Morphogenetic Designs and a Theory of Bryophyte Origins and Divergence

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In the plant kingdom, the four major levels of anatomical organization and complexity are those circumscribed by the terms thallophyte, bryophyte, pteridophyte, and spermatophyte. Each level possesses some structural specialization suggestive of evolutionary advancement from the level preceding it. Thus, the thallophytes, at the level of origin, lack the well-defined tissues and multicellular gametangia that the bryophytes possess; the bryophytes lack the root, stem, and leaf differentiation in the sporophyte (traits common in pteridophytes); and the pteridophytes lack seeds, an improvement left to the spermatophytes.

Diversification of form occurs at each organizational level, producing distinct morphological units. In the bryophytes, these units are the mosses, hepatics, and anthocerotes. As indicated by their position just above thallophytes, bryophytes are structurally simple, terrestrial plants, generally of small size. Although some, like the peat mosses, are associated with wetland or bog habitats, most are mesic organisms, and a few are well-adapted to the xeric conditions of exposed rocks and even deserts.

Classical texts of the early to middle 1900s—such as the Fitting et al. rewrite of Strasburger's *Textbook of Botany* (1930), introductory treatments by Fuller and Tippo (1954) and Sinnott and Wilson (1955), and a two-volume treatment of cryptogams by Smith (1955)—placed mosses, hepatics, and anthocerotes in the single division Bryophyta, which in turn was positioned between the algae and the "true" land plants. Such alignments, still employed in some introductory texts, reflect the view that these organisms share ancestral commonality and that they are the most primitive or least evolved of the land plants. Their oneness as a phyletic unit is based on their uniform possession of an alternating life cycle in which the haploid phase is the persistent, photosynthesizing generation and the diploid phase is incapable of independent existence.

Further, in all three groups, prostrate growth habits are common, a true cutin-containing cuticle and cutinized walls are absent in the mature haploid generation, motile sperm facilitate fertilization, and sporophytes are homosporous. Temporal and nutritional dominance of the gametophyte phase and simplistic organization of both generations are regarded as major features still shared with their filamentous algal progenitors (Fritsch 1945). Thalloid hepatics, like *Riccia*, being both semiaquatic and structurally uncomplicated, are placed near the point of origin of this monophyletic unit, whereas anthocerotes and/or mosses are regarded as direct antecedents of the pteridophytes (Bower 1908).

Although this concept of bryophyte phylogeny has prevailed in general treatments, bryologists have advanced alternate hypotheses, both in past and recent times. That erect, radially symmetric gametophytes are primitive and dorsiventral forms have evolved by reductive processes are the most notable of these substitute proposals. Whether a massive green alga with isomorphic generations (Campbell 1971) or a *Horneophyton*-like pteridophyte (Haskell 1949) served as progenitor, these theories view modern bryophyte forms as diminished structures with little evolutionary potential. Indeed, in the absence of verified fossil records, either perspective may be debated.

THE MODERN THEORY

During the past two decades, data have emerged which suggest still another hypothesis, namely, that extant mosses, hepatics, and anthocerotes are representatives of separately evolving lines of independent origins (Bold 1956, Steere 1969) and should, thus, be recognized as comprising three plant divisions: Bryophyta, Hepatophyta, and Anthocerotophyta, respectively (Stotler and Crandall-Stotler 1977). In each line, successful adaptation to competition and environmental stress has involved sporophyte retention by the gametophyte and subsequent reduction in sporophyte mass and lifespan. In this way, the sporophyte can provide each species with colonizing r-selection attributes, while the gametophyte functions locally as a perennating K-species. In optimal growing conditions, a taxon may reproduce sexually, be an aggressive colonizing competitor, and maintain a high degree of genetic polymorphism. In more stressful or isolated niches, the same species may succeed only as a vegetative gametophyte; nonetheless, even in this less hospitable habitat, it can persist and preserve its hereditary units for later recombination. Conceivably, such a life cycle represents not a primitive level of organization, but rather a different type of evolution that produces the same structural, physiological, and genetic variability in bryophytes as in other land plants.

