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THE POTTIACEAE S.STR. AS AN EVOLUTIONARY LAZARUS TAXON

RICHARD H. ZANDER¹

Abstract: Genomic studies have shown that evolution can be based on clusters of genes that may be silenced and reactivated by regulator genes or promoter sequences. Thus, apparent phylogenetic homoplasy may actually represent a single complex developmental response to selection, involving many genes or gene clusters and one or more regulating sequences, and as such may be called multiplex homoiology. Evidence for such complex exaptations (pre-adaptations) in many organisms is discussed, and two features of the Pottiaceae (Bryopsida), the complex gametophytic morphology characterized by the pleisiomorphic *Timmiella*, and the twisted peristome complex of 32 filamentous, spiculate teeth, distal to a basal membrane are suggested to be likewise homoiologous. The latter complex trait may have reappeared in the family 4 to 7 times. Inasmuch as exaptations may skip branching events tracked by nested sets of non-coding traits, and because genetic isolation alone is not a good basis for classification, this paper re-evaluates past evolutionary schema in light of this theoretically acceptable exception to Dollo's Law that complex traits are never re-evolved.

Key Words: exaptation, Dollo's Law, evolution, homoiology, Pottiaceae, phylogenetics.

INTRODUCTION

With a change during the 1700's and 1800's towards probabilistic thinking in science (Pap, 1962), philosophical or logical support for certainty or relative certainty about "truth" in science began to be replaced by a pragmatic attitude that science does not establish truth, but identifies theories that are so well supported by facts (well-corroborated observations) that they may be acted upon (used as a basis for additional research) and alternative theories may be ignored, even though some facts support them. The new probabilistic science is centered around a phenomenon of distribution of random events in physics described by the Central Limit Theorem, and is the basis for probabilistic theory and statistics. Statistics as a field is well established today and, although there are conflicts between the different schools (Gigerenzer et al., 1989) of frequentist, Bayesian, and hypothesis testers, the basic requirements for assessing reliability are clear. There are, however, commonly today many phylogenetic studies that

¹ Missouri Botanical Garden, PO Box 299, St. Louis, MO 63166-0299, U.S.A. E-mail: richard.zander@mobot.org

fail to provide adequate statistical evaluation, often focusing on only one or two of several requirements for establishing reliability.

Bayesian Philosophy and Science

Although the result of Bayes' Formula is the posterior probability and that is commonly regarded as the chance of a solution being correct, the Bayesian philosophy also requires no bet (i.e., no confidence in the pragmatic value of the results) except after evaluation of risk. Bayesian betting in the phylogenetic context means taking the study out of the realm of speculation and deciding whether to view the solution as sufficiently reliable to base additional work (biogeography, etc.) on it. The risk of one's science being wrong (requiring a high posterior probability of being right) also depends on the chance of any assumptions being wrong, which affects the final probability involved in the decision to make the bet or not (the posterior probability of a branch arrangement of interest must be multiplied by the chance that the arrangement is wrong because an assumption may be wrong).

There are two major methods of phylogenetic analysis that now compete with funding for taxonomy and biodiversity studies: analysis of morphological phenotypic expression commonly using maximum parsimony, optimality, Bremer support, and, recently, Markov chain Monte Carlo Bayesian analysis ("datatype = standard"); and sequence analysis focusing on many apparently evolutionary neutral or nearly neutral independent and independently (i.e., randomly) distributed (I.I.D.) traits. Each has particular reliability problems. Morphological characters are relatively few and commonly convergent, optimality alone does not take into account nearly optimal alternative solutions, Bremer support needs branch length data to be even slightly meaningful, and Bayesian analysis shows too high posterior probabilities for short branch lengths (e.g. from typical morphological data) due apparently to a hard polytomy not being an alternative (Lewis et al., 2005). DNA sequence analysis suffers from major problems, e.g., (1) assumption that the data is independent and randomly distributed when it may not be, at least in part; (2) that the data is sufficiently copious to reflect a chi-squared distribution; (3) that the evolutionary model being used is correct or adequate; (4) that conclusions are not based on pre-selecting for further probabilistic study branch arrangements or groups with high probability scores from a set of many, i.e., multiple test problems; (5) ignoring the effect of implicit, often unaccounted assumptions (Zander, 2005) in introducing uncertainty because of an emphasis on the likelihood principle that the data provide all that is needed for evaluation of the truth of an hypothesis (because the likelihood of the hypothesis is the likelihood of the data); (6) ignoring contrary data, such as branch arrangements from other studies that are less than 0.50 Bayesian posterior probability (BPP) or nonparametric bootstrap (BP); (7) conflicting results from different methods of analysis; and (8) falling back on philosophy or logic when statistical support is low. There are dozens of unaccounted assumptions that affect the reliability of phylogenetic analysis (Zander, in preparation), and the present paper provides an across-the-board penalty of one percent to the BPP (or 20 percent of the reliability window if 0.95 BPP is the accepted minimum level of reliability).

Problems with statistics and phylogenetic estimation

Regarding using either total evidence (Allard & Carpenter, 1996; Eernisse & Kluge, 1993; Nixon & Carpenter, 1996) or the comparison of individual gene studies (Chen et al., 2003), total evidence may be better because, in evaluating gene studies with

Bayes' Formula, one arrangement at high reliability in BPP by chance alone will never be refuted by a few additional studies that show ca. 0.50 BPP because no matter how many 0.50 priors there are, the high score does not change. Only when a low BPP by chance alone occurs can the high score be refuted. Therefore, many studies must be made to establish a chi-square distribution, and low scores retained (not discarded if below 0.50). Consider a 4-taxon branch arrangement with the branches labeled A, B, C, and D, and possible branch lengths AB, AC, and BC when D is outgroup. With total evidence, in the 4-taxon case with random data or in the case of real data with a hard polytomy, it is possible to find or contrive an arrangement supported by chance alone with, for instance, a 0.98 CI reliability of a branch length of 7 steps where $AB+AC+BC = 10$; doubling the data will reduce the chance down to 0.96 in a branch length of 11 with $AB+AC+BC = 20$. This assumes the additional data is random from additional studies of the hard polytomy (or from another contrived data set) and shared about equally by AB, AC and BC. Thus, for branch lengths of about 10 steps, rather highly reliable scores that may have occurred by chance alone are not corrected by total evidence involving a hard or soft polytomy until the data set relevant to that branch arrangement is more than doubled in size.

Multiple test problems (Felsenstein, 2004) occur when selection is made on the chance of being correct. For example, flipping many coins many times to determine if any are loaded will result in several coins coming up heads several times in a row even if all coins are fair. In the context of a large number of coins analyzed, this is to be expected. But selecting only that group of coins and their associated data that generates a high reliability measure and reanalyzing from that data will falsely show high reliability out of context, and the high possibility of this being random data is hidden. In phylogenetic analysis, preselecting taxa for study based on morphological analysis can associate taxa with randomly established convergent gene traits that are reflected in morphology, and reliability measures associated with molecular analysis of just that group are impacted. The same is true with all molecular data in that both maximum parsimony and likelihood analysis will group taxa, sometimes on the basis of imbalanced but random data, and each group is a preselection for succeeding studies. If the first molecular analysis resulted in a BPP of 0.95, then the second analysis based on just this group, to reach 0.95 BPP, requires Bonferroni correction (i.e. a BPP of 0.975 is needed), such that both analyses are correct (show acceptably non-random variation) at the same time. Any preselection of taxa is a candidate for examination for introduction of multiple test problems.

