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Source: *The Bryologist*, Vol. 98, No. 3 (Autumn, 1995), pp. 363-374

Published by: American Bryological and Lichenological Society

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Phylogenetic Relationships of *Hyophiladelphus* gen. nov. (Pottiaceae, Musci) and a Perspective on the Cladistic Method

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Abstract. *The moss Barbula agraria Hedw., a discordant element in the genus Barbula, is recognized as distinct at the generic level by upgrading the monotypic Barbula sect. Hyophiladelphus C. Müll. Cladistic analysis supports a removal to the subfamily Pottioideae wherein Hyophiladelphus is related to one of two circum-Tethyan groups of genera. This study details the several necessary methodological steps for reclassifying this problematic species.*

Barbula agraria Hedw. is a small, nearly stemless moss endemic to islands and mainland shores of the Caribbean area. It has been described, discussed, and illustrated by Bartram (1949), Breen (1963), Crum and Steere (1957), Steere (1938), Crum and Anderson (1981), and Zander (1979, 1993, 1994). It is particularly common in the West Indies, whence I have seen specimens from Barbados, Cuba, Dominican Republic, Guadeloupe, Haiti, Jamaica, Martinique, Puerto Rico and the Virgin Islands. It is one of a distinctive group of Pottiaceae, including the essentially Caribbean species *Luisierella barbula* (Schwaegr.) Steere, *Quaesticula navicularis* (Mitt.) Zand., and *Plaubelia sprengelii* (Schwaegr.) Zand., that have a similar morphology apparently adapted to a shared sun-drenched, dry habitat of tropical and subtropical islands and the shores of nearby mainlands. That morphology includes a rosulate, short-stemmed habit, broad leaves with plane or incurved margins, ventrally bulging upper laminal cells, and papillae small or entirely absent.

In the genus *Barbula* (authorities of the supraspecific taxa throughout are according to Zander 1993), *B. agraria* has long been recognized as incongruous because of its broadly elliptical or spatulate leaves, but its two costal stereid bands have not, in the past, been taxonomically acceptable in the *Tortula* relationship, which is characterized by such leaves but with a single band. C. Müller (1849) placed *B. agraria* in *Barbula* sect. *Hyophiladelphus* C. Müll., together, significantly, with *Barbula spathulata* Dozy & Molkenb. (a synonym of *Hyophila involuta* (Hook.) Jaeg.), citing as distinctive the involute, more or less spatulate leaves, and both basal and upper laminal cells small and lacking papillae. Zander (1979) raised Müller's section to the subgenus level, and noted a clear resemblance to *Luisierella barbula* through the "similar strongly colliculate adaxial

laminal surface and nearly smooth abaxial surface." Steere (1938) placed *B. agraria* in its own group, *B. sect. Agrariae*, saying of the species that it "approaches *Barbula* in the structure of its costa, but on the basis of leaf-shape it is frequently placed in *Tortula*. It is sufficiently distinct from both genera, however, to justify, perhaps, the eventual erection of a new genus."

A cladistic analysis of the family Pottiaceae at the genus level (Zander 1993) demonstrated the existence of a lineage of taxa similar to *B. agraria* in morphology, especially in the leaves often tubulose when dry, leaf margins plane or incurved or involute, and upper laminal cells ventrally bulging. The leaf shape was commonly elliptical or spatulate, but also occasionally lanceolate, and the number of stereid bands was either one or two. Included were the 18 genera *Aloina*, *Aloinella*, *Crossidium*, *Gangulea*, *Globulinella*, *Hymenostyliella*, *Hyophila*, *Hypodontium*, *Luisierella*, *Molendoa*, *Plaubelia*, *Pterygoneurum*, *Quaesticula*, *Stegonia*, *Teniolophora*, *Weisiopsis*, *Weissia*, and *Weissiodicranum*. The group occurred either as comprising the base of the Pottioideae subclade (Zander 1993, pp. 41, 42) when analyzed with *Timmia* or *Ptychomitrium* as outgroups, or as a separate branch of the Pottioideae subclade (1993, pp. 40, 46) with *Polytrichum* as outgroup or *Timmiella* as functional outgroup. Viewing the last cladogram of the four as best, Zander (1993) recognized the group as the Hyophileae.

Barbula agraria has no relatives with intermediate morphology in the genus *Barbula*. With the expectation that *B. agraria* might well be placed in the Hyophileae if the family were reanalyzed with this species segregated as a monotypic genus (see synonymy in treatment of *B. agraria* by Zander 1979, 1994), new analyses were carried out.

METHODOLOGICAL REVIEW

A cladistic study, involving the principles of special similarity (Farris 1977a), monophyletic classification (Hennig 1966), and congruence of characters due to common ancestry (Patterson 1982; Kluge 1989), was performed at the genus level. An emphasis on using only presumed derived characters (Hennig 1966) as a basis for phylogenetic analysis has been extensively rationalized recently, and has been used in many studies of mosses since Koponen (1968).

The methodology of this paper is the same as that used in *Genera of the Pottiaceae* (Zander 1993), but the several critical methodological choices made there are here explained in detail because few bryological authors give reasons for their decisions one way or another regarding particular methodological issues discussed in the present paper. Avoiding areas of major controversy, one hopes to keep to the "straight and narrow" (Cranston 1991). As concerns the scientific method alone, the chief decisions that must be made during a study involve selection of methodology, modification of standard methods (because of unusual features such as any known introgression), selection of outgroup(s), homology of characters, and character weighting (both prior to the exact algorithm and after it).