The three groups of bryophytes are morphologically distinct from one another (Chopra 1968), but it is rarely recognized that such distinctions are due to fundamental differences in morphogenetic design. Indeed, the disparities in ontogenesis among the mosses, hepatics, and anthocerotes are central to the argument for separate origins, and the physiological complexities of development support advanced evolutionary progress in all three lines.

Morphogenetic Patterns and Spore Germination

Evident morphogenetic dissimilarities begin with the first phase of gametophyte growth, i.e., spore germination. The ex-

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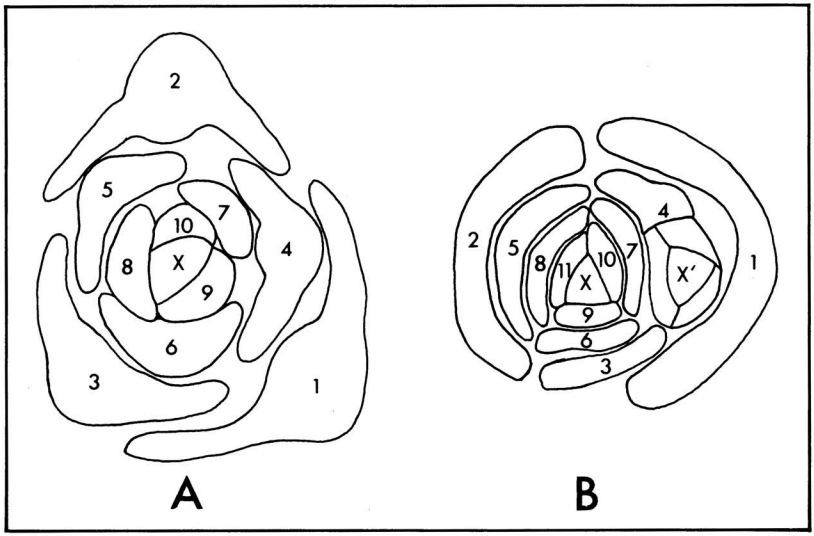

Figure 1. A: Apical organization of the moss *Plagiomnium* in transverse section, illustrating an oblique segmentation pattern and resultant 3/8 phyllotaxy. B: Apical organization of the hepatic *Bazzania* in transverse section showing, in contrast, a parallel segmentation pattern and three-ranked leaves. Key: X = pyramidal apical cell; X′ = branch apical cell.

tensive studies of Nishida (1978) on patterns of germination in mosses have shown that, with only rare exception, sporeling development will include an exosporic filamentous phase. In the vast majority of taxa, the complete protonema is filamentous, and a heterostichous differentiation of green chloronemal and brown caulonemal filaments is apparent. Several leafy shoots arise in fairy-ring fashion from each highly branched spore-product through the formation of pyramidal apical cells from physiologically specialized caulonemal target cells. Both the induction of caulonema differentiation and the subsequent triggering of bud development are complex physiological events that involve highly refined phytochrome, cytokinin, auxin, and protein interactions (Bopp 1977). In a few discordant groups, this primal pattern is modified, either by the insertion of a nonfilamentous secondary protonemal phase (e.g., Sphagnaceae) or by an initial globose endosporic phase preceding the filamentous phase (e.g., Andreaeaceae). The latter modification is generally restricted to epiphyllic or epipetric taxa.

The fundamental pattern of spore germination in hepatics, on the other hand, involves exosporic divisions in three planes to produce an undifferentiated, globose protonemal phase from which but a single juvenile plant develops (Nehira 1966). In some genera (e.g., *Cephalozia*), an unspecialized filamentous protonema occurs, whereas in others (e.g., *Scapania*), the protonema may combine short filaments with interspersed, globose cell masses. However, there is never heterostichous specialization or fairy-ring production of leafy shoots. As in mosses, this basic exosporic pattern is variously modified in derived groups, with endosporic development predominating in epiphyllic and epipetric forms.