A totally artificial data set of 50 taxa and 50 random 2-state characters was contrived with RANDSET (Zander, 1999). Analysis with PAUP* under maximum parsimony (hs with 20 random sequence additions) produced 159 equally parsimonious trees from this totally random data set, and a largely unresolved strict consensus tree with, however, two distinct lineages (A,B) and ((C,D)E). An analysis of a subset of these 5 taxa, under maximum parsimony (bandb), produced one lineage of ((C,D)E) with 0.58 BP support for (C,D) and 0.81 BP for (C,D,E). Bayesian MCMC analysis (MrBayes 3.1, datatype = standard, ngen = 500000) of the 5 taxon data set provided 0.74 BPP and 0.94 BPP for the same groups. Clearly, preselection of a subset on the basis of a reliability measure for further analysis introduces multiple test problems.

Contradictions between morphological and molecular analysis

Some molecular data is equivalent to morphology in being subject to evolutionary pressures, but other data (most non-coding DNA) are not contributing to phenotypic traits of the organism but are supposedly randomly generated mutations that are segregated on speciation. Actual speciation has to do with the coding mutations not the non-coding mutations. Nested non-coding mutations and what are taken to be independent and random mutations of genes are used to track events of genetic isolation. This paper deals with contradictions between phenotypic features associated with speciation and cladistic events of speciation.

Casual inspection of a cladogram allows the following three kinds of apparently reliable information (given the data): (1) branch arrangements distant on a cladogram are probably reliably separated; (2) branch arrangements that are distal to an internode of 0.95 CI (or BPP) are probably reliably monophyletic; and (3) if the molecular result agrees with prior morphological analysis, the branch arrangement is probably reliable.

Contributions of genomic analysis

Homoiology is a kind of parallelism in which organs that are developmentally the same converge to the same kind of phenotype, e.g. wings of birds and bats are homoiologous as tetrapod forelegs but convergent as wings. It may be applied (e.g. Stuessy et al., 2003) to recent theorization based on data from evolutionary development (“evo-devo”) work that indicates that clusters of genes controlled by one regulator or promoter may be silenced then reactivated later in a phylogenetic lineage (Caporale, 2003a, 2003b; Stuessy et al., 2003). Such gene clusters may determine the existence of major organs and be more highly or immediately adaptive than incremental selection and accumulation of traits (Caporale, 2002, 1999). Incremental evolution, a basic assumption of all present parsimony and likelihood analyses, is thus not necessarily always the case. There may be many “hopeful monsters” (Bateman & Dimichele, 1994) among our taxa, and much apparent homoplasy may be reactivation of silenced traits, not independent new mutation. As reviewed by Stevens (1980), there is early discussion of “evolutionary recall” (Robson, 1972), this possibly by developmentally based violation of Dollo’s Law that complex traits are not re-evolved. Because the definitions of much terminology in phylogenetics includes a theoretical first cause, the use of the word “homoiology” is various, and occasionally tendentious as in the redefinition: “Homoiologies are phylogenetically misleading resemblances among a group of taxa that can be ascribed to phenotypic plasticity. That is, homoiologies are homoplasies that result from the expression by a genotype of different phenotypes in response to different environmental conditions” (Lycett & Collard, 2005). In the present paper, homoiology is “evolutionary recall.”

Examples of phylogenetically distant but developmentally homologous traits include apparent re-evolution of shell coiling in snails (Collin & Cipriani 2003); reactivation of wings in wingless walking sticks (Whiting et al., 2001); modes of vulva formation in nematodes (Srinivasan et al., 2001); ancestral features of the lateral lines, muscles and gill rakers of cichlid fishes (Stiassny, 1992); eyes in eyeless copepods (Dingle, 2003); and occurrence of a second molar in lynx (Kurtén, 1963). Not all similar atavisms are developmentally associated, as vestigial hips in snakes and whales have been shown to ultimately depend on quite different developmental pathways (Bejder & Hall, 2002). The Pottiaceae (Bryopsida) is a large and diverse family of mosses characteristic of harsh habitats. The Pottiaceae (less *Timmiella*) may well be a “Lazarus

taxon” (Wignall & Benton, 1999), not in the geologic sense as a group that has skipped a long fossil epoch but as a resurfacing in evolutionary time of a major developmental adaptive complex contrary to Dollo's Law (Hall, 2003). Such silenced-gene reactivation has recently been estimated as restricted to 0.5--6.0 million years before full or partial degradation to non-functionality (Marshall et al., 1994). According to a review by Stevens (1980), several studies have supported the idea that the “genetic capacity to produce structures now no longer visible” can be retained for 200 million years or more in vertebrates. If traits evolve as silenced-reactivated clusters, then the independent and random distribution assumption critical to reliability measures, and the idea of incremental evolution itself, is affected at both morphological and coding DNA levels.

Possible homoiologous traits in the Pottiaceae

There were many reversals in traits in Zander's (1993) maximum parsimony cladogram of Pottiaceae morphology. These involved length of stem; stem sclerodermis and hyalodermis presence; leaf stance when dry or wet; leaf shape and length; conformance of leaf ventral surface and costal groove; leaf base shape; number of rows of cells across ventral surface of costa; transverse section shape of dorsal stereid band; dorsal costal epidermis presence; costal hydroid strand presence; width of medial upper laminal cells; superficial wall width of upper laminal cells; sexual condition; perichaetial leaf shape; seta twisted or not; theca length; annulus type; peristome type; length of calyptra; and spore diameter.

Hypothetically, these traits could be changed from one state to another and back again via direct mutation of the gene or through a silencing-reactivation method, but if simple the traits can be treated as incrementally accumulated. If of definitely complex morphology, reversals are more likely to be homoiologous. Homoiologous clusters of traits can also be lumped by maximum parsimony into the same lineage. For instance, a multiple trait reversal through reactivation in a species that was pottiaceous but not *Tortula* involving the major gametophytic traits of *Tortula* would place that taxon in *Tortula* or at least in the close relationship. Multiple trait reversal would thus be hidden to a large extent in phylogenetic analysis. We know that genes are silenced during cell differentiation, so silencing is not debatable, and any reversal may involve reactivation. Evidence for multigene complex reactivation may be sought in identifying major phenotypic trait clusters that are at a distance on a molecularly based cladogram and apparently contravene Dollo's Law that complex traits cannot be expected to re-evolve.