The Pottiaceae are difficult to conceive as a monophyletic unit because the major synapomorphic character, the twisted peristome, has been reversed quite separately in different subclades (Zander 1993, p. 26). The family may be paraphyletic as opposed to holophyletic (Meacham & Duncan 1987) because species in the Ditrichaceae may be inappropriately excluded (Zander 1993). Ideally, in monothetic terms, lack of characters unequivocally supporting monophyly of the Pottiaceae should lead to breakup of the family (see discussion of Swofford & Maddison 1987, p. 225). The presence of several ancestral nodes on the stem below the branching of the two major lineages—Merceoideae and Pottiioideae (Zander 1993, pp. 47–49)—however, serves to support monophyly of the family. Also, the general morphology, including the distinctive but not unique papillose leaves with enlarged basal cells and complex costal anatomy, and the existence of many clear transformation series as apparently co-adapted suites of characters that relate taxa with twisted peristomes and those with non-twisted peristomes or peristomes absent or capsules cleistocarpous, provide other support that makes the twisted peristome (as a transmodal character *sensu* Micevich & Weller 1990) a probable shared apomorphy at the family level.

Very similar morphological structures and certain chemical color reactions were selected as potential

homologous traits, following Stevens' (1991) "criteria of similarity." The characters were examined for variation within each operational taxonomic unit (OTU) and between OTU's, with a view to determining clear discontinuities between variation patterns of the character states, while comparisons were made between character states bounded by like discontinuities. This maximized the likelihood of character independence. The moss family Pottiaceae is unusually rich in number of characters (Zander 1993) and this is of value in analysis: Landrum (1993) concluded that it is normally best to include as many characters as possible in a phylogenetic study.

The phylogenetic inference method used is that of parsimony (various methods reviewed in detail by Swofford & Olsen 1990), assuming least evolutionary change thereby minimizing the need for *ad hoc* hypotheses of homoplasy. Farris (1977b) has demonstrated that "the usual criticisms of the parsimony criterion (that it assumes that evolution proceeds parsimoniously, or that parallelism is improbable) are quite groundless." I agree with Hull (1983, p. 184) and others that, in view of the simplistic nature of the Hennigian method, true advances in classification and phylogenetics must be consilient, that is, guided by the generally concurring results of different classes of inductive methods. The traditional syncretic method seeks to explain observations by a complex neo-Darwinian theory of evolution, even if there is considerable disagreement about such theory (e.g., Smith 1992), and seeks to erect a classification that reflects such relationships. Stuessy (1990, p. 131) has noted that cladistics has contributed a valuable importance to testing classifications, and I also agree with him that any classification is testable, whether they be derived from cladistic (shared apomorphy), phenetic, or phyletic methods.

The cladistic method has been criticized recently (see Farris 1979 for refutation of early criticisms of cladistics) for lacking provision for dealing directly with introgression, convergence, fossils, anagenetic change, or more than two lines from a single ancestor (Scott-Ram 1990, but see W. Maddison 1989 on polytomous cladograms). It apparently cannot reconcile Popperian and Hennigian methodology, ignores estimates of evolutionary history, fails to classify ancestors, and does not promote stability in classification (Meacham & Duncan 1987 but see de Queiroz & Gauthier 1990 on cladistic classification). According to Rieseberg and Bruiliet (1994), inasmuch as species are mainly paraphyletic, at least at first, "a species classification based on the criterion of monophyly is unlikely to be an effective tool for describing and ordering biological diversity." Following the arguments of Rieseberg and Bruiliet (1994), speciation by founder effects and population

subdivision (undoubtedly common in mosses associated with patchy environments) leads to derivative species sharing apomorphies with the ancestral population, producing paraphyletic species, while allopolyploidy (possibly the source of the high chromosome numbers in reduced arid-land species of *Tortula*), leads to polyphyletic species. And according to Humphries (1983), "we have no 100% certainty of distinguishing between multiple speciation, living ancestors, reticulation, or homoplasy . . ." Moore (1990) argued that "as a heuristic for evolution, it [cladism] breaks down at the lowest taxonomic levels." In addition, the cladistic method is associated with rigor, reproducibility, and high resolution, but this does not mean it necessarily produces the best phylogenetic tree, since character selection may be poor and methodology faulty.

It is clear, however, that the cladistic method does group organisms by shared innovations, and to this extent reflects descent with modification (cf. Micevich & Weller 1990, p. 161), or at least "relative recency of common descent with modification" (Nelson 1989), while it theoretically maximizes information content of the classification (Farris 1979). Following Panchen (1992, p. 344)—who has argued cogently in defence of a cladogram as a tree directly representing the phylogeny of life—cladistics reflects basic evolutionary theory and thus is valuable and powerful as at least a first step in rigorously (as opposed to Gestalt or omnispersion methods) evaluating the many characters involved in complex phylogenetic relationships (Zander 1993, p. vi). According to Panchen (1992, p. 8), "if the hierarchical pattern of the natural order of organisms, and the hierarchy of characters on which it is based, are accepted *a priori*, then cladistics is the only valid technique for discovering that order [his emphasis]." Although cladograms are not directly testable without reference to a pedigree, the predictive value of cladistics can be tested, at least by implication, by the genetic similarity of terminal taxa associated on the cladogram. Evolution is not a "central tenet from which the principles and methods of taxonomy are to be deduced" (as per de Queiroz 1992), but is merely our most powerful central explanation of perceived hierarchies in nature, a data-rich elaboration of "like produces like." The analytical power of the cladistic method is clear, but may be extended by some enthusiasts, uselessly, into idealism (e.g., Scott-Ram 1990; Smith 1992).

The cladistic method may be modified to incorporate unmodeled evolutionary information if and when such is known, e.g., hybridity as discussed by Wagner (1983) among others. Problematically, there is evidence for reticulate evolution in at least some mosses (Wyatt et al. 1992). Although a few hybrids in the Pottiaceae have been reported (listed by Zan-

der 1993), the implication for actual introgression in parent species is unknown. Shaw et al. (1994) found no isozyme genotype evidence that the morphological intergradation evident between two species of *Climacium* (Climaciaceae) in North America was due to ongoing interspecific hybridization. Population studies like this (also see Shaw 1994) may help delimit for critical species or populations the tokogenetic "line of death" (Vrana & Wheeler 1992) of reticulate genetic relationships below which hierarchical classification is theoretically impossible.