Spore germination in anthocerotes is likewise exosporic except in the epiphyllic genus *Dendroceros* (Renzaglia 1978). Early divisions in this group produce a small, globose cell-mass from which first rhizoids and then flattened lobes arise in a manner strikingly like prothallial growth of certain filicalean ferns (see Bierhorst 1971). Mature plants emerge, one per spore, with the establishment of a segmenting apical cell in the prothallus stage.

Apical Organizations in Mosses and Leafy Hepatics

As patterns of spore germination are dissimilar, so also is the fundamental organization of the mature gametophytic growth system. Both in mosses and leafy liverworts, histogenesis begins with regular, albeit slow, mitotic divisions of a single pyramidal apical initial; that is, all cell lineages can be traced back to a single generative center (Hallet 1977). The process of segmentation and subsequent orientation of cell divisions in newly formed derivatives, however, differs substantially in the two groups. Distinctive apical organizations result (Figure 1).

In mosses, the apical cell varies in shape from broadly obovoid in the acrocarps to narrowly fusiform in the pleurocarps, and in transverse section it appears to be from three- to five-sided (Bonnot 1968, Frey 1971). The variation in cross-sectional appearance is correlated with an obvious obliquity of segmentation that characterizes most mosses. During cytokinesis the phragmoplast of the developing derivative extends from a point of intersection of two sides of the apical cell to a predetermined position on the wall opposite the point of intersection, rather than extending in a plane parallel to an existing wall. This obliquity produces a derivative, then, that is triangular in outline in surface view, with the base of the triangle forming the anodic portion of the cell, i.e., lying in a plane contiguous with the long axis of the next formed derivative.

Apical cell enlargement, accompanied by organellar migration (Hébant et al. 1978), follows each segmentation and reestablishes the polarity necessary to the next oblique division. These very exact angles of segmentation are, in turn, responsible for the phyllotaxy characteristic of the species and for what some authors have termed apical torsion. These angles of segment divergence generally approach the 137° ideal angle and produce typical Fibonnaci orthostichies and contact parastichies. A $^2/_5$ phyllotaxy with 2 + 3 contact parastichies and a $^3/_8$ phyllotaxy with 3 + 5 contact parastichies are the most common phyllotaxes in the mosses. Presumably through different causes, the mosses mimic the flowering plants in the production of helical leaf arrangements.

In leafy liverworts, in contrast, the apical cell is nicely tetrahedral, with a constant three-sided, triangular outline in transverse section (Crandall 1969). Segmentation always produces derivative walls that run parallel to the lateral walls of the apical cell, even in erect, radially symmetric taxa. Such a pattern of wall formation produces derivatives that are arranged in three ranks and, subsequently, a potential for only three orthostichies. In dorsiventral taxa, ventrally ranked derivatives may be reduced so that no leaves develop and a distichous leaf arrangement occurs. Only in the hepatic *Pleurozia* is distichy associated with a lenticular apical cell. Such ranking of sequential derivatives in the

mosses occurs only in the three-ranked aquatic *Fontinalis*, which displays parallel rather than oblique segmentation, and in the two-ranked *Fissidens*, which like *Pleurozia* possesses a two-sided apical cell. Even in the distichous taxa *Schistostega* and *Bryoxiphium* (Chamberlin 1979, Leitgeb 1874), derivatives arise in spiral sequence through oblique segmentations and are later reoriented to ranked positions.

In all mosses, the first division wall of the derivative extends from the anodic to the cathodic surface—i.e., from one lateral wall to the other—in an approximately periclinal plane and divides it into inner and outer initials (Figure 2). The inner cell may divide rapidly to form cortex and stele initials, while the outer cell divides anticlinally to form an apically oriented, acroscopic foliar initial and a posteriorly oriented, basiscopic caulogenic initial (Berthier 1972). Histogenic determination is profound, even at this stage.