Zander's (1993) maximum parsimony analysis of the morphology of all 76 then known genera of the Pottiaceae showed re-evolution of the twisted peristome complex of 32 filamentous, spiculate teeth arising from a basal membrane at four distant nodes on the cladogram. The molecular cladogram of Werner et al. (2004) based on *rps4* chloroplast DNA showed scattered and apparently re-evolution of the twisted peristome complex. The latter cladogram also showed one pottiaceous genus, *Timmiella*, treated as basal by Zander (1993), to be phylogenetically distant from the Pottiaceae s.str. Because *Timmiella* evinced a full range of characteristic, pleisiomorphic Pottiaceae traits, its morphology may be determined by the same gene cluster that informs the Pottiaceae s.str. Intermediate nodes, however, shared lineages of quite different morphology, in the families Calymperaceae, Dicranaceae, Ditrichaceae, Fissidentaceae, and Grimmiaceae. Although the Werner et al. (2004) cladogram was fully resolved, the reliability of phylogenetic distance was difficult to ascertain as only some nodes showed high values

for Bayesian credibility intervals and the cladogram required reduction to show only reliable relationships.

The way phylogenetic analysis has itself evolved apparently parallels recent changes in the way history proper is studied. Fischer (1989) pointed out that three generations ago, there was a standard paradigm for doing historical work consisting of narrative reports of a fairly narrow class of variables (authority and power in politics through time), based on thorough, Gestalt knowledge of the literature, with major findings offered as interpretations discovered by intuition underlain by testimony. Early in the 20th Century, the topics of history expanded greatly and historical relativism became central (1930--60), though unsatisfactory because static. In the 1960's the French school of the "Annales" invented a radical new method that examined change in all of social history, requiring rigorous methods of logic and empiricism. As a synthesis, however, in the 1980's this newest paradigm failed by devolving into competing special fields with narrow focuses and philosophies of study. Fischer's solution was to combine as well as possible the best elements of all previous syntheses. Both interpretation and empiric evaluations contribute to a more broadly based, interdisciplinary view of history, combining fact-based, interpretive story-telling and rigorous empiric problem-solving as a "braided narrative." A history of phylogenetics (e.g. as related by Felsenstein, 2004) follows approximately this nutshell historiography. Originally, evolutionary work was based on thorough, Gestalt evaluation of the facts, resulting in reasonable scenarios. Then, emphasis on data from crossing experiments, common gardens, reciprocal transplants, cytology, and other fields supported a "New Systematics" with more robust, empirically based narratives. Phenetic analysis of the 1970's introduced a rigorous mathematical method emphasizing similarity, with prediction focused on predicting phenetic similarity. Cladistics, with a competing new rigorous method based on maximum parsimony, then gained popularity, and proponents ridiculed the older descriptive methods (e.g. Crowe, 1994) as overly subjective and similar to the "just so stories" of Kipling (1966), e.g. "How the Leopard Got His Spots." Today, well-known methods such as maximum parsimony, maximum likelihood, and Bayesian Markov chain Monte Carlo methods all have their own partisan schools and somewhat different results with the same data, while new techniques both complex, e.g., codon substitution (Ren et al., 2005) and simplistic, e.g., DNA bar-coding (Hebert & Gregory, 2005; Will et al., 2005), vie for researchers' attention, and but all commonly relegate morphology into the background or at best include it submerged in total evidence studies.

METHOD

A Bayesian MCMC analysis of 48 exemplar species of the Pottiaceae and 24 species in other haplolepideous families was done by Werner et al. (2004), based on *rps4* chloroplast DNA sequences. The results were here subjected to the five-step "operative transform" procedure of Zander (submitted), which creates a cladogram with only 0.95 CI branch arrangements, all other branch arrangements being collapsed. The original cladogram was fully resolved, and thus "speculative," and the transform provides a reliable core on which a taxonomist can base classification and further research. *First*, morphological and molecular results are combined with Bayes' Formula when "uncontested" morphologically based branch arrangements, assigned a probability of 0.95 match molecularly based arrangements, and the posterior probability must be therefore greater than 0.95 if the molecular Bayesian posterior probability (BPP) is

greater than 0.50. *Second*, the BPP is taken as equivalent to the chance that the arrangement is correct, even though the BPP of short branches are commonly expected to be too high (Lewis et al., 2005; Suzuki et al., 2002; Zander, 2004). *Third*, a small (0.01) reduction in probability is made to reflect unaccounted assumptions that contribute uncertainty, as a general penalty applicable to BPPs of each branch arrangement, and also additional individual penalties are made when necessary for suspicious branch arrangements. *Fourth*, distance on the cladogram comprised of internodes of less than 0.95 BPP is evaluated for reliability in the following way. Chained internodes with BPPs lower than 0.95 are combined into one implied reliable internode (IRR) using a formula that determines the chance that at least one internode among two or more is correct, by calculating an implied reliable confidence interval (IRCI). The formula for the IRCI is simply one minus the product of the chances of each of all concatenated arrangements being wrong (where the chance of being wrong is one minus their BPP). A spreadsheet is available for easy calculation of the IRCI (Zander, 2003). *Fifth*, at least two intervening internodes must be true at once for taxa to be distinguished as separate from a particular clade as opposed to being merely a basal branch, and the calculation used is similar to standard Bonferroni correction for multiple tests (i.e., the BPPs or IRCIs when multiplied together must reach 0.95). These five evaluations determine that one or more reliably resolved branch arrangements exist in a published cladogram, and that two or more are correct at once when distance is evaluated.

The morphologically based phylogenetic analysis of Zander (1993) was re-examined for homoiologous traits as complex traits that appear to re-evolve separately in distant parts of the cladogram. A cluster analysis (UPGMA) was performed (using PAST, Hammer & Harper, 2003) on the same data set (less *Hypodontium*, definitely excluded from the Pottiaceae by Werner et al., 2004), using the clustering method (Dice, a.k.a. Sorensen) that best kept uncontested or accepted groups together. A subset of that data set containing *Timmiella* as outgroup and only the genera with at least some species with the complex pottiaceous twisted peristome was used to generate (with PAUP*, Swofford, 1998) a constraint tree with maximum parsimony (default settings, including ACCTRAN). Then, a neighbor-joining tree (NJ---Saitou & Nei, 1987) of all taxa (less *Hypodontium*) was made with PAUP* with genera with twisted peristomes forced into basal positions by that constraint.

