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MACROSYSTEMATICS OF *DIDYMODON* SENSU LATO (*POTTIACEAE*, *BRYOPHYTA*) USING AN ANALYTIC KEY AND INFORMATION THEORY

Zander R.H. *Macrosystematics of Didymodon sensu lato (Pottiaceae, Bryophyta) using an analytic key and information theory*. Ukr. Bot. J., 2016, 73(4): 319–332.

Abstract. Evolutionary trees (caulograms) and phylogenetic cladograms for both morphological and molecular analyses of certain species in the moss genus *Didymodon* (*Pottiaceae*, *Bryophyta*) were compared. A new two-step macrosystematic (macroevolutionary systematics) method of calculating statistical support for both linear order and lineage direction of evolution is introduced. This involves clustering of taxa in sets by minimization of redundancy using cladograms and minimum parsimony, then building an often-branched linear model by maximization of information on gradual evolution by ordering species through adding informational bits for advanced traits and subtracting them for reversals. Cladistic analysis is considered to be similar to cryptographic code-breaking, with that code key then used for model-building following theory. Very high Bayesian support was computed for lineages in the morphological analyses, which stand up well to high support for past molecular studies. The caulogram allowed for predictions not possible with cladograms. The importance of using information on both shared and serial descent is discussed.

Key words: analytic key, cladogram, classification, evolution, information theory, macrosystematics, paraphyly, phylogenetics, *Didymodon*, *Pottiaceae*

Introduction

The cladistic classification practice requiring direct matching of clades and taxa has been criticized in the past by a series of publications by myself (e.g., Zander, 2004, 2007, 2008a,b, 2010a,b, 2013, 2014a,b,c,d), and others (e.g., Brummitt, 1997, 2002, 2003, 2006, 2010; Farjon, 2007; Hörandl, 2006, 2010; Hörandl, Emadzade, 2012; Hörandl, Stuessy, 2010; Mayr, Bock, 2002; Nordal, Stedje, 2005; Rieppel, 2010; Robinson, 1986; Sosef, 1997; Stuessy, Hörandl, 2014; Stuessy, König, 2008). Although the critiques address many problems, I suggest that, fundamentally, cladistic analysis is problematic because it is only the first and incomplete part of a full analysis of the information available on evolution, in the context of evolutionary theory. It is an «insufficient statistic» because all information relevant to evolutionary relationships is not addressed.

Basically cladistic analysis focuses entirely on data relevant to shared descent, that is, advanced homologous traits shared by taxa. Traits not shared

or which are isolated on a cladogram, are termed autapomorphies and are largely ignored. These autapomorphies, however, are very informative of serial descent. This paper demonstrates how information on both serial and shared descent may be used to complete an evolutionary tree of stem taxa (a caulogram, or stemma) showing both serial descent in lineages of one taxon being progenitor of the next, and shared descent in two or more lineages branching from a jointly shared progenitor species. This paper is an attempt to provide examples of a new method of systematic analysis of actual taxa to supersede papers of criticism that only point out problems with phylogenetics.

Using both shared and serial descent as analytic criteria. There are two steps in macrosystematics (evolutionary systematics focused on relationships of stem taxa) that involve use of information about both shared and serial ancestry to develop an evolutionary tree that is useful in classification. (1) Shared descent is addressed by clustering taxa by similarity, best served by phylogenetic methods of establishing multiply-embedded sets of taxa with closest shared ancestors. The idea is to minimize redundancy of advanced traits such

that taxa related by shared descent have a maximum number of advanced traits that are alike, this being a signal of evolutionary relationship, a specialty of cladistic methodology. Redundancy in information theory is «wasted information» in a message, and as used here is similar to mutual information in information theory, or phylogenetic profiling, see discussions in Wikipedia. Minimization of redundancy is a condensation of repetitive evolutionary messages that helps maximize entropy. Informational redundancy is reduced by explaining duplicate traits as having been created only once through shared ancestry, i.e., they are homologous, which makes them essentially the same information. (2) Once sets of taxa that minimize redundancy of traits are established, the difference between taxa in the sets is used to determine direction and order of evolution. This is done by assigning one informational bit to each new trait with a penalty of one bit for each reversal back to the primitive traits of an outgroup, and order is established by maximizing numbers of information bits for each lineage. Parallelisms, which, like, reversals are redundant information, are minimized by cladistic clustering by shared traits.

Basically cladistics establishes major groupings and general contiguity of taxa by implied shared ancestry of two or more taxa, while an evolutionary analysis determines linear order of taxa from information implying descent of one taxon from another. This analysis using information theory has a parallel in cryptanalysis. Suppose we have a cryptogram message «eftdfoq xjui npejgdbujpo,» and we decrypt just the pattern of letter substitutions. Suppose it is $a = b$, $b = c$, $d = e$, etc. That pattern has much information in it about the message, and is similar to the information-rich patterns generated by cladistics. Cladistics uses the pattern impressed by the analytic method as a basis for classification. But the message still needs to be read. By assigning the code identities to the letters in the cryptogram, the order of presentation becomes important and the message becomes «descent with modification». The language of the evolutionary message is called «theory» and the arrangement of plaintext letters is similar to the modeling of an evolutionary tree based on both shared and serial traits. The point of a macrosystematic analysis is to model evolution of a group so that it fits into everything else we know about evolution, and is not a «discovery process» like determining code letter identities.

Species definitions and dissilient genera. A species may ultimately be based on any of a number of criteria

depending on the author's choice of a species concept for the group studied. In this paper, a practical criterion is used: a species is a group of individuals possessing a minimum of two otherwise unlinked traits that may be considered linked by some evolutionary process, known or unknown. It helps, of course, for the group of individuals to have some «evolutionary trajectory» or specialized habitat, but two traits are minimal and sufficient. A genus is here defined as the «dissilient genus» of Zander (2013: 92), being the result of a speciation burst. Groups of species, at least in the groups I have studied (*Pottiaceae*, *Bryophyta*), often may be seen as some central, generalist, sexually reproducing species of wide distribution and many biotypes surrounded by two or more advanced, stenomorphic descendant species with unique traits, sometimes asexual and found in specialized or recent environments. These descendant species may have descendants of their own to form linear series, usually short, of two or three species in length (for examples see Zander 2008a, 2009, 2013, 2014c). Each evolutionarily radiative group of species is here considered a genus, which is an empirical definition that may be applied to families (i.e., a radiative group of genera).

Cladogram versus caulogram. A cladogram is a dichotomously branching tree with the tips of the branches ending in the taxa studied. It may be entirely replaced by a nested set of parentheses, annotated with branch lengths and other information (e.g. the Newick format). It represents only shared descent (as implied by a series of gradually less inclusive traits) and treats any indication of serial descent as unwanted paraphyly.

A caulogram is an often-branching tree with taxa comprising the stem and branches, and with many taxa lined up in linear series. The branches of a caulogram show shared traits and evolutionary radiation, the lineages of stem taxa show order and direction of evolution. A caulogram maximizes paraphyly, which is taken to signal a progenitor-descendant relationship. Simplistically, a cladogram minimizes the differences between taxa, a caulogram interprets the differences left. Caulograms as diagrams of direct descent of extant and inferred extinct taxa are fully explained by Zander (2008a, 2010a, 2013).