There have been various attempts to justify parsimony as a method of selecting one of many possible hypotheses derived from a single data set (Scott-Ram 1990; Sober 1975, 1983, 1986, 1988), none completely acceptable according to Donoghue (1990), either methodological in minimizing assumptions (see Farris 1983) or requiring the assumption that homoplasy is generally uncommon (see Felsenstein 1978). Abbott et al. (1985) felt that "authoritative reconstruction" of a phylogeny on the assumption of parsimony is "doomed." On the other hand, I find compelling Sober's (e.g., 1983, 1986) closely reasoned argument that parsimonious trees are trees of "maximum likelihood," nicely demonstrated through "backward inequality"; the latter similar to Farris optimization; see also Farris' (1973) and Swofford & Olsen's (1990, p. 480) discussion of maximum likelihood, and I find justified Carpenter's (1992) explanation of how "parsimony corresponds to degree of corroboration in phylogenetic analysis and measures evidential support."

Because multiple states for a character are generally the rule at least when examining many taxa (Micevich 1982), the additivity question was evaluated. There is more phylogenetic information in additive (or ordered, cf. Wilkinson 1992) characters but *ad hoc* judgements must be made about processes (Mabee 1989); the extreme environmental conditions implied at the beginning or end of a transformation (Kluge 1991) are readily associated with "stature gradient" transformations described for the Pottiaceae (Zander 1978, 1993). All multi-state characters were treated as additive, reflecting the "method of intermediates" (Wilkinson 1992), which theorizes a probable evolutionary distance and a gradualistic evolutionary model. Mishler (1990) ordered multiple states on the basis of ontogenetic evidence (Mishler & de Luna 1991, but see critical review of this method by Hauser & Presch 1991, p. 255) in his study of *Tortula*, and he correctly viewed gemmae types as unordered.

Hyvönen and Enroth (1994) used non-additive states "in order to avoid *a priori* assumptions about the nature of the characters" without further explanation. Likewise, Mishler and Churchill (1987) emphasized that "postulating reduction series . . . de-

depends on the use of outgroup comparison, not appeal to an *a priori* evolutionary scenario." On the contrary, rejection of all relevant scientific reasoning prior to analysis using one of the presently available exact algorithms is an example of "hasty monism," a common logical fallacy in science (Cohen & Nagel 1934, p. 384), being an attempt to address and explain everything through one principle or method. It is also a form of the fallacy of exclusive particularity—in this case, the presumption that because a given method expresses an important truth about a subject, every other method must fail. Systematics, I feel, will gain predictive power through a melding of the theoretical depth of evolutionary systematics and the resolving power of the exact parsimony algorithm provided by cladistics. I here avoid the use of the phrase *a priori* to refer to weighting before the exact algorithm, as has been accepted by numerical taxonomists and cladists since the 1960's, because it implies unscientific practices: "1) by reasoning from definitions formed or principles assumed: deductively, 2) without examination or analysis: presumptively, 3) independently of experience: intuitively." (Gove 1976). Powerful, compelling, simplifying explanations based on a wealth of information should not be dismissed as *a priori* evolutionary "just-so stories."

The phrase "*a posteriori*" is, in kind, usually used in the literature for any weighting done after parsimony analysis. This Latin phrase actually means reasoning from facts. Are there any more facts available after parsimony analysis than before? Certainly there are more (and better) explanations because of the resolving power of the exact algorithm, but hardly more facts about the terminal taxa. Apropos of this, Swofford and Olsen (1990, pp. 466, 499) cautioned against successive, iterative re-weighting after the cladistic analysis, such as estimation of optimal weights by successive approximations (Farris 1969, also see Goloboff 1993a, b) citing circularity and giving an example of a failure of this method, but recommending instead methods of weighting prior to the exact algorithm such as the compatibility method of Penny and Hendy (1985, 1986). Weighting highly those characters with best fit as determined after the parsimony analysis, may be done in various ways: Ladiges et al. 1989 used both the consistency index (c) over the patristic unit character length (Farris 1969) and also the product of character consistency and character retention index as determined in Hennig86 (Farris 1989). Goloboff's (1993a) PEE WEE software weights reliable characters using a constant for the concave function that may be modified. No method now exists to recommend the *best* weighting by character fit (Farris' 1969 example works for an artificial data set with a known random element). Since any large data

set with relatively simple characters, as in the present study, will have homoplasy reflecting both true convergence and taxonomic noise, the latter is randomized and therefore incongruent and minimized through parsimony. Homoplasy based on convergence is important information and should not be masked by post-parsimony analysis deweighting, which is not used here.

The cladograms were generated in this study both with all characters weighted (prior to the exact algorithm) the same and with weighting of characters along the lines used and discussed by Zander (1993), reflecting an entirely reasonable apprehended convergence in several lineages in many characters through morphological reduction. This is in spite of and counter to the statement of Kluge and Farris (1969) that "Certainly one could not objectively detect parallelism by assuming that it existed prior to the analysis!" although details of parallelism are detected and mapped by parsimony analysis (Farris 1977b) within the above limitations of the Hennigian method. Landrum (1993) has cautioned against errors in analysis caused by a co-adaptive set of character states (cf. discussion of Rensch 1960, p. 127) in taxa that is related to habitat. Swofford and Olsen (1990, p. 498) advise low weight for rapidly evolving characters that contribute to long-branch attraction. Just such a set of 22 characters (fully 30% of the total data set!) is identified (Zander 1993) for arid-land Pottiaceae. This particular stature-related transformation series was selected prior to the exact algorithm through perceived strong correlation of morphology and habitat. This is probably a reduction series, but the weighting does not favor any direction of transformation since control by possible suppressor genes would obviate the necessity for postulating re-evolution of complex structures like peristomes. Swofford and Maddison (1987) indicated that the presumption is arguable that cladistic methodology involves "freedom from assumptions about the nature of the evolutionary process," and as "transformed cladistics" this presumption is further countered by Hull (1983, p. 183) and at length by Scott-Ram (1990). A rigid requirement of methodological neutrality (cladistics being purely a discovery procedure, e.g., Nelson 1989) fails because "if any reference to a Platonic world view is to be avoided, such methods are only intelligible in the light of evolution" (Scott-Ram 1990, p. 175). The cladistic method thus directly models descent with modification, and does so in a narrow manner. Relating evolutionary process and cladistic pattern through distinct, cladistic "bridge principles" (e.g., the "evolutionary species" of Wiley 1981, pp. 22, 25), implies that the pattern is something apart from the theory when in fact one hopes the pattern is

TABLE 1. *Hyophiladelphus*, character states 0 through 74, as added to the data set of Zander (1993: 50) and used in this study.

| 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| 012345678901234567890123456789012345678901234567890123456789012345678901234 | | | | | | | |
| 0001000001210020000100111010011100000002000--10-----00100-21011111221101000 | | | | | | | |

developed from the theory through the strongly coupled method.

