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HYDROSTATIC AND FLUID DYNAMIC CONSTRAINTS ON EXTERNAL CAPILLARY WATER CONDUCTION IN THE DIVERSIFICATION OF LAND PLANTS; BRYOPHYTE COLONIES, A MODEL SYSTEM

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by

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A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

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ABSTRACT

Hydrostatic and Fluid Dynamic Constraints and External Capillary Water Conduction in the Diversification of Land Plants: Bryophyte Colonies, a model system

by

Paul S. Mankiewicz

Advisor: Dominick V. Basile

For photoautotrophs, the transition from aquatic to terrestrial habitats required a fundamental reconfiguration of the plant body. The hypothesis is presented that in this transition, the cell wall became a macromolecular matrix with high surface forces capable of moving water throughout a continuous apoplast, while at the same time maintaining its function as a tensile structural element. This apoplastic surface is the major structural innovation for water conduction in the land plants. This feature permits two different strategies for water conduction in the terrestrial environment: a low resistance system utilizing the rapid flow of water along paths between plant axes and organs; and a high resistance system utilizing the lowconductance of cell membranes and other mechanisms to decrease and regulate flow rates of water through the system. Apoplast then permits three types of water conduction: 1) within the micellular structure of the cell wall itself; 2) between cell walls but mainly within the lumenae of empty cells (trachaeophyte strategy); and 3) between cell walls between axes and organs in external capillary systems (bryophyte strategy).

This study uses fluid dynamics, hydrostatics, and packing geometries to predict fundamental bounds on the morphology and functional properties of colonies of small plants. This context indicates limits on the scale and organization of the land plant body derived from equations of flow rate, hydrostatics, wettability, Reynolds number, and close and open packing geometries.

Predictions are tested with the following methods: 1) direct visualization of boundary layer velocities using smoke tracers; 2) direct measures of external capillary spaces in bryophyte colonies; 3) measures of maximum water flow through bryophyte colonies; 4) calculation of the upper limit of external capillary water conduction in the earliest fossil land plants based on published dimensions of these organisms together with measures taken from published photographs of these organisms; 5) comparison of published photographs of early land plant fossils with artifically fossilized bryophytes; 6) measurement of the water volume held within the external capillary spaces in a bryophyte colony at known forces; 7) measurement of hydrostatic forces and water movement in filling and emptying bryophyte colonies.

Acknowledgements

"The way to teach science is to do it". These words marked the beginning of my studies in the plant sciences, and still afford guidance, weather teaching myself, or others. While they were hardly the only gift I received from Professor Dominick V. Basile, they were first. Inspiration for this project arose in Professor Basile's plant morphology and morphogenesis courses. Here I gleaned that while morphology and size might separate bryophytes and larger land plants, the form generating processes of development appear the same in both. Through Professor Basile, I became familiar, and then indebted to the elegant work of his mentor, Edwin B. Matzke, on the geometry of cell packing. Eventually, an elemental question could be asked: if there is a geometry of cell packing in tissues, is there an analogous geometry to the packing of plant axes in colonies? The answer is yes, and the next obvious question is, why should plant axes pack at such a larger scale than cells? Answers require the right questions, and these I have been given. To repay the most longstanding of the intellectual debts I have incurred, I would hope to contribute to the spirit of Professor Matzke's original work. With this project, and endeavours in the botanical sciences which follow, I would hope to begin to do justice to the breadth and depth of the knowledge I have received from my mentor, Professor Dominick Basile.

Members of my committee deserve appreciation for the carefully rigorous and critically helpful reading each devoted to my dissertation. While my gratitude does not end there, it begins much earlier. Conversations ranging from germs of ideas to elaborate theories of plant evolution and biogeography with Professor Cronquist kept me in contact with clarity of thought and bredth of knowledge in the botanical sciences, in a word, with the primal sources of my education. In courses and conversations from biometry to higher level multivariate techniques, Professor Marcus permitted my imagination to begin to grasp some central limits on statistical method, and at the same time, to appreciate whatever capacities I may have in conceptualizing the geometry of form in causal terms. With Professor Salthe, I have enjoyed the best of company in exploring the limits, inconsistancies, and potentials of modern biology. But more, as my endeavours carried me far afield in the theory and methods of the sciences of life, I always knew that there was least one intelligence interested in what I might find. From my first meeting with Professor Kincaid, he has been a continuous source of novel perspectives, very recent references, new methods and techniques. These have come in enlightening discussions on how to frame theoretical problems in technical terms. Professor Kincaid did me a special service by inviting Professor Steve Vogel from Duke University to give a seminar at Lehman College. This talk, conversation, correspondence, and reading his Life in Moving Fluids made this work possible and thoroughly engaging.

I have the good fortune to be related to Charles A. Soriano, engineer and inventer extrordinaire. His enthusiasm, technical insight, proficient craftsmanship, and well equiped workshop moved instrument design and construction through generations of prototype to final form.

There are others I take this opportunity to thank: Professor Thomas Jensen provided support for my graduate career when it was most needed; Jean LeCorbeiller led me in conversations and seminars to grasp something of the profound meaning of number; technical assistance with photographic work was provided at key moments by John Hills; Michael Kucher contributed admirable organizational skills, care and patience in the layout of the figures.

My earliest botanical inspirations were my mother's gardens. Any lived understanding I have of plants comes from these. My brother Tom accompanied me on walks through years of seasons, seeking wildflowers, birds, fish, and, lately, bryophytes. This work is testamony to the direction in our wanderings.

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Finally, I am grateful to Julie Downey. Her help in finishing this project has led me to rediscover rewarding intensity in research, writing, and thinking. May gratitude be measured in the breadth, depth, and number of works to follow.

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INTRODUCTION

This study is grounded in a perspective in which the land plants are taken to be water conducting axes connecting the substratum with the gaseous atmosphere (Lemon et. al. 1971; Gates 1976, 1980; Raven 1977). In other words, to the degree that form follows function in the structure of the land plants, they may be seen as interfacial connections of substratum, atmosphere, and liquid water. The morphological consequences of these inevitable conditions of terrestrial life make up the body of this exploration.

The question of scale and the origin of the land plants

More than 400 million years ago, embryophytes differentiated from green algal ancestors (Banks 1968, 1970, 1975; Grey and Boucot 1977). This statement implies two well accepted and complementary hypotheses: one temporal, the other structural. The temporal hypothesis is based on fossil remains of verified land plants localized in their respective strata indicating the minimum age of the group. The structural hypothesis is based on the small scale of these earliest terrestrial inhabitants. This study utilizes the temporal hypothesis of the fossil record together with the well supported hypothesis that the embryophytes differentiated from phragmoplastic green algal ancestors as a context in which to explore questions and hypotheses implied by the comparative biology of plants and the fossil record. The structural hypothesis is used to initiate an investigation of the fluid dynamic and hydrostatic meaning of scale for multicellular terrestrial autotrophs.

For photoautotrophic organisms, the transition from aquatic to terrestrial habitats required some rather specific reconfigurations of the plant body. It is hypothesised that this transition was only possible after the cell wall became a macromolecular matrix with high surface forces capable of moving water throughout a continuous apoplast, while at the same time maintaining its function as a tensile structural element (Preston 1974). By extension, the hypothesis states that apoplastic or external capillary water conduction within and between cell walls is the primitive or generalized state of the land plants. One of the prime functions of proteinaceous cellulosic cell walls in aquatic algae involves generating tensile forces equal and opposite to the osmotic pressure generated by cell contents (Preston 1974). While this function is maintained in the land plants, the terrestrial environment exerts much lower water potential than the cell itself. Since the cell is an essentially aquaeous entity, the 'problem' a cell confronts in terrestrial habitats is to maintain a water potential outside of the cell that is equal to or greater than the osmotic potential of the cell contents. Terrestrial plants universally accomplish this by surrounding the cell contents with a proteinaceous-cellulosic microfibrillar matrix with high surface free energy (Adamson 1976; Zettlemoyer 1967), and, correlatively high adhesive bonding to the universal solvent of this planet, water (Stillinger 1980). These adhesive bonding forces together with the cohesive integral forces in water make up its capacity for exerting hydrostatic force. This translates readily into the somewhat more familar water potential by a direct eqivalence: centimeters of capillary rise or hydrostatic force times (-100) equals water potential in pascals (Pa). In other words, any specific configuration of apoplastic matrix has an equivalent force in water potential. This microfibrilar arrangment of cell walls has been detected in a Carboniferous land plant by Smoot and Taylor (1984), but the pattern is probably very much older.

The earliest land plants of upper Silurian times, best exemplified by such genera as *Cooksonia* and*Steganotheca*, are diminutive organisms of relatively simple structure, consisting of more or less naked cylindrical axes reaching apparent heights of from less than one to a few centimeters. This implies that any constraints on their form would be analogous to constraints imposed on present day plants existing at the same scale as these early embryophytes. In general, the smallest extant embryophytes are in the bryophyte phyla. Therefore, the major focus of this study is the set of constraints on the water conduction, fluid dynamics, and hydrostatics of Gimingham and Birse 1957; Proctor, 1982) and present evidence suggest that in general, at the scale of bryophytes, the colony, as opposed to the individual axis is the functional unit in nature. At the same time, many of the earliest land plant fossils at the scale of bryophytes are found grouped in lithic contexts suggestive of colonial growth forms. The scale and colonial nature of bryophyte axesand, by analogy, early land plants, imply strategies for water conduction differing from larger land plants. These strategies are described in terms of well established principles of fluid dyanamics, hydrostatics, and the geometry of packing, together with the propositions and hypotheses derived from these.

An ecological hypothesis on the origin of the apoplast

An ecological hypothesis is offered in connection with the evolution of the embryophytes: the aquatic habitat is taken to be primitive or generalized for the progenitors of the land plants, while the terrestrial habitat is taken to be derived. Since metabolically active cells require an isosmotic or hyposmotic milieu, functioning in the terrestrial environment necessitates regulation of osmotic pressures and extracellular water potential. In animal systems this is accomplished by mechanisms which reciprocally adjust ionic and water concentrations in extracellular fluid. To achieve similar ends, terrestrial plant systems utilize the tensile forces of cell walls to counterbalance the expansive osmotic forces of the cell contents which act as complementary compressive structural elements. At the same time, terrestrial plant systems utilize the matric potential and the adhesive attraction between water and the proteinaceous-cellulosic extracellular matrix to transport water and maintain the water and solute concentration of the cells surroundings. The specific hypothesis offered here in regard to water balance in land plants is that the matric properties of the proteinaceous-cellulosic cell wall are primary regulators of water balance by acting as tensile structural elements, as they do in aquatic algae as well, and by acting as the apoplastic energy surfaces which bring water and solutes to the cell (Stamm 1967; Thomas l977). This latter is the hypothesised primitive or generalized state of the embryophytes as a clade.

Apoplast is capable of transporting water and solutes very quickly and with very low resistance to flow. Flow follows the high surface energy of the protenaceous-cellulosic microfibrilar extracellular matrix. Resistance to flow is minimized if the surface is shaped such that elongated rectilinear or curvilinear spaces are formed which are bound by plant axes and organs over their length, but open to water at base and the atmosphere at the apex. In other words, if fibrils or plant axes are packed together to make a wick of capillary spaces, water will flow into these spaces, given an interface with the atmosphere. While the parameters and variables involved will be discussed at length below, it should be emphasised here that certain shapes and packing strategies of such surfaces have much greater capacity to move water than others.

Structural constraints on water conductivity in the embryophytes

Each structure of the plant body has a unique range of capacities for conducting water. Specifically, cytoplasm (Gunning and Overall, 1983), cell membranes, cell walls (Preston 1974; Carpita et. al. 1979; Tepfer and Taylor 1981; Nobel 1983), lumenae within empty trachaeid cells (Zimmerman, 1978, 1983; Nobel 1983), and the space between plant axes each have a characteristic conductance and resistance to the flow of water. These may be given in terms of the pressures needed to drive a given amount of water through each of the structures listed. The first three examples in table 1 describe the resistance to lengthwise water conductance through a cylindrical cell 1 mm long by 20 µm in radius.

TABLE I: Resistance of plant structures to water conductivity

Plant Structure	Resistance in Mega Pascals (MPa)
Plasmalemma	2×10^{3}
Cell wall interstices 6 μm thick (2x3μm)	2
Tracheid lumen r=20μm,L=1mm	2×10^{-5}
Small external capillary space r = 200μm, L=1mm	2×10^{-9}

r= radius of the cell, L= length.

The first three resistances are taken from Nobel (1983, p 498), the last was extrapolated based on the Hagen-Poiseuille relation (see section on Fluid Dynamic Principles below).

These figures indicate that it would take the walls of one billion cells or 10,000 tracheids to conduct as much water as one small external capillary space. This indicates that until multicellular land plants reached sizes in cross section of a few thousand cells or more, external capillary conduction systems would be more efficient at moving water.

A relatively small external capillary space exerts twelve orders of magnitude less resistance than a cell membrane, and nine orders of magnitude less than the cell wall matrix. Since these plant structures have intrinsic conductances and resistances to the flow of water, the way they are organized can have dramatically different outcomes in terms of the resistance to water movement in the whole plant. Since resistance may be maximized or minimized by plant form, this points to two fundamentally different strategies for water conduction in the land plants. At small scale land plants employ a very low resistance system utilizing the rapid flow of water along paths between plant axes and organs. At large scale, plants adopt a very high resistance system utilizing the low conductance of the micellular structure of cell walls, coupled with cutin and suberin coatings (Kolattukudy 1980), cell membranes and other mechanisms (Mansfield and Davies 1985) to regulate movement of water through the system by reducing the flow of water through the plant and into the atmosphere. Both systems must hydrate plant cells, move solutes, and exchange carbon dioxide, but at different scales, two very different morphologies are necessary to achieve the same end. This potential for two fundamentally different strategies may have acted to constrain the cladogenesis of the embryophytes to the so called 'tracheophyte' and 'bryophyte' lineages. In basic terms, large scale plants (>5 cm), exist where the concentration of water vapor is low, temperature is high and variable, and wind velocity is high. These variables together at their extremes maximize evaporation, and, since water is limiting, large scale plants are structured to provide abundant and variable resistance to excessive water loss through evapotranspiration. Small scale plants, on the other hand, live in environments where water concentration in the aqueous and vapor phase may be quite high, and wind speed and thermal differentials low. Therefore, all biological exchange would be low because of the nearly laminar flow of the atmosphere, and small plants confront this low exchange potential by minimizing resistance to flow. This may be seen in table 2.

TABLE 2: The kinds of terrestrial environments with respect to scale and fluid dynamic properties.

Small scale, near atmosphere/substratum interface (<5cm)	Large scale, extending beyond atmosphere/substratum interface (>5cm)
generalized or primitive	specialized or derived
low wind velocity	high wind velocity
laminar air flow	turbulent air flow
low evaporative potential	high evaporative potential
Requirements for water conducting systems	
low resistance to water flow	high resistance to water flow
water absorptive surface equal to the sectional area of the conducting spaces (i.e., no roots)	water absorptive surface roughly 10^4 larger than the sectional area of the conducting tissue (i.e. roots)

The question of the significance of the size relations between bryophytes and the larger land plants has long been of interest to plant morphologists. In the last one hundred years, leading morphologists from Goebel (1905) and Kerner Von Marilaun (1896), to Bower(1930), have taken an interest in this question, but it has yet to find satisfactory resolution. Half a century ago, Bower, following D'arcy Thompson (1942), suggested that the surface to volume ratio of the bryophytes, at their scale, was sufficient to effect exhange without the internal differentiation characteristic of the 'tracheophytes'. As evidence, Bower (1930) cited the incipient differentiation of the larger bryophytes such as *Marchantia polymorpha* as evidence that as bryophytes became larger, stomates (or air chambers, their functional equivalent. See also Haupt 1926; Paton and Pierce 1957), together with internal conducting tissue, became necessary in order to continue to function as photoautotrophs. This implies that smaller bryophytes, lacking such structures, are below some specific size at which such differentiations became necessary. While this argument still appears to be substantially correct, the meaning of surface at the scale of the bryophytes has changed dramatically in the last fifty years.

Specifically, while surface area is a fundamental geometric concept, to understand its import here we must refer area to the fundamental parameter of surface energy, or, in its thermodynamic form, surface free energy , and the interfacial properties of the cell wall (Tollenaar 1967). The following historical introduction to the topic leads to a consideration of this presently active area of research on plant structure and function.

Brief history of the study of the cell wall

The importance of the organization and orientation of the cell wall in growth and differentiation has long been recognized by students of plant morphology and plant development. Henshaw (1661) is often credited with the first observation of the walls of vessels in the wood of walnut, but the recognition of the widespread distribution of the cell and illustration of the cell wall must be attributed to the 1667 publication of Robert Hook's Micrographia. This tradition was continued in England with the publication of The Anatomie of Plantes in 1682 by Nehemiah Grew, and in Italy with Anatomae Plantarum in 1675 by the great anatomist and illustrator Marcello Malpighi. The 'Enlightenment"' of the seventeen hundreds brought few apparent substantive contributions to the understanding of the structure of the cell wall. The 19th century, however, records several striking discoveries. First amongst these in the context of this study was the work of von Nägeli, who in Starkekörner, published in 1858, presented what we would describe as the matric potential of starch grains and cell walls, investigated in part through their swelling reactions during hydration. These observations led to the postulation of submicroscopic crystalline structures he termed micelles. This appears to be the first demonstration of the pressure produced by the adhesive forces which connect cellulosic structures with water. The concept of the active participation of the cell wall in the life of the plant is, however, a more recent development, and to describe these relations we must move to the 20th century.

While many recent workers have explored the properties of the plant cell wall, studies may be grouped in two methodological approaches to plant structure and function: the morphological tradition has investigated water conduction from the scale of aggregates of cell wall molecules (Wainwright et al.1976) to the scale of groups of cells, organs, and organismic integration (Nobel 1983, Raven 1977, Walter & Stadelmann 1968, Zimmerman & Brown 1971, Zimmerman 1983); while a portion of the cell biology tradition has concerned itself with the ultrastructure and surface physical chemistry of the cell wall (Domozych et. al.1980; Pickett-Heaps 1969; Preston 1974; Stewart & Mattox 1975). These two traditions have proceeded in relative independence. Considered together, however, they open the ground for a synthetic investigation of how the elaborate three dimensional and surface architecture of the cell wall embodies constraints and potentials for the ontogeny and phylogeny of the land plants.

Synthetic positions often require shifts in perspective, and this is so here with regard to the origin of the land plants. These organisms may be said to originate with one developmental or evolutionary move. This may not have been, however, the origin or differentiation of a new compound or cell type (as in Banks, 1968; or Chaloner, 1970), but rather, the elaboration of apoplastic interface (Raven 1977). While the terrestrial habitat requires several tissues and organ groups to keep the drying atmosphere away from living cells, the primary water holding and moving structure in the plant body is the apoplast Given this, the origin of the embryophytes should be marked by the elaboration of cell surfaces with the shared derived character of apoplastic water regulating properties, a character shared by all land plants (Trachtenberg and Zamski, 1979; Raven, 1977; Lauchli 1976), instead of the more commonly sought differentiation of the lignified tracheid as the sine qua non of terrestrial autotrophic organization (Banks 1975).

The problem of 'cause' in evolutionary studies: attempts to avoid circular reasoning

The intended aim of the synthetic position presented here is to derive the size limits of bryophytes or any diminutive plants using external capillary water conduction in terms of one macromolecular property: the surface tension of water, but even with success this would not be a complete description of the causes of the evolution of the land plants. Water limits life not only in terms of availability, but even more profoundly, in terms of its characteristic properties. But while these properties are literally the fundaments of life, these are not the causes of phylogenesis or ontogenesis in the restricted sense of the word. This synthesis of morphology and the physical chemistry of the surfaces of cells, however, is essentially incomplete without the processes of morphogenesis, since the 'causes' of evolutionary change are to be found here. These causes are not referable to the constraints of physics and chemistry, but to the form generative and regulative processes of ontogeny.

The positioning of active and suppressed centers of growth generates the distribution of plant axes and organs in time and space. This implies that the three dimensional morphology of plants is a function of selective suppression of specific meristematic regions in the course of development. Only morphogenetic regulation yields or 'causes' form in ontogeny. This line of research has been actively pursued by Basile (1979) who has offered the hypothesis that hydroxyproline-rich protein regulates morphogenesis by suppressing cell division and/or enlargement, perhaps indicative of multiple functional properties of proteinaceous-cellulosic cell walls. This is a 'causal' hypothesis complementary to the fluidic constraints described in this study.

Form can only derive from developmental processes. While the focus of this study remains the functional constraints of scale on land plant morphology, it must be noted that function is not a causal explanation of form (Salthe 1985). The present study can only contribute that suppression of meristems in plants at the scale of bryophytes and similarly scaled early land plants utilizing external capillary conduction would produce inter-axial and inter-organ distances within the bounds set by the surface tension of water. Can such processes result in 'adapted' organisms? The often unasked question is 'adapted compared to what? "Adaptation" has often been invoked as an ad hoc explanation, albeit tautological, of those structures which confer fitness on populations of organisms, measured, circularly, by their survival.

