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A Survey of Morphological Characters for Phylogenetic Study of the Transition to Pleurocarpy

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Abstract. *Although the number of family or generic cladistic studies in bryophytes is increasing, there have so far been few cladistic analyses of moss relationships at the ordinal level. Cladistic methods and theory provide powerful analytical tools in the study of character variation, and are used here to provide the basis for studies of morphological characters for the phylogeny of the transition to pleurocarpy, a problem at the ordinal level in mosses. Morphological characters from the gametophyte and sporophyte are assessed, and discussed in the context of cladistic analysis based on morphological data and molecular data from* rbc*L sequences. In order to understand the evolution of branching systems we have deconstructed the traditional concept of pleurocarpy into its constituent elements. These we have included in the analysis as independent characters. Among features potentially important to the understanding of the transition to pleurocarpy are: modular architecture, hierarchy of the archegonial module, length of fertile module, differentiation of perichaetial leaves, formation of sub-perichaetial branches, and intrusion of the foot into the supporting module. Position of the branch primordium is found to be less informative than previously thought. Further study of the pleurocarpous members of the Bryales, especially* Pyrrhobryum *and its relatives in the Rhizogoniaceae, will be crucial for extending our understanding of the transition to pleurocarpy.*

One critical area in which cladistic methods and theory provide powerful analytical tools is the study of character variation and the development of hypotheses of homology. In cladistic analysis both characters and phylogenies represent hypotheses, to be tested by congruence with additional data or taxa, and therefore are potentially falsifiable. Every process of character selection should represent a "best estimate" of a character as a potential homology for a systematic group. As additional information on variability or distribution becomes available the character or one or more of its states may be subject to alteration or rejection. Phylogenies may similarly be modified or rejected following the addition or revision of characters, or on the addition of taxa.

The development of a character and definition of its states equates to the development of a hypothesis of homology. The selection of characters consists of two stages, an empirical stage in which observational and other criteria are used to develop a first "best estimate," and an inferential stage in which each character is tested by the use of congruence and the principle of parsimony (de Pinna 1991; Funk & Brooks 1990). Initially we need only to know that, under the criteria of positional and structural similarity, the states appear to be homologous. We do not need to ascertain *a priori* if a character or states have a common origin, or if states are homologous. These are hypotheses that result from the cladistic analysis, not *a priori* conditions. Rejection of characters on the basis of *a priori* conjectures of non-homology or polarity, rather than on the basis of observational criteria and testing by congruence, is theoretically insupportable and should be avoided (see below.)

Each morphological feature that can be discerned may potentially contribute systematic information at an appropriate taxonomic level. The primary criterion for recognition of a feature as a potential homology is similarity, both positional and structural, and is in effect from the earliest stages of character recognition. Features that are unusable in a cladistic analysis because they cannot be described ("gestalt"), that are invariant in the taxa concerned, or that are excessively variable at the level studied may then be rejected (Mishler & De Luna 1991). However, invariant features may provide systematic information at higher levels, while variability may be due to phenotypic plasticity or environmental pressures, or may represent systematic information more appropriately studied at a lower level. Statistical, phenetic, or other numerical studies of variation can be used, but frequently the preliminary phases of character selection are based solely on observational methods. Consequently, characters that may not have been perceived by ear-

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lier workers, or that were seen but ignored or rejected, may be found to be informative by later researchers.

Following the preliminary phases of character recognition, different empirical criteria may be employed in the study and description of any given feature to determine taxonomic characters and their states in the taxa studied. Similarity, both positional and structural, may be more explicitly studied, using (for example) anatomy and ontogeny. Heritability and independence of characters should preferably be studied using breeding and common garden experiments to determine the genetic basis. However, this is more frequently inferred through herbarium and field observations of large numbers of specimens from a wide range of habitats.

The conjunction test (Patterson 1982) or criterion (de Pinna 1991) may also be used to make decisions on independance of characters. According to this criterion, the states (homologues) of a single character represent a transformation series, and consequently cannot co-exist in a single individual. Two separate structures that occur in a single individual must therefore be considered to be independent characters (de Pinna 1991). Caution must be used in such considerations—for example, in plants there may be many identical parts (e.g., leaves) that represent serial homology (homonomy, mass homology – Patterson 1982). In such a situation different ontogenetic stages may be present, resulting in failure of the conjunction criterion if states correspond with those ontogenetic stages. Consequently only comparable ontogenetic stages should be used for character and state description. In addition, structures invariably found together may not be independent, representing the effect of environmental, functional, developmental, or genetic constraints, including pleiotropy, and so will not add additional data to an analysis. However, such correlations may also reflect evolutionary history. Statistical tests are available for the study of such correlations ("morphological integration," – Cheverud et al. 1989), but have mostly been used in morphometric studies by zoologists.

Selection and rejection of characters, reduction, and convergence.—The *a priori* selection or rejection of characters on the basis of theoretical assumptions can lead to multiple problems in an analysis. In particular, the use of a restricted data set in a cladistic analysis can result in unreliable or incomplete results. There are two types of character rejection—use of a single suite of characters (thereby rejecting all others) or rejection of a suite of characters (but including all others available). In one example of the use of a restricted suite of characters, Garbary et al. (1993) conducted a cladistic analysis using only data from the ultra-structure of motile male gametes. The pattern of relationships found was controversial, with *Selaginella* as the sister-group to the bryophytes, which were placed together in a monophyletic group. The use of such single suites of characters to explain the evolution of groups of taxa seems powerful, due to the reduction of conflicts, and is tempting, but may reflect functional constraints rather than evolutionary pattern. Even the use of such data for study of the evolution of the character system should preferably be carried out in the context of a well-resolved phylogeny based on additional data (Funk & Brooks 1990).

The second type of restriction of data involves the rejection of one or more suites of characters. The consequent problems and the limitations of the resulting cladogram(s) may not be so severe as in the first type, since other characters are available to permit congruence testing. However, this type of data restriction can still lead to problems with uneven results, poor resolution, and multiple most-parsimonious trees.

An example concerns the rejection of peristome characters in mosses with reduced peristomes. Since it seems probable that adaptations to epiphytism in mosses have occurred repeatedly, the value of all related characters for understanding the relationships between taxa has been questioned (Buck 1991). In pleurocarpous mosses in particular, the extent of reduction of the peristome may be associated with habitat, with erect capsules that have reduced peristomes being found more frequently in epiphytic and xerophytic species (Buck 1991; Buck & Vitt 1986; Vitt 1981). Consequently, epiphytic taxa with erect sporophytes tend to have peristomes with either or both the endostome and exostome reduced or lost, with reductions occuring in the basal membrane or segments or cilia of the endostome, or with reduction, erosion, change of shape or fusion of exostome teeth. Patterns of surface ornamentation also change, frequently from highly ornamented to poorly ornamented to smooth. Ornamentation includes horizontal or vertical striae and papillae of various sizes, shapes and distribution, and may occur on the inner or outer surface of either or both the exostome and endostome. The walls (remnants of the PPL) on the inner surface of the exostome may project to a greater or lesser degree, with various patterns of thickening. In addition, the size, relative proportions and numerical ratios of the cells in the three principle cell layers forming the peristome may differ between taxa. These changes are, however, not restricted to epiphytic mosses, but may also be found in epilithic, terrestrial, and aquatic mosses.

In cladistic analyses of various groups of pleurocarpous mosses Hedenäs (1994, 1995, 1996*a, b*)

treated sporophyte and peristome character states from taxa with "specialized" (i.e., reduced) sporophytes as "unknown". He argued (Hedenäs 1995) that "peristome characters in reduced peristomes should be treated as unknown if it is not apparent which basic (perfect) peristome type one deals with . . ." on the assumption that all such characters would reflect convergent evolution. Although many of Hedenäs' empirical observations of characters are valuable, inferential testing of the characters in his restricted analysis was inadequate. Consequently the results of his analyses provided little additional contribution to our understanding of pleurocarp phylogeny or the evolution of the characters involved.

Although convergent evolution of character complexes is an important consideration, there is no theoretical or empirical justification for the incorporation of these or other conjectures on the history of evolution into a cladistic analysis. The use of *ad hoc* hypotheses of polarity, homology and non-homology, which are established as principles and thus protected from further analysis (e.g., Edwards 1984; Schofield 1985; Schuster 1984; Vitt 1984) is unfortunately common in evolutionary systematics. In cladistic methodology, hypotheses of homology and non-homology are the result of a cladistic analysis, not *a priori* conditions, and the rejection of some similarities as being unreliable as markers of shared ancestry invalidates the power of parsimony and character congruence.

In addition to theoretical considerations, empirical arguments also invalidate the *a priori* dismissal of similarities as convergent. Many different characters are involved in the form of the sporophyte and peristome, each of which may have a separate evolutionary origin and history and may be free to vary independently of all other characters, resulting in a mosaic of different states. Such reductions in the sporophyte may indeed have happened more than once, but these reductions can still represent separate evolutionary events, and as such can each potentially follow different routes. Even if the end results are very similar, sufficient historical markers may remain, especially in complex characters, to identify these routes. Again, in cladistic methodology the resolution of these historical events relies on parsimony and character congruence, methods which are invalidated by *a priori* assumptions about the value of any given set of characters.

The logical consequence of such problems with the limitations of incomplete data sets is that all possible characters need to be used before the phylogeny of a group can be reliably understood. However, although highly desirable ("omega" classification – Davis & Heywood 1973) this is not currently (or potentially) obtainable, nor does it even seem to be necessary. Many different problems may result from poor character selection or state definition, poor taxon sampling, poor outgroup selection, or poorly planned or incomplete analyses, but for the most part, the same general patterns seem to appear in widely differing analyses. Consequently it must be concluded that the information derived from the shared evolutionary history of the organisms, and reflected in the pattern of character change (the "historical signal") is sufficiently strong that it takes a large amount of uninformative or misleading data ("noise") to obscure the pattern. Nevertheless, the use of all available phylogenetically informative data, including multiple gene sequences, will provide more support, through congruence, to the resulting phylogenies.

Congruence, homology, and polarity.—The characters that result from observational studies, and that meet the criteria of positional and structural similarity, heritability, and independance can be considered to represent putative homologies, and as such represent hypotheses of synapomorphy. Of the three "tests" (similarity, conjunction, and congruence) proposed by Patterson (1982) the first two allow the empirical identification of putative homologies, but only congruence provides an inferential test of homology (de Pinna 1991).

Characters resulting from a shared evolutionary history will be congruent, while characters that represent the effect of different forces (e.g., environmental pressures) will show variation in different, non-congruent patterns that conflict and represent "noise." Congruence of putative homologies with other characters allows the identification (through character optimization) of the most parsimonious distribution of states, that is, the minimum number of evolutionary events required to explain the data. Consequently congruence and parsimony allow the identification of characters that represent meaningful comparisons (homologies) to be discriminated from characters that represent parallelism or convergence (homoplasies – Patterson 1982). Any given character can be tested through comparison with the distribution of all other characters, and rejected as a homology (or restricted to localized homology, de Pinna 1991) if it is not congruent.

The identification of a character as homoplasious in a given analysis does not necessarily mean that it should be rejected as uninformative, since characters that prove to be homoplasious at higher, more inclusive, or global levels (deeper branches e.g., between orders) of the analysis may potentially be informative at lower, less inclusive or local levels (distal branches e.g., between genera). Thus, even if a character state is homoplasious, it should not be rejected from the analysis. Examination of character distribution on a given cladogram may

show several small groups of terminal taxa that share the same character state—although the distribution between the groups is homoplasious, representing different evolutionary events, the members of each group share the state as a homology within the group. Identification of a character as homoplasious may also result in the character being subjected to additional or more critical scrutiny, or in a search in additional taxa to assess the generality of the character in the taxonomic groups involved.

In cladistic terms, homologies represent synapomorphies for groups in which the taxa have a common and unique evolutionary history, while homoplasies are characters found in taxa that have multiple evolutionary histories. However, this interpretation is dependent on the polarity of the cladogram, since a change in orientation may potentially change the circumscription or membership of any given group. Ontogenetic criteria may often be used *a priori* to determine polarity of a given character, but should more appropriately be used in the process of character and state description. In earlier, manual methods of cladistic analysis, a decision on polarity for each character was a preliminary step in the analysis. As a consequence, *a priori* theories on evolutionary history (for example, such as the antithetic versus homologous evolution of the moss sporophyte) could have a profound effect on the resulting phylogenies, or their acceptance (Robinson 1985). Determination of polarity, *a posteriori,* based on the distribution of taxa and characters on a phylogeny by reference to the outgroup taxa, is dependent on outgroup selection. Pre-existing higher level cladistic analyses allow the identification of a succession of sister groups to act as proximal and distal outgroups to the ingroup, and also establish the monophyly of the ingroup. In the absence of such higher level analyses, outgroup selection has to be based on the current best estimate of relationships (DeLuna et al. 1999). One of the aims of the current project is to develop a robust phylogeny of "anchor" taxa, which will provide a cladistic topology and outgroups for further studies at the ordinal and family level, and will also facilitate resolution of the relationships of highly autapomorphic or volatile taxa.

Materials and Methods

The characters presented in this paper represent our preliminary empirical estimates of character and state delimitation, through reference to the literature and examination of the expression and distribution of the characters in a wide range of taxa. As such, they should be considered experimental, and potentially subject to modification and rejection, as should all characters used in cladistic analysis. The characters and states are then tested through congruence with the complete morphological character set and the molecular characters derived from *rbc*L data (De Luna et al. 1999). Detailed examination of certain character sets will be published separately at a later date.

Choice of representative families and exemplar taxa.—The systematic criteria for the choice of taxa and outgroups were based on existing classifications (Buck & Vitt 1986; Crosby 1980; Robinson 1971) and are discussed in detail in De Luna et al. (1999) so will not be discussed further here. Fewer outgroup taxa were used for the morphological studies than in the molecular studies because of the difficulties in determining states in groups that are morphologically very dissimilar.

Exemplar taxa for this study were chosen partly on the basis of availability of recently collected material, so that the same specimen could be used for both morphological and molecular studies. Another criterion was the availability of material with sporophytes, in part on the basis of the completeness of the peristome, so that as many characters could be scored as possible. For example, of the species of the genus *Neckera* available to us, *N. urnigera* possesses endostome segments, while *N. angustifolia* lacks an endostome. Consequently, the former species was used, to reduce the number of endostome characters coded as unknown.

In three cases "supplementary" species from the same genus were used when material in good or complete condition could not be obtained. Initially *Leucodon curvirostris* was used to supplement peristome characters for *Leucodon julaceus,* where only poorly preserved peristomes were available. Three species of *Spiridens, S. vieillardii, S. reinwardtii,* and *S. balfourianus* were used to compare sporophytes, and in an attempt to find axillary hairs. The calyptra of *Thuidium tomentosum* was examined to supplement *T. delicatulum.* In several cases our initial studies were carried out on species that lacked sporophytes, but as additional material became available, we changed to species that were more complete. In the case of molecular data originating in other labs (De Luna et al. 1999) the species used was occasionally not specified, or was not available to us for morphological study. For example, the only material of the Splachnaceae available to us was *Tayloria splachnoides,* which was used as an alternative to *Splachnum ampullaceum* used to extract *rbc*L. The "supplementary" species were chosen with reference to floras or monographs (e.g., Crum & Anderson 1981; Flowers 1973; Sharp et al. 1994) for information on relationships among the taxa. In future studies we will obtain the morphological data for species for which only molecular data is currently available, and vice versa.

The characters and states were developed over 10 years through observation of many species and specimens, and not all material seen could be cited here. Consequently the specimens included in Appendix 2 should be regarded as vouchers rather than as a comprehensive list. Duplicates are deposited in XAL, and specimens were also consulted in BM and US. Where herbarium material was studied, care was taken to choose specimens that were identified or annotated by current experts for each group, where possible.

Morphological data.—In the current study, the morphological characters used were based in part on previous work by the authors, in part on characters described in the literature, and in part on current studies by the authors. Certain groups of characters were given particular attention—the architecture of the branching system, rhizoid distribution and morphology, and the development and structure of the vaginula and calyptra. Characters related to branching architecture were in large part based on previous work by the authors (De Luna 1990, 1995, Newton 1993) or our current studies. Reference was also made to

the characters proposed by La Farge-England (1996), many of which have been included here, allowing them to be tested in a phylogenetic framework.

Coding of states for taxa in which a character is missing or inapplicable is problematic, and can cause various undesirable effects (Maddison 1993). In some cases where there were doubts about the homology of a structure (e.g., the single-celled stomate in *Funaria,* character 63) an autapomorphic state was used, rather than coding the character as absent.

Many of the characters in this paper are not novel, and have been used at various taxonomic levels by different authors. However, only a selection of references to the literature could be included here. Further review of published descriptions of many characters is necessary to extend coverage of generality and variability. Certain characters from the literature were not included because of insufficient time to assess the characters and to study the states and their distributions in the taxa used, but these will potentially be included at a later date. Other characters, especially those relating to leaf and cell shape and size, were not used because of the extent of variation of these characters at lower taxonomic levels (within families or genera). No characters were used solely or largely on the basis of published descriptions, although in a few cases, for example where complete sporophytes could not be obtained, published illustrations, or photographs were consulted. Each character and its states is described below.

