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The Use of Ontogenetic Data in Phylogenetic Analyses of Mosses

by

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With 7 Figures

Abstract: This review examines the nature of development in mosses, as well as theoretical frameworks for the use of information about development in studies of systematics, phylogeny, and evolution. Ontogeny in moss gametophytes is recognized to be both hierarchical and modular. Of particular interest in phylogenetic comparisons is the prolonged heteroblastic series of *metamers* (i.e., fully differentiated merophytes, each including a leaf) produced as a *module* (i.e., the product of a single stem apical cell) matures. Potential uses of ontogenetic data in systematics and phylogenetic reconstruction include the discovery and definition of taxonomic characters, the evaluation of homology between characters, and determination of evolutionary order and polarity of character states. These uses are illustrated with several examples taken primarily from our work, including studies of protonemal development, heteroblastic leaf series, and branching patterns.

Zusammenfassung: Diese Übersicht behandelt die Entwicklungsgeschichte bei Laubmoosen, wie auch den theoretischen Rahmen für den Gebrauch solcher Ergebnisse in Systematik, Phylogenie und Evolution. Die Ontogenie des Moosgametophyten ist sowohl hierarchisch wie modular. Die verlängerte heteroblastische Reihe von *Metameren* (d.h. voll differenzierte Merophyten, die je ein Blatt darstellen), die als *Modul* (d.h. das Produkt einer einzigen Scheitelzelle) reifen, ist von besonderem Interesse für phylogenetische Vergleiche. Möglichkeiten im Gebrauch von ontogenetischen Resultaten in der Systematik und für die phylogenetische Rekonstruktion schließen die Entdeckung und Definition taxonomischer Merkmale, Bewertung von Homologie von Merkmalen und die Bestimmung evolutionärer Ordnung und Polarität von Merkmalszuständen ein. Diese Anwendungen werden mit Beispielen hauptsächlich aus unseren eigenen Arbeiten auch über Protonemalentwicklung, heteroblastische Blattreihen und Verzweigungsmodelle, vorgestellt.

Keywords: bryophytes, character analysis, cladistics, growth forms, Hedwigiaceae, heteroblasty, heterochrony, homology, mosses, ontogeny, phylogeny, plant architecture, protonema, *Tortula*.

Contents

Introduction

Developmental data have frequently played a special role in the systematics of bryophytes, particularly at high taxonomic levels. However, there remains a need for careful examination of the nature of ontogenetic data and its valid uses in bryophyte systematics. Our goals in this paper are therefore not to review physiological or morphological aspects of bryophyte development per se (for which see Renzaglia 1978, 1982; Bopp 1981, 1983; Frey 1981; Crandall-Stotler 1981; Knoop 1984; Chopra & Kumra 1988), but rather to review theoretical frameworks for the *use* of developmental data in bryophyte systematics. We illustrate these frameworks with selected examples, taken primarily from our work. Our empirical focus is therefore on mosses, but the concepts presented should prove useful throughout bryophytes.

The mosses are a "gold-mine" for the empirical evaluation of theoretical issues such as taxonomic character recognition, ordering, and polarity; homology; and heterochrony. Biologically, mosses have a relatively simple morphological construction, yet a prolonged ontogeny in most parts of the life cycle. Practically, mosses have the advantage of small size, ease of growth under controlled conditions, ease of study, and a long history of developmental research. We think that the thoughtful application of ontogenetic data will continue to greatly assist moss systematics, and conversely, that the study of mosses will contribute to a general understanding of the relationships among ontogeny, phylogeny, and systematics.

Potential uses of ontogenetic data in moss systematics include the following: (1) a source of new taxonomic characters in juvenile phases; (2) a source of information for clarifying homologies and defining character states in mature phases; (3) a source for determining transformational homology among character states within a character (ordering); (4) a source for hypothesizing evolutionary directionality among character states within a character (polarization). Furthermore, given a phylogenetic hypothesis, ontogenetic data can be used in evolutionary studies focused on changes in timing of developmental events (heterochrony).

In this review we first examine the complexity of ontogeny in mosses, then discuss and demonstrate each of these uses of ontogeny in moss systematics and evolution, taking a cladistic approach throughout. Such an approach is becoming standard in systematic biology, but is still unusual and widely misunderstood within bryology, despite a long (if sparse) history of bryophyte cladistic studies (e.g., Koponen 1968, 1973, 1980; Bremer 1981; Churchill 1981; Mishler & Churchill 1984, 1985; Mishler 1985a; Hyvönen 1989). The cladistic approach is tightly interwoven with the uses of ontogenetic data examined in this paper. Therefore, we define terms and explicitly describe this approach to systematics in a separate section. However, we want to emphasize

that at least the first two (and probably all four) of the above listed systematic uses of ontogeny are relevant under *any* approach to systematics.

Ontogeny in Mosses

Bryophytes have been favored organisms for anatomical and developmental studies since the earliest days of light microscopy (see comprehensive reviews by Frey 1981 on mosses; by Crandall-Stotler 1981, and Schuster 1984, on liverworts; and by Renzaglia 1978 on hornworts). A solid body of comparative data at the light microscopic level exists for apical cell segmentation patterns and differentiation of major organs: protonemata (Nishida 1978, Nehira 1983), thalli (Crandall-Stotler 1981, 1984; Renzaglia 1982), shoots (Bonnot 1968, Frey 1970, Berthier 1972, Hébant & Berthier 1972, Hébant 1977), leaves (Pottier 1925, Frey 1974, Bopp 1984), gametangia (Janzen 1921), and sporophytes (Shaw et al. 1987).

Recently, use of electron microscopy has allowed comparative studies of differentiation at the cellular level. Such studies have not yet been as comprehensive as the above mentioned surveys of histogenesis using light microscopy, but at least in certain areas, rapid progress has occurred, e.g., in spermatogenesis (Carothers & Duckett 1980, Duckett et al. 1983, Carothers & Rushing 1988), the gametophyte/sporophyte junction (Chauhan & Lal 1987; Ligrone & Gambardella 1988a, b), and sporogenesis (Neidhart 1979, Brown & Lemmon 1988). The net result of these studies is an increasing realization that the three major groups of bryophytes (liverworts, hornworts, and mosses) are quite different from each other developmentally, and presumably phylogenetically (Crandall-Stotler 1980, 1984; Duckett & Renzaglia 1988), yet comparable to the other land plants in significant ways.

A convenient point of departure for a summarization of the generalized moss life-cycle is spore germination. Haploid spores germinate (usually exosporically, but sometimes endosporically) to form the first phase of the gametophyte generation, the protonema. The protonemal system is extensive and multi-branched, producing a large number of leafy shoots (the second phase of the gametophyte generation) per system. A typical moss shoot grows from an obovoidal or fusiform apical cell with three cutting faces (Frey 1970, 1981). Each merophyte or segment derived from the apical cell differentiates into a leaf initial, a secondary branch initial, and epidermal stem layers to the outside and internal stem tissue (often with differentiation into a central strand of conducting cells) to the inside. Gametangia (antheridia and archegonia) usually terminate the growth of the stem on which they are produced (whether a main stem or a lateral one). Fertilization of the egg by the swimming sperm occurs within the archegonium.

The sporophyte generation develops in place and remains attached to the gametophyte throughout its existence; the fertilized archegonium and associated gametophytic tissues develop in concert with the sporophyte to form the placenta and calyptra. The diploid sporophyte grows initially from an apical cell with two cutting faces. At maturity it consists of a foot, a seta (usually with a central strand of conducting tissue), and a capsule. Meiosis occurs in the capsule to produce spores, which are usually released through an apical opening (mouth) of the capsule, which is exposed after the operculum falls away. The mouth is surrounded by a complex ring of teeth (the peristome), although some species lack a peristome and/or an operculum.

As discussed by Mishler (1988a), development in mosses (at least in the gametophyte) is distinctly hierarchical. Growth consists of a sequence of repeated parts, i.e., modules as defined by Hallé et al. (1978; see White 1984, for a full discussion of modularity and metamerism in tracheophytes), and these modules occur at a number of levels of inclusiveness. Because of the diversity of levels at which development occurs, comparative study of development can be confusing. Therefore, a careful description of observed patterns is necessary, along with the adoption of a standardized set of hierarchical levels and comparative terms to describe development at each level.

At least five distinct hierarchical levels of ontogeny have been noted in the moss gametophyte generation (Fig. 1), although some levels may not occur in a given species. In comparative studies of development it is important to keep track of this hierarchy for two reasons. First, patterns of differentiation at one level depend not only on events at lower levels but also on the developmental stage of *higher* levels because of positional controls on development (Bopp 1984). Second, patterns of differentiation at each of these levels may be important phylogenetically, in that evolutionary change could presumably affect patterns at any level during evolution of particular clades.

In the ontogeny of moss gametophytes (Fig. 1) each *cell* differentiates, but the pattern of differentiation followed by a particular cell depends on its position in the next higher level, the *metamer*. Following the concept of White (1984), we use metamer to refer to the repeated units that make up a branch. White used to term to refer to the node-leaf-axillary meristem-internode complex in angiosperms. The concept can be cleanly applied to mosses because the metamer corresponds morphologically to a single *merophyte* (i.e., a unicellular derivative of an apical cell and all subsequent cells derived from it, also called a segment). The metamer usually includes a single leaf with axillary hairs, lateral bud, epidermis, cortex, and conducting cells.

The pattern of differentiation of a metamer depends on its position in the next higher level, the *module* (i.e., the product of a single apical meristem, White 1984) in which the merophyte is initiated. In mosses a module includes all metamers produced by a single stem apical cell, i.e., a gametophytic branch. A distinct and prolonged *heteroblastic* series (Goebel 1900; see discussion of heteroblastic development in tracheophytes by Allsopp 1965) is pro-