From the foliar initial, the leaf apical cell will be formed by two oblique divisions: The first will generally occur in the anodic portion of the initial, whereas the caulogenic initial, after a variable period of dormancy, will form a branch and internodal epidermal tissue, only internodal epidermal tissue, or caulogenic regenerants. As the undivided leaf begins to grow from regular segmentations of the single leaf apical cell, a filamentous, chloronema-like mucilage hair is formed from the anodic basal leaf cell, and differentiation of a multilayered costa, often containing special water-conducting cells (or hydroids), begins at the leaf base. Further cellular differentiation proceeds acropetally.

In contrast, the first derivative division in all leafy hepatics is anticlinal, extending from near the middle of the free surface wall to the middle of the anodic lateral wall, in a plane generally parallel to the cathodic wall (Figure 2). A second division, which rapidly follows the first, produces a periclinal wall in the larger cathodic cell. The derivative now consists of a single inner cell and two outer cells. The former will give rise to internal stem tissues, and each of the latter two enlarges, divides periclinally, and produces an outer foliar initial and an inner epidermal initial.

The formation of two primary foliar initials in each derivative is responsible for the basically divided nature of liverwort leaves. Leaf growth begins when apical cells are obliquely segmented from the foliar initials. After a rather brief period of apical growth, a generalized basal meristem is established. The parted portion of the unistratose leaf, derived from apical activity, begins to differentiate as the basal meristem forms laminal cells. Continued differentiation proceeds basipetally.

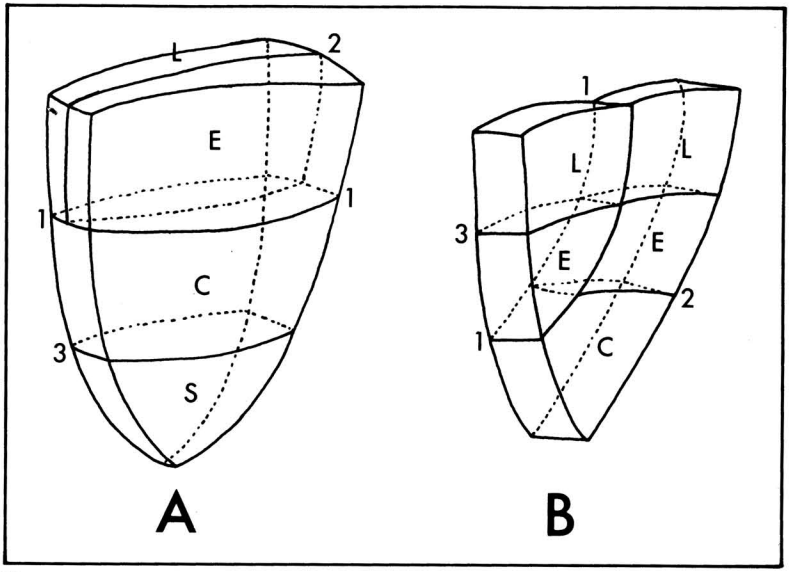

Figure 2. A: Diagram of a four-celled derivative in a moss showing the position of the first divisions and histogenic initials. B: Diagram of a comparable five-celled derivative in a leafy hepatic. Walls are numbered in sequence of appearance. Key: C = initial from which internal parenchymatous stem tissue is derived; E = initial from which stem epidermis and moss branches are derived; L = foliar initial; S = stele initial.

These distinctions in derivative morphogenesis are absolute; no mosses display the hepatic pattern, and no hepatics display the moss pattern, even in cases when external morphology might suggest overlap. In a related manner, patterns of branch morphogenesis are likewise different in mosses and hepatics (Berthier 1972, Crandall 1969). In the former, branches develop along exact cladotaxies, form only from the caulogenic initial of a derivative, and appear axillary to leaves, generally along the N-3 parastichies; in the latter, branch patterns are irregular, branches may form from foliar initials, epidermal initials, or internal stem initials, and they appear axillary, usually only if of internal origin.