Sequence data.—Gene sequences from *rbc*L were obtained in three laboratories, by Brent Mishler at the University of California, Berkeley; Alison Withey at Duke University, Durham; and Dolores Gonzalez at the Instituto de Ecología, Xalapa. Details of procedures are discussed fully in De Luna et al. (1999) and are not repeated here. In this study the morphological data was supplemented by data from only one gene sequence, but it is intended in future work to include sequences from additional chloroplast and nuclear genes.

Phylogenetic analysis.—Three groups of analyses were carried out, using the molecular, morphological, and combined data sets. The molecular and combined data analyses, and the issues concerning the combination of different types of data, are discussed in De Luna et al. (1999) and will not be included here.

The morphological character set for 39 taxa consisted of 91 characters, many multistate with up to eight states, and was input to a data matrix in MacClade 3.07 (Maddison & Maddison 1992; Appendix 1). All characters were weighted equally and were unordered. Multistate data were coded as polymorphic. The data were analysed using PAUP 3.1.1 (Swofford 1990) on a Macintosh Quadra 800 and a Power Macintosh G3. After various preliminary runs, heuristic searches were performed using the "Random" search option with 100 replicates and TBR branch swapping. A further heuristic search, saving trees four steps longer than the most parsimonious trees, was used to calculate the decay index (Bremer 1994). The "Random Trees" option in PAUP was used to find 10,000 random trees to estimate the g1 statistic of skewness. Character states were optimized using the ACCTRAN option in PAUP. Further methodological and theoretical considerations are discussed in De Luna et al. (1999) and are not repeated here.

Character descriptions and character states

1. Archegonium position. There has been much discussion and controversy concerning the nature of acrocarpy, cladocarpy, and pleurocarpy (see the recent discussion by La Farge-England 1996). For this analysis, a strict definition of the character is used.

Archegonia normally terminate the module on which they are borne, whether this be the primary module or a secondary module. All cases in which the fertile module is the primary module (whether short or elongate) were considered to be "acrocarps". Where the fertile module is the secondary module the branch may be long ("cladocarps") or very short ("pleurocarps"). Fertile modules that are already elongated when the archegonia begins to develop, and that have at least some normal secondary module leaves below the perichaetium were coded as cladocarp. Confusion of long branch cladocarpy with acrocarpy may occur if the distinction between primary and secondary modules is not made. In contrast, pleurocarp fertile modules are extremely short, so that the archegonia appear to develop from a lateral bud on the subtending module, and virtually all leaves are differentiated as perichaetial leaves (see char. 47). All taxa in which archegonia develop as a lateral bud surrounded only by modified juvenile leaves, with the majority of perichaetial leaves developing after fertilization, were coded as pleurocarpous for this analysis. An alternative coding would be to use two characters (position and length) each with two states. (0 = Primary module; 1 = secondary module, long branch; 2 = secondary module, short branch.)

2. Subperichaetial innovations. Branch primordia on the fertile module may develop to form innovations, and were considered by La Farge-England (1996) to be associated with cladocarpous and acrocarpous taxa, and normally absent (but see Hedenäs 1998) in pleurocarpous taxa. Subperichaetial innovations frequently develop directly under the perichaetium, but in most taxa also develop elsewhere on the module. Very rarely only distal innovations were found. The innovations may develop into primary or secondary modules. (0 = absent; 1 = distal and general; 2 = distal only.)

3. Primary module growth. The primary module (*sensu* Mishler & De Luna 1991) represents the primary element of a hierachical branching system, with dependent secondary modules which normally have a different orientation, leaf form, and stance. Third and fourth order modules may also be formed. Where no differentiation of stance, leaf form etc. occurs all modules are considered primary. In some taxa stolons and erect shoots are found, with each giving rise to the other in a relationship that is not obviously hierarchical. However, the plagiotropous stolon can be considered ontogenetically and functionally primary, and is treated here as the primary module, and the relationship

between plagiotropous and orthotropous modules is considered reiterative (see char. 6.)

The primary module can be indeterminate, with growth normally continuing indefinitely in the absence of damage or disease. In many mosses, however, growth from the apical cell of the primary module ceases, and a lateral branch primordium continues growth with the characteristic orientation and leaf form of a primary module. Termination of growth in acrocarpous taxa, whether vegetative or because of the development of archegonia, was coded as the same state, to avoid over-weighting the position of the archegonium on the primary module. However, it may be possible to identify determinate or indeterminate modules in acrocarpous taxa by the variation in module length and the distribution of gametangia or sporophyte remnants on old modules, and future studies will address this problem. (0 = determinate; 1 = indeterminate.)

4. Secondary module growth. Most secondary modules are determinate—only in the aquatic *Fontinalis* do the secondary modules appear to be indeterminate. (0 = determinate; 1 = indeterminate; 2 = secondary modules absent.)

5. Insertion of module. Three distinct forms of insertion of modules on subtending modules were observed on the mature plants. These may reflect differences in development of the branch primordium, but confirmation of this will require anatomical and developmental studies. In many taxa the base of the module is little differentiated and projects cleanly from the primary module ("enate") while in others the base is swollen, forming a slightly grasping or clamp-like structure ("haptate"). In *Spiridens,* the base is unswollen, but lies closely adherent to the subtending module ("adnate"). (0 = haptate; 1 = enate; 2 = adnate.)

6. Reiteration. Reiteration is the repetition of an earlier level of the hierarchy of modules, or of the entire architectural system and all associated elements. In these situations, the new primary modules develop from branch primordia on secondary modules, rather than on the primary modules. More specifically, where the form of the primary module changes through the course of maturation (shoot heteroblasty), earlier phases of the primary module may develop out of sequence, so that a branch primordium on a stipe (the "middle" phase of a dendroid determinate module) may develop to form the initial, stolon, phase of the primary module. Since these growth patterns may not necessarily occur under all environmental regimes, observational data was obtained from specimens from a range of habitats and locations. (0 = reiteration absent; 1 = reiteration present.)

7. Orientation of the primary module. The orientation of the primary module is a significant element of the characteristic appearance of the plant, and is not necessarily related to the position of the archegonium. Since the plant is normally oriented relative to the substrate, which may be horizontal, sloping or vertical, the use of the terms "erect" and "prostrate" are avoided. The orientation may be simple (orthotropous or plagiotropous), or the primary module may change orientation as it matures. Three changes in orientation were inferred from the architecture of mature plants. One pattern is illustrated by *Pterobryon*—early in shoot ontogeny the primary module is plagiotropous, forming a creeping stolon that turns away from the substrate to become orthotropous as the shoot matures. A second pattern is illustrated by *Thuidium*—here the primary module is orthotropous, becoming plagiotropous distally. The third pattern was seen only in *Hypopterygium,* which initially follows the *Pterobryon* pattern, but the distal region of the branching frondose shoot undergoes a second change of orientation to become plagiotropous, at right angles to the direction of growth of the stolon. The stems of *Dicranum* were found to frequently change orientation with all modules changing at the same point. This was provisionally interpreted as an "orthotropous" orientation, with the modules reacting to disturbances in the plant's position, but needs experimental confirmation. (0 = plagiotropous; 1 = plagiotropous becoming orthotropous; 2 = orthotropous; 3 = orthotropous-plagiotropous; 4 = plagiotropous-orthotropous-plagiotropous.)

8. Origin of the primary module. In nearly all plants, whether the primary module is determinate or indeterminate, and in the absence of damage to the apical cell, a branch primordium will eventually develop to form a replacement primary module. The point of origin of this module has important implications for plant architecture, and results in characteristic growth forms. Where the point of origin is not restricted to one region the resulting growth form is rambling and tangled, regardless of orientation of the module. Where the origin of the primary module is proximal the plant has a fasciculate appearance, while distal origin results in a linear, moniliform or chain-like appearance. Midpoint origin is strongly associated with the *Pterobryon* pattern of primary module orientation (character 7: 1). La Farge-England (1996) classified proximal (basitonous) and distal (acrotonous) branch positions with the axillary and cauline positions of the branch primordium, but this is a separate character system (see char. 12) (0 = primary module origin not specific; 1 = proximal; 2 = distal; 3 = midpoint.)

9. Origin of the secondary module. When secondary modules (branches) are formed, their point of origin is apparent in the architecture of the

plants, contributing to the appearance of plants as matted, frondose, or dendroid. (0 = non-specific; 1 = basal; 2 = distal.)

10. Origin of the female module. The point of origin of the female module has little influence on plant architecture, but is characteristic of different taxa. Plants with archegonia terminating the primary module were coded as "not applicable" to avoid overweighting the origin of the primary module, which in this case is identical to the female module. (0 = non-specific; 1 = basal; 2 = distal; 3 = flush or seasonal.)

11. Orientation of secondary modules. Although frequently the same as the primary module, the orientation of the secondary module may differ. In the case of plants with orthotropous primary modules, the branches may adopt a "neutral" stance that is neither orthotropous or plagiotropous. (0 = plagiotropous; 1 = orthotropous; 2 = neutral.)

12. Position of branch primordium. The apical cell of the branch primordium results from divisions in the second cortical cell below a leaf, corresponding to the proximal portion of the merophyte. However, further divisions and growth of the cortical cells distal to the branch initial result in the primordium becoming displaced from its original position below the stem leaf, so that it may frequently appear axillary to the leaf of the merophyte below (Crandall 1969; Crandall-Stotler 1972; Leitgeb 1868; Mishler & De Luna 1991). Although Buck and Vitt (1986) considered that axillary branch primordia are characteristic of certain Bryalean pleurocarps, Withey (1996*a*) disagreed with this observation. Hedenäs (1994) also noted that the branch primordia of many other pleurocarps appear to be axillary. In this study, the term axillary was restricted to those branch primordia in which the cells of the primordium seemed to be in direct contact with the cells of the subtending leaf. Where the primordium was apparently in the leaf axil but several cells distant from the leaf insertion it was termed "proximal", while primordia clearly located between the proximal and distal leaves were termed "cauline". It was necessary to take care that this character was scored only when the branch primordia were dormant and on a fully mature stem, since as the branch primordium begins to develop it enlarges and its apparent position can change, while in immature stems the leaf primordia and branch primordia are too closely adjacent to determine proximity reliably. (0 = axillary; 1 = proximal; 2 = cauline.)

13. Buds. In taxa with scale leaves surrounding the branch primordia the stance of the scale leaves can differ. Closely wrapped scale leaves form a domed bud, but in some taxa the outermost scale leaves are erect. In other taxa all scale leaves are erect, forming a loose bud. The scale leaves may be minute, and arranged on a slightly elongated axis, so that very little protection is afforded to the apical cell. Care must be taken that this latter state is not confused with a naked primordium in the first stages of development. (0 = domed; 1 = outer erect; 2 = all erect; 3 = minute.)

14. Branch primordium. Branch primordia, their locations, and their associated structures are one of the most troublesome character complexes in pleurocarp phylogeny (see characters 15 & 16). In many cases the characters appear to be highly informative (e.g., Allen 1987), but the problems of interpretation can be serious. The various descriptive and survey papers available (see below) are helpful where SEM photos or careful line drawings are supplied, but interpretation of cladistic characters from the descriptions or coded tables is usually not reliable.

Although branch primordia may be classified as "naked" (or *Bryum* type) and "bud" (or *Climacium* type) (Akiyama 1990 *a,b*; Akiyama & Nishimura 1993 *a,b*) this is probably overly simplistic. "Naked" primordia may be partly immersed in the cortex, flush with the surface, or domed, and the number and stance of scale leaves associated with "buds" is variable (see also character 13). Additional work, preferably anatomical studies similar to those developed by Crandall (1969) for the study of hepatic branching patterns, are badly needed. Interpretation of the state of dormancy of primordia may also lead to problems, especially in taxa with obscure immersed primordia, which may be scarcely visible until development commences. (0 = naked; 1 = scale leaves present.)

15. Scale leaves. The interpretation of structures surrounding branch primordia, either as "scale leaves" or as "foliose pseudoparaphyllia", is often difficult. In this study, structures on the epidermal cells are interpreted as pseudoparaphyllia (see char. 16), while structures on the pale, thin-walled cells surrounding the branch primordium are interpreted as potentially scale leaves. This character (15) relates only to these latter structures, and is an attempt to determine which are scale leaves and which may be pseudoparaphyllia. Consequently, the "states" used here are experimental.

Axillary hairs are normally present in the axils of developing leaves and scale leaves, and although the hairs may be lost as the leaves or primordia mature, the basal cells may persist and can often be located. Where the structures around the branch primordium possess axillary hairs they should be interpreted as scale leaves (Newton 1993; Withey 1996*a*), rather than as foliose pseudoparaphyllia. Some of the outer leaf-like structures lack axillary hairs, but are clearly located on the pale zone of

thin-walled cells surrounding the branch primordium. These outer scale leaves may in addition be lanceolate, but grade into the foliose scale leaves. Consequently, three states are used—scale leaves with axillary hairs, foliose structures resembling scale leaves but lacking axillary hairs, and outermost lanceolate structures that are least like the scale leaves, but nevertheless occur on the thin-walled cells surrounding the branch primordium. An alternative coding would be to divide this character into two: shape, and possession of axillary hairs. (0 = all scale leaves with axillary hairs; 1 = outer scale leaves lack axillary hairs; 2 = outer scale leaves lanceolate.)

16. Pseudoparaphyllia. For this study, pseudoparaphyllia were interpreted as those structures originating on the dark, thick-walled cells of the epidermis, outside the pale zone of thin-walled cells associated with the branch primordium. Existing surveys of pseudoparaphyllia are only useful as a source of information for cladistic analyses where line drawings or SEM photos are included. The term "filamentous" is particularly problematic, frequently being used for any structures that are not obviously foliose, and ranging from true, uniseriate filaments to lanceolate pseudoparaphyllia several cells wide. In this study most pseudoparaphyllia were lanceolate, that is, bi- or tri-seriate throughout much of their length, and no truly filamentous (uniseriate) pseudoparaphyllia were seen. Leaf-like pseudoparaphyllia, multiseriate and approximately as wide as long, were coded as broad foliose. This last type is that most easily confused with the scale leaves of the branch primordium. In addition to noting the position relative to the cells of the branch primordium and epidermis, the presence or absence of axillary hairs (char. 15) may be helpful in resolving their identity. Despite these criteria, the structures in many taxa are difficult to interpret, and further work on this character complex must include detailed anatomical and developmental studies. (0 = pseudoparaphyllia absent; 1 = pseudoparaphyllia lanceolate; 2 = pseudoparaphyllia broad foliose.)

17. Surface. The structures associated with the branch primordia in the Hedwigiaceae lack axillary hairs, originate on the thin-walled branch primordia cells and are lanceolate. In addition, unlike all other taxa, the cells are papillose like those of the leaves. (0 = smooth; 1 = papillose.)

18. Stem central strand. The cells of the stem may be virtually uniform, but frequently several different zones can be distinguished. An extensive series of studies of stem anatomy by Kawai (e.g., 1977) suggests several characters that might be developed for cladistic analysis. During our initial assessment of the stem characters for this study various kinds of differentiation were noted (e.g., internal rows of stereid cells), but were represented only in single taxa. Since these states could not be clearly related to other autapomorphic states they were not used in this analysis. Further study of differentiation in the tissues of the stem, especially using morphometric methods to study variation and develop states, is necessary for this and the following two characters.

For this analysis, central strands with few to many cells that were slightly smaller, thin walled and more or less collapsed were termed "weak". Central strands with cells thin-walled and strongly differentiated with corner thickenings were termed "elaborate". These are probably hydroids (Duckett, pers. comm.). Further subdivision of "elaborate" into small and large may prove to be arbitrary, however, inclusion of two separate states in the analysis allows this to be assessed through character congruence. (0 = central strand absent; 1 = central strand weak; 2 = central strand elaborate, small; 3 = central strand elaborate, large.)

19. Cortex differentiation. The cells of the outer layers of the stem are normally thicker walled and smaller than those of the medulla, but in many taxa they are further differentiated to form a region of stereid cells. Rarely the cortical cells may be undifferentiated from the medulla cells. (0 = undifferentiated; 1 = differentiated; 2 = stereid cells.)

20. Epidermis. A single outer layer of cells may be differentiated from the inner cortical cells to form an epidermis. These included inflated, hyaline epidermal cells with all walls thin, frequently referred to as the hyalodermis (for example, by Buck 1987). An epidermal layer of dark colored stereid cells, differentiated from cortical stereid cells, was seen in some taxa, while others had "U-shaped" cells (with the inner walls thickened and the outer wall thin, hyaline and frequently collapsed). Taxa in which all stem cells were inflated and hyaline were provisionally coded as having an undifferentiated cortex with a hyalodermis. (0 = epidermal cells not differentiated; 1 = stereid cells; 2 = hyalodermis; 3 = U-shaped cells.)