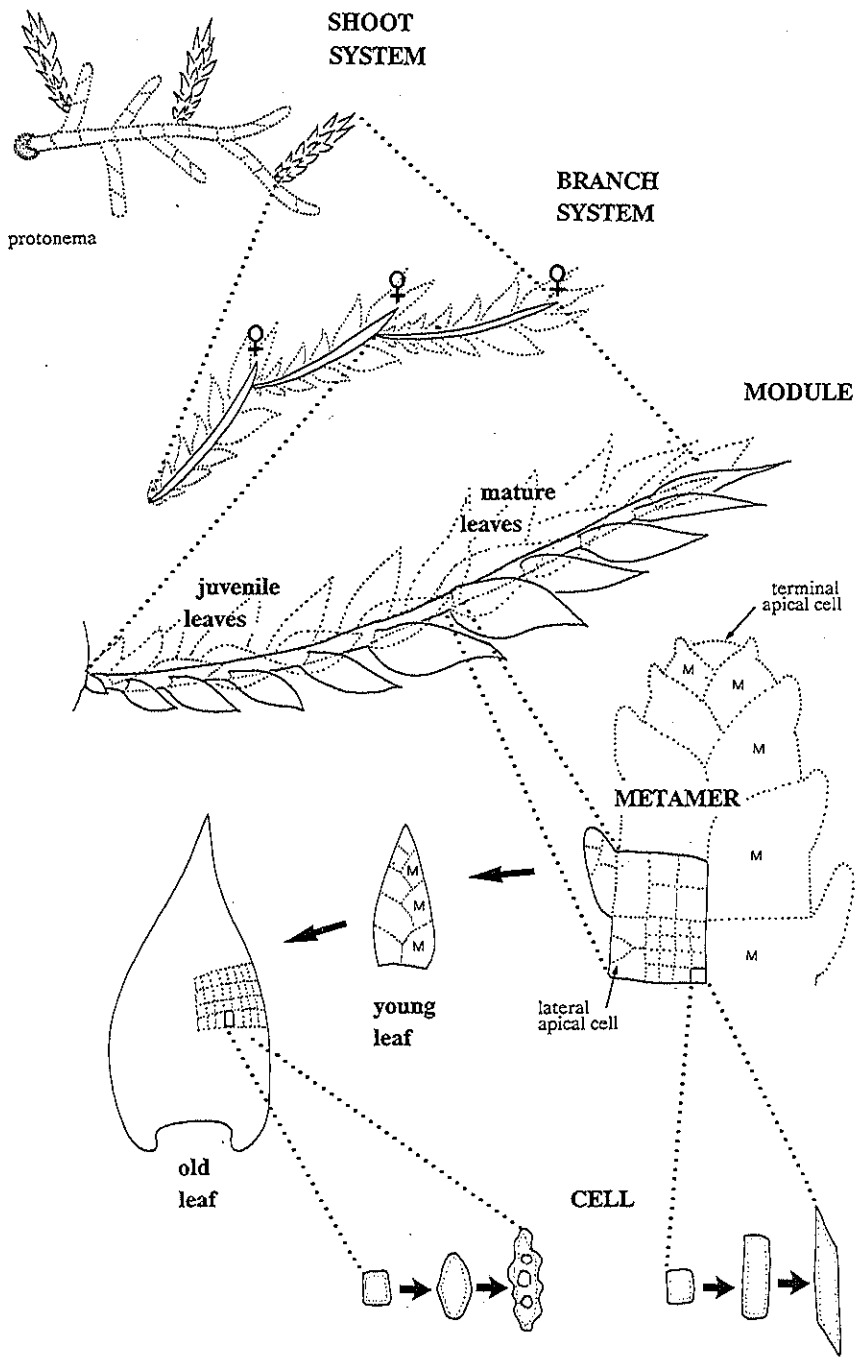
duced as a branch matures. The pattern of merophyte development and that of associated leaves changes depending on the ontogenetic stage of the branch module. "*Juvenile*" will be used to refer to leaves produced by early metamers on the branch module; "*mature*" will be used to refer to the final leaf-form of the heteroblastic series (Mishler 1988a).

The fourth hierarchical level in moss gametophyte ontogeny is that of the *branch system,* which consists of a sequence of connected modules together making up a single leafy shoot. In *Tortula* and most acrocarpous mosses examined the same heteroblastic leaf series is repeated in each new branch (which in acrocarpous mosses arise either as an *innovation* just beneath the archegonia or as an *adventitious branch* from dormant buds in older tissue). All branch modules are thus morphologically equivalent. However, a variety of specializations occurs in pleurocarpous mosses and in the acrocarpous moss *Polytrichum* (according to Wigglesworth 1947). Unlike the situation in most acrocarpous mosses, secondary and later branches may have a different pattern of heteroblastic development than that of the primary branch to which they are sequentially connected. Thus all branch modules may not be equivalent; in such cases, the pattern of differentiation of a branch depends on the ontogenetic stage of the branch system.

A fifth possible hierarchical level in moss gametophyte development has been noted by Meusel (1935; see discussion by Watson 1971, p. 123). Meusel reported cases of a regular progression of morphologically (and reproductively) different types of leafy shoots produced by a single developing protonemal system. In such a case the development of each successive shoot depends on its position in the protonemal system as a whole. We term this highest level of gametophyte development the *shoot system.*

Development in moss sporophytes is not so obviously modular and hierarchical, because of determinate growth and lack of appendages. However, a form of heteroblastic maturation is apparent in the apical part of the sporophyte. The sporophyte (which could be regarded as a single module, in the sense of the terminology introduced above for gametophytes) grows initially by means of a two-sided apical cell that produces only 10-20 merophytes. An intercalary meristem is then formed, from which the seta and foot tissues develop (Crandall-Stotler 1984). The developmental pattern followed by apically

Figure 1. The hierarchy of ontogeny in moss gametophytes. Differentiation occurs on five levels; the pattern of differentiation in each repeated unit depends in part on the ontogenetic stage of higher levels. *Cells* differentiate within each *metamer* (M, merophyte); a heteroblastic series of metamers (each with an associated leaf) is produced as a branch *module* matures; a series of different types of branches may be produced as the *branch system* (shoot) develops; a series of different types of shoots my be produced as the *shoot system* develops on a protonema derived from a single spore.



derived sequential merophytes differs as the capsule, peristome-forming region, and operculum differentiate. The generality of this pattern and its possible phylogenetic significance has been little explored.

Ontogeny and Systematics

A revived interest in relating ontogeny to studies of phylogeny and systematics occurred during the 1970s and 1980s as part of a general rethinking of theories and methods for reconstructing phylogeny (Kaplan 1971; Lundberg 1973; Nelson 1978, 1985; Fink 1982; Patterson 1983; Kluge 1985; Kluge & Strauss 1985; Humphries 1988). Ontogeny has been explicitly linked to three particular areas within systematics: homology, ordering, and polarity. It appears that complex character systems with an elaborate ontogeny retain more traces of history than other, simpler systems such as molecular sequence data (particularly at higher taxonomic levels — Mishler et al. 1988, Bremer 1988, Donoghue & Sanderson in press), and that such complex character systems will continue to be characters of choice in systematics.

Bryologists have generally reacted favorably to new methods for the collection of systematic data. The reviews by Anderson (1963, 1964), Koponen (1978), Smith (1978), Clarke and Duckett (1979), Geissler and Greene (1982), Frey (1984), Wyatt and Stoneburner (1984), and Miller (1985) summarize the advances of biosystematic studies in bryology. However, the majority of bryologists have not been concerned with discussions about methods for the analysis of systematic data (see also Clarke & Duckett 1979, Preface). The reviews mentioned above and others by Szweykowski (1978), Horton (1984), and Mishler (1986a) give the impression that only recently and only in a few instances have diverse methods of systematic analysis been explicitly discussed and applied by bryologists.

It is important to realize that regardless of how bryophyte systematists make taxonomic decisions, explicitly or not, they are also implicitly making and endorsing theoretical statements about the nature of taxonomic groupings, phylogenetic relationships, and evolution. Thus, bryophyte systematists need to be equally concerned with, and explicit in, their selection of data types *and* their choice of approaches to analyze data.

This section establishes the theoretical basis for our particular approach to systematics, including its interrelationships with ontogeny. We first discuss debates on alternative methods of analysis in order to highlight the "theoretical shift" that we think is necessary in bryophyte systematics (cf. Mishler 1986a). Later, in the Case Studies section, we incorporate these basic concepts with examples from our work to illustrate the multiple levels of character and group analysis that are commonly labeled as "phylogenetic" or "cladistic" analysis.

Controversies in Systematics

Most systematists agree that their principal aim is to produce a classification system that orders and describes biological diversity (see Stevens 1984a, 1986 for a lucid discussion of the history of botanical systematics). However, there is disagreement among systematists as to how to proceed in two fundamental areas of systematic research. The first area is operational, involving the recognition of taxonomic groups (*grouping*) along with the construction of hierarchical classifications (*ranking*). The second area is theoretical and includes the generation and testing of phylogenetic hypotheses, which can potentially be used as a basis for both classification and studies of evolutionary processes (Eldredge & Cracraft 1980).

Contemporary schools of systematics are divided according to their immediate goals in constructing classifications. Information on principles and basic methods of "traditional," "phenetic," and "cladistic" approaches can be found in the texts of Mayr (1969), Sneath and Sokal (1973), and Wiley (1981), respectively (more recent and brief accounts are Sokal 1986 for phenetics; Humphries & Funk 1984, Funk & Brooks 1990 for cladistics).

Traditional (sometimes known as "evolutionary") and cladistic (sometimes known as "phylogenetic") systematists agree that the immediate goal in constructing a classification is to interpret patterns of diversity in terms of theories of evolutionary biology. Consequently, the groups constructed based on similarities must have a biological meaning, particularly in terms of known evolutionary processes. In other words taxonomic groups should also be evolutionary groups (Simpson 1961, Mayr 1969). Thus, evolutionary and phylogenetic systematists agree that it is possible to infer the evolutionary history of organisms. However, they disagree on the way to recognize "evolutionary groups," and how inferences of phylogenetic relationships are developed (Felsenstein 1979, Hull 1981, Mayr 1981, Farris 1983, Heywood & Moore 1984, Brooks & Wiley 1985, Stuessy 1987). Evolutionary systematists use overall similarity in homologous characters; phylogenetic systematists use only "special" similarity, i.e., shared-derived, homologous characters (Hennig 1966, Wiley 1981).

Another group of systematists (pheneticists) claims that it is not possible to reconstruct the evolutionary history of organisms, and thus, that phylogenetic relationships should not be the basis for classification. The construction of classifications should be free of any type of evolutionary inference and theory, thereby producing a theoretically neutral system of classification. Pheneticists argue that theory-free classifications are more useful in terms of information content, predictability, and stability (Sneath & Sokal 1973, Dunn & Everit 1982).

A recent trend among evolutionary systematists is to integrate available methods at different levels of systematic analysis. Mayr (1982) suggested an

"eclectic taxonomy" based on traditional methods, but combined with certain numerical (phenetic) methods and cladistic analysis of characters. Stuessy (1987) argued for an "explicit" approach and suggested that results of both phenetic and cladistic analyses should be incorporated into an explicit basis for "evolutionary" classification.

In view of these controversies in systematics several authors have evaluated advantages and disadvantages of phenetic, evolutionary, and cladistic methods. Among the factors considered are: the type of character data used (Stuessy & Crawford 1983, Bremer et al. 1987); taxonomic level analyzed (Jones & Young 1983, Rodman et al. 1984); the stability and congruence of results (Duncan et al. 1980, Farris 1982, Whalen & Caruso 1983, Eckenwalder & Barrett 1986); and the practicality of the resulting classification (Mayr 1974, Wiley 1979).

In the remaining part of this section we will argue that the phylogenetic approach to systematics alone allows a rigorous, explicit, and, at the same time, theoretically sound evaluation of systematic relationships. Justification for this phylogenetic approach to bryophyte systematics has been presented previously by Mishler and Churchill (1984) and Mishler (1986a). The primary reason for adopting the cladistic or phylogenetic approach is its treatment of *homology*. Indeed, cladistics could be defined as the study of homology: every statement about a homologous character is necessarily a statement about a phylogenetic group at some level. Thus a cladogram in this sense is simply the summation of the patterns shown by all postulated homologies. Empirical considerations about characters such as division into states, coding, ordering, and polarity, are fundamental to implementing this theoretical approach and are discussed below, with special emphasis on ontogenetic data.

Homology

The general concept of homology, a correspondence between two or more characteristics of organisms that is caused by a historical continuity of information (Van Valen 1982; Roth 1984, 1988) has been greatly clarified in recent years, and it has become recognized that several types of homology exist. *Iterative homology* is a historical correspondence between different structures within a single organism, and includes, for example, serial homology (repeated morphological parts) and paralogous molecules (duplicated genes within the same genome) (Roth 1988). Following a further distinction made by Eldredge (1979) and Patterson (1982), *taxic homology* should be separated from *transformational homology*. Taxic homology is historical correspondence in a feature among different organisms, due to inheritence from a common ancestor that had that characteristic (in the most rigorous formulations equivalent to the cladistic concept of synapomorphy — e.g., Patterson 1982, Stevens 1984b, Roth 1988). Transformational homology is a correspondence

between two different features due to a historical modification of one into the other (equivalent to the relationship between an apomorphy and its plesiomorphy — see Fig. 2).