Details of problems with cladistics-only analysis. Firstly, there is a difference between cladistics and phylogenetics. The former simply desires a branching tree that groups taxa in the simplest manner by minimizing required shared character state transformations. A cladogram maximizes synapomorphies (shared

advanced traits). The resultant tree has a goodly amount of evolutionary information on shared descent, but evolution, particularly evolutionary theory, is not particularly important to cladists who apparently feel that a tree with the least number of trait changes is a practical basis for classification. Phylogenetics, however, adds evolutionary significance to elements of the cladogram, where branch length (in terms of trait changes) implies evolutionary distance, and each node in the dichotomous tree represents a shared ancestor giving rise to (and ending in) two branches. The resulting interpreted cladogram is termed a phylogram, and is often presented as an evolutionary tree although seldom called by that name.

Clarity in understanding the limitations of cladistics is important, and is hard-won. «Tree thinking» can be overwhelming in its complex methodological detail, nearly full acceptance by the systematic community (either enthusiastic or cynical), and the availability of copious funding by granting agencies. There are, however, certain major crippling aspects that are largely ignored or even accepted as positive features because of simplistic solutions provided in the methodology.

1. Phylogenetic trees are not evolutionary trees nor can they truly model monophyly because shared descent alone does not track serial aspects of evolution.
2. Phylogenetic analysis generates «sister groups» for each split in the tree, but for, say, two taxa as sister to each other, phylogenetics cannot tell if one taxon is the progenitor of the other, or not. This is because the phylogenetic data set includes only information about shared descent. Even when data are available on progenitor-descendant relationships, they are generally ignored.
3. Continuity in a phylogenetic tree is through nodes, which are often interpreted as shared ancestors, and taxa are then related by degree of their shared descent. Nodes, however, are neither named nor characterized as natural entities, and recency of shared descent is problematic. What they really represent are splits in the raw minimum spanning tree or Markov chain that is used in the computerized software to gather the taxa involved into hierarchical sets that increasingly share advanced traits. A phylogenetic tree or cladogram can be completely represented by groups of taxa in nested sets of parentheses to show the inclusiveness of sets, similar to the well-known phylogenetic Newick format. There is no evolutionary tree, there are no ancestral nodes, and the «tree» simply represents an

easy way to visualize the nested sets of parentheses; e.g., ((A, B)(C,D)) may be represented by a bone-shaped diagram (>—<) with A and B at one end and C and D at the other.

4. Important evolutionary information is lost with cladistics, and the more taxa are involved, the more information is lost. Consider $A > B > C$, where species A speciates B and B speciates C (the angle bracket shows the direction of evolution). The cladogram for this is A(B, C) given that B and C share at least one trait advanced over those of A (unless there is a reversal). In this case and more generally, information is lost when data on serial descent are ignored.
5. Because the method of phylogenetics uses only data on shared descent, the differences between taxa are only indirectly addressed as which taxa are lower in a cladogram or toward the outside of a set of taxa in nested parentheses. Thus, when a taxon is embedded in a cladogram of a taxon of a different name, it is either lumped with that taxon under one name, or the taxon in which it is embedded is split into many taxa to avoid direct embedding. The taxon with another taxon of the same rank or higher embedded in it is called a «paraphyletic» taxon. The method of strict phylogenetic monophyly has been invented to justify such lumping and/or splitting. This is the result of a classification method invented to shore up the blind spot of reliance only on shared descent, and is not a result of a well-supported evolutionary theory. Cladistically embedded species and genera have had the same criteria in describing species and genera as have paraphyletic species and genera, and there is no natural reason to distinguish them.
6. Multifurcations are considered failures of resolution in cladistics, yet are expected and informative in evolutionary systematics. Multifurcations of otherwise serial lineages may be reflected in macroevolutionary classification as named genera.

Cryptanalysis parallel. Cryptanalysis is translation or interpretation of hidden meanings in secret codes (Good, 1979; McGrayne, 2011: 134, 168, 205). In breaking codes, minimizing redundancy means to discover which letters in the coded message always mean «a», which mean «b», and so on. Minimizing redundancy in systematics means creating a cladogram or an equivalent diagram as a guide to sharing of homologous traits through joint descent. Traits that last over two or more speciation events are valuable for tracking the flow of evolution.

The correct mapping of the cladistically derived code key to patterns developed through interpretation by theory «saves» (in terms of philosophy of science) both cladistics and evolutionary theory by melding them as two steps in the macrosystematic method. That mapping will be done in this paper using an «analytic key» as described below.

In sum, cladistics is a kind of discovery process that «cracks the code» by creating a minimally redundant arrangement of taxa, a cladogram, which condenses otherwise redundant information by sharing traits among taxa. Evolutionary systematics accepts that decoding of arranged closely related taxa with informative non-redundant traits left over and «reads the message» through the language of evolutionary theory. The dichotomous cladogram of the mechanical code redundancy analysis is transformed into a branching linear arrangement of taxa, a caulogram, that reflects both shared and serial descent.

Problems with molecular analysis. Species have their phenome of expressed traits often sculpted by stabilizing and purifying selection (see review by Popadin et al., 2007) over time such that the species' basic identity remains intact and singular. Gradual change and biotype development over time is understood through well-supported theory. The «bell-shaped curve» of morphological variation is cut off at the tail ends by selection against overly burdensome mutations, a kind of phyletic constraint. On the other hand, the molecular traits used for tracking evolutionary changes in taxa in molecular cladistic analysis are apparently or are hoped to be under little selection, and mutations may remain in the genome of molecular races indefinitely or until that molecular race is overwritten through accumulated mutations or otherwise rendered extinct.

This leads to molecular paraphyly such that one species may appear to be in two or more different places on a cladogram at once. This is common in molecular analysis and is usually dealt with by strict phylogenetic monophyly by calling molecular races «cryptic species» and naming them. Paraphyly is information that the paraphyletic species gave rise to the embedded species, a progenitor-descendant relationship. The problem is that molecular races can go extinct, and the place on a molecular cladogram of one instance of a species does not rule out other places on the cladogram that a molecular race of that species may have occupied, except for being extinct or otherwise unsampled. The BPP supporting a molecular clade can be considered valid if one judges the taxa to be very recent and extinct

paraphyly is doubtful because there has been little time for speciation between instances of molecular races. Given the caulogram below, one might expect one to three speciation events during the lifetime of a species, which one might estimate at an average of five million years (as a rule of thumb). See also discussion of paleontological time scales of Zherikhin (1998): «If about 50% of living insect species exist since the Pliocene, it is improbable that none of them gave rise to any different species during the last 5 million years.»