21. Paraphyllia. Paraphyllia are found in families and genera throughout the "pleurocarpous" mosses, and have a wide range of forms. Many are lanceolate or narrowly foliose, and they are frequently branched or forked. Highly branched, uniseriate filaments with papillose cells occur in the Thuidiaceae. (0 = absent; 1 = lanceolate.)

22. Axillary hair terminal cell shape. Axillary hairs are usually present in the axils of leaves in actively growing and healthy stem and branch apices, but may be lost in older parts of the plant. Much variation exists in the axillary hair character complex, although it may not be informative at all

taxonomic levels. Hedenäs (1989), in an extensive survey of axillary hairs in the Hypnales, found the number of terminal cells and basal cells useful at the genus level but not at the family level. However, he included few representatives of other pleurocarpous taxa, all in the Leucodontales, and none of the Hookeriales or of other orders. Axillary hair morphology has been used for family level studies by Buck (Hookeriales; 1987), and by Griffin and Buck (Bartramiaceae; 1989). In a study of the Phyllogoniaceae and Pterobryaceae, Lin (1983) combined hairs per axil, basal cells and terminal cells in one composite character with four complex states.

Various features of the axillary hairs seem to be potentially useful characters, including shape, color, and number of basal and terminal cells, number of hairs per axil, distribution of the hairs across the leaf base, and branching of the axillary hairs, but only number and shape of terminal cells and branching have been used in this analysis. Terminal cells of axillary hairs are frequently thin walled and hyaline, but may be colored or verrucose, or contain red crystals (in *Hookeria acutifolia*). The terminal cells in many taxa are ovate-cylindric, varying somewhat in relative length and width and in the curvature of the walls, but with no discontinuities that allowed the recognition of separate states. In small groups of taxa, however, clearly distinct cell shapes were observed. (0 = ovate-cylindric; 1 = short-inflated; 2 = elongate; 3 = quadrate.)

23. Branching of axillary hair. In the majority of taxa, axillary hairs are straight and uniseriate, but in the papillose members of the Meteoriaceae they may be curved with additional lateral cells, or strongly branched with two or three sub-equal branches. This latter state has also been observed by Hedenäs (1998). Further observations of the ontogeny and distribution of these states may be useful in studies at the generic level in this family. (0 = straight; 1 = angled; 2 = branched.)

24. Axillary hair terminal cell number. The number of terminal cells is variable, but patterns seem to exist at higher taxonomic levels. In each state the number of terminal cells represents a range about a mean, based on observational data. Although most specimens can be allocated to a state without difficulty, quantitative studies of this character may improve state definition. It was occasionally observed that the central hair(s) located at the costa base have both more basal cells and more terminal cells than the other hairs. Consequently only lateral hairs were scored for terminal cell number in this study. This variation, together with the distribution of hairs across the leaf base, requires more study but may prove informative. (0 = one cell only; 1 = cells 1–3; 2 = cells 3–5; 3 = cells 5–9; 4 = cells 11–13.)

25. Axillary hairs per leaf. The number of hairs per leaf axil was determined by examining well developed but immature leaves that were still attached to the plant. Folding back leaves in situ at the stem apex exposes the axillary hairs, and the basal cells at least can normally be clearly seen and counted, and their distribution noted. Removal of the leaves may allow the hairs to be seen more clearly, but the count may be less reliable, since axillary hairs are frequently removed with the leaves, and the hairs may be obscured by the stem. In the Spiridentaceae, axillary hairs were not found, and were coded as absent, but are apparently numerous, long, and highly deciduous (Withey, pers. comm.). (0 = absent; 1 = one axillary hair; 2 = 2–3 axillary hairs; 3 = 4–8 axillary hairs; 4 = 12–14 axillary hairs.)

26. Axillary hair basal cell number. The basal cells are frequently well differentiated, small, dark-walled, and persistent. In many taxa studied, one basal cell per hair was the normal pattern, as found by Hedenäs (1989), but in other pleurocarpous taxa most hairs had two basal cells (but see 24: terminal cell number). Many of the acrocarpous taxa had several basal cells, or the axillary hairs were not differentiated into basal and terminal cells.

Although considerable variation is apparent in the shape of the basal cells, both in relative length and width and curvature of the walls, and in the attachment of the basal cells to the underlying epidermal cells or to the cells of the leaf base, this variation requires more study and was not used at the present time. (0 = not differentiated; 1 = one basal cell; 2 = 1–2 basal cells; 3 = 2 or more basal cells.)

27. Micronemata. Rhizoid structure in the Mniaceae was described by Koponen (1968), who used the variation in structure and position to differentiate macronemata (on branch primordia) and micronemata (highly branched, on epidermal cells). Features of rhizoid structure and distribution were discussed by Crundwell (1979) and illustrated by Whittemore and Allen (1989). In this study, leaf tip rhizoids were not used because the relationship of this feature to vegetative reproduction (for example, in *Hookeria*) requires additional study. Four types of rhizoids, based on position, (macronemata, micronemata, adaxial and abaxial rhizoids) were included here. In many taxa more than one type of rhizoid occurs, in different combinations, and so can be considered as separate characters (conjunction test of independance, Patterson 1982).

Micronemata originate from single epidermal cells, normally scattered across the surface of the stem or branch, with no apparent affinity for leaf

bases or branch primordia. In stoloniform taxa they may be restricted to the ventral surface of the stolon. Considerable variation was observed, but several principal branching patterns were used here, as with the other types of rhizoids. The "trunk-and-branches" type of Crundwell (1979) has a strong primary axis with sparse to abundant but fairly simple lateral branches. Alternatively the lateral branches were abundantly and sub-dichotomously branched to form a diffuse tomentum. Normally one primary axis developed from each epidermal cell, but in a few taxa the primary axis divided to form a basal fork. In other taxa the single primary was short, dividing repeatedly to form a sub-dichotomous tomentum. (0 = absent; 1 = primary with laterals; 2 = basal fork; 3 = primary with diffuse branching; 4 = sub-dichotomous branching.)

28. Macronemata. This term is restricted to those rhizoids originating from cells around the branch primordia, usually from enlarged hyaline cells adjacent to the primordium, but sometimes also in a line extending along the stem from the primordium. Macronemata are frequently detectable as isolated tufts scattered along the module and closer examination reveals the branch primordium in the center of the tuft. Branching patterns are as described for micronemata. (0 = absent; 1 = unbranched; 2 = primary with laterals; 3 = primary with diffuse branching.)

29. Adaxial rhizoids. These rhizoids originate in the axils of leaves, often in tight groups in positions where branch primordia would normally be formed, and sometimes in highly branched fans from a single point, but careful examination of the tufts shows that no branch primordium is present. Unlike the tufts of macronemata, which are relatively few, adaxial rhizoids normally occur in the axils of every leaf. They may however be absent where a branch primordium is developed. Branching patterns are as described for micronemata.

In certain taxa, bases of stems and branches are densely surrounded by rhizoids, but the cells from which the rhizoids originate are obscure. The rhizoids may be macronemata on the stem associated with the branch base. However, the rhizoids appear to be located on the branches, rather than around the branch base on the subtending module. Alternatively, the rhizoids may be macronemata associated with primordia on the branch itself, although few primordia were seen on branch bases. A further alternative is that the rhizoids are adaxial, in the axils of the juvenile leaves of the branch, and they are provisionally coded as such here. (0 = absent; 1 = unbranched; 2 = primary with laterals; 3 = primary with diffuse branching.)

30. Abaxial rhizoids. In many pleurocarpous mosses rhizoids are formed in a fourth location, at the abaxial base of the leaves (Crundwell 1979; Damanhuri & Longton 1996; Koponen 1968). Different codings for this character were used by Hedenäs–as a kind of micronemata (char. 7, 1994), or unspecified rhizoid (char. 36, 1996*a*; char. 34, 1996*b*), or as several states in association with rhizoids in other locations on the leaf (char. 39, 1995).

In the taxa observed in this study the rhizoids abaxial to the leaf were either associated primarily with the cells of the costa, or associated with the epidermal cells immediately adjacent to the leaf and costa base. In other taxa adaxial rhizoids have been noted at the basal corners of the leaves (see also Crundwell 1979). (0 = absent; 1 = on costa; 2 = basal to costa.)

31. Abaxial rhizoid branching. The primary axes of abaxial rhizoids are normally long and fairly straight, remaining unbranched until they contact the substrate. They then develop numerous distal anastomosing branches (rhizoidal disk, Damanhuri & Longton 1996; lobed, Whittemore & Allen 1989). Alternatively, branching patterns as described for the other rhizoid types may occur. (0 = distal-contact; 1 = primary with laterals; 2 = primary with diffuse branching; 3 = sub-dichotomous branching.)

32. Papillosity. Surface features (papillosity and color), density and distribution of the rhizoids were coded for all rhizoid types jointly. Papillosity was scored for "medium" rhizoids, since variation in this character was related to rhizoid diameter. Very fine surface features below the level of effective resolution of the light microscope were coded as "smooth". Larger surface features could be separated into coarsely verrucose, with scattered, large but irregular flattish plaques and warts; minutely verrucose rhizoids with similar but smaller and more regular ornamentation; spiculose rhizoids with fine points on rounded bases, and papillose rhizoids with very fine, regularly arranged spherical papillae. (0 = smooth; 1 = coarse verrucose; 2 = spiculose; 3 = minutely verrucose; 4 = papillose.)

33. Color. The colors of the "medium" rhizoids, as seen freshly mounted in Hoyer's solution, were grouped into approximate color classes. This character however leaves much to be desired in terms of accuracy of delimitation of the states, and it is highly possible that the "same" color could be due to different chemical pathways. Various simple techniques to improve the accuracy of this character could be followed (Crundwell 1979). (0 = orange-brown; 1 = yellow-brown; 2 = red-brown; 3 = red; 4 = red-purple; 5 = purple; 6 = pink; 7 = yellow.)

34. Density of tomentum. The density of the tomentum was assessed for all forms of rhizoids

jointly, simply as low—where clearly isolated tufts were visible, or high—where the rhizoids formed a dense covering hiding the stem. The appearance of plants as densely covered in tomentum or rhizoids is a reflection of the interaction between rhizoid type, branching pattern, density and distribution. As with the following character, differences in expression related to habitat can be resolved by examination of variation in material from different locations. (0 = low; 1 = high.)

35. Distribution of tomentum. Distribution of the rhizoids on the primary module was scored for all rhizoid types. Rhizoids restricted to the module base were scored as proximal while those present and persistent along the length of the module were scored as general. Rhizoids initiated distally (in the actively growing region of the stem) but lost in older regions of the stem were scored as distal. (0 = proximal; 1 = general; 2 = distal.)

36. Differentiation of basal cells of stem leaves. The basal cells of the leaf (above the zone of attachment) may be enlarged, yellow or orangish in color, thicker walled, and more strongly pitted than the adjacent cells of the lamina. Variation in expression of this character was frequently seen, and as with other leaf characters it was necessary to use only mature, fully developed stem leaves (Mishler & De Luna 1991). The basal cells were considered differentiated if three or more of these features were seen. Potentially each feature should be scored separately. (0 = undifferentiated; 1 = differentiated.)

37. Differentiation of alar cells. The alar cells in the basal corners of the leaf may differ in shape, size, and color from the other cells of the leaf base and the lamina, and also differ in number and pattern of differentiation. These features are variable and provide many characters at lower taxonomic levels, but only shape (char. 38) and pattern of differentiation were used in the current analysis. The patches of alar cells may be similar to the other cells, differ gradually so that no abrupt transition is seen, or may be sharply differentiated and clearly distinct. (0 = undifferentiated; 1 = gradually differentiated; 2 = sharply differentiated.)

38. Shape of alar cells. Where differentiated, the shape of the alar cells was scored. (0 = rhombic; 1 = rectangular-quadrate; 2 = oblate; 3 = inflated.)

39. Juxta-costal cells. The cells immediately adjacent to the costa are usually slightly more elongate than other lamina cells, but in a few taxa a zone of differentiated cells several cells wide is also seen. This character was problematic in certain taxa lacking a costa, where cells resembling juxta-costal cells occupy most of the leaf base. (0 = undifferentiated; 1 = differentiated.)

40. Cell profile, stem leaves. Surface features of the lamina cells can be divided into the shape of the underlying cell (profile), and the presence of thickenings of the cell wall (papillae). Symmetrical, centrally placed bulging of the cell profile is termed mammillose, while swelling that is distally or proximally displaced so that the tip of the cell juts out like the prow of a boat is termed prorose. (0 = smooth-flat; 1 = mammillose; 2 = prorose.)

41. Position of papillae. Where papillae are present, they may be located over the lumen of the cell or over the cell walls. In prorose taxa a papilla may be located on the tip of the prora, emphasizing the projection. (0 = absent; 1 = over cell lumen; 2 = on tips of prorae.)

42. Distribution of papillae. Where more than one papilla is found on each cell face, they may be clustered in the center of the cell, distributed as one or more lines along the length of the cell, or scattered. (0 = central; 1 = lines; 2 = scattered.)

43. Pit shape. Thin places or holes in the lateral walls between adjacent cells are termed pits. Very little structure is visible, and in taxa with thin walls, pits may only be seen in the thicker cells of the leaf base. In many taxa the pits appear simple, but in others a secondary zone is seen around the pit ("circular") with wall material visible on either side. These may not be homologous with the other pit type but inclusion of this state allows homology to be assessed through character congruence. (0 = absent; 1 = simple; 2 = circular.)

44. Alignment of laminal cells. The cells of the lamina can normally be seen to be aligned, orientated in rows that are parallel or oblique relative to the costa, regardless of the shape or size of the cells. In questionable cases, following a cell row along the length of the leaf will normally lead out towards the margin where the cells are oblique, but remain parallel to the costa where the cells are parallel. The pattern in immature or juvenile leaves can also be used to clarify this question. (0 = parallel; 1 = oblique.)

45. Costa. Costa development is highly variable, and it is consequently necessary always to use mature, fully developed stem leaves (Mishler & De Luna 1991) and to use the most fully developed expression of the costa. This character is widely used, but possibly homoplasious, and may be better restricted to lower levels of analysis. Complete absence of the costa is rarely seen—usually one to a few elongated cells in the leaf base can be found in at least some leaves. Short double costae are frequently seen, varying in length and sometimes with additional forks or spurs, but rarely exceeding the middle of the leaf. Single costae may be short or long, reaching the apex of the leaf or excurrent. Long to excurrent costae may be associated with differentiation of the costa section. Long double

costae are found primarily in the Hookeriales. (0 = absent or very short; 1 = short and double; 2 = single; 3 = long and double.)

46. Costa transverse section. Sections of the costa may be uniform ("homogenous" leaf nerve, Hedenäs 1994) or show zones of differentiated cells. These zones include enlarged "deuters" continuing the line of the leaf cells, one or more zones of cells ventral or dorsal to the plane of the leaf with somewhat or very strongly thickened cell walls and reduced lumens (sub-stereids and stereids), ventral or dorsal enlarged cells, and a central patch of thin walled, minute and fragile cells (hydroids and leptoids). In many of the taxa used here the costae were uniform, with no differentiation of the cells from those of the lamina. In simple costae there is either a line of larger cells ("deuters") across the center of the costa, or a zone of rather smaller, thicker walled cells dorsal or ventral to the central line, but since these conditions tend to blend into each other they were coded as a single state. In elaborate costae two or more features were seen, normally at least with clearly differentiated deuters and stereids or sub-stereids. Hedenäs (1994) used the character of "deuters divided", following Frey (1977) who regarded this as a character separating Bartramiaceae and Timmiaceae from the Bryaceae, Mniaceae, and Hypnodendraceae. However, double rows of deuters are seen in other taxa, for example the Polytrichales, indicating that this character may be more general. The work of Kawai in a series of papers (e.g., 1968, 1977) on the transverse sectional anatomy of the costa and stem suggests many additional potential characters, although as given in these papers are not usable as cladistic characters. A simple coding of costa transverse section was used here. (0 = uniform; 1 = simple; 2 = elaborate.)

47. Perichaetial leaf differentiation. The leaves on the fertile module may be scarcely or not differentiated from vegetative leaves, but in most taxa at least the distal leaves are differentiated, or the leaves throughout the module are modified. From observation of archegonia and the embryonic, juvenile, and mature stages of the sporophytes, it appears that differentiation of the perichaetial leaves reflects a process of leaf initiation and differentiation in coordination with the development of the fertilized embryo and the differentiation of the vaginula and foot (see characters 54–57, 89). In taxa lacking differentiated perichaetial leaves, the foot of the embryo appears to push down into the apex of the stem, and few or no additional leaves are initiated. In taxa with differentiated perichaetial leaves distal on the fertile module, additional leaves seem to be initiated subsequent to the fertilization of the embryo, and differentiation of the vaginula involves at least some growth of the stem apex around the foot. In a variant of this, in taxa such as *Plagiomnium,* the archegonia are borne at the center of "splash-cups" formed from greatly enlarged comal leaves, while the perichaetial leaves s.s. are minute lanceolate structures.