There are thus four sources, all somewhat different, of possible evolutionary relationships that can inform a pragmatic classification, (1) intuitive or Gestalt as discussed for most genera by Zander (1993); (2) the operative transform of the Werner et al. (2004) molecular cladogram (Figure 1); (3) the NJ reanalysis of the original cladogram of Zander (1993) with genera with twisted peristomes constrained basally (Figure 2); and (4) the UPGMA-Dice cluster analysis (Figure 3). Hypothetical branch arrangements based on morphological traits are not assigned formal probabilities as these are simply optimal trees and there may be many barely less likely alternative trees, also significant nonparametric bootstrap proportions are usually impossible to get from morphological data sets with large numbers of taxa; on the other hand, intuitively uncontested groups for which alternative branch arrangements are apparently not supported by any morphological evidence may be informally assigned a high confidence level as a kind of Bayesian prior. The object was to create the most highly resolved tree that is both reliable and reflects all relevant data. In this case, given problems with (1)

implicit assumptions of model and data integrity, (2) the work of Baptiste et al. (2005) and Salamin et al. (2005) critical of the ability of sequence data to generate reliable phylogenetic trees, (3) the suggestion by Wortley et al. (2005) that as many as 10,000 base pairs are needed to fully resolve and support a difficult phylogeny, and by Rokas et al. (2003) that as many as 20 genes may be necessary to derive a supported, resolved phylogeny for such groups, then a much simplified evolutionary tree informed by apparently reliable branch arrangements in molecular studies is in this case the best to be hoped for. For taxa not treated in the molecular study or otherwise equivocal, the intuitive or Gestalt evaluations of Zander (1993) are followed, based on a strong a priori weighting of morphological traits through biologically well-founded character analysis as justified by Szalay et al. (1987). The multi-stemmed core of the evolutionary tree reflects multiple reappearance of the twisted peristome in the NJ tree with twisted peristome genera constrained basally, but relationships of taxa otherwise indicated by general proximity. The final tree (Figure 4) is presented as an evolutionary tree showing only relationships between extant taxa. Any lines of relationship must be interpreted by the reader as having been established by unknown ancestors.

Given the lack of adequate confirmation of the results of morphological study through fossils or statistics, and the number of unaccounted assumptions that plague molecular analysis, the taxonomist developing a classification must be prepared to accept only a rather poorly resolved evolutionary tree (not based on weakly founded speculation) as in any way reliable and suitable for basing further research.

RESULTS

The operatively transformed molecular tree is given in Figure 1. The Pottiaceae s.str. is grouped terminally in the cladogram. The genus *Timmiella*, however, which was a basal branch in the Zander (1993) morphological cladogram, is reliably placed (given the data set) towards the base of the cladogram, separated from the Pottiaceae s.str. by three reliable (BPP 0.95) internodes. Details of the transform will be given in another publication. The genus *Timmiella* has a large array of the pleisomorphic traits of the Pottiaceae, including the filamentous, twisted peristome with a basal membrane. Although it is distant by at least three speciation events (and probably many more that lack reliable data tracking them), it is a candidate for interpretation as having a homoiologous relationship with the Pottiaceae s.str., sharing the same many developmental, little-changed traits. Although both *Timmiella* and the Pottiaceae s.str. are possible Laxarus taxa, the absence of branching lineages connecting *Timmiella* with the main line of the cladogram indicates this genus may be frozen in time, a living fossil.

The transform shows to some extent those major infrafamilial groups of the Pottiaceae recognized by Zander (1993), with clustered taxa in lineages approximating his Timmielloideae, Trichostomoideae, Leptodontieae, and Barbuleae. A major group identifiable as the Pottiae including *Tortula* is clear, but *Syntrichia* and relatives are less well differentiated from the Barbuloideae (sensu Werner et al., 2004, is the same as Merceyoideae sensu Zander, 1993). The Barbuloideae is somewhat exploded, with some members scattered among other lineages, and *Scopelophila*, exemplar of the type genus (*Merceya* is a synonym of *Scopelophila*) is isolated as a basal branch. As *Scopelophila* is so reduced morphologically that it may be a member of a different family, the Merceyoideae can be restricted nomenclaturally to that isolated genus and the more familiar Barbuloideae used for the remainder of the subfamily. The complex twisted

peristome is scattered among the several apparently reliable lineages of Pottiaceae. Figure 1 shows in bold face those genera known to have a twisted peristome in at least some member species, and those species that actually have such are marked with a square bullet. Clearly all ancestors of the reliable nodes would have to have twisted peristomes to *avoid* an interpretation as homoiologous gene complex reactivation; this extends down to *Pseudocrossidium hornschuchianum* and even further to *Timmiella*. Given the various expressions of the peristome known for the Pottiaceae, it is improbable that no similar variation would occur in the ancestors, and that other families evolving from the line between *Timmiella* and the Pottiaceae s.str. would not have at least some twisted peristomes. Thus, an interpretation of multiplex silencing and reactivation is a good hypothesis. The phylogenetic distance between *Timmiella* and the Pottiaceae can be interpreted as events of genetic isolation associated with the Biological Species Concept (doubtless accumulating minor incremental trait changes) that do not affect the major evolutionary contribution of the transmission of the set of now activated pleisiomorphic traits, including the twisted peristome, of the ancestor of *Timmiella* to those of the Pottiaceae s.str.

The four instances of apparent re-evolution of the twisted peristome found in the original cladogram of Zander (1993) are reflected in the neighbor-joining tree with genera (in at least some species) with twisted peristomes constrained basally of Figure 2. Genera with at least one species with a twisted peristome are given in bold face. The NJ tree is much like that of the original tree, but points out well that even though taxa are forced into a form that will not contradict Dollo's Law, NJ requires seven more or less separate groups of taxa with twisted peristomes, which indicates that the twisted peristome contributed developmentally by a direct ancestor of *Timmiella* may be been reactivated as many as seven times in the Pottiaceae. The neighbor joining method is fast and allows different branch lengths, but is not guaranteed to produce the shortest tree. The results, however, are commonly close to the maximum parsimony result, and unlike UPGMA, a molecular clock is not assumed.

The cluster analysis of Figure 3 that best kept uncontested or accepted groups together (and by extension may best keep groups of unknown relationships in correct proximity assuming similarity reflects genetic relationship either homologous or homoiologous) is UPGMA with the Dice (or Sorensen) method. Again seven groups of genera, identified with bold face, exhibit twisted peristomes in at least some member species.

A reclassification of the Pottiaceae

The molecular analysis, the neighbor-joining tree, and the cluster analysis can be used to develop a new classification of the Pottiaceae that reflects at the subfamily and tribal levels reliable features of the molecular work in light of the possibility of developmentally identical reactivated homoiologous trait clusters tracked on molecular cladograms only by general morphological similarity. A low resolution is warranted by these theoretical possibilities, and genera with twisted peristomes and no particular reduction in morphological complexity of the gametophyte are here considered central to a "halo" of related taxa with reduced peristomes and gametophytes, some being otherwise reduced genera with special, apparently secondary features adapted to arid climates. Included in this classification are taxa found by the molecular study of Werner et al. (2004) to be almost certainly members of the Pottiaceae, such as *Clinclidotus*

(Clinclidotaceae) and *Sphachnobryum*. On the other hand, *Ephemerum* (Ephemeraceae) and *Goniomitrium* (Funariaceae) though suggested as Pottiaceae by Werner et al. (2004) may be excluded by their large, non-papillose leaf cells (elongate in Ephemeraceae) and campanulate calyptrae. Although these two taxa are highly reduced in morphological complexity, long-branch attraction and paucity of non-pottiaceous taxa in the data set, together with possible adaptive pressure on the coding sequences used in the analysis may have placed them in the Pottiaceae s.str. of the Werner et al. (2004) cladogram, while their correct placement may be lower in the cladogram (Funariaceae may not be well represented in its entirety by *Funaria hygrometrica* as outgroup). If further study indicates the contrary, however, the taxon closest to these is *Bryocephospora*. *Scopelophila*, representing a basal branch, may well belong to the Dicranaceae or Ditrichaceae (it lacks a peristome) and has equivocal morphological features.

