Growth Form, Branching Pattern, and Perichaetial Position in Mosses: Cladocarpy and Pleurocarpy Redefined

CATHERINE LA FARGE-ENGLAND

Cryptogamic Herbarium, Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

Abstract. *The terminology for growth form, branching pattern, and position of the perichaetia has been inconsistently used in the literature. This terminology, used for the structural organization in Bryopsida, is reviewed, classified, and redefined. The following interpretations are proposed 1) Growth form is differentiated from life form. 2) Direction of growth does not necessarily infer perichaetial position, for there are prostrate acrocarps or erect pleurocarps. Pseudo-pleurocarpy is not considered a formal perichaetial position. 3) Cladocarpy is distinct from acrocarpy or pleurocarpy, and defined as perichaetia terminal on lateral branches with juvenile leaf development similar to that on vegetative branches. The perichaetial branches have lateral primordia that potentially develop subperichaetial branches. Cladocarpy is interpreted as functional pleurocarpy that has evolved in a number of independent lineages. 4) Pleurocarpy is defined as perichaetia terminal on lateral innovations that appear sessile and swollen along the supporting axes. The juvenile leaves are morphologically different from those of the vegetative branches. The perichaetial innovations lack lateral branch primordia and thus do not produce subperichaetial branches. These innovations may represent a type of heterochrony—a paedomorphosis in branch development. Pleurocarpy is restricted to the Hypnales, Hookeriales, and Leucodontales, including the Spiridentaceae and Racopilicaneae.*

The structural organization of the moss gametophyte is diverse, despite the comparatively simple organism. Generally, mosses have erect or prostrate leafy stems with respect to horizontal substrates, whereas they often develop perpendicular or pendulous stems on vertical substrates (i.e., cliffs, tree trunks, branches, and lianas). Mosses form unbranched to multibranched axes with diverse patterns of length, frequency, and position of the branches (Meusel 1935). The development of a structural hierarchy of branches from the main axis is common, with some mosses having secondary or even tertiary branches.

Branches originate from lateral initials that occur in the outer cortical tissue (Berthier 1972). Along the developed branch, the first leaves are reduced in size and can be morphologically distinct from leaves produced later (Mishler & De Luna 1991). This heteroblastic sequence of leaves differentiates each connected branch. Most often, branches develop along the stem in two directions: from the apex downward and from the base upward. These developmental sequences ultimately affect the branching pattern.

Two basic branching patterns are found in mosses; one is a chain of connected branches of the same hierarchy; the other is a series of independent (or unconnected) branches developed along a supporting axis of a lower hierarchy. These two patterns can potentially be found at any given level of structural hierarchy.

In mosses, perichaetia are found in one of three basic positions 1) terminal on the primary axis; 2) terminal on lateral branches; or 3) terminal on lateral innovations that appear sessile and lateral along the primary or supporting axis. Individual species are characterized by a single position, indicating that the distribution of perichaetia is conservative.

Structural analyses of growth form, branching pattern, and perichaetial position form an integral component of systematic revisions. However, in the recent literature, authors have used the same terms with different inferences (i.e., life form for growth form, pleurocarpy for prostrate growth form, pseudo-pleurocarpy for cladocarpy, pleurocarpy for cladocarpy), resulting in a confused terminology. Consistent use of terminology in comparative and phylogenetic analyses is essential and will help determine the systematic value of these features as potential homologues. The objectives of this paper are to 1) review how terms have been applied to growth form, branching patterns, and perichaetial position, with a re-evaluation of cladocarpy and 2) provide a classification of terms with amended definitions.

PREVIOUS CONCEPTS OF TERMINOLOGY

Life and growth form.—One of the earliest papers on bryophyte "growth forms" was based on

tropical rainforest epiphytes (Giesenhagen 1910). A critical treatise on growth form ("Wuchsformen") of european mosses emphasized the general, structural organization of the plant (Meusel 1935). Subsequent literature on the classification of growth form has had an ecological emphasis (During 1979, 1990; Gimingham & Birse 1957; Horikawa & Ando 1952; Iwatsuki 1960; Mägdefrau 1982; Proctor & Smith 1995; Richards 1984). A comprehensive review of growth forms from an ontogenetic perspective was presented by Mishler and De Luna (1991). Other systematic studies have examined branch development in association with related structures—pseudoparaphyllia and scaly leaves, rhizoids, and phenology (Akiyama & Nishimura 1993; Ireland 1971; Koponen 1982; Stark 1985; respectively). However, there are few detailed systematic studies on growth form (Deguchi 1978; Nishimura 1985; Zomlefer 1993).

Mägdefrau (1982) restricted the germane use of the term growth form (Gimingham & Birse 1957) by the introduction of the term life form. He defined life form as "the habit of a plant in harmony with its life conditions, . . . the morphological structure of the colony of individuals, the growth form, and modification by external factors." Growth form was defined as the moss shoot or individual, which "has a genetically fixed method of ramification, depending on species, genus or family" (Mägdefrau 1982). His distinction between growth form and life form is clear. The former refers to the individual plant, whereas the latter refers to the aggregate or colony of individuals.

In Mägdefrau's (1982) classification of growth forms, direction of growth was the primary division: orthotropic versus plagiotropic. The misleading concept of his classification was that he equated orthotropic and plagiotropic with fruit terminal versus lateral, respectively. This feature of growth form—direction of growth—has often been included in the definition of pleurocarpy and acrocarpy (Flowers 1973; Magill 1990; Schofield & Hébant 1984; Smith 1978). As well, acrocarpy and pleurocarpy have been described as the two basic "growth forms" in mosses (Mishler & De Luna 1991). However, growth form is based on the structural development of the shoot and branches of an individual plant, including frequency, length, and orientation of the branches (branch system, *sensu* Mishler & De Luna 1991). Perichaetial position is independent of growth form and should be treated separately (Table 1).

Recently, Buck and Vitt (1986) defined two types of branching in pleurocarpous mosses: cauline and axillary. Cauline branches develop on the stem between the leaves, whereas axillary branches develop in the axils of the stem leaves. They designated

cauline lateral branching, and pseudoparaphyllia as unique synapomorphies to distinguish the true pleurocarpous clade (Hypnales, Hookeriales, and Leucodontales), from the acrocarpous and pleurocarpous clade (Bryales). The "pleurocarpous" taxa within the Bryales were defined as having axillary branching.

Subsequently, Hedenäs (1994) considered cauline versus axillary branches in a phylogenetic analysis of selected pleurocarpous taxa, and he observed that both cauline and axillary branch position occur in pleurocarps. He concluded that branch position was too variable to be informative. Beside the variability, many pleurocarps have densely leaved axes, which may preclude the determination of an axillary versus cauline position (i.e., *Spiridens flagellosus*).

A single type of lateral branch development has been described for mosses, whether cauline or axillary in position (Berthier 1972; Chamberlain 1980—*Fissidens*; Crandall 1969—*Fontinalis*; *Leucoloma* pers. observ.). The ultimate position of a lateral branch is determined by the amount of cell elongation and number of cell divisions between the branch primordium and the leaf above it, and the primordium may be displaced to an axillary position of the leaf below it (i.e., *Funaria hygrometrica, Hypnodendron marginatum*).

The terminology used for growth form has been intermixed with life form, perichaetial position, and branching patterns or types. The separation of the terminology into distinct categories facilitates a better understanding of the terms (see Terminology).

Branching pattern.—Fragile subapical or lateral innovations have been described as "epigametophytic plants" in *Leucophanes* (Salazar-Allen 1985). Transverse sections have shown a basal constriction of the branches at the attachment to the main axis, and this constriction causes the branches to be fragile and easily detached. The fragile or tenuous nature of the branches has led to their interpretation as "epigametophytic" plants. Until now, the origin of these branches has not been well understood. These "epigametophytic" plants are derived from loosely attached, fragile, deciduous branches. This type of fragile branching is common in *Leucoloma* (i.e., *L. holstii*) and has been reported for other genera in the Dicranaceae (Newton & Mishler 1994). These branches form either a sympodial pattern from subapical innovations or a monopodial branching pattern from lateral innovations not associated with a terminal perichaetium (i.e., *Leucophanes hildebrandtii* and *L. octoblepharoides*). In *Leucoloma,* the sequence of branch development is from a nonprotruding lateral primordium, to a protruding primordium, to an immature branch

TABLE 1.   The classification and definitions of terms related to life and growth form, branching pattern, and perichaetial position.

I. LIFE FORM
   The structure of an assemblage of individual shoots, branching pattern, and direction of growth, with modification by its habitat (i.e. cushion, dendroid, mat, pendant, tail, turf, weft).
II. GROWTH FORM
   The structure of an individual shoot, including direction of growth, with the length, frequency, and position of branches.
   A. DIRECTION OF GROWTH
      a. orthotropic
         primary axes with erect growth
      b. horizontal
         primary axes growing perpendicular to vertical substrates
      c. plagiotropic
         primary with prostrate growth
      d. pendulous
         primary axes with downward outspreading or pendent growth

   B. BRANCH FORM
      a. Length
      b. Frequency
      c. Position
         1) basitonous
            branches formed at the proximal end of a module
         2) acrotonous
            branches formed at the distal end of a module
         3) axillary
            branches positioned distinctly in the leaf axils
         4) cauline
            branches positioned between the leaves

III. BRANCHING PATTERN
   A. SYMPODIAL
      A branch system that consists of a chain of connected modules of the same level of hierarchy. It occurs at different levels within the branch level hierarchy. Each connected module is defined by a heteroblastic series of leaves.

   B. MONOPODIAL
      A branch system that consists of a module with independent (or unconnected), subsidiary modules (lateral branches) of a different level of the branch hierarchy, derived along the supporting axis. Along the supporting module, an uninterrupted series of leaves is evident at each branch node.

IV. PERICHAETIAL POSITION
   A. ACROCARPY
      A single perichaetium is produced at the terminus of the primary module of the branch system. Subperichaetial primordia may develop for continued growth.

   B. CLADOCARPY
      One or more perichaetia are produced per primary module of the branch system. The primary modules terminate in vegetative growth. The perichaetia are produced at the terminus of lateral branches (secondary or tertiary modules) that have subperichaetial branch primordia or developed branches. Fertile branches do not appear swollen and differentiated from vegetative branches. The juvenile leaf development at the base of fertile branches is morphologically similar to that of the vegetative branches.