Suppose from many taxa, cladistics groups taxa D, A, and T as having many redundant traits. There may be two molecular races of one species A, or two species of genus A, so there are two terminal taxa «A», that is, D, T, A, and another A. Problematically, if the code key is «D, A, T, A,» perhaps in the form ((D, A)(T, A)), to avoid paraphyly (and theory) the paraphyletic taxon «A» may be split into two (two species if molecular races or two genera if species) by cladists to give «DZTA,» or ((D, A)(T, Z)), which is not interpretable in the language of scientific theory. (One can usually find *some* minor biotype traits that distinguish two populations of different molecular races of one taxon, but, because the morphological traits cannot stand alone, they are not real support.) The correct interpretation may be $A > T > D$, where additional information not in the phylogenetic data set reveals that ancestral taxon A (progenitors are boldfaced) gave rise to T, and T to D. Ancestral taxon A may include two molecular races, or include two species that are somewhat distant on a cladogram but nevertheless are clear in that genus as representing a stem taxon.

Like cladistic introduction of cryptic or nearly cryptic species, ignoring the possibility of extinct paraphyly introduces a lack of resolution in molecular cladograms. This is not such a problem in morphological cladograms because of stabilizing selection. The degree of poor resolution may be gauged by the amount and degree of molecular paraphyly known for the group. If a known paraphyletic molecular taxon spans three nodes on a cladogram, then all except the most recent species must be suspected of having up to the same level of paraphyly in the past. This is because of similar sensitivity of their genomes to mutation of the particular DNA sequence used in the analysis.

Two features of molecular analysis may be relied on. (1) Paraphyly or short-range molecular polyphyly implies that the embedded taxa are linear descendants of the paraphyletic taxon. (2) Long-range polyphyly, such as species of one genus split between two

families, suggests a true polyphyly such that contrary morphology-based taxonomy needs to be re-evaluated.

***Didymodon* s. l. as exemplar.** An intensive macrosystematic analysis of the moss genus *Didymodon* Hedw. was made in three previous studies by Zander (1998, 2013, 2014a,b,c). These studies evaluated the 24 North American species, and divided them (Zander, 2013) into six genera, based on estimated centers of adaptive radiation («dissilient genera»). This was done in the following manner: A cladogram of these taxa (Zander, 1998) was modified into a caulogram of their serial and shared evolutionary relationships under the simple rubric that if a cladogram node can easily be taxonomically named as the same as one of the two sister groups, this is more parsimonious than positing an unknown unnamed shared ancestor. On naming a node, the cladogram was collapsed into a serial relationship of one of the sister groups ancestral to the other. Two nodes were left unnamed as unknown shared ancestral taxa, with the proviso that this practice retrodicts the past existence of such unknown taxa and predicts the possibility of discovering a taxon with that general circumscription. Later, another study (Zander, 2014a,b,c) evaluated the statistical support for the caulogram lineages.

Although the macrosystematic method involves first doing a cladogram or equivalent, the practice of doing no more than simply naming nodes as one of the terminal taxa on a cladogram is not advisable as much information on serial descent is never used in cladistics analysis.

Justification of bit-based Bayesian measures of support. No definite assignment of support for lineage estimations in terms of Bayesian credible intervals were made in the Zander (2013) study as the relationships seemed overwhelmingly clear, but this was remedied by Zander (2014a,b,c). In the 2014 papers, exact probabilities were assigned to advanced traits using the deciban (dB) unit. Decibans are logarithmic units (exponents at base 2) equivalent to certain Bayesian posterior probabilities (BPP), see Table 1, and fully explained in the 2014 papers. Because decibans are logarithmic, they can be added, and the sum of decibans can be translated to a final posterior probability without using Bayes' formula.

In the case of 2014a,b,c study, the deciban value of support for each advanced trait in a species was assigned intuitively based on long experience with the genus and with the rarity of traits. One deciban has been described as the minimum detectable information beyond 50:50

support for two hypotheses. It was considered a «hint,» equivalent to 0.56 BPP. Decibans were then assigned in the 2014 paper as numbers of decibans for each trait, because evolutionarily important traits are commonly more than just hints. Adding these decibans may reach a sum (interpreted by Table 1) suggesting a very high posterior probability of the direction and order of evolution of some particular series of taxa

The study of Zander (2014a,b,c) gauged support for each branch of the *Didymodon* caulogram. This involved the estimation of how uncommon an advanced trait was. The more rare, the greater support for the direction of evolution away from a generalized ancestor. The generalized ancestor was determined by comparison with some outgroup taxon, as in cladistics. Some categories of critical traits informative of direction of evolution are:

Primitive: (1) A species generalist or centralist in morphology that might easily generate specialized descendants. (2) A widely distributed species that is found in many habitats and may be relatively old. (3) A species of multiple subspecies or varieties. (4) A major morphological differentiation that signals a new relationship with the environment that opens evolution of radiative lineages.

Advanced: (1) A habitat specialist. (2) A species with asexual reproduction common and sexual reproductive organs rare or absent. (3) A species of local distribution, often of recent or specialized habitats. (4) A species with a burdensome physiological or morphological adaptation not conducive to further speciation.

The above criteria certainly call for judgment guided by established theory. Additional discussion of identification of progenitor-descendant species pairs has been provided by Crawford (2010). In the Zander (2014) papers, each trait in each species matching a category above was assigned credible intervals approximating the following schema:

1. «Five Sigma» (**0.998** or better) super-certainty (i.e., «quite certain,» «damn sure»). Statistical certainty is a real feature of some analyses.
2. Almost certain. Say, only once wrong out of a hundred times would the hypothesis be wrong. Expected level of correctness in critical research. Assigned credible interval is **0.99**.
3. Acceptable as a theory, being the lower limit of reliable information. Expected to be correct 19 out of 20 times, good for non-critical, easily reversible decisions. Credible interval is **0.95**.

Table 1. Equivalency of bits and decibans (dB) with Bayesian posterior probability (BPP)

| Bits | dB | BPP |
|-----------|-----------|--|
| 0 | 0 | 0.500 |
| 0.33 | 1 | 0.557 |
| 0.67 | 2 | 0.613 |
| 1 | 3 | 0.666 or nearly 1 S.D. (0.683) |
| 1.33 | 4 | 0.715 |
| 1.67 | 5 | 0.759 |
| 2 | 6 | 0.799 |
| 2.33 | 7 | 0.833 |
| 2.67 | 8 | 0.863 |
| 3 | 9 | 0.888 |
| 3.33 | 10 | 0.909 |
| 3.67 | 11 | 0.926 |
| 4 | 12 | 0.940 or nearly 2 S.D. (0.955) |
| 4.33 | 13 | 0.952 |
| 4.67 | 14 | 0.961 |
| 5 | 15 | 0.969 |
| 5.33 | 16 | 0.975 |
| 5.67 | 17 | 0.980 |
| 6 | 18 | 0.984 |
| 6.33 | 19 | 0.987 |
| 6.67 | 20 | 0.990 |
| 7 | 21 | 0.992 |
| 8 | 24 | 0.996 or 0.99+ |
| 9 | 27 | 0.998 3 S.D. (0.997) |
| 10 | 30 | 0.999 |
| 20 | 60 | 0.999999 (odds of 1 million to one) |

Note. The decimal fractions of bits are equivalent to adding one or two dBs to each bit, where dBs, if one wishes to use them in addition to bits, are equivalent to poor data that cannot be ignored. Standard deviations are indicated, and serve to show how much variation is eliminated by the analysis.