Examination of the Werner et al. (2004) data set, graciously provided by Olaf Werner, shows that *Anoetangium aestivum* and *Gymnostomum viridulum* differ by seven sites (2 first position, 2 second, 3 third), but the two specimens of *Splachnobryum obtusum* (the only species of which two specimens were analyzed) differ by 21 sites (4 first position, 7 second, 10 third). Although the rates of change of sites, especially in the codon, surely differ, it is doubtful that the former two samples are not in the same genus, or the latter is a misidentification for *A. handelii*. Given that the word “exemplar” implies example representation of the molecular sequence characteristic of other specimens in the species and genus, one might wonder in view of the (unusually?) large internal variation in *Splachnobryum obtusum* that the specimens studied might not be samples from a more heterogeneous molecular assemblage at both species and genus level than expected. *Erthyrophylopsis fuscula* and *Erythrophyllastrum andinum* differ by only six sites (3 first position, 1 second, 3 third), and, given the uncomfortable similarities of morphology, this second look requires the synonymy of *Erythrophyllastrum* R. H. Zander as a genus with *Erthyrophylopsis* Broth.

The appropriate tree (Figure 4) that best represents a reliable hypothesis (or theory) of evolution in the Pottiaceae given both morphological and molecular study would be a low-resolution diagram similar to that of Chen (1941), namely Figure 4, in which the morphologically based NJ tree is most informative, but modified by reliable features of the molecular study of Werner et al. (2004), intuitive Gestalt evaluations of Zander (1993), and lastly the UPGMA-Dice cluster analysis. The classification, therefore, advanced here can be summarized as a combination of judicious melding of reliable (“operative”) features of the analyses of the molecular and morphological data. Those surprised that more definite lineages are not shown should remember that the molecular cladogram commonly had only one or two reliable internodes to distinguish genera, and the genera are often heterophyletic, i.e., species of one morphologically uncontested genus are scattered among the lineages of a molecular cladogram. Given the fact that there are commonly few informative characters in the Werner et al. (2004) molecular study of one locus, it is likely that reliable branching patterns of species within a genus are superposed across two or more generic branching patterns. Thus, although it may well be that the genus *Streblotrichum* should be revived and transferred to the Trichostomoideae because *Barbula* species with plane leaf margins are placed there in the molecular cladogram, the separation of these from the *Barbula* species with recurved margins may be an artifact that is correctable with more data (more genes analyzed). The

tree of Figure 4 is not a speculation but summarizes reliable elements at the subfamily and tribal levels of past work. In the classification given below, genera with unclear relationships are marked with an asterisk. For full nomenclatural citations, see Zander (1993).

POTTIACEAE Schimp., *nom. fam. cons.*

Timmielloideae Zand.

Timmiella (De Not.) Limpr.,

Trichostomoideae (BSG) Limpr. in Broth.

Astomaceae Schimp.; Astomataceae Magill, *orth. err. pro* Astomaceae Schimp.; Chionolomoideae Zand., syn. nov.; Eucladieae Chen; Eucladioideae Chen; Euweisiaceae Hampe, *nom. illeg.*; Phascaceae Schimp.; Tetracoscinodontieae Zand., syn. nov.; Tortelleae Chen; Trichostomaceae Schimp. "Trichostomeae"; Trichostomataceae Crosby & Magill, *orth. err. pro* Trichostomaceae Schimp., 1860; Trichostomeae BSG in Schimp.; Trichostomeae Dix.; Trichostomeae Limpr., rank not given; Weissiaceae Schimp.

Aschisma Lindb.

* *Bryocephospora* Crum & Anders.

* *Calymperastrum* Stone
Calyptopogon (Mitt.) Broth.

Chionoloma Dixon

Eucladium B.&S. in BSG

* *Leptobarbula* Schimp.

* *Neophoenix* Zand.

Pachyneuroopsis H. Miller

Pleurochaete Lindb.

Pottiopsis Blockeel & A. J. E. Smith

Pseudosymblepharis Broth.

* *Quaesticula* Zand.

Streptocalypta C. Müll.

* *Tetracoscinodon* R. Br. ter.

* *Tetrapterum* Hampe ex Jaeg.

Tortella (Lindb.) Limpr.

* *Trachycarpidium* Broth.

Trichostomum Bruch (including
Paraleptodontium D. G. Long)

Tuerckheimia Broth.

* *Uleobryum* Broth.

Weissia Hedw.

Weissiodicranum Reese

Barbuloideae (Herz.) Hilp.

Barbuleae Herz..

Erythrophylllopoideae Zand., syn. nov.; Gertrudielloideae Zand., syn. nov.; Anoectangiaceae Schimp.; Gymnoweisieae Limpr., rank not given; Pleuroweisieae Limpr.; rank not given; Pleuroweisioideae (Limpr.) Broth.; Pleuroweisieae (Limpr.) Chen

Anoectangium Schwaegr.

Barbula Hedw.

Bellibarbula Chen

Dialytrichia (Schimp.) Limpr.

Cinclidotus P. Beauv.

Didymodon Hedw. (includes
Kingiobryum H.
 Robinson)
Erythrophyllopsis Broth. in Herz.
 (*Erythrophyllastrum*
 Zand., syn. nov.)
Gertrudiella Broth.

Gymnostomum Nees & Hornsch.
Gyroweisia Schimp.
Hymenostyliella Bartr.
Hyophiladelphus (C. Müll.)
 Zand.
Molendoa Lindb. (including
Ozobryum Merrill)

Bryoerythrophyllae Zand.

Bryoerythrophyllum Chen
Mironia Zand.

Pseudocrossidium Williams
 * *Sarconeurum* Bryhn

Hyophileae Chen

Hyophilaceae Hampe, *nom. nud.*, *nom. rejic.*.

Ganguleea Zand.
Gymnostomiella Fleisch.,
Hyophila Brid.
Luisierella Thér. & P. Varde

Plaubelia Brid.
Splachnobryum C. Müll.
Teniolophora Reese
 * *Weisiopsis* Broth.

Leptodontieae Herz.

Leptodontioideae (Herz.) Hilp.

Hymenostylium Brid.
Leptodontiella Zand. & E.
 Hegew.
Leptodontium (C. Müll.) Hampe
 ex Lindb.

Rhexophyllum Herz.
Reimersia Chen
Streptotrichum Herz.
Trachyodontium Steere
Triquetrella C. Müll.

Pottioideae (Limpr.) Broth.

Pottieae (Limpr.) Dix.

Eupottiaceae, *nom. illeg.*; Tortuloideae Visotska, *nom. inval. typ. non. cit.*;
 Pottieae Limpr., rank not given.

Aloinella Card.
Crossidium Jur. (includes
Microcrossidium
 Guerra & Cano)
Globulinella Steere
Pterygoneurum Jur.
Stegonia Vent.