Developmental similarity is one time-honored criterion for determining homology (Remane 1952, Stevens 1984b, Kaplan 1984), although it is important to realize that homologs do not *necessarily* develop in similar fashion (Roth 1988). Detailed similarity in mature structure and development constitutes the *similarity test* of taxic homology (Patterson 1982) and is also important in hypothesizing transformational homology (Stevens 1984b; a pair of transformationally homologous characters are known as a *transformation series*; Wiley 1981). Putative taxic homologies (i.e., those that pass the similarity test), must then be evaluated by the *congruence test* (i.e., the most parsimonious phylogenetic hypothesis based on *all* putative taxic homologies; Patterson 1982, Stevens 1984b).

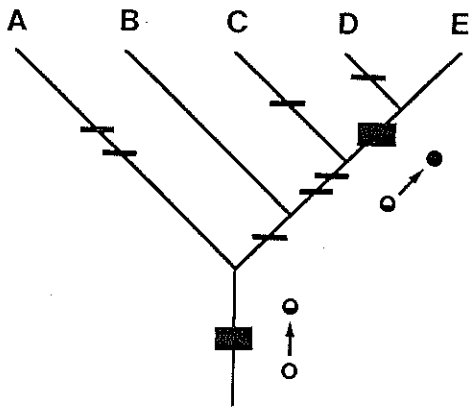


Figure 2. A hypothetical cladogram of a monophyletic group of five species, illustrating concepts of taxic and transformational homology. Synapomorphies (taxic homologies) supporting this hypothesis of relationships are shown by cross-bars. Transformational homology in one character is illustrated: ◒represents a synapomorphy for the whole group, relative to the symplesiomorphic state O; at a less inclusive level, ● represents a synapomorphy for the monophyletic group (D, E), relative to the state ◒, which is now seen to be a symplesiomorphy at that level.

Character Analysis

Characters and character states are the basis of description and comparison in systematic biology. Thus, despite differing opinions on how to analyze character data, all systematists need to classify raw observations about individual organisms into a system of characters and character states. When classifying observations into characters and states, systematists implicitly or explicitly develop hypotheses of taxic and transformational homology. Therefore, these hypotheses must be developed in a formal and explicit way to be accessible for evaluation. Indeed, as discussed by Neff (1986) and Bryant (1989), character analysis is the most important part of cladistic analysis.

"Character" can be defined in several different ways. In order to be consistent in our discussion, we will adopt a standardized terminology for various types of similarity (see Fig. 3). It is important to emphasize throughout that, in order to avoid confusion, any comparisons between organisms must be made between equivalent ontogenetic stages, at all the hierarchical levels of development detailed in a previous section (Fig. 1).

The most general observation (Fig. 3) is of *features*: any characteristic of the organism. Observed features can be divided into those that are describable or quantifiable in some comparative manner, and those that (at least without further study) remain only a "gestalt" perception. Of the *describable features,* some are *potential taxonomic characters* if they are variable within the study group. By "variable," we do not simply mean differences among specimens, but rather discrete patterns of variation, with significantly greater differences among specimens than within a single specimen. Patterns of variation in describable features can be studied using various ordination and statistical techniques (Neff & Marcus 1980, Wiley 1981). Invariant features are of course of no use within a study group, but may be of use at some more inclusive taxonomic level.

Potential taxonomic characters can be regarded as *taxonomic characters* (= potential taxic homologies) if they are heritable and independent of other characters. Reciprocal transplants, growth experiments, and biometric studies of patterns of variation and correlation can help to evaluate potential taxonomic characters (see Davis 1983, 1988; Mishler 1985b). Taxonomic characters that are congruent with a cladogram based on all characters are considered to be taxic homologies; those that are not congruent are considered to be *homoplasies* (the congruence test of homology — see discussion above).

An important realization is that a taxonomic character is necessarily a system of at least two homologs, since as discussed above, they by definition must vary in a discrete manner within the study group. For each taxonomic character recognized there is an implied hypothesis of transformational homology linking at least two features (known as *character states*) that are considered the same or transformed from a common ancestral state.

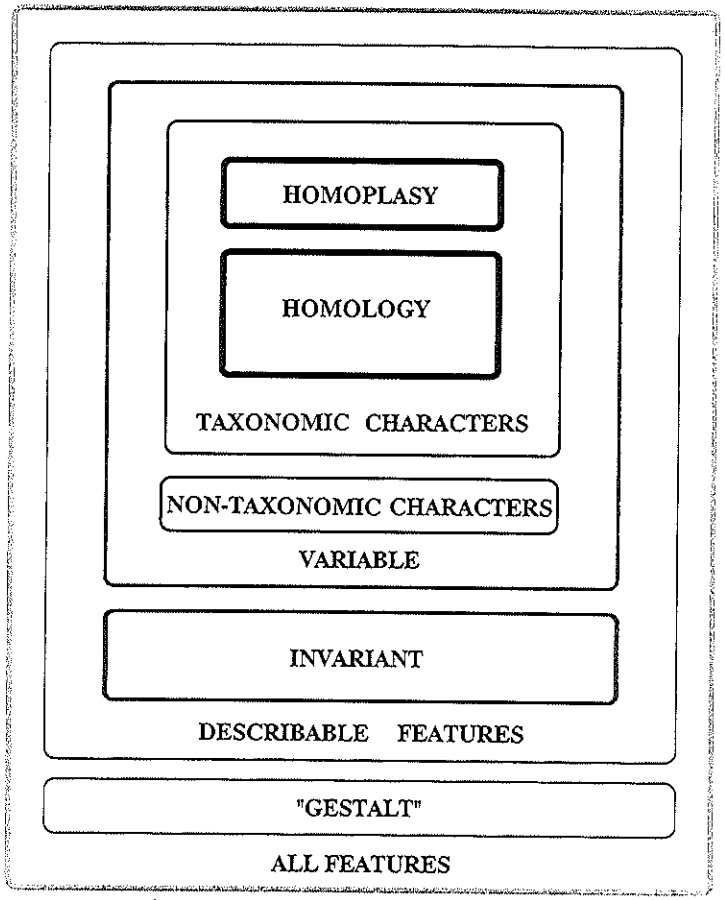


Figure 3. Character analysis. This is the standardized terminology used in this paper for various types of similarity among organisms. In order to be considered a homology a similarity must meet several criteria: it must be describable, variable within the study group, heritable and independent of other characters, and congruent with a cladogram based on all available characters (see text for explanation).

When taxonomic characters are selected, a basic step is to group the variation found in that character into a hierarchy of similar scores (i.e., to define character states). This step involves an initial "phenetic" evaluation of similarity (morphological, ontogenetic) between "corresponding" features of many organisms. The raw observations must be summarized and grouped into character states. Some systematists feel that the choice of character states is

the most arbitrary and subjective step in systematics, particularly in the case of continuously varying characters (e.g., Crovello 1974).

In an attempt to make character state descriptions and comparisons explicit and repeatable, several quantitative methods have been proposed. Some quantitative methods for analysis of character variation are variously included in discussions on phenetics (Sokal 1986), taximetrics (Abbott et al. 1985, Chapter 4), and morphometrics (Bookstein 1982). Specific methods for partitioning character states have been discussed by Archie (1985), Chappill (1989), and others cited therein. On the other hand, some systematists argue that only very discrete, qualitative character states are suitable for phylogenetic analysis (Pimentel & Riggins 1987, Chappill 1989).

We favor a simple and straight-forward alternative method for quantitatively partitioning characters that is based on the concept of homology discussed above. (A complete description and justification of this method will be offered elsewhere, Mishler & De Luna, in preparation.) Following from the tenet that a hypothesis of taxic homology is also a hypothesis of a monophyletic group, a taxonomic character (or character state, given that these are also hypotheses of taxic homology at a less inclusive level) can be defined as *a piece of evidence for the existence of a monophyletic group.* All describable features are in principle quantifiable. Thus the usual distinction between "qualitative" and "quantitative" characters (e.g., Pimentel & Riggins 1987, Chappill 1989) is only a matter of degree, a spectrum between characters showing a highly discrete pattern of variation among taxa and those showing much overlap. We urge the use of standard statistical methods designed to test whether some quantified measure (in this case a taxonomic character) is associated with some a priori designated groups (in this case taxa). This provides a rigorous test of the question of whether a given character (or state) should be regarded as a valid bit of evidence for grouping (monophyly).

In brief the method we advocate uses relatively discrete taxonomic characters (in the sense defined above) to recognize tentative taxa (OTU's, or operational taxonomic units). Then less obvious differences (i.e., taxonomic characters showing greater overlap between specimens) are tested for their association with (and thus support of) these OTU's using analysis of variance (ANOVA) followed by multiple range tests (Sokal & Rohlf 1981). An example is shown in Figure 4, in which basal leaf-cell width is compared among six tentative species of the *Tortula ruralis* complex that were initially distinguished on the basis of various other discrete character states of costa and stem anatomy, leaf-cell ornamentation, etc. The scores from specimens of the six species fall into four statistically distinct groups for this character; these were then treated as four character states. Such a character state, based on a *mean* of measurements made on repeated units within an individual, can be diagnostic of a monophyletic group, even if the *ranges* of measurements on different monophyletic groups overlap.

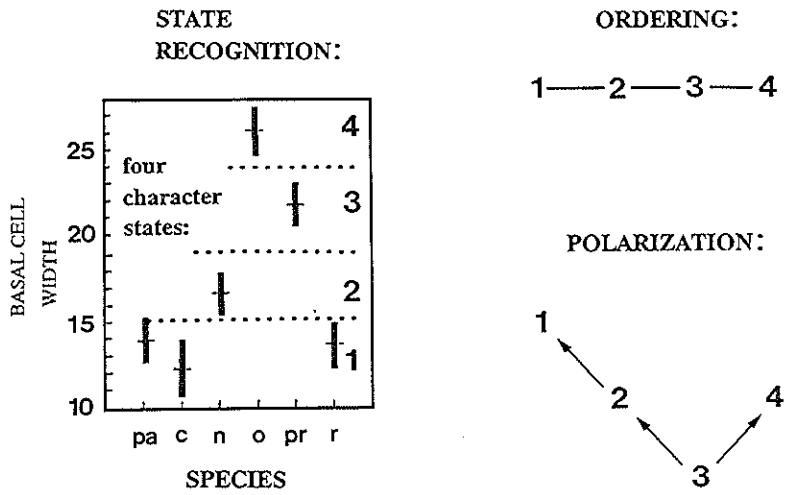


Figure 4. An example of character state recognition, ordering, and polarization, based on data from six species of the *Tortula ruralis* complex. The character is cell width (in ocular micrometer units) measured in the middle of the group of basal cells; given for each species is a mean (plus 95% confidence intervals) of 10 measurements made on each of 10 plants (selected from throughout the range of the species); species in order from left to right are: *T. papillossisima, T. caninervis, T. norvegica, T. obtusissima, T. princeps,* and *T. ruralis.* ANOVA and multiple range tests suggest the existence of four groups (character states) with significantly different means. These character states can be linearly *ordered* based on developmental observations; they can be *polarized* by outgroup comparison with related species of *Tortula,* which happen to have character state 3.