4. Substantial support alone is not decisive for action, but can be a working hypothesis. It can be narrowed down to half-way between certain (1.00) and totally equivocal (0.50), or 0.75. Using 0.75 as prior and 0.75 as probability yields 0.90, then using that as prior and 0.75 again as probability yields 0.96 as posterior. Thus empirical use of Bayes Formula with the answer to the first instance being the prior for the second and so

on indicates that perhaps three occurrences of «some support» with no contrary evidence is sufficient for use as a theory. Credible interval is then **0.75**.

5. A «hint» of support is barely acceptable as a hypothesis, and is certainly not actionable alone, nor are even several hints impressive. Using 0.60 probability as representative of a hint, being just beyond totally equivocal, requires 0.60 to be used as a prior seven times in successive empirical analyses with Bayes' Formula, with no contrary information, to reach 0.96. The credible interval for very minor support is **0.60**.
6. Totally equivocal support probability (assuming only two reasonable alternatives, yes or no, support or refutation) is **0.50**.
- 7 to 10. Support against a hypothesis, is the reverse of the above, that is, **0.40, 0.25, 0.05, 0.01** in support «for» the hypothesis (leaving the remainder «for» any opposing hypothesis of two hypotheses).

Comparing this analysis of intuitive estimation to the additive use of decibans as in Table 1, justifies to a large extent the more mechanical assignments of these logarithmic units. That is, the range of credibility seems about the same.

Informational bits. The entirely intuitive (Zander, 2013) or multiple deciban judgmental assignment (Zander, 2014a,b,c) methods are, of course, not replicable by anyone but another researcher familiar with the taxa. Also, decibans are too fine a measure of credibility. In addition, a less arbitrary assignment of credibility is desired. The present paper introduces a *more objective method*, meaning one more easily used to attempt replication of the study. This includes an evaluation of support by accumulation of advanced traits indicating direction of evolution away from a generalized ancestral taxon. In this case, the order of any two taxa in a series is simply the number of advanced traits of one taxon more than that of the second, given polarization of trait changes with the presumed progenitor of the lineage as functional outgroup of primitive traits. Each advanced trait is assigned one informational bit (exponent of base 10). Because bits are logarithms, they may be added together. Reversals are assigned negative bits. Recursively comparing contiguous pairs of taxa along a series of taxa will order than in gradual advancement of traits, given comparison with the primitive traits of an outgroup (or functional outgroup such as the central progenitor).

Summing the bits provides a measure of support of one particular order in evolution, with Bayesian posterior probabilities obtained from a table (Table 1). The assigned probabilities of a particular order generally match the intuitive evaluation by an expert. Each bit is nearly exactly equal to 3 dB. Thus, 1 bit is equivalent to 0.67 probability, about half way between a hint and substantial support — given that two advanced traits are required to distinguish a species in this study, one can expect each species to contribute at least 2 bits, or 0.80 BPP to analysis of the evolutionary order. This may not seem great, but many species are distinguished by four traits (0.94 BPP). Adding bit support for the order of all species in the lineage is a good measure of direction of evolution, given theoretical gradual accumulation of traits. A detailed discussion of this simple use of information theory in systematics is given by Zander (2014c). This is a very specialized use, and is not the same as analysis of entropic aspects of evolution (e.g., Brooks, Wiley, 1988).

We can now see if the intuitive assignments of support from advanced traits for the position in the *Didymodon* s. l. caulogram published by Zander (2014c: 9ff., 14) were in the right ball park.

Materials and Methods

Analytic key. An «analytic key» was developed to determine order and direction of evolution of the serial lineages. Bits were assigned to descendant species' traits that were advanced compared to those of the generalist ancestral taxa of each of the segregate genera.

The bits assigned to progenitor species (of Zander, 2014c: 14) are those advanced traits distinguishing the genus from the immediate ancestral taxon. These traits mostly were given in a serial and multichotomous «natural key» by Zander (2013: 82). This natural key was combined with the format of the «tables of monophyly» in Zander (2014c: 9ff) to devise an analytic key. This is given below, and, I hope, is an intuitively easily understandable analysis of serial and shared descent, and support for those evolutionary relationships among the segregate genera of *Didymodon* s. l. The reader should note that the analytic key may be multichotomous or, at times, «monochotomous» with just one indented description of advanced traits of the single descendant. The positions of genera on the morphological cladogram were checked in the analytic key for minimum redundancy of traits and minimum reversals.

Order and direction of evolution. Order and direction of evolution are only evaluated once the species involved are minimally redundant in terms of traits. That is, grouped such that homologous traits are maximally shared. Once species and their traits are most similar, their differences can be used to further analyze evolution. *Order* of any two species in a lineage is evaluated by awarding position of greatest advancement in the lineage to that species with the greater bit count relative to the next lower species. Reversals require subtraction of one bit per reversal, which aids in modeling gradual evolution and fine-tuning the minimal redundancy. *Direction of evolution* for a lineage is simply summing all the bits for each species in the lineage after best ordering. It is intuitively acceptable that two or more species in a group or lineage reify that group or lineage over having just one species. A randomized group species (i.e., that are not first rendered minimally redundant with maximum parsimony) may have a large bit count, but a preliminary clustering study is critical to a successful model of evolution because an attempt at linear ordering would then reduce information from random orderings because of many reversals.

Data for analytic key. Data sets of unique or uncommon traits may be used to create an analytic key (Zander, 2013: 82, 2014c: 4ff), or, as in the present paper, parallelized descriptions of taxa from modern works (mainly FNA, 2007) are evaluated for taxa that appear to be the same as another taxon but with advanced traits. From these descriptions, a central progenitor of widespread distribution was selected. The progenitor generally has common and generalist traits, being fully sexual, and capable of generating both sexual and asexually reproducing descendant species.

The reason descriptions rather than data sets are used to better advantage in macrosystematics is because descriptions (rather than telegraphic data sets, e.g., characters labeled 1 or 0) differentiate better between similar traits, which is critical when order of linear descent is evaluated. Such traits are usually not included in cladistic data sets, where shared descent through shared homologous traits is the analytic focus, and unique or uncommon traits are autapomorphies or otherwise «phylogenetically uninformative.» Two or more descendants are postulated from one ancestral taxon when traits of the putative descendants are rather different and arranging them linearly would add positive bits for advanced traits and negative bits from reversals summing to zero or nearly so. That is, when information

on order and direction of evolution is lacking, under constraint of minimal redundancy.

A special case of branching is when an unknown shared ancestor is suggested when two descendants sharing advanced traits are different from each other and are also equally different from the only extant possible ancestral taxon; so an intermediate taxon with those shared advanced traits that lower the difference between the ancestor and descendants (given gradual evolution as a model) is then a valuable hypothesis, see the genus *Fuscobryum* in the caulogram (Fig. 1).