   C. PLEUROCARPY
      One or more perichaetia are produced per primary module of the branch system. The primary modules terminate in vegetative growth. Perichaetia are produced along the primary module or secondary modules at the terminus of lateral innovations that lack subperichaetial branch primordia or developed branches. Perichaetial leaf development is ± immediate. Fertile branches commonly appear swollen and differentiated from vegetative branches. Juvenile leaf development on the perichaetial branches is morphologically different from that of the vegetative branches.

→

FIGURE 1.   Perichaetial positions (♀) and branching patterns. — a. acrocarpous (terminal perichaetia), sympodial branching with 1° modules developed from a single subapical innovation. — b. acrocarpous, sympodial branching with 1° modules developed from 2 subapical innovations. — c. acrocarpous, sympodial branching with 1° modules developed from a single subapical innovation and monopodial branching with determinant 2° modules developed from several
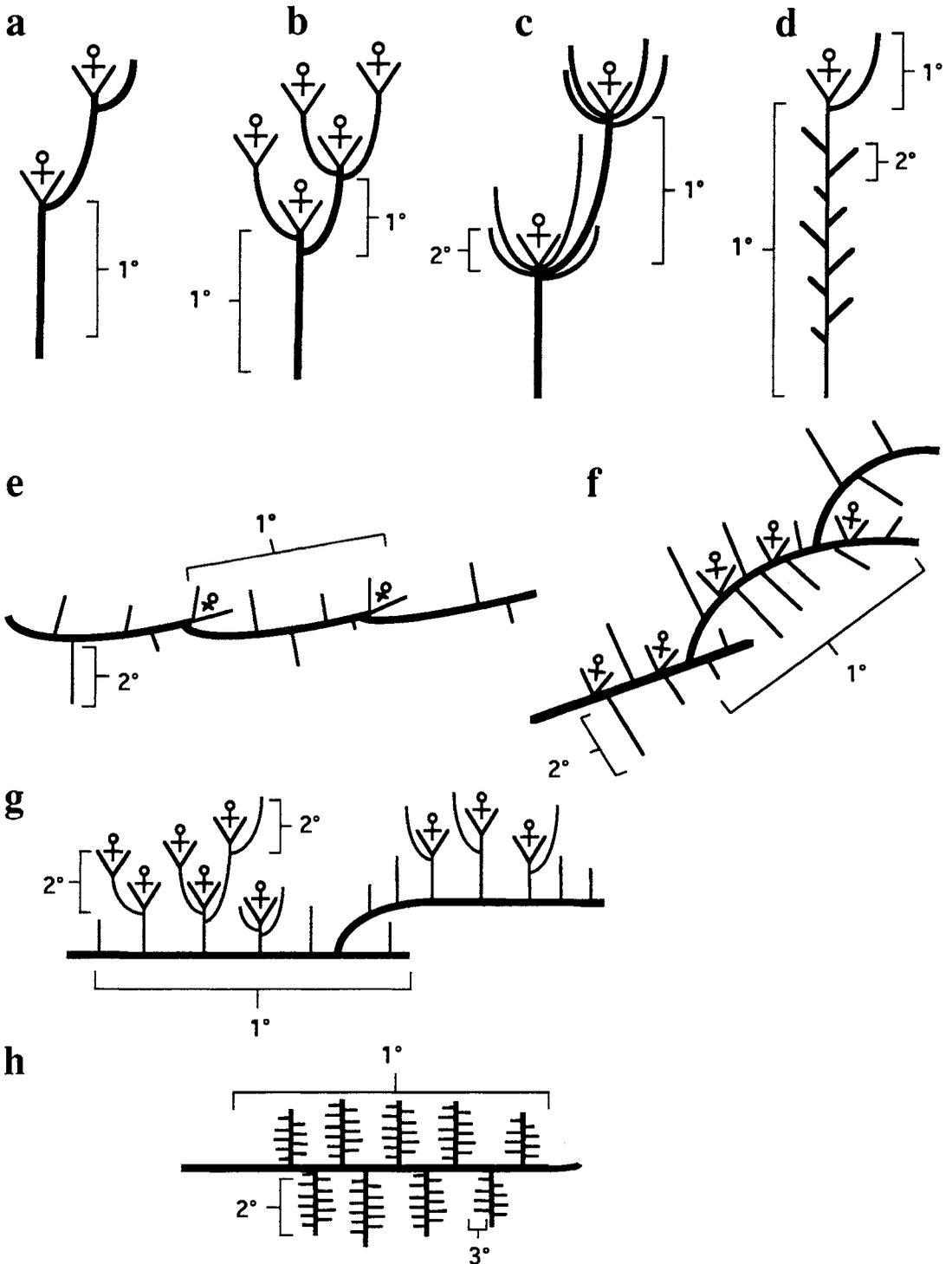
subapical innovations. — d–e. acrocarpous, sympodial branching with 1° modules developed from a single subapical innovation and monopodial branching with 2° modules developed as determinant lateral branches. — f. pleurocarpous (perichaetia terminal on lateral innovations), sympodial branching with 1° modules developed from a lateral innovation, 1° modules have vegetative apices, monopodial branching with 2° modules developed as determinant lateral branches. — g. cladocarpous (perichaetia terminal on lateral branches), sympodial branching with 1° modules developed from a lateral innovation, 1° modules have vegetative apices; sympodial branching with 2° modules developed from subapical innovations; monopodial branching with 2° modules developed from lateral innovations on 1° module. — h. monopodial branching with 2° and 3° modules developed from lateral innovations on 1° or 2° modules, respectively.

DIRECTION		PERICHAETIAL POSITION		
		acrocarpy	cladocarpy	pleurocarpy
SYMPODIAL	orthotropic	Funaria Fissidens Orthotrichum Leucoloma	Cinclidotus Anoectangium Fissidens	Hylocomium Hypnodendron Climacium
	plagiotropic	Hedwigia Sclerodontium Leucoloma Plagiomnium	Macromitrium Fissidens Mesotus	Hylocomium Thuidium
MONOPODIAL	orthotropic	Leucoloma Racomitrium Leucophanes Dicranum	Fissidens Racomitrium	Hylocomium Cratoneuron Calliergon
	plagiotropic	Leucoloma Dicranoloma Rhacocarpus	Macromitrium Fissidens Racomitrium Bryowikia	Ptilium Hypnum Neckera Thuidium
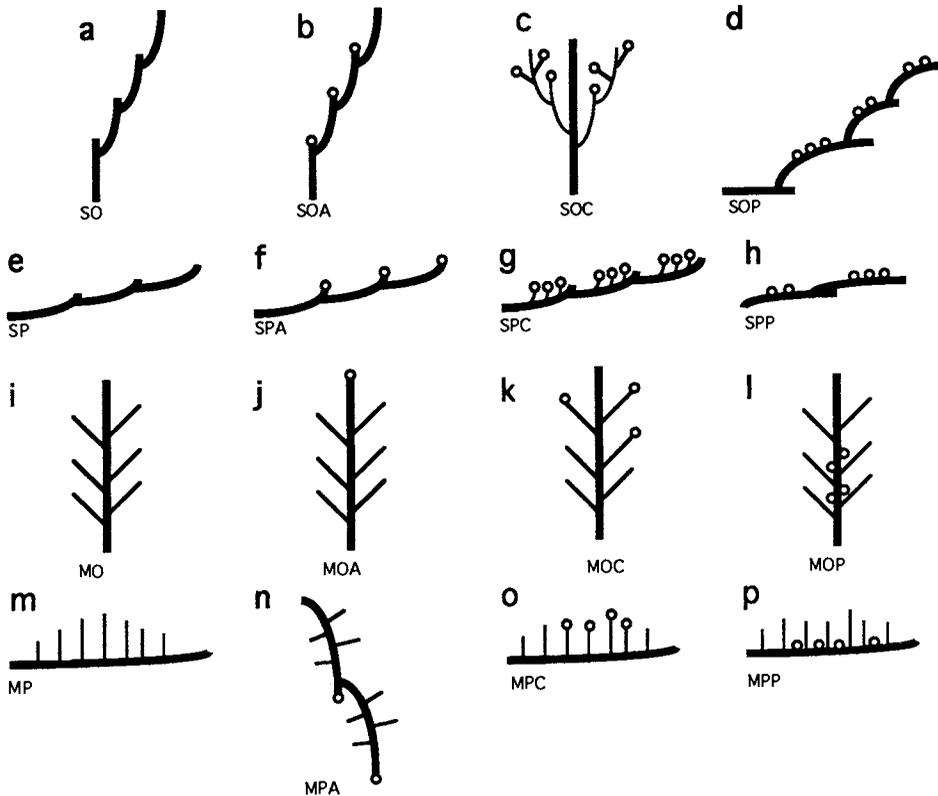
with juvenile leaves, to a mature, branch that is fragile.

Sympodial branching has been misinterpreted as monopodial in a number of revisionary studies (i.e., Horton 1982; Lewinsky 1993). In both *Encalypta* and *Orthotrichum,* the subapical innovations develop a chain of primary modules that form the primary branch system, which is a sympodial pattern.

Branching patterns have often been associated with perichaetial position; acrocarpy with sympodial branching and pleurocarpy with monopodial branching (De Luna 1995). Although there is general correspondence, the terms should be considered separately, for both types of branching can and do occur in plants with all types of perichaetial positions (Fig. 2). Sympodial branching is not restricted to subterminal innovations, rather it is formed by a chain of branches of the same hierarchy (i.e., basal innovations in *Climacium dendroides*). As well, monopodial and sympodial branching often occur in a single species (i.e., *Hylocomium splendens, Leucoloma dichelymoides*).

A system for analyzing the hierarchy of branches in mosses was presented by Mishler and De Luna (1991). The structural organization of an individual moss includes the shoot, branch, modular, and metamer (at the cellular level) systems. These ontogenetic components provide useful tools for analyzing gametophyte structure. Meusel (1935) was the first person to provide a comprehensive survey of branching patterns in mosses and little has followed in the interim. Branching patterns in mosses have been little studied and warrant further investigation to evaluate the evolutionary significance of these patterns.