In taxa with a highly modified lateral perichaetial branch [pleurocarps s.s. (*sensu stricto*)] all leaves on the fertile module are modified. Initially the archegonia are surrounded by juvenile branch leaves in a modified form as archegonial bracts. Following fertilization and the commencement of the development of an embryo, some extension of the perichaetial branch occurs and additional often highly modified perichaetial leaves are formed in coordination with the development of the foot and vaginula in most taxa. Extensive study of the development of the embryo, vaginula, and calyptra was carried out by Roth (1969), and this work suggests several potential characters. (0 = leaves not differentiated; 1 = distal on module; 2 = throughout module.)

48. Lamina of perichaetial leaves. Shape and size of perichaetial leaves may differ from that of the vegetative leaves in several ways. In the majority the lamina of the innermost and fully mature perichaetial leaves were similar in shape to the vegetative leaves, but enlarged or reduced in one or more dimensions. Minute, erect lanceolate leaves were seen in some taxa. (0 = undifferentiated from vegetative leaves; 1 = minute, shape lanceolate; 2 = reduced, shape similar to vegetative leaves; 3 = enlarged, shape similar to vegetative leaves.)

49. Apex of perichaetial leaves. The apices of the innermost and fully mature perichaetial leaves were frequently differentiated, and were usually more abruptly and narrowly acuminate than the apices of the vegetative leaves. (0 = undifferentiated from vegetative leaves; 1 = acute; 2 = acuminate.)

50. Texture of inner perichaetial leaves. In many taxa the perichaetial leaves are clearly differentiated in texture, appearing relatively glossy and scarious when compared with the vegetative leaves. In a few cases the vegetative leaves are also normally scarious. (0 = not scarious; 1 = scarious.)

51. Surface of inner perichaetial leaves. This character has been used by Hedenäs (1989; char. 25, 1994), but the taxonomic level at which it is informative is not clear. Variation does occur within families, and even within genera in the taxa used in this study (e.g., in *Brachythecium* and *Spiridens*). (0 = smooth; 1 = plicate.)

52. Stance of inner perichaetial leaves. This character was also initially described by Hedenäs (1989; char. 24, 1994), and is used in a slightly modified form here. The tips of the outer perichaetial leaves of many taxa are recurved (or reflexed),

and only the innermost leaves of the fully mature perichaetium were scored for this character. (0 = inner perichaetial leaves straight and erect; 1 = tips of inner perichaetial leaves recurved.)

53. Ochrea. A delicate membranous ring of tissue, the ochrea, is found at the apex of the vaginula in the Orthotrichales and some Hedwigiaceae (De Luna 1995). In some taxa (e.g., in species of *Macromitrium*), the ring may become detached and slide freely on the seta. Evanescent membranous fringes have also been observed in other taxa. In *Racopilum tomentosum* a dense matted ring develops at the apex of the vaginula, but this is formed by rhizoids and so by empirical criteria (lack of structural similarity) cannot be considered an ochrea. (0 = absent; 1 = present.)

54. Distribution of perichaetial leaves. The distribution of perichaetial leaves on the vaginula seems to be related to the development of the vaginula-foot complex subsequent to the formation of the embryo (see also characters 47, 55–57, 89). Here the vaginula is considered to be all tissues, of whatever origin, surrounding the sporophyte foot. In *Fontinalis,* sometimes considered to be cladocarpous (Buck & Vitt 1986), the archegonia clearly originate on a lateral bud surrounded by juvenile leaves modified as archegonial bracts, but the form of the vaginula is unusual, with the most distal perichaetial leaves located on a collar raised up around the base of the seta. (0 = leaves to top of vaginula; 1 = leaves half way up vaginula; 2 = leaves restricted to base of vaginula; 3 = leaves on vaginular collar.)

55. Paraphyses. Prior to fertilization the archegonia are normally surrounded by uniseriate, hyaline paraphyses, but these may be absent in the mature perichaetium. Axillary hairs associated with the perichaetial leaves can be differentiated by their restriction to the leaf bases and their shorter, less variable length. (0 = absent; 1 = uniseriate.)

56. Distribution of aborted archegonia. Initially all archegonia are clustered at the apex of the fertile module. As the fertilized embryo develops, the remaining aborted archegonia are displaced by the development of the vaginula. The distribution of the aborted archegonia seems to indicate the location of zones of expansion relative to the original module apex, and appears to be independent of the original position of the fertilized archegonium. (0 = archegonia to top of vaginula; 1 = archegonia part way up vaginula; 2 = archegonia restricted to base of vaginula.)

57. Foot width. This character was mentioned by La Farge-England (1996) who stated that pleurocarpous taxa are defined by "perichaetia terminal on lateral innovations that appear sessile and swollen . . .". Care is needed with this character, since the extent of swelling appears to differ with maturity of the vaginula-foot complex, or the foot may be narrow but the surrounding stem tissues swollen. In several acrocarpous taxa examined both the foot and the stem appear swollen. (0 = both foot and stem narrow; 1 = foot narrow, stem swollen; 2 = both foot and stem swollen.)

58. Seta central strand. Although various levels of differentiation of the seta in transverse section were seen, only the presence or absence of a central strand was used in the present study. (0 = central strand absent; 1 = present.)

59. Capsule orientation. It has been observed that orientation of the capsule seems to be correlated with habitat, with erect capsules found more frequently in epiphytic and xerophytic species, and that other features of the sporophyte, such as the extent of reduction of the peristome, may also be associated with habitat (Buck 1991; Vitt 1981; see Selection and Rejection of Characters).

Hedenäs (1994) used capsule orientation and shape as one character, but coded all erect capsules as "unknown" since he considered all such capsules as derived and modified from an unknown original shape, and that they therefore could not be homologized. Elements of the capsule shape do seem correlated with orientation, and are consequently not coded separately here. (0 = erect-inclined; 1 = horizontal; 2 = pendulous.)

60. Neck shape. The development of the neck appeared to be at least partly independent of capsule orientation, and is used as a separate character. In the majority of taxa studied, the neck of the capsule tapers moderately from the urn to the seta, while in others the neck is short, with the urn connecting directly to the seta. In other taxa studied, the neck is elongated, representing a third to a half of the total length of the urn. (0 = absent; 1 = normal; 2 = long.)

61. Surface of capsule. In the majority of taxa studied the surface of the moist capsule was smooth or with slight and irregular wrinkles. In a few taxa the surface of the capsule was strongly furrowed longitudinally, with differentiation of exothecial cells in the furrows. (0 = smooth or irregularly wrinkled; 1 = furrowed longitudinally.)

62. Operculum base. The shape of the operculum consists of at least two separate components, the shape of the base, and the presence, shape and angle of the rostrum or beak. The operculum base may be almost flat to slightly convex or concave, or if strongly convex, may have straight sides resulting in a conical shape, or curved sides resulting in a mamillose shape. (0 = flat; 1 = conic; 2 = mamillose.)

63. Stomate position. Several characters related to the stomates are potentially useful, including po-

sition in the capsule wall, distribution in different zones of the sporophyte urn, pore shape, and the number of cells involved. Position and pore shape were used in this analysis. There are normally two kidney-shaped or curved "guard cells", with a pore between them. The guard cells may be superficial (phaneropore), lying in the same plane as the other exothecial cells of the capsule wall, or they may lie slightly below the plane of the other exothecial cells. In the latter case the surrounding exothecial cells may protrude to a greater or lesser extent over the stomate (cryptopore). In one of the study taxa, each stomate consists of a single ovate guard cell perforated by a central pore. These structural differences do not allow a robust hypothesis of homology of these stomates with those in the other taxa studied (under the similarity criterion) and these stomates were consequently coded with the autapomorphic state "single cell" rather than coding as "unknown". (0 = absent; 1 = superficial; 2 = immersed; 3 = single cell.)

64. Pore shape. The shape of the stomate pore seems rather variable, with a range of shapes and sizes within each capsule. The majority state was scored in each case, but this character may prove to be unreliable. (0 = round; 1 = oval; 2 = elongate.)

65. Exothecial cell shape. The surface cells of the capsule in the majority of taxa examined are roughly oblong to rectangular in shape. In some taxa the cell shape was highly variable, while in others the cells were smaller and quadrate. In *Tayloria,* the cells were strongly differentiated with transverse thickenings between minute cells, an autapomorphic state that could not readily be related to the other states. (0 = oblong-rectangular; 1 = quadrate-isodiametric; 2 = irregular; 3 = minute.)

66. Alignment of exothecial cells. The exothecial cells in the majority of taxa are weakly or strongly aligned in longitudinal rows, independently from the presence of longitudinal furrows. Rarely the cell arrangement was highly irregular, so that no such cell rows could be traced. (0 = strongly aligned; 1 = weakly aligned; 2 = not aligned.)

67. Exothecial cell wall thickness. The lateral walls of the exothecial cells in the majority of taxa are of uniform thickness (whether thick or thin), but some taxa, especially in the Hookeriaceae and Sematophyllaceae, have thickenings either in the cell corners ("collenchymatous") or along the lateral walls, respectively. (0 = walls uniform; 1 = walls collenchymatous.)

68. Annulus. Cells between the rim of the urn and the operculum may be differentiated, facilitating dehiscence of the operculum. Dehiscence may occur by breakage across cells, but more normally the walls between the cells separate. The cells of the annulus may be small or large, form a single or multiple layer, may remain attached to the capsule, or may separate, either as individuals or as a curling strip of cells (a "revoluble" annulus). However, it was observed that the method of dehiscence of the annulus was more variable than the size and layering of the annular cells, and so only this latter variation was scored for the present study. (0 = absent; 1 = single-layer small; 2 = single-layer large; 3 = multi-layer.)

69. Exostome teeth. Buck and Vitt (1986) considered that the presence of a shoulder on the exostome tooth was characteristic of the Hypnales, but we agree with the observation of Hedenäs (1994) that shouldered exostome teeth are also present in members of the Bryales. Although a shoulder was undoubtedly present in several taxa used in the current study, considerable variation was seen in the height, angle, and distinctness of the shoulder. This information could not be satisfactorily separated into states for cladistic analysis, and consequently was excluded. Several taxa lack either or both the exostome and endostome, or sporophytes were unavailable or of poor quality. These cases were coded as "−" or "?" respectively, but these codings were treated alike by the analysis.

In the ingroup taxa for this study, the exostome normally consists of 16 separate teeth. These may be completely separate, or contiguous in several cells at the base ("base of exostome broad", Buck & Vitt 1986). In the two members of the Meteoriaceae included the exostome teeth were irregularly fused above. Other variations in the character states used here represent uniformative autapomorphies for individual out-group taxa. (0 = absent; 1 = 16 separate teeth; 2 = 16, contiguous at base; 3 = 16, partly fused; 4 = 8 pairs; 5 = split into 32; 6 = forked above.)

70. Membrane. In certain taxa the mature exostome teeth were seen to be mounted on a basal membranous ring. (0 = membrane absent; 1 = membrane present.)

71. Position of exostome in mouth. The exostome may be attached at the inner rim of the mouth of the urn, or at a point deeper within the mouth. (0 = superficial; 1 = immersed.)

72. Border on exostome teeth. The presence of a border on the exostome teeth represents differences in width of the inner surface (PPL) and the outer surface (OPL) of the teeth. Consequently a border may be present due either to a wider inner layer (e.g., in some Hookeriaceae) or to a wider outer layer (e.g., in some Sematophyllaceae) (Buck & Vitt 1986). Additionally, the border may be more apparent in the lower regions of the teeth in some taxa, and nearer the tips in other taxa. The presence or absence of all types of border was used here, but

with considerable reservation. Further study is required to determine reliable character states. (0 = absent; 1 = present.)

73. Color of exostome teeth. Color was observed in exostome teeth freshly mounted in Hoyer's solution, but, as noted for rhizoid color (char. 33), it needs to be used with caution. (0 = whitish; 1 = yellow-brown; 2 = orange-brown; 3 = red-brown.)

74. Median line. The majority of the taxa included had relatively little thickening on the outer surface of the exostome, and only in some members of the Hookeriaceae (*Brymela* in this analysis) was there sufficient thickening to form a furrow. The exostome teeth in *Tayloria* were split along the median line. (0 = zig-zag line visible; 1 = thickened, furrow present; 4 = exostome split.)

75. Ornamentation of exostome outer surface–striae. Ornamentation of the exostome is highly varied, ranging from striate, through partially or completely papillose, to partially or completely smooth. Partially or completely papillose or smooth peristomes are considered to be a consequence of reduction, which may have occurred repeatedly (Buck 1991; Vitt 1981). The distribution of striae, reticulations, and papillae on the exostome is frequently emphasized in moss taxonomy.

The morphology of the ornamentation, rather than the distribution, was emphasized for this character. Papillae were considered separately from striae (char. 76). Since the pattern of ornamentation of exostome teeth normally differs between the tips and the base and between the interior and exterior, only ornamentation of the outer surface at the base is considered here. Several patterns of morphology of the striae were noted in the taxa used in this study. In some taxa striae appear to be formed by fusion of papillae, while in others the striae exist separately from the papillae, which may occur on the surface of the striae. "Multi-directional" striae appeared to be composed of tall papillae that radiate in lines, somewhat like a hairbrush. Massive striae, seen only in *Entodon,* are coarser than other striae, and may also be oblique or vertical rather than primarily horizontal. Taxa that lacked striae were coded as "not applicable" (−). (0 = striae by fusion of papillae; 1 = striae separate; 3 = massive striae; 4 = multi-directional striae.)

76. Ornamentation of exostome outer surface–papillae. The majority of taxa, including those that were largely striate, also possess papillae. Papillae at the tips of the exostome teeth frequently differ from those lower down, and only those in the base and lower middle region were scored for this character. The majority of taxa had papillae that were small, rounded, and very regular in size, shape, and distribution. Further small groups of taxa shared states (1–3), and some individual taxa showed autapomorphic states (4–7). (0 = small regular papillae; 1 = domed; 2 = coarse; 3 = spiculose; 4 = columnar; 5 = coralloid; 6 = granular; 7 = smooth.)

77. Trabeculae. The inner surface of the exostome has transverse ridges (trabeculae) that represent the walls of the PPL cells. The area between these ridges is variously thickened, and the ridges themselves may be extended into transverse plates. Since the development of the trabeculae varies along the length of the exostome teeth, the midpoint of each tooth was used to score these structures. In certain taxa the trabeculae were very elongate in the distal half of the exostome teeth, as described by Hedenäs (1994). The relative height and width of the trabeculae showed almost continuous variation in the taxa used, and no discrete states could be identified using this information. However, discrete states were seen in the profile of the trabeculae, resulting from the distribution of wall thickenings on and between the trabeculae. An even layer between and over the surface of the trabeculae resulted in a rectangular or square shaped profile. Thickening that was deeper in the corners between the trabeculae, which frequently projected beyond the thickenings, resulted in a concave profile (see Hedenäs 1994, fig. 4a & c). In a variant of this the trabeculae were very close together and very tall. In the third group, the thickenings in the area between the trabeculae was more or less even in depth, producing a flattish or very slightly convex or concave profile, but with the trabeculae shorter than the thickening to produce an emarginate apex. Again, this could be separated into low and high states. (0 = absent; 1 = rectangular; 2 = concave low; 3 = concave tall; 4 = emarginate low; 5 = emarginate high.)

78. Transverse walls. The distribution of papillae on the outer surface of the exostome teeth was not always even. In the majority of taxa the papillae appeared primarily on the face of the exostome teeth between the transverse walls, while in other taxa the papillae were located preferentially on the transverse walls. *Funaria* had "fimbriate" transverse walls, with tufts of long papillae. (0 = smooth; 1 = papillose; 2 = fimbriate.)

79. Movement of exostome teeth. The exostome teeth flex when wet, in a manner that reflects the relative thickness of the thickenings on the inner and outer surface of the exostome. Many variants of relative position were seen, reflecting in part the length of the exostome teeth. (0 = straight; 1 = erect, tips reflexed; 2 = recurved; 4 = incurved; 5 = incurved, tips erect; 6 = convolute.)

80. Endostome. The outgroup taxon *Dicranum* is haplolepideous, with a single ring of peristome teeth that is interpreted as an endostome (Edwards

1979). All other taxa included are diplolepidous, with endostome segments either opposite the exostome teeth, or alternating with the exostome teeth. (0 = absent; 1 = opposite; 2 = alternate.)

81. Basal membrane. The basal membrane of the endostome varies in height, both relative to the segments and/or exostome teeth and in absolute terms. Various methods of coding for this character complex have been used. In a study of the Spiridentaceae and related taxa, all with well developed, nonreduced segments, Withey (1996*b*) expressed the height of the basal membrane as greater or less than half the total height of the endostome. Hedenäs (1995) calculated the height of the basal membrane as a proportion of the height of the endostome segments (his character 78). The height of the basal membrane seems frequently to be dependent on the height of the endostome, so in a species with a low endostome the basal membrane may have the same relative proportion as in a species with a high endostome. Consequently, where taxa with dissimilar peristomes are included, measurements of relative height are problematic—a reservation expressed by Hedenäs in his 1996 papers.