The previous cladistic study (Zander 1993) of the Pottiaceae at the level of genus found considerable homoplasy and specialization in the Pottiaceae. Note, however, that Sober (1988) demonstrated that "shared derived characters provide evidence of relationship regardless of the level of homoplasy" (as discussed by Donoghue 1990), while Goloboff (1991) pointed out that decisiveness of a tree is not a function of relative amounts of homoplasy but of the number of equally parsimonious trees, fewer being more decisive. Also, according to Mickevich (1982), convergent characters contributing to homoplasy are highly phylogenetically informative, even if some contradict the cladogram on which they are based.

Inasmuch as all characters theoretically have different phylogenetic importance (as per discussion by Farris 1983, p. 11), equal weighting prior to the exact algorithm is equivalent to arbitrary weighting (Swofford & Olsen 1990, p. 464). Thus, the more the characters are (reasonably) weighted differently, the less arbitrary is their weighting; Kluge and Farris (1969) recommend weighting by degree of variability of a character within OTU's, this being a measure of the rate of evolution of that character. Also, weighting makes optimal solutions more readily found (increases apparent resolution of the cladogram), since it increases the variability in cladogram length (Platnick 1989).

It is, however, an unfortunate fact that most bryophyte characters cannot be readily apprehended as very different in phylogenetic importance on the basis of their relative complexity (complex characters being probable composites of several traits). Thus, in this study, except for weighting against the clearly convergent transformation series of apparently co-adaptive characters forming 30% of the data set, all characters were weighted as equal prior to the exact algorithm in accordance with the "principle of indifference" (as discussed by Wilkinson 1992, *contra* Hauser 1992 and Hauser & Presch 1991).

As Sober (1986) pointed out, "good" characters cannot be identified easily prior to the exact algorithm; such characters are more apt to be retained in evolutionary situations that minimize anagenetic change (e.g., fixed mutation pressure changing gene

frequency) and thus do not mask character history as do (according to Sober) random drift, selection for a particular predominating trait, a one-locus model with heterozygote inferiority, or multilocus models with many adaptive peaks. I feel that this reasoning is support for low weighting of all characters that are part of an apparently co-adaptive set of characters forming a transformation series correlated with environmental extremes. Lowered weighting delays transformation of the character states of the co-adaptive set of characters into the subclades of the cladogram, where they may yet prove to be synapomorphic. Buck (1980) eliminated entirely from analysis the apparent convergent characters in his generic revision of the Entodontaceae, but the present differential weighting scheme allows use of a maximum number of characters.

METHODS

Because *Barbula agraria* was clearly incongruous in the genus *Barbula*, its character states were not reflected in the original data set of Zander (1993, p. 50). For the present study the same Pottiaceae genus data set was used except for the addition of the coding for the 75 characters scored for *B. agraria* (as *Hyophiladelphus*—Table 1). All multistate characters were treated as additive (ordered).

The results of twenty different orderings of data presentation of the 77 genera (OTU's) were examined for each analysis. These orderings were pseudorandomized using a shuffle program to avoid being trapped in local optima (D. Maddison 1991; Swofford & Olsen 1990, p. 488). The analyses were done (following Zander 1993) with the program Hennig86 (Farris 1988, 1989) using the commands "mh*;bb*" for heuristic branch-swapping, or "ie*", an exact algorithm, for the small data sets (associated with Analysis 2). The maximally parsimonious tree or trees were selected.

Cladograms that were generated in the present study were both consensus-collapsed and single character-trees. Consensus trees are not phylogenies as such (Miyamoto 1985), but show topologies common to all equally parsimonious trees found. The single character-trees were necessarily segregated from multiple equally maximally parsimonious trees by means of the functional-outgroup/in-group (Watrous & Wheeler (1981) method and reciprocal illumination (Hennig 1966) as was done in the previous study (Zander 1993). Support for consensus trees was searched for through any clear congruence with geographic distributions of the taxa. At the genus level (Zander 1993), geographic congruence has been difficult to find because of the wide ranges of the supraspecific groups, wide ranges not being relevant sources of information (Kluge 1988).