Perichaetial position.—Bridel (1819) classified species based on the position of the perichaetium. The terms *acrocarpi* and *pleurocarpi* were introduced by Nees von Esenbeck et al. (1823). In Latin, the terms mean terminal and lateral fruit, respectively (Stearn 1983). Mitten (1859) was the first to question the phylogenetic significance of acrocarpy and pleurocarpy and established a classification based primarily on peristome characters. The primary divisions, *acrocarpi* and *pleurocarpi,* were

also rejected by Fleischer (1900–1923) and replaced by peristome criteria.

Pleurocarpy (*sensu lato*) has been recognized as a feature, independently derived within the separate lineages of mosses (Brotherus 1924–1925; Cavers 1911; Crosby 1980, Crum & Anderson 1981; Dixon 1932; Mitten 1859). In the most recent synopsis of the Bryopsida, Vitt (1984) designated the following families to have independently derived "pleurocarpy": Calymperaceae, Fissidentaceae, Gigaspermaceae, Leucobryaceae, Pleurophascaceae, Pottiaceae, Rhizogoniaceae, and Spiridentaceae. The Hookeriales, Hypnales, and Leucodontales were defined as completely pleurocarpous (true pleurocarpy). Crum has viewed the Orthotrichales as the transitional order between acrocarpous and pleurocarpous orders (Crum & Anderson 1981). The occurrence of pleurocarpy within so many disparate lineages (Vitt 1984) has prompted a re-examination of the definition of pleurocarpy and its distribution within mosses.

Superficially, the distinction between acrocarpy and pleurocarpy is not always obvious (De Luna 1990; Mitten 1859, p. 3). Some prostrate mosses have been misclassified initially as pleurocarps (*Leucoloma* Bridel 1827; *Sclerodontium* Crum 1986), but later determined as acrocarps (*Hedwigia ciliata* De Luna 1990; *Rhacocarpus purpurascens* this paper). Prostrate acrocarps that have laterally displaced, terminal perichaetia due to subperichaetial branching have been termed pseudo-pleurocarpous. Vitt (1984) referred to the Orthotrichineae as an acrocarpous suborder with a pseudo-pleurocarpous condition in some of the genera. Two genera referred to as pseudo-pleurocarpous, *Macromitrium* and *Schlotheimia,* are cladocarpous (see below). Proctor and Smith (1995) defined *Cinclidotus* as a "pseudo-pleurocarpous" genus, even though Smith (1978) described the Cinclidotoideae as cladocarpous. Thus, the distinction between cladocarpy and acrocarpy has remained unclear in the literature. Pseudo-pleurocarpy is a growth form modification and does not represent a distinct perichaetial position. It is proposed here that this term be dropped to avoid further confusion. A similar term that has

---

←

FIGURE 2. Genera that have species with the various combinations of growth direction, branching pattern, and perichaetial position. — a–p. Schematic diagrams of sympodial (S), monopodial (M), orthotropic (O), plagiotropic (P), acrocarpous (A), cladocarpous (C), and pleurocarpous (P) features. Circles represent perichaetial position. — a. sympodial orthotropic. — b. sympodial orthotropic acrocarp. — c. sympodial orthotropic cladocarp. — d. sympodial orthotropic pleurocarp. — e. sympodial plagiotropic. — f. sympodial plagiotropic acrocarp. — g. sympodial plagiotropic cladocarp. — h. sympodial plagiotropic pleurocarp. — i. monopodial orthotropic. — j. monopodial orthotropic acrocarp. — k. monopodial orthotropic cladocarp. — l. monopodial orthotropic pleurocarp. — m. monopodial plagiotropic. — n. monopodial plagiotropic acrocarp. — o. monopodial plagiotropic cladocarp. — p. monopodial plagiotropic pleurocarp.

TABLE 2. List of species examined. All La Farge-England specimens are from the private herbarium of C. La Farge-England, the remaining are from ALTA, unless otherwise indicated.

Family	Species	Specimen
ACROCARPOUS TAXA		
Bryaceae	*Leptobryum pryiforme*	*Peterson 4548*
	Mielichoferia macrocarpa	*La Farge-England 5186*
Bartramiaceae	*Bartramia halleri*	*La Farge-England 3537*
	Bartramia pomiformis	*La Farge-England 4144*
	Bartramia sticta	*La Farge-England 4121*
	Leiomela africana	*La Farge-England 5342*
Calymperaceae	*Leucophanes candidum*	*Tan & Tandang, 1982 82–09*
	Leucophanes hildebrandtii	*Pócs & Kornas 6531/E*
	Leucophanes octoblepharoides	*Vitt 33433a*
Dicranaceae	*Dicranoloma blumei*	*Weber & McVean B–34890*
	Dicranum scoparium	*Ireland 21330*
	Leucoloma dichelymoides	*La Farge-England 5960*
	Leucoloma fontinaloides	*La Farge-England 6328*
	Leucoloma holstii	*La Farge-England 5525*
	Leucoloma humbertii	*La Farge-England 6325*
	Leucoloma sanctae-mariae	*La Farge-England 6103*
	Sclerodontium clavinerve	*Petics s.n.* FH
	Sclerodontium pallidum	*Schofield 51446*
Ditrichaceae	*Distichium capiillaceum*	*Vitt 34153*
Encalyptaceae	*Encalypta procera*	*Vitt 33836*
	Encalypta spathulata	*Vitt 35445*
Fissidentaceae	*Fissidens bryoides*	*Olsson 18/483*
Funariaceae	*Funaria hygometrica*	*Turner 9773*
Grimmiaceae	*Racomitrium canescens*	*MacFadden s.n.*
	Racomitrium ericoides	*Horton 5643*
Hedwigiaceae	*Hedwigia ciliata*	*La Farge-England 5255*
	Hedwigidium imberbe	*Cleef 6942*
Mitteniaceae	*Mittenia plumula*	*Fife 7079*
Mniaceae	*Cryptopodium bartramioides*	*Vitt 29618*
	Leucolepis menziesii	*La Farge-England 8125*
	Mnium spinulosum	*Handke s.n.*
	Plagiomnium ciliare	*Churchill 9350*
	Rhizomnium glabrescens	*La Farge-England 8138*
	Rhizomnium punctatum	*Florin s.n.*
Orthotrichaceae	*Orthotrichum lyellii*	*La Farge-England 8124*
	Orthotrichum obtusifolium	*Vitt 15158*
	Orthotrichum speciosum	*Vitt 13779*
	Zygodon cf. microtheca	*La Farge-England 8097*
	Zygodon gracillimus	*Bartlett 15148*
Pottiaceae	*Leptodontium viticulosoides*	*Zander 1972*
Rhacocarpaceae	*Rhacocarpus purpurascens*	*Griffin PV–1292*
Timmiaceae	*Timmia bavarica*	*La Farge 308a*
Splachnaceae	*Tayloria hornschuchii*	*La Farge-England 3829*
CLADOCARPUS TAXA		
Bryaceae	*Mielichoferia bryoides*	*Fife 7269*
Dicranaceae	*Mesotus celatus*	*Fife s.n.* ex CHR *103959*
Cryphaeaceae	*Acrocryhaea gardneri*	*Wright 150*
	Acrocryhaea coffeae	*Clayton B-390*
	Acrocryhaea robustum	*De Sloover 18.717*
	Cryphaea dilatata	*Vitt 27229*
	Cryphaea exannulata	*Vitt 27416*
	Cryphaea exigua	*De Sloover 18555*
	Cryphaea fasiculosa	*Lopez 8697*
	Cryphaea filiformis	*Buck 7899*
	Cryphaea glomerata	*Allen & Magill 4702*
	Cryphaea orizabae	*Larsen, Santisuk, Warncke 2719*
	Cryphaea tenella	*Vitt 28067*
	Dendrocryphaea tasmamanica	*Vitt 29343, 29400*
Eropodiaceae	*Venturiella sinensis*	*Noguchi 117*
Fissidentaceae	*Fissidens adianthoides*	*La Farge-England 3540*
	Fissidens cristatus	*Schofield 53205*
	Fissidens taxifolius	*La Farge-England 3484*

TABLE 2.   Continued.