To avoid this dilemna, this investigation does not assume that structure is all 'adaptation'. Instead, a hypothesis with testable implications is offered (Jaksic, 1981): the structural novelty that differentiates the land plants from the algae is the presence of an apoplastic interface of liquid water and atmosphere. This hypothesis provides the ground for a synthesis of two traditions in the plant sciences. Specifically, since the physical chemical architecture of cell walls provides the continuum of apoplastic surface in land plants (Raven 1977), the major morphological variants in the water conducting systems of land plants may be seen to be regulative arrangements of this surface. Thus the ultrastructural and morphological traditions, in the context of water conducting systems, may be taken to share the central concept of apoplastic organization, at scales appropriate to the methodologies involved. This continuum of proteinaceous-cellulosic matrix, by virtue of its macromolecular constituents, provides the surface energy taken to be the primary regulator of water balance in the land plants. Characteristics of the morphology of tissues, organs, organisms, and colonies organize and regulate this continuous film of water and the apoplastic interface of water and atmosphere. It is well known that water conducting systems in the embryophyte clades, bryophytes and 'tracheophytes', are not entirely similar. Do these morphological differences represent poles in a continuum or functional 'optima' of apoplastic organization? Rather than assume that water conducting structures are adaptive, the hydrostatic and fluid dynamic consequences of scale are investigated. These consequences are then used to predict measurable properties of hydrostatic pressure and water content of colonies of terrestrial plants. These properties can then be directly measured in colonies of bryophytes which utilize different packing strategies and orientations. If these strategies are functions of developmental homologies involved in phyletic differentiation and cladogenesis, and if modifications of the strategies differentiate the ecological roles such colonies play, they may be termed adaptations. On the other hand, if these strategies are indicative of limits on the kind of organization permitted at different magnitudes, they represent 'grades of organization' (Simpson 1953), not adaptations, but requirements of scale. Such grades were probably of importance in the original differentiation of the land plants. If the strategies and structures which characterize such grades were involved in the cladogenic events which produced higher taxa, they are generalized or primitive characteristics which then cannot be used to distinguish species or lower level taxa.

The hypothesis here presented is that bryophytes exploit the terrestrial environment at and below the laminar surface boundary layer, while the remaining phyla of land plants in general exploit the region above the laminar limits of the surface boundary layer in the region of high wind velocity and turbulance. All forms, in passing from small to large scale, must first embody strategies adequate to the smaller to ensure their survival to the greater. To make use of environmental potentials at small scale, however, requires branching strategies and colony forms adequate to the demands of these spaces, and these will be introduced below.

Bryophytes and early embryophytes of small stature: analogous structures with analogous constraints

Since the earliest land plants were diminutive organisms of relatively simple structure, any constraints on their form would be analogous to constraints imposed on present day plants existing at the same scale as these early embryophytes. In general, the smallest embryophytes are in the bryophyte phyla. This study therefore focuses on the structures that effect water conduction in extant bryophyte colonies, evaluated in the terms of fluid dynamics and hydrostatics. Groups of bryophyte axes or colonies are chosen as the subject of investigation instead of individual axes because earlier investigations and present evidence suggests that, in general, at the scale of bryophytes, the colony, as opposed to the individual axis is the functional unit in nature (Magdefrau, 1982; Proctor, 1982). At the same time, many of the earliest land plant fossils at the scale of bryophytes are found grouped in lithic contexts suggestive of colonial growth forms. The scale and colonial nature of bryophyte axes and, by analogy, early land plants, imply strategies for water conduction differing from larger land plants. These strategies are described in terms of the the following set of well established principles of fluid dynamics and hydrostatics and the propositions and hypotheses derived from these (Goldstein, 1938; Gates, 1980; Vogel, 1981).

Fluid Dynamic Principles Germane to Understanding Terrestrial Environments

I All fluids adhere to their surroundings forming an interface, and a surface boundary layer of still fluid extending outward from the interfacial surface.

II All fluids flow in slow, laminar streamlines near an interface.

III All fluids break streamlines into vortices at the higher velocities encountered at greater distances from an interface.

These principles together with the geometry and behavior of fluids are used to generate well grounded propositions which are used to characterize terrestrial environments, terrestrial plants and their water relations in terms of scale.

Proposition 1; The thickness of the surface boundary layer of the earth is the first constraint on evaporation and water movement in terrestrial environments. Small plants at a scale of millimeters to centimeters, including most bryophytes and early land plants, exist within the surface boundary layer of the substratum. This boundary layer is characterized by low velocity gradients of the atmosphere, i.e. low wind speeds. Because the boundary layer near the substratum is relatively unstirred by wind, gradients which depend on the velocity gradient of the atmosphere are comparatively gradual. Specifically, for small organisms near the substratum, the relative humidity gradient is regulated more by the surface boundary layer than by specific structural features of the plants themselves. The larger land plants at a scale of centimeters to meters extend into the turbulent segment of the atmosphere. In this area of high to awesome velocity gradients where boundary layers are comparatively thin, structural features of the plant body dramatically affect evaporation and water loss. Where water is limiting, such regulation is essential. In sum, the steepness of velocity gradients of the atmosphere and the concomitant gradient of relative humidity are dependent on height above the substratum. The thickness of this layer of unstirred air is the primary impediment to evaporation and the concomitant movement of water and minerals in the transpirational stream. The requirement for regulation of the rate of flow of this stream, and the steep gradients of water potential of large scale land plants centimeters to meters above the substratum are necessarily coupled (Lauchli, 1976; Mansfield and Davies, 1985). The power to run the transpirational pump and the need to limit the amount of water loss come from the same high evaporative potential of the turbulent atmosphere. On the other hand, small plants such as bryophytes and early lands plants exist within relatively flat water potential gradients millimeters to centimeters above the substratum (Potzger, 1939; Proctor, 1982). Here, there is relatively low evaporative capacity because diffusion is limited by laminar flow. This implies the following propositions.

Proposition 2; Water potential is a function of scale. Between the substratum and the upper edge of the laminar flow boundary, the concentration gradient of water vapor is flat, and wind velocity is low, together providing little energy to power evapotranspiration. Between the substratum and the turbulent atmosphere, the concentration gradient of water vapor is steep, and, coupled with high wind velocity and temperature, this provides a very steep water potential gradient.

Proposition 3; In order to move water efficiently, small plants must have water conducting systems with low resistance to flow because there are only low water potential differences between base and leaf tip. For large plants, to move water efficiently means to conserve it by limiting evaporation rates with water conducting systems with high resistances necessitated by the large water potential differences between root and leaf.

These propositions describe the properties of the terrestrial environment as a set of fluid dynamic parameters. These parameters, as such, constrain the morphological variables of any terrestrial autotroph.

The principles and propositions which follow apply specifically to small scale plants, and, amongst extant plants, to bryophyte colonies in particular. The classical literature on the kinds of bryophyte colonies specifies five growth forms: turfs, cushions, mats, canopies and wefts (Gimingham & Robertson 1950; Gimingham & Birse 1957) (See figure 1). These studies conclude that the distributions of these growth forms are correlated with habitat, specifically with light and humidity gradients. An intrinsic problem with such characterizations, however, is that these growth forms are merely structural (Watson 1971). The present study investigates the hydrostatic and fluid dynamic behavior of these growth forms. Also, a more general model of growth forms in diminutive plant colonies is presented which utilizes only two parameters: packing strategy of axes; and, their orientation in relation to substratum. The packing of plant axes when viewed in cross section varies from the limit of close packing to open packing to non-packed open growth forms (see figure 2). Orientation of bryophyte axes may vary from vertical to horizontal. Because of the scale of bryophytes, packing strategy between bryophyte axes structures the largest component of the external capillary conducting system for water movement. In turfs and cushions this component of the external capillary conducting system is oriented vertically and approximates close packing, in mats the orientation is horizontal to vertical and approximates close to open packing, while in canopies and wefts the orientation is mixed and the axes are arranged in open growth or non-packed form. This model rests on the euclidian geometry of spheres or cylinders packed in a plane, and so it is based on axioms of two dimensional geometry (Thompson, 1942; Dormer 1980), together with the auxilliary assumption that the spheres are of the same size. This framework is coupled with the theory of hydrostatics. Together these are used to arrive at a first approximation of comparative water conducting capacities of the kinds of bryophyte colonies based on the packing and orientation of plant axes and the hydrostatic forces such packing strategies generate.

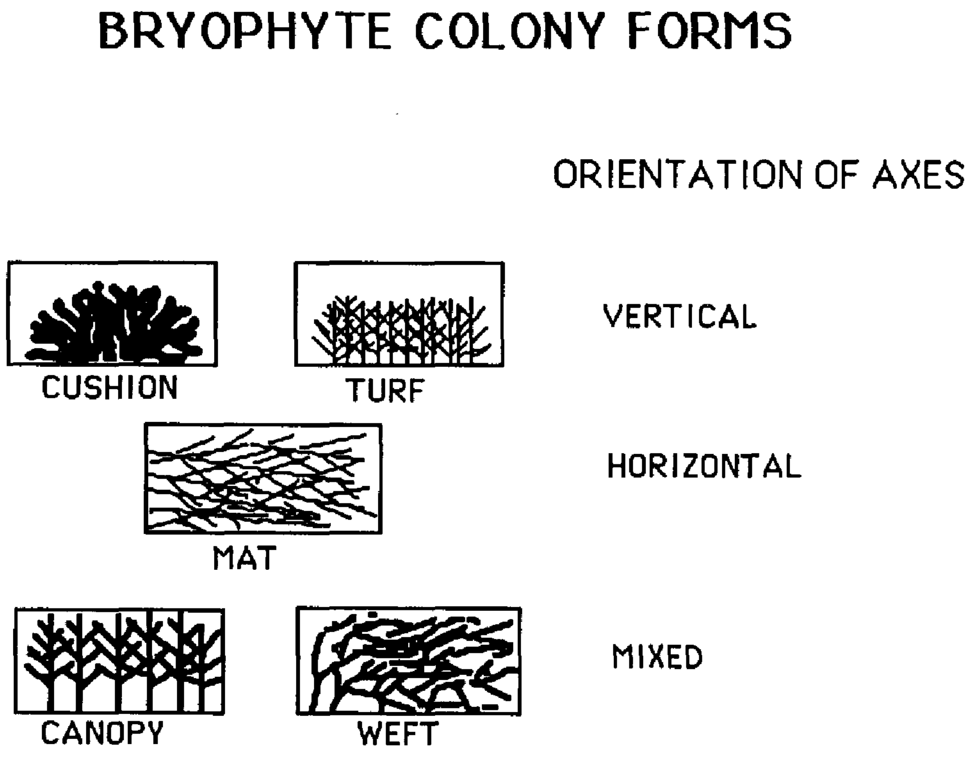
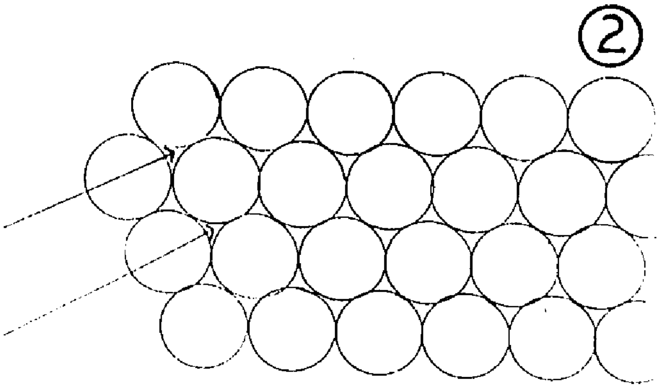


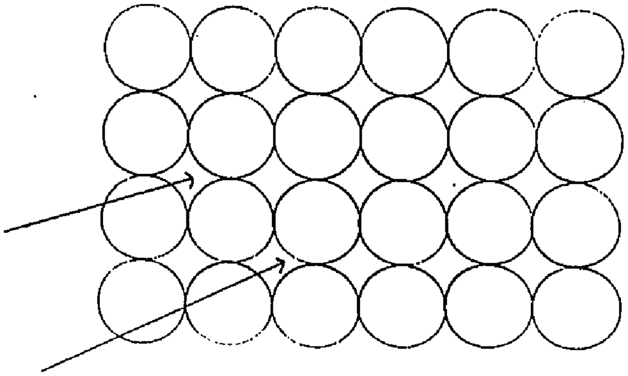
Figure 1. Bryophyte colony forms. The classical literature describes five kinds of bryophyte colony: cushion, turf, mat, canopy and weft. Axes in cushions and turfs tend towards the vertical, mats are horizontally oriented, canopies and wefts have mixed orientation of axes. Orientation as well as packing strategy are the subject of this study, with cushions, turf, and some mats found to be close packed to open packed, while other mats, canopies and wefts are non-packed (see figure 2)

Figure 2. Geometric packing strategies. There are geometric limits on the packing of bodies in two dimensions. Circles, sections of cylinders or of plant axes can be close packed, where each body is in contact with six others (top figure), open packed, where each body is in contact with eight others (middle figure), or non-packed (bottom figure), where, on average, each body is in contact with less than eight other such bodies. The arrows point to the spaces between the packed bodies. These have characteristic sizes. In close packing, these spaces are 0.155 times the radius of the bodies, in open packing, 0.414 times the radius. These outcomes are utilized in estimating the possible height to which water could be conducted in fossil early land plants (see tables 5 and 6).

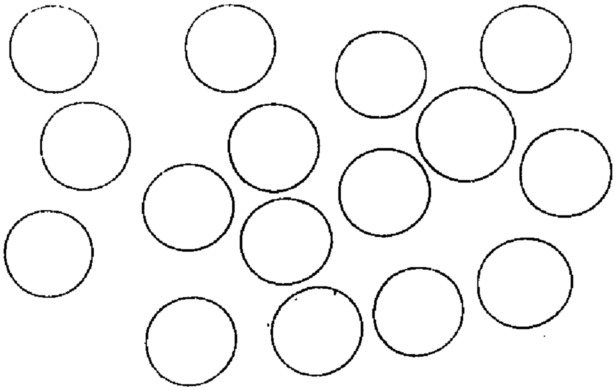
Close packing



Open packing



Non-packing



Two dimensional geometric and hydrostatic principles germane to understanding colony organization in diminutive land plants

IV Geometric close packing minimizes the distance between spheres or capillaries.

V The height of capillary rise is inversely proportional to the radius of the capillary. The smaller the capillary, the greater the rise.

The following propositions follow from these principles.

Proposition 4; Close packing minimizes the distance between axes thereby maximizing hydrostatic forces in the external capillary conducting system between plant axes. Non-packed forms contain larger spaces between axes and exert much lower hydrostatic forces (and therefore, much higher water potential, since hydrostatic force in cm X (-100)= water potential in pascals (Pa)).

Proposition 5; The greater the hydrostatic forces, the greater the heights to which water may be lifted above the substratum and the water table. Close packed plant axes will therefore raise water to greater heights in the interaxial spaces than open-packed and non-packed forms.

Proposition 6; Close packed external capillary conducting systems exert the greatest hydrostatic pressures, while non-packed systems exert much lower pressures. Close packed turfs and cushions would then have the capacity to move water to the greatest vertical heights, and to the greatest heights above the water table at a given depth. Open growth non-packed canopies and wefts would have the least such capacities. The horizontal orientation of mats permits them to move water laterally, with the vertical height limited by the degree of close packing.

Since external capillary conduction of water is dependent upon the presence of free liquid water, bryophytes and other plants of the same scale that utilize this system for water movement must maintain quantities of free liquid water in capillaries between axes and other organs (Burr et. al., 1974; Monzingo et. al., 1969). Complete saturation with water does not permit evaporation or the formation of interfaces and the concomitant 'pumping' of the transpirational stream. On the other hand, the absence of liquid water would break continuity between plant and substratum and begin to dissicate cells and shut down photosynthesis (Hinshiri and Proctor 1971; Dilks and Proctor 1974, 1975, 1976 a,b; Proctor 1982; 1979). Because of these conditions of the terrestrial environment, to maintain active photosynthetic capacity, land plants utilizing external capillary water conduction must balance the forces filling and emptying the system. This is accomplished by matching the hydrostatic capacity to fill interaxial water conducting spaces against the evaporative potential of the habitat which acts to empty these capillaries. From a hydrostatic perspective, this strategy of land plant water balance can be described in terms of the different curves on the graph of liquid water content and hydrostatic pressure of depth to water table (see figures 30-31). The curve describing the emptying of the external capillary spaces within a bryophyte colony differs from the refilling curve because hydrostatic pressure depends on capillary diameter, and any bryophyte colony contains capillaries of several different diameter magnitudes. However, the curves for any given group of capillaries are unique. This leads to the following:

Proposition 7; Bryophyte colonies of different growth forms embody characteristic frequencies of capillaries in different size ranges. Each of the size ranges of these capillaries exerts a characteristic hydrostatic pressure for a given volume of water. Therefore, the sum of the distribution of hydrostatic forces in each colony type determines a specific surface on the graph of water content against hydrostatic pressure or depth to the water table. Bryophyte colony growth-forms may thus be differentiated by the characteristic shapes of each form's graph of hydrostatic pressure vs water content of the colony.

The bryophytes have long been a group surrounded by considerable controversy in regard to their phyletic relations with the so called tracheophytes (Remy and Remy, 1980; Remy, 1982; Stebbins and Hill 1980; Taylor 1982; Mishler and Churchill, 1984, 1985). The question has been asked by various authors at different times as to whether the bryophytes are the earliest group to differentiate from the green algal ancestors of the embryophytes; whether the bryophytes are ancestral to the rest of the embryophytes, whether bryophytes and 'tracheophytes' arose independantly from some phragmoplastic green algal ancestor; and whether the bryophytes themselves are monophyletic in various senses of the concept.

While the present study cannot possibly answer all of these problems in the phylogeny of the land plants, it does address the question of the scale of the early embryophytes and their concomitant requirement for differentiated water conducting structures. The propositions presented above provide a framework for the interpretation of information on water balance in small plants. The first three propositions address the question of scale with regard to: 1) the surface boundary layer; 2) water potential; and 3) the resistance to flow in water conducting systems. These three propositions are so well corroborated at this point as to constitute a well supported theoretical framework grounded in more than five decades of empirical research in fluid dynamics and boundary layer effects on diffusion. This framework serves to outline the fluid dynamic constraints of the terrestrial environment. Specifically, from the first two propositions, boundary layer constraints on diffusion and water potential were primary limits on the functional capacities of early land plants if these were of similar scale to either extant bryophytes or the early plant fossils found thus far. The third proposition regarding resistance to flow characteristic of different water conducting systems is based on the constraint space described by the first two propositions. It points to a specific size range at which high resistance water conducting systems characteristic of the so called tracheophytes becomes necessary in fluid dynamic terms. Specifically, this occurs when a plant axis reaches a height of relatively constant contact with the high evaporative potential in zone of turbulent flow of the atmosphere where only high resistance to the flow of water from substratum to atmosphere limits demand to match supply. On the other hand, strategies to lower the resistance to water conduction need not always result in external capillary systems. The presence of vessels in the roots of *Selaginella* and several species of ferns may be examples of the same strategy in internal conducting ystems. The argument presented here is that the low water potential differences and the low evaporative potential of surfaces within the non-turbulent boundary layer of the substratum provide an environment where the size of water conducting channels tends to be maximized because the potential difference and evaporative forces which drive water conduction are at a minimum, and the resistance to the flow of water therefore needs be minimized.

While several mathematical techniques underlie virtually all of the methods here presented, a fundamental group of equations has been utilized throughout to characterize the parametric constraints bounding the bryophyte strategy. These equations describe boundary layers, hydrostatic pressure and flow rates in terms of the properties of water and parameters of scale. The equations are as follows:

$$Q = \frac{\pi \Delta P r^4}{8 \mu l} \qquad h = \frac{2 \partial \cos a}{r P g} \qquad h^2 = \frac{\partial r t \cos a}{2 n}$$

and the equation defining the relative thickness of the surface boundary layer

$h/x = 5\ \mathrm{Re}_x^{-1/2}$

where

Q = flow rate, cm^2/s
ΔP = pressure differential, in pascals
μ = dynamic viscosity, g/cm/s
l = length, cm
h = height, cm
∂ = surface tension of water, 72.8 dyn/cm @ 20º C
a = angle of meniscus with capillary surface, $\cos a \approx 1$
r = radius of capillary, cm
P = density of water, g/cm^3
t = time, s
n = kinematic viscosity, cm^2/s
Re = Reynolds number, Vx/n, where
V = velocity of fluid, cm/s
x = characteristic dimension, or distance from leading edge of a surface
Re_x = Reynolds number at distance x from the leading edge

The latter equation implies that a bryophyte growing on a flat rock a meter across would have a laminar boundary layer ≈ 5cm thick over the center of the rock, a prediction in general accord with the hypothesis that bryophytes are land plants at the scale of the laminar flow surface boundary layer of the atmosphere against the substratum.

The former equations imply a set of relations between the flow rate through a capillary system, the radius of the conducting channels, the height to which the capillary conducting system can move water, and the temporal constraints on the velocity of flow through channels of given radii. More water flows through a larger capillary than a smaller capillary, and fluid moves more quickly through a system of large capillaries than of small capillaries. However the height of capillary rise is greater in small than in large capillary systems.

The purpose of these mathematical endeavours is to gain some synthetic understanding of the theoretical limits on water conducting systems and to make predictions with regard to the organization and scale of colonies of small plants. In this system of four simultaneous equations it should be noted that r, the radius of conducting capillaries, occurs in the first three equations, while h, height occurs in the last three. In fact, since P = (height)(gravity)(density of water), h occurs in all four equations. Because of this, given the assumptions of laminar flow and of close packing, we are in a position to predict the maximum height range of colonies of small plants utilizing external capillary conduction, and the maximum size of interaxial capillary spaces within close packed plant colonies at various heights. This is simply accomplished by setting the appropriate equations equal to one another.

Specifically, the height of laminar flow may be set equal to the height limit due to hydrostatic forces.

Since $h/x = 5\,Re_x^{-1/2}$ may be restated, $h = 5\,Re_x^{-1/2}\,(x)$

and since $h = \frac{2\partial \cos a}{r P g}$, $\frac{2\partial \cos a}{r P g} = 5\,Re_x^{-1/2}\,(x)$

By algebraic manipulations, $r = \frac{2\partial \cos a}{P g\, 5\,Re_x^{-1/2}\,(x)}$ The fluid geometry of the situation thus sets a reciprocal limit on the laminar flow of the atmosphere and the structure and scale of the hydrostatic forces responsible for moving water in external capillary systems in small plants.

Simply stated, the scale of an external capillary conduction system is essentially limited by the surface tension of water and the thickness of the laminar surface boundary layer of the atmosphere. This 'defines' bryophytes for the first time in terms of the geometry of fluids and the intrinsic properties of water. It is perhaps the first attempt to grasp the differentiation of the land plants in terms of the lawful relation of the constraints inherent in the terrestrial environment.