The Cladograms.—Maximally parsimonious clado-

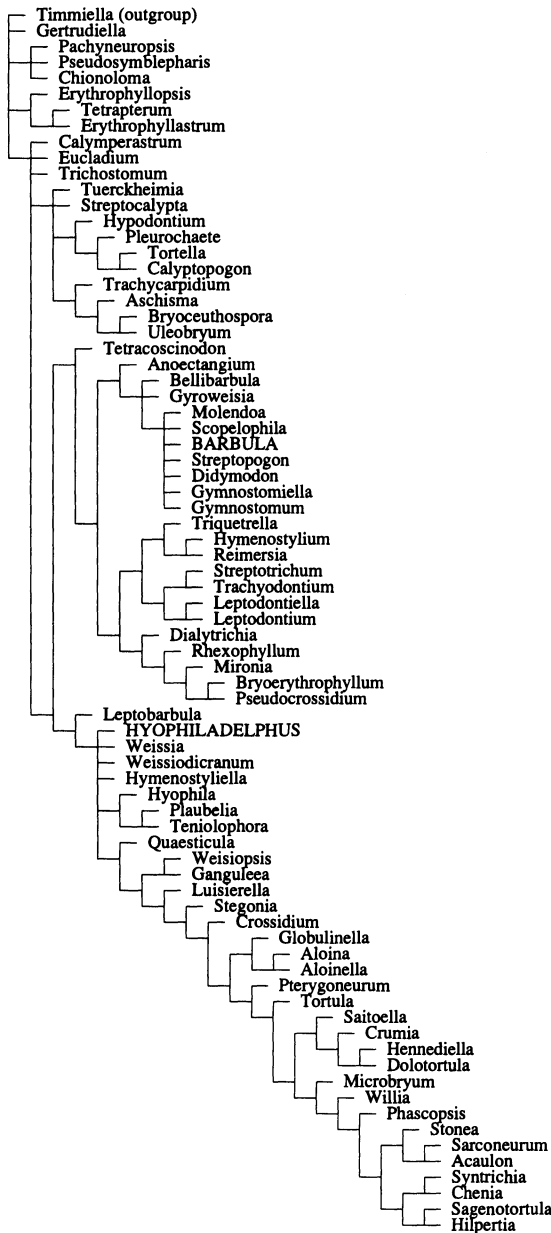


FIGURE 1. Analysis 2. Strict consensus tree of Pottiaceae genera. *Timmiella* is functional outgroup, 22 reduction-related characters weighted at 1:15, tree length is 5,367, number of equally parsimonious trees greater than 1241.

grams were produced for the full Pottiaceae data set (Zander 1993) (here including *B. agraria* as *Hyophiladelphus*, Table 1) in two different analyses: Analysis 1 (not illustrated), being Pottiaceae with *Ptychomitrium* as outgroup (the most morphologically similar sister group of the Pottiaceae) and Analysis 2 (Fig. 1), being Pottiaceae with *Timmiella* as functional outgroup (the pottiaceous genus sharing the most plesiomorphic characters with *Ptychomitrium*, see Zander 1993, p. 27). Partial data set analysis

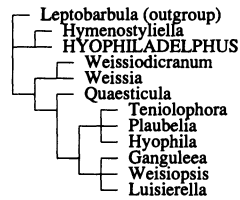


FIGURE 2. Phylogenetic evaluation of eleven genera at the base of the Pottiioideae mostly characteristic of tropical shores and islands. Strict consensus tree of 4 equally parsimonious trees, *Leptobarbula* is outgroup, consensus trees identical with both 1:1 and 1:15 weightings.

was also done: Analysis 3 (one tree of which is selected as Fig. 3) the Pottiioideae with *Tetracoscinodon* as outgroup (sister group of the subfamily Pottiioideae), with the Pottiioideae subclade consisting of the 33 genera (Fig. 1) recognized as such in both Analyses 1 and 2, and Analysis 4 (Fig. 2) of eleven related genera characteristic of tropical shores and islands. The final tree (Fig. 3) consists of the selection of a single tree from the multiple maximally parsimonious trees resulting from Analysis 3, being the one most similar to Figure 2 and otherwise to Cladogram 15 of Zander (1993).

Analyses 1-4 were done with all characters weighted identically (1:1) and also with 22 reduction-related characters (as listed by Zander 1993, p. 19) weighted low (1:15) to force transformations based on these characters into the subclades. The weight of 1:15 was selected as that ratio beyond which resultant maximally parsimonious cladograms ceased to change in topology as the weighting ratio is incremented.

RESULTS

The maximally parsimonious cladograms of Analyses 1-3 place *Barbula agraria* at the base of the Pottiioideae subclade, demonstrating that it is not closely related to the genus *Barbula* nor is it a member of the Merceyae (= Barbuleae), but is instead most properly placed at the base of the Pottiioideae subclade. Analysis 1 is not figured as a cladogram here because the base of the Pottiioideae subclade was highly unresolved in the consensus tree at either 1:1 or 1:15 weighting of 22 reduction-related characters.

The base of the Pottiioideae subclade was likewise largely unresolved in the consensus tree of Analysis 2 at 1:1 weighting of 22 reduction-related characters, but sufficiently less so with 1:15 weighting to be instructive (Fig. 1) in the extent to which it reflects or did not reflect Cladogram 14 of the previous study (Zander 1993), done at the same weighting and on which the present suprageneric classification is based. Inasmuch as the Hyophileae subclade of the previous study is not evident in any cladogram generated with the new data set (i.e., including *Hyophiladelphus*), this tribe becomes merely a paraphyletic group, although the name is a convenient label for the morphologically fairly distinct base of