Family	Species	Specimen
Gigaspermaceae	*Gigaspermum repens*	*Oliver, Tolken, Venter 649*
Grimmiaceae	*Racomitrium lanuginosum*	*Schofield 93253*
Orthotrichaceae	*Macromitrium loamense*	*Hegewald 7458*
	Schlotheimia apressifolia	*Weir 72* NY LT!
	Schlotheimia robusticuspis	*Schofield 64722, Ule 1417* H LT
	Schlotheimia serricalyx	*Ule 902* H LT
	Schlotheimia torquata	*Allen 11949, Vitt & Buck 11441, Yano 1237*
	Ulota magellanica	*Schäfer-Verimp & Verimp s.n.*
Pleurophascaeae	*Pleurophascum grandiglobum*	*Vitt 29235*
Pottiaceae	*Anoectangium aestivum*	*Vitt 19766*
	Cinclidotus fontinalioides	*De Sloover 45168*
	Ganglea angulosa	*Vital & Buck 20053*
	Molendoa sendtneriana	*Vitt 10939*
Rhizogoniaceae	*Hymenodontopsis streimannii*	*De Sloover 46780*
	Pyrrhobryum spiniforme	*La Farge-England 5375, 5377*
	Rhizogonium dozyanum	*Ando, Oct. 24, 1976*
	Rhizogonium novae-hollandiae	*Vitt 10360*
(?)	*Bryowijkia ambigua*	*Larsen, Santisuk, Warncke 2877*
PLEUROCARPUS TAXA		
Amblystegiaceae	*Calliergon giganteum*	*Steere 15507*
	Campylium stellatum	*Vitt 23943*
	Cratoneuron filicinum	*La Farge-England 3491*
	Drepanocladus aduncus	*Hermann 26506*
Brachytheciaceae	*Kindbergia oreganum*	*La Farge-England 8141*
	Eurhynchium pulchellum	*La Farge-England 2957*
Climaciaceae	*Climacium dendroides*	*Moxley 103*
Cryphaeaceae	*Cryphaea borneensis*	*van Zanten 57*
	Cryphaea patens	*Frahm, 23.3.79*
	Cyptodontopsis obtusifolia	*Suzuki 1612*
Cryptopodiaceae	*Bescherellia elegantissima*	*Koponen 33971*
Fontinalaceae	*Dichelyma capillaceum*	*Ley 961*
	Dichelyma japonica	*Toyohara s.n.*
	Fontinalis neomexicana	*Naas, May 14/17*
Hookeriaceae	*Daltonia angustifolia*	*La Farge-England 5360*
	Hookeria luscescens	*La Farge-England 8143*
	Hookeriopsis papillosulum	*La Farge-England 5752*
	Lepidopilidium attenuatum	*La Farge-England 5823*
Hylocomiaceae	*Hylocomium splendens*	*La Farge-England 2873*
Hypnaceae	*Hypnum hamulosum*	*Vitt 5474*
	Leucomium sp.	*La Farge-England 5527, 5823*
	Ptilium crista-castrensis	*La Farge-England 5051*
Hypnodendraceae	*Hypnodendron marginatum*	*Schofield 49036, Vitt 29689*
	Hypnodendron spininerve	*Schofield 49052*
Hypopterygiaceae	*Hypopterygium novae-seelandiae*	*Vitt 8281*
Leptodontaceae	*Pseudocryophaea flagellifera*	*Frahm 1997*
Leucodontaceae	*Alsia californica*	*Schofield 76048a*
	Dozya japonicum	*Mizutani 13730*
	Leucodon julacea	*Vitt 33710*
Meteoriaceae	*Aerobryidium subpiligerum*	*La Farge-England 5359*
	Meteorium miquelianum	*Streimann & Tamba 12210*
Neckeraceae	*Neckera douglasii*	*La Farge-England 2876*
	Neckera pennata	*Harms & Wright 25782-G*
	Porothamnium bigelovii	*La Farge-England 8132*
	Porothamnium stipitatum	*La Farge-England 6326*
Plagiotheciaceae	*Isopterygium elegans*	*La Farge-England 8135*
	Plagiothecium undulatum	*La Farge-England 8130*
Racopilaceae	*Racopilum convolutaceum*	*Vitt 27429*
Rhytidiaceae	*Rhytidiadelphus loreus*	*La Farge-England 8137*
Spiridentaceae	*Spiridens baliforianus*	*Gardner s.n.*
	Spiridens flagellosus	*Fleischer 1162*
	Spiridens muelleri	*Vitt 28480*
	Spiridens reinwardtii	*De Sloover 42867*
Thuidicaeae	*Claopodium crispifolium*	*La Farge-England 8129*
	Heterocladium macounii	*La Farge-England 8140*
	Thuidium abietinum	*Redfearn 36411*
	Thuidium tamariscinum	*La Farge-England 3448*

been applied to the Hedwigiaceae and Orthotrichaceae is "pseudoakrocarp" (Meusel 1935, p. 266), although a formal definition of the term has not been found.

Cladocarpy is another term that has been used for perichaetial position. It was designated as one of six classes for the perichaetial position in *Sphagnum* and *Archidium* (Bridel 1826). Mueller (1949) did not use *cladocarpi* as a formal division, although he designated several taxa within the subclass of acrocarpous taxa as cladocarpous, and stated that some pleurocarpous taxa often approach cladocarpi. As well, Schimper (1860) did not use cladocarpi as a formal division of mosses. In an artificial classification of the genera, Lesquereux and James (1884) used the term cladocarpi for *Fontinalis, Dichelyma,* and *Cryphaea.* Fleischer (1900–1923) used the term cladocarp with reference to mosses that produce terminal perichaetia on lateral branches. Commonly, cladocarpy has been defined as a type of pleurocarpy (Frey 1971; Magill 1990; Mishler & De Luna 1991).

The distinction remains unclear between cladocarps and acrocarpous taxa with basitonous branches that produce terminal perichaetia. The Rhizogoniaceae were included within the concept of pleurocarpy (*sensu lato*) by Buck and Vitt (1986), whereas Koponen (1988) considered them an acrocarpous family. Koponen (1988) interpreted the perichaetial position of taxa in *Pyrrhobryum* sect. *Pyrrhobryum* as acrocarpous. These taxa develop terminal perichaetia on branches of determinant sterile shoots or branches of other fertile shoots (see cladocarpy in Terminology). Buck and Vitt (1986) described the family as pleurocarpous based on the interpretation of "non-terminal perichaetia," because the primary axis does not terminate with perichaetia.

Additional confusion exists between cladocarpy and pleurocarpy. Cladocarpy is commonly referred to as perichaetia on short lateral branches and pleurocarpy as perichaetia lateral. If the only difference between cladocarpy and pleurocarpy is the length of the lateral branch, when is there sufficient branch development to determine a cladocarp? For example, Lawton (1971) defined pleurocarpy as "having archegonia and later seta and capsule on short side branches and not at the apices of stems or branches" (i.e., *Homalothecium megaptilum* and *Hylocomium splendens*). Her definition of cladocarpy, "having fruit terminal on short lateral shoot," is difficult to differentiate from her definition of pleurocarpy. Dixon (1924) noted the difficulty of many pleurocarpous mosses with perichaetia that "appear to be terminal on very short lateral" branches. He explained that examination of the axis will show that it is "only an elongation of the perichaetium,

originating in a lateral bud on the stem, containing the archegonia; the elongation taking place after fertilization . . . ." This difference warrants clarification.

This difficulty in distinguishing cladocarpy from pleurocarpy is exemplified by the following: True pleurocarps (*sensu* Buck & Vitt 1986) are typified by lateral perichaetia that lack branch elongation. Hand sections through the lateral perichaetial axes of species of *Aerobryidium, Daltonia, Drepanocladus, Hypnum, Leucomium, Neckera,* and *Rhytidiadelphus* show minimal development below the unfertilized perichaetium. Yet in some cladocarpous species, the perichaetial axes of *Anoectangium aestivum, Fissidens crisatatus,* and *Mielichoferia bryoides* are extremely reduced. The question remains, are the perichaetial axes of true pleurocarps developmentally the same as cladocarps with extremely reduced axes, or is the reduced axis length an example of convergent evolution (Tables 1, 2; Terminology)?

Hedenäs (1994) defined a pleurocarpous, diplolepideous moss as "a diplolepideous moss . . . where the sporophytes are inserted on shortened and laterally inserted, specialized, perichaetial branches, with only more or less specialized leaves (perichaetial leaves)." He does not distinguish cladocarpy. This is evident from his character analysis where he defines perichaetial position as having two states: "archegonia terminal on shoots or on apparently undifferentiated branches (0) or archegonia on short specialized branches (always with more or less strongly modified perichaetial leaves) (1)." His classification of *Schlotheimia,* coded as state (0 or 1), indicates that he considers it polymorphic-cladocarpous and pleurocarpous (Hedenäs 1994, p. 235). My examination of *S. appressifolia, S. robusticuspis, S. serricalyx,* and *S. torquata* indicates that all of these species are cladocarpous. The perichaetia are terminal on lateral branches of the primary axis and have subperichaetial innovations. In Hedenäs' analysis, acrocarpy and cladocarpy are coded as the same state.

With respect to the evolution of acrocarpy, cladocarpy, and pleurocarpy, a number of conceptual differences are present. Vitt (1984) described a "hypothetical, primitive Bryalean moss" as acrocarpous and interpreted pleurocarpy as an "derived" condition, whereas Miller (1971) was noncommital. Cladocarpy has been inferred as a transitional state between acrocarpy and pleurocarpy (Crum & Anderson 1981; De Luna 1995—the use of ordered character states; Hedenäs 1994). Elsewhere, cladocarpy has been defined as a specialized type of pleurocarpy (Mishler & De Luna 1991).

Several questions arise from the current usage of terminology of perichaetial position 1) Is pleuro-

carpy distinct from cladocarpy? 2) Is cladocarpy related to acrocarpy? 3) Should cladocarpy be recognized as a distinct category of perichaetial position? 4) Are there any attributes of cladocarpy, acrocarpy, or pleurocarpy that have been overlooked as distinguishing features? and 5) Are there any evolutionary implications based on the distribution of the perichaetial types within the Bryopsida?

TERMINOLOGY

The terms related to moss structure and perichaetial position can be classified into four categories: life form, growth form, branching pattern, and perichaetial position (Table 1). The amended definitions presented here are based on the examination of specimens cited in Table 2. These categories provide a terminology that can be applied independently to each species examined.

Life Form.—Life form is the overall organization of growth form, branching pattern, general assemblage of individuals, and modification of a population by the environment (i.e., cushions, turfs, wefts; Table 1). There is a diverse range of moss life forms that have an integral relationship with their microhabitat (During 1990; Mägdefrau 1982; Richards 1984). For example, cushions are compact tufts of erect stems that commonly form in dry exposed habitats (i.e., *Grimmia anodon,* on rock outcrops). The density of the stems provides protection against desiccation of the individual plants (During 1990). Thus, the aggregate population functions as a single life form providing an adaptation to its xeric habitat. Environmental modification of the life form of a population is evident in *Hylocomium splendens,* which forms prostrate wefts under mesic forest conditions or erect turfs in exposed, tundra habitats (During 1990; Schofield & Hébant 1984). Life form is the overall structure of a group of individuals occurring in a specific habitat.

Growth form.—Growth form is the structural architecture of the individual moss plant (Table 1). The structure of an individual plant can be analyzed as a hierarchy of modules (Fig. 1; Mishler & De Luna 1991). A module is the product of a single apical meristem (White 1984).

The direction of growth in mosses is diverse and depends on factors such as gravity, phototropism, and substrate. Orthotropic taxa have erect growth, whereas plagiotropic taxa have prostrate growth. Ascending stems are an intermediate direction. Horizontal growth, defined as perpendicular on vertical substrates, is common for epiphytic mosses in the tropics (i.e., *Rutenbergia* on tree trunks, *Daltonia* on bamboo stems). Within taxa classified as pendulous ("drooping", i.e., Meteoriaceae), some species have downward, outspreading stems (i.e.,

Leucoloma sanctae-mariae, Neckera pennata). The direction of growth may change during the maturation of an individual plant.