Conductive Tissues and Stem Anatomy

In addition to gross dissimilarities in the development of leaves and branches in mosses and hepatics, differentiation of specialized stem tissues also varies. In mosses, cells that issue from the innermost initial of the four-celled derivative usually differentiate into either water-conducting hydroids or thick-walled stereids of the stele or central strand (Hébant 1977). Cells to the outside differentiate as typical parenchymatous ground tissue, specialized food-conducting parenchyma (i.e., deuters), or highly specialized sieve-element-like leptoids. As the hydroids differentiate, lysosomal acid phosphatase activity leads to protoplasmic degeneration so that the fully differentiated cell is devoid of cellular contents. When the functional stage is reached, the hydroids further possess oblique, partially hydrolyzed cellulosic end walls, lack pores, and sometimes develop "secondary" polyphenolic thickenings on lateral walls only (Scheirer 1975). Leptoids, as they occur in representative polytrichales, display oblique sieve-plates, organized marginal endoplasmic reticulum, and partial nuclear degeneration.

In hepatics, distinctive water-conducting cells are a rarity found in only two foliose and two simple thalloid families, and differentiated food-conducting cells are never produced. For the most part, tissue specialization is restricted to development of collenchymatous support tissue in erect taxa or formation of a hyalodermic epidermis in prostrate forms. Even though lysosomal acid phosphatases cause protoplasmic degeneration in the water-conducting cells of the hepatics that have them, wall morphogenesis is distinct from that found in the mosses. The hepatic water-conducting cells display no wall hydrolysis,

possess numerous plasmodesmata-derived pores on all walls, and never develop polyphenolics (Hébant 1978).

DIVERGENT HORNWORT DESIGNS

Hornwort gametophytic growth systems bear no similarity to those of either mosses or leafy hepatics, but do resemble those of some thalloid hepatics (Renzaglia 1978). In all genera except *Dendroceros,* a five-sided, wedge-shaped apical cell, located in a mucilage-protected notch, serves as the generative center of the vegetative thallus. In vertical longitudinal section, this cell appears triangular, whereas in all other planes, it has a rectangular outline. Segmentation walls are parallel to initial walls and are regular in sequence. This type of growth system also occurs in complex thalloid hepatics, but was probably derived independently in the two groups from the pyramidal systems of respective leafless axial progenitors, as suggested by Schuster (1977, 1979) and mathematically simulated by Niklas (1979). In *Dendroceros,* the wedge-shaped apical initial of the juvenile phase is converted to a hemidiscoid cell with three surfaces of segmentation in the foliose adult.

In contrast to both mosses and hepatics, segmentation and subsequent derivative divisions involve not only nuclear segregations, but also very exact divisions of the large, pyrenoid-containing plastids (Wilsenach 1963). Further, as ventral epidermal initials divide and differentiate, they form unique clefts that open into mucilage-filled cavities. Each cleft is associated with two reniform epidermal cells and, hence, superficially resembles a stoma. It is through these permanently open clefts that *Nostoc* colonies enter the cavities and establish the symbiosis so characteristic of all hornworts. In the absence of a cuticle, the presence of these stomate-like associations is puzzling.

Ontogenetically, the most important divergence between anthocerote and hepatic gametophytes occurs in gametangial development. In the former, antheridia develop from dorsal scattered subepidermal initials; in the latter, superficial initials are involved. Several antheridia differentiate from a single anthocerote initial, and antheridial buds proliferate at the base of already mature antheridia, whereas in hepatics each antheridium originates from an independent initial. Spermatozoids likewise reflect major developmental divergence, with unique spline and lamellar strip shapes and basal body positions occurring in anthocerotes (Carothers and Duckett 1979). Archegonial development, which proceeds internally rather than externally, is more akin to a pteridophyte prototype than to any pattern found in extant bryophytes.

