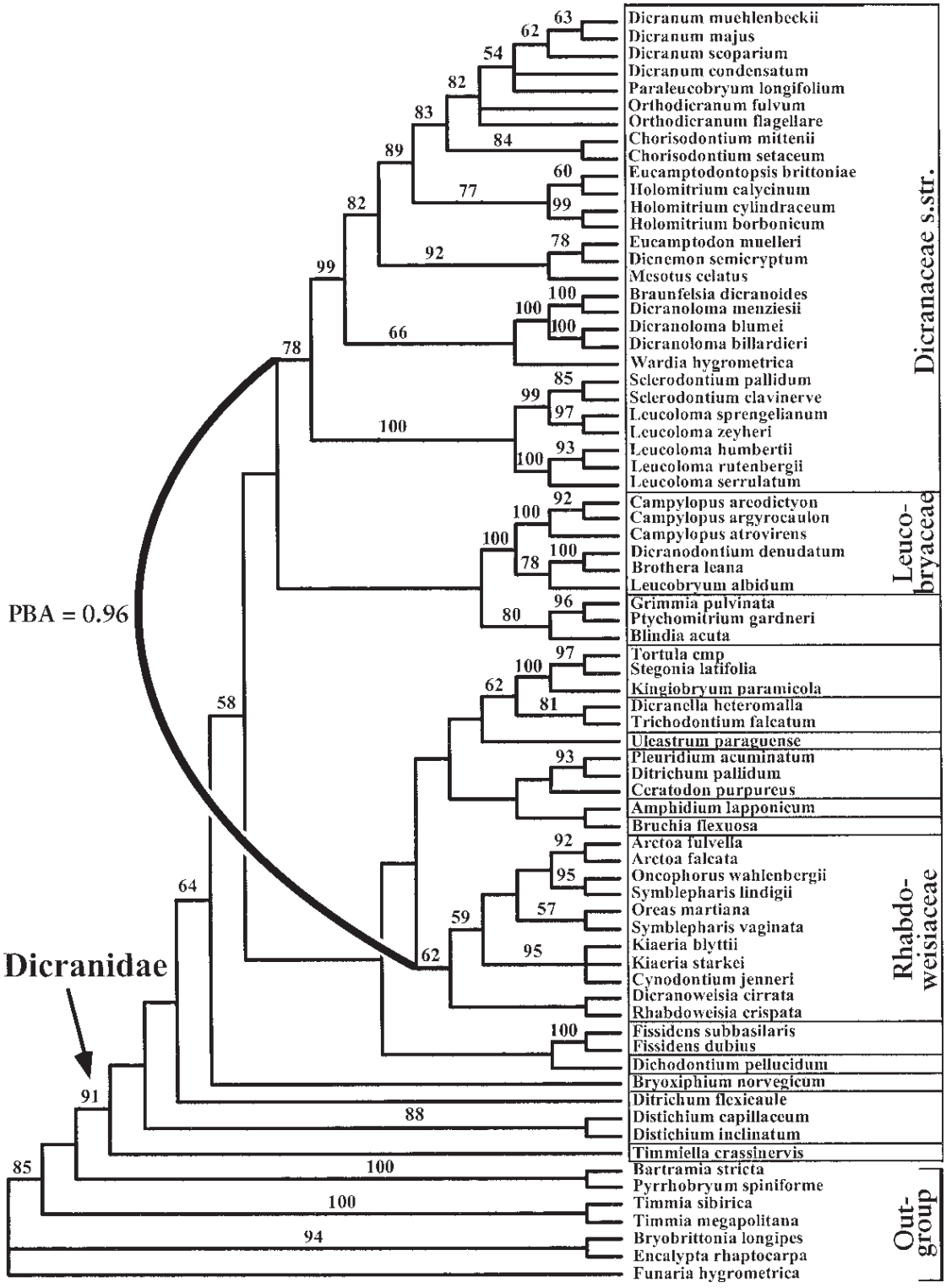

Figure 1. Cladogram based on that of La Farge et al. (2002) showing that the Dicranaceae s.str. and Rhabdoweisiaceae, when not rooted in the Dicranidae, are reliably distinguished at branch arrangement probability 0.96. Numbers above branches are original bootstrap values.