Absolute measures may be more reliable where taxa with dissimilar endostomes are used. The height of the individual cells in the basal membrane could be potentially informative. Hedenäs (1995) calculated a figure based on the height of the basal membrane divided by the number of horizontal walls in the PPL (his character 82). In taxa in which the lowest cells of the basal membrane were variable in size he excluded the cells of this zone from the calculation. The replication of this character is therefore difficult, but he considers the feature to be still under evaluation (Hedenäs 1995; 1996 *a,b*). Various other absolute measurements are possible. One alternative is to count the number of cells forming the basal membrane. The walls of the IPL and the PPL can usually be distinguished from each other with a little care, and either set of cells could be used. The PPL cells are normally narrower and so more numerous than the IPL cells, but more difficult to see. The ratio of IPL to PPL cells may also prove informative, potentially reflecting basic developmental processes in the formation of the endostome.

In the current study the average number of IPL cells in the basal membrane was used, noted at several positions in several endostomes for each taxon (depending on availability) with states determined by gap coding. (0 = basal membrane absent; 1 = low, 1–3 IPL cells; 2 = mid, 4–6 IPL cells; 3 = high, 8–10 IPL cells; 4 = very high, 12 IPL cells.)

82. Segment height. The height of the endostome was expressed relative to the height of the exostome. (0 = no segments; 1 = short, less than half the height of teeth; 1 = tall, more or less equal to teeth.)

83. Fenestration. The endostome may be entire or perforated. Two distinct types of perforation are evident, but these have not always been differentiated (see also character 85). Fenestration refers to perforation through the face of the IPL cells, and may occur in the cells of the basal membrane between the segments, or in the cells of the segment (including segment cells at the level of the basal membrane). The "basket-work" endostome of *Fontinalis* is interpreted as highly perforated, with all IPL cells perforated. (0 = IPL cells intact; 1 = fenestration in basal membrane cells; 2 = fenestration in segment cells; 3 = fenestration in all cells.)

84. Segments keeled. The segments of the endostome are normally weakly or strongly keeled along the midline where the PPL cells join. The keel reflects expansion of the PPL cells and displacement of the IPL cells during the development of the peristome (Shaw et al. 1989). (0 = flat; 1 = weakly keeled; 2 = strongly keeled.)

85. Gaping keel. Perforation along the keel of the segments reflects gaping between the walls of the PPL cells, and is independent of fenestration. Both gape and fenestration may occur in the same endostome (conjunction test, Patterson 1982). The gape may be narrow or wide, with slight to strong separation between the longitudinal walls of the PPL, but with the transverse IPL walls intact. The IPL walls may also separate, so that the two halves of the segment become detached, either below, with the tips joined (see Shaw & Rohrer 1984, fig. 9), or throughout their length. Where variation was seen, the widest gape was scored. (0 = no gape; 1 = narrow gape; 2 = wide gape; 3 = separating below; 4 = separating throughout.)

86. Cilia development. Cilia represent additional divisions in the IPL, between the cells that provide the walls forming the segments. In many taxa, the cilia are reduced or lost, but cell columns representing the divisions can be traced in the basal membrane (Shaw & Rohrer 1984). Cilia have frequently been used only when well developed, as "nodulose" or "appendiculate", and when poorly developed have frequently been ignored. The number of cilia varies, and is reflected in the following character (87) so is not scored separately. Cilia may be represented only by the cell divisions in the basal membrane, or may be rudimentary, with short and delicate or eroded stubs between the segments. Better developed (or less reduced) cilia may be mid-length, or almost as tall as the segments, with the transverse walls short (nodulose) or long (appendiculate). Although the development of transverse walls could be treated as a separate character, they are here used as indicators of the reduction of

the cilia. (0 = absent; 1 = cell divisions in basal membrane; 2 = cilia rudimentary; 3 = cilia mid-length; 4 = cilia long, nodulose; 5 = cilia long, appendiculate.)

87. Ratio of IPL:PPL cells. In anatomical studies of the developing peristome in juvenile sporophytes, the ratio of cells in the Outer, Primary and Inner layers is expressed as a peristomial formula, giving the number in each layer of cells in one quarter of the peristome (Edwards 1979). This same ratio for the IPL and PPL can be seen, though less clearly, in the endostome of the mature peristome under the optical microscope (Shaw & Rohrer 1984). Each PPL cell extends from the keel of one segment to the keel of the adjacent segment, while one IPL cell normally covers the inner face of the segment, so that for each segment the IPL cell coincides with two half PPL cells, which meet at the mid-line of the endostome segment. Columns of IPL cells are also seen between segments, and are continuous with the cilia when present. The PPL walls can normally be clearly distinguished from the IPL walls, allowing the ratio to be observed. IPL cells that form the cilia may be variable in number, so that the mean of several counts for each species must be used. (0 = 2:1; 1 = 3:1; 2 = 4:1; 3 = 5:1.)

88. Calyptra shape. Calyptrae show a wide variety of forms, but these are frequently grouped into just two shapes, mitrate and cucullate. Size of the calyptra relative to the operculum and capsule may also be informative, but was not used in this analysis. Several other characters are potentially informative. Hedenäs (1995) used information from the transverse section and the marginal cells of the calyptra, characters that seem potentially informative for the relationships of the Hookeriales. (0 = mitrate; 1 = conic; 2 = cucullate; 3 = campanulate.)

89. Paraphyses on calyptra. Prior to fertilization the archegonia are surrounded by uniseriate hyaline paraphyses. As the fertilized embryo grows, the calyptra develops from the remnants of the fertilized archegonium and part of the stem apex (see characters 47, 54–57). If the zone of expansion is in the stem apex below the aborted archegonia and the paraphyses, these will be carried up and appear on the calyptra surface. (0 = absent; 1 = present.)

90. Calyptra surface. In the majority of taxa the calyptra surface is smooth, but in certain taxa the surface is longitudinally folded. (0 = smooth; 1 = plicate.)

91. Calyptra margin. The margin of the calyptra may be entire, or variously lobed or dissected. This is in part correlated with the folding of the calyptra surface. (0 = entire; 1 = lobed-laciniate.)

Results

Comparison of the results of the analysis for the molecular and combined data sets, and details of the tree statistics used for all analyses is included in De Luna et al. (1999) and is not repeated here. Using the morphological data alone, with 91 characters for 39 taxa, two most parsimonious trees were found, with a length of 665 steps and a consistency index of 0.328. Using both morphological and molecular data ("combined data") for the 28 taxa common to both data sets, two most parsimonious trees were found by the analysis, with a length of 1162 steps and a consistency index of 0.373. The consistency index was slightly lower in the morphological data than in the *rbc*L (CI = 0.366) or combined data, suggesting slightly higher levels of homoplasy, but not sufficient to indicate any significant disparity between the data sets. These levels in the consistency indices for these numbers of taxa are congruent with phylogenetically informative data (Klassen et al. 1991). The g1 statistic measure of tree-length frequency distribution (Skewness, Huelsenbeck 1991), indicates the distribution of tree lengths for all possible trees, and can be used as an estimate of phylogenetic signal. Values less than zero indicate a left skewed distribution of tree lengths i.e., that there are relatively few minimal and sub-optimal trees, and therefore relatively few alternative most-parsimonious phylogenetic hypotheses found by the data. The g1 statistic for the morphology data, based on 10,000 random trees, was −0.3818, closer to zero than either the *rbc*L data (g1 = −0.5594) or the combined data (g1 = −0.4668), but still indicative of relatively few alternative phylogenetic hypotheses.

Tree topologies.—A single transition to pleurocarpy (node P on Figs. 1–2) was found by the morphological and combined data sets (discussed in De Luna et al. 1999): characters supporting this transition will be discussed below, with reference to the topology of tree 2 found by analysis of the combined data (Fig. 1).

The "Clade A" found by Withey (1996*b*) was found by the *rbc*L data (De Luna et al. 1999), was found in part (lacking the Bartramiaceae and *Plagiomnium*) by the combined data analysis, and was not retrieved by the morphological data. The principle difference between the topologies of the molecular and combined trees is the placement of the Bartramiaceae and *Plagiomnium,* which were placed with the Bryaceae and Splachnaceae by the combined analysis, but nested within the Clade A taxa by the molecular analysis. As a consequence, the molecular data found two transitions to pleurocarpy, but this topology requires the reversal of many morphological characters, especially those

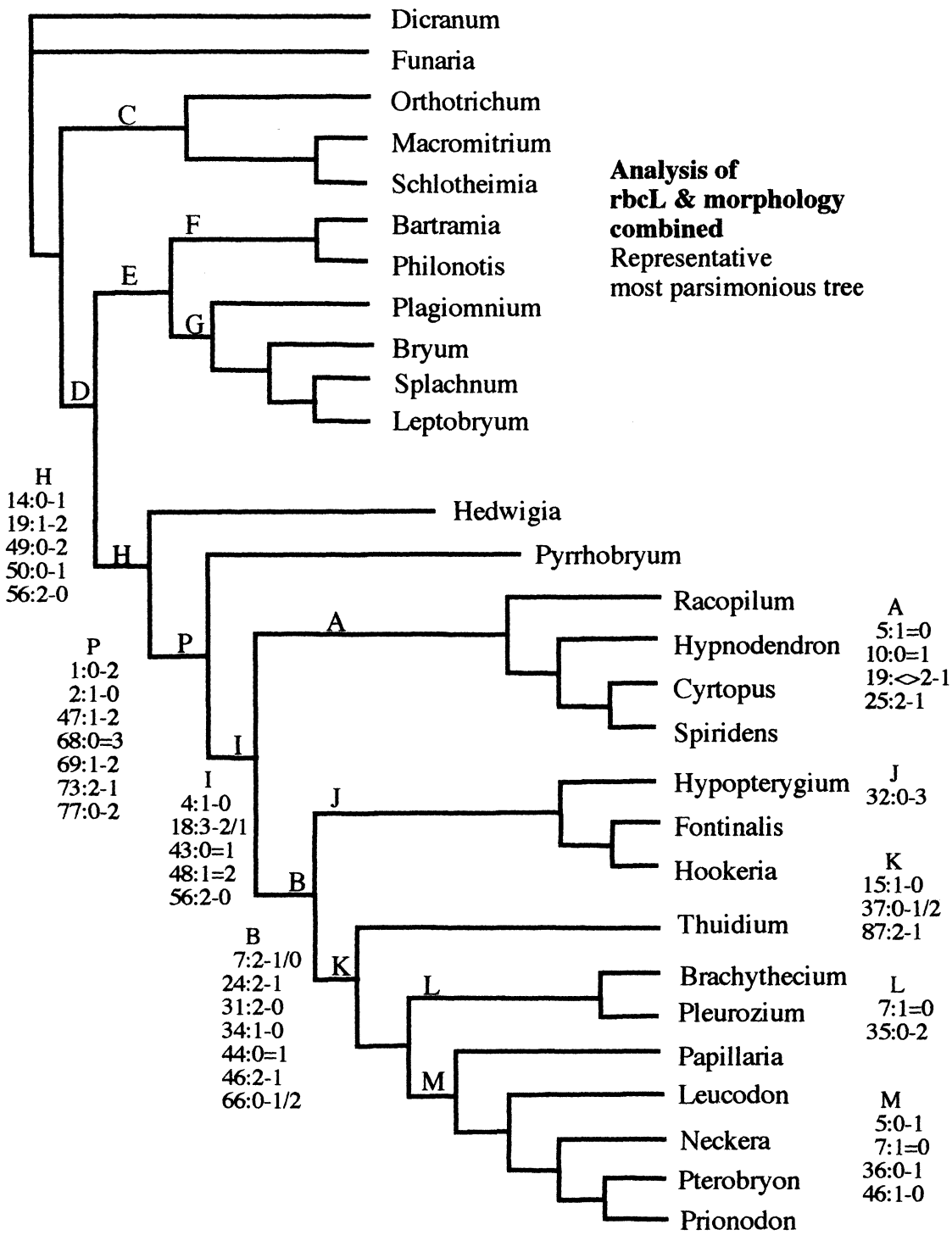

FIGURE 1. Tree 2 (of 2) from analysis of combined morphological and molecular data. State changes are indicated for characters on the principle nodes associated with pleurocarpy. Principle state changes for pleurocarp clades and outgroup clades are also shown in Table 1 and discussed in the text. Support for this tree is discussed in De Luna et al. 1999 (Fig. 2).

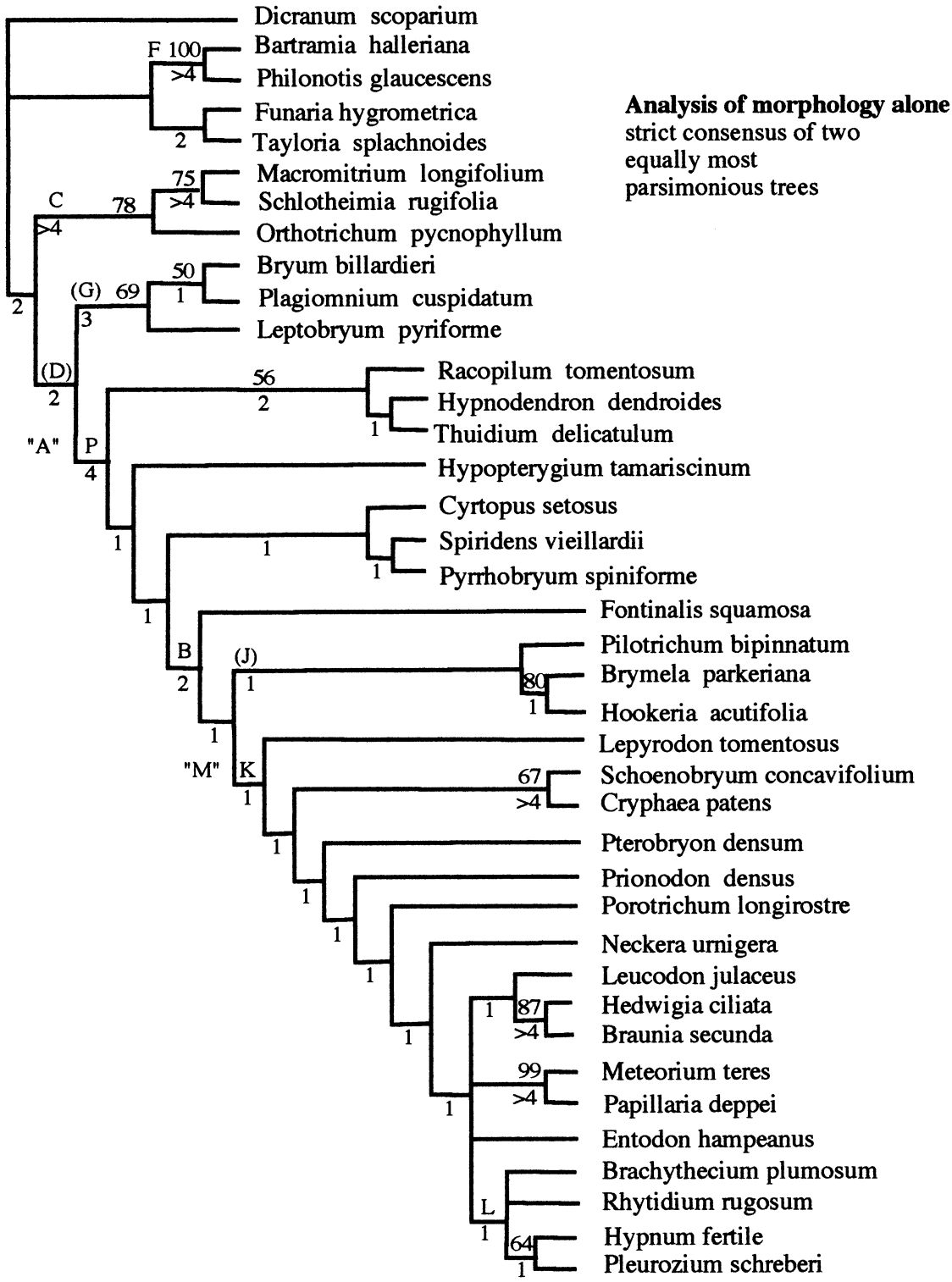

FIGURE 2. Strict consensus of the two trees from analysis of morphological data. Lettered clades correspond with those in Fig. 1. Clades (G) and (D) lack the Bartramiales and Splachnaceae, and Clade (J) lacks *Fontinalis*, taxa that were included in these clades in Fig. 1. Clades "A" and "M" are paraphyletic in the morphological trees. Decay Index and bootstrap values are shown.

associated with pleurocarpy. The two trees found by analysis of the morphological data reflected a somewhat more traditional topology, as might be expected, although different elements of Clade A were associated with the pleurocarps rather than in the Bryineae (Fig. 2). The Bryaceae and Mniaceae formed a clade basal to the pleurocarps, while the members of Clade A were basal within the pleurocarps and paraphyletic. The Bartramiaceae were placed at the base of the tree, with *Funaria* and *Tayloria.*

The Clade B pleurocarps were monophyletic, for the most part, in all analyses, but different relationships were found between the groups. Both the molecular and the morphological data placed the representatives of the Hookeriales in a basal position, the Leucodontales paraphyletic, and the Hypnales in a terminal, mostly monophyletic clade. The combined data, however, found two monophyletic groups, the Hookeriales and the Leucodontales, while the Hypnales were unresolved. A monophyletic group of Leucodontales was not found by either the morphological or the molecular data sets independently, but was found in analysis of the combined data. In the three trees found by the combined data, the Hypnalean taxa, *Brachythecium* and *Pleurozium,* were either placed together or adjacent, while *Thuidium* was either associated with these taxa or placed basal to the Hookeriales and other pleurocarps. Because of the low level of sampling of the pleurocarpous taxa in the combined analysis, this lack of resolution in the Hypnales should not be regarded as important. The taxa from the Leucodontales were always placed together, but the relationships between them showed two different patterns (see tree 1 from this analysis, in fig. 4 of De Luna et al. 1999).