The Sporophyte Generation

These substantial dissimilitudes of morphogenetic designs in gametophytes are compounded in the sporophyte generation. Beginning with embryogenesis, divergence is obvious. In mosses and hepatics, the zygote is polarized along a vertical gradient, and the first division is transverse to the long axis of the archegonium. Anthocerote embryos lack such polarity and, like leptosporangiate fern embryos, divide first along their longitudinal axes (Renzaglia 1978).

Typically, in mosses a lenticular apical cell forms from the upper or epibasal cell, as the lower or hypobasal cell divides to form a suspensor-like mass of vacuolated cells (Roth 1969). After a short period of apical growth (e.g., 18–19 segmentations in *Pogonatum*), an intercalary meristem is established in the midzone of the elongate, flattened embryo. Cells differentiating basipetally from this meristem form a dagger-shaped foot and the lower part of the stem-like seta, while acropetally derived lineages differentiate into upper seta and capsule cells. The foot is surrounded by dividing cells of the archegonial stalk and receptacle (i.e., the vaginula), and the upper portion of the embryo is covered by the archegonial venter (or calyptra). Interdigitating transfer cells develop between the foot and the vaginula (Wiencke and Schulz 1977). The upper part of the embryo, through continued meristematic activity, emerges from the gametophyte, and eventually the apical portion, covered by the persistent calyptra, forms the sporangial capsule.

Sporophyte histogenesis is complex and results in the differentiation of a cutinized cuticle in the epidermis of seta and capsule, hydroids and conducting parenchyma in the seta, a spongy photosynthetic zone and stomates at the seta-capsule juncture (Garner and Paolillo 1973), and a highly specialized columellate capsule with an endothecial sporogenous zone. Meiospores develop externally deposited perines of sporopollenin (Mueller 1974), and spore dispersal, effected by the slow, hygroscopic movements of the peristome, occurs for an extended period.

In hepatics, a three- to four-celled filamentous embryo succeeds the two-celled embryonic stage. Typically, the basal cell of the filament differentiates into an enlarged haustorium or suspensor (Schertler 1979), the distal cell functions as a capsule initial, and the median cell (or cells) produces the seta and foot. All cells, except the haustorium, possess equal division potential; no defined meristematic zone is discernible. Gametophytic tissues near the developing sporophyte are variously modified as enveloping structures and, regardless of form, remain intact around the sporophyte until sporogenesis is terminated. The bulbous-to-rapiform foot often develops a haustorial collar at its juncture with the seta; the seta is composed entirely of parenchyma; and the capsule is simply organized into a one- to seven-layered wall and internal sporogenous region. Meiospores are intermixed with sterile elaters, and no perine is externally deposited during sporogenesis (Horner et al. 1966). Auxin-influenced seta elongation occurs only after spore maturation; capsule dehiscence and spore dispersal rapidly follow.

Hornwort ontogeny progresses from the 2-celled stage to a 12-celled embryoid, organized in three tiers. Rapid, regular divisions in the upper tier establish a basal meristem and acropetally differentiating cells of the columella, amphithecial sporogenous zone, and sporangial wall. The lower tier cells divide more slowly and form a massive sporophyte foot, which remains embedded in the gametophyte thallus. Since the basal meristem remains active throughout the life of the sporophyte, upper regions may be dispersing spores while meiosis is still occurring in the lower regions.

Clearly, mosses, hepatics, and anthocerotes possess distinctive morphogenetic designs, regulated by genetic and physiological mechanisms as complex as those described for flowering plants. Bopp (1977) has shown that interactions of growth regulators like ethylene, c-AMP, abscisic acid, auxins, and cytokinins are responsible for morphogenetic transitions in mosses, and that the cellular mechanisms involved in these events are comparable to those occurring in flowering plants. In hepatics, auxins regulate cell cycle rates in undifferentiated cells (Stange 1977); the dihydrostilbenes lunularin and lunularic acid function in a manner comparable to the activity of abscisic acid in mosses and flowering plants (Valio et al. 1969); and hydroxy-

proline is a morphogenetically significant cell wall component (Basile 1979).