Morphological cladogram. The morphological cladogram of *Didymodon* s. l. (Zander, 2013: 80) was recreated using the data set of Zander (1998) and the same reported software settings. Also a non-parametric bootstrap analysis was done using 2000 replicates and «faststep» settings. The names of segregate genera of *Didymodon* were used as in the 2013 publication. The serial relationships of the genera were based on contiguity of nodes on that morphological cladogram, which minimized redundancy of traits following theory that most species evolve through gradual accumulation of advanced traits.

Molecular cladogram. A molecular cladogram of *Didymodon* s. l. species from Werner et al. (2005) was duplicated as reduced to taxa in the morphological cladogram. Bayesian posterior probabilities obtained by the 2005 authors were appended for values greater than 0.50. This cladogram was compared to the morphological cladogram, and interpreted in terms of serial evolution.

Results

Macroevolutionary analytic key. Descriptive information was used to develop an analytic key listing the genera and species in evolutionary order. Key entries are preceded with the progenitor identifier (a number), a right angle bracket indicating evolutionary direction, and a unique identifier for the descendant species (which itself may be a progenitor of its own descendants). By convention progenitors in evolutionary formulae are given in boldface, e.g., **A** > **B** > C. Equal indentation indicates taxa that are all derived from one progenitor, and extra indentation indicates a descendant taxon of the one above and less indented in the key. The features are those different from the progenitor and from the preceding species, therefore presumed advanced. Each trait advanced over those of the earlier species in the lineage was scored as one positive informational bit.

In the present optimized order of the analytic key, there are no reversals, therefore no negative bits to detract from support measures. To see the effect of assigning negative bits, simply reverse the order of two paragraphs in optimal arrangement of the key, and compute the differences.

The bits associated with each advanced trait (1 bit per trait) were summed for each species, listed after the taxon name, and interpreted as Bayesian posterior probabilities. After each genus the bits are summed for the support for that genus. Note that some indentations in the key are monochotomous (species 1aa, 3ca, 5aa, 5ca, 5caa, 6a), meaning only one descendant from a previous species in the lineage. The caulogram (Fig. 1) summarizes visually the information in the analytic key.

Analytic Key to *Didymodon* and related genera

1. *Vinealobryum* progenitor: Differing from outgroup *Barbula unguiculata* by axillary hairs with brown basal cells, leaves lanceolate, adaxial costal epidermal cells quadrate, with a distinct costal groove or window adaxially near the leaf apex, and gemmae multicellular, obovate, borne on the stem*Vinealobryum vineale* (Brid.) R.H. Zander 5 bits, 0.97 BPP

1 > 1a. Immediate descendant: Leaves shorter, leaf base squared; more arid habitats; gemmae present; peristome short and twisted or rudimentary*Vinealobryum brachyphyllum* (Sull.) R.H. Zander 4 bits, 0.94 BPP

1a > 1aa. Secondary descendant: Leaves with multilayered photosynthetic cells on ventral surface of mid-costa; leaf margins loosely revolute; sporophytes absent; highly restricted distribution in arid region*Vinealobryum nevadense* (R.H. Zander in R. H. Zander et al., L.R. Stark & Marrs-Smith) R.H. Zander 4 bits, 0.94 BPP

1 > 1b. Immediate descendant: Plants large; leaves bistratose medially; leaves distally very broad*Vinealobryum nicholsonii* (Culm) R.H. Zander 3 bits, 0.89 BPP

1 > 1c. Immediate descendant: Very restricted northern distribution; leaf apex sinuose or toothed, bi-tri-stratose, deciduous as a propagule; sporophytes unknown; growing on wood or bark*Vinealobryum murrayae* (Otnyukova) R.H. Zander 4 bits, 0.94 BPP

Total support for *Vinealobryum* lineage is 21 bits, or 0.99+ BPP.

1 > 2. *Trichostomopsis* progenitor: Plants green (not reddish); costa much flattened, ventral stered band absent; distal laminal cells with simple papillae

..... *Trichostomopsis australasiae* (Hook. & Grev.) Rob. 4 bits, 0.94 BPP

2 > 2a. **Immediate descendant:** Leaves very long acuminate-lanceolate, basal laminal cells hyaline and with slits; human distributed

Trichostomopsis umbrosa (Müll.Hal.) Rob. 3 bits, 0.89 BPP

2 > 2b. **Immediate descendant:** Leaves short-ovate, margins loosely revolute; unicellular propagula in leaf axils; peristome absent to short, straight; restricted distribution *Trichostomopsis revoluta* (Card.) R.H. Zander 5 bits, 0.97 BPP

Total support for *Trichostomopsis* lineage is 12 bits, or 0.99+ BPP.

1 > 3. **Didymodon s.str. progenitor:** Leaves green or occasionally reddish in nature, more broadly channeled; costa flat or convex dorsally, not convex; distal laminal cells only weakly and simply papillose or smooth *Didymodon acutus* (Brid.) K. Saito 4 bits, 0.94 BPP

3 > 3a. **Immediate descendant:** Leaves distally thickened, long-elliptical; gemmae abundant; peristome short and straight; hygic habitats *Didymodon rigidulus* Hedw. 5 bits, 0.97 BPP

3 > 3b. **Immediate descendant:** Leaf apex acuminate, cylindric, fragile in pieces as a propagule, laminal cells large; strong northern distribution, hygic habitat, growing on wood *Didymodon johansenii* (Williams) Crum 5 bits, 0.97 BPP

3 > 3c. **Immediate descendant:** Leaves long-acuminate, basal cells quadrate *Didymodon icmadophilus* (Müll.Hal.) K. Saito 2 bits, 0.80 BPP

3c > 3ca. **Secondary descendant:** Leaf apex turbinate, deciduous as a propagule; sporophytes absent; restricted distribution *Didymodon anserinocapitatus* (X.J. Li) R.H. Zander 3 bits, 0.89 BPP

Total support for *Didymodon* lineage is 19 bits, or 0.99+ BPP.

1 > 4. **Exobryum progenitor:** Leaves narrowly channeled, carinate; distal laminal papillae simple; moist areas *Exobryum* sp., unknown ancestral taxon 3 bits, 0.89 BPP

4 > 4a. **Immediate descendant:** Mountainous areas; deep red plant coloration; leaves strongly recurved; stem central strand often absent, peristome short and straight *Exobryum asperifolius* 5 bits, 0.97 BPP

Total support for *Exobryum* lineage is 8 bits, or 0.99+ BPP.