The Hagen-Poiseuille equation indicates that the flow rate of larger capillaries is much greater than that of small, in proportion to the forth power of the radius of the conducting element. As stated above, flow

rate, $Q = \frac{\pi \Delta p r^4}{8 \mu l}$

This indicates the importance of the scale of the conducting element, but again, this equation may be manipulated to make this point in an even more powerful way. What is important here is the ratio of the drop in pressure per flow rate. Following Goldstein (1965), we may write:

$$\frac{\Delta p}{Q} = \frac{8\mu l}{\pi r^4} = R$$

This ratio indicates the resistance to flow within the system, and once again, by inspection it is apparent that a relatively small increase in the radius of a capillary conducting element will dramatically reduce the resistance to flow in the system. The ten to hundredfold increase in scale from tracheids to external capillary spaces dramatically underscores the low resistance of external capillary systems.

To conclude, while land plants inhabit the terrestrial environment, liquid water is essentially limited in quantity and spacially limited in its distribution in these landscapes. Continued presence of concentrations of liquid water occur only in contact with the substratum. The fluid behavior of the atmosphere, its interface with apoplastic water, and the relation of conduit size to rate of water flow must be integrated by the water conducting systems of plants because of these limits on supply and distribution. Near the substratum where the atmosphere flows in laminar sheets and liquid water is concentrated, there is little difference in relative humidity, and only a flat gradient of the concentration of water vapor to power evaporation and water flow from base to apex of the small plants in this milieu. Where the atmosphere tears into vortices at considerable velocities some distance above the substratum, the relative humidity may be extremely low, supplying a steep water vapor concentration gradient between the apex and base of the plant. Such evaporative potential could empty most terrestrial environments of liquid water. Under these circumstances, conduits must be scaled down, exposure to atmosphere of aqueous apoplastic capillaries regulated, and evaporation closely coupled to supply by a system which resists the unproductive loss of a limited, essential resource.These are consequences, not of evolutionary process, but of the behavior of fluids and interfaces, of the geometry of flow and the surface tension of water.

METHODS AND MATERIALS

Patterns of flow: movement of atmosphere around bryophyte colonies

Flow patterns of the atmosphere around bryophyte colonies have received relatively little attention in part because such patterns are difficult to measure directly. In order to demonstrate the pattern of laminar and turbulent flow of the atmosphere in the vicinity of bryophyte colonies a classical technique from fluid dynamics (Shapiro 1961) was adapted to the study of bryophytes. Specifically, smoke was utilized to make stream lines visible and to differentiate laminar from turbulent flow photographically. To this end, smoke candles (Forestery Suppliers, Inc. catalogue number 85004) were fit into a split sapling or similar holder, lit, and the stream of smoke was aimed into a bryophyte colony and its surroundings at a distance of roughly 30cm. Care was then taken to move the candle quickly to an area downwind of the line between camera and colony to avoid obfuscating the photograph, and the dissipation of the smoke layer was photographed at appropriate intervals, from once every three seconds to once every eight seconds depending on the velocity of the wind in the microhabitat of the plants. The photographs were taken with a Nikon F camera fitted with a Micro-Nikkor 55mm lens, using Kodak Pan X or high speed ectochrome for contrast. Shutter speed is important, since the turbulent eddies must be 'stopped' in the photographic record. In general, 1/30th of a second is the minimum speed for such results, improving results at successively higher shutter speeds.

Direct visualisation methods

Direct visualization methods involved photographs of the space filling distribution of the plant axes in a colony. Here, the colony was photographed within a circle of known diameter, 8.89 or 6.35 cm, from a distance of either approximately 25 or 21 centimeters. Between fourteen and one hundred twenty three axes were included in each photograph. The photographs were taken at f stop 3.5, minimizing the depth of field. With both circle sizes, the depth of field was approximately 5 mm. The photographs were taken such that the image completely filled the frame of a 35 mm SLR camera. The tip of each axis together with their surrounding organs was then circled on transparent overlays of these photographs. The distribution of these circles was then characterized in terms of close packing, open packing, and non-packing models, and the uniformity of the size of the packing unit.

An additional direct visualization method involved fixing whole colonies in paraffin and sectioning relatively large blocks of up to one square centimeter or more. Colonies of *Leucobryum glaucum* (6), *Thuidium delicatulum* (5),*Grimmia sp.* (3), *Conocephalum conicum* (2), *Bazzania trilobata* (3), and *Tetraphis pellucida* (2) all yielded adequate replicates of this technique, represented by the number in parentheses. Eight other moss and liverwort colonies were tested, with less than adequate results. The method permits reconstruction of the external capillary conducting spaces in series from base to apex. While in theory this is the method of choice for directly visualizing and measuring the sizes of external capillary spaces within colonies, in practice it is excessively time consuming and most appropriate for close packed bryophyte colonies. It is not yet practical for weft and canopy colony types. *Leucobryum glaucum* colonies provided sections most adequate for photographic representation, so these were included here. The method involves the following modificaton of Johansen's (1940) paraffin infiltration: apply negative pressure (15 minuits of aspiration) to all stages of dehydration followed by mild agitation to increase diffusion rates into the colony. Doubling the number of dehydration steps gives comparable results with smaller blocks ($\approx$ 1 cm^2).

Evaporation with free water access

Many studies have characterized water loss in bryophytes under natural conditions or at low evaporative potentials (Blaikley, 1932; Hadley I980; Dilks and Proctor 1974, 1975, 1976a,b; Proctor, 1979, 1982, 1984). In order to estimate the maximum evaporative capacity of bryophyte colonies together with their low resistance to water flow, it was necessary to develop a technique which permitted the colonies free access to a water source while moving the whole colonies at the same time to an environment in the turbulent flow of the atmosphere. This was accomplished by utilizing empty tin cans (Ocean Spray Whole Berry Cranberry Sauce, one pound size) 11.3 cm in height by 7.2 cm in internal diameter. These cans were fitted with styrofoam discs of 7.0 cm diameter by 2.3 cm in thickness. In the center of these discs was punched a hole 2.54 cm in diameter, and in the experimental condition a plug of bryophyte colony of the same size was fitted into this hole. The evaporative rates of twenty two different species of mosses and hepatics were evaluated using this technique, with a minimum of six trials per sample. only those seven species of bryophyte are included in table 4 for which sixteen or more samples were taken. The controls utilized both the 'doughnut' type styrofoam discs without the bryophyte plug, and, a solid disc to control for evaporation at the edges between can and disc. The variable of interest was evaporation over time. Water was measured and poured into each of the cans, and after periods of from 4 to 36 hours water was measured from each can using a graduated cylinder.

Prediction and measurement of capillary spaces in early fossil land plants

When fossil land plants are collected, their description typically includes measures of the width of plant axes as well as photographs of the lithic context in which the organisms were discovered. Three to eight published records of each fossil taxon were investigated, but measures reported here derive from forty to more than one hundred measures of the clasical photographs reported in Boureau (1967). From these records, estimates are generated of the height to which such organisms could have raised water by external capillary conduction by axes in the reported size range utilizing various packing strategies. The height predictions are based on the fundamental relation of hydrostatics discussed earlier, namely that the height to which water may be raised in a capillary is proportional to the reciprocal of the radius of the capillary. Close packing refers throughout the text to the condition where each plant axis is in contact with six adjoining axes. Such packing between any three axes in mutual contact yields a capillary space equal to 0.155 times the radius of the plant axis (see fig. 2). Open packing is here taken to be the condition where four cylinders are square packed to form a capillary between them, which by plane geometry yields a capillary space of 0.414. Given the size of the fossil stem or axis, utilizing the assumption of close packing (six axes in mutual contact) or open packing (four axes in 'square units'), together with the equation for hydrostatic rise, predictions may be made as to the maximum height to which water could be moved by external capillary conduction. These are given below in Tables 5 and 6.

Artificial bryophyte fossils

In order to compare the earliest land plants with extant organisms of similar scale, compressions were made of two to four samples of each of the five bryophyte colony types. The intent here was to present compressions of known external capillary conducting systems to which fossil land plants could be compared. This was done by placing bryophye colonies approximately three to five centimeters in diameter between two square pieces of plate glass 15 cm on an edge. These plants were then treated with hydrochloric, sulfuric, or nitric acid (0.01 - 0.1N), and an applied pressure of up to 0.2 kg/cm^2. The colonies were thus compressed for three weeks to two months, then photographed with Kodak Pan X film under uniform lighting. The photographs were printed to achieve comparable tone to the published photographs of the fossils (Boureau 1967).

Centrifugation studies

Measurement of the volume of water held within a bryophyte colony by the surface forces of the external capillary conduction system has been accomplished by several methods in the past, from nuclear bombardment to weighing and air drying specimens. The present study utilized a top pan balance (Mettler P1200) as well as centrifugation to measure the weight and volume of water held in the larger capillary spaces within a bryophyte colony. Weight and volume of water extracted by centrifugation were utilized both independently and in tandem as mutually corrective measures. An International refrigerated centrifuge (International Portable Refrigerated Centrifuge Model PR-2) was used for measurement in part of this study, but, because of the limits on the size of a specimen that may be treated in even a large centrifuge tube, and because such centrifuges are not available for fieldwork, a more simplified instrument was adapted here. This device is a salad spinner, normally utilized for removing the liquid wash water from salad materials. Such devices are inexpensive (≈\$10) and they have the advantage of portability in the field. The rapidity of measure (30 seconds) permits a rather large sampling, with N greater than or equal to 100 samples for each species measured, including multiple measures per sample. Besides this, although they are limited in terms of the amount of force they may generate, The gear ratios of most of the commonly available models permit 1600 rpm or more, with a concomitant force of roughly 300 times gravity. Utilizing the well known equation for capillary rise, $h = 2 S \cos a / r P g$ (where h is height, S the surface tension of water, a the contact angle of meniscus and cell wall, r the radius of the capillary, P the density of water, and g the gravitational constant), the maximum amount by which a capillary system may be emptied by centrifugation at a given force is equal to the reciprocal of the force in Gs, or h/G, where G equals centrifugal force in multiples of the gravitational constant. The maximum force utilized in this study with this modified centrifuge was a little less than 300 Gs, thereby emptying the capillary water conducting system by a factor of ≈ 1/300, or, to roughly 0.3 % of full capacity.

Field porometer

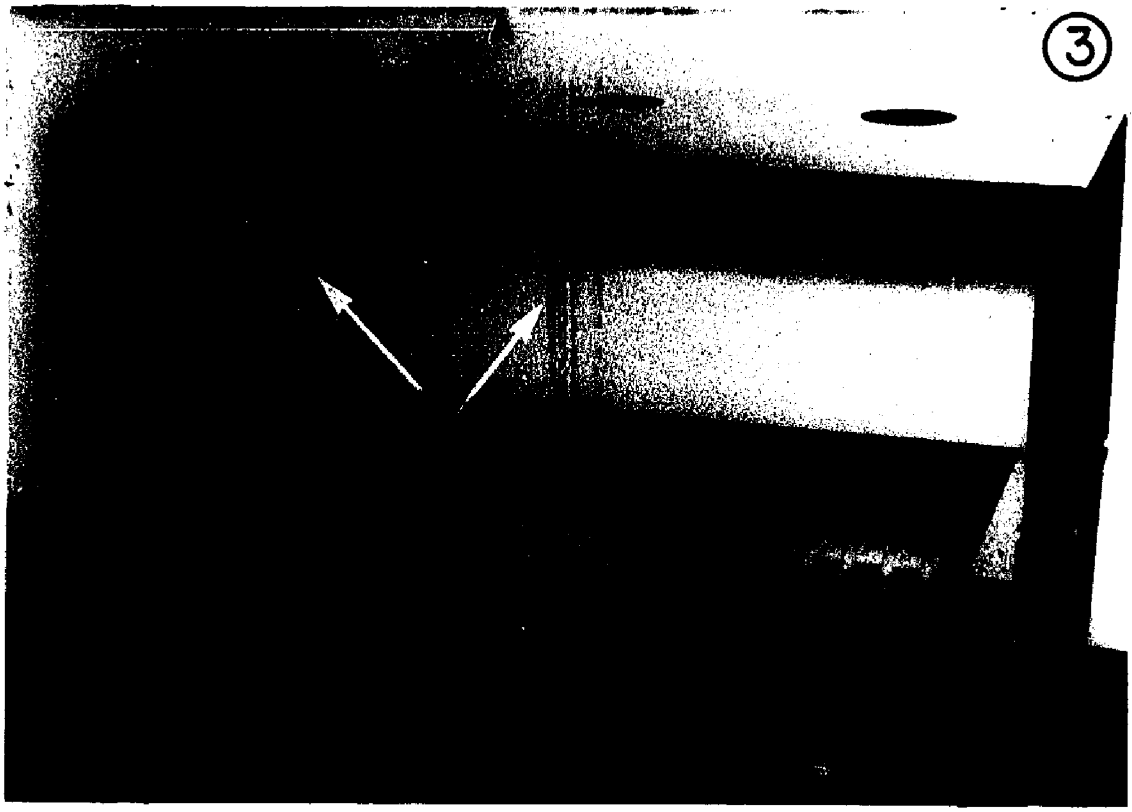
The measurement of hydrostatic forces involved constructing a modified field porometer with a capacity to generate up to about 25cm of head. This device is a modification of the the instruments utilized in the characterization of capillary forces in soils (Haines, 1925, 1927, 1930; Fisher, 1926, 1928; Childs, 1969). This particular instrument was constructed to measure the filling and emptying volumes of the same colony in order to characterize the graphic surface of water content against hydrostatic pressure, a relationship here taken to be fundamental to the habitat requirements of plants of small scale utilizing external capillary conduction of water.

The instrument consists of a scintered glass filter 3.8cm in diameter set in a plastic and wood frame with adjustable legs to permit leveling of the apparatus. The scintered glass filter is connected by tygon tubing to two Penn Plax Loc-tite non-corrosive aquarium gang valves attached in series. Four of the leads of each of these are connected to one millimeter pipettes arranged such that the meniscus in the pipette can be varied from the same height as the surface of the scintered glass filter on which the bryophyte colony is placed, to 20cm below the colony, applying a pressure of -2.0 kPa., equivalent to the hydrostatic pressure of a capillary of radius 0.075 mm. The menisci can be raised or lowered independently utilizing a syringe imparting pressure to the system through a serum bottle stopper. Using the variable setting of the mensci in the pipettes, a negative hydrostatic pressure of up to -2 kPa may be applied to the bryophyte colony, or, conversely, the colony may pull water from zero pressure with each miniscus beginning at the same level as the plant itself, down to some negative pressure.

While the instrument itself is constructed of relatively simple materials and is relatively inexpensive to build (<$40 not including the scintered glass filter), the design utilizes some rather sophisticated principles of fluid dynamics. First amongst these is the principle of continuity which states that the quantity of any incompressable fluid entering a system in one place is equal to the quantity of fluid leaving the system by any output channels. Since water is incompressable at the pressures encountered in terrestrial environments, pressure exerted at a surface in a bound system is transmitted to all other surfaces within the system. In this case, the principle is invoked to indicate that a bryophyte of positive, neutral, or negative hydrostatic pressure will transmit this pressure through the scintered glass filter housing to the water within the apparatus, thus bringing about the changes in volume in the pipettes. It is most important to note, however, that this is a partially closed system in which equal and opposite hydrostatic forces between apparatus and bryophyte come into equilibrium. There is a time dimension to this response which must be accounted for, namely, for any given liquid at a given temperature, the height of capillary rise is a function of a constant times the square root of the time. In terms of measurement technique, this means that beyond the segment where the square root curve begins to flatten, error is a roughly linear function of time, and the rate of change or the derivative of the graph of capillary rise is equal to the reciprocal of the square root of the value of the graph at that point. This may be used to advantage in the following way: by fixing the time of measurement relative to the beginning of each experiment, error is limited if near equilibrium in hydrostatic pressure occurs between the organism and apparatus. The time span of one minute was chosen because in this span the system would usually approach equilibrium. Therefore, while in a non-equilibrium situation, a three second variation in a one minute experiment could lead to a coefficient of error of ≈20%, the same variation in this apparatus would lead to an error of ≈0.5%.

Previous studies have utilized various methods to characterize the water conducting capacities of bryophytes (Blaikley, 1932; Bowen, 1931, 1933a, 1933b, 1933c; Deloire et. al., 1979; Magdefrau, 1935; Rifot and Barriere, 1974; Rycroft et. al., 1975 a, b; Trachtenberg and Zamski, 1979; Zacherl, 1956). Most of these methods have been destructive of colony morphology. One study which utilized intact colonies (Clymo and Hayward 1982; Hayward and Clymo 1982) involved measuring gamma radiation transmittance as a function of water content. Such methods are apparently quite accurate, but the techniques involved require bringing the bryophytes to the apparatus in the laboratory and, therefore, not appropriate to fieldwork. While the present study is indebted to these earlier works, the methodology presented here is, in part, an original contribution. The major difference between the present and previous methodology is the inexpensive simplicity and field orientation of the techniques developed, and the use of intact bryophyte colonies and segments of colonies. The apparatus described and pictured in figure 3 can be used anywhere in the field to measure negative hydrostatic pressure in a bryophyte colony, or, conversely, to apply a negative hydrostatic head and measure the volume of water held in a bryophyte colony at that pressure or less. The versatility of the apparatus allows a colony to be emptied and filled in series. This permits the direct measure of the change in hydrostatic pressure or water potential with water content of a bryophyte colony. While this can only be done for relatively low pressures, these are in the functional range of bryophyte colonies under field conditions (Proctor 1979, 1982; Hayward and Clymo 1982; Clymo and Hayward 1982).

Figure 3. Photograph of the field porometer designed and constructed by the author. The instrument pictured here is the first of its kind used in the study of small plants. This apparatus is capable of measureing hydrostatic pressures up to 20 cm (which equals a water potential of -2000 Pa, -2 kPa). It is fully portable and may be used in tandum with the field centrifuge described above. It consists of a scintered glass filter (arrow at A) 3.8cm in diameter, set in a plastic and wood frame with adjustable legs to permit leveling of the apparatus. The scintered glass filter is connected by tygon tubing to two Penn Plax Loc-tite non-corrosive aquarium gang valves attached in series (arrow B). Four of the leads of each of these are connected to one millimeter pipettes (C) arranged such that the miniscus in the pipette can be varied from the same height as the surface of the scintered glass filter on which the bryophyte colony is placed, to 20cm below the colony, applying a pressure of -2.0 kPa., equilivalent to the hydrostatic pressure of a capillary of radius 0.08 mm., or 80µm. The menisci can be raised or lowered independently utilizing a syringe imparting pressure on the system through a serum bottle stopper (D). By lowering the mensci in the pipettes to below that of the plant on the scintered glass filter, a negative hydrostatic pressure of up to -2.0 kPa may be applied to the bryophyte colony, or, conversely, the colony may pull water from zero pressure with each miniscus begining at the same level as the plant itself, down to measureable negative pressures which depend on the hydrostatic structure of the colony. This is the first such piece of portable equipment capable of generating the emptying and refilling curves of external capillary conducting systems in the field or the laboratory. These curves describe the area of hydric exchange with the environment where the plants are generally involved in active photosynthesis.


③

RESULTS AND DISCUSSION

Patterns of flow: atmospheric movement around bryophyte colonies

Immersing bryophyte colonies and their surroundings in layers of smoke offers strong support that such plants live largely within the laminar flow surface boundary layer of the substrate (see figs. 4-23). While the exact position of this layer of slowly moving air changes with the velocity of the wind, within the time frame of these photographs, the laminar strata of smoke remain within and around the colony.