Physiological advancement is also suggested by biochemical data (Markham and Porter 1978). Complex flavonoids like the aurone glycosides, exotic allergenic sesquiterpene lactones, and diversified polyunsaturated fatty acids suggest extensive biochemical diversification. Further, in all three groups, starch-gel electrophoresis has demonstrated multiple molecular forms (i.e., isozymes) to exist for most enzyme systems, even though the genetic base is haploid (Crandall-Stotler and Zehr 1979). These organisms display extensive intra- and interpopulational polymorphism as well as surprising levels of isozyme heterogeneity. Such data suggest that bryophytes, like other advanced organisms, have undergone gene duplication and are genetically pleomorphic.

BRYOPHYTE ORIGINS

Morphogenetic analyses, both of pattern and regulation, support a view of separate origins and advanced—somewhat divergent—evolutionary positions for mosses, hepatics, and anthocerotes. In a very real sense, most mosses are vascular plants, conducting tissue being absent only in some highly reduced and pleurocarpic taxa. Their gametophytes display organographic specializations comparable to those of pteridophyte sporophytes, while their terete, leafless sporophytes recall certain rhynialean features.

That both mosses and primitive pteridophytes arose from a common vascularized progenitor, characterized by homologous, leafless, axial, alternating generations seems plausible. During the course of evolutionary divergence, the sexual haploid generation served as the persistent genetic unit in mosses, while the pteridophyte line elaborated on asexual diploid phases. In particular, the similarity between moss gametophyte and sporophyte hydroids and incipient tracheids of primitive pteridophytes supports this view.

Hepatics, in contrast, were probably derived from an unrelated, nonvascular archegoniate ancestor, which also may have possessed homologous, leafless, axial sporophytes and gametophytes. The ubiquitous presence of unique membrane-bound oil bodies, poor starch-producing capabilities (Suleiman et al. 1979), and certain biochemical idiosyncracies attests to their metabolic separation from other archegoniates. The anomalous presence of conducting tissue in a few unrelated taxa and the distinctive form and histogenesis of this tissue point to later specialization.

Finally, the enigmatic hornworts seem to have arisen from a remote group of plants, unrelated to either modern day hepatics and mosses or to pteridophytes. Since their origin, hornworts have been an isolated group (Schuster 1977). They have demonstrated only slight diversification as compared to other extant groups and appear the least modified, both structurally and metabolically, from their presumptive ancestors.

The distinctiveness of modern bryophyte forms and the total absence of fossilized intermediates among mosses, hepatics, and anthocerotes surely strengthen the argument for separate origins during the "explosive" synchronous colonization of early land habitats. Indeed, as Schuster (1979) has recently suggested, various groups "may well have evolved simultaneously as a number of moves towards colonization of the land at different places" took place. Unfortunately, a completely acceptable solution to the problem of bryophyte origins and divergence may remain remote, as Watson (1964) maintains. Nonetheless, as we gain greater understanding of the biology of these plants, our data-base for hypothesizing will broaden and our postulates will gain a firmer support.

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Morphogenetic Designs and a Theory of Bryophyte Origins and Divergence

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Morphogenetic patterns involved in spore germination, indeterminant leafy shoot growth, including leaf and branch formation and histogenesis, gametangial development, embryogenesis, sporophyte maturation, and sporogenesis show that mosses, hepatics, and anthocerotes are fundamentally different from each other. Such patterns support the hypothesis that the three groups of bryophytes originated from unrelated ancestors, and that their common features are due to similar reductive evolutionary processes, an alternative type of land plant advancement. *(Accepted for publication 24 April 1980)*