A hypothesis of homology among character states does not necessarily imply any particular evolutionary transformation series among the states. The elaboration of hypotheses of character state transformation (*ordering,* i.e., the specification of character state "adjacency" without any implied directionality) is often inferred from observations of character state transformations in ontogeny, based on assumptions about conservative evolutionary processes in development (see Mabee 1989a, for detailed discussion of the assumptions involved). For example, the four states in Figure 4 can logically be treated as linearly ordered based on their ontogenetic transformations. If no reliable evidence for ordering character states is available (e.g., alternative bases at a homologous site in molecular sequence data), then they can be left *unordered.*

Character state ordering is thus different from *polarity.* Hypotheses about polarity (i.e., evolutionary directionality among states) are a logical extension of hypotheses of transformational homology in the sense that they describe

the assumed evolution of one homolog into another homolog. Thus, to polarize a taxonomic character is to postulate that a prior or ancestral (*plesiomorphic*) state gave rise to one (or more) posterior or derived (*apomorphic*) states along a transformation series. Hypotheses of polarity will thus depend on the hypothesized order of character states. Polarity statements are always relative and applicable only to a particular level within the study group. In a multistate transformation series, an apomorphic state at one level is in turn the plesiomorphic state in relation to the next apomorphic state (see Fig. 2).

Methods for elaborating hypotheses of evolutionary polarity or direction of change in a character transformation series are controversial. Several authors have discussed the relative merits of in-group, out-group, ontogenetic, paleontological, functional, and adaptive criteria (e.g., Lundberg 1973, Stevens 1980, Crisci & Stuessy 1980, Watrous & Wheeler 1981, Maddison et al. 1984, Meacham 1984, Nelson 1985, De Queiroz 1985, Wheeler 1990).

The most theoretically sound method for polarizing character state transformation series is out-group comparison (Stevens 1980). The plesiomorphic state within a study group is judged to be the state that is also present in closely related groups. To continue with the example in Figure 4, out-group comparison with close relatives based on the cladogram presented by Mishler (1985a) leads to the conclusion that state three of the four state transformation series is plesiomorphic for the *Tortula ruralis* complex.

Critical application of this method depends on sound a priori selection of out-groups. When this selection is problematic because higher-level relationships are poorly known, several possibilities remain. In the case of complete lack of out-group knowledge, character states (ordered or unordered) can be compared without polarization, which results in an unrooted parsimony *network*. If a restricted set of possible out-groups is available (but without any hypothesis of relationships among them), the out-group substitution method of Donoghue and Cantino (1984) may be used. Another possibility is to use ontogenetic progression (the ontogeny criterion) to help in assessing tentative polarity, or in narrowing the number of potential out-groups.

Ontogenetic order of precedence has been taken as one important criterion for determining the evolutionary polarity of a transformation series (e.g., Hennig 1966, Stevens 1980); indeed some cladists have taken it as the primary criterion (Nelson 1978, 1985). The relative merits of the latter position were exhaustively debated in the volume edited by Humphries (1988). We feel that while numerous empirical falsifications of the biogenetic law (sensu Nelson 1978) have been demonstrated (Kluge 1985, Alberch 1985, De Queiroz 1985, O'Grady 1985, Mishler 1988a, Mabee 1989b), close parallels often have been demonstrated between ontogeny and phylogeny, and thus the ontogeny criterion is a useful supplement to the more primary out-group criterion in cases where out-group comparison is difficult (see Mishler 1988a).

Hypotheses of homology and character state ordering for a given study group are usually presented in a character × taxon matrix. A coding system is needed to represent information adequately about the states recognized and their transformational relationships. Several coding methods are used, with letters or integers, depending on the number, order, and type of character states, presence of missing data, and requirements of particular computer programs. It should be pointed out that coding of states in a transformation series does not in itself imply a particular evolutionary polarity of states. Hypotheses of the direction of character state change are incorporated in a data matrix by the inclusion of one or more rows ("taxa") representing actual out-groups, or by a row representing a hypothesized ancestor if generalized out-group comparison or the ontogeny criterion is being used. These rows can include codes representing "unknown" states for some characters, if these are to be left unpolarized.

Classification

The elaboration of hypotheses of phylogeny based on character analysis is the most fundamental aspect of cladistic analysis. The *Hennig Principle,* the explicit distinction between ancestral (plesiomorphic) and derived (apomorphic) character states as indicators of phylogenetic relationship, is simple, yet profound in its application to biological classification. Only shared apomorphic character states indicate relative recency of common ancestry of taxa. *Monophyly,* in the restricted Hennigian sense, refers ontologically to groups consisting of all and only descendants of a common ancestor, which are epistemologically recognized by synapomorphies. The elegant correspondence between hypotheses of homology, congruent patterns of synapomorphies, and monophyletic classifications (Fig. 2) is the driving force behind the cladistic revolution in systematics.

Hypotheses about character evolution (homology, ordering, polarity) are the only basis for phylogenetic reconstruction. Each available hypothesis of apomorphy indicates a potential grouping of organisms within a hierarchical pattern of phylogenetic relationships. Some apomorphies (known as *autapomorphies* are found only in the terminal groups (i.e., least inclusive); other apomorphies (*synapomorphies*) co-occur in more inclusive groups. A character state (e.g., ⊖ in Fig. 2) is a synapomorphy at one level of inclusion, but at the same time, it is a symplesiomorphy (ancestral) in relation to a transformationally homologous character state (e.g., ● in Fig. 2, which is a synapomorphy at that level). Thus, nested hypotheses of synapomorphy are clues for different levels of genealogical groupings.

Individual character state trees can be combined into a phylogenetic tree (cladogram) that depicts the best supported hypothesis of relationships (i.e., relative recency of common ancestry) among the groups studied. Once character analysis has been performed to the point of constructing a data matrix,

most of the important aspects of cladistic analysis have been completed. The generation of cladograms from the matrix is in this sense only a graphical summarization of information already present in the matrix. Thus, in this context the cladogram is the least important product of a cladistic analysis! Care must be taken to examine published "cladograms", critically since these are sometimes produced without the support of explicit character analysis.

Algorithms used to find cladogram topologies are based on a *parsimony* criterion: in case of conflicting patterns of synapomorphy, the topology that requires the smallest amount of homoplasy (i.e., independent gains or secondary losses) is favored. This methodological criterion is justified because it retains the maximum number of the original, independently specified hypotheses of taxic homology. It is not circular, because the original hypotheses of homology are based (as discussed above) on observations of organisms without any preconception of their higher-level relationships (Funk & Brooks 1990). It does not assume that evolution proceeds parsimoniously (contra Robinson 1985, Buck 1986, Cronquist 1987), but it does assume that an apparent homology (i.e., a detailed similarity) between organisms is more likely to be due to true homology than to independent, non-homologous origin, unless evidence (i.e., a majority of incongruent taxonomic characters) exists to require a hypothesis of homoplasy. In fact the most parsimonious cladogram may well have many postulated homoplasies and can thus serve as a useful tool for demonstrating that evolution is *not* proceeding parsimoniously! Several computer programs are now available that use parsimony algorithms for the generation of cladograms (Magill, this volume).

In a cladogram branches (internodes) represent ancestor-descendant relationships, nodes represent hypothetical ancestors, and tips of external branches represent the least inclusive groups studied (usually known as OTU's, or operational taxonomic units). A monophyletic group is a taxonomic grouping that includes all and only descendants from a particular internal node (i.e., hypothesized ancestor), for example the group (D, E) in Figure 2. Non-monophyletic groups can be either *paraphyletic* (if some descendants of the common ancestor are left out), for example a group (A, B, C) in Figure 2, or *polyphyletic* (if no immediate common ancestor exists), for example a group (A, E) in Figure 2. The nature of species in a cladistic classification system is beyond the scope of this review; see Mishler & Donoghue (1982), Donoghue (1985), Mishler & Brandon (1987), and Cracraft (1989) for discussions of phylogenetic species concepts.

Evolutionary, phenetic, and cladistic schools of thought differ in the criteria used to delimit taxa. Phenetic grouping criteria are the most relaxed in that all similarities (homologs plus non-homologs) are used. Evolutionary grouping criteria are stricter because only homologs (ancestral and derived) are employed for taxon delimitation. In both approaches inferences about character evolution and genealogical relationships are problematic due to the non-

correspondence of classifications and phylogenies. The cladistic grouping criterion is the strictest. Cladistic classification includes the additional level of character analysis that adds explicit statements of character polarity. Hypotheses of synapomorphy provide a rigorous basis for distinguishing monophyly from non-monophyly. This is an important distinction, since only monophyletic taxa are useful as "models" of historical events for biogeographic, ecological, and evolutionary studies.

Once a cladogram indicating nested monophyletic groups has been recognized, there is still the problem of assigning taxonomic ranks and deciding what groups to recognize formally. Hennig (1966) advocated naming each monophyletic group, with its rank in the taxonomic hierarchy determined by geological age. Because of practical problems with the large number of ranks required, recent cladists have relaxed these ranking criteria. Present opinion is that all named taxonomic groups should be monophyletic, but that not all monophyletic groups need be named. Only the most "important" nodes are named, i.e., those nodes with greatest character support and/or those of particular evolutionary, ecological, or biogeographic significance. A convention known as "phyletic sequencing" allows a classification to reflect exactly a cladogram without naming every node (see Wiley 1981, for this convention and others dealing with fossils, hybrids, known ancestors, etc.). The particular taxonomic rank employed for a given monophyletic group is arbitrary from a cladistic point of view; criteria used for this decision should include consistency with previous practice within a group.

Problems in Phylogenetic Reconstruction

The feasibility of phylogenetic studies has been the subject of much debate in botany (e.g., Cronquist 1987, Donoghue & Cantino 1988). Some bryologists have argued that too little is known (or even knowable) about characters in bryophytes to attempt phylogenetic analysis (Anderson 1984, Smith 1986). Other bryologists have argued against the validity of specific assumptions or methods in cladistic analysis (Allen 1984, Robinson 1985, Buck 1986, Whittemore 1987).

It is true that reconstruction of past historical events is fraught with difficulties: taxonomic characters are incompletely understood; taxa belonging to a study group go extinct without leaving a fossil record; evolutionary parallelisms, reversals, and losses obscure patterns of homology; and hybridization causes reticulate patterns of homology. However, it is important to separate those difficulties that are general problems for systematics from those that might cause *particular* problems for cladistics. As has been discussed by Mishler (1986a), the above listed difficulties are problematic for *all* systematic approaches, and are therefore no reason to prefer, for example, a phenetic approach.

Character polarization is one area that *is* of particular importance for cladistic analysis (although as discussed above, rudimentary cladistic analyses can be done with unpolarized characters). While indeed critical, we feel that polarization is no more subjective than any other decision made in systematics. Decisions about polarity made in a cladistic framework are explicit, guided by logically sound criteria, and testable with further data. This is not to say that wrong polarity decisions are rare, but that wrong decisions, being explicitly stated, can be detected and corrected by additional study of outgroup relationships, ontogeny, and taxonomic characters.

Much further study of characters and relationships is needed before a complete hypothesis of phylogeny can be produced for the bryophytes and other land plants. However, regardless of how much or how little data are available the most rigorous method should be used to arrange and compare them. The cladistic approach provides an explicit framework for demonstrating what is known about relationships, and what taxa and characters are especially in need of further study.