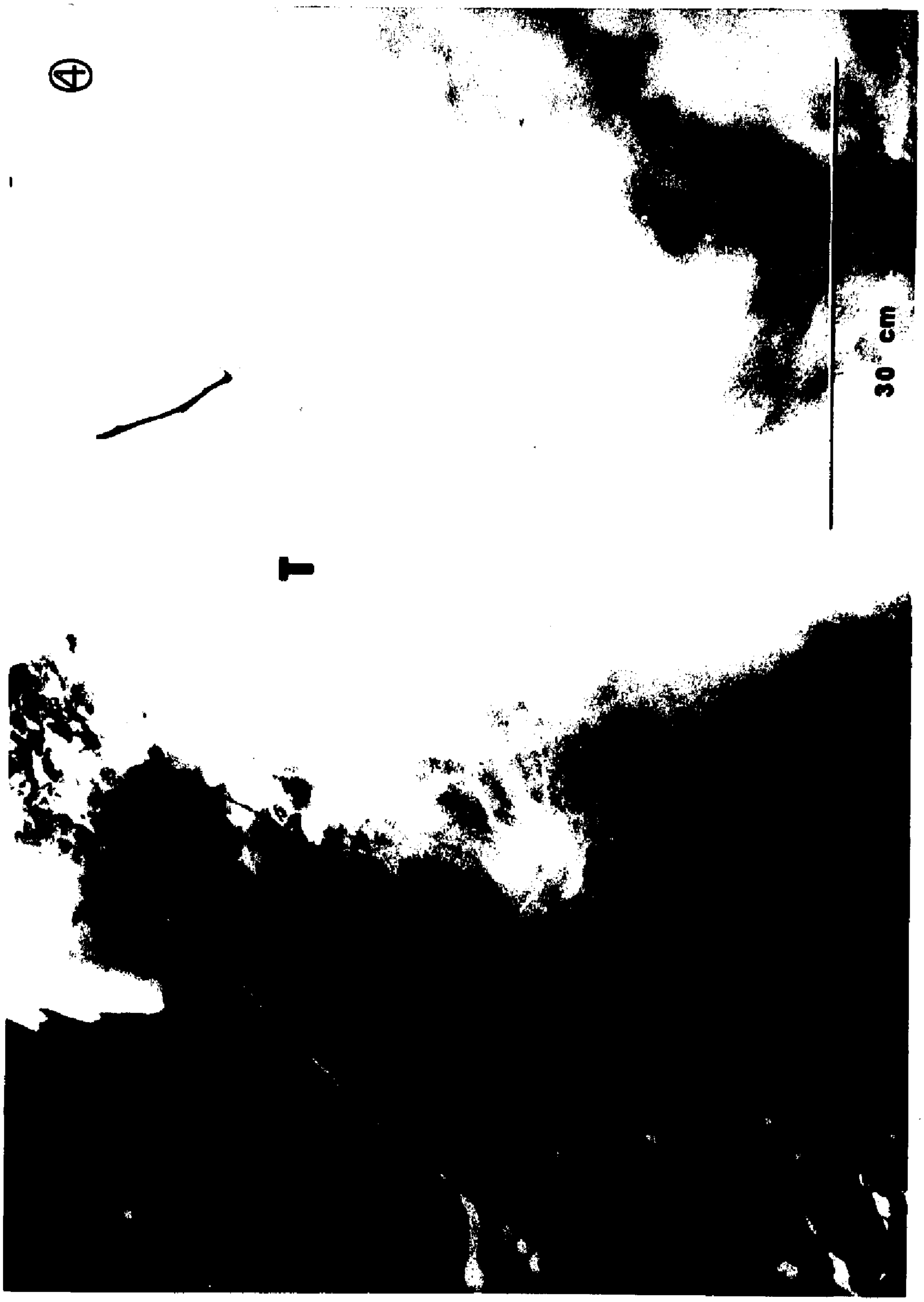
These photographs provide a visualization of the atmosphere surrounding several kinds of bryophyte colonies. They indicate that there are several strategies with regard to the laminar surface boundary layer. Specific colony types appear to have different relations to the steep velocity gradients at the laminar boundary, and the morphology of some forms appears to organize the surrounding atmosphere. Turfs and cushions seem to be largely contained by the laminar boundary (see photos) except for the important exceptions of leaf tips. *Climacium* and *Hylocomium* , canopy and weft respecively, appear to be organized such that their surfaces are near the turbulent/laminar boundary while the atmosphere below these surfaces is laminar or even relatively still. Both *Climacium* and *Hylocomium* show this pattern of external/internal ordering of fluid movement, even though the ravine streamside habitat of *Hylocomium* was protected from strong direct winds while the forest floor after leaf fall where *Climacium* occurred was swept by driving westerlies.

In conclusion, while *Climacium* and *Hylocomium*, canopy and weft, have apparent internal exchange rates of less than once every six seconds and once every 15 seconds, respectively, the more densely packed turf and cushion have apparent rates of less than once every 20 seconds and less than once every several minutes. *Climacium* and *Leucobryum* were photographed on the same windy day, although in different habitats, but the effects of packing of axes are still apparent.

One present difficulty with this method is recording the easily discernable behavior on the smoke photographically. Special lighting, florescent smoke, fast or infrared sensitive films, or these in combination with various filters will be utilized in the next set of trials. Readily quantifiable data might be gathered with motor drive or video equipment, and these avenues could also be explored. The two limits on the present study are lack of a continuous record, and the lack of contrast between plant background and smoke foreground in the photographs.

Figures 4-23. Photographs of the dissipation of smoke from the surroundings of bryophyte colonies indicative of the region of laminar flow and the laminar/turbulent transition. The following series of photographs were taken after bryophyte colonies and their immediate surroundings were filled with smoke. The photographic record of the several seconds following this event depicts how the velocity gradient of airspeed above bryophyte colonies rapidly shears away the layers of smoke at heights above the plant but leaves intact an area of laminar air flow bounded by the body of the bryophyte colony. While each photograph represents a different microhabitat, all contain laminar flow boundary layers and areas of turbulence (arrows S and T, respectively). The specific laminar boundary layer patterns seen in each photrograph are a function of wind speed and direction together with the surface properties of the colony body and its surroundings. The steepness of the velocity gradient varies with the wind speed, but the shape of the laminar envelope is set by the shape and size of the microhabitat and bryophyte colony together. The rate of complete exchange of air between bryophyte colony and surroundings is given based on the periodicity of the photographs. This is indicated in each of the descriptions which follow.

Figures 4-8. *Dicranum scoparium and Brachythecium sp.* colonies on a large rockface. This series of four photographs depicts a large rockface tending from near vertical to 45º with a mixed colony of *Dicranum scoparium* and *Brachythecium sp*. In figure 4, smoke is blown into and around the habitat filling the surroundings volume of atmosphere. The curved lines and eddies indicate the turbulence (T) of the strata of atmosphere above the rockface. Relatively still air is in general difficult to visualize within a bryophyte colony, however, in the figures 5 & 6, each taken at five second intervals, very slow moving (« 3 cm/sec) 'pools' of smoke may be seen collected in microhabitat 'valleys'. These hollows within the bryophyte colony, measurable in millimeters, may be seen in figures 5 and 7 (S). Figure 7 indicates that some of these residual pockets of smoke are surrounding colonial turfs of *Dicranum* (D) while covering mats of *Brachythecium* (B). The area several centimeters above the substratum shows a rather different pattern. Here, in the areas marked T in fig. 6 the laminar stream lines are beginning to diverge and bend as the still air boundary within the bryophyte colony is accelerated through the ≈3 cm/sec laminar/turbulent transition zone. The smoke technique may be used as a semi-quantative method. By way of example, in figure 5, taken five seconds after figure 4, nearly all the smoke in the more than two meters between camera and bryophytes has already been dissipated. Since the whole two meter space had been previously filled, calculation yields a minimum wind speed of 0.4 meters per second. By contrast, the continued presence of smoke in the areas marked S in figure 8 indicates that the atmosphere within the colonies is not fully exchanged in twenty seconds under the conditions at hand.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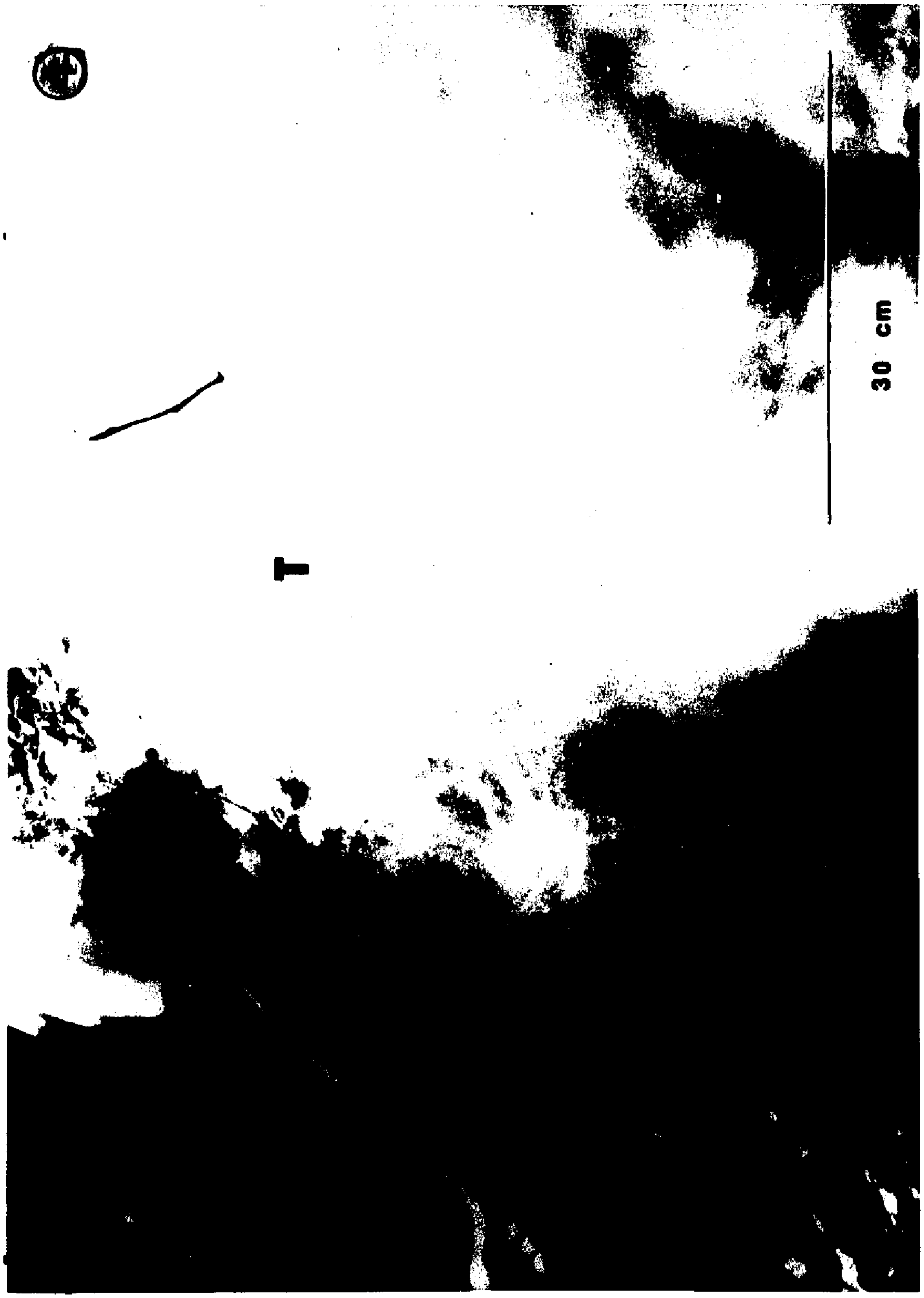
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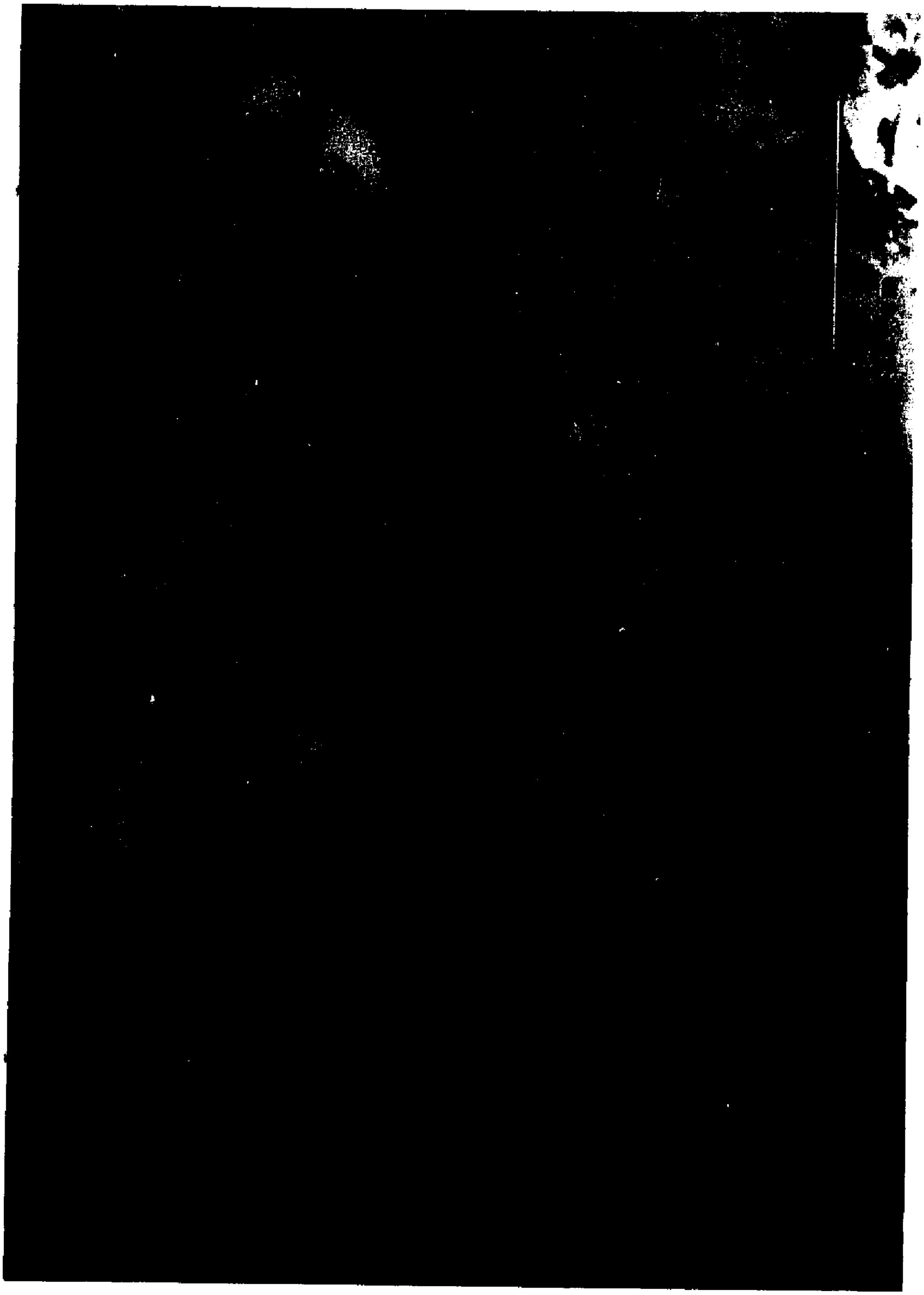

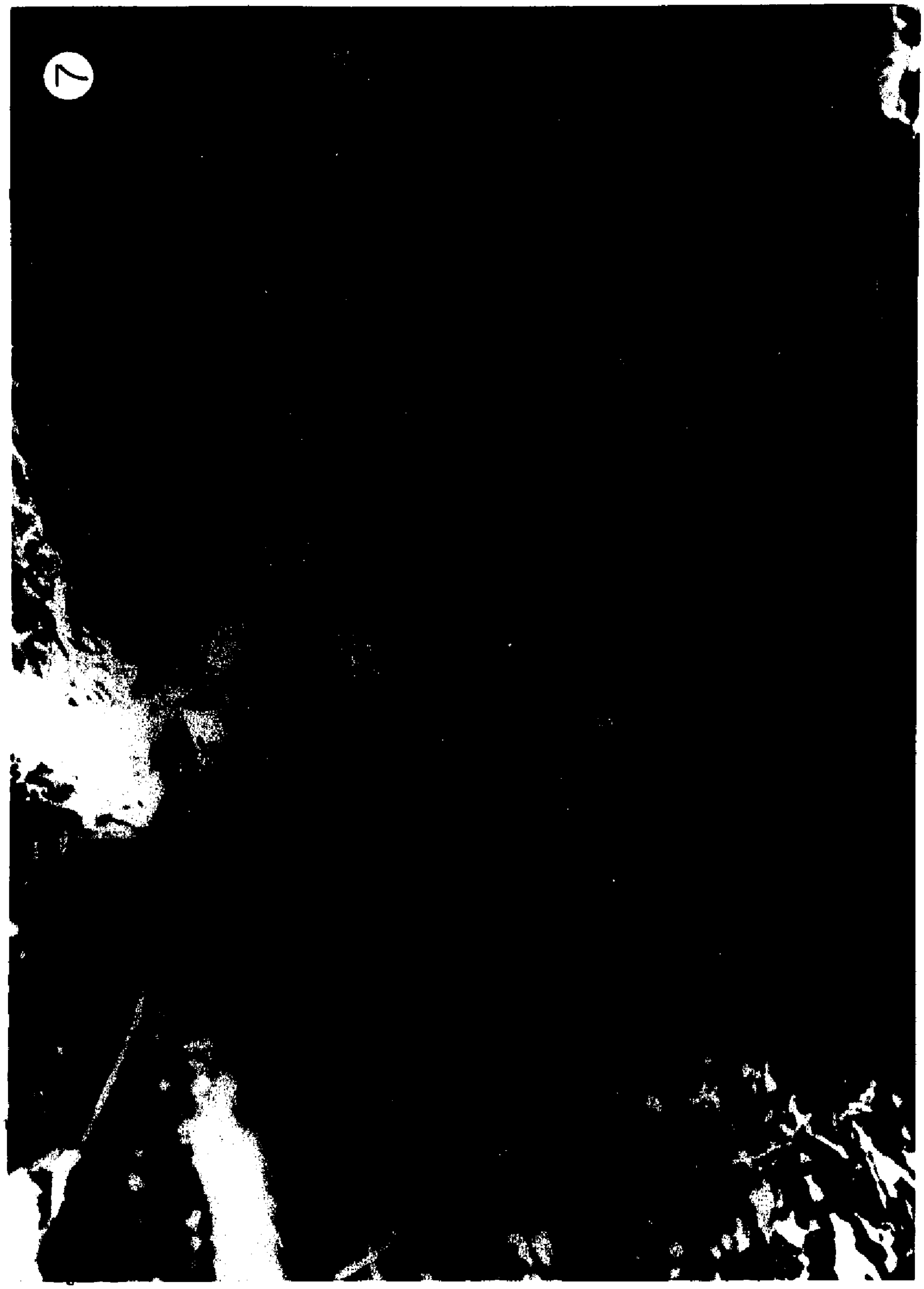

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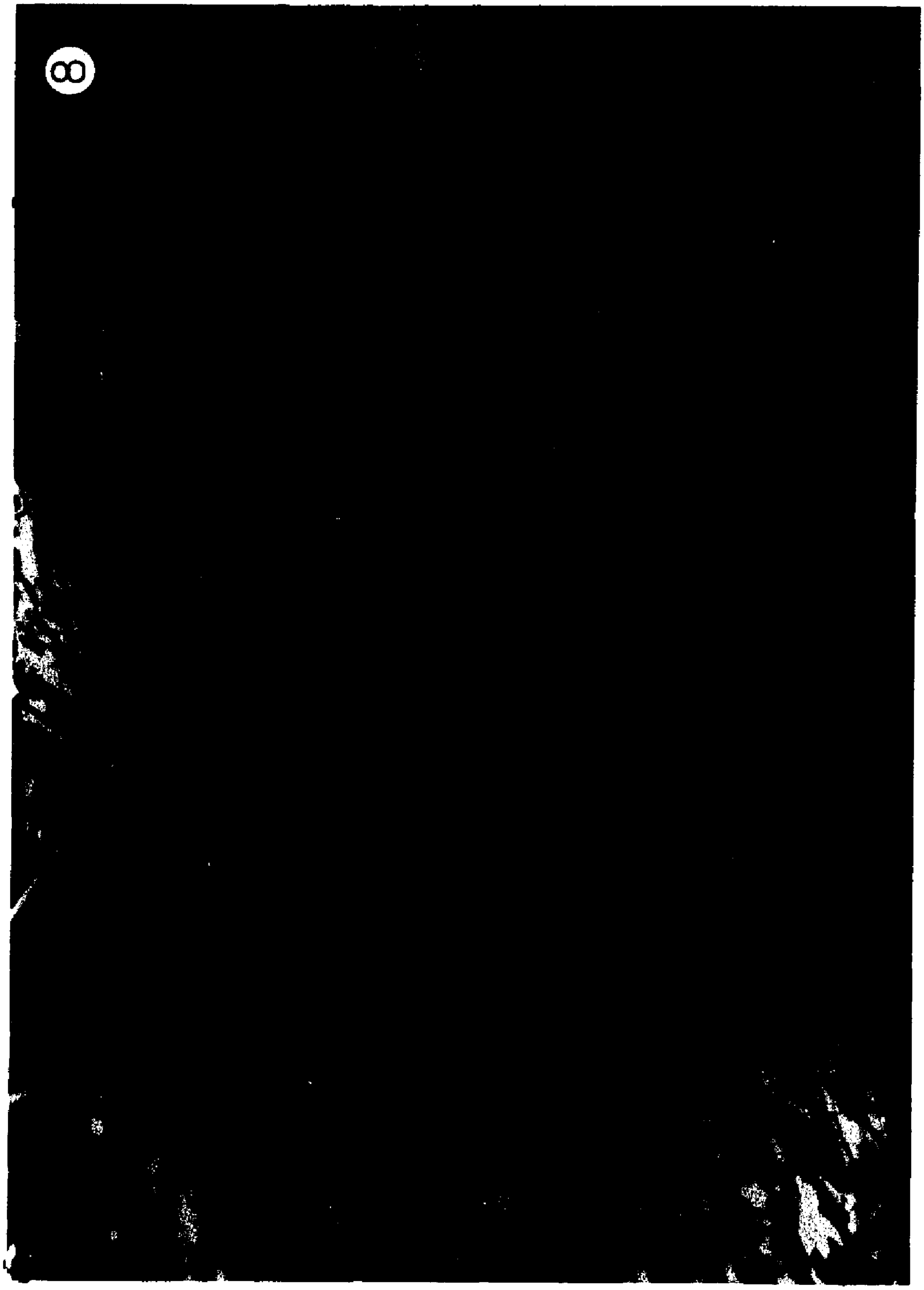
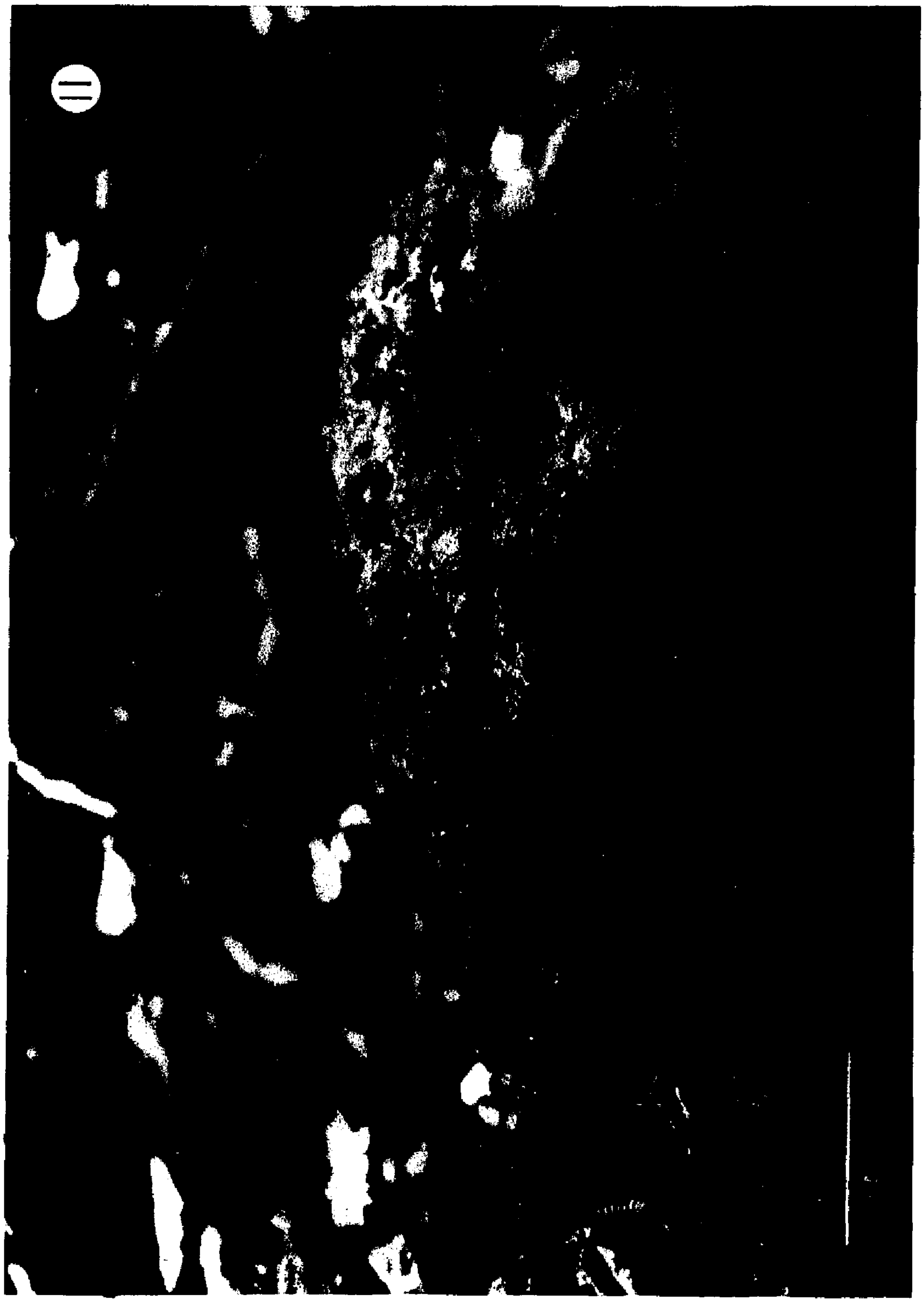