In certain mosses, the stems are unbranched (i.e. *Leptobryum pyriforme;* Fig. 1a), while other mosses develop simple branched stems by one to several subapical innovations for continued growth (i.e., *Dicranum, Grimmia, Orthotrichum);* Fig. 1b). Some mosses produce subapical whorls of branches (i.e., *Philonotis fontana;* Fig. 1c). Mosses with complex branch development (cladotaxies) produce lateral, secondary branches at either irregular or regular intervals (i.e., *Amblystegium* spp., *Cinclidotus fontinaloides,* respectively) or pinnate branches (i.e., *Ptilium crista-castrensis).* *Heterocladium macounii* is tripinnate, developing a hierarchy of four branch levels. The frequency of branch primordia does not necessarily imply the development of branches. In acrocarpous or cladocarpous species naked primordia or innovations with the initial juvenile leaf development are usually visible when the leaves are removed from a stem or branch (*Leucoloma, Macromitrium).* In pleurocarps, the lateral primordia develop immediately into branches or lie dormant as buds or primordia along the axes (i.e., *Climacium, Neckera).* The distribution of the primordia or buds varies between taxa, resulting in diverse cladotaxies (Table 2; Koponen 1982). The branch length can be highly variable within a species (i.e., *Racomitrium lanuginosum,* Tallis 1959) or follow a predictable pattern (i.e., *Ptilium).* Physiological factors have a direct effect on the patterns of development, maturation of branches, and ultimately growth form (Chopra & Kumra 1988).

Basitonous and acrotonous branching are two specialized branch positions (Table 1). Mosses with basitonous branches develop branches at the proximal end of a module (i.e., *Rhizogonium novae-hollandiae;* Bryineae—Fig. 3), whereas mosses with acrotonous branches have branch development restricted to the distal end of a module (i.e., *Orthotrichum* spp.; Figs. 1a–c).

Branching pattern.—There are two basic patterns of branching—sympodial and monopodial, each consisting of a hierarchy of modules (Table 1). A sympodial pattern has a chain of connected modules from the same level of branch hierarchy. For example, a primary branch system consists of a series of primary modules. A primary module is the first axis of a gametophore, or it is the product of a lateral initial that forms the primary branch system (Figs. 1a–g). The sympodial pattern occurs in acrocarps, cladocarps, and pleurocarps at various levels of the branch hierarchy (Meusel 1935; Figs. 1b, g; 2a–h, n).

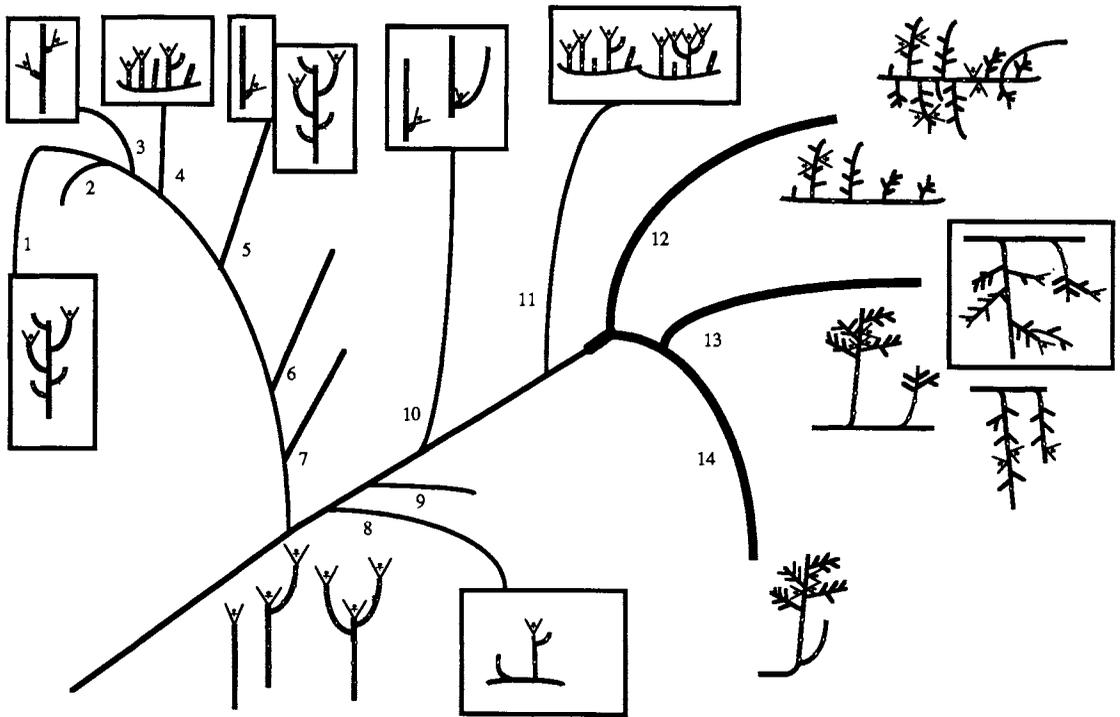The most common sympodial pattern in acro-

FIGURE 3. A proposed cladogram based on Vitt (1984) and Buck and Vitt (1986), illustrating the 14 major lineages of arthrodontous mosses. The boxes indicate lineages where cladocarpous taxa occur. The thickened line indicates the pleurocarpous lineages. The thinner lines represent the acrocarpous lineages. The corresponding taxa for the numbered lineages are as follows: 1—Grimmiineae, 2—Seligeriineae, 3—Fissidentineae, 4—Dicranineae, 5—Pottiineae, 6—Encalyptineae, 7—Buxbaumiineae, 8—Funariineae, 9—Splachnineae, 10—Bryineae, 11—Orthotrichineae, 12—Hypnineae, 13—Leucodontineae, 14—Hookeriineae.

carps is the primary branch system, derived from subapical innovations. The apical meristem of a primary module is consumed in the production of the archegonia, or vegetative if the apical cell has been damaged. *Leucoloma albo-cinctum* develops a single subapical innovation, whereas *L. sanctae-mariae* commonly has two subapical innovations that form the primary branch system.

In pleurocarps, the terminus of a primary module is vegetative (Figs. 1f; 2d, h, l, p). A common sympodial branching pattern in pleurocarps is from the development of a lateral initial that develops a functional primary module. Examples of pleurocarpous species that can develop sympodial branching include *Climacium dendroides, Hylocomium splendens* (Fig. 1f), and *Thuidium matarumense* (Touw 1976). These species also have monopodial branching (see below).

Sympodial branching often occurs in secondary branch systems in some cladocarpous species (Fig. 1g). Chamberlain (1980) has observed up to five, repeated secondary modules in *Fissidens cristatus* that form a sympodial pattern. Lateral branches with terminal perichaetia produce subapical innovations that in turn produce innovations below the

terminal perichaetia (i.e., *Macromitrium loamense,* Fig. 4h).

In monopodial branching, the branches are produced along the main axis by subsidiary, lateral innovations (Table 1). These lateral branches form a series of unconnected 2° or 3° modules along a 1° or 2° module, respectively, whereas sympodial branches are a chain of connected modules of the same hierarchical level (Figs. 1h, 2i–m, o–p). Pinnately branched taxa are elegant examples of monopodial branching (*Ptilium crista-castrensis*). Bipinnate or tripinnate branches in Thuidiaceae are examples of secondary and tertiary monopodial branches (Fig. 1h).

Monopodially branched axes are common in pleurocarpous mosses, yet are not restricted to them. In monopodial development, there is no interruption of leaf size at the branching points along the supporting axis. Examples of monopodial branching in acrocarpous and cladocarpous taxa include: Dicranaceae: *Dicranoloma blumei, Dicranum scoparium, Leucoloma holstii, L. dichelymoides, L. humbertii, Leucophanes candidulum*; Fissidentaceae: *Fissidens* spp.; Grimmiaceae: *Racomitrium lanuginosum*; Pottiaceae: *Cinclidotus fontinaloides*; Rhacocarpaceae—

Rhacocarpus purpurascens; and *Bryowijkia ambigua* (Fig. 2).

Perichaetial position.—Acrocarpy, cladocarpy, and pleurocarpy are the three perichaetial positions in mosses. The definitions are presented in Table 1. The schematic illustrations of acrocarps (Figs. 1a–d, 2b, f, j, n), cladocarps (Figs. 1g, 2c, g, k, o), and pleurocarps (Figs. 1f, 2d, h, l, p) illustrate a range of growth forms, but are not exhaustive.

In some acrocarpous mosses, a single subapical innovation develops and laterally displaces the terminal perichaetium (Figs. 1c, 2f). These sympodially branched, prostrate acrocarps possess a chain of primary modules, each terminating with a perichaetium (i.e., *Hedwigia ciliata, Racomitrium canescens, Rhacocarpus purpurascens*). Confusion with pleurocarpy is clarified by the heteroblastic leaf series along the single chain of primary modules (Berthier 1972, Mishler & De Luna 1991). At the base of each primary module, a series of juvenile leaves is present that indicates the development of a new branch. These leaves are generally reduced in size and differ morphologically from mature leaves. These subperichaetial branches are easily removed for the examination of the juvenile leaves. In contrast, pleurocarps have a branch system that has lateral perichaetia along a single module, with an uninterrupted leaf series. The leaf series does not change size or shape at the fruiting points.

The similarity of pleurocarpy to cladocarpy is that the apical meristem of the primary module (or axis) continues to grow during the production of the perichaetia at the terminus of lateral meristems (Table 1). However, distinction between cladocarpy and pleurocarpy is found in the sequence of leaf development on the perichaetial branch. In cladocarps, the lateral innovation initially develops juvenile leaves at the base of the branch, followed by a series of mature leaves that grade into perichaetial leaves and terminates with the production of archegonia (Fig. 4i). The development of the juvenile leaves through mature leaf development is the same on a vegetative or perichaetial branch of cladocarps. The terminal development of the perichaetial leaves and perichaetium is equivalent to that in acrocarps.

In true pleurocarps, the sequence of leaf development is modified. The lateral innovation develops juvenile leaves that are morphologically different from the juvenile leaves of a vegetative branch (Fig. 5). The transition from juvenile leaves to the perichaetial leaves is typically abrupt. The lack of elongation between the leaf nodes is in contrast to those of the vegetative branches. The perichaetial leaves and archegonia develop at the terminus of the innovation as in acrocarps and cladocarps, and

the result is the production of lateral perichaetial branches (or buds—Ireland, 1982) along the primary module, that appear sessile (Fig. 4a, b). The perichaetial leaves are typically enlarged and strongly differentiated from the mature vegetative leaves; as well the perichaetial branch is commonly swollen. These features differentiate vegetative branches from perichaetial branches in pleurocarps (Fig. 4a).