4 > 5. **Geheebia progenitor:** Leaves weakly recurved; adaxial cells of costa elongate *Geheebia fallax* (Hedw.) R.H. Zander 2 bits, 0.80 BPP

5 > 5a. **Immediate descendant:** Leaves ovate-lanceolate, usually without papillae, costa ending before apex, with small basal auricles or long decurrencies; peristome short and straight, occasionally rudimentary or absent; calciphile, wet habitats *Geheebia tophacea* (Brid.) R.H. Zander 6 bits, 0.98 BPP

5a > 5aa. **Secondary descendant:** Leaves long-acuminate lanceolate, with large auricles; sporophytes absent; restricted northern distribution *Geheebia leskeoides* (K. Saito) R.H. Zander 4 bits, 0.94 BPP

5 > 5b. **Immediate descendant:** Leaved catenulate when dry, small spherical gemmae in leaf axils; sporophytes absent *Geheebia maschalogena* (Ren. & Card.) R.H. Zander 3 bits, 0.89 BPP

5 > 5c. **Immediate descendant:** Plants yellow to red; leaves usually without papillae, very wet habitats *Geheebia ferruginea* (Besch.) R.H. Zander 3 bits, 0.89 BPP

5c > 5ca. **Secondary descendant:** Leaves much enlarged; sporophytes absent; very restricted distribution *Geheebia maxima* (Syed & Crundw.) R.H. Zander 3 bits, 0.89 BPP

5ca > 5caa. **Tertiary descendant:** Leaves and plants much enlarged, leaves long-acuminate; laminal cells with large, bulging trigones; sporophyte absent .. *Geheebia gigantea* (Funck) Boulay 4 bits, 0.94 BPP

Total support for *Geheebia* lineage is 25 bits, or 0.99+ BPP.

5 > 6. **Fuscobryum progenitor:** Leaves dark brown to black in nature, distal marginal cells crenulate; costa thin; hyperoceanic northern distribution *Fuscobryum nigrescens* (Mitt.) R.H. Zander 4 bits, 0.94 BPP

6 > 6a. **Immediate descendant:** Leaves ovate, apex broadly rounded *Fuscobryum* spp., unknown ancestral taxon 2 bits, 0.80 BPP

6a > 6aa. **Secondary descendant:** Clusters of unicellular gemmae in leaf axils; sporophytes absent; very restricted distribution *Fuscobryum perobtusum* (Broth.) R.H. Zander 3 bits, 0.89 BPP

6a > 6ab. **Secondary descendant:** Leaves dimorphic, the smaller strongly concave in series in some parts of the plant; sporophytes absent *Fuscobryum subandreaoides* (Kindb.) R.H. Zander 3 bits, 0.89 BPP

Total support for *Fuscobryum* lineage is 12 bits, or 0.99+ BPP.

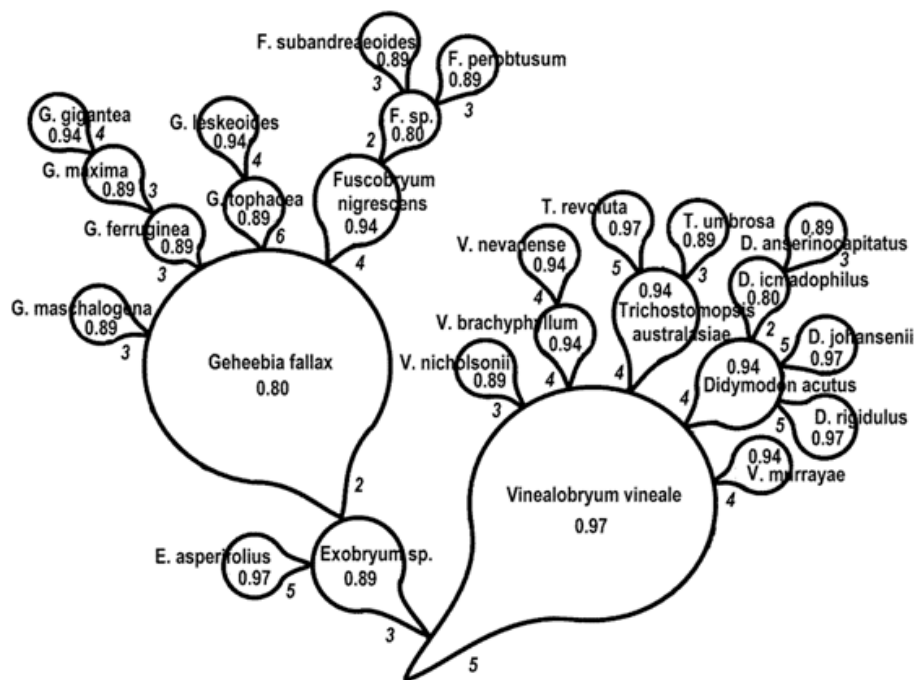


Fig. 1. Caulogram of *Didymodon* s. l. Segregate genera are identified. Each species is identified with the Bayesian posterior probability of the species evolutionary order. At base of each species balloon is number of bits supporting order of an advanced species over the next lower in the cladogram based on primitive traits of the central progenitor as functional outgroup; adding these gives bit support for a lineage (not shown)

The study (Zander, 2014) that used intuitive assignments of decibans for each trait for each species of *Didymodon* created «tables of monophyly» that included BPPs for linear order for each pair of contiguous species, as well as various combinations of species. The optimal order of species is the same as in the present study, and a comparison of those judgmentally assigned deciban-derived BPPs with the one bit per trait method used here is given in the table below (Table 2). The scale of credibility is about the same. The credible intervals awarded in the Zander (2014) study are clearly more variable than those of the present study. The variation is due in part to the fact that one or two decibans are less than one bit in terms of BPP, while four or more are greater. Whether the additional judgment involved in the 2014 study was better than the present method of equal weighting may be evaluated by additional study with more species. I think the method used here is a stabilizing influence, as the BPP of a bit seems in the center of BPPs correlated with the number of decibans commonly awarded in the 2014 study.

Morphological analysis. The morphological cladogram (Fig. 2) shows the shared relationships of the species optimized under maximum parsimony. Thick lines connect central progenitors. Nonparametric bootstrap proportions greater than 50 are added at base of splits together with translation to equivalent Bayesian

posterior probabilities (Zander, 2004) in parentheses. If taxonomically lumped by strict phylogenetic monophyly, genera of taxa marked «paraphyly» would lose their names and attendant macroevolutionary information, with the species lumped into *Geheebia* (upper part of cladogram) or *Didymodon* (lower part of cladogram except *Exobryum*) — the correct cladistic name would be *Didymodon* because it is, following the Code, an earlier name for the paraphyletic *Vinealobryum*.

Compare low bootstrap support here from only shared descent with that from serial descent (Fig. 1). Clearly, shared descent in *Didymodon* s. l. morphological studies is far more informative than shared descent.