8

Figures 9-12. *Hylocomium splendens.* This set of four photographs indicates the behavior of a large weft in a stream side revine. While the wind shifted during the sequence, turbulence (T) and a laminar surface boundary region (S) may be discerned. In this as well as the other smoke study photographs it must be remembered that the laminar/turbulent transition zone is always overlaid by turbulence. In the five seconds between figures 9 and l0, the density of the turbulent zone greatly diminishes. In figures ll and l2, a laminar cascade of smoke is seen to move from the center right to the lower right of the frame. The slow dissipation rate for the smoke is indicative of a very slowly moving laminar flow front. The left-most pocket marked S in the first two photographs can be seen residually in figures 11 and 12, indicating that the weft of a *Hylocomium* colony is an open packing strategy capable under certain conditons of ordering laminar flow across and through the fronds while maintaining still air pockets within, with an exchange rate between interior and exterior air occuring less than once every 15 seconds.

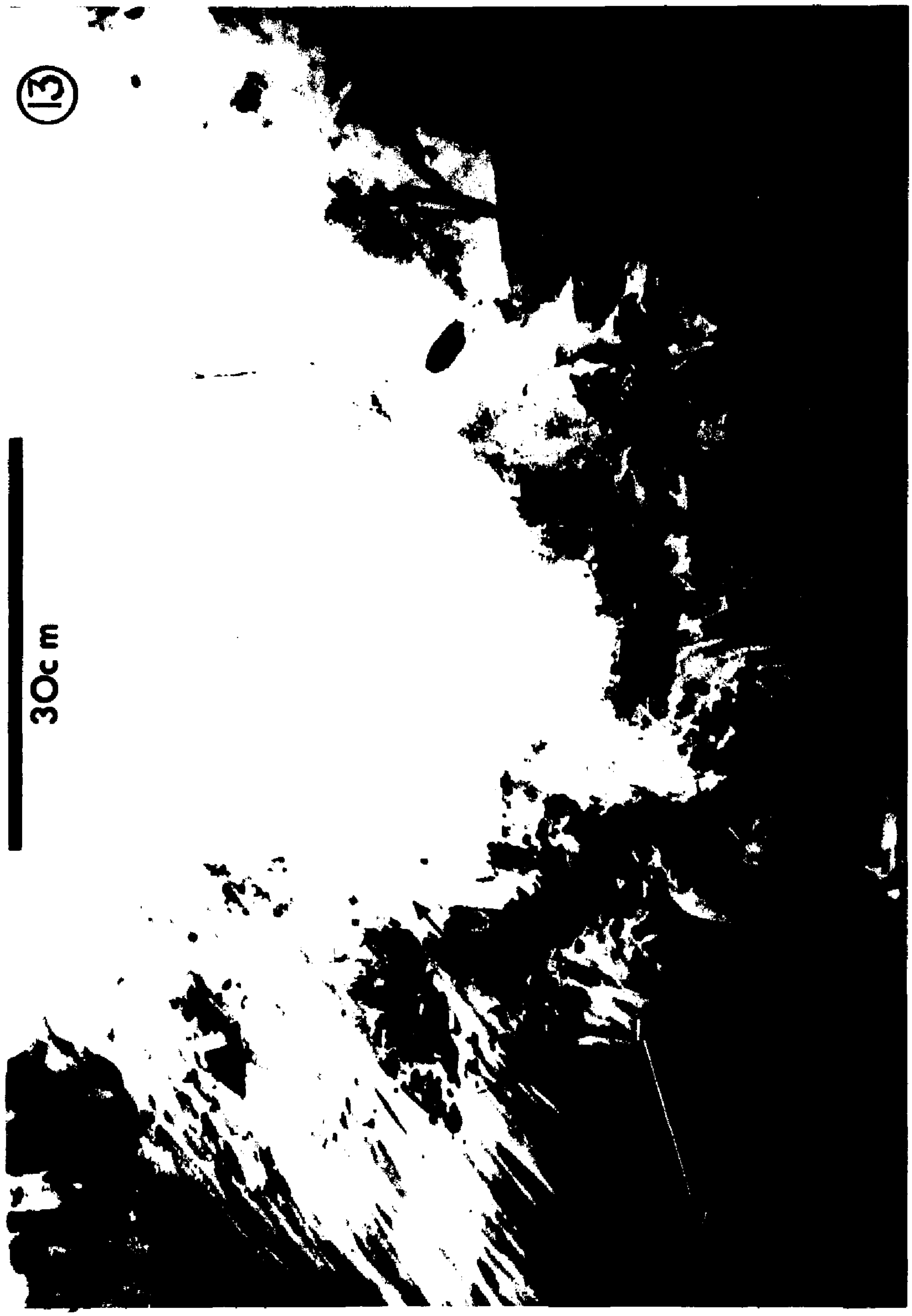

T
T
T
T
S
S
S


⑩
T
10 cm


II


12

Figure 13-15. *Climacium dendroides.* A relatively large colony of *Climacium dendroides* was partly submerged in a temporary shallow pond. In the first photograph (fig. 13), laminar stream lines can be seen against the surface of the water, and extending down wind along the interface (arrows marked S). Turbulence can be seen tearing off the tip of the canopy and extending downwind at heights above the substratum (T). The second photograph (fig. 14) shows a lesser amount of smoke in a similar pattern three seconds later. A standing wave of turbulence may be seen clinging to the upper portions of the *Climacium* canopy under these conditions. Below this turbulence, distinct laminar boundary flow lines may be discerned in the lee of the canopy, especially in the pockets indicated by the arrows. While the wind is moving relatively rapidly here as evidenced by the minimal height of the laminar boundary layer on the water surface, residual still pockets of smoke may be seen within the *Climacium* canopy, although vortices are apparently tearing off the tip of the colony under these conditions. The third photograph (fig. l5) indicates that these residual pockets are more stable than the water surface streamlines, and that the atmosphere within a *Climacium* colony is exchanged less than once every six seconds even in a windy macrohabitat.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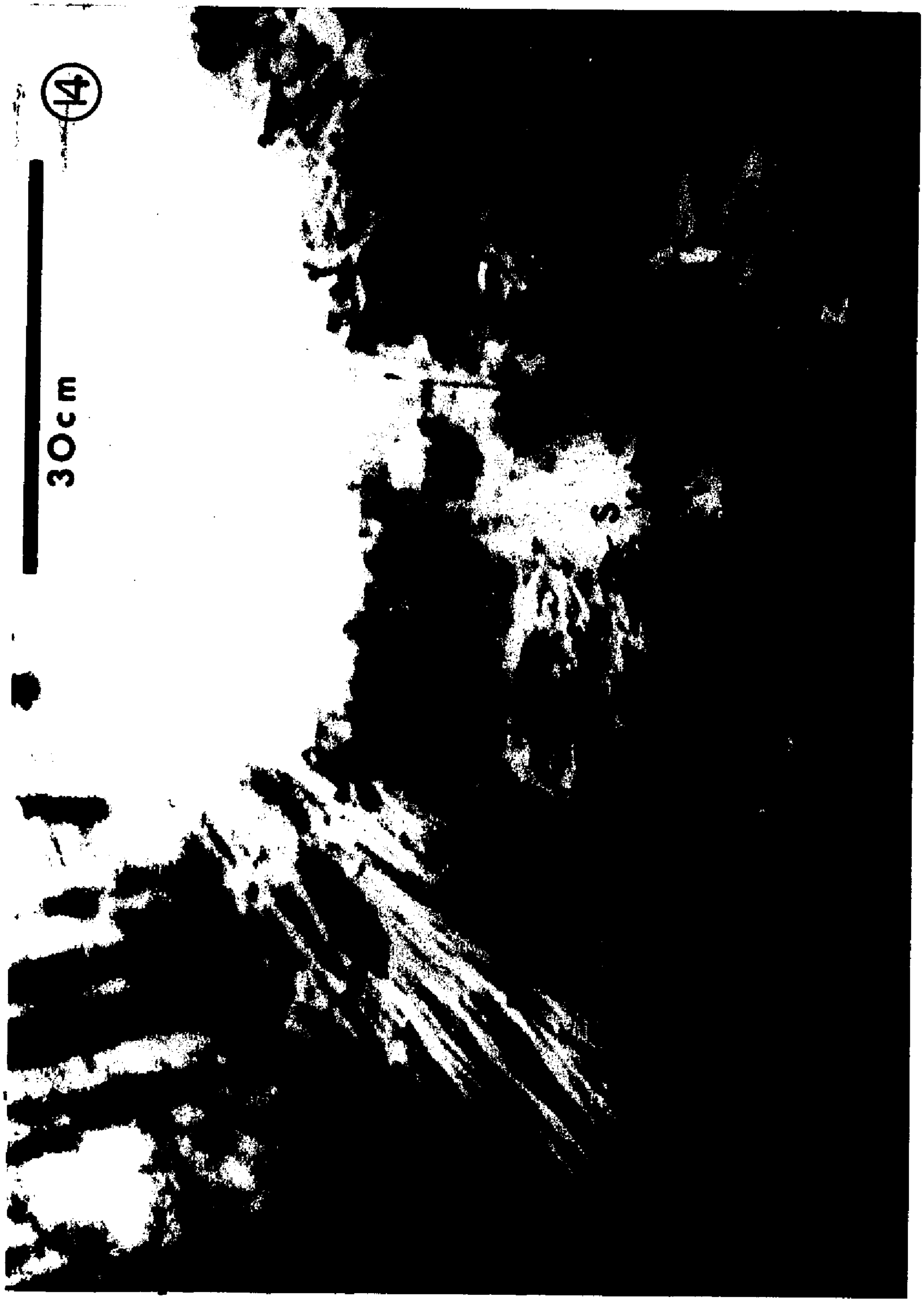
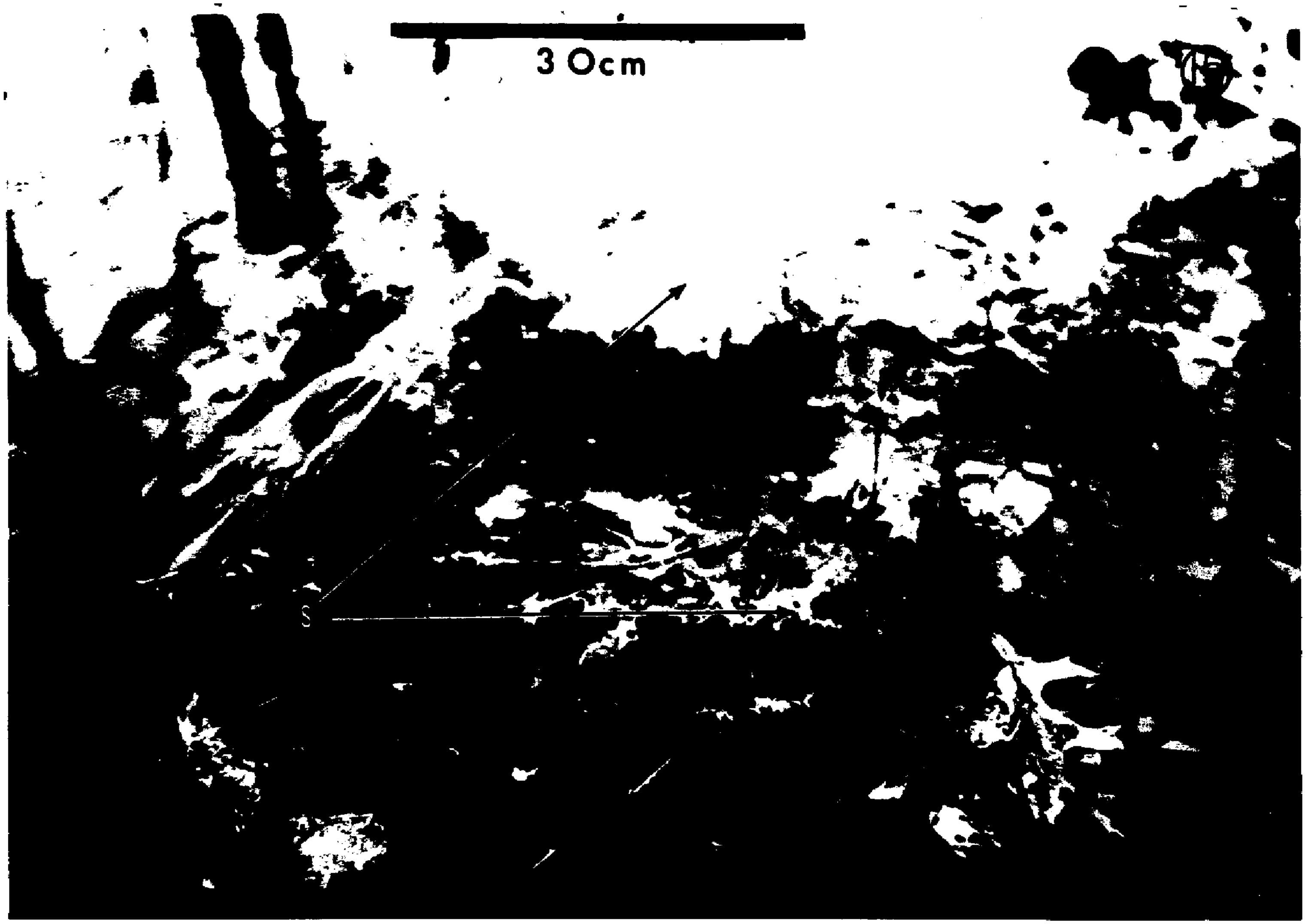
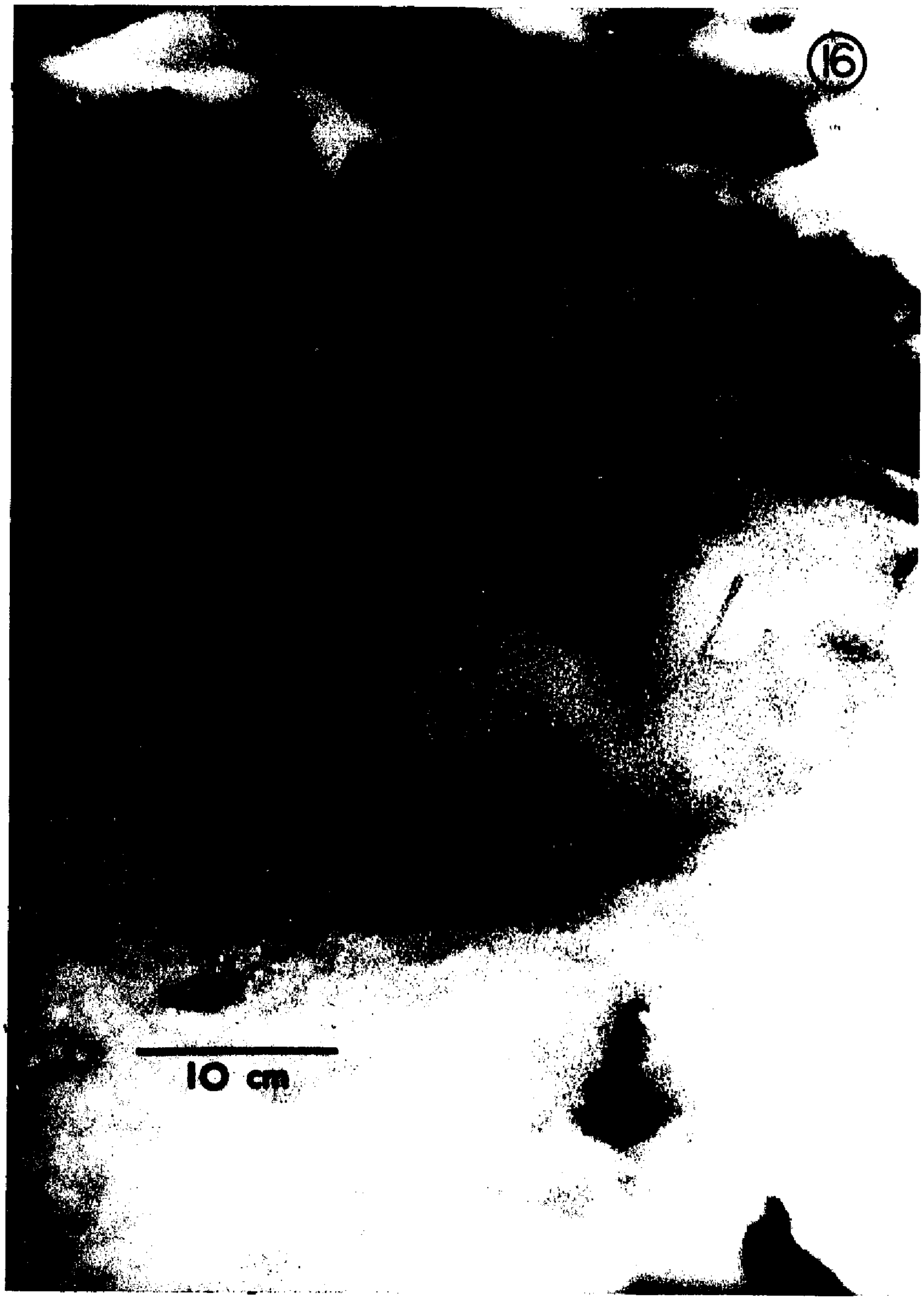
30cm


⑭
30cm
S


30cm
S

Figures 16-20. ***Dicranum scoparium.*** This series of five photographs demonstrates two different smoke inundations of the same colony. What this set uniquely demonstrates is the continued presence of turbulence at distances from the colony and the substratum. The turf colony form of *Dicranum scoparium* releases smoke in laminar sheets, as in figure I8, and while such sheets are not always visible, their presence may be presumed at this scale. The vortices to the left of the rounded colony (slightly left of center, all frames) are apparently derived from streamlines passing over the rounded colony surface (see especially S and T, figure 20, and the position of T, all frames). The rounded forms of many of the close packed colonies may be involved in moving streamlines together and thus, like an airfoil or airplane wing, minimizing turbulence and therefore dissication in dryer more rapidly moving air. Such a strategy could act to extend the dissication range of plants utilizing external capillary conducting systems.