There was incomplete overlap in the data sets used for the different analyses, since for some of the taxa for which *rbc*L was sequenced in Berkeley and Durham we did not have specimens available in Xalapa for morphological analysis. Conversely, we could not extract DNA and sequence *rbc*L for all taxa that we had morphological data for because the material available was too old for extraction to be successful. Consequently only 28 of the total of 48 taxa were common to both molecular and morphological data sets. Experimental removal of taxa from the *rbc*L data set indicated that the failure of the morphological and combined data to retrieve Clade A may reflect the absence of taxa for which we had no morphological data from these analyses (De Luna et al. 1999). Although the principle clades found by the analysis were well supported, the relationships between them were less strong, indicating the possibility that Clade A could be found in future analyses with more complete taxon sampling. The combined data set included all the basal and outgroup taxa used in the morphological analysis, but only 17 of the 28 taxa from the pleurocarps and Hedwigiaceae. Studies of the effect of the number of taxa on the results of phylogenetic analyses indicate that increasing the number of taxa included can both decrease computation time and increase robustness of the resulting phylogenetic trees (Hillis 1993, 1995; Lecointre et al. 1993; Wiens 1998). Consequently, it seems likely that the reduced resolution seen in the results of the analysis of the combined data, as compared to the morphological analysis, may in part be due to the absence of 11 pleurocarpous taxa.

Character distribution.—The two trees for the combined data were identical in the basal regions and differed only in the relationships within the distal pleurocarps (see above). Principle characters supporting the groups are plotted on tree 2 of the combined analysis (Fig. 1) and listed in the accompanying table (Table 1) but only certain characters will be discussed here. The principle clades and nodes between sister groups are identified by bold, upper case letters, sequentially from the base of the tree, with the exception that Clades A and B of Withey (1996*b*) are identified by those letters, and the principle pleurocarp clade is identified as P. To facilitate the study of character distribution among the distal taxa, occasional reference was made to a "combined + morphology" tree (Fig. 3). This consisted of the topology found using the combined data (tree 2), with the taxa for which only morphological data was available placed on the tree in the groupings most nearly corresponding to those seen on tree one from the morphological analysis.

The tree was rooted on *Dicranum scoparium* representing the haplolepideae, as the most basal outgroup. The outgroup and "place-holder" taxa fell into two principle clades. The most distant outgroup clade (c), the Orthotrichales, (represented by *Orthotrichum, Macromitrium,* and *Schlotheimia*) was well supported (DI > 4) and was found by all analyses. Important characters include loss of the stem central strand (18:3 = 0), presence of an ochrea (53:0–1), erect capsules (59:1 = 0) with exostome teeth with "multi-directional" papillae (75: 0–3), and the shape (88:2 = 0) and margin (91:0 = 1) of the calyptra. The lack of trabeculae (77:0) on the exostome and the short (82:1), flat (85:0), unperforated (83:0, 85:0) endostome segments are interpreted as plesiomorphic.

The relationship (node D) of the adjacent outgroup clade (the Bryineae s.s.) with the ingroup taxa is poorly supported (DI = 1), but is marked by the unambiguous character of the swelling of the vaginula and foot (57:0–2) in the majority of taxa examined, indicating that this character is more

general than indicated by La Farge-England (1996). An additional interesting set of characters includes the appearance of well developed trabeculae on the exostome (77:0–2), a strongly keeled endostome (84:0–2) with well-developed cilia (86:0–3/4) and a high IPL:PPL (87:0–2/3) ratio. However, different optimization of this character complex may indicate that it evolved in parallel in the Bryineae and the Hypnineae. Either optimization would support the hypothesis that the Orthotrichales represent an early phase of peristome evolution (Buck & Vitt 1986; Vitt 1984), lacking the derived peristome features, rather than having affinities with the Isobryales and peristomes secondarily reduced, as suggested by the older classifications of Brotherus (1924) and Fleischer (1904). Various members of the Orthotrichaceae have relatively well developed endostomes, sometimes with keeled segments, but always lack cilia (Lewinsky 1993; Vitt 1984).

The adjacent outgroup (clade E), composed of the representatives of the Bartramiaceae, Bryaceae, Mniaceae, and Splachnaceae (the Bryineae s.s.), was weakly supported (DI = 1), but the members possess micronemata with diffuse or dichotomous branching (27:0–3/4), and verrucose or spiculose rhizoids (32:0–1/2), archegonia distributed to the mid-part of the vaginula (56:2–1), elongate pores in the stomata (64:0–2), and a widely gaping and separating keel on the endostome (85:1–3/4).

The Bartramiaceae (clade F) was strong (DI = 4) with good support by several unambiguous characters (for example, prorose cells (40:0–2) and a fenestrate basal membrane (83:0 = 1), in addition to autapomorphies for the family not used in the analysis), but its placement is problematic. Whether the Bartramiaceae are placed with the Bryaceae and Mniaceae, as in the combined analysis, or with the members of Clade A, as in the *rbc*L analysis, study of the distribution of the morphological characters shows reversals, parallelisms, or other ambiguities, indicating that the characters or states may be homoplasous. For example, the presence of scale leaves around the branch primordia is anomalous in the Bryinae but also among the members of Clade A (Akiyama & Nishimura 1993*a*), and may represent a parallel gain. If the scale leaves indicate a relationship within the pleurocarps, then the large suite of acrocarpous features must represent reversals.

The clade (G) consisting of *Plagiomnium, Bryum, Leptobryum,* and *Tayloria* was well supported (DI = 3) and shared several characters, including minute lanceolate perichaetial leaves (48: 2–1), and the capsule becoming pendulous (59:1–2) as a derived feature. Most members of this clade have the lamina cells aligned obliquely (44:0 = 1), a character seen in the majority of the pleurocarps and possibly a synapomorphy at node E rather than within the Bryineae. The lamina cells are aligned longitudinally in the Bartramiaceae, an additional indication that this family may be misplaced in the Bryineae. The placement of *Tayloria* reflects the influence of the molecular data for *Splachnum*—many of the morphological characters are reversed, and there are several autapomorphous characters.

In the combined analysis, the ingroup was composed of two strongly supported clades, one consisting of the Clade A pleurocarps (*Spiridens, Cyrtopus, Hypnodendron,* and *Racopilum*) and the other of the Clade B pleurocarps (Hypnales, Leucodontales, and Hookeriales), with *Hedwigia ciliata* and *Pyrrhobryum spiniforme* basal to these clades. The acrocarpous *Hedwigia* (node H) shares with the pleurocarps perichaetial leaves becoming elongate with acuminate to awl-like apices (49:0–2), and scarious in texture (50:0–1). Scarious perichaetial leaves also occur in some taxa currently placed in the Orthotrichineae (Vitt 1984) but not included in this analysis (e.g., *Helicophyllum*)—study of the distribution of this character in taxa basal to node H would be useful. Several characters at this node and the two subsequent nodes are ambiguous, with reversals or parallel gains, indicating a possible rapid radiation. This is complicated by the absence of a peristome in *Hedwigia,* which restricts the study of the peristome characters at this point. Two characters, the presence of scale leaves around branch primordia (14:0–1), and the development of stereid cells in the stem cortex (19:1–2), are interesting but problematic here. Both the Hedwigiaceae and the Clade B pleurocarps possess scale leaves, while *Pyrrhobryum* and the Clade A pleurocarps lack them. Clade A taxa have the cortical cells of the stem somewhat differentiated, but in the Hedwigiaceae, *Pyrrhobryum,* and Clade B pleurocarps the cortical cells are further differentiated to form a well defined zone of stereid cells. This does, however, occur also in more basal taxa, and the generality of this character complex needs to be investigated further.

Characters associated with pleurocarpy, the differentiated lateral fertile module (1:0–2) with specialized perichaetial leaves throughout (47:1–2), and the absence of sub-perichaetial branching (2: 1–0), group *Pyrrhobryum* with Clade A and Clade B at node P. *Pyrrhobryum* has been interpreted as acrocarpous (Koponen 1988) while La Farge-England (1996) reported that fertile modules may develop as branches on other fertile modules, that is, with sub-perichaetial branches. The data matrix for the morphological analysis does not reflect the presence of sub-perichaetial branching in this taxon, but such a situation would be congruent with a hypothesis that *Pyrrhobryum* represents the transi-

TABLE 1. Character and state distributions in principle clades, (alt. = alternate).

Clade	Character	State
C	18:3 = 0	Stem central strand lost (also *Hedwigia,* some Clade L)
(Orthotrichales)	43:0 = 1	Weak pits between lamina cells normally present
	53:0–1	Ochrea present
	59:1 = 0	Capsule erect (also in some Hypnalean pleurocarps)
	75:0–3	Exostome papillae "multidirectional"
	88:2 = 0	Calyptra mitrate (also seen in Hookeriales, in part)
	91:0 = 1	Calyptra margin lobed laciniate
D	57:0–2	Foot and stem swollen
(Bryineae +	77:0–2	Exostome trabeculae well developed and concave
Hypnineae)	84:0–2	Endostome strongly keeled
	86:0–3/4	Cilia well developed
	44:0–1	Lamina cell alignment oblique (alt. optimization)
	61:1–0	Capsules smooth (alt. optimization)
	87:0–2/3	IPL:PPL ratio high (4/5:1) (alt. optimization)
E	27:0–3/4	Micronemata with diffuse or dichotomous branching
(Bryineae including	32:0–1/2	Rhizoids coarsely verrucose or spiculose
Bartramiaceae)	56:2–1	Archegonia distributed to middle of vaginula
	64:0–2	Pores of stomata elongate
	85:1–3/4	Keel of endostome separating below or throughout (also some Clade A)
F	14:0 = 1	Branch primordium with scale leaves (also pleurocarps)
(Bartramiaceae)	40:0–2	Lamina cells prorose
	60:1–2	Capsule neck reduced (also some Leucodontales)
	77:2<>1	Exostome trabeculae rectangular (also in outgroups)
	83:0–1	Basal membrane fenestrate
G	5:1 = 0	Insertion heptate (also in Bryalean pleurocarps)
(Bryineae without	28:0–2	Macronemata with lateral branches
Bartramiaceae)	44:0 = 1	Lamina cell alignment oblique (also in Clade B)
	48:0–1	Perichaetial leaves minute lanceolate
	54:2–1	Perichaetial leaf insertion to middle of vaginula
	59:1–2	Capsule orientation becoming pendulous
	68:0 = 3	Annulus multilayered (also in Clade A, in part)
	87:0–2/3	IPL:PPL ratio high (4/5:1) (alt. optimization)
H	14:0 = 1	Branch primordium with scale leaves (also Bartramiaceae)
(Pleurocarps +	19:1–2	Cortical cells of stem differentiated into stereids
Hedwigiaceae)	30:0–1	Abaxial rhizoids on costa
	43:0 = 1	Weak pits between lamina cells normally present
	49:0–2	Perichaetial leaf apex elongate, acuminate to awl-like
	50:0–1	Perichaetial leaf texture shining and scarious
	56:2–0	Archegonia distributed to top of vaginula
	61:1–0	Capsules smooth (alt. optimization)
P	1:0–2	Archegonia on short secondary module
(Hypnalean, Bryalean,	2:1–0	Loss of sub-perichaetial branching
and *Pyrrhobryum*)	47:1–2	Differentiation of perichaetial leaves throughout module
	68:0 = 3	Annulus multilayered (also in Clade G)
	69:1–2	Exostome teeth becoming contiguous at base
	73:2–1	Exostome teeth paler (yellow brown)
	77:0–2	Exostome trabeculae well developed (alt. optimization)
I	4:2–0	Determinate secondary modules frequent
(Bryalean and Hypnalean	18:3–2/1	Stem central strand reduced from elaborate to weak
pleurocarps	87:3–0/1	IPL:PPL ratio reduced (2/3:1)
A	5:1 = 0	Insertion haptate (also seen in Bryineae & *Pyrrhobryum*)
(Bryalean	19:2–1	Cortical cells of stem differentiated
pleurocarps)	25:2–1	Axillary hairs reduced to 1 per leaf
	75:0 = 1	Papillae form striae (also in Hypnales, Bryales, in part)
B	7:2–1/0	Primary module plagiotropous or plagio > orthotropous
(Hypnalean	10:0–2	Lateral fertile modules developing distally
pleurocarps)	24:2–1	Axillary hair terminal cells reduced to 1–3 per hair
	31:2–0	Abaxial rhizoids with "distal contact" branching
	34:1–0	Tomentum density low
	44:0 = 1	Lamina cells alignment oblique (also seen in Bryineae)
	46:2–1	Leaf costa section with simple differentiation of cells
	66:0–1/2	Exothecial cells in capsule weakly or not aligned
J	22:0–1/2	Axillary hair terminal cell inflated or elongate
(Hookeriales with	24:1–0	Axillary hair terminal cell single
Hypopterygium)	32:0 = 3	Rhizoids minutely verrucose (also in *Fontinalis*)
	67:0–1	Exothecial cells collenchymatous

TABLE 1. Continued.

Clade	Character	State
(Hookeriales *s.s.*)	20:0–2	Stem with hyalodermis
	45:2–3	Costa double and long
	46:1 = 0	Costa section uniform (also in some Clade K)
	54:1–0	Perichaetial leaf insertion to top of vaginula
	88:2 = 0	Calyptra mitrate (also Orthotrichales)
	90:0–1	Calyptra plicate (also Orthotrichales)
	91:0–1	Calyptra margin lobed-laciniate (also Orthotrichales)
K	37:0–1/2	Alar cells differentiated
(Hypnales and Leucodontales)	15:0–1	Outer scale leaves lacking axillary hairs
L	7:1 = 0	Primary module plagiotropous (in part)
(Hypnales)	35:0–2	Tomentum distribution distal
M	6:0–1	Reiteration
(Leucodontales)	7:1 = 0	Primary module plagiotropous (in part)
	36:0–1	Lamina basal cells differentiated
	46:1–0	Costa section uniform (also Hookeriales)

tion to true pleurocarpy through a phase of cladocarpy.

The two pleurocarp clades (Clade A and Clade B) were each strongly supported, but the relationship between them (node I) was weak (DI = 1). Characters supporting this node also are not strong, some occurring in parallel elsewhere (especially in the Bryales) or lost in several taxa. However, a general pattern of increased secondary branching (4:2–0), weakening of the central strand in the stem (18:3–2/1) and reduction of the IPL:PPL ratio (87:3–0/1) was found in these pleurocarp taxa.

Clade A was strongly supported (DI = > 4) but since there were few unambiguous morphological characters for the clade this was presumably due to support from the *rbc*L data. Morphological characters include reduction in the number of axillary hairs (25:2–1), with *Racopilum* and *Hypnodendron* having only one per leaf. However, *Thuidium* (Clade B) also has one hair per axil, as do many other taxa not included in this analysis. Both *Spiridens* and *Cyrtopus* possess numerous axillary hairs, but in *Spiridens* these are extremely ephemeral. The branch insertion is somewhat swollen and clamp-like ("haptate", 5:1 = 0) or adpressed ("adnate", 5:0–2) in Clade A, as opposed to the simple ("enate") insertion of the majority of taxa, but members of the Bryineae also have the haptate type of insertion.

The Clade B pleurocarps formed a strong group (DI = 4), supported by several morphological characters. Interesting characters include the possession of abaxial rhizoids with the "distal-contact" type of branching (31:0–2), reduction of the leaf costa from elaborate to simple (46:2–1, cf. the "homogenous leaf nerve", Hedenäs 1994), and increased irregularity in the alignment of exothecial cells on the capsule (66:0–1/2). Additional characters include an increasingly prostrate habit (7:2–1/0), with a pattern of a reduced number of terminal cells in axillary hairs (24:2–1), and reduced tomentum density (34:1–0). Abaxial rhizoids also occur in *Braunia,* which has extremely sparse "distal-contact" branching, in the Macromitriaceae (*Macromitrium* and *Schlotheimia*) and in two Clade A taxa (*Racopilum* and *Hypnodendron*). However, in the Macromitriaceae and Clade A taxa the branching is diffuse rather than "distal-contact", suggesting that abaxial rhizoids in these groups are not homologous with those in Clade B pleurocarps.