Ontogeny and Evolution

Interest in the relationship between ontogeny and phylogeny, long a staple in evolutionary biology but largely out of favor since the Modern Synthesis, has been rekindled through the influence of Gould's important historical and theoretical treatment of the subject (1977). Much progress has been made recently in attempts to fuse development and evolution, two very different biological disciplines (Alberch 1983). Investigations are proceeding into the epigenetic basis of evolutionary novelties (Raff & Kaufman 1983), ontogenetic connections to life history studies (Stearns 1982) and phenotypic plasticity (Smith-Gill 1983), patterns and mechanisms of heterochronic change (Alberch et al. 1979, Ambros & Horvitz 1984, Kluge & Strauss 1985, Atchley 1987), and developmental canalization as a constraint on natural selection (Alberch 1980, 1982; Smith et al. 1985).

These recent theoretical advances in relating ontogeny to phylogeny have as yet had few applications in botany when compared to zoology. This is in part because of intrinsic differences between plants (e.g., modularity, hierarchical organization, indeterminate growth, and phenotypic plasticity — see Guerrant 1988, Mishler 1988a) and animals. Nonetheless, plants have been used in a few recent studies of heterochrony and/or the ontogenetic criterion for polarity, for example Guerrant (1982, 1988), Lord and Hill (1987), Mishler (1986b, 1987, 1988a), and Blackmore and Crane (1988).

The relationship between ontogeny and phylogeny is a reciprocal one. As discussed in the previous section, ontogenetic studies are an important part of a rigorous approach to phylogenetic reconstruction. On the other hand, once a robust phylogeny has been reconstructed and tested, it can serve as the framework for studies of evolutionary process, including studies of the evolution of developmental programs. The latter use, while not central to the aims of this volume, is worthy of some discussion here.

The study of heterochrony, defined as evolutionary changes in the timing and rate of development, has advanced considerably in recent years, because of two analytic breakthroughs. One was the development of a quantitative framework for explicitly comparing ontogenies (Alberch et al. 1979). The other was a linking of cladistic analysis to ontogenetic comparisons (Fink 1982, Kluge 1988). Empirical studies have lagged behind these theoretical advances, but it is clear that a framework is now available for an eventual evaluation of the importance of heterochronic change in evolution.

A standardized set of terms and a quantitative methodology for heterochronic studies has emerged (Gould 1977, Alberch et al. 1979, Fink 1982, Kluge 1988). The terminology can be summarized briefly as follows. Inferred ancestral and derived developmental sequences (as determined by out-group comparison) are compared graphically in a bivariate plot comparing "shape" as a function of "size" at different ages. Developmental trajectories can be visualized on such a graph by means of three parameters: onset of growth, cessation of growth, and growth rate.

Two "pure" *patterns* of heterochrony might be seen: *paedomorphosis,* referring to cases where a mature descendant has the form of a juvenile ancestor; and *peramorphosis* (also known as recapitulation), referring to cases where a juvenile descendant has the form of a mature ancestor. These patterns can be caused by six different "pure" processes of heterochrony. Paedomorphosis can be caused by *neoteny* (relatively slow growth rate in the descendant), *progenesis* (early cessation of growth in the descendant), or *postdisplacement* (late onset of growth in the descendant). Peramorphosis can be caused by *acceleration* (relatively rapid growth rate in the descendant), *hypermorphosis* (late cessation of growth in the descendant), or *predisplacement* (early onset of growth in the descendant).

Most real evolutionary comparisons between ontogenies of ancestors and descendants are likely to be less clear than the idealized cases of heterochronic change described above (Alberch et al. 1979). Different characters are likely to evolve through different mechanisms, and within a single character more than one developmental parameter may vary at once.

Application of this theoretical and methodological framework is accomplished as follows. A well-supported cladogram for the study group is generated based on all available characters. The evolution of individual character systems is then mapped onto the cladogram using a parsimony criterion (keeping in mind that multiple, equally parsimonious asignments of character states to nodes is sometimes possible). In this manner polarized phylogenetic comparisons can be made between plesiomorphic and apomorphic developmental pro-

grams (Fink 1982). Inferences are then made about the mode of evolutionary change, whether one of the "pure" models of heterochrony, or some other modification of development. After many such comparisons general conclusions about the importance of various types of heterochronic processes in evolution may be possible.

Bryophytes, because of their prolonged, easily observable ontogeny, seem particularly suited to such research. A few examples of this approach applied to shoot development in acrocarpous mosses have been presented by Mishler (1986b, 1987, 1988a). The best studied example is in the moss *Tortula*. A distinct heteroblastic series occurs in branch development (see further description in Case Studies, below). Many similarities can be seen between juvenile leaves produced in various stages of shoot development in *Tortula* and mature leaves characteristic of a wide range of related taxa. When developmental sequences are mapped onto a cladogram of the genus (Mishler 1986b), both paedomorphic and peramorphic patterns are seen. Interestingly, all observed evolutionary changes involve terminal stages of ontogeny, whether deletion, addition, or modification. This is in contrast to similar comparisons made in animal groups, whereby non-terminal changes are frequently observed (O'Grady 1985, Mabee 1989b). Cases of paedomorphosis observed in *Tortula* seem best interpreted as neoteny, slowing of rates of shoot differentiation resulting in the retention of an ancestral juvenile leaf form at maturity.

Bryophytes may also be particularly suited for experimental studies of ontogeny and phylogeny. Basile and co-workers have shown that the study of morphoregulatory proteins can test specific hypotheses about phylogenetic changes in ontogeny (Basile 1969, Basile & Basile 1984, Stebbins & Basile 1986).

There are a number of possible connections between heterochronic change and the relationship of organisms to their environment (Gould 1977). While beyond the scope of this paper, we will mention a few possible examples in mosses to spur further research.

Some preliminary data (Mishler 1986b, and unpublished) indicate that juvenile leaves of *Tortula* have a much greater ability to regenerate protonema and new shoots than do mature leaves. Thus neoteny (i.e., a delay in production of mature leaves in the heteroblastic series) may be adaptive when asexual propagation by fragmentation and regeneration is advantageous. It was further argued by Mishler (1988b) that many of the specialized types of asexual propagules produced in bryophytes are a result of an evolutionary process of neoteny.

Heterochrony appears to be involved in the evolution of moss sporophytes. Evidence for this is a series of developmental studies of the peristome-forming region (Shaw et al. 1989, Schwartz 1989). Merophytes in the capsule region undergo a very conservative pattern of cell division, expansion, and differentiation. As in moss shoot development, close parallels are seen between ontogenetic sequences and presumed phylogenetic transformations among the mature peristome types. The evolution of the hygroscopic, arthrodontous peristome types of true mosses from a plesiomorphic, non-hygroscopic nematodontous peristome appears to have involved several ontogenetic modifications, additions, and deletions (terminal and non-terminal). This process, as well as many cases of secondary peristome loss through paedomorphosis in the true mosses, may well be influenced by selection for effective spore dispersal in different environments.

Case Studies

This section presents in detail a few examples of moss gametophyte development, demonstrating the relationship of ontogenetic data to specific systematic problems at different taxonomic levels. For each example, we describe the systematic background for mosses in general and for a few specific taxonomic groups, and then we summarize the application of data from these cases to the four general uses of ontogeny in bryophyte systematics discussed in the Introduction.

Protonemal Development

Although spore germination and protonemal development are a continuous process, for practical reasons the transition from spore germination to protonemal development is usually defined as the occurrence of the first mitosis (Fulford 1956, Inoue 1960, Nehira 1983). Protonemal development continues with the differentiation of extensive chloronemata, caulonemata, and rhizoids and "concludes" with the formation of buds. Data are available on protonemal development for more than one hundred genera of diverse families (Nishida 1978, Nehira 1983).

Fourteen protonemal types are known in mosses. These are defined on the basis of the overall morphology of the mature protonema, whether the germination is endosporic or exosporic, and the shape of chloronemal cells, particularly those at the earliest stages of protonemal development (Nishida 1978, Nehira 1983). According to these authors, the protonema in the Sphagnidae is exclusively thallose (*Sphagnum*-type), and in the Andreaeidae the protonema is massive (i.e., endosporic germination produces a globose cell mass which then produces filamentous elements — the *Andreaea*-type). In contrast the protonema is completely filamentous (*Funaria*-, *Bryum*-, and *Macromitrium*-types) in a majority of the Bryidae. In a few taxa within the Bryidae the protonema, at least in part, is non-filamentous (e.g., in the Schistostegales and Tetraphidales, as well as in a few genera in the Grimmiales, Dicranales, Orthotrichales, Hypnobryales, and Isobryales; Nishida 1978, Ne-

hira 1983). Determining the systematic significance of protonemal development requires a full understanding of patterns of variation and the levels of homology among the different patterns.

The protonemal phase is one of the best investigated morphogenetic systems in experimental bryological research (Knoop 1984). Available information, recently summarized by Chopra and Kumra (1988), indicates that the filamentous protonemal types are extremely variable in response to different culture conditions. For example, the shape of cells, polarity of growth, rate of mitosis, differentiation of chloronema into caulonema, and the branching frequency of the filamentous protonema can be easily modified by changes in light quality and quantity, photoperiod, temperature, hydration and pH of the substratum, hormonal levels, and interaction with microorganisms (Chopra & Kumra 1988). Consequently, protonemal development has often been considered of limited or no phylogenetic significance. However, this generalization is based only on the study of filamentous protonemal types.

Plasticity in non-filamentous protonemal patterns has remained little studied, but it seems that the basic patterns are stable in cultures under a variety of conditions (Nishida 1978, Nehira 1983). For example, Anderson and Crosby (1965) studied protonemal development in *Sphagnum meridense* (Hampe) C. Müll. in laboratory cultures. They described variation in the length of the initial filament, rate of prothallial differentiation, and rhizoid production. However, the characteristic thallus-like growth was unchanged. Similar limited variation has been observed in *Andreaea,* and other genera with massive protonemal types (Nehira 1983). Thus, seemingly heritable, stable differences between various non-filamentous protonemal patterns make these patterns potentially useful as taxonomic characters.

Nishida (1978) and Nehira (1983) have interpreted the different "massive" protonemal types of unrelated mosses as ecological adaptations, and therefore argued that these are of limited phylogenetic value. One possible implication of this generalization is that taxa with similar massive protonemata do not belong together in one monophyletic taxon, i.e., they do not share a unique recent common ancestor. However, this reasonable implication needs to be evaluated cladistically before an understanding of the "phylogenetic value" of protonemal types at particular taxonomic levels can be gained.

A plausible interpretation of character-state evolution in the protonema of mosses can be based on current ideas of relationships among mosses (Mishler & Churchill 1984). All protonemal types in mosses seem homologous as protonemata, i.e., states that can be considered transformed from a common ancestral protonemal type. Polarization at this inclusive level must be based on out-group comparison with the "charophyte" green algae (e.g., a paraphyletic assemblage including *Coleochaete, Chara,* and *Nitella* — Mishler & Churchill 1985; Graham et al., this volume), liverworts, hornworts, and some tracheophytes. Such a comparison suggests that a basically thalloid protonema produced via exosporic germination and an initial few-celled uniseriate filament (such as the *Sphagnum*-type) is likely to be plesiomorphic in relation to the synapomorphic, extensive filamentous protonema found in the majority of true mosses. At the inclusive level of the peristomate mosses, the presence of an extensive and elaborate filamentous protonema can in turn probably be interpreted as a plesiomorphy relative to the various independently derived non-filamentous types in phylogenetically scattered genera in the Bryidae, even though cladistic relationships within the true mosses are poorly known.