16
10 cm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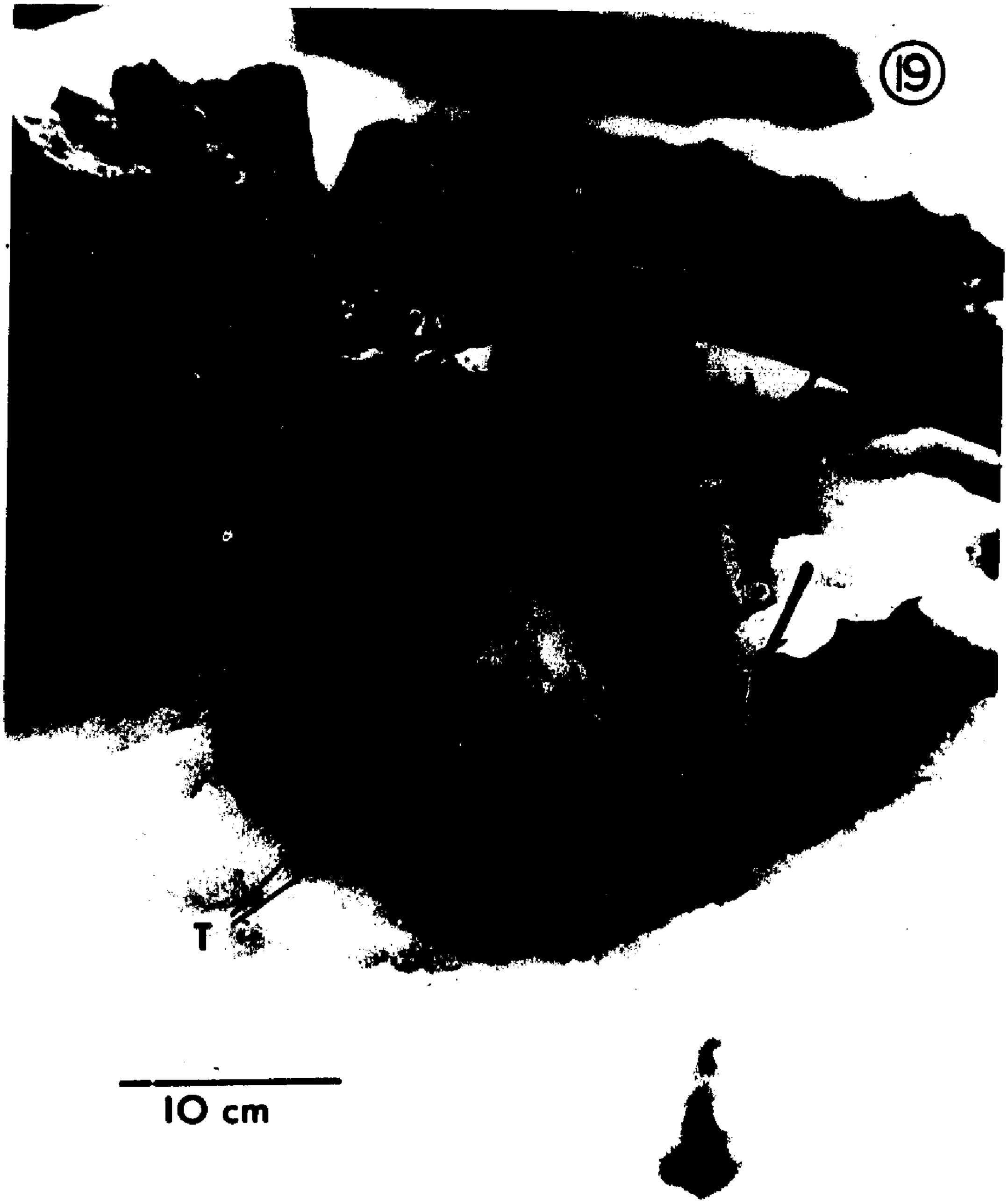
T
10 cm


⑱
10 cm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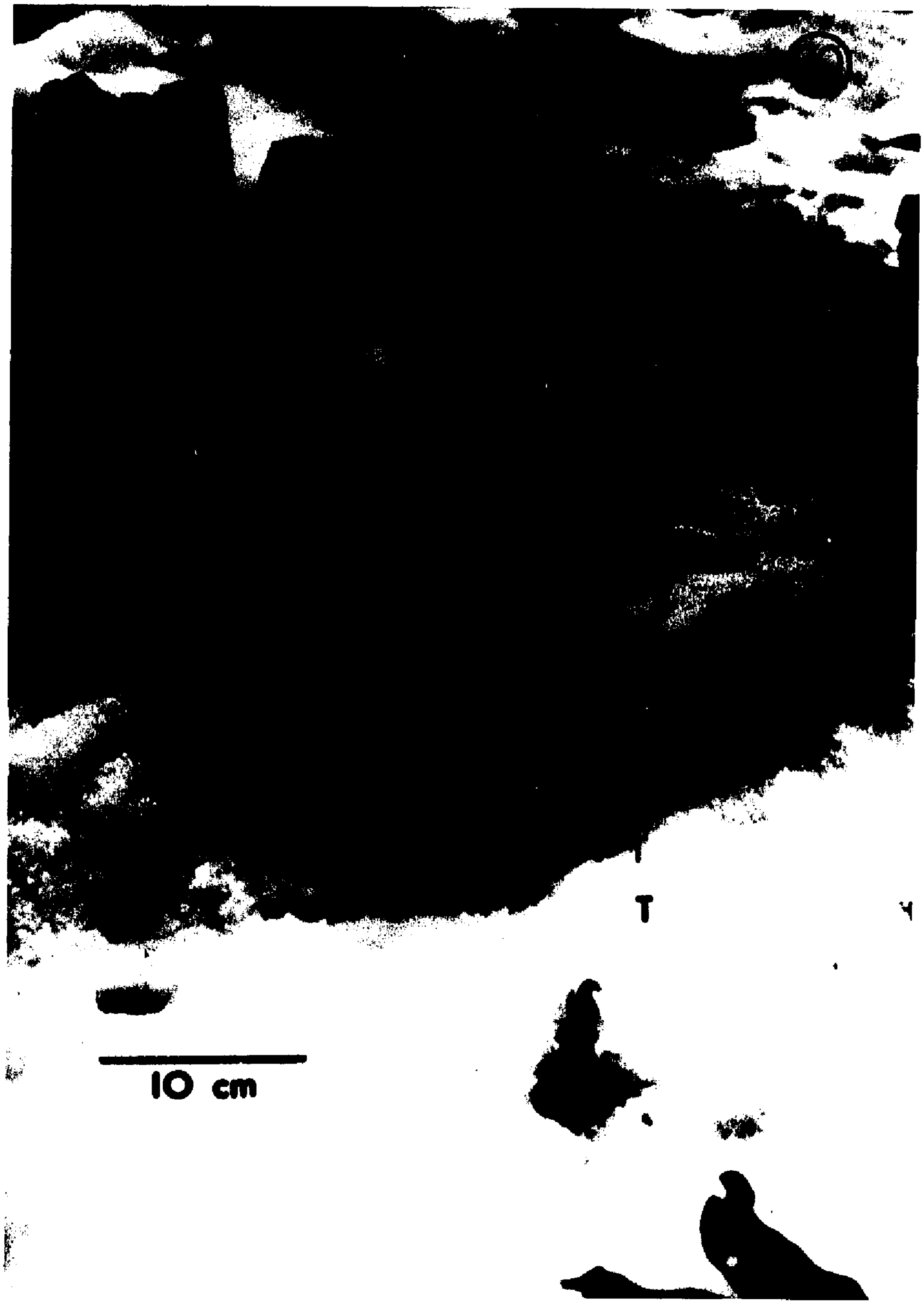
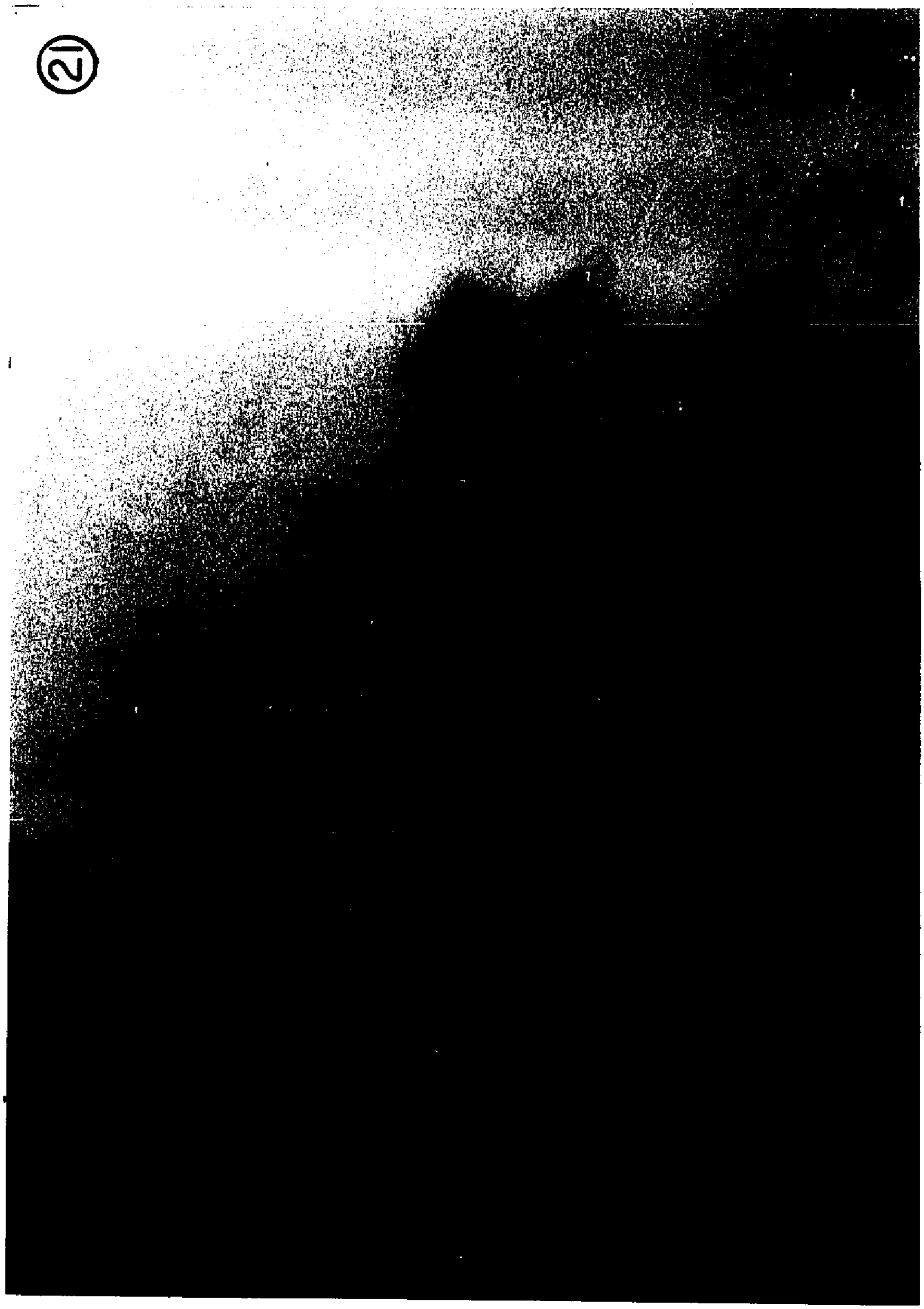

T
10 cm

Figures 21-23. *Leucobryum glaucum.* The three photographs of *Leucobryum glaucum* indicate the same patterns of turbulance and laminar flow as the other figures, but here the special effects of close packing and the cushion colony form are in evidence. In all three photographs, but particularly the second (fig. 22), a very fine layer of smoke occurs at the border of the cushion. This may indicate how this moss of woodlands holds water in external capillaries very near the surface yet retards water loss through the streamlines of the cushion habit and exceedingly dense close packing. On the extremely windy day this photograph was taken, *Leucobryum* colonies were emitting smoke for minutes after the end of the test.



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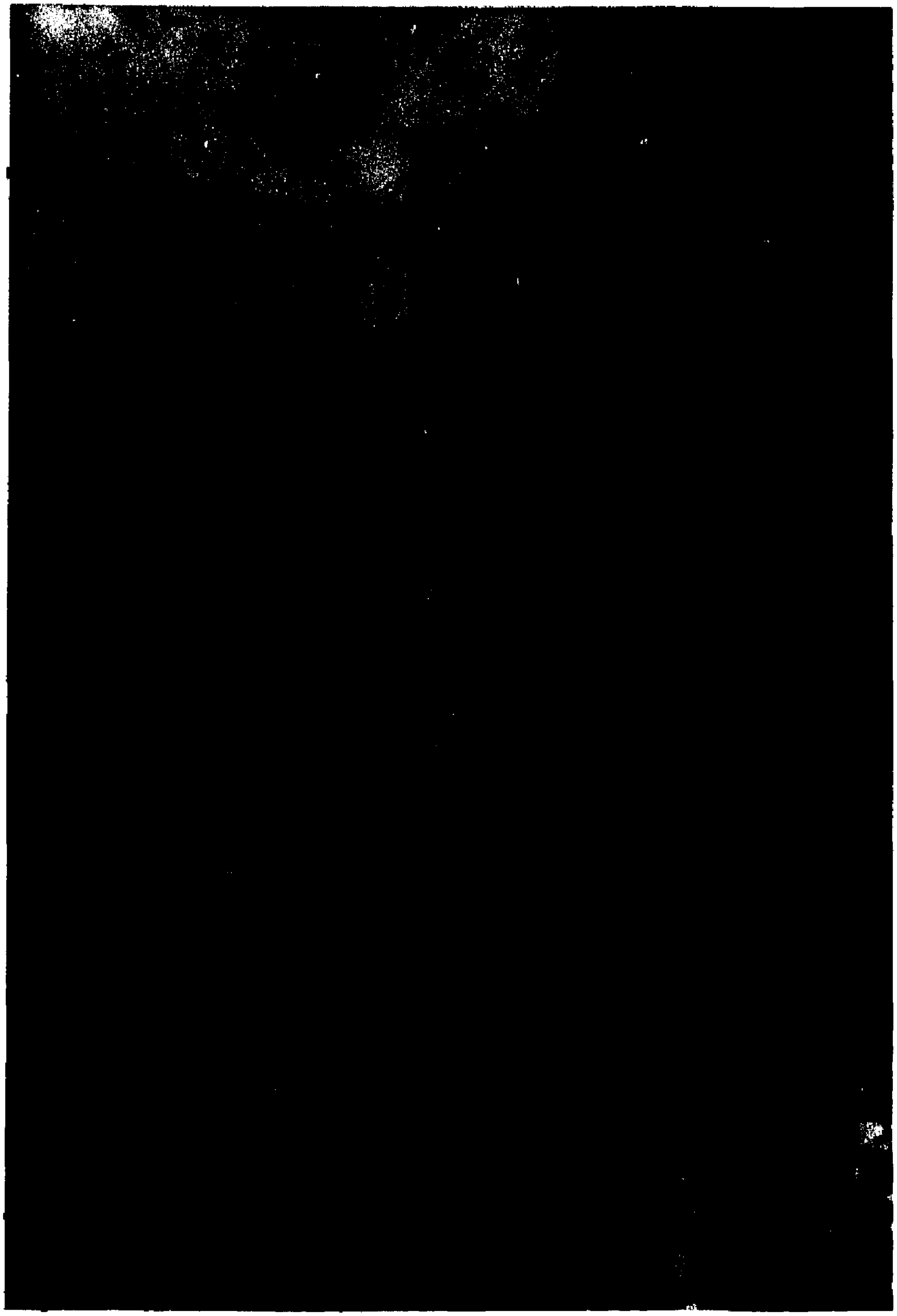


Direct visualisation of bryophyte packing strategies

Photographic records of the spacing of leafy axes in bryophyte colonies are compared here in terms of the geometry of packing. The anaylsis used is based on the parameters of the frequency distribution of the circles surrounding the axes and their size classes. Of the organisms considered in this study, four were chosen for inclusion here: *Hylocomium splendens, Pleurozium schreberi, Dicranum scoparium,* and *Hypnum imponens.* These were included because, although they are different from one another, the scale of these colonies and axes permits ready application of this macroscopic, photographic method. Table 3 demonstrates the order of magnitude differences between different growth forms and packing strategies. Cushions and turfs generally follow the pattern described for the turf below, but mats and wefts are much less definite descriptors of colony morphology and packing frequency. While it would be difficult to apply the method as used here to such organisms as *Bryum argenteum* or *Leucobryum glaucum* at present because their axes would require microscopic analysis (see microscopic cross sections of *Leucobryum glaucum* colonies below). These organisms and the other cushions and turfs preliminarily investigated support the pattern presented of large numbers of axes of these vertical growth forms concentrated per unit surface area. In fact, such forms appear to be hyper-packed, with hugh numbers of axes per unit surface. *Climacium dendroides* presents the opposite problem, with only a few axes occuring in the 9 cm diameter circles used for the other colonies, there are not enough circles for analysis. The area for analysis here would have to be much larger, and since individual axes are difficult to determine photographically, sampling would probably have to be destructive. In any case, while sample size is small, the findings are suggestive for the packing of axes in bryophyte colony growth forms.

TABLE 3: Packing of axes in bryophyte colony growth forms.

Species	Growth form	Number of plant axes in a circle of 8.89 cm diameter (248 cm^2)	% Error (N=4-6)
Dicranum scoparium	turf	241*	3
Hypnum imponens	mat	49	7
Pleurozium schreberi	mat	34	8
Hylocomium splendens	weft	14	3

(*Based on a count of 123 for 127 cm^2)

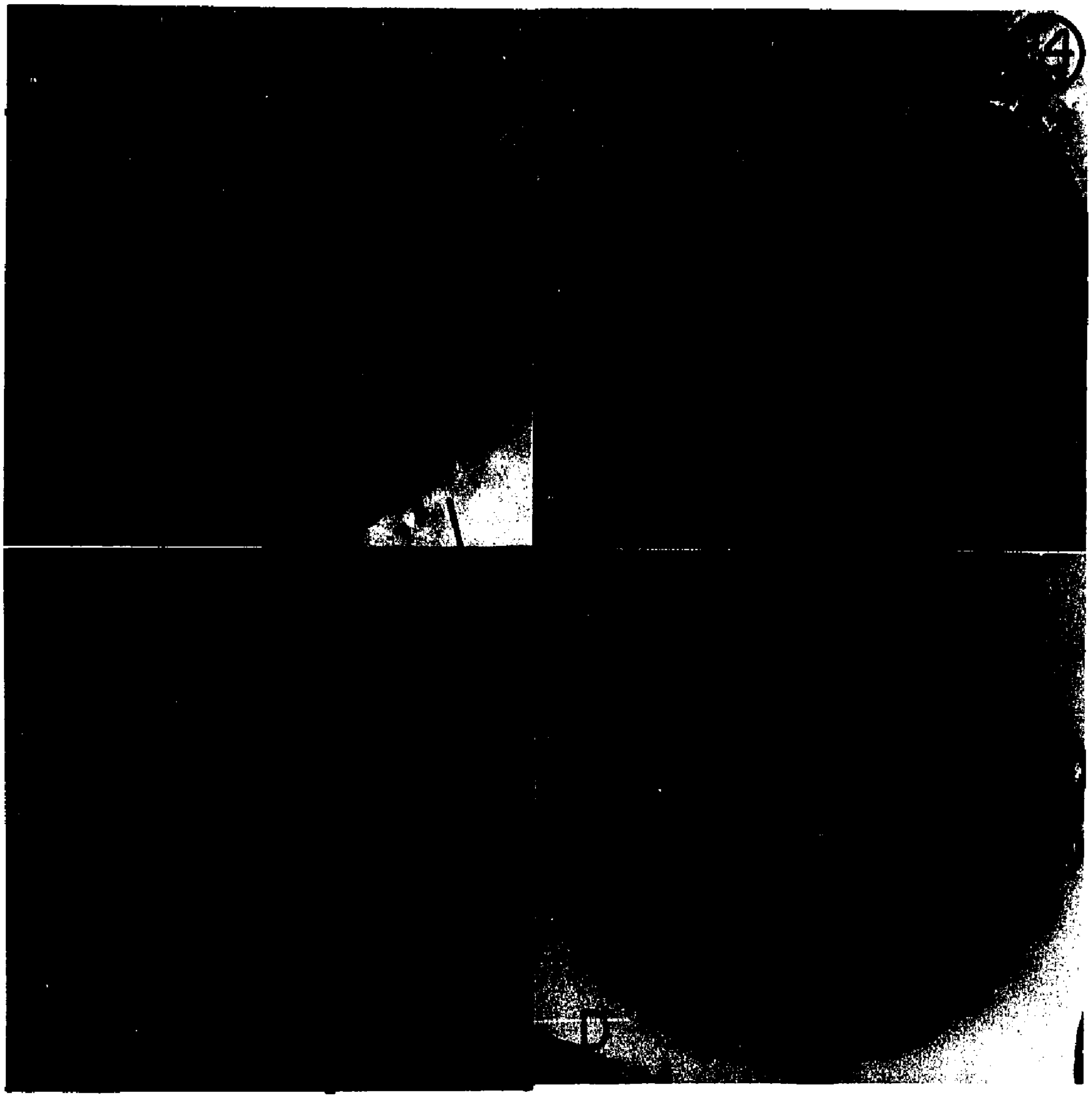
The results of table 3 are given graphically in figures 24-26. Here, overlays of circles on individual bryophyte axes within a fixed area circle and the frequency histogram of the number of circles at any given size suggest that turfs (and probably also cushions) utilize axial elements, stems plus leaves, which are roughly isodiametric. This is a primary requirement for geometric close packing. While the circles used to overlay fronds of Hylocomium are isodiametric, these do not appear to be close packed. At the very least, this method demonstrates a qualitative difference in the packing strategies of a turf which approximates close packing, and mats and a weft, which do not. The frequency histogram (figure 26) indicates that the frequency of any given size range of plant axial segments in focus in a plane in the photograph shows considerable variation in certain of the growth forms but not others. The uniformity of the turf and weft is very different from the scatter of the two mats analyzed. The order of magnitude differences exhibited between different colonial forms indicates that axial packing is a major variant in colony morphology, and, in light of findings presented below, function.

The cross sections of a *Leucobryum glaucum* colony demonstrate the presence of maximally scaled external capillary conduction channels approximating the 600 µm predicted maximum which would be capable of raising water to the colony height of 2.5 cm.

The majority of the capillary spaces visible in the cross sections presented in figures 27-28 are in the 0.1 mm range, with a radius of 0.05 mm, or 50µm. This is common of capillary spaces between leaves and within clusters of axes. On the other hand, large capillary spaces between clusters are typically one to two orders of magnitude larger than the inter-cluster spaces shown. While these larger capillary spaces are easy to see, they occur at a scale difficult to photograph. Nonetheless, the presence of two rather different size classes of capillaries may indicate that the larger acts as a kind of reservoir for the smaller. The combination of capillaries in different size classes will act to collect or gather liquid water only under a milieu exerting lower hydrostatic forces than the colony itself. Also, the larger capillaries with an average radius of 0.6 mm would be capable of raising water from 2.5 cm below the colony, or, to a similar height, while the 0.05 mm capillaries would be capable of raising water above a water table 30 cm below ground surface, thus providing water in dryer times.