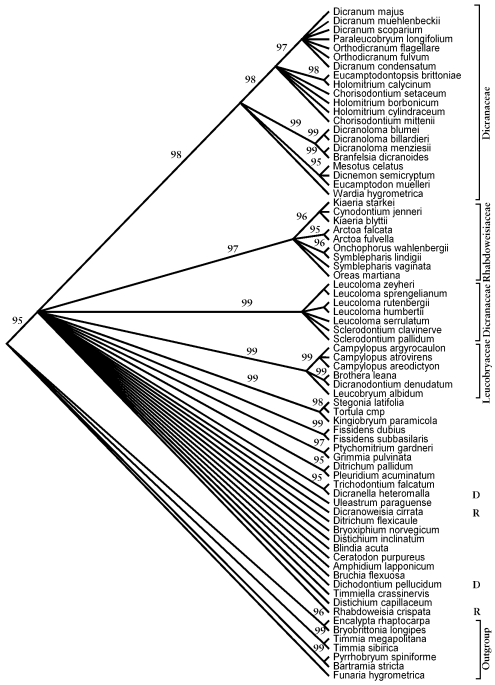

Figure 2. The same cladogram reduced to only branch arrangements supported at 0.95 probability or above, using the nine-step statistical procedure. When rooted in the context of the Dicranidae, the original Rhabdoweisiaceae are dissected, with *Rhabdoweisia* itself placed elsewhere in the tree. Other families are derived as multifurcations at the base of the Dicranaceae. The numbers are probabilities of branch arrangements, isolated members are identified as D = Dicranaceae and R = Rhabdoweisiaceae.

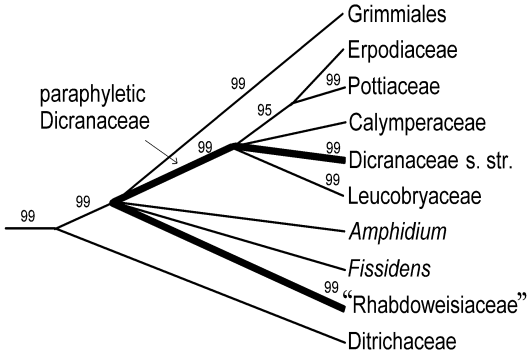

Figure 3. Cladogram based on that of Tsubota et al. (2003), but including only taxa relevant to the distinction of Dicranaceae s.str. and Rhabdoweisiaceae. Both families are molecularly reciprocally monophyletic at 0.98 probability (Step 7), and reliably are not sister groups at the same level of reliability (Step 8).

are scattered elsewhere. The Dicranaceae s.str. of La Farge et al. (2002), less *Dichodontium pellucidum* and *Dicranella heteromalla*, thus form a reliable group with respect to the Dicranidae root, not including the Rhabdoweisiaceae. The Rhabdoweisiaceae, less *Rhabdoweisia* (the type genus) and *Dicranoweisia cirrata*, also are reliable with respect to the root. Both are apparently reciprocally monophyletic, i.e., as a set (the product of their PBAs is 0.95).

To demonstrate a separate taxonomic identity of the Rhabdoweisiaceae subclade, it is necessary for it to have a clear-cut morphological description, which is unavailable, or by Step 8 show that the Rhabdoweisiaceae are not merely a basal branch by demonstrating it is not a sister group of the Dicranaceae s.str.; although **Fig. 2** shows two reliable internodes between the Dicranaceae s.str. and the trimmed version of Rhabdoweisiaceae, these are with respect to the root and there is no clearly different intermediate lineage (they are sister groups in a multifurcation). In the context of eliminating speculation, this leaves the Rhabdoweisiaceae sensu La Farge et al. (2002) as a somewhat dissected lineage in the Dicranidae bush basal to the main portion of the Dicranaceae s.str. and lacking its name-bringing exemplar (*Rhabdoweisia*).