Thus, the *Tetraphis-, Schistostega-, Diphyscium-,* and *Buxbaumia*-types and several different "massive" protonemal types (found in *Andreaea, Drummondia, Ptychomitrium, Encalypta,* and the Hedwigiaceae) cannot be interpreted as the "same protonemal type" (i.e., a taxic homology) taken together. They are neither developmentally similar nor phylogenetically congruent if considered a single taxic homology. Alone, each of these protonemal patterns *is* a potential synapomorphy in relation to the filamentous plesiomorphic state, but only at a less inclusive taxonomic level. For example, non-filamentous sporeling types seem useful in the diagnosis of taxa such as *Sphaerotheciella* (Manuel 1977, 1982), *Muelleriella* (Vitt 1976), *Drummondia* (Allen 1987a), and the Dicnemonaceae (Allen 1987b), even though none of these applications represents an explicit evaluation of homology and polarity. A recent example of an explicit analysis of the systematic significance of non-filamentous protonemal patterns at the family level comes from recent work on the Hedwigiaceae (De Luna 1990a).

The Hedwigiaceae have been characterized by eperistomate capsules, ecostate leaves, leaf cells irregularly short-oblong, and branched leaf papillae. Phylogenetic relationships within the family, its circumscription, and its ordinal relationships have been problematic on the basis of comparative adult morphology. The Hedwigiaceae have been variously classified within either of the two main groups of true mosses (Haplolepidae or Diplolepidae). Also, the inclusion of *Bryowijkia* and *Rhacocarpus* in this family has been controversial. Based on characters of the mature plants, *Bryowijkia* has been transferred from the Hedwigiaceae to the Trachypodaceae (Vitt & Buck 1984). Debate remains over whether *Rhacocarpus* belongs to the Hedwigiaceae (Barthlott & Schultze-Motel 1981; Koponen & Norris 1986), or whether it represents a monotypic family (Buck & Vitt 1986).

In view of uncertainty about the circumscription of the Hedwigiaceae and the doubtful familial relationships of *Rhacocarpus,* studies of protonemal developmental patterns in selected species of each genus were initiated to help clarify the taxonomy of the family (De Luna 1990a). A unique type of protonema was observed in *Braunia secunda* (Hook.) B.S.G., *Hedwigia ciliata* (Hedw.) Ehrh. ex P.-Beauv., *Hedwigidium integrifolium* (P.-Beauv.) Dixon and *Pseudobraunia californica* (Lesq.) Broth. Germination of this new type

is exosporic, leading to formation of a three-dimensional, globular mass of cells. In contrast the development of protonemata in *Bryowijkia* is endosporic (De Luna, in press); in *Rhacocarpus purpurascens* (Brid.) Par. it is the basic exosporic filamentous pattern known in a large number of moss species (the *Macromitrium*-type sensu Nehira 1983). The *Macromitrium*-type is similar to the filamentous *Funaria*- and *Bryum*-types, and it has been observed in several pleurocarpous mosses, namely in the Leucodontaceae, Pterobryaceae, Neckeraceae, Leskeaceae, and some species in the Thuidiaceae (Nishida 1978).

Interpreting the globular protonema shared by *Hedwigia, Hedwigidium, Braunia,* and *Pseudobraunia* as "the same state" implies a taxic homology (therefore common ancestry) linking the four genera. The alternative interpretation would be that similarities among these genera in protonemal development are a result of ecological convergence (i.e., non-homology), instead of an indication of common phylogenetic origin. Obviously, choosing one hypothesis over the other greatly influences the interpretation of the systematic significance of globular protonema, in terms of character state evolution and taxonomic groupings.

For these four genera (Hedwigiaceae in the restricted sense), the globular protonema is phylogenetically congruent with other similarities of mature gametophytes and sporophytes (such as branching patterns, leaf cell shape, papillae, and spore surface morphology). Thus, the application of both the similarity and congruence tests of homology suggests that the globular protonema is a taxic homology between *Hedwigia, Hedwigidium, Braunia,* and *Pseudobraunia.* In this example ordering is simple because only two states (filamentous and globular) are considered. To hypothesize synapomorphy, however, a polarity assessment is needed. In other words, what is more likely to be derived, the filamentous or globular type of protonema?

The Leucodontaceae and Cryphaeaceae have been suggested to be the most closely related out-groups to the Hedwigiaceae within the Isobryales (Leucodontales). According to the studies of Nehira (1983) and Nishida (1978) the protonema is filamentous in most species of the Isobryales. This is also true at a more inclusive level, viz., subclass Bryidae *sensu* Schofield (1985). Therefore, character state polarization by out-group comparison suggests a phylogenetic transformation at the family level (Hedwigiaceae) from an ancestral filamentous protonema to a relatively derived globular one. These results suggest the hypothesis that the globular protonema is a synapomorphy that would help to circumscribe the Hedwigiaceae as a monophyletic group, including only the species currently classified in *Hedwigia, Hedwigidium, Braunia,* and *Pseudobraunia* (De Luna 1990a).

In contrast any hypothesis of homology (e.g., Allen 1987a) between the *Hedwigia*-type protonema and the superficially similar "massive" types of protonema found in various other mosses passes neither the similarity nor the congruence tests of homology. The details of development of the *Hedwigia*-type protonema are unique, and there are no other putative homologies linking the Hedwigiaceae to other groups with a "massive" protonema.

Shoot Development

The differentiation of an apical cell from a protonemal cell marks the initiation of the development of the foliose gametophytic shoot in mosses. Merophytes produced by regular segmentation of the apical cell differentiate in a stereotyped manner into leaves, axillary hairs, stem tissue, conductive cells, gametangia, and lateral branch apical cells. Extensive studies have described different morphological aspects of the development of shoots, such as patterns of apical segmentation (Bonnot 1968, Berthier 1972), leaf development (Frey 1970, 1974), differentiation of conductive cells (Hébant 1973), differentiation of axillary filaments and lateral buds (Berthier 1978), and differentiation of gametangia (Janzen 1921).

While all of these developmental patterns are potentially useful in systematic studies, we will focus on the development of the *module* as a whole, in terms of the heteroblastic series of *metamers* (see Fig. 1). This level of the ontogenetic hierarchy has been relatively understudied, particularly in a comparative manner. The development of the heteroblastic leaf series and the development of conducting tissue are examined in detail to illustrate the systematic significance of ontogenetic data of this type at different taxonomic levels.

Heteroblastic Leaf Series. Most studies of shoot and leaf development have described segmentation patterns and cell differentiation in apices of mature shoots (e.g., Berthier 1972). For example, Frey (1974), Bopp (1984), and many others, have carefully described leaf development as observed in a succession of leaves from an apex of a mature shoot. However, it has been known for a long time that leaf developmental patterns are heteroblastic (Goebel 1900, Wigglesworth 1956, Berthier 1972). The pattern of differentiation followed by a given leaf depends on its position in the branch module; juvenile leaves are often strikingly different from mature leaves on the same branch. These differences can be seen most easily in culture studies but are also readily observable in herbarium specimens.

Only a few comparative observations have been made of heteroblastic shoot development in mosses (Mishler 1986b, 1987, 1988a). We first present a summary of these initial observations, followed by a more extensive description of recent work on the Hedwigiaceae.

Mature leaves of mosses in the *Tortula ruralis* complex have a long, hyaline hairpoint, recurved margins, a strong midrib, and two types of cells in the lamina. At the base of the leaf is an area of large, rectangular, smooth cells; in the upper part of the leaf there are small, isodiametric, papillose cells. Juvenile leaves (i.e., those produced early on a module) are extremely different,

resembling the mature leaf-form of another order of mosses, the Funariales (interestingly, an order sometimes suggested as the basal lineage in the true mosses; Crosby 1980). These juvenile leaves of *Tortula* have plane margins, a weak midrib, only one type of cell on the lamina (large, rectangular, smooth cells), and no hairpoint (Mishler 1986b).

The heteroblastic leaf series described in *Tortula* has a number of systematic and evolutionary implications (Mishler 1986b, 1988a; see also the above section on Ontogeny and Evolution). To take one example, it has been difficult to establish homologies between the extremely tall leaf-cell papillae in mature leaves of *Tortula papillosissima* (Coppey) Broth. and the normal papillae of the *Tortula ruralis* complex (Mishler 1987). Study of the heteroblastic leaf series in *T. papillosissima* (Fig. 5) showed that juvenile leaves of this species have a leaf-cell ornamentation identical to that in the mature leaves of other members of the *T. ruralis* complex, with a moderately tall mammilla (i.e., bulging cell surface) bearing approximately four branched papillae per cell. The uniquely derived (as determined by out-group comparison) ornamentation of mature leaves of *T. papillosissima* appears later in the heteroblastic series and can be determined to be composed of two independent taxonomic characters: (1) a significantly taller mammilla, and (2) a reduction in the number of papillae to one or two (since these two characters appear separately in the heteroblastic series; Fig. 5). Thus, a clarification of homologies in leaf-cell ornamentation within the complex was possible.

While the heterochronic pattern shown by both characters is peramorphic, two different heterochronic processes may be occurring at the module level (Mishler 1987). The very early reduction of papilla number in *Tortula papillosissima* as compared to its relatives may be due to acceleration. However, the relatively late appearance of the tall mammilla, apparently as a prolongation of the normal development of the mammilla in the *T. ruralis* complex, may be due to hypermorphosis.

Heteroblastic leaf series of systematic significance in other mosses (*Fissidens, Atrichum, Sphagnum, Scouleria, Eustichia, Neckera*), and a liverwort (*Fossombronia*) were discussed by Mishler (1988a). *Fissidens* provides a particularly good example of the systematic utility of such data in evaluating transformational homology. The mature leaf morphology of this genus is bizarre, with three laminae instead of the normal two found in all other mosses. A cross-section taken in the lower part of the leaf is "Y" shaped, with two "vaginant" laminae clasping the stem, and a "dorsal" lamina projecting on the other side of the midrib from these. While this unique leaf form is undoubtedly a synapomorphy of the genus, the transformational homologies of this leaf form to that of related mosses has long been controversial (Salmon 1899, Robinson 1970, Chamberlin 1980). Observations of the heteroblastic leaf series in *Fissidens* shows clearly, however, a transformation from juvenile leaves with a completely "normal" leaf form (typical of families related to the

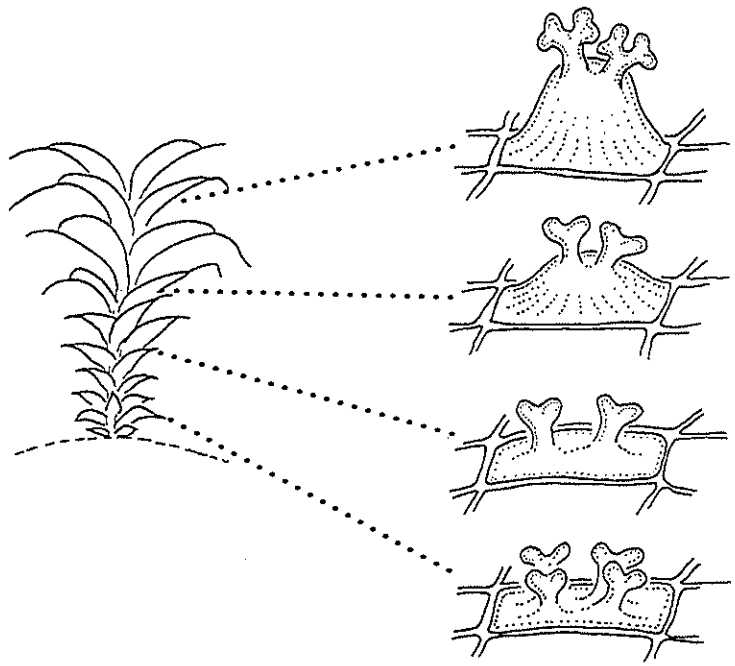


Figure 5. Leaf-cell ornamentation of *Tortula papillosissima* as it varies through the heteroblastic leaf series. Shown are leaf cells from fully differentiated leaves. Early juvenile leaves (bottom) have a normal ornamentation for the *T. ruralis* complex, with only a slightly bulging cell surface and four branched papillae per cell; later juvenile leaves have a reduced number of papillae; mature leaves have an extremely tall bulge in the cell surface.