Figures 24-26. Surface packing of bryophyte colonies. Each bryophyte colony was photographed within the circumference of a reference circle of known diameter (figure 24) which surrounded between fourteen and one hundred twenty three axes, depending on the species. Then on an acetate overlay a circle was drawn around the tip of each plant axis together with whatever surrounding appendages were in focus in the photograph (figure 25). The distribution of these circles was then analysed with regard to the size variation of the axes and to their packing in the two dimensional plane of the photograph. It can readily be seen that the leftmost histograms in figure 26, that of *Dicranum* and *Hylocomnium* show very little variation in the size of the their axes in the plane of focus, while both mats, represented in the rightmost histograms, show considerable scatter. This indicates that while uniformity of axis size is necessary for close packing, it is not a sufficient condition for this state. Non-packed mats, however, do show a scatter which characterizes variation in position, size, and orientation of the axes within the colony.

a. *Dicranum scoparium* b. *Hypnum imponens* c. *Hylocomium splendens*
d. *Pleurozium schreberii*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D

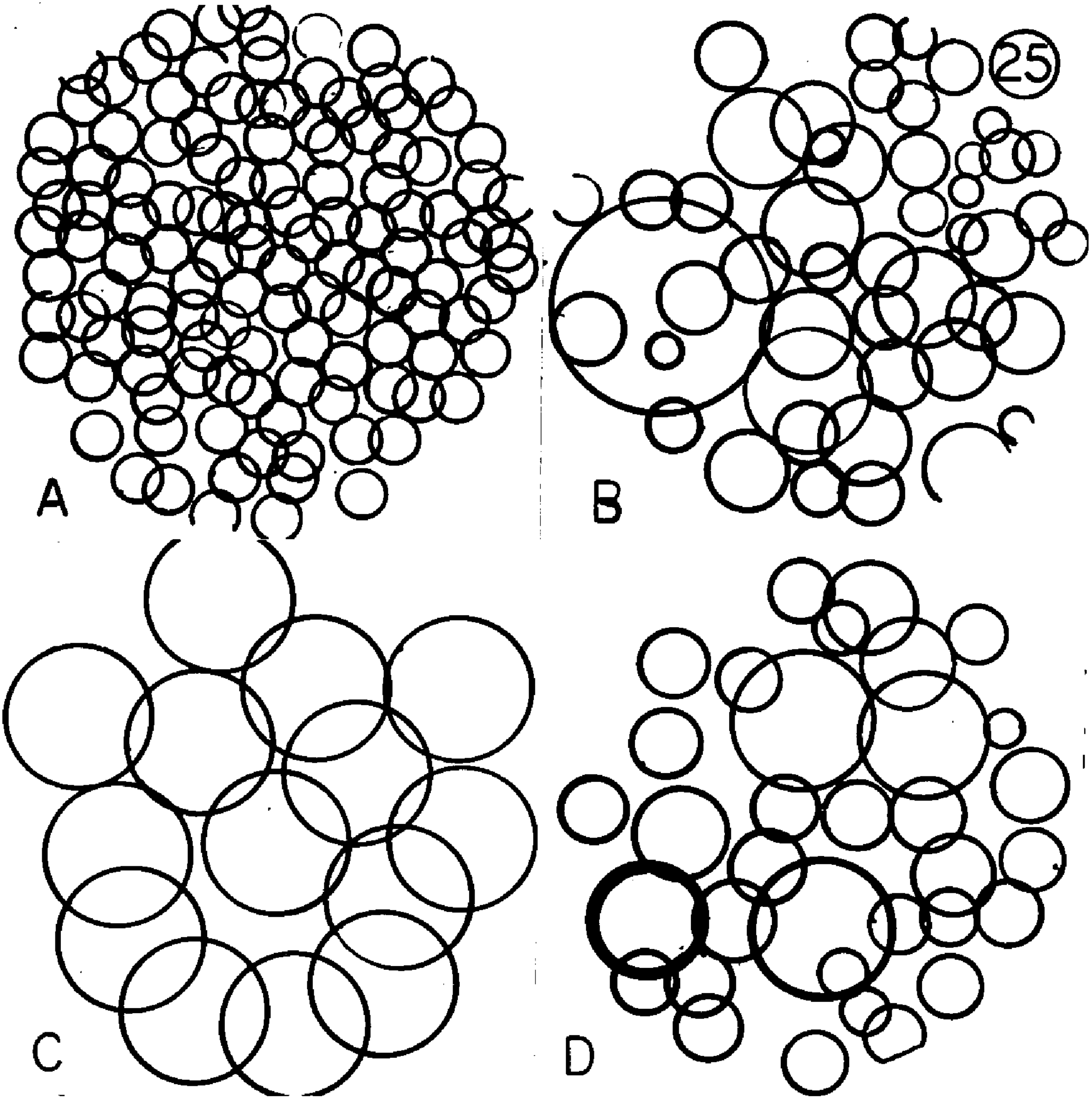
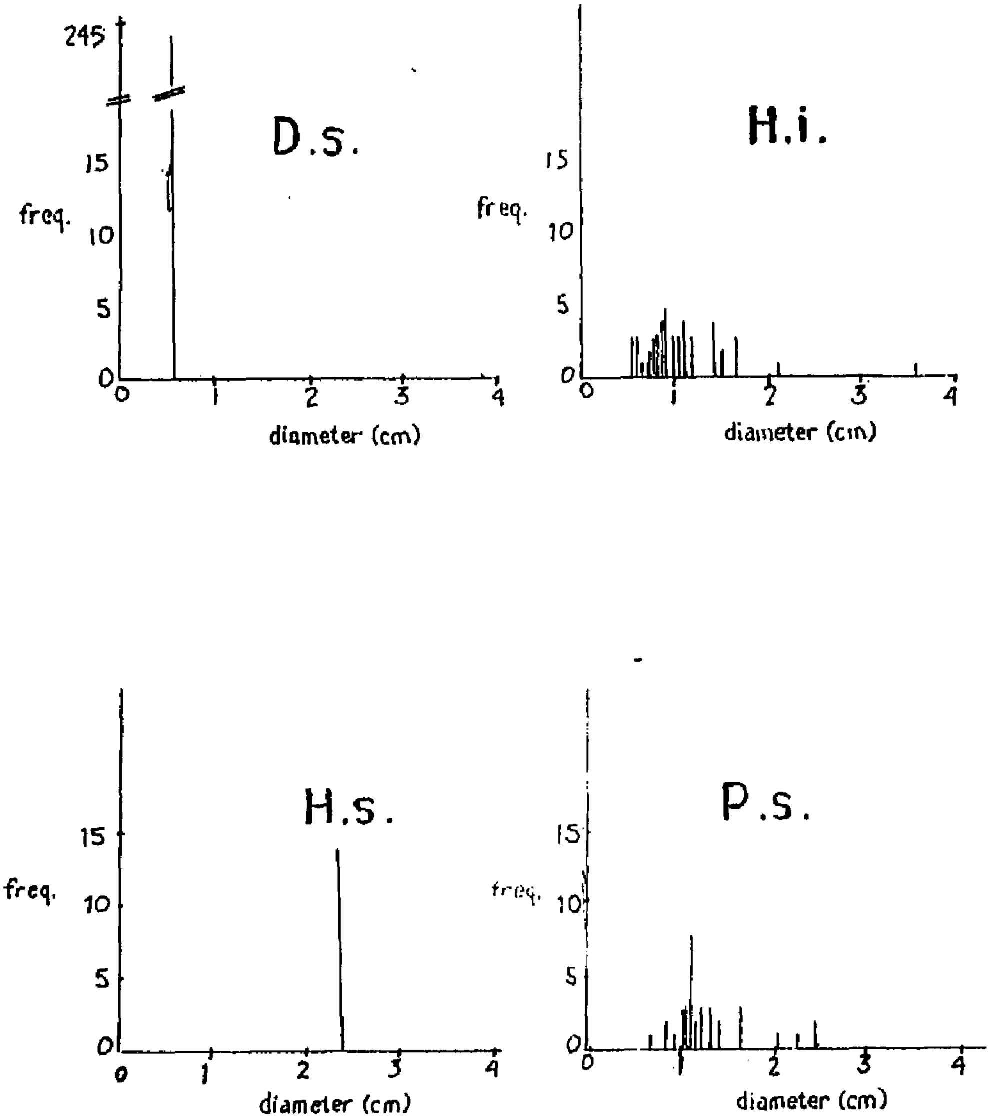
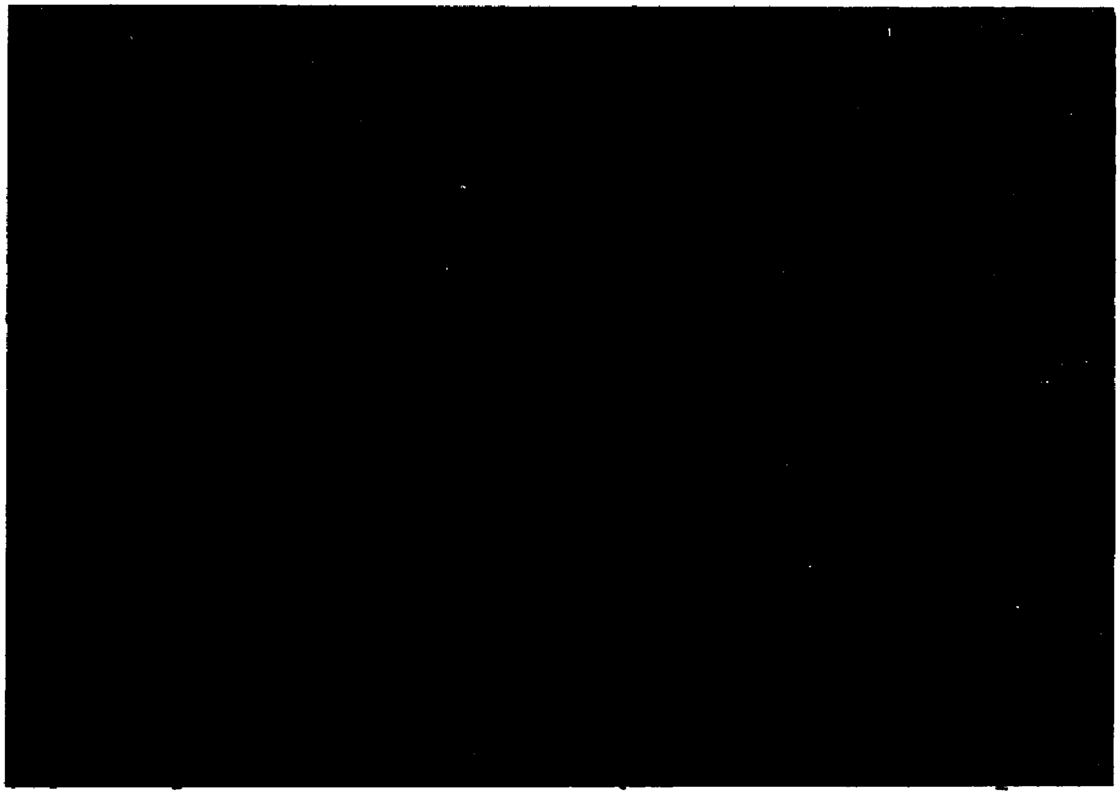
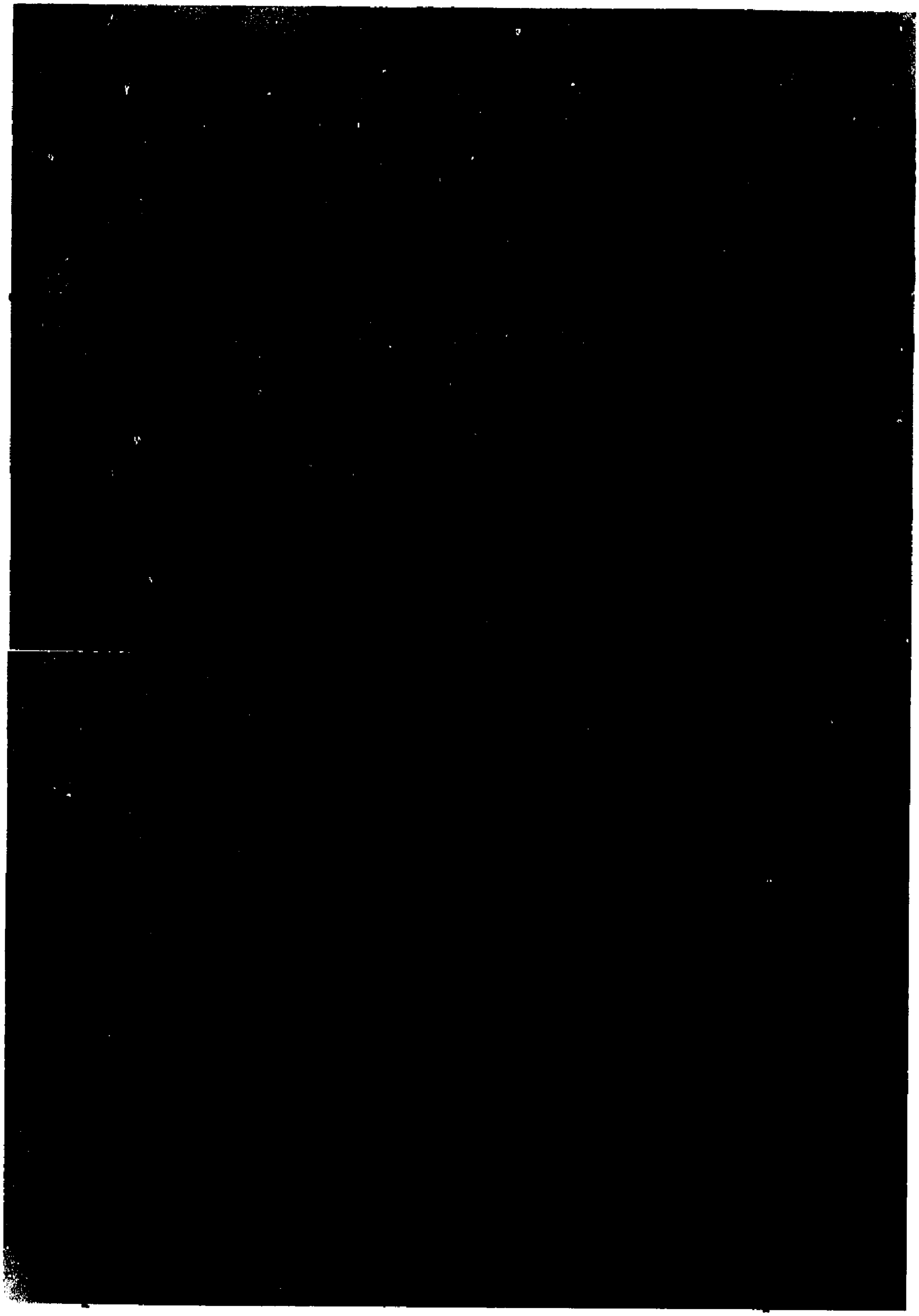

A
B
25
C
D

Figure 26. Frequency Histogram. Key: D.s. *Dicranum scoparium*; H.i. *Hypnum imponens*; H.s. *Hylocomium splendens*; P.s. *Pleurozium schreberi.*



Figures 27-28. Cross-sections through a *Leucobryum* colony showing the distribution and size of capillary water conducting spaces between leaves and axes within the colony. In the first photograph (fig. 27), two axes (A) can be seen at centerfield. Surrounding these are groups of crescent shaped bodies which are cross sections of the leaves (L). External capillary conducting spaces may be seen between the leaves and axes and between leaves. Those marked with the white '0' are on the order of 0.1 mm. Larger inter-axial spaces are prevalent between groups of axes, and one of these is marked by the 0.5 mm grid bar at lower right. Such spaces are typically twice as large or more than the space pictured here. In the second frame (fig. 28.), three axes (A) are present, with the spaces between interspersed with leaves. The spaces between leaves and those between axes are seen to form a continuous network of medium sized capillaries. The four capillaries marked with a white '0' between the lower and leftmost axis in these two photographs may be seen to be continuous for several millimeters along the length of the colony. These two cross sections are separated by nearly a millimeter. In this distance, it can be seen that the ≈0.1 mm diameter capllaries change relatively little in shape, spatial orientation and scale over this length.





Evaporation with free water access

A basic measure of the capacity of plants to move water through their conducting systems is evaporative rate. The results given below in table 4 indicate this capacity of bryophyte colonies vis a vis a free water surface. These results are compared to results from the literature for tracheophytes. What this demonstrates is that a bryophyte colony is capable of evaporating more water than a free water surface if moved into the turbulent flow region of the atmosphere. This demonstrates that bryophyte colonies have considerably less resistance to flow than tracheophytes.

TABLE 4: Evaporation as a percentage of an open water surface ($N \geq 16$)

Species	Colony Growth Form	Percentage evaporation	N
Bryum argenteum	turf	113-116	33
Dicranum scoparium	turf	133-143	37
Leucobryum glauca	cushion	131-147	52
Eurynchium riparioides	mat	111-127	19
Climacium dendroides	canopy	58-90	26
Thuidium delicatulum	weft	112-134	24
Hylocomium splendens	weft	62-96	16
Rye Grass field	--	≈60*	
Open Water Surface	control	100	

(* from Pruitt and Angus 1961)

The range was chosen as descriptor of percentage of evaporation over mean or median to indicate that no matter how plants were arranged in the apparatus, some colonies demonstrated consistant capacity to move more water than the free liquid surface. While the amount of water evaporated and the percentage difference between experimental and control group differed as complex functions of wind speed, colony length, surface area and radiation flux, for the plants studied, the range in its entirety fell on one side or the other of the control. Using the binomial theorem, the probability of divergence from the null hypothesis that evaporation is equal in experimental and control group $\leq 1/2^N$ for a predicted distribution on one side of the control, or $1/2^N/2$ for a distribution on either side of the control. In all cases listed, the probabability p varies from a maximum of 3×10^{-5} to a minimum of 7×10^{-12}.

The absolute amount of water evaporated from the surface of a bryophyte colony is dependent on several factors, including relative humidity, temperature, and wind speed. Because of this multiple dependence on factors that can vary over orders of magnitude, evaporative rate necessariily shows dramatic variation. However, the ratio of evaporation compared to a fixed control, a free liquid water surface, is quite limited. While there are considerable differences among various colony types, it should also be noted that colonies of the same type do not all exhibit similar evaporative behavior relative to the control. Most interestingly, while so called tracheophytes show the regulatory capacity demonstrated by rye grass in the table above, some bryophytes exhibit the same limitation of evaporation. While it must be emphasized that the bryophytes in this set of experiments are operating in an 'unnatural' circumstance, projected with their water supply into the turbulent zone of the atmosphere more that 12 cm above the substrate and less than 2 cm from the leading edge of their container, the results demonstrate that in these circumstances the evaporative capacity of certain bryophytes is not only greater than that generally recorded for 'tracheophytes', it is also greater than a free surface of water itself. Most importantly, this is evidence that the resistance to the movement of water is lower in bryophyte colonies than in large scale plants, in fact lower than water itself, and this constitutes strong but indirect evidence that the water conducting strategies of bryophyte colonies are structured in terms of the flat gradients of evapotranspiration within the laminar flow boundary layer near the substratum, and that colony morphology is capable of moving water under quite unfavorable energetic conditions.

Prediction and measurement of capillary spaces in fossil early land plants

These predicted values for the height to which these samples of fossil plants could conduct water by external capillary systems are in general well within the assumed heights of these organisms (see tables 5 and 6). Plants like *Rhynia*, for which axes have been found 30 cm and more in length/height, contained considerable internal differentiation of xylem. Other predicted heights in the <1cm range indicating a wide stem or thallus belong to *Sciadophyton* and *Taenocrada,* genera which are strap shaped and could have conducted water by external capillarity in the

TABLE 5: Axial measures and prediction of external capillarity in early land plant fossils.