Within the Clade B pleurocarps there was some variation between analyses in the membership of the different clades, more so than was seen among the taxa of the outgroups and basal regions. This probably is in large part a reflection of the taxon coverage. Most of the outgroup and basal taxa were included in both the morphological and molecular data sets, and so were well represented in the combined data set and analysis. Molecular data was available for only 11 of the 21 Clade B taxa for which morphological data was available, so only this subset could be included in the combined analysis. Nevertheless, broad similarities between the three analyses are apparent.

The "Hookeriales" were recognized in all analyses (Clade J), but in the trees found by the molecular data this group consisted of *Hookeria* and *Hypopterygium,* while in the combined analysis *Fontinalis* was added to this group. No other Hookeriales were included in these two analyses. The *Hookeria* + *Hypopterygium* clade was very weak (DI = 1). In the morphological analysis the Hookeriales consisted of *Hookeria, Brymela,* and *Pilotrichum* (DI = 2), while *Hypopterygium* was placed in a basal position within the pleurocarps, and *Fontinalis* was placed as the sister group to the Hookeriales and all other pleurocarps. Morphological characters common to the Hookeriales (*sensu lato*),

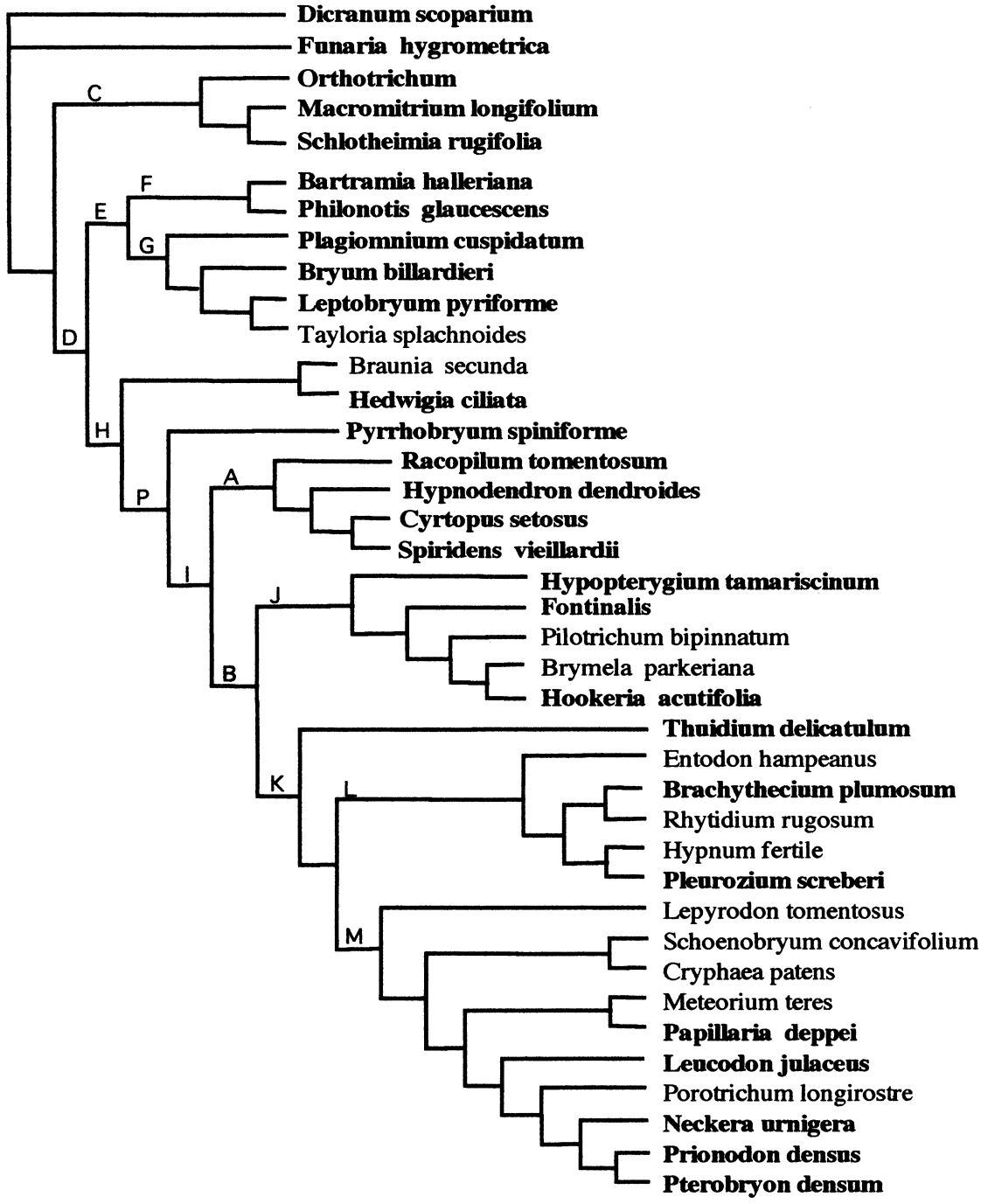

FIGURE 3. "Combined + morphology" tree. Tree 2 from analysis of the 28 taxa for which both morphological and molecular data were available (see Fig. 1) with taxa added for which only morphological data was available. "Combined data" taxa are in bold and lettered clades are those from Fig. 1. Relationships within the clades of pleurocarp taxa are approximate and represent "best estimates" from the morphological trees.

that is, with *Hypopterygium,* include characters of the axillary hairs, which have single terminal cells (24:1–0) that are inflated or elongate (22:0–1/2), rhizoids that are minutely verrucose (32:0–3, also in *Fontinalis*), and collenchymatous exothecial cells (67:0–2, except *Pilotrichum*). In the Hookeriales sensu stricto (*Hookeria, Brymela, Pilotrichum*) characters found in two or more of the taxa include stems with a hyalodermis (20:0–2), a double long costa (45:2–3) with the transverse section

uniform (46:1 = 0), perichaetial leaves inserted at the top of the vaginula (54:1–0) and characters of the calyptra.

In the Hypnales and Leucodontales (Clade K, DI = 2), a majority of taxa have alar cells either gradually or sharply differentiated from the lamina cells (37:0 = 1/2), and loss of axillary hairs in the outermost scale leaves on the branch primordia (15:0–1). Many taxa have reiterative growth (6:0–1), or the primary module completely plagiotropous (7:1–0), and the costa section uniform (46:1–0). Many of the Leucodontales have the basal cells of the lamina differentiated (36:0–1). The Hypnales frequently have rhizoids ("tomentum") distributed distally (35:0–2) i.e., with rhizoids developing in small clusters near the tips of the stems, especially in the completely plagiotropous taxa, serving to anchor the wefts to the substrate.

Discussion

Problematic and uninformative characters.—Several characters that have been considered characteristic of certain groups of plants were found to have more general or uninformative distributions in these analyses.

1. Position of branch primordium. As discussed above (character 12) the position of the branch primordium ("axillary" or "cauline") has been considered characteristic of bryalean pleurocarps. A character of this kind might be expected to reflect very fundamental differences in development and growth of the plant, and consequently to be relatively invariant and reliably informative at high taxonomic levels. However, many primordia are less clearly axillary or cauline than others, and variation in position occurs on single stems in some taxa. The distinction between these two states is therefore somewhat subjective. In addition, as discussed above, developmental state can be critical in accurately determining the position of the primordium relative to the leaf. An additional state, "proximal," was added to the existing states, for branch primordia that are located in the axil of the subtending leaf but not closely adjacent to the leaf base. The resulting distribution of states showed "proximal" to be plesiomorphic, with multiple small groups or individual taxa having either "axillary" or "cauline" branch primordia. Since "proximal" could easily be interpreted as "cauline" or "axillary" it would be too easy to make decisions that fulfill subconscious perceptions of pattern, especially combined with the expectation that such a pattern would be informative. Including the state "proximal" in the analysis highlights the ambiguity of this character. Studies of variability, quantitative analysis of the number and enlargement of epidermal cells involved, and anatomical studies of the developmental processes resulting in the eventual position of the branch primordium, are necessary to determine whether reliable states can be found for this character.

2. Border of exostome. The border on the exostome (character 72) was coded solely as present or absent in this study, which was overly simplistic. Many of the taxa included in this analysis possessed at least a trace of border, and this character was consequently rather uninformative in this study. Potentially several characters and states could be used to describe the variation in this feature. The widening of the border at the "transition zone" was used by Hedenäs (1987, 1995, 1996*a*), while Buck and Vitt (1986) noted that greater width of either the OPL or the PPL layer could result in the appearance of a border. In the current study it was noted that in some taxa the border was better developed in the basal region of the tooth, while in others it was stronger distally.

3. Perichaetial module. The characters associated with the differentiation of a highly reduced perichaetial module, with loss of sub-perichaetial branching and perichaetial leaves differentiated throughout, are strongly correlated and seem to represent a single functional element in the majority of pleurocarpous taxa. The situation in *Pyrrhobryum spiniforme* is particularly interesting. Branching in this species is basal and very compact, with numerous condensed branches in a dense mat of tomentum. The archegonia are located on a highly reduced basal module in a compact complex of basally branched primary modules. The fertile module is extremely short prior to fertilization, but at sporophyte maturity an additional basal portion is apparent, and sub-perichaetial branches may be formed (La Farge-England 1996). The fertile module could be interpreted as an extremely short primary module, and consequently as not homologous with fertile modules that represent condensed secondary modules. Within the Rhizogoniaceae, fertile modules appear in several different positions—terminal with sub-perichaetial branching in *Cryptopodium,* terminal in *Leptotheca,* basal in *Rhizogonium,* basal or lateral in *Pyrrhobryum,* and lateral in *Mesochaete* (Churchill & Buck 1982; Koponen 1988). Obviously the pattern in this family is complex, and given the location of the one exemplar in the tree derived from the combined analysis, it is tempting to speculate that this situation represents parallel diversifications in the direction of pleurocarpy. A phylogenetic perspective is necessary to transform such speculations into specific hypotheses of topological relationships (homology and monophyly) and evolution of character systems (polarity of character transformation and character

state optimization). Koponen (1988) presented "cladograms" illustrating the distribution of 15 characters in the Mniaceae and Rhizogoniaceae, but these were "handmade" and consequently lack this phylogenetic perspective. Extensive study of the morphology of the Rhizogoniaceae and its relatives in the context of phylogenetic analyses must be the next step in the study of the evolution of pleurocarpy.

4. Reduced peristomes. Peristome characters were used for all taxa studied, including those that have peristomes that are reduced to a greater or lesser extent. A large number of characters are involved and there are many different patterns of variation that may be phylogenetically informative. There was no indication that taxa with reduced peristomes were placed together by the analysis as an artifact of convergence in these characters. Even if parallel patterns of reduction occur in the taxa involved, the characters were not sufficiently congruent to obscure the information derived from other characters. The avoidance of these characters in taxa with reduced peristomes (Hedenäs 1994, 1995, 1996*a,b*) does not therefore seem to be necessary.

Use of the Combined Phylogeny to study the Evolution of Pleurocarpy in Diplolepidous Mosses.—Pleurocarpy has been considered to be an homology supporting a group that includes the Hypnales, Leucodontales, and Hookeriales (Buck & Vitt 1986; Hedenäs 1994; La Farge-England 1996). Since the advent of cladistic theory and methodology, a rigorous approach to the study of evolution has become possible, so that speculations on character evolution that are not based on a phylogenetic framework can only be considered as general approximations. Under the cladistic paradigm, decisions on optimizations of state changes and polarity of transformations depend on parsimony and topological relationships, and statements of character evolution are always relative to outgroups and a specific plesiomorphic state. Without cladistic analyses, alternative polarities of character state transformations and multiple optimizations cannot be selected formally.

The phylogenetic hypothesis that we present here, based on our combined data from *rbc*L gene sequences and morphological characters, represents a summary of our current thinking on the possible relationships of the diplolepidous pleurocarp mosses. It is clear that the ordinal outline of phylogenetic relationships among pleurocarp mosses remains inconclusive with the data, taxon sampling and cladistic analyses at hand. Our interpretations on the evolution of "pleurocarpy" rely on the cladogram in Figure 1, which includes only the taxa sampled for both sequences and morphology, as an hypothesis of phylogenetic relationships among diplolepidous mosses. Character states associated with pleurocarpy were optimized parsimoniously onto this phylogenetic tree using MacClade 3.06 (Maddison & Maddison 1992). This procedure provides hypotheses of the direction of evolutionary transformations and the most parsimonious estimate of the number of times a feature has evolved within a group of interest. Such a phylogenetic approach is central to our studies of the evolution of pleurocarpy among diplolepidous mosses, since only a cladogram provides the methodological robustness to reconstruct patterns of evolutionary transformation of features. These patterns can then be used to study the evolutionary processes involved (Donoghue 1989; Wake & Larson 1987).

In order to fully understand the evolution of branching systems we have deconstructed the traditional concept of pleurocarpy into its constituent elements. These we have included in the cladistic analysis as independent characters. Among features potentially important to the understanding of the transition to pleurocarpy are: hierarchy of archegonial module (char. 1), formation of sub-perichaetial branches (char. 2), and differentiation of perichaetial leaves (chars. 47, 49, 50). A most-parsimonious reconstruction for the evolution of these features indicates a single origin of pleurocarpy among diplolepidous mosses. These character changes are mapped on the branch supporting the clade including all eleven exemplars of the Leucodontales-Hypnales-Hookeriales group and the subset of five pleurocarp taxa from the Bryales (Node P, Fig. 1). There are no alternative optimizations for these characters on this topology. Other features, such as the swollen foot associated with a short lateral perichaetial module (La Farge-England 1996), were found to be more inclusive (branch D, Fig. 1).

The combination of character states related to branch architecture in *Hedwigia* and *Pyrrhobryum* seem to be crucial in the evolution to pleurocarpy. Our current ACCTRAN optimization on branches H and P suggest the hypothesis of sequential changes in several features from acrocarpy (branches C, D, H) to a specific form of cladocarpy (*Pyrrhobryum*). Cladocarpy in other taxa, associated with long branches, appears to have occurred repeatedly in parallel. The transition to pleurocarpy can be interpreted as the accumulated result of an initial phase of differentiation of perichaetial leaves (as in *Hedwigia*), a second phase of progressive shortening of the female module (as in *Pyrrhobryum*), followed by an eventual loss of sub-perichaetial branches. The hypothetical ancestor of the pleurocarps (branch P) is reconstructed as already having differentiated perichaetial leaves and a short female module, but still with sub-perichaetial branches.

The present phylogenetic hypothesis allows an unambiguous transition from cladocarpy to pleurocarpy, in which the loss of sub-perichaetial branches is a synapomorphy for the pleurocarps. This is an important historical marker of a shared evolutionary history of families that traditionally have been placed in the different orders of Leucodontales, Hypnales, and Hookeriales, and also those pleurocarps that have been placed in the Bryales.

Within diplolepidous mosses, the "cladocarpous" position of archegonia evolved separately at least twice from ancestral "acrocarpous" mosses, and in addition, several times by reversal from "pleurocarpous" mosses. One of these transitions from acrocarpy to cladocarpy occurred early in the history of diplolepidous mosses within the Orthotrichales (Macromitriaceae, represented here by *Macromitrium* and *Schlotheimia*). The transition from acrocarpy that resulted in the growth form seen in *Pyrrhobryum* seems to have been a separate evolutionary event, so that the cladocarpous/pleurocarpous condition here is an independently derived feature. Within the Macromitriaceae the archegonial branches are considerably longer than in *Pyrrhobryum* and the pleurocarpous mosses. This is associated with several additional characters related to differentiation of the perichaetial leaves, the vaginula and foot of the sporophyte. However, details of the anatomy of the archegonial module, and ontogenetic studies of female branches and sub-perichaetial branches may provide useful additional information as to the timing of elongation of the female module and development of associated branch buds.

Additional transitions from acrocarpy seem to have occurred. The Bartramiaceae may be primitively acrocarpous (if included in the Bryineae s.s.) or may have reverted to acrocarpy from pleurocarpy (if included in Clade A.) The Mniaceae, as represented by *Plagiomnium cuspidatum,* could be seen as having developed a quite distinct form of cladocarpy, with a determinate orthotropous "rosette" module forming as a branch on an indeterminate plagiotropous, laterally symmetrical primary module. However, the traditional interpretation of the orthotropous module as primary (which occurs elsewhere in the family and is the normal situation in the sister group) and the plagiotropous module as a secondary and novel innovation, would leave this taxon as acrocarpous. Within the pleurocarps, cladocarpous members of the Cryphaeaceae seem to have developed a strategy in which both primary and secondary modules may be terminated by archegonia. Character congruence indicates that this may be a reversal from true pleurocarpy. The analysis using the morphological data alone places the Hedwigiaceae distally, associated with *Leucodon.* This may represent a case of "long-branch attraction" with multiple homoplasies adding up to a false similarity in distantly related taxa. Alternatively, the Hedwigiaceae may also represent a group that has undergone secondary reversal from pleurocarpy to a state that resembles acrocarpy.