Fissidentaceae such as the Ditrichaceae) to the derived leaf form in the mature leaves. The vaginant laminae appear to be taxically homologous to the normal moss leaf, and the apical and dorsal laminae appear to be novel additions to the plesiomorphic leaf ontogeny (Mishler 1988a).

The mature leaves of *Hedwigia, Hedwigidium, Braunia,* and *Pseudobraunia* lack a costa and have short-oblong, papillose cells not strongly differentiated at the margins or in the alar region. The mature leaves of *Rhacocarpus* also lack a costa, but the leaf cells are not papillose and are elongate in the middle of the leaf, linear at the margins, and inflated in the alar region.

In *Hedwigia, Hedwigidium, Braunia,* and *Pseudobraunia,* a branch produces a regular and prolonged heteroblastic sequence of leaves as it matures. In a primordium (bud) the leaves have smooth, short-rectangular cells when fully differentiated. In an older branch, fully differentiated juvenile leaves have two types of cells: in the upper half of the leaf, cells are short-quadrate

to pentagonal and bear 3-5 papillae; in the basal half of the leaf, cells are rectangular and smooth. Mature leaves have approximately 3-5 papillae per cell in *Hedwigidium* and *Braunia.* However, only one papilla per cell occurs in mature leaves of *Hedwigia* and *Pseudobraunia.* Leaf development and the heteroblastic series in *Hedwigia* are illustrated in Figure 6.

Significant differences in module development were observed between the Hedwigiaceae in the strict sense (i.e., the four genera described above) and *Rhacocarpus.* The first juvenile leaves in *Rhacocarpus* do not develop a costa, but very early the cells are differentiated in different parts of the lamina. The basal cells are rectangular and elongated, the middle cells are elongate, rhombic to hexagonal, grading to short rhombic in the acumen, and the marginal cells are large, oblong to elliptical at the base, becoming smaller and oval at the apex. Further differentiation of alar, basal, marginal, and apical cells occurs in later leaves.

Differences in gametophyte ontogeny thus appear to support the phylogenetic hypothesis derived by outgroup comparison (discussed under Protonemal Development, above) that *Rhacocarpus* does not share a recent common ancestor with *Hedwigia, Hedwigidium, Braunia,* and *Pseudobraunia.* However, phylogenetic interpretations of branch ontogeny are premature at this point. It will first be necessary to study the sequence of differentiation of papillae and other characters in more detail in additional species of each genus (including *Bryowijkia*) and in likely outgroups. Nevertheless, preliminary results of studies of cell differentiation and papilla formation show that shoot ontogenetic data provide promising sources of taxonomic evidence, allowing a means to identify homology among character states found in mature gametophytes.

In future studies of module ontogeny, particularly in pleurocarpous mosses, it may be necessary to take into account both the branch system and the shoot system levels of ontogeny (Fig. 1). For example, A. Newton (pers. com.) has noted that patterns of leaf development in *Pireella* appear to depend not only on the development of a branch but on the branching order. Secondary modules in this pleurocarp develop a different heteroblastic series from that of the primary modules. In contrast, in the acrocarpous mosses we have examined, all modules are morphologically equivalent. For example, Mishler (1988a) noted that in *Tortula* the same heteroblastic leaf series is developed in each new branch.

Development of Conducting Tissues. The relationship of the conducting tissues of bryophytes to those of tracheophytes is one of the most controversial issues in bryophyte phylogeny today. Opinions range widely, in both research papers and textbooks. Most general biology texts simply state that the mosses are non-vascular plants. Specialized botany texts acknowledge the obvious fact that many mosses have conducting tissues, but opinions differ on the

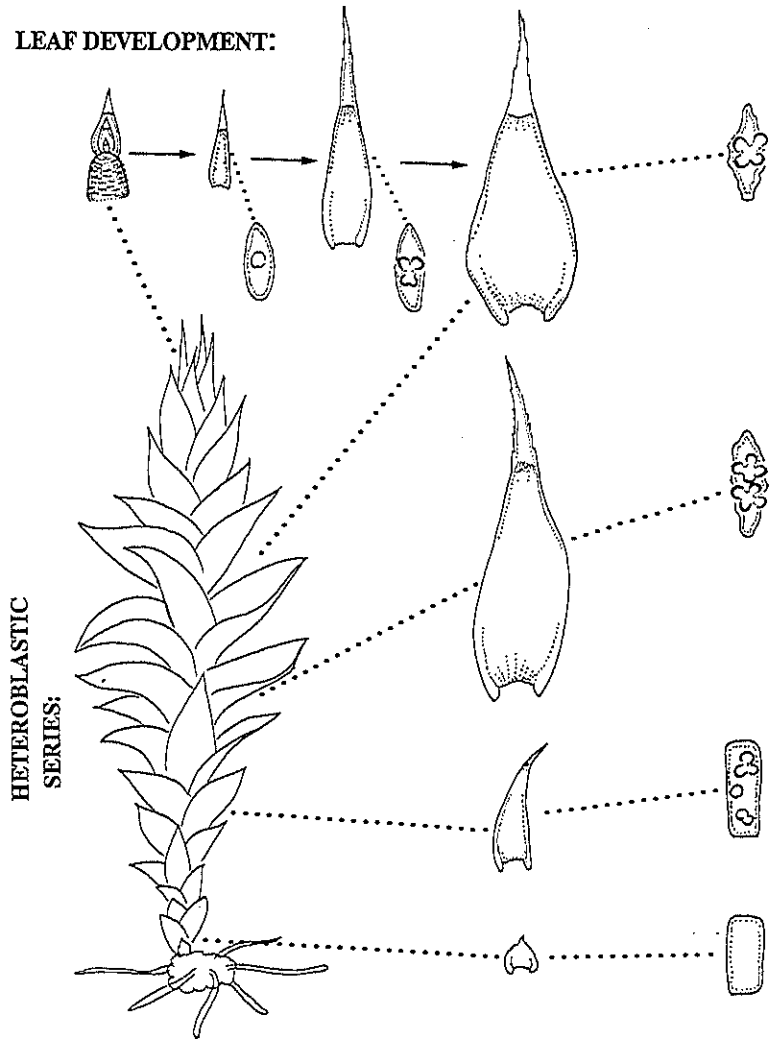


Figure 6. Heteroblastic leaf development in *Hedwigia ciliata.* Shown ascending at right are fully differentiated leaves (and a representative upper leaf-cell of each) taken from different positions on the branch. Shown across the top is the pattern of differentiation of a single mature leaf. Developmental patterns in leaf characters seen at these two different hierarchical levels are quite different.

question of whether these tissues are homologous to the xylem and phloem of tracheophytes (e.g., see Kaufman et al. 1989 for a negative answer, and Raven et al. 1986 for an affirmative answer). Opinions of researchers interested in

bryophyte phylogeny have ranged from the view that moss conducting tissue is reduced from more complicated xylem and phloem (e.g., Haskell 1949; Miller 1974, 1982; Richards 1978), to the view that the moss conducting tissue is the result of parallel evolution (e.g., Khanna 1965, Campbell 1971, Schofield, 1985). A building consensus seems to be a middle ground position: that mosses and tracheophytes shared a common ancestor, and this ancestor had conducting tissues much like the tissues present in extant polytrichaceous mosses (Hébant 1977, Scheirer 1980, Crum 1983: 378-379, Mishler & Churchill 1984). In this view the moss grade of conducting tissues (hydroids and leptoids) is transformationally homologous to the more complex tissues of the tracheophytes, and thus study of conducting tissue in mosses could provide a model system of evolutionary pathways followed in primitive land plants (Scheirer 1980).

These issues are far from settled, however. Even though many studies have emphasized bryophyte conducting tissues (reviewed by Hébant 1977; more recent literature is summarized by Scheirer 1980, 1990), much more work needs to be done to characterize the mosses as a whole. This is because the bulk of published work has dealt with the Polytrichales and has dealt with the gametophyte generation rather than the sporophyte. The last point is particularly important because, as discussed in Mishler and Churchill (1985), the taxic homology between conducting tissue in mosses and tracheophytes is likely to be only in the sporophyte generation (since the tissue is lacking in almost all tracheophyte gametophytes, with the exception of occasional polyploid *Psilotum* gametophytes; Bold et al. 1987). Mishler and Churchill hypothesized that expression of vascular tissue in moss gametophytes occurred as a secondary "transference" from the sporophyte. Thus one might expect differences between the expression of the tissues in the two generations, with the sporophyte perhaps retaining more primitive features.

Most comparative studies of vascular tissue in mosses have focused on mature cells and tissues. In his important book on conducting tissues in bryophytes, Charles Hébant (1977) summarized the status of knowledge of these tissues and pointed out less well studied areas, including development. Developmental studies include Hébant (1973, 1974, 1976) and Stevenson (1974), although the coverage of taxa to date is incomplete, since a great majority of developmental studies focus on the Polytrichales. Furthermore, little has been published regarding development of conducting tissue in the sporophyte (e.g., Schulz & Wiencke 1976). An additional gap is that virtually all of these studies have focused on the mature stage of branch development (i.e., the apex of a mature branch is examined; see Hébant 1977). Such studies have contributed important information on differentiation and ultrastructure at the cell level. However, other juvenile stages of module development also need study.

Based on the work of Wigglesworth (1956), there is some indication that branch development may provide data of considerable phylogenetic interest. The prolonged heteroblastic development of the branch has mostly been documented with respect to leaf sequences but appears to involve changes in other parts of the metamers as well. Heteroblasty appears to be reflected in the differentiation of the conducting tissues in successive metamers (Wigglesworth 1956, Hébant 1977). The earliest juvenile stems of *Polytrichum* are without any internal differentiation (reminiscent of the mature stem in many mosses in the Bryales). Later juvenile stems have hydroids only (reminiscent of the mature stem of other mosses in the Bryales). The mature plants have both hydroids and leptoids. As pointed out by Hébant (1977), this situation is of phylogenetic interest in that the shoot ontogeny of *Polytrichum* passes through the full set of character states found taxonomically across the mosses. Hébant suggested neoteny as a mechanism whereby mature stems of an "advanced" moss such as *Orthotrichum* might have lost vascular tissue in the phylogenetic sense.