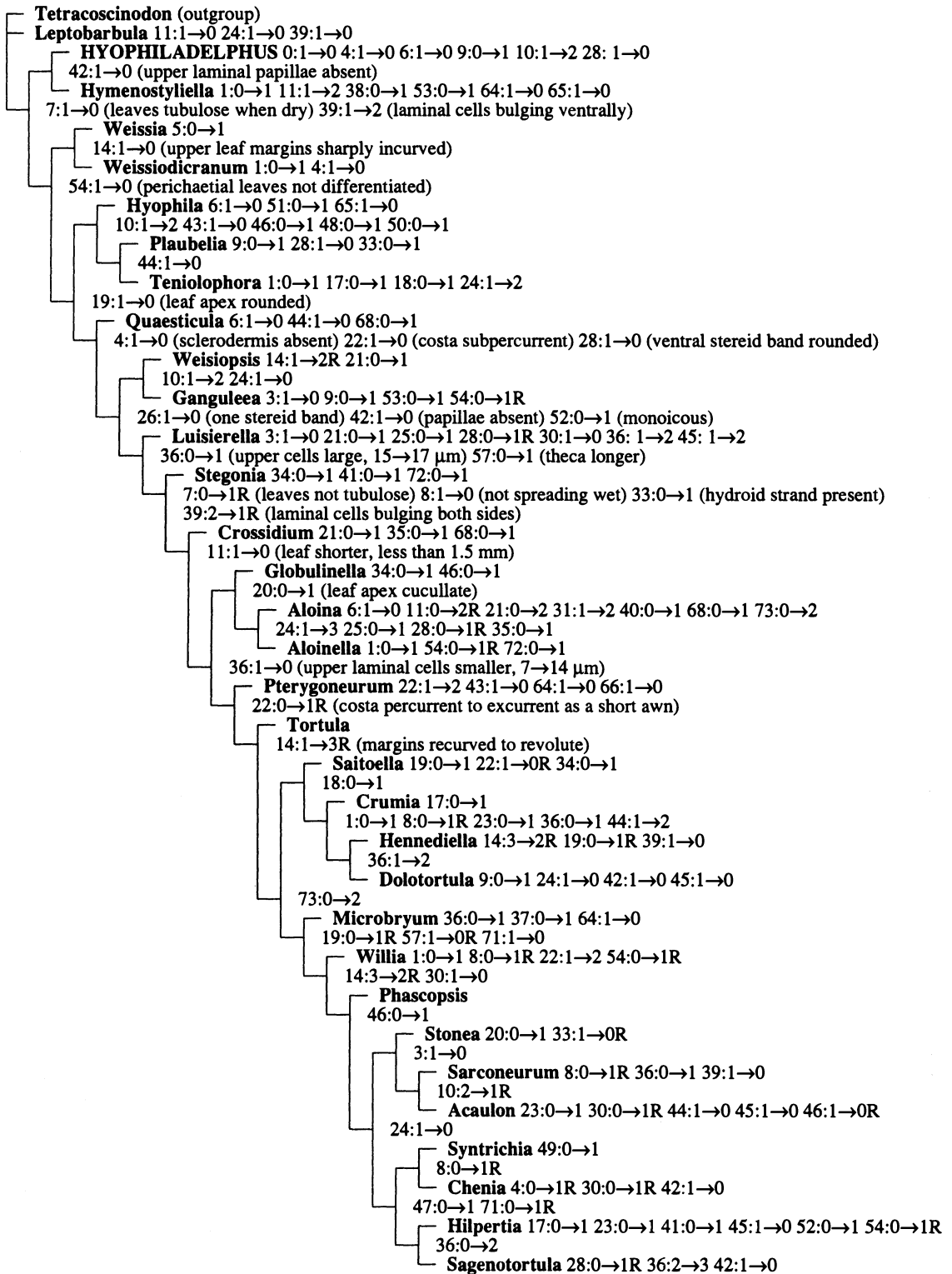


FIGURE 3. Analysis 3b. Cladogram of the Pottiioideae (*sensu* this publication), *Tetracoscinodon* is outgroup, 22 reduction-related characters weighted at 1:15, length 2,448, consistency index 0.35, retention index 0.58, tree number 3 of 15 trees, being the one most similar to Figure 2 and otherwise to Cladogram 15 of Zander (1993). R = reversal within the subclade; state changes of critical nodes explained in words, otherwise for codes see Zander (1993, p. 19).

the Pottioideae subclade. Long-branch attraction may be involved, however, and further study is necessary. In spite of a call by various authors (e.g., de Queiroz & Gauthier 1990) to base nomenclature more exactly on cladistic results, cladistic analysis may lead to instability in classification because of the many ways in which the data may be analyzed. Past stability is largely due to a general lack of expert opinion because the data was difficult to evaluate with Gestalt methods. Because the cladistic classification of Zander (1993) is not much different from past classifications or from the present one, it is still serviceable and no changes in suprageneric taxa are recommended here. The next major changes should await large-scale analysis at the species level.

In all cladograms resulting from the full data set, the extant relative closest to *Barbula agraria* was not discernible (e.g., Fig. 1). A focused analysis (Analysis 3) of just the Pottioideae subclade with *Tetracoscinodon* as outgroup was done in an effort to resolve the basal branches. In Analysis 3a (not figured), in which all characters were equally weighted (at 1:1), *Barbula agraria* was paired with the likewise Caribbean taxon *Quaesticula* in all 15 equally maximally parsimonious trees. Because the analysis was done with all characters equally weighted, certain taxa identified prior to the exact algorithm as much reduced morphologically were closely associated: *Acaulon*, *Stonea*, *Phascopsis*, *Sarconeurum*, *Pterygoneurum*, *Stegonia*, and *Microbryum*. These were more finely distributed in a second analysis (Analysis 3b) in which characters were differentially weighted.

Analysis 3b, also of the Pottioideae subclade alone, was done with 22 reduction-related characters weighted low (at 1:15), and gave a consensus tree exactly like that of the Pottioideae subclade in Figure 1, but of only 15 equally maximally parsimonious trees. Of these 15 trees, a single tree (Fig. 3) was selected in the following manner:

An additional study (Analysis 4) was done to examine the relationships of eleven basal genera of Hyophileae. These were associated by Caribbean lowland distribution or are found elsewhere in low to medium elevation tropical areas but not in inland desert habitats (thus excluding desert taxa like *Crossidium* and *Stegonia*), and lack the several character states listed as changes in the immediate ancestral node of *Stegonia* in Figure 3. These taxa were: *Ganguleea*, *Hymenostyliella*, *Hyophila*, *Hyophiladelphus*, *Luisierella*, *Plaubelia*, *Quaesticula*, *Teniolophora*, *Weisiopsis*, *Weissia*, and *Weissiodicranum*, with *Leptobarbula* as outgroup. Two taxa, *Ganguleea* and *Hymenostyliella* have outlier distributions in Brazil and India, while *Hyophila* is found nearly world wide in tropical and temperate areas. Identical consensus trees were derived with both 1:1