Molecular analysis. The molecular cladogram of Werner et al. (2005) after reduction to only species also in the present morphological study (Fig. 3) demonstrated rather high support for splits based on shared descent. The segregate genera largely hang together as given in the caulogram (Fig. 1). *Vinealobryum* may appear to be widely split as paraphyletic, but given that it is basal and ultimate progenitor to the remainder of the taxa, all the nodes between *V. murrayae* and *V. vineale* may be taken to be taxonomically *V. vineale*, or extinct or unsampled monophyletic biotypes of *V. vineale*. This may also explain the paraphyly of *Geheebia*, with *G. fallax* somewhat isolated but easily a descendant of *V. vineale* as well as the remainder of *Geheebia* species. *Exobryum*

Table 2. Comparison of Bayesian posterior probabilities awarded to evolutionary order of linear pairs of species on the caulogram, comparing judgmentally variable numbers of decibans used in the Zander (2014) study and the present use of one bit per trait

| Species | BPP 2014 | BPP present |
|-------------------------------------|----------|-------------|
| <i>Didymodon acutus</i> | 0.99+ | 0.94 |
| <i>D. anserinocapitatus</i> | 0.83 | 0.89 |
| <i>D. icmadophilus</i> | 0.93 | 0.80 |
| <i>D. johansenii</i> | 0.97 | 0.97 |
| <i>D. rigidulus</i> | 0.93 | 0.97 |
| <i>Exobryum asperifolius</i> | ? | 0.97 |
| <i>Exobryum</i> unknown progenitor | ? | 0.89 |
| <i>Fuscobryum nigrescens</i> | 0.94 | 0.94 |
| <i>F. perobtusum</i> | 0.98 | 0.89 |
| <i>Fuscobryum</i> shared ancestor | 0.72 | 0.80 |
| <i>F. subandreaeoides</i> | 0.95 | 0.89 |
| <i>Geheebia fallax</i> | 0.99+ | 0.80 |
| <i>G. ferruginea</i> | 0.93 | 0.89 |
| <i>G. gigantea</i> | 0.72 | 0.94 |
| <i>G. leskeoides</i> | 0.99+ | 0.94 |
| <i>G. maschalogenia</i> | 0.93 | 0.89 |
| <i>G. maxima</i> | 0.76 | 0.89 |
| <i>G. tophacea</i> | 0.99+ | 0.89 |
| <i>Trichostomopsis australasiae</i> | 0.94 | 0.94 |
| <i>T. revoluta</i> | 0.61 | 0.97 |
| <i>T. umbrosa</i> | 0.95 | 0.89 |
| <i>Vinealobryum brachyphyllum</i> | 0.72 | 0.94 |
| <i>V. murrayae</i> | 0.98 | 0.94 |
| <i>V. nevadensis</i> | 0.99+ | 0.94 |
| <i>V. nicholsonii</i> | 0.96 | 0.89 |
| <i>V. vineale</i> | 0.99+ | 0.97 |

is isolated rather far from its contiguous neighbors in the caulogram, *Vinealobryum* and *Geheebia*, and is in fact embedded in *Didymodon*. However, the position of *Fuscobryum* nearby, associated with the rather different species *D. rigidulus*, indicates that much more sampling of surviving molecular races is needed. One should remember that only heterophyly (paraphyly or patristically close phylogenetic polyphyly) and great distance on the cladogram contribute positive or negative information about serial descent (Zander, 2013).

Some species in Fig. 3 are represented by two exemplars (specimens) each. Certainly *Didymodon acutus* has two different molecular sequences, since the two entries are paraphyletic. One should realize, however, that specimens that are sister groups, such as *D. icmadophilus* and *Trichostomopsis australasiae* do not necessarily have the same molecular sequence. These are potentially paraphyletic to some yet unanalyzed species, and therefore would be evolutionarily informative.

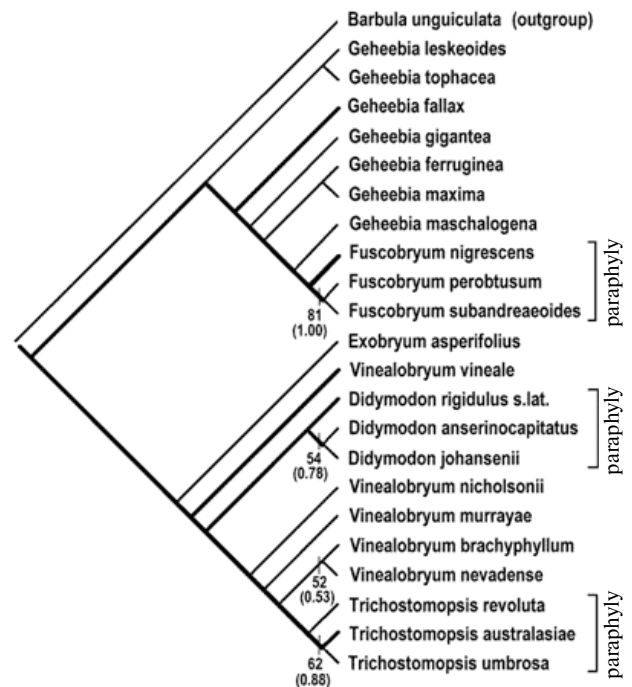


Fig. 2. Morphological cladogram of *Didymodon* s. l. based on the study of Zander (1998). Bootstrap support for proportions greater than 50, and equivalent Bayesian posterior probabilities (in parentheses), were awarded to four sister groups

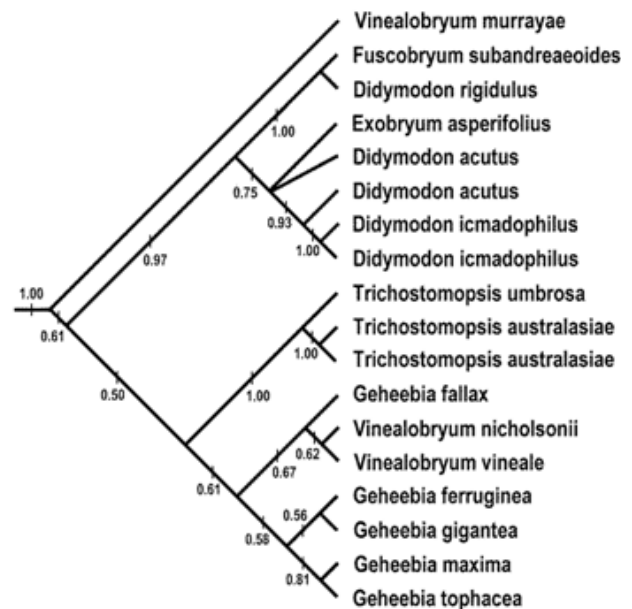


Fig. 3. Cladogram of *Didymodon* from Werner et al. (2005), reduced to only taxa that are present in the analytic key, with Bayesian posterior probabilities appended

Discussion

Cladograms use only data on advanced shared character states (i.e., phylogenetically informative) plus an optimization procedure that groups taxa with advanced character state transformations on a dichotomous tree. Caulograms use all data relevant to evolutionary relationships, both of shared and serial descent. To the extent possible, taxa are arranged in linear series, with branches made when a generalist ancestral species radiates two or more descendant taxa or lineages. Unknown taxa are interpolated when a missing link seems necessary to complete modeling the gradual evolution of a chain, or when two species require a shared ancestral taxon not now extant to explain their evolutionary nearness but separate evolutionary directions.

The macrosystematic method takes two steps. First, species are grouped to maximize shared advanced traits, and minimize differences between taxa. Cladistic analysis is a good way to do this. The ultimate minimal redundancy is when individuals are found to have all the same traits, and are therefore one taxon. Then, step two: When differences between species are minimized, the traits left over are those characteristic of the species, and often revelatory of monophyly through details of order and direction of evolution. Species need to be ordered serially so that every species contributes information. Conveniently, this reflects evolutionary theory that species mostly evolve by accumulated gradual transformations of character states. This is done using an analytic key by arranging the order of species so that they gradually add more traits as they evolve away from some outgroup, which is either a nearby taxon, or a generalized putative progenitor. This maximally informative order of species is ensured by adding one informational bit for each trait different from the last in order and subtracting one bit for each reversal.