The Tsubota et al. (2003) cladogram. Relevant branch arrangements in the Tsubota et al. (2003) study were similar to and in many cases better supported than those of the first study. The likelihood bootstrap values were accepted here as equivalent to posterior probabilities and reduced 0.01 for unaccounted assumptions (Steps 1 and 5). For Step 2, Bayes' formula was used to increase support for shared branch arrangements supported by both studies. In this case, molecular support for four families, Dicranaceae, Leucobryaceae, Pottiaceae and Rhabdoweisiaceae was increased to 0.99 or greater each. Using FIR, support for Grimmiales and Leucobryaceae was also increased to 0.99 or greater, and support for the sister lineage of the Ditrichaceae increased to 0.99. These calculations were done with the Silk Purse Spreadsheet (Zander 2003b), which eases both FIR and Bayes' formula calculations.

A summary diagram of the second transformation, now combining the two studies, is presented as **Fig. 3**. This addresses only the relevant

branch arrangements and thus minimizes the number of multiple tests that are involved. Clearly by Step 7 there are two internodes each of 0.99 probability between Dicranaceae and Rhabdoweisiaceae (one supporting the Dicranaceae at 0.99 and another supporting it and its sister lineages) in the Tsubota et al. (2003) study after combination with La Farge et al. (2002); joint probability is 0.98. Also, by Step 8, the Dicranaceae s.str. and Rhabdoweisiaceae are reciprocally monophyletic at 0.98 joint probability. Based on the two studies now combined, Rhabdoweisiaceae are reliably not a sister group of Dicranaceae, but the Leucobryaceae and Pottiaceae plus Erpodiaceae lineages are.

Summary of results. The molecular studies that are here analyzed are, in combination, not perfectly decisive because not enough taxa were included to confidently distinguish many possible candidates in the Dicranaceae for inclusion in Rhabdoweisiaceae or vice versa, and because *Glyphomitrium* (Ptychomitriaceae) is included in the Tsubota et al. (2003) study as terminal in the Rhabdoweisiaceae lineage. The position of *Glyphomitrium* may be correct, or due simply to long-branch attraction, and if the latter its inclusion may well have increased the apparent support for the Rhabdoweisiaceae lineage. Additional molecular studies with different loci and additional taxa are needed to resolve this problem.

In the molecular studies, La Farge et al. (2002) recognized *Arctoa*, *Cynodontium*, *Dicranoweisia*, *Kiaeria*, *Onchophorus*, *Oreas* and *Rhabdoweisia* for the Rhabdoweisiaceae, but excluded *Amphidium* (traditionally recognized in the Orthotrichaceae) and *Dichodontium*, much the same as in the study of La Farge et al. (2000). Tsubota et al. (2003) included *Arctoa*, *Cynodontium*, *Dicranoweisia*, *Glyphomitrium* (traditionally recognized in the Ptychomitriaceae), *Kiaeria* and *Rhabdoweisia* and also excluded *Amphidium*. Other studies using the same loci are not well enough supported internally for reliable results.

The original description by Limpricht (1890) included *Amphidium*, *Cynodontium*, *Dichodontium*, *Oreas*, *Oreoweisia* and *Rhabdoweisia*. The recent treatment for sub-Saharan Africa by Frahm (2000) included *Amphidium*, *Cynodontium*, *Oreoweisia* and *Rhabdoweisia*. La Farge et al. (2000) distinguished the Rhabdoweisiaceae as autoicous genera with entire or bifid, smooth, striate or papillose peristome teeth, with or without developed alar laminal cells, but Buck and Goffinet (2000) characterized the family as small to medium plants, lacking stem central strand, with ribbed capsules that are widest at the mouth. These particular combinations of taxa are phylogenetically rather disparate, given the present studies, and what is or is not to be included is yet to be determined.

It is not clear to me how to define the Rhabdoweisiaceae morphologically such that it excludes similar taxa in the Dicranaceae; the description of Rhabdoweisiaceae by Frahm (2000) allows great variability in important traits. One might also point out that *Dichodontium olympicum* is autoicous, and splitting the genus among the two families may be correct but begs the question. Relevant here is the fact that the Werner et al. (2004) cladogram included four Dicranaceae s.str. genera and two Rhabdoweisiaceae genera, but of the latter, *Dichodontium* (placed in Rhabdoweisiaceae by Buck and Goffinet (2002) was reliably well embedded in the Dicranaceae s.str. (Zander 2006b, 2007a).