Taxon	predicted average radius of axis mm.	predicted r of capillary (close packed) mm.	predicted capillary rise (close packed) cm.	predicted r of capillary (open packing) mm.	capillary rise (open packing) cm.
Eogaspesiea gracilis	0.2-0.8	0.03-0.1	12.0-48.1	0.08-0.3	4.5-18.0
Sporogonites exuberans	0.8	0.1	12.0	0.3	4.5
Zosterop. myretonionum	0.9-1.1	0.1-0.2	8.8-10.7	0.4-0.5	3.3-4.0
Zosterophyllum minor	1.2	0.2	8.0	0.5	3.0
Z. fertile	1.1-1.3	0.2	8.8	0.5-0.53	2.8-4.0
Cooksonia crassiparietalis	0.7-1.4	0.1-0.2	6.9-13.8	0.3-0.6	2.6-5.1
C. sp.	0.8-1.5	0.1-0.2	6.4-12.0	0.3-0.6	2.4-4.5
Z. llanoveranum	1.6	0.2	6.0	0.7	2.2
Gosslingia breconensis	0.6-1.8	0.09-0.3	5.3-16.0	0.2-0.7	2.0-6.0
Hicklingia edwardii	1.9	0.3	5.1	0.8	1.9
Z. rhenanum	1.6-2.0	0.2-0.3	4.8-6.0	0.7-0.8	1.8-2.2
Yarravia oblonga	2.1	0.3	4.6	0.9	1.7
Sciadophyton laxum	0.3-2.5	0.05-0.4	3.8-32.1	0.1-1.0	1.4-12.0
Hedeia corymbosa	1.5-2.5	0.2-0.4	3.8-6.4	0.6-1.0	1.4-2.4
Sciadophyton steinmanni	0.9-2.7	0.1-0.4	3.6-10.7	0.4-1.1	1.3-4.0
Y. subsphaerica	2.1-2.7	0.3-0.4	3.6-4.6	0.9-1.1	1.3-1.7
Zosterophyllum longum	2.8	0.4	3.4	1.2	1.3
T. dubia	3.5-4.8	0.5-0.7	2.0-2.7	1.4-2.0	0.7-1.0
Rhynia gwynne-vaughnii	2.0-5.7	0.3-0.9	8.8-1.7	0.8-2.3	0.6-1.8
Taenocradia decheniana	1.2-5.8	0.2-0.9	1.7-8.0	0.5-2.4	0.6-3.0
average heights of close and open packing respectively			$\bar{h}$ = 6.0cm		$\bar{h}$ = 2.1cm

TABLE 5 (con't) The fossil plants here examined are arranged according to scale, from small to large. Measurements were taken of the width of the plant stems or axes. From this we may derive an estimate of the radius of the plant axis (column 1), given that it is cylindrical in shape. From such measures, the radius of the capillary between these axes may be derived (columns 2 and 4). Then, the equation for capillary rise,

$$h = \frac{2 \partial \cos a}{rPg}$$

may be used to calculated the maximum height to which water might be moved under given regimens of packing of axes (columns 3 and 5) utilizing hydrostatic forces in external capillary conducting systems. For the twenty fossil land plants studied, the average height to which such organisms in close packed strategy could have conducted water by external capillarity, based on measures of the widths of fossil axes, is 6.0 cm, with a minimum range of from 1.7 to 12 cm. Sub-optimal open packing yields an average of 2.1 cm with a range of 0.6 to 4.5 cm.. Such external capillary conducting systems are more than sufficient to fully hydrate diminuitive early land plants, if the early land plants were only a few centimeters in height, as the fossil evidence strongly suggests. *Cooksonia* and *Steganotheca* in the Silurian, and *Zosterophyllum sp.*, *Gosslingia, Sciadophyton, Taenocradia,* (but for the latter two taxa, see below) and other taxa from the lower Devonian all appear to be from less than one to at most a few centimeters in height. Exceptions in this list may include plants like *Rhynia,* for which axes have been found 30 cm and more in length/height. These axes contained internal differentiation of xylem in the form of a central stele. In two other genera the stem or thallus was relatively wide, leading to predicted heights of external capillary rise of <1 cm. These taxa, *Sciadophyton* and *Taenocrada,* apparently formed strap shaped thalli analogous to metzgerialian and marchantialian hepatics (McConaha 1941), and therefore the original assumption of cylindrical axes is wrong. The extant forms with which these fossils are compared here conduct water by external capillarity between strips of overlapping thalli, and between these and the substratum.

TABLE 6. Measures of inter-axial spaces and prediction of external capillarity in early land plant fossils.

Species	measured spaces between axes in fossils (mm)(N>50)	radius of spaces (mm)	predicted capillary rise (cm)
Sporogonites exuberans	0.3	0.15	9.9
Zosterophyllum myretonionum	0.4-0.9	0.20-0.45	3.3-7.5
Eogaspesiea gracilis	<0.1-1.0	0.05-0.50	3.0-29.8
Taenocradia decheniana	<1.0	0.50	3.0
Hicklingia edwardi	0.5-1.2	0.25-0.60	2.5-6.0
T. dubia	1.5	0.75	2.0
average height of predicted capillary rise	h = 3.9		

The left column lists average widths of actual spaces between plant axes. These are here interpreted as fossilizations of potential external capillary conducting spaces between axes, the radius of which is derived in the middle column. The predicted maximum capillary rise in such capillaries is given in the right column. It should be noted that the results are simliar to those given in the previous table. However, in that case, the widths of the axes were measured and the height of capillary rise predicted. Here, similar predictions were based on the magnitude of the spaces themselves between the axes. The agreement between these two sets of predictions, one based on axis width alone, and the other based on measures of spaces between axes found in the lithic matrix, may be taken as initial corroboration, through internal consistancy, of the methodology here employed. Early land plants could have moved water from base to apex using external capillary conduction if their average height was less than 3.9 cm, an estimate supported by the fossil record.

or Marchantialian hepatics or Anthocerotes, between strips of overlapping thalli, and between these and the substratum (Clee, 1939, 1943; Isaac, 1941).

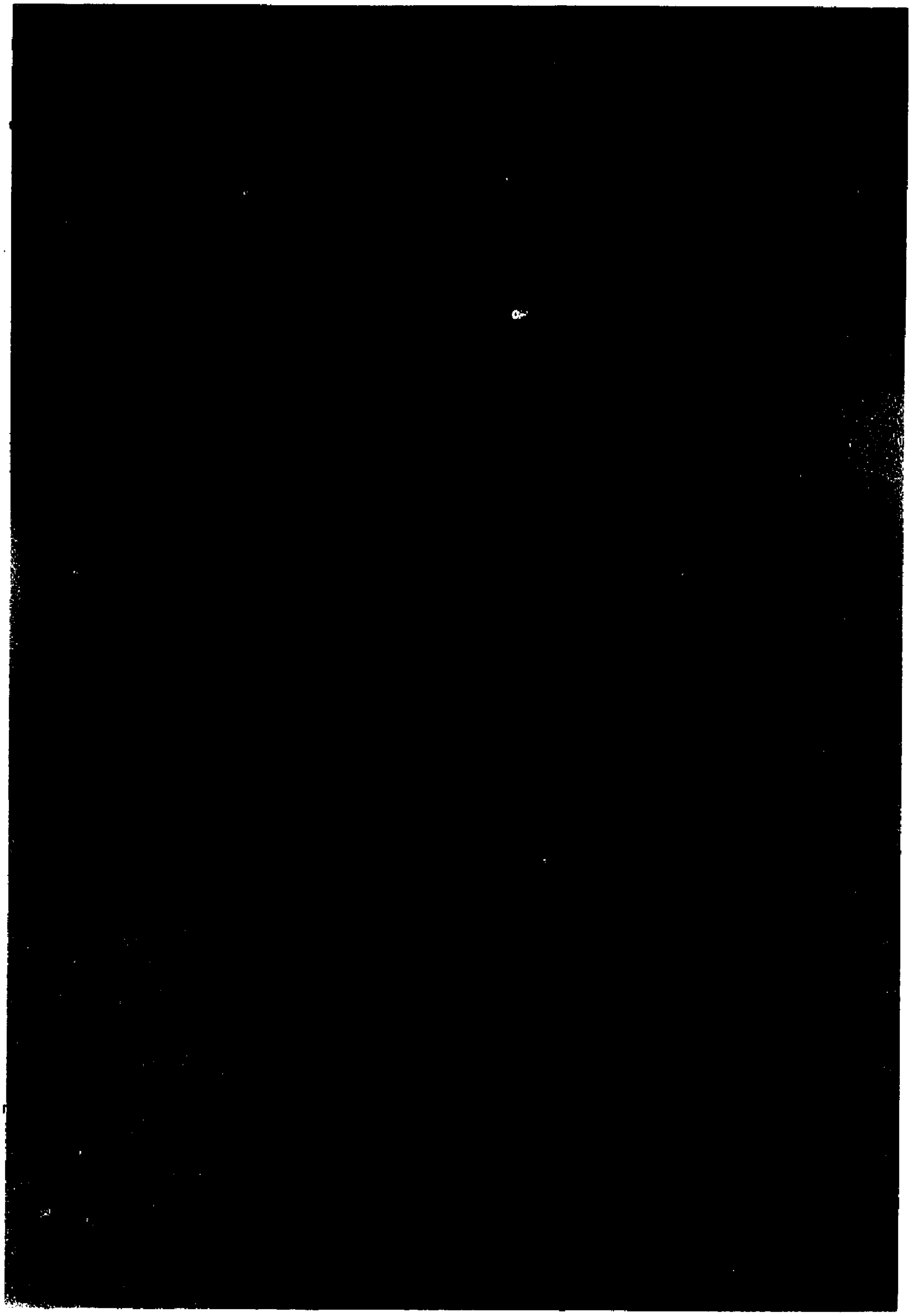
For the twenty fossil land plants studied, the average height to which such organisms in close packed strategy could have conducted water by external capillarity is 6.0 cm, with a minimum range of from 1.7 to 12 cm. Sub-optimal open packing yields an average of 2.1 cm with a range of 0.6 to 4.5 cm. Where the spaces between axes were measured directly from photographic records of the fossils, and the height of capillary rise calculated from these measures (as opposed to from the assumption of close and open packing as in the above examples), the average height of capillary rise falls between those based on the close and open packing assumptions at 3.9 cm. Together these values indicate that the hydraulic capacities of external, apoplastic structures could have moved water from base to apex given packing of the plant axes. Such external capillary conducting systems are more than sufficient to fully hydrate diminuitive early land plants. *Eohostinella*, *Cooksonia*, and *Steganotheca* from the Silurian epoch are very small plants indeed (Stewart 1983), and these calculations suggest that, if these and other early land plants were only a few centimeters in height, as the fossil evidence strongly suggests (see figure 5), hydrostatic and fluid dynamic constraints would compel these organisms to utilize external capillary conduction because of the intrinsic capacities of such systems. The measures given below offer some support of this conclusion based on the general distribution of fossil land plants in the lithic context as compared to compressed external capillary conducting systems, the bryophytes.

Artificial Bryophyte Fossils

Photographs of manufactured bryophyte fossils compared to similarly scaled photographs of fossil land plants show some strikingly similar characteristics (see fig. 29). Specifically, in areas where previously contiguous axes of bryophytes have been compressed in a plane, there are relatively few spaces greater than 2 mm. Two millimeters was taken as a cutoff point because if such a space acted as an external capillary conducting channel, it would be the equivalent of a capillary space capable of raising water to a height of 1.5 cm, a height generally well within the laminar flow envelope of the surface boundary layer, and equivalent to the height/length of many early land plants. While the method of artifically 'fossilizing' bryophyte colonies is new to this study, it was undertaken here to offer some indication as to whether compressed axes of known external capillary conducting systems resembled fossilized early land plants. While the sample size is limited, the results suggest that compressed bryophyte colonies and several diminutive fossilized early land plants exhibit interaxial spaces of similar

Figure 29. Comparison of artificial 'fossil' bryophytes with early land plant fossils. Photographs of manufactured bryophyte fossils are printed adjacently to similarly scaled photographs of fossil land plants. Where contiguous axes of bryophytes have been compressed in a plane, Threre are relatively few spaces greater than 2 mm. The two millimeter openings could act as an external capillary conducting channel capable of raising water to a height of 1.5 cm, a height generally well within the laminar flow envelope of the surface boundary layer, and equal to or less than the height/length of the earliest land plants. While the method of artifically 'fossilizing' and compressing bryophyte colonies is new to this study, it was undertaken here to find out whether compressed axes of known external capillary conducting systems resembled fossilized early land plants. The distribution of the 2 mm markings indicate similarities of scale . The results are suggestive that compressed bryophyte colonies and diminutive fossilized early land plants exhibit interaxial spaces of similar dimensions.

early land plants: a. *Sciadophyton steinmanni* b. *Hinglickia edwardi*
c. *Zosterophyllum minor*
artificial 'fossils' : d. *Hylocomium splendens* e. *Brachythecium sp.*
f. *Oncophorus wahlenbergii*



dimensions. Since bryophytes utilize interaxial external capillary conduction spaces as a primary means for moving water, the comparative method suggests that early land plants at the same scale and organized in similar colonial forms could have done likewise.

Centrifugation studies

Centrifugation was used to apply a force to bryophyte colonies. Using the hydrostatic equation,

$$h = \frac{2 \partial \cos a}{r P g}$$

an equivalence was generated between the force in gravities, g in the above equation, applied with the centrifuge, and the size of capillaries completely emptied. The same relation tells how much all capillaries were emptied, as a percentage of capillary height. In the data below, it is calculated that all apoplastic capillaries ≥ 0.22 mm in radius are emptied by centrifugation, while all capillaries < 0.22 mm in radius should be emptied to 0.3% of their full capacity. The amount of water held in each of the bryophyte colonies studied is given below in terms of the proportion of grams of water in a fully saturated colony to grams of bryophyte colony after spinning.

TABLE 7: Water holding capacity of bryophyte colonies as determined by centrifugation in gram of water per gram of spun colony.

Species	Growth form	Mean of water holding capacity g/g ($p < 0.01$, $N \geq 100$)*	variance (g H_2O/g plant)
Bryum argenteum	TURF	2.00	0.004
Leucobryum glaucum	CUSHION	2.03	0.013
Dicranum scoparium	CUSHION	2.73	0.017
Eurynchium riparioides	MAT	4.05	0.043
Climacium dendroides	CANOPY	2.85	0.012
Pleurozium schreberi	WEFT	2.24	0.059
Rhytidiadelphus triquetrus	WEFT	2.62	0.069
Hylocomium splendens	WEFT	2.44	0.009

* The large sample size permitted quite adequate statistics to be done on the variability of the measure of grams of water held per gram of spun colony. A comparison of variances in general separated turf and cushion from mat canopy and weft, with variances low in the former and high in the latter. But this was not universally true, again raising difficulties with the verification of this system of classifying bryophyte colonies into growth forms.

For the species studied, these results indicate a broad overlap in the water holding capacity of the different strategies. It should be noted however, that water holding may be accomplished by close and non-packed forms, while hydrostatic pressure is a function of the packing of organs and axes. This means that a plant may have reservoirs which hold water from precipitation, dew , or fog, but which are incapable of filling themselves using the hydrostatic forces of their capillary structures. These results must be taken together with the hydrostatic capacities of the colonies, a topic taken up below in the section on the field porometer.

Field porometer

The field porometer developed for these studies was used to demonstrate for the first time in bryopohyte colonies the emptying and refilling curves for bryophyte colonies other than *Sphagnum.* The findings indicate that small scale plants such as bryophytes utilize hydrostatic forces to resist the loss of water and to refill external capillary spaces when free liquid water becomes available. Specifically, the paired curves for emptying and refilling in bryophyte colonies support the hypothesis that external capillary water conducting spaces are low resistance hydrostatic conduits. This system is capable of acting within minutes to refill proportions of water lost (fig. 30-31), and to resist water loss caused by lowered hydrostatic pressure of the surroundings. A surface is described by the emptying and refilling curves for bryophte colonies or any colony of diminutive plants, limited on the left by the amount of water per gram that the specific plant colony can hold, and on the right, by the limits of dissication of the colony.

The traditional catagories of growth forms in bryophytes are, from the findings of this study, problematic in that different growth forms have similar relations between water content and water potential, while it is reported that the distribution of these forms is correlated with moisture and light factors. No measures of the latter were taken here, but the different shapes of the paired emptying and refilling curves indicates that there are different hydrostatic strategies operative in these organisms . Specifically, colonies may maximize their capacities to catch and hold water by maximizing water content, or to extract it from their surroundings by maximizing internal hydrostatic forces. While the generalizations are not complete, turfs, cushions and mats are better at mining water from the water table, while canopies and wefts are relatively better at holding volumes received from above as rain, dew, fog, meltwater, or spray. Leafy and thalloid hepatics and anthocerotes behave like turfs, cushions and mats, but, in general, at heigher water potentials, with lower resistance to water loss. In sum, these studies suggest that the traditional division of bryophyte colonies into 'growth forms' may not provide adequate catagories for these organisms as functional participants in their habitats. In terms of the water relations of colony types, turf, cushion, mat, canopy and weft don't appear to separate these organisms systematically in terms of their capcities to empty and refill external capillary systems. It appears that strategies for packing axes are more relevant to the water relations of these organisms than the purely morphologic character of growth form. How this may fit with the coupling of water and light regimes is a matter for future study.

Figure 30. The emptying and refilling curves of bryophyte colonies expressed as plots of grams of water per gram of centrifuged bryophyte colony versus depth to water table. Each organism is represented by paired emptying and refilling curves, emptying curve always to the right of the filling curve. The paired curves describe a surface which characterizes the hydrostatic forces a given colony exerts dependant on how much water it has already lost or gained. The solid lines represent high density data points, while the dotted lines represent hydrostatic equilibrium between plant and apparatus. The results are presented in pairs here to stress some similarities in hydrostatic behavior between different sets of samples and to underscore some problems with the classical classification of growth forms of bryophyte colonies. The flat curves in a) represent small tightly packed axes in close packed turf and cushion. The flatness represents low water holding capacity together with resistance to water loss against external hydrostatic pressures. The much steeper curves in b) represent close packing in a large mat and turf capable of holding considerable amounts of water given up relatively easily in the high and middle ranges of water content, accounting for the steepness of the emptying curve, but offering hydrostatic resistance as the depth to water table nears 20 cm. Graph c) depicts a so-called canopy and a mat, and d), two wefts. While there are differences here (note especially the doubly curved emptying curves in d) versus the single curves in c)), all of these open packed forms have considerable overlap in the surfaces characterizing their hydrostatic behavior. In all cases, the paired curves are examples of hysteresis, behavior of a system which is dependant on previous history. These are the first such curves presented for any bryophyte colonies with the exception of *Sphagnum*. The similarities of cushion and turf in a), mat and turf in b), and canopy and mat in c), serves as strong indication that so called growth-form of the classical literature may not characterize qualities as fundamental as water balance and hydrostatic behavior of bryophyte colonies. Key: L(s)= small colonies of *Leucobryum glaucum*; B= *Bryum argenteum*; E= *Eurynchium riparioides*; D= *Dicranum scoparium*; C= *Climacium dendroides*; P= *Pleurozium schreberi*; R= *Rhytidiadelphus triquetrus*; H= *Hylocomium splendens.*

(30)

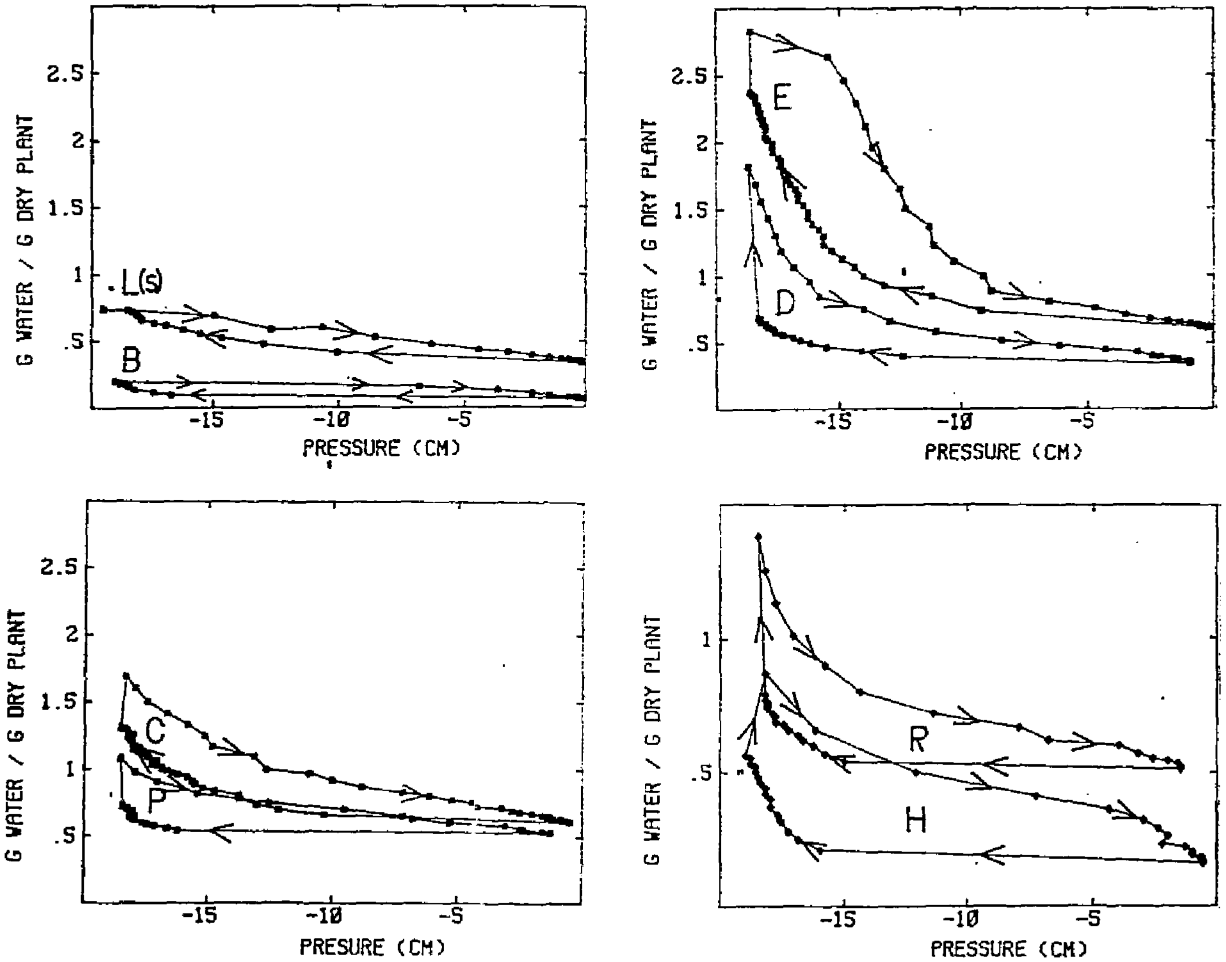

G WATER / G DRY PLANT
2.5
2
1.5
1
.5
L(s)
B
-15
-10
-5
PRESSURE (CM)
E
D
C
P
PRESURE (CM)
R
H

Figure 31. Emptying and refilling curves for a cushion and a turf expressed as plots of grams of water per gram of centrifuged bryophyte colony versus depth to water table. The sample sets here are from larger colonies that differ by no more than 5% of their centrifuged weight. Again, the similarities call into question the colony growth form classification used to characterize bryophytes in the classical literature. Both colony types presented consist of close packed axes, which may account for the similarities of hysteresis curves. Note that scale is an important parameter here also, as the large or tall *Leucobryum* colonies differ considerably from the small colonies represented in figure 30., a). Key: L(t)= *Leucobryum glaucum* tall or large; M= *Mnium sp.*

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