weighting and 1:15 differential weighting of reduction-associated characters, and *Hyophiladelphus* was found to be at the base of the clade paired with the Asian *Hymenostyliella* (Fig. 2). The latter genus, although it has an similar tropical lowland or island distribution, differs significantly from *Hyophiladelphus* by the following characters: peristome absent, perichaetia borne laterally, stem elongate, leaves long-lanceolate and upper laminal cells trigonous. The disparate morphologies of these twelve distinctive basal Pottioideae genera of one or few species in each indicates a probable long and event-filled (island-related isolation and drift with strong environmental pressures) history of evolution probably coupled with extinction of taxa of intermediate morphology. As previously discussed (Zander 1993, p. 31), the Hyophileae may be members of a "Circum-Tethyan" floristic zone (Frey & Kürschner 1983, 1988) including many species of Circum-Mediterranean, central Asian and western North American Pottiaceae. That *Leptobarbula* is an essentially Mediterranean taxon further qualifies it as an appropriate outgroup. There are clearly two phylogenetically related groups of Circum-Tethyan Pottiaceae forming the base of the Pottioideae subclade: a tropical island and shores element (including *Hyophiladelphus* and at least ten others) and a more highly evolved inland desert element (including such taxa as *Stegonia* and *Crossidium*).

Based on the information provided by analysis of the twelve taxa above, which resulted in Figure 2, a single tree was selected from the 15 trees of Analysis 3b (with 22 reduction-related characters weighted low, at 1:15). This single tree is given in Figure 3, together with mapped character state changes (see Zander 1993, p. 19 for a list of characters and their states). Figure 3 is now the best hypothesis of the phylogeny of the Pottioideae.

Although Vrana and Wheeler (1992) make a case for doing all analyses at the individual specimen level, a general analysis involving a large number of specimens and species presently requires that taxonomic evaluation of individual specimens be based on a degree of judgement and experience with purely methodological, explicit analysis limited to major differences between groups of organisms. In the case of the present study, cladistic study at the level of genus supports transfer of a single species from one named subclade to another, while the several autapomorphic characters for the terminal taxon listed in Figure 3 allow recognition (see discussion of Mishler 1990, p. 87) of *Hyophiladelphus* as a distinct, though monotypic genus. The fact that *Hyophiladelphus* is near the base of the subclade further supports recognition of it as a monotypic genus representing a now mostly extinct lineage.

An additional analysis (not illustrated) was done

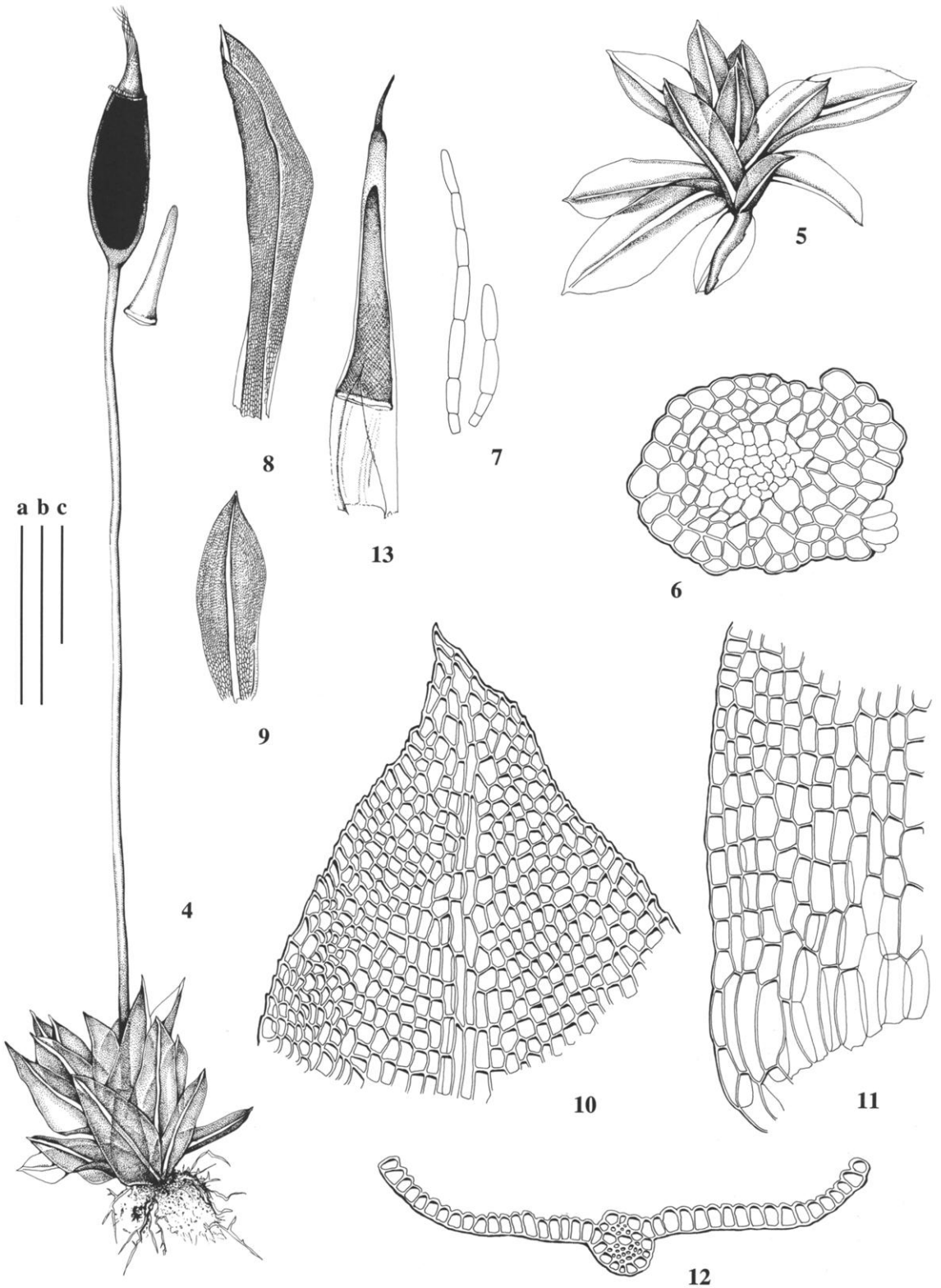


FIGURE 4-13. *Hyophiladelphus agrarius*. — 4. Habit, fruiting plant. — 5. Habit, perigoniote plant. — 6. Transverse section of stem. — 7. Axillary hairs. — 8-9. Two leaves. — 10. Leaf apex. 11. — Leaf margin at base. — 12. Laminal section at midleaf. — 13. Calyptra, with retained operculum. Scale bars: A = 0.5 mm, Fig. 6-7, 10-12; B = 1.0 mm, Fig. 8-9; C = 1 mm, Figs. 4-5, 13.