To further explain ordering of taxa in modeling serial descent, if a progenitor has primitive traits 00000, the next species in order would be 00001, then 00011, then 00111, then 01111, then 11111, where 1 is an advanced trait. Each species contributes one bit, totalling 5 bits for the lineage. If we made the arrangement with the last species first, that is the outgroup 00000, then the last species in order put first 11111, the other three species would not contribute information as their traits would be totally redundant with the species with 11111 advanced traits. Requiring a penalty of 1 bit for each reversal then would make the 00000 then 11111 first order, add to zero bits when the remaining three species are appended.

This is 5 bits for the first order, but minus one for each of the other species that contribute reversals. Doubtless there are other ways of ordering species, such as adding to any positive bit an additional one bit for each species' distance from the progenitor, and not using negative bits at all.

A minimum of two linked traits per species (two bits equals 0.80 BPP) may not seem sufficient to confirm the linear order of species, but radiation of additional descendant species in a lineage or dissilient genus adds to the credibility, given a theoretical assumption of gradual accumulation of advanced traits.

This study demonstrated rather good support for order of evolution between pairs of contiguous species in a lineage (difference between numbers of advanced traits), and excellent support (total summed bits) for the direction of evolution for each lineage. Morphological cladistic analysis helped establish the linear and branching relationships of the main progenitor taxa. The molecular cladogram was interpreted as not an evolutionary tree because the basal nodes could be assigned to one taxon (*Vinealobryum vineale*) based on morphological information that was not phylogenetically informative but was instead macroevolutionarily informative.

Predictions are possible with macrosystematic analysis. For instance, the unknown taxon posited through inductive inference as ancestral to *Exobryum asperifolius* may be found with further study. The same obtains with the inductively inferred unknown shared ancestral taxon for *Fuscobryum subandreaeoides* and *F. perobtusum*. As in any evolution-based classification, further discoveries should match the present groupings to a great extent, each newly discovered species with expected similar physiological features and evolutionary potentials.

One may also note that generative generalized species generate other generative species. Although it is possible that advanced, specialized descendant species may prove to grade into generative new species in other habitats, this has not been shown the case in the present study. It is quite possible that there is a path of maximum evolutionary potential running through every large group that is comprised of generative species. The elucidation of this path should be of great importance in biodiversity study as elimination of generative species reduces expected numbers of descendant species that explore and exploit smaller niches. For instance, a generalized species of limited distribution in a habitat that is expected to expand and grow more arid over time is a good candidate for long-term protection.

This macrosystematic study supported the integrity of the study (Zander, 2013) that splits off from the large genus *Didymodon* five segregate genera based on dissilience (centers of radiation) around progenitor species. The caulogram model of evolution of *Didymodon* s. l. is helped to some extent by minimalization of redundancy with cladistics, and the analytic key can corroborate such redundancy. The model also can explain most of a molecular cladogram's apparent incongruity in relationships of the same species.

Support values for the order of taxa and for direction of evolution of the lineages in the caulogram were in the range expected by expert intuition (my own, after years of familiarity), and compared well with previous intuitive study (Zander, 2014a,b,c). It is concluded that a somewhat more mechanical therefore more easily replicable analysis, as was done here with the analytic key above, is a successful way to model evolutionary transformations at both species and genus level, so to inform a more information-rich classification than with cladistic methods alone.

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Submitted 24.04.2016

Зандер Р.Г. **Макросистематика *Didymodon sensu lato* (*Pottiaceae*, *Bryophyta*) з використанням аналітичного ключа та теорії інформації.** – Укр. ботан. журн. – 2016. – **73(4)**: 319–332.

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Проведене порівняння еволюційних дерев (каулограм) та філогенетичних кладограм як для морфологічних, так і молекулярних аналізів деяких видів мохоподібних роду *Didymodon* (*Pottiaceae*, *Bryophyta*). Запропонований новий двоступеневий макротаксономічний метод (метод макроеволюційної систематики) розрахунку статистичної підтримки як лінійного порядку, так і напрямку еволюції певної філогенетичної лінії. Метод включає кластеризацію таксонів у наборах шляхом мінімізації повторності (надмірності) з використанням кладограм та мінімальної парсимонії, з наступною побудовою часто розгалуженої лінійної моделі через максимізацію інформації про поступову (градуалістичну) еволюцію шляхом упорядкування видів через додавання інформаційних бітів для просунутих ознак і віднімання їх для еволюційних реверсій. Кладистичний аналіз розглядається як аналог криптографічної операції злому коду, при цьому кодовий

ключ потім використовується для побудови наступної теоретичної моделі. Дуже висока байєсівська підтримка обчислена для еволюційних ліній при морфологічному аналізі, що добре корелює з високою підтримкою попередніх молекулярних досліджень. Каулограма дозволила здійснити передбачення (прогнози), які були неможливими за допомогою кладограм. Обговорюється важливість використання інформації щодо як походження від спільного предка шляхом дивергенції (кладогенез), так і походження внаслідок «відбруньковування» нових таксонів та лінійних послідовних змін (анагенез).

Ключові слова: аналітичний ключ, кладограма, класифікація, еволюція, теорія інформації, макросистематика, парафілія, філогенетика, *Didymodon*, *Pottiaceae*

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Проведено сравнение эволюционных деревьев (каулограм) и филогенетических кладограмм как для морфологических, так и молекулярных анализов некоторых видов мохообразных рода *Didymodon* (*Pottiaceae*, *Bryophyta*). Предложен новый двухступенчатый макротаксономический метод (метод макроеволюционной систематики) расчета статистической поддержки как линейного порядка, так и направления эволюции определенной филогенетической линии. Метод включает кластеризацию таксонов в наборах путем минимизации повторности (избыточности) с использованием кладограмм и минимальной парсимонии, с последующим построением часто разветвленной линейной модели путем максимизации информации о постепенной (градуалистической) эволюции посредством упорядочивания видов через добавление информационных битов для продвинутых признаков и вычитание их для эволюционных реверсий. Кладистический анализ рассматривается как аналог криптографической операции взлома кода, при этом кодовый ключ впоследствии используется для построения следующей теоретической модели. Очень высокая байесовская поддержка вычислена для эволюционных линий при морфологическом анализе, что хорошо коррелирует с высокой поддержкой предыдущих молекулярных исследований. Каулограмма позволила осуществить прогнозы, которые были невозможными при помощи кладограмм. Обсуждается важность использования информации относительно как происхождения от общего предка путем дивергенции (кладогенез), так и происхождения вследствие «отпочковывания» новых таксонов и линейных последовательных изменений (анагенез).

Ключевые слова: аналитический ключ, кладограмма, классификация, эволюция, теория информации, макросистематика, парафилия, филогенетика, *Didymodon*, *Pottiaceae*