In the development of an apical meristem, or in this case a lateral meristem (innovation), each metamer (*sensu* Mishler & De Luna 1991) produces a lateral branch initial cell (Berthier 1972). In cladocarpous taxa, primordia develop from the branch initials below the perichaetium that either remain dormant or develop further lateral branching (i.e., *Bryowijkia ambigua, Cinclidotus fontinaloides, Cryphaea exigua, Fissidens taxifolius, Macromitrium longifolium, Mesotus celatus, Pyrrhobryum spiniforme, Racomitrium lanuginosum*; Figs. 4c–i). The dormant primordia (pale patches or protuberances of small meristematic cells) or dormant buds are visible along the axes. Often there is abundant rhizoid development at the base of the perichaetial branch in cladocarps.

In true pleurocarps (i.e., *Hypnum, Hookeria,* and *Brachythecium*), the perichaetial branches have lateral branch initials that do not develop primordia below the perichaetia, and therefore lack subperichaetial branches (Figs. 4a–b). The lateral innovations in pleurocarps have truncated branch development in which the perichaetium develops from a lateral bud (Dixon 1924). This pattern of development is termed paedomorphosis, or specifically progenesis—a process of heterochrony that exhibits an early cessation of growth in the descendent (Mishler & De Luna 1991). Heterochronic processes that alter rates of development provide potential for new phenotypes that are dramatically different from those of ancestors (Rothwell 1987). The distinctive features of pleurocarpous perichaetial branches are 1) the development of juvenile perichaetial leaves that are morphologically different from juvenile leaves of vegetative branches (Fig. 5); 2) the lack of primordia or branching below the perichaetium (Fig. 4); 3) the appearance of swollen fertile branches in comparison to the vegetative branches; and 4) a general lack of rhizoid development at the base of the lateral perichaetial innovation.

Genera that have representative species for each of the combined categories—direction of growth, branching pattern, and perichaetial position are designated (Fig. 2). Previously, these categories have been interpreted as linked, however, no strict correlation occurs between any two terms. Therefore, pleurocarps are not restricted to a prostrate growth form, nor do acrocarps only have sympodial
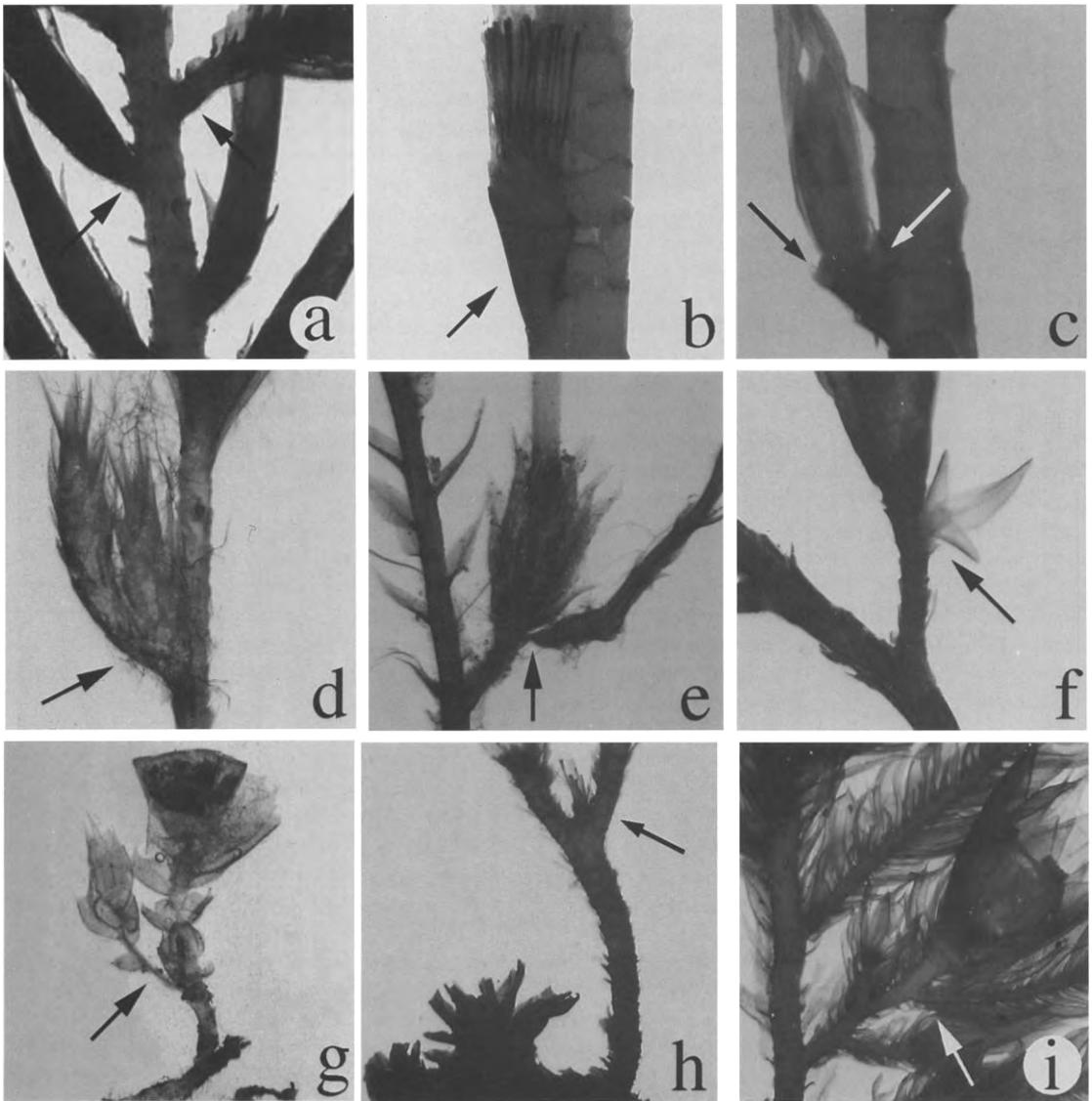
FIGURE 4.   Perichaetial position. Specimen citation for each species is found in Table 2. — a–b. Pleurocarpy. — a. *Dozya japonica,* left arrow indicates perichaetial innovation lacking subperichaetial primordia or branches. Right arrow indicates a vegetative branch. — b. *Spiridens muelleri,* perichaetial innovation lacking subperichaetial primordia or branches. — c–i. Cladocarpy. — c. *Fissidens cristatus,* black and white arrows indicate subperichaetial buds in early development. — d–i. Black or white arrow indicates subperichaetial branches. — d. *Anoectangium aestivum.* — e. *Mielichoferia bryoides.* — f. *Cinclidotus fontinaloides.* — g. *Pleurophascum grandiglobum.* — h. *Macromitrium loamense.* — i. *Bryowijkia ambigua.*

branching. A schematic diagram representing each possible combination of branching pattern, direction and perichaetial position is presented (Figs. 2a–p). Thus an independent assessment of growth form, branching pattern, and perichaetial position is advocated to evaluate the structural elements of a taxon for potential systematic value.

IMPLICATIONS OF THE TERMINOLOGY

The terminology commonly used for the structural organization of mosses has been classified and presented with amended definitions. When defined precisely, these terms can be evaluated as potential synapomorphies for phylogenetic analyses. For example, what is the pattern of distribution for the multistate character, perichaetial position? Although the phylogenetic arrangement of the Bryopsida suborders (excluding Tetraphidales, Polytrichales, and Archidiineae) is provisional, and not meant as a rigorous cladistic analysis, it is used here as a framework for 14 major suborders of mosses (Vitt 1984, figs. 28, 29). Subsequent mod-
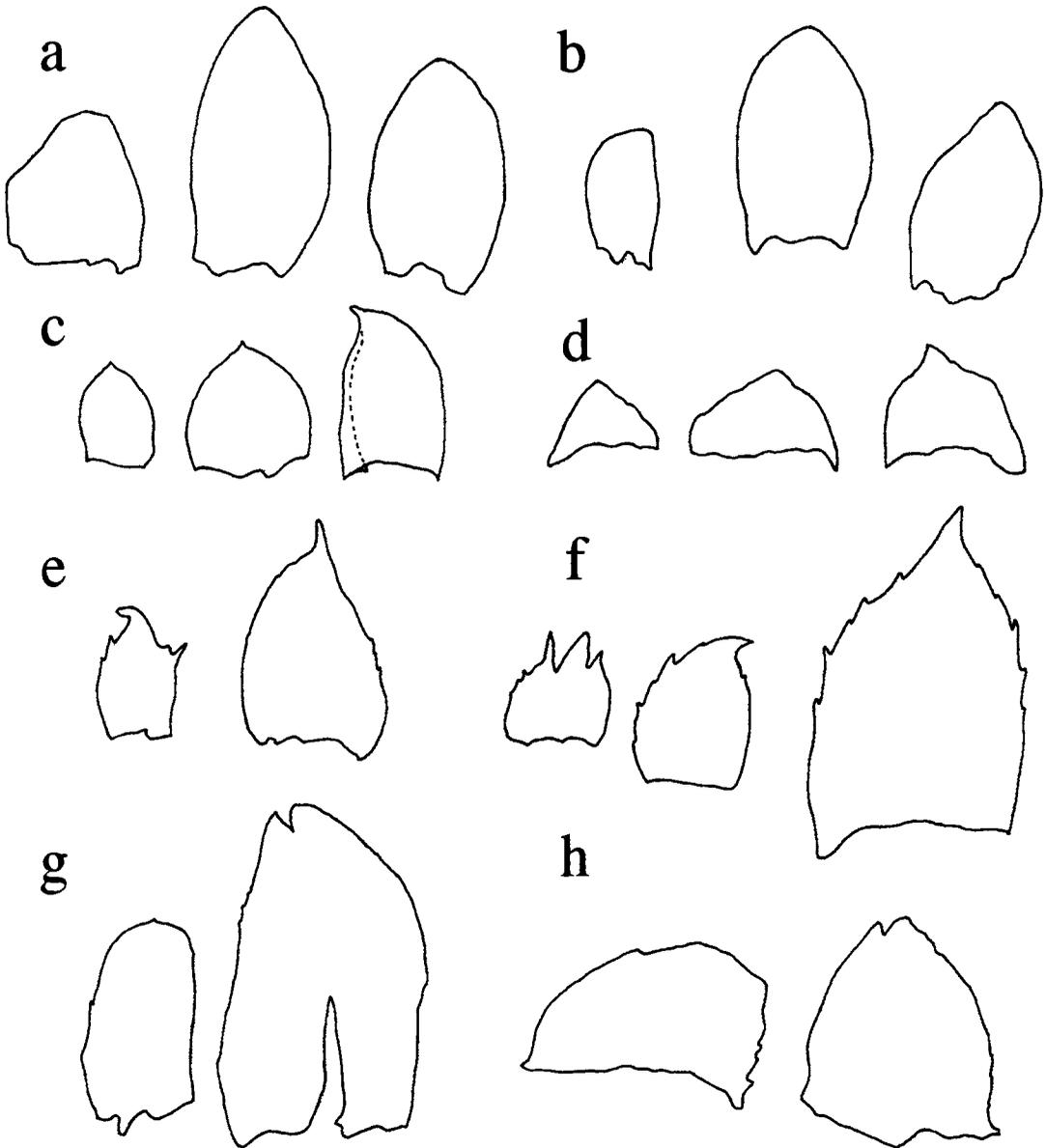
FIGURE 5. Juvenile leaves. — a, c, e, g. Leaves of vegetative branches. — b, d, f, h. Leaves of perichaetial branches. — a–b. cladocarpous, *Cryphaea tasmanica* (*Vitt 29343* ALTA). — c–d. pleurocarpous, *Porothamnium stipitatum* (*La Farge-England 6326*, priv. herb). — e–f. pleurocarpous, *Bescherellia elegantissima* (*Koponen 33971* ALTA). — g–h. pleurocarpous, *Aerobryidium subpiligerum* (*La Farge-England 5359*, priv. herb.).