with the Pottioidae data set of Analysis 3 weighted as in 3b (reduction-related characters at 1:15), *Tetracoscinodon* being functional outgroup, and with one additional character in the data set: "alar cells inflated," scored as "present" for *Hyophiladelphus*, *Weissia*, and *Weissiodicranum*. There was no clarification of the relative positions of the three genera, these being unresolved (as above *Leptobarbula* in Fig. 1). This indicates that the enlarged alar cells of *Hyophiladelphus* remain of unclear homology in relating this genus to the other two. This additional character also made no difference in the results of Analysis 4 of the twelve taxa basal to the Pottioidae.

In conclusion, *Barbula agraria*, as the new genus *Hyophiladelphus*, belongs with the Pottioidae rather than the Barbuleae, with closest relationship demonstrated to be with the Asian genus *Hymenostyliella* when characters clearly involved in convergence are weighted low.

HYOPHILADELPHUS (C. Müll.) Zander, *stat. et gen. nov.*

BASIONYM: *Barbula* sect. *Hyophiladelphus* C. Müll., Syn. 1: 604. 1849. **LECTOTYPE:** *Barbula agraria* Hedw., *fide* Zander, *Phytologia* 44: 201. 1979.

Barbula subg. *Hyophiladelphus* (C. Müll.) Zand., *Phytologia* 44: 201. 1979.

Tortula sect. *Hyophiladelphus* (C. Müll.) Broth., *Nat. Pfl.* 1(3): 429. 1902.

Barbula sect. *Agrariae* Steere in Grout, *Moss Fl. N. Amer.* 1(3): 173. 1938, *nom. illeg.* **TYPE:** *Barbula agraria* Hedw.

The genus is monotypic and has the characters of the species.

HYOPHILADELPHUS AGRARIUS (Hedw.) Zander, *comb. nov.* [Fig. 4–13]

BASIONYM: *Barbula agraria* Hedw., *Spec. Musc.* 116. 1801. **TYPE:** "Jamaica et Domingo," Swartz s.n. (lectotype, g!; isotype, BM!).

Tortula agraria (Hedw.) P. Beauv., *Prodr.* 91. 1805. (For full synonymy, see Zander 1979.)

Plants loosely caespitose to gregarious, *blackish green above*, brown below. *Stems* not branching, *very short*, to 0.2 cm in length, transverse section rounded, *central strand present*, *sclerodermis absent*, *hyalodermis absent*; axillary hairs 2–3 cells in length, all hyaline; densely rhizoidiferous. *Leaves* appressed and involute when dry, *weakly spreading when moist to rosulate*, *oblong*, *elliptical or spatulate*, 1.2–2.0 mm in length, *upper lamina broadly channeled to deeply concave*, *margins plane*, *entire*, occasionally weakly serrulate near apex, occasionally bistratose on margins or medial portion of the lamina, marginal cells rhomboidal and thick-walled near apex; *apex broadly acute*; *base oblong or not differentiated*, alar region often enlarged and bulging; costa percurrent to shortly and stoutly excurrent, superficial cells elongate and smooth on both sides, (2–)4 rows of cells across costa ventrally at midleaf, costal transverse section oval to circular, *two stereid bands present*, ventrally small, epidermis differentiated ventrally, present

or occasionally absent dorsally, guide cells 2 in 1 layer, hydroid strand absent, *upper laminal cells subquadrate to subrectangular*, *occasionally rhomboidal*, (8–)11–13(–15) μm in width, 1–2:1, walls thin, occasionally evenly thickened, *superficially ventrally bulging*, *dorsally flat*; *papillae absent*; basal cells differentiated across leaf in a small area or up to $\frac{1}{2}$ leaf length, *alar cells often sharply bulging*, basal cells rectangular and curved, 20–25 μm in width, 2–4:1, walls thin. Propagula absent. Dioicous. *Perichaetia terminal*, inner leaves ovate, ca. 1.5 mm in length, weakly sheathing in lower $\frac{1}{2}$ to $\frac{2}{3}$, lower cells rhomboidal. Perigoniate plants of same size or smaller than the archegoniate. Seta 0.4–1.0 cm in length, solitary, red-brown, twisted clockwise below, often also counterclockwise above; theca 0.3–1.7 mm in length, red-brown, cylindrical to elliptical, commonly sulcate, exothecial cells rectangular, 16–23 μm wide, 3–5:1, walls thin, stomates phaneropore, at base of theca, annulus deciduous, revolvable, 1–2 rows of strongly vesiculose cells; *peristome teeth of 32 narrow rami*, *filamentous*, *closely and evenly spiculate*, 500–1,200 μm , with many articulations, twisted 1.5–2.0 times counterclockwise, basal membrane low, 45–100 μm in height, granulate to spiculate. Operculum long-conic, 0.8–1.5 mm in length, cells twisted counterclockwise. Calyptra cucullate, smooth, 1.4–2.1 mm in length. Spores 9–11 μm , light brown, weakly papillose. Laminal color reaction to 2% KOH strongly yellow-orange, occasionally medium orange.

Habitat and range.—Calcareous soil, walls, coral, limestone, sandstone, and brick in low elevation (sea level to 350 m.s.m.) in the American Caribbean region, including the Gulf Coast of United States, eastern Mexico, West Indies, Central America and northeastern South America (Zander 1979).

ACKNOWLEDGMENTS

The plate was illustrated by Patricia M. Eckel. I appreciate the comments of J. Hyvönen and another, anonymous reviewer.

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