The exemplars in a group phylogenetically reliably well isolated on the basis of molecular data should provide a guide to help determine the morphological definition of the family. If such morphological traits cannot be found, then a paraphyletic classification of the Dicranaceae should be considered as both a practical solution and perhaps better representative of evolutionary reality. The Rhabdoweisiaceae are, on the basis of two molecular studies, demonstrably not imbedded in the Dicranaceae nor are they a sister group. Even given somewhat different sets of exemplars in the two studies, it apparently is well supported as molecularly monophyletic. As noted above, there are various morphological definitions of the Rhabdoweisiaceae. It may, however, be possible to resolve the morphological-molecular differences by viewing the Dicranaceae as paraphyletic with taxa referred to the Rhabdoweisiaceae actually being within the Dicranaceae but mostly basal, and the Leucobryaceae and Pottiaceae (plus Erpodiaceae) simply derived from advanced elements of the Dicranaceae. This

would be a worthwhile avenue to pursue if Dicranaceae and Rhabdoweisiaceae prove impossible to distinguish either morphologically or in evolutionary ecology (e.g., see the rationale of Zander 2007a, b). Hypothetically, the small size and autoicy of genera assigned to Rhabdoweisiaceae might simply be a result of the senescence and partial extinction of basal lines in the Dicranaceae.

Discussion

The number of internodes between the Dicranaceae s.str. and Rhabdoweisiaceae in the original La Farge et al. (2002) cladogram of maximum parsimony was five. Two correct internodes are needed to establish phylogenetic isolation in a cladogram based on molecular data alone, to support the status of the Rhabdoweisiaceae as a separate family. The first internode is simply that of the terminal lineage and insures its monophyly, the other isolates the Rhabdoweisiaceae taxa (whether the taxa are monophyletic or not) from the base of the Dicranaceae and assures that the Rhabdoweisiaceae are not a sister group, i.e., not just a basal branch of the Dicranaceae. Three of the La Farge et al. (2002) internodes were not assigned reliability values, and other two were 0.62 and 0.78 BP. These translate to 0.71 and 0.86 PBA, respectively, after correction for unaccounted assumptions. Only one reliable internode can be assembled from this data, of implied PBA 0.96, demonstrating only one inferred reliable internode between the two putative families, and Rhabdoweisiaceae could be molecularly a basal branch of the Dicranaceae, requiring further information (morphological) to distinguish it. In the context of a rooted cladogram, the two families were further dissected by excision of two genera from each, including the name-bringing exemplar of *Rhabdoweisia* itself. Therefore, from the La Farge et al. (2002) study alone, no reliable evidence for a phylogenetic distinction between the Dicranaceae and the Rhabdoweisiaceae could be demonstrated. The possibility that the lineage is a basal branch is also dubious because all the taxa are not reliably supported as a single lineage.

The Tsubota et al. (2003) study, however, presented critical data. The Dicranaceae s.str. were provided with additional molecular evidence that they were monophyletic, and the subtending internode was also found to be strongly supported such that Step 7 was satisfied.

I cannot presently determine a unique or even fairly good morphological description of a group of species that fits the monophyletic molecular circumscription of the Rhabdoweisiaceae. This is not to say that such does not exist, but this is a task for specialists in the Dicranaceae and rests on future studies. Given no adequate description of the Rhabdoweisiaceae based on expressed traits, I here recognize the Dicranaceae as a paraphyletic group (**Fig. 3**) with distinctive families evolved from taxa intermediate in the Dicranaceae.

Although high statistical power (e.g., optimality alone, or identification of BAs with PBAs higher than, say, 0.70) is needed to identify potential new facts about evolution for continuing investigation, there is a need to quantify the exact level of reliability of distance between lineages of interest on a cladogram as judged from published support values. The use of a nine-step transformation of published phylogenetic analyses can be of considerable aid to taxonomists and others who need to distinguish well-grounded theoretic results from speculation, and is particularly important to researchers such as biogeographers, who may not have training or interest in the complex techniques of phylogenetic analysis. Critical to all this is the onerous stricture of monophyly. If monophyly is in some cases relaxed, however, the classification may prove a better explanation of relationships.

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