ifications and interpretations of the phylogenetic relationships of the diplolepideous mosses have been recently published (Buck & Vitt 1986; De Luna 1995; Hedenäs 1994). Using the amended definitions presented here, the following hypotheses are proposed: 1) acrocarpy is the plesiomorphic state, with the Funariineae as the basal group (outgroup comparison: Polytrichales, Tetraphidales, and Andreaopsida; Vitt 1984); 2) cladocarpy has evolved independently within selected taxa of at least 11 distinct families (Table 2); and 3) pleurocarpy is

restricted to the Hookeriineae, Hypnineae, and Leucodontineae; these lack any acrocarpous taxa (De Luna 1990, 1995; see below). Several implications follow from these proposals.

— Buck and Vitt (1986) defined the Rhizogoniineae to include the Rhizogoniacanae and the Racopilacanae. After examination of representative species of *Racopilum* and *Hypopterygium,* I agree with Koponen (1988) that the Racopilanae should be classified in the pleurocarpous clades (as Vitt 1984). The Rhizogoniacanae consists of the Rhi-

zogoniaceae and the Spiridentaceae (Buck & Vitt 1986). Koponen (1988) interpreted the Rhizogoniaceae as acrocarpous, not pleurocarpous. Cladocarpy occurs in genera of the Rhizogoniaceae, with the perichaetia terminal on lateral, basitonous to acrotonous branches (Koponen 1988). *Pyrrhobryum spiniforme* and *Rhizogonium novae-hollandiae* have subperichaetial primordia and branching, that indicate cladocarpy. The Spiridentaceae and the Hypnodendraceae are interpreted here as pleurocarpous. Brotherus (1909) placed *Spiridens* near *Bescherellia* and *Cryptopus*. This relationship should be reconsidered. With the removal of the Racopilacanae, Spiridentaceae, and Hypnodendraceae (Buck & Vitt 1986), the Bryales represent an acrocarpous-cladocarpous clade, concordant with the Dicranales, Fissidentales, Funariales, Grimmiales, Pottiales, and Orthotrichales.

— *Rhacocarpus purpurascens* previously has been classified as a pleurocarp (Brotherus 1925; De Luna 1995; Vitt & Buck 1984). It is a prostrate acrocarp, with a monopodially and sympodially branched axis (Fig. 2f). Hence, the systematic position of the monotypic Rhacocarpaceae should be re-evaluated and its relationship to the Hedwigiaceae reconsidered.

As well, *Bryowijkia ambigua* has been classified as a pleurocarp and removed from the Hedwigiaceae (Hedwigiaceae—Brotherus 1925, Trachypodiaceae—De Luna 1995, Vitt & Buck 1984). The rationale for removing *Bryowijkia* from the Hedwigiaceae was based partially on a pleurocarpous interpretation (De Luna 1995) and its lack of subperichaetial branching (Vitt & Buck 1984). Vitt and Buck (1984) excluded it from all acrocarpous mosses based on profuse branching and from the Orthotrichaceae based on the lack of subperichaetial branching, elongate leaf cells, and differentiated alar cells. However, the perichaetia are terminal on well developed branches and subperichaetial branching is evident (Fig. 4i). Consequently, *Bryowijkia ambigua* is a cladocarpous species that has a creeping primary axis and densely leaved, highly branched secondary axes with terminal perichaetia on tertiary branches. The dimorphic, primary versus secondary branch leaves, the densely papillose leaf cells, strong single costa, profusely branched plants without pseudoparaphyllia, densely leaved branches, and cladocarpy comply with the Orthotrichales. Therefore, a re-evaluation of the phylogenetic relationship of this genus should be considered.

— *Cryphaea* (*Acrocryphaea* and *Dendrocryphaea* included) has a minimum of 11 cladocarpous species within the Leucodontineae (Table 2). It should be noted that the Hedwigiaceae and the Orthotrichaceae, two acrocarpous or acro-cladocarpous lineages, were once included within the Leucodontineae (Fleischer 1900–1923). Two explanations for the occurrence of cladocarpous taxa within predominantly pleurocarpous lineages are possible—1) the Cryphaeaceae are basal within the Leucodontineae and the suborder is basal within the pleurocarpous lineages. This interpretation would support an evolutionary sequence: acrocarpy → cladocarpy → pleurocarpy; or 2) the cladocarpous taxa within the Cryphaeaceae were derived from pleurocarpous ancestors: acrocarpy → pleurocarpy → cladocarpy. Detailed phylogenetic analyses of the family and suborder will determine which evolutionary hypothesis is applicable for the cladocarps within the Cryphaeaceae. The results from De Luna (1995) suggest that *Cryphaea* represents a more derived genus within the Leucodontineae. As well, Vitt (1984) and Buck and Vitt (1986) have considered the placement of the Cryphaeaceae well within pleurocarpous families.

The data matrix of De Luna (1995) includes several critical taxa for testing perichaetial position. A re-analysis of De Luna's (1995) data matrix with perichaetial position recoded for *Rhacocarpus, Bryowijkia,* and *Cryphaea* (Table 2), indicated 3 reversals for this character (PAUP, Swofford 1993). Two interpretations of his cladogram are possible—1) The position of these taxa are phylogenetically correct, thus the genetic control(s) determining perichaetial position is (are) less stringent than considered here, with reversals commonly occurring. These reversals weaken the rationale to order the character states (De Luna 1995); or 2) the position of these taxa are not phylogenetically correct, and should be re-evaluated.

The distribution of perichaetial position within the 14 major clades of Bryopsida (Vitt 1984), shows three basic patterns: 1) 11 acrocarpous-cladocarpous lineages; 2) Two pleurocarpous lineages; and 3) one cladocarpous-pleurocarpous lineage. Within the predominantly acrocarpous lineages, (i.e., Grimmiineae), a single genus can have two species with different perichaetial positions—acrocarpy versus cladocarpy (*Racomitrium canescens* and *R. lanuginosum,* respectively). As well, cladocarpy has evolved independently in four disparate (or non-sister group) genera of the acrocarpous Pottioideae (Pottiaceae): *Anoectangium, Ganguleea, Molendoa,* and *Pleurochaete* (Zander 1993). The development of cladocarpy from acrocarpy has apparently occurred repeatedly in unrelated lineages and at various taxonomic ranks (Fig. 3).

An alternative hypothesis that should be considered is the evolution of pleurocarpy directly from acrocarpy (Fig. 3). Both cladocarpy and pleurocarpy have vegetative apices on the primary axis and produce lateral innovations with terminal perichae-

tia. The control of branch length in these two groups may be the result of different developmental constraints (in cladocarpy—reduction, or in pleurocarpy—paedomorphosis, the "immediate" development of the perichaetium). Differences in the shape and the cellular arrangement of the apical cell region has been observed in acrocarpous and pleurocarpous taxa (Frey 1971, 1974). Developmental studies of the perichaetial branches in strongly reduced cladocarps and pleurocarps are needed to further clarify the distinctions. The phylogenetic position of the cladocarpous species in the Cryphaeaceae is central to the question of evolution of pleurocarpy. Therefore in choosing an outgroup for the pleurocarpous mosses, both acrocarpous and cladocarpous species should be considered. Detailed systematic analyses, such as on the subfamily Pottioideae (Zander 1993), are needed to evaluate the possible evolutionary pathways for perichaetial position.

CONCLUSIONS

A consistent use of terminology regarding growth form, branching pattern, and perichaetial position provides a foundation for improved systematic analyses. The terms are classified into four distinct categories to emphasize independent assessment.

The classification of the terminology for the structure of mosses and the amended definitions of perichaetial position in mosses present a framework for a more rigorous assessment of the structural organization of mosses. These will provide more robust characters in future phylogenetic analyses. The clarification of three distinct perichaetial positions may provide useful insights regarding the evolutionary relationships between mosses. Unless strict definitions of terms are applied, the terms may lack critical phylogenetic information.

LITERATURE CITED

AKIYAMA, H. & N. NISHIMURA. 1993. Further studies on branch buds in mosses; "pseudoparaphyllia" and "scaly leaves". Journal of Plant Research 106: 101–108.

BERTHIER, J. 1972. Recherches sur la structure et le développment de l'apex du gamétophyte feuillé des mousses. Revue Bryologique et Lichénologique 38: 421–551.