Tortula Hedw. (including
Protobryum
 Guerra &
 Cano, syn.
 nov.)

Syntrichieae R. H. Zander, trib. nov. Pottieis similis sed lamina superna in solutione KOH atque in statu vivo rubrescenti differt. Typus: *Syntrichia* Brid. (*Syntrichia ruralis* (Hedw.) Web. & Mohr).

* <i>Acaulon</i> C. Müll.	<i>Phascopsis</i> Stone
* <i>Aloina</i> Kindb.	<i>Sagenotortula</i> Zand.
<i>Chenia</i> Zand.	<i>Saitobryum</i> Zand.
<i>Crumia</i> Schof.	<i>Stonea</i> Zand.
<i>Dolotortula</i> Zand.,	<i>Streptopogon</i> Wils. in
<i>Henediella</i> Par.	Mitt.
<i>Hilpertia</i> Zand.	<i>Syntrichia</i> Brid.,
<i>Microbryum</i> Schimp.	<i>Willia</i> C. Müll.

Merceyoideae Broth.

Merceyaceae Casares-Gil; Merceyeae (Broth.) Chen

* *Scopelophila* (Mitt.) Lindb.

DISCUSSION

There are two scenarios for which *Timmiella* is related to the Pottiaceae. First, following optimization thinking using maximum parsimony and Bayesian MCMC modeling incremental evolution of morphological and molecular traits, *Timmiella* was elaborated from ancestors that were much reduced, and the Pottiaceae was incrementally re-elaborated. Second, in an evo-devo scenario, both *Timmiella* and the Pottiaceae are based on one multiplex genetic package the expression of which is controlled by a regulatory gene or promoter sequence, elaborated in the past, then switched off and on again, resulting in the two extant groups that have responded to at least similar selective pressures with the gene cluster that codes for pottiaceous phenotypy. The intermediate groups are phylogenetically discernable by tracking with non-coding sequences but are evolutionarily trivial, where the major evolutionary event is identified by developmentally identical adaptive phenotypes that are not explained by plasticity. Naturally, this hypothesis needs confirmation by developmental analysis of a possible genetic linkage and control.

Of 53 Pottiaceae genera in the molecular analysis, 12, or 1/4, have twisted peristomes, including *Timmiella*, placed distantly near the cladogram base. To avoid a hypothesis of re-evolution of this complex peristome, all 9 reliable internodes from *Timmiella* through the remainder of the distal Pottiaceae clade of the operatively transformed cladogram would have to represent ancestors with twisted peristomes, 6 of these in the Pottiaceae-less-*Timmiella* group. Figure 1 is the most highly telescoped cladogram, and the true tree or at least a more reliable tree from additional data would have many more internodes, all internodes connecting *Timmiella* and Pottiaceae s.str. necessarily representing ancestors with twisted peristomes. This seems doubtful, unless we also postulate that the proportion of ancestral species with twisted peristomes is totally unlike that of modern taxa, and also that the ancestors of genera in the Calymperaceae, Dicranaceae, Ditrichaceae, Grimmiaceae, and Ptychomitriaceae all had twisted peristomes.

Morphology and associated patterns of morphogenesis may be the key to real understanding of evolutionary relationships. Dollo's Law (Dingle, 2003; Hall, 2003) states that it is improbable (or probabilistically impossible) that particular apparently very highly adaptive complex combinations of traits would re-evolve through gradual accumulation of mutations a second time. This can be countered by demonstrations in the evo-devo literature that complexes of genes can be controlled by one or a few genes or a strongly conserved non-coding promoter sequence, which can be suppressed or silenced, and later, perhaps after millions of years, reactivated. Many genes also have been shown to be ancient, either active or potentially resurrected later in a lineage. There is thus an ability of gene complexes and their silenced controlling genes to slide past speciation events, perhaps in part as paralogs or pseudogenes. Taxa with such exaptations (pre-adaptations) to selection pressure would have an evolutionary advantage (Caporale, 2002, 2003b). The many morphological characters of the Pottiaceae that are shared with the more basal *Timmiella* may well be developmentally homologous in that it is improbable that all these would re-evolve gradually and prove to be in combination the plesiomorphic traits of the Pottiaceae.

A parallel situation occurs with humans and orangutans, which share many critical morphological characters (Schwartz, 1988), yet humans are demonstrably more distant from orangutans than from chimpanzees and gorillas on the basis of reliable molecular data, and the traits are apparently atavistic in humans. An explanation that would deal with conflicting morphological and molecular evidence is that there are two phylogenetic patterns that must be studied : (1) a phyletic tree revealed by gradual accumulation of mutations in introns, junk DNA and variable sites of exons, which record events of speciation based on the Biological Species Concept, i.e., inferred events of reproductive isolation; and (2) an evolutionary tree or network incorporating evidence that massive convergence is probabilistically due to shared fellow-traveler (suppressed in the lineage but potent) homoiologous complexes, and is revealed by morphology determined by activated or desuppressed controlling genes. At times, both trees may be the same, but contraindications of incremental evolution must be dealt with. The best way to evaluate morphology as revelatory of not-to-be-expected-by-chance-alone evolutionary relationships is to map morphological traits on a molecularly based cladogram and look for complex-trait homoplasy. Then, search for re-evolution of complex traits violating Dollo's Law. Constraining the involved genera basally and re-optimizing with all taxa is an obvious hypothesis to consider. Certain branch arrangements on this morphologically based cladogram may be changed as informed by reliable molecular studies, but it remains a theoretical structure only partially reliable. Additional context is provided by techniques of phenetic cluster analysis popular in the 1970's. After reduction, sometimes extreme, to a cladogram that shows only reliable branch arrangements, it may be sufficiently reliable to be of use in further study. The two contrary but improbable-by-chance-alone phenomena of molecularly based phylogenetic patterns (with high Bayesian posterior probabilities or high bootstrap proportions) versus morphological patterns (massive convergence) may be supported by continuing research in development, and if so then phylogenetic analysis will no longer find sufficient simply mapping morphological trait changes on a molecular tree (e.g., Buck et al., 2000).

Other studies appear to support the importance of silenced genes or gene complexes in evolution. The molecular study of pleurocarpous mosses of Buck et al.

(2000) found the trait “peristome lacking” scattered among 78 exemplar taxa in many families. If ancestors were similarly diverse in this character, it is difficult to imagine no reversals. The molecular study of *Didymodon* (Pottiaceae) by Werner et al. (2005a) found the twisted peristome in several taxa scattered throughout the cladogram. Likewise, in a similar molecular study (Werner et al., 2005b) on the Trichostomoideae, of the many taxa involved, the characteristic pottiaceous twisted peristome was present in many of the outgroup taxa, and again at a distance (highly reliable given the many 1.00 BPPs) in the center of the tree in several species of *Tortella*. In these three studies, although it is possible, it is improbable that all of the deeper branches and up to half of the more recent ones were of peristomate taxa. This needs further investigation.