Conclusions

Many characters have previously been described and used in the study of the relationships between groups of mosses at different taxonomic levels, but in the absence of robust phylogenetic hypotheses based on cladistic analysis, these characters cannot be tested other than by observation of general patterns. This analysis represents a preliminary study at the ordinal level of a group of characters in a phylogenetic context, and will provide the basis for our further studies of characters and groups. Careful description and definition of characters and their states is essential for the evaluation of homologies, and the more precisely characters are described and defined, the easier it will be to assess their phylogenetic value. The evolution of pleurocarpy is highly complex, and by deconstructing the various elements of pleurocarpy it is possible to obtain a more precise understanding of the evolution of this suite of characters.

We used a range of data from different character systems for the taxa included in our analyses, although many more could potentially be added. As far as possible we avoided rejecting characters or defining states on the basis of *a priori* ideas about homology or evolutionary value. Features that were not used fell into several different categories (Mishler & De Luna 1991). Poorly studied features, either because of rare occurrence or because of novelty, need additional work to determine variability and generality, and to identify characters and states. Continuously variable features need rigorous statistical or morphometric studies to define states for cladistic analysis. Highly variable features may be appropriate for study at lower levels, for example within or between genera, or even at the population level, but may introduce excessive homoplasy to a study at the ordinal level. Additional gene sequences, from nuclear, mitochondrial and chloroplast DNA, need to be used to avoid the risk of obtaining gene trees rather than phylogenies. Current work by Cox and Hedderson (1999) indicate that trnL and rps4 gene sequences may be informative in studies of pleurocarpous phylogenies. Many characters that were used in this analysis need further modification or study, and some, in light of the current results, should perhaps be rejected as problematic or uninformative.

We included characters of reduced peristomes

that were rejected by other workers on the basis of *a priori* theories as to the evolutionary value of those characters. Our results show that such *a priori* exclusion is unwarranted, and that the use of such data does not result in artificial grouping of taxa on the basis of environmental convergence. Use of molecular data in addition to morphological data has increased the explanatory power of our analyses by providing additional sources of character congruence. Congruence of characters in a diverse data set of this kind reveals that there is a historical signal in the data, which is not obscured by the "noise" of non-congruent characters.

The phylogenies based on morphological data are less resolved and less robust than those based on characters from *rbc*L sequence data or on the combined data. In part, this reflects the ratio of characters to taxa, since the more data is available, the more robust and the better resolved the resulting trees. However, use of either data set alone constitutes a form of character suite rejection—by restricting the range of characters used, congruence testing is reduced. Although there are many practical and theoretical problems associated with morphological characters, these characters represent a large element of the interest in an evolutionary study, and should not be ignored in favor of an entirely molecular approach. Phylogenies based on multiple data sets, including both morphological characters and multiple gene sequences, will be necessary both to resolve the relationships of the pleurocarps and to fully understand the evolution of the characters related to pleurocarpy.

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In memory of Mike Adler, 1954–1996.

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ms. received April 2, 1998; accepted March 17, 1999.

APPENDIX 1. Data matrix of morphological characters used in "morphological" and "combined" analyses. - = inapplicable character; ? = character state unknown.

Bartramia halleriana	02021 022-	-1210 0-301 00032 33000 -2211 00-02 30002 21200	00021 10112 12121 00011 1120- 01042 22124 112000
Brachythecium plumosum	20101 10002	00110 0-220 00012 20200 -0000 01100 0-012 12221	01021 12111 01100 10120 01101 02012 32022 312000
Braunia secunda	01001 10{23}0 -	02112 21020 00013 20001 00000 11200 12100 -1321	10001 01?01 01110 1000- ----- ----- ----- --2000
Brymela parkeriana	20101 10002	21210 0-022 02002 10001 03001 11000 0-013 02221	00001 02011 01100 11020 01110 23052 22020 110111
Bryum billardieri	01020 02{02}- -	-2-0- 0-210 00023 14220 -1011 00-00 0-312 21100	00011 02121 01220 20310 01101 02012 42023 532100
Callicosta bipinnata	20001 11322	21212 00020 01002 10001 03000 10-02 0-113 02221	00001 02101 010-1 10110 0100- 32122 22010 000111
Cryphaea patens	20001 11322	21212 00020 00012 20002 00000 01200 0-012 12321	00020 02?02 010-0 10310 0000- 44012 11000 001000
Cyrtopus setosus	20000 02122	22-0- 20111 00033 30030 -3010 00-00 --112 12221	10021 22101 0?100 10010 0020- 02022 22020 112000
Dicranum scoparium	01021 02{02}- -	-1-0- 0-310 00042 30330 -0711 02300 0-302 21311	00021 21111 11100 0006- ----- --0-- 1-000 002000
Entodon hampeanus	20101 00002	02110 0-110 00022 10001 00001 01100 0-111 02321	00021 02101 01110 10010 01202 -5052 12021 002000
Fontinalis squamosa	20111 01322	02010 0-010 00033 10200 -3000 00-00 0-110 -2311	00031 02?02 010-0 10010 0020- 12122 02320 000000
Funaria hygrometrica	00020 020-	-0??? 0-313 02002 21000 -0000 00-00 0-002 20300	00000 ?0110 12320 00011 00200 01241 22001 0-2000
Hedwigia ciliata	01021 00{02}- -	-0112 21020 00022 10100 -0300 11000 12100 -1221	10001 01?02 00100 0000- ----- ----- ----- --1100
Hookeria acutifolia	20121 001-2	-2210 0-102 02002 10001 03601 00-00 0-110 -2???	0?0?? ???1? 01100 110?? 0120? ????2 22020 110101
Hypnum fertile	20101 00101	01210 30120 00013 10002 00002 02300 --111 02321	10021 02111 01100 10020 01101 02022 22021 312000
Hypnodendron dendroides	20000 52222	02311 00211 10021 20021 20011 01100 --002 22321	10021 02111 12110 00320 00101 22052 32024 512???
Hypopterygium tamariscinum	20001 04322	0131- 0-300 01002 14000 -3010 00-00 0-112 12321	00021 02111 01101 11021 01100 03042 32021 422000
Leptobryum pyriforme	0?02? ?2?-	-?-0- 0-??? 0???? ????? ?1?00 00-?0 0-??2 21???	??0?? ????2? 021?? ?031? ?1101 ????2 42023 5?2000
Lepyrodon tomentosus	20021 122-0	-131- 20221 01002 10030 -3011 01000 0-112 12211	00011 12000 01010 1030- ----- ----2 12014 002000
Leucodon julaceus	20101 10002	12010 20020 00012 20001 00000 11200 0-110 -2321	00020 02?01 01102 20010 1100- 14012 200-- 002000
Macromitrium longifolium	11101 10200	02-0- 0-023 00032 20002 24011 00-01 10102 21200	00121 20101 01101 00010 00103 ?0002 21000 010011
Meteorium teres	20101 00002	01110 0-120 03122 30001 00102 11100 11112 02321	00021 02102 01100 10031 0100- 34122 21101 00210
Neckera urnigera	20001 10302	01010 20020 12012 20002 00000 11100 0-111 02221	00021 02101 02100 10010 01000 05042 22001 012000
Orthotrichum pycnophyllum	01021 02{02}- -	-0-0- 2-010 00022 10330 -0000 02100 10102 00---	--12? 20?01 12110 00040 00103 ?0002 01000 0-0111
Papillari deppei	20101 00002	01110 0-120 03232 20001 00101 11100 11112 02221	00021 02101 01100 10031 0100- 34142 22101 002100
Philonotis rigida	01001 0212-	1121? 0-310 00013 13000 -2211 00-02 3-002 01200	0002? 12112 10121 00011 1120- 01042 22124 002000
Plagiomnium cuspidatum	11100 100-0	11-0- 0-310 00022 32200 -2210 00-00 0-012 21100	00011 12121 01220 00310 01201 02012 32223 432000
Pleurozium schreberi	20101 00201	01210 0-120 00022 20002 00002 12100 0-111 02321	00011 12111 02100 10021 01101 02042 22022 412000
Porotrichum longirostre	20001 11322	2131- 0-120 00012 10002 00000 10-00 0-012 02221	00021 02?11 01100 10011 01000 05012 22011 212000
Prionodon densum	20001 11322	20010 3-020 03012 10002 10200 01100 10112 22221	00021 02?02 01??1 10210 0100- 64012 12011 112000
Pterobryon densum	20001 11322	21010 20020 00012 10002 11000 11000 0-112 02321	00021 02?02 010-2 20210 0110- 75-12 10--- 000000
Pyrrhobryum spiniforme	20020 021-1	-0-0- 0-321 00032 10200 -1410 00-00 0-002 22221	00021 22111 02100 00320 01100 02052 32021 422?00
Racopilum tomentosum	20101 00000	0131- 0-210 00021 20002 20011 00-10 10012 22321	00001 02110 12100 00320 01101 02052 22023 522100
Rhytidium rugosum	20001 00202	01210 20220 00012 20002 00102 01102 0-112 12221	10021 02?11 01210 10?20 01101 020?2 32020 312000
Schoenobryum concavifolium	01021 010--	-231- 20020 00022 20002 00000 02210 0-012 11321	01000 02-02 010-0 10310 0010- 55012 ----- --1000
Schlotheimia rugifolia	11101 10000	10-0- 0-020 00023 10002 24000 01100 0-102 10---	--121 20?01 1?100 00021 00203 ?0012 21000 003001
Spiridens vieillardii	20002 02123	20-0- 0-311 0---0 -2200 -0510 00-00 0-002 22{23}21	10021 12101 01101 10010 11101 020?2 22020 120?00
Tayloria splachnoides	01020 020-	-1310 0-310 02014 31220 -1501 00-00 0-012 20---	--010 11100 01123 02050 10340 0?06? 00— 0-4000
Thuidium delicatulum	20001 03020	02311 0-120 10011 10001 00000 00-00 10112 12321	10021 02111 02100 20320 01101 22052 32021 322000

APPENDIX 2. Specimens included as vouchers to verify morphological characters of the exemplar species included in the present study, with supplementary taxa.

Bartramia halleriana Hedw. INDIA. Darjeeling. Fleischer *B3243* (XAL)
Brachythecium rutabulum (Hedw.) BSG. CANADA. BRITISH COLUMBIA. *MacFadden* (XAL)
Brachythecium plumosum (Hedw.) BSG. MEXICO. DISTRITO FEDERAL. *Rzedowski 19468* (XAL)
Braunia secunda (Hook.) BSG. MEXICO. VERACRUZ. *De Luna 1655, 1803; De Luna & Keller 2245* (XAL)
Brymela parkeriana (Hook. & Grev.) Buck. GUYANA. Potaro, *Newton 3483* (US, XAL)
Bryum billardieri Schwaegr. MEXICO. VERACRUZ. *De Luna 1235* (XAL)
Cryphaea patens C. Müll. COLOMBIA. Santander, *De Luna 1824* (XAL). MEXICO. VERACRUZ. *De Luna 1631, 2243; Delgadillo 4208* (XAL)
Cyrtopus setosus (Hedw.) Hook. f. *Berggren 1756* (US)
Dicranum scoparium Hedw. MEXICO. *Nuevo León. Valdéz 808* (XAL); SCOTLAND. Grampian. *Newton & Newton 4319* (XAL)
Entodon beyrichii (Schwaegr.) C. Müll. MEXICO. Edo. México, *Cárdenas 4145* (XAL). COAHUILA. *De Luna & Mishler 2171* (XAL). NUEVO LÉON. *De Luna & Mishler 2217* (XAL)
Entodon hampeanus C. Müll. MEXICO. VERACRUZ. *De Luna & Newton 550* (XAL)
Fontinalis bogotensis Hamp. *Gradstein 3807* (XAL)
Fontinalis squamosa Hedw. ENGLAND. DEVON. *Newton 1982* (XAL)
Funaria hygrometrica Hedw. MEXICO. VERACRUZ. *Juárez 38* (XAL)
Hedwigia ciliata (Hedw.) P. Beauv. MEXICO. VERACRUZ. *De Luna & Newton 2271* (XAL)
Hookeria acutifolia Hook. MEXICO. VERACRUZ. *Juárez 1318a* (XAL)
Hypnodendron dendroides (Brid.) Touw. PAPUA NEW GUINEA. WEST SEPIK. *Newton 1700* (XAL)
Hypnum fertile Sendtn. *Schofield 10375* (XAL)
Hypopterygium tamariscinum (Hedw.) Brid. MEXICO. VERACRUZ. *Newton 3877* (XAL)
Leptobryum pyriforme (Hedw.) Wils. *Ochyra 43* (BM)
Lepyrodon tomentosus (Hook.) Mitt. COLOMBIA. Boyac. *Florschütz 4185; Cleef 7100* (XAL). MEXICO. VERACRUZ. *De Luna & Keller 2246* (XAL)
Leucodon curvirostris Hamp. MEXICO. VERACRUZ. *De Luna 1722* (XAL)
Leucodon julaceus (Hedw.) Sull. MEXICO. NUEVO LEÓN. *De Luna & Mishler 2160, 2164* (XAL)
Macromitrium longifolium (Hook.) Brid. MEXICO. HIDALGO. *Cárdenas 105* (XAL)
Meteorium teres Mitt. MEXICO. VERACRUZ. *De Luna & Newton 2277, 2280* (XAL); *Newton & De Luna 3861* (XAL)
Neckera angustifolia C. Müll. MEXICO. VERACRUZ. *Newton & De Luna 3859* (XAL)
Neckera urnigera C. Müll. MEXICO. VERACRUZ. *De Luna 2235* (XAL)
Orthotrichum pycnophyllum Schimp. MEXICO. VERACRUZ. *De Luna 436* (XAL)
Papillaria deppei (Hornsch.) Jaeg. MEXICO. VERACRUZ. *De Luna & Newton 2267* (XAL); *Newton & De Luna 3858* (XAL)
Philonotis glaucescens C. Müll. MEXICO. VERACRUZ. *Juárez 1312b* (XAL)
Pilotrichum bipinnatum (Schwaegr.) Brid. GUYANA. Upper Mazaruni. *Newton 4246* (US, XAL)
Plagiomnium cuspidatum Hedw. U.S.A. TENNESSEE. *Juárez 663* (XAL)
Plagiomnium rhynchophorum (Hook.) T. Kop. MEXICO. VERACRUZ. *Newton 4310* (XAL)
Pleurozium schreberi (Brid.) Mitt. MEXICO. VERACRUZ. *De Luna 791* (XAL). U.S.A. SOUTH DAKOTA. *Anderson 24114* (XAL). SCOTLAND. Grampian. *Newton & Newton 4316* (XAL)
Porotrichum longirostre (Hook.) Mitt. MEXICO. VERACRUZ. *De Luna & Newton 2266* (XAL); *Newton & De Luna 3857, 3876* (XAL)
Prionodon densus (Hedw.) C. Müll. PERU. AYACUCHO. *Hegewald & Hegewald 9016* (XAL) MEXICO. HIDALGO. *Cardenas 4073* (XAL) VERACRUZ. *Newton & De Luna 3872* (XAL)
Pterobryon densum (Schwaegr.) Hornsch. BRAZIL. SAÕ PAULO. *Frahm 1514* (XAL). MEXICO. VERACRUZ. *Newton & De Luna 3856* (XAL). *Juárez 1047* (DUKE)
Pyrrhobryum spiniforme (Hedw.) Mitt. MEXICO. VERACRUZ. *Newton 4397; Ramirez* 19 Dic. 1978 (XAL)
Racopilum tomentosum (Hedw.) Brid. MEXICO. VERACRUZ. *De Luna 1242, 1558b, De Luna & Newton 2259, 2279, Newton 4284* (XAL)
Rhytidium rugosum (Hedw.) Kindb. MEXICO. NUEVO LEÓN. *De Luna & Mishler 2193* (XAL). VERACRUZ. *De Luna & Newton 2256, Newton & De Luna 4261* (XAL). NORWAY. OPPLAND. Kaurin & Ryan, 1897 (US)
Schlotheimia rugifolia (Hook.) Schwaegr. (as *S. jamesonii* (Arnott) Brid.) BRAZIL. SANTA CATARINA. *Frahm 1695* (XAL)
Schoenobryum concavifolium (Griff.) Gangulee. MEXICO. VERACRUZ. *De Luna 1173* (XAL)
Spiridens balfourianus Grev. ILES DE LA SOCIETE. MOORÉA. *De Sloover 21143* (XAL)
Spiridens reinwardtii Nees. PAPUA NEW GUINEA. WEST SEPIK. *Newton 1915* (BM, DUKE)
Spiridens vieillardii Schimp. NEW CALEDONIA. Mt. Rembai. *Turner 36* (XAL)
Tayloria splachnoides (Schwaegr.) Hook. MEXICO. PUEBLA. *De Luna 209* (XAL)
Thuidium delicatulum (Hedw.) Mitt. MEXICO. Edo. de México. *Cruz 1659.* VERACRUZ. *De Luna 1079* (XAL)
Thuidium tomentosum Besch. MEXICO. VERACRUZ. *Newton 4387* (XAL)