BRIDEL, S. E. 1819. Muscologiae Recentiorum Supplementum Pars IV. Seu Mantissa naturae normam melius instituta et muscologiae recentiorum accomodata. Gothae.

———. 1826–1827. Bryologia universa seu Systematica ad Novam Methodum Dispositio, Historia et Descriptio omnium Muscorum Frondosorum Hucusque cognitorum cum Synonymia ex Auctoribus Probatissimis. Volumen Primum; Volumen Secundum. Leipzig.

BROTHERUS, V. F. 1901–1909. Musci (Laubmoose). III. Unterklasse Bryales: II. Spezieller Teil, pp. 277–1246. In A. Engler & K. Prantl (eds.), Die Natürlichen pflanzenfamilien 1(3,I,II). Leipzig.

———. 1924–1925. Musci (Laubmoose). Unterklasse Bryales: II Spezieller Teil. 10 Band, 1 Hälfte, pp. 143–478; 11 Band, 2 Hälfte, pp. 1–542. In A. Engler & K. Prantl (eds.), Die Natürlichen pflanzenfamilien. Leipzig.

BUCK, W. R. & D. H. VITT. 1986. Suggestions for a new classification of pleurocarps. Taxon 35: 21–60.

CAVERS, F. 1911. The inter-relationships of Bryophyta. The New Phytologist 9–10: 1–200.

CHAMBERLIN, M. A. 1980. The morphology and development of the gametophytes of Fissidens and Bryoxiphium (Bryophyta). M. Sc. Thesis, Southern Illinois University, Carbondale.

CHOPRA, R. N. & P. K. KUMURA. 1988. Biology of Bryophytes. New Delhi.

CRANDALL, B. J. 1969. Morphology and development of branches in leafy Hepaticae. Beihefte zur Nova Hedwigia 30: 1–261.

CROSBY, M. R. 1980. The diversity and relationships of mosses, pp. 115–129. In R. J. Taylor & A. E. Leviton (eds.), The mosses of North America. Pacific Division, American Association for the Advancement of Science. California Academy of Science, San Francisco.

CRUM, H. A. 1986. A survey of the moss genus Sclerodontium. Hikobia 9: 289–295.

——— & L. E. ANDERSON. 1981. The Mosses of Eastern North America. Vol. 1. New York.

DE LUNA, E. 1990. Developmental evidence of acrocarpy in Hedwigia ciliata (Musci: Hedwigiaceae). Tropical Bryology 2: 53–60.

———. 1995. The circumcription and phylogenetic relationships of the Hedwigiaceae (Musci). Systematic Botany 20: 347–373.

DEGUCHI, H. 1978. A revision of the genera Grimmia, Schistidium, and Coscinodon (Musci) of Japan. Journal of Science of the Hiroshima University Series B, Div. 2 (Botany) 16: 121–256.

DIXON, H. N. 1924. The Student's Handbook of British mosses. Eastbourne.

———. 1932. The Classification of Mosses, pp. 397–412. In F. Verdoorn (ed.), Manual of Bryology, The Hague.

DURING, H. 1979. Life strategies of bryophytes: a preliminary review. Lindbergia 5: 2–18.

———. 1990. Clonal growth patterns among bryophytes, pp. 153–176. In J. van Groenendael & H. de Kroon (eds.), Clonal Growth in Plants: Regulation and Function, The Hague.

FLEISCHER, M. 1900–1923. Die Musci der Flora von Buitenzorg (Zugleich Laubmoosflora von Java). Vols. 1–4. Leiden.

FLOWERS, S. 1973. Mosses: Utah and the West. Provo, Utah.

FREY, W. 1971. Blattenwicklung bei Laubmoosen. Dissertation Tübingen, pp. 463–556. Lehre.

———. 1974. Vergleichende entwicklungsgeschichtliche Untersuchungen an Laubmoosbättern als Beitrag zur Systematik der Laubmoose. Bulletin de la Société Botanique de France 121: 29–34.

GIESENHAGEN, K. 1910. Mosstypen der Regenwälder. Annales du Jardin botanique de Buitenzorg, Supplement 3: 711–790.

GIMINGHAM, G. H. & E. M. BIRSE. 1957. Ecological studies on growth form in bryophytes. I Correlations between growth form and habitat. Journal of Ecology. 45: 533–545.

HEDENÄS, L. 1994. The basal pleurocarpous diplolepidous mosses. A cladistic approach. THE BRYOLOGIST 97: 225–243.

HORIKAWA, Y. & H. ANDO. 1952. A short study on growth-forms of bryophytes and its ecological significance. Hikobia 1: 119–129.

HORTON, D. G. 1982. A revision of the Encalyptaceae (Musci) with particular reference to the North American taxa Part I. Journal of the Hattori Botanical Laboratory 53: 365–418.

IRELAND, R. R. 1971. Moss pseudoparaphyllia. THE BRYOLOGIST 74: 312–330.

———. 1982. Moss Flora of the Maritime Provinces. Publications in Botany, No. 13. National Museum of Natural Sciences, Ottawa.

IWATSUKI, Z. 1960. The epiphytic bryophyte communities in Japan. Journal of the Hattori Botanical Laboratory 22: 159–348.

KOPONEN, T. 1982. Rhizoid topography and branching patterns in moss taxonomy. Nova Hedwigia 71: 95–99.

———. 1988. The phylogeny and classification of Mniaceae and Rhizogoniaceae (Musci). Journal of the Hattori Botanical Laboratory 64: 37–46.

LAWTON, E. 1971. Moss Flora of the Pacific Northwest. Nichinan, Japan.

LESQUEREUX, L. & T. P. JAMES. 1884. Manual of Mosses of North America. Boston.

LEWINSKY, J. 1993. A synopsis of the genus Orthotrichum Hedw. (Musci, Orthotrichaceae). Bryobrothera 2: 1–59.

MÄGDEFRAU, K. 1982. Life forms of bryophytes, pp. 45–58. In A. E. J. Smith (ed.), Bryophyte Ecology, London.

MAGILL, R. E. 1990. Glossarum Polyglottum Bryologiae: A multilingual glossary for bryology. Monographs In Systematic Botany from the Missouri Botanical Garden 13: 1–297.

MEUSEL, H. 1935. Wuchsformen und Wuchstypen der europäischen Laubmoose. Nova Acta Leopoldina Neue Folge 3: 123–277.

MILLER, H. A. 1971. An overview of the Hookeriales. Phytologia 21: 243–252.

MISHLER, B. D. & E. DE LUNA. 1991. The use of ontogenetic data in phylogenetic analyses of mosses. Advances in Bryology 4: 121–167.

MITTEN, W. 1859. Musci Indiae Orientalis. An enumeration of the mosses of the east Indies. Journal of the Proceedings of the Linnean Society (London), Supplement Botany. 1: 1–171.

MUELLER, C. 1948. Synopsis Muscorum Frondosorum omnium hucusque cognitorum. Pars prima. Berolini.

NEES VON ESENBECK, C. G., FR. HORNSCHUCH, & J. STURM. 1823. Bryologia Germanica, oder Beschreibung der in Deutschland und in der Schweiz washsenden Laubmoose. Erster Theil. Nürnberg.

NEWTON, A. E. & B. D. MISHLER. 1994. The evolutionary significance of asexual reproduction in mosses. Journal of the Hattori Botanical Laboratory 76: 127–145.

NISHIMURA, N. 1985. A revision of the genus Ctenidium (Musci). Journal of the Hattori Botanical Laboratory 58: 1–82.

PROCTOR, M. C. & A. J. E. SMITH. 1995. Ecological and systematic implications of branching patterns in bryophytes. Monographs In Systematic Botany from the Missouri Botanical Garden 53: 87–110.

RICHARDS, P. W. 1984. The ecology of tropical forest bryophytes, pp. 1233–1270. In R. M. Schuster (ed.), New Manual of Bryology, Vol. 2. Nichinan, Japan.

ROTHWELL, G. W. 1987. The role of development in plant phylogeny: a paleobotanical perspective. Review of Paleobotany and Palynology 50: 97–114.

SALAZAR-ALLEN. N. 1985. The life-form and presence of epigametophytic plants in the genus Leucophanes. THE BRYOLOGIST 88: 94–97.

SCHIMPER, W. P. 1860. Synopsis Muscorum Europaeorum praemissa introductione de elementis bryologicis tractante. Vol. 1. Introductio I–CLIX, Vol. II. Speciarum descriptio. Stuttgartiae.

SCHOFIELD, W. B. & C. HÉBANT. 1984. The morphology and anatomy of the moss gametophore, pp. 627–657. In R. M. Schuster (ed.), New Manual of Bryology, Vol. 2. Nichinan, Japan.

SMITH, A. E. J. 1978. The Moss Flora of Britain and Ireland. Cambridge.

STARK, L. R. 1985. Phenology and species concepts: A case study. THE BRYOLOGIST 88: 190–198.

STEARN, W. T. 1983. Botanical Latin. London.

SWOFFORD, D. L. 1993. Phylogenetic analysis using parsimony, ver. 3.1.1. Computor program distributed by the Illinois Natural history Survey, Champaign, Illinois.

TALLIS, J. H. 1959. Studies in the biology and ecology of Racomitrium lanuginosum Brid. II. Growth, reproduction and physiology. Journal of Ecology 47: 325–350.

TOUW, A. 1976. A taxonomic revision of Thuidium, Pelekium, and Rauiella in Africa south of the Sahara. Lindbergia 3: 135–195.

VITT, D. H. 1984. Classification of Bryopsida, pp. 696–759. In R. M. Schuster (ed.), New Manual of Bryology, Vol. 2. Nichinan, Japan.

——— & W. R. BUCK. 1984. The familial placement of Bryowijkia (Musci: Trachypodiaceae). Brittonia 36: 300–306.

WHITE, J. 1984. Plant metamerism, pp. 15–47. In R. Dirzo & J. Sarukhán (eds.), Perspectives on Plant Population Ecology, Sunderland, MA.

ZANDER, R. 1993. Genera of the Pottiaceae: mosses of harsh environments. Bulletin of the Buffalo Society of Natural Sciences 32: 1–378.

ZOMLEFER, W. 1993. A Revision of Rigodium (Musci: Rigodiaceae). THE BRYOLOGIST 96: 1–72.