The functional effect of natural selection on *cis*-acting regulators on single genes have been recently demonstrated in human evolution (Rockman et al., 2005). A silenced gene cluster is thought to degrade over the passage of time, and if so, it may be that the trait complex may degrade in stages. If so, then one might expect to see a central group of taxa with the intact trait cluster, surrounded by a group of taxa with gradually a reduced trait complex. In fact, we do see this in published cladograms of *Didymodon* and the Trichostomoideae mentioned above, where taxa or groups of taxa with long, filamentous, twisted peristomes are deeply embedded in the cladogram among related taxa of short, long-triangular, straight peristomes, rudimentary peristomes, or none at all. Thus, it may be that the arrangement of a tree core with a halo of reduced forms is the evolutionary group in the Pottiaceae (not necessarily a lineage but a spray or a series of multifurcations).

Genes commonly are more strongly conserved and their sequences vary less with time than do non-coding sequences. Given that genes can be significantly modified by selection or internal pressures such as codon bias, molecularly based phylogenetic trees are here treated as unreliable in decisively selecting among problematic branching patterns with confidence intervals requiring independent and random segregation, at least in deeper branches best informed by genes, and in fact only represent events of genetic isolation.

Given apparent genetic continuity in the lineage from *Timmiella* to the Pottiaceae s.str., but probabilistic support for the considerable patristic distance between that genus and the Pottiaceae s.str., then the pottiaceous complex of characters necessarily reappeared and had considerable phylogenetic valence. Given Dollo's Law regarding the improbability of major trait complexes re-evolving, it is possible that the pottiaceous gene complex survived genetic degradation, was epigenetically silenced on the tree between *Timmiella* and the Pottiaceae s.str., and was reactivated on selection involving regulatory genes or promoter regions. There is evidence that the twisted peristome, and perhaps the entire complex of pottiaceous traits, was re-evolved four to seven times. Such an explanation is needed and indeed necessary given the joint improbability of both phyletic distance and morphological similarity.

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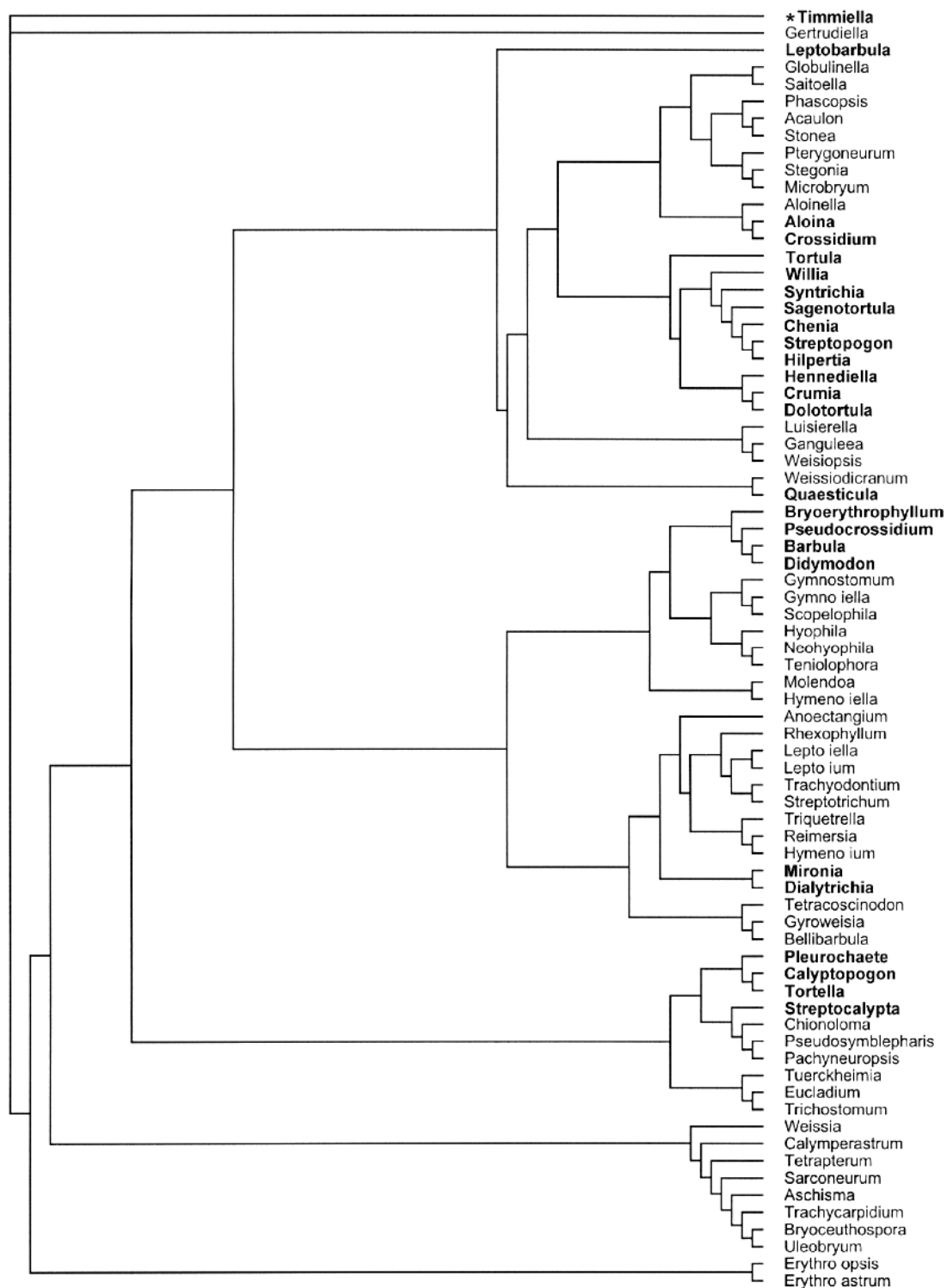


Fig. 2. Neighbor-joining reanalysis of the original cladogram (less *Hypodontium*) of Zander (1993) with genera with twisted peristomes constrained basally. Bold-faced are names of genera including at least some species with twisted peristomes.