Branching Patterns

After the development of a primary shoot, the majority of mosses produce branches. The development of several branches of regular length, frequency, and orientation is the structural basis of the various *growth forms* of mosses. The aggregation of several branching shoots gives in turn the structural basis of the various types of *life forms* of mosses. We follow Mägdefrau (1982), who clearly differentiated the meaning of these two terms to describe the morphology of a shoot and the shape of a colony, respectively. However, we develop and discuss in more detail his approach to the classification of growth forms that was in turn based on Meusel's work (1935). We emphasize that the study of branching patterns involves not only an assessment of the mature morphology of the shoot and its orientation but also the dynamic aspects of branch development.

The branching system of mosses has been commonly described only from observations of mature specimens. Features typically observed include leaf sequences in relation to branch primordia, degree of pinnate branching, presence of pseudoparaphyllia, relative length and frequency of branches, and symmetry of branching, among others (Correns 1898, Koponen 1982b, Meusel 1935, Stark 1985).

Branches are started by secondary apical cells differentiated along the primary stem, and thus they constitute a new module in the sense of White (1984). The search for regularities in the branching patterns of mosses is therefore a search for types of modular organization. Consequently, we want to stress the significance of an "architectural analysis" (Hallé et al. 1978) of branching patterns in mosses. Such a developmental approach is necessary to determine the structural components (modules and metamers) and to under-

stand processes that account for a particular branching pattern (De Luna 1990b).

Morphologically, there are two basic growth forms in mosses: *acrocarpy,* i.e., with capsules terminal on main stems, and *pleurocarpy,* i.e., with capsules terminal on lateral branches (Schofield & Hébant 1984). A subtype of pleurocarpy, known as *cladocarpy* (Frey 1970), has been recognized in a few mosses, where the lateral branches terminating in capsules are elongated (e.g., *Fontinalis*). Developmentally, in acrocarpic mosses after a period of branch growth the terminal apical cell and surrounding merophytes differentiate archegonia, thus terminating shoot growth. In these mosses branching is *sympodial,* i.e., lateral apical cells differentiated during shoot development initiate further growth and produce subterminal innovations, adventitious (basal) branches, or both (Fig. 7). In contrast pleurocarpous mosses have indeterminate shooth growth, since the main apical cell does not differentiate archegonia. In these mosses development of branches is *monopodial,* i.e., lateral apical cells produce determinate branches, often in a pinnate pattern, as in *Ctenidium* (Nishimura 1985). Archegonia eventually differentiate from the apical cell of these lateral branches.

In addition to these morphological and developmental aspects, growth forms of mosses are modified by the plant's habit (i.e., spatial orientation of growth). The habits of mosses can be grouped into two general types (Meusel

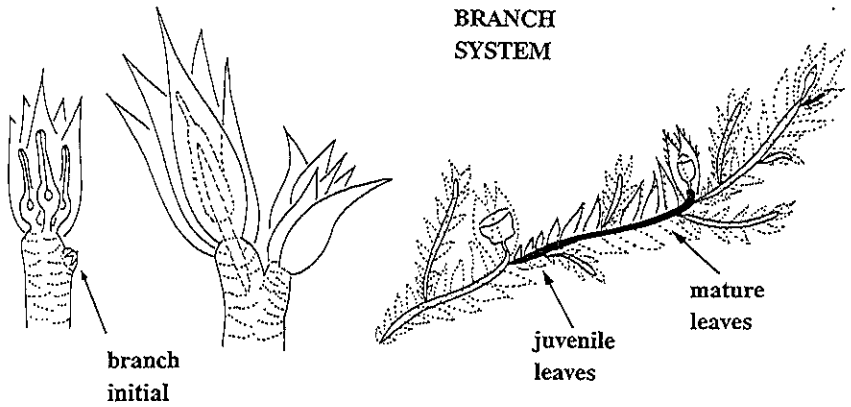


Figure 7. The pseudo-pleurocarpous branching patterns of *Hedwigia ciliata.* A branch initial develops from a lateral apical cell below the archegonia that terminated growth of the previous module. The new branch module grows vigorously and pushes aside the old branch terminus (and associated sporophyte). Even in observations of herbarium specimens, this growth pattern can be confirmed by the position of the juvenile leaves produced on the new branch; in a true monopodial pleurocarpous moss, no such interrupted pattern of juvenile and mature leaves would be seen.

1935). Acrocarpic mosses are commonly, but not always, erect (*orthotropic*), whereas pleurocarpic mosses commonly, but not always, develop a prostrate (*plagiotropic*) habit. A gradient of stem habits from totally erect to prostrate is often observed, and thus this criterion alone is problematic for determining if a moss is acrocarpous or pleurocarpous.

There are other types of growth habits in mosses that illustrate the importance of considering morphological, developmental, and habit criteria together for a precise description of branching patterns. In many species in the Grimmiaceae and Orthotrichaceae an initial acrocarpous (sometimes erect but frequently prostrate) shoot develops terminal archegonia, which are soon displaced laterally by sympodial, plagiotropic innovations. At maturity the shoots look pleurocarpous because of the prostrate habit and apparently lateral capsules. This growth form has been called *pseudo-pleurocarpous* (Meusel 1935, Buck & Vitt 1986).

Other mosses have alternate phases of orthotropic and plagiotropic growth. Some have a prostrate phase (stolons and rhizomes) but are developmentally acrocarpic and sympodial, for example, species in the Bryaceae and Polytrichaceae. Conversely, some mosses are erect during some phase of their development, but pleurocarpic and monopodial in their branching pattern, for example in the Pterobryaceae and Hypnodendraceae. Mosses of these two families alternatively combine phases of monopodial and sympodial growth. An initial erect shoot develops monopodially with several branches forming an open dendroid growth. Subsequent growth is by a basal lateral branch that initially is plagiotropic and behaves like a stolon or rhizome. Later this branch turns to vertical growth, producing branches in a similar dendroid form.

Variation in branching patterns observed in mature plants can be attributed to developmental differences at the level of merophyte differentiation. Branch initials are differentiated laterally on the primary stem from an outer cell of a merophyte. In some mosses each merophyte differentiates a branch initial along with the leaf, as in *Mnium* (Koponen 1982a). In other mosses only a few merophytes, regularly spaced along the stem, differentiate branch initials. This spacing can be very precise and result in taxon-specific cladotaxies (Berthier 1972). Physiological differences, particularly of apical dominance and the hormone system, are also a presumably important factor in the observed variation in branching patterns (Nyman & Cutter 1981).

Strong environmental effects on branching have always been suspected. But surprisingly, there are few studies that have demonstrated plasticity in critical developmental and morphological aspects of branching. Often, environmental effects are reflected in length, frequency of branches, and the life form, but the position of archegonia (acrocarpic or pleurocarpic) and the type of branching (sympodial and monopodial) are not modified (Schoenau 1912, Birse 1957, Gimingham & Birse 1957, Berthier 1965, Schofield 1972, Pitkin 1975, Mägdefrau 1982, Stark 1985).

Detailed morphological aspects of branching patterns are known only for the few European taxa studied by Meusel (1935), and other taxa studied by several authors who used the position of archegonia in relation to the shoot apex and the type of branching as characters of taxonomic significance at different levels (e.g., Lindberg 1873, Koponen 1972, Tuomikoski & Koponen 1979, Koponen 1982b, Nishimura 1985, Stark 1985, Sastre-De Jesús 1987). The example discussed below comes from recent work in the Hedwigiaceae (De Luna 1990b).

Analyses of the phylogenetic relationships of the Hedwigiaceae are problematic, in part because of uncertainty about the growth form and the lack of a peristome. The growth pattern in the Hedwigiaceae (*s.l.*) has been interpreted as acrocarpous (Hedwig 1801), pseudo-pleurocarpous (Meusel 1935), cladocarpous (Frey 1970), and pleurocarpous (Vitt 1984). Anatomical study was necessary to determine if the archegonia are truly lateral, or if they are initially terminal and only appear lateral because of subterminal innovations. Plants of *Hedwigia ciliata* were studied to describe the arrangement of leaves, distribution of gametangia, and frequency and localization of branches. Also, stems were sectioned to study the anatomy of the apex and branching points (De Luna 1990b).

These observations suggest that the development of archegonia is acrocarpic, i.e., from the main apex, and thus that the branching system in *Hedwigia ciliata* is sympodial (De Luna 1990b). All plants develop a primary shoot that is extended by one or two subterminal innovations (Fig. 7). Also, one or two adventitious and stoloniferous branches develop from the basal part of the oldest branch. The same pseudo-pleurocarpic branching system seems to occur in *Hedwigidium, Braunia,* and *Pseudobraunia,* although size and frequency of branches varies.

These results suggest that this branching pattern may be of value in the systematics of the Hedwigiaceae. It is likely that a pseudo-pleurocarpous branching pattern is homologous at the level of the family (Hedwigiaceae). However, it still remains to be evaluated by out-group comparison whether this is a synapomorphy for the family or for some more inclusive level.

Summary and Conclusions

In the Introduction we outlined four general uses for ontogenetic data in systematics. Here we summarize the examples we have presented of each of these uses, along with a few other examples from the literature.

(1) A source of new taxonomic characters in juvenile phases. The unique globular protonema of the Hedwigiaceae is one of the best characters currently supporting the monophyly of the family. Other examples of characters only

evident in immature phases include: the synapomorphic multicellular rhizoids of mosses, only retained in the protonemal stage of *Sphagnum* (Mishler & Churchill 1984), and the remarkably uniform early development of the peristome-forming region of the sporophyte, shared among mosses of extremely divergent mature capsule morphology (Shaw et al. 1989).

(2) A source of information for clarifying homologies and defining character states in mature phases. The growth form of the Hedwigiaceae (and other mosses) is hard to interpret based only on appearance of mature shoots; developmental studies were necessary to demonstrate its acrocarpous nature. The unique cell ornamentations of *Tortula papillosissima* were discovered to consist of two distinct taxonomic characters by means of developmental studies. Similar clarification is possible in peristome development. *Diphyscium* was considered to have a distinctive peristome type, transitional perhaps between nematodontous and arthrodontous types, until developmental studies showed that the peristome is arthrodontous in all respects, and in fact close to the well-known haplolepideous type (Shaw et al. 1987).

(3) A source for determining transformational homology among character states (ordering). The transformational homologies between the leaf-type of *Fissidens* and that of related mosses is best demonstrated by examining heteroblastic leaf series. Similar examinations have proven useful in ordering leaf characters in *Tortula* and the Hedwigiaceae. Heteroblastic development of conducting tissues provides evidence for ordering character states of the leptoids and hydroids.

(4) A source for hypothesizing evolutionary directionality among character states (polarization). As we have indicated, ontogenetic progression can be a useful supplement to the outgroup criterion. This seems particularly true of heteroblastic development of branch modules; in the cases known to us, evolutionary changes at this level (when they can be evaluated independently by out-group comparison) seem to occur in terminal stages of ontogeny. Protonemal evolution, on the other hand, seems to violate this basic assumption of the ontogeny criterion (Mishler 1988a). Evolutionary transformations of the filamentous moss protonema into the various derived non-filamentous types are developmentally non-terminal and include additions, deletions, and substitutions (sensu O'Grady 1985).

Given the ease with which mosses can be grown in culture, and the fact that many leaf and shoot developmental processes we have discussed can be observed directly from herbarium specimens without culturing, we think there is good reason to include ontogenetic data in systematic studies at any taxonomic level. These data add a new dimension to systematic studies based on mature plants and help to provide a truly sound foundation for phylogenetic reconstruction and therefore for systematics.

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