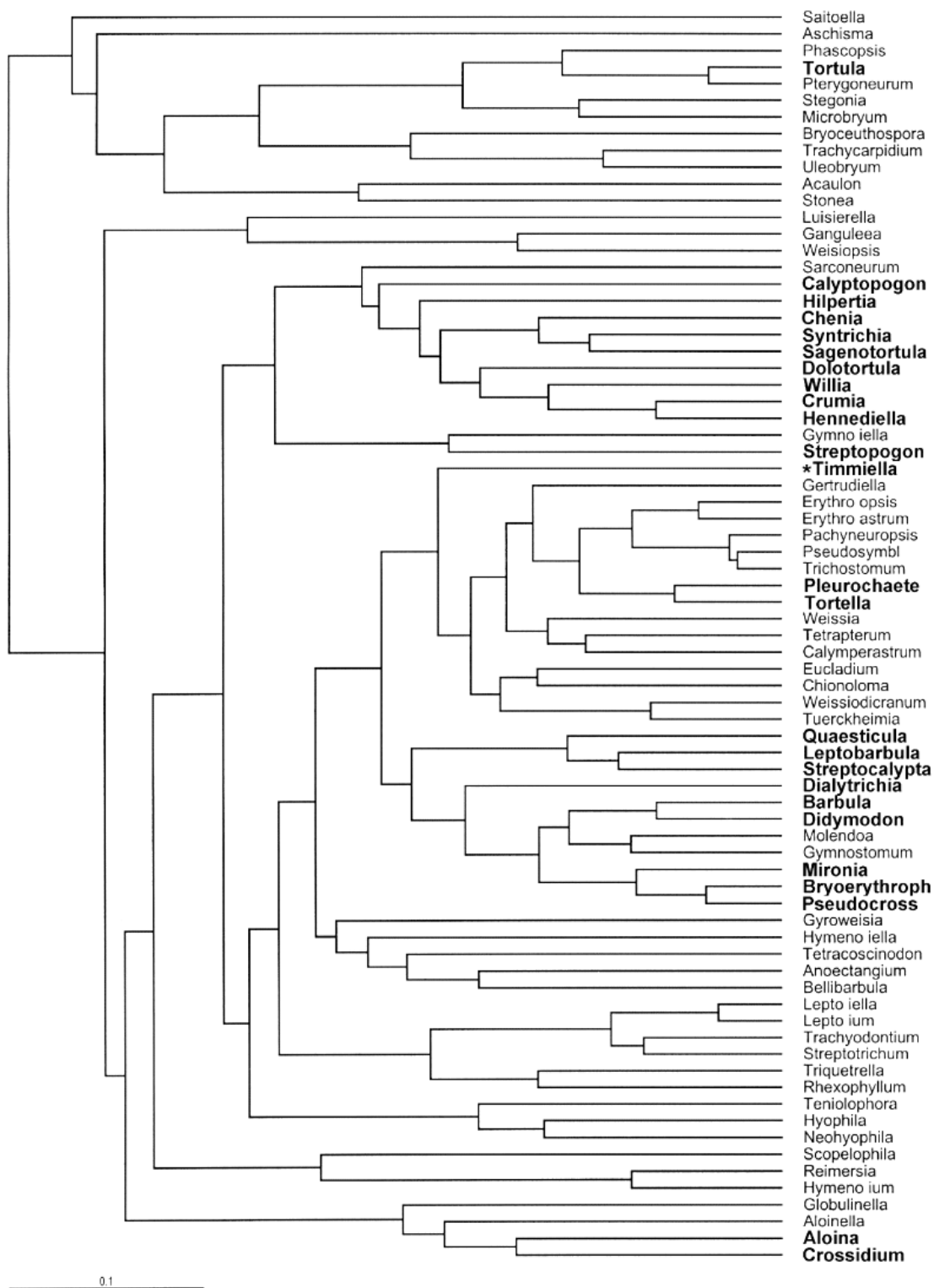


Fig. 3. UPGMA cluster analysis with Dice (Sorensen) method selected as best retaining uncontested (accepted) branch arrangements. Bold-faced are names of genera including at least some species with twisted peristomes.

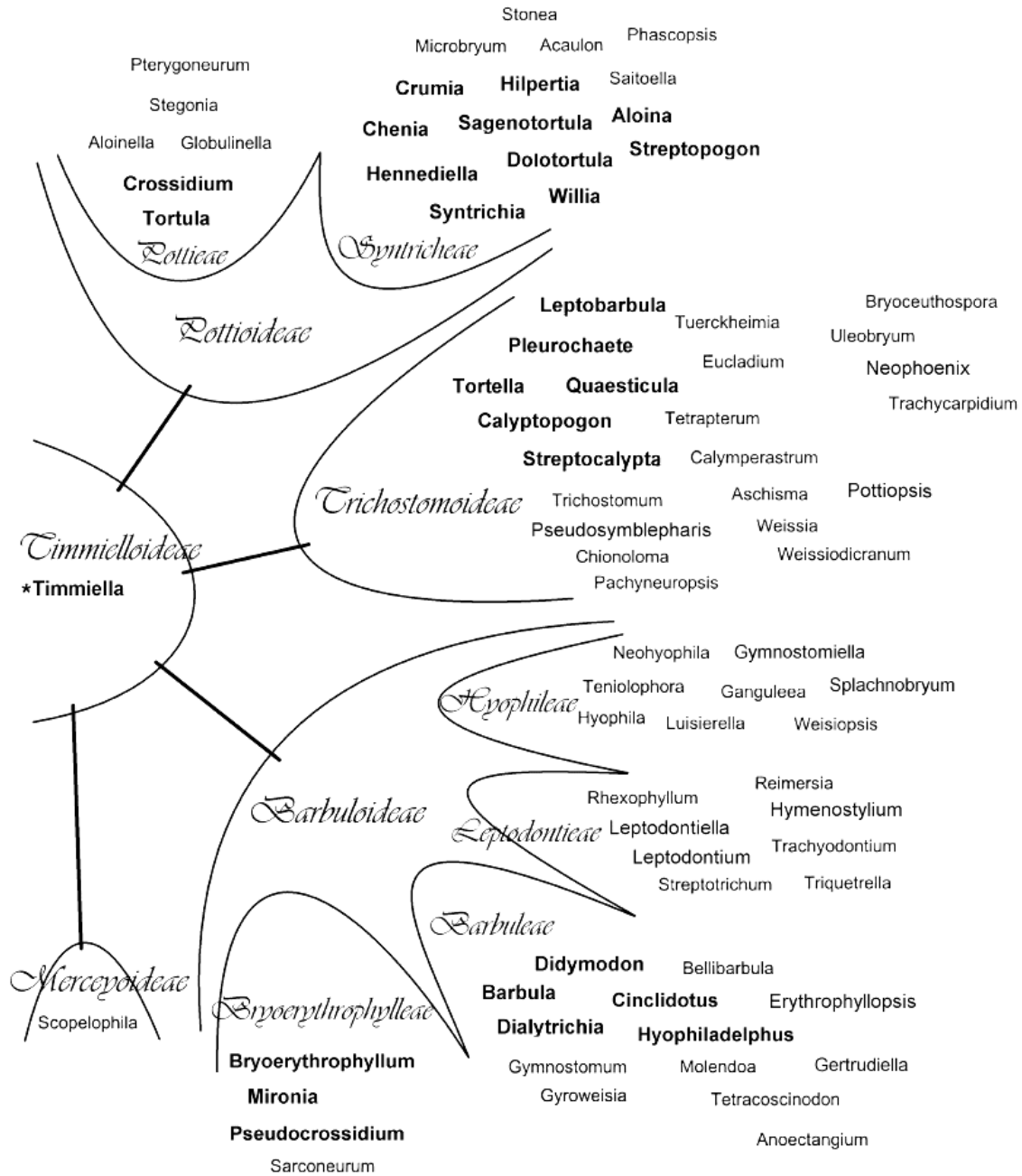


Fig. 4. Evolutionary tree best combining reliable aspects of morphological and molecular analyses. Bold-faced are names of genera including at least some species with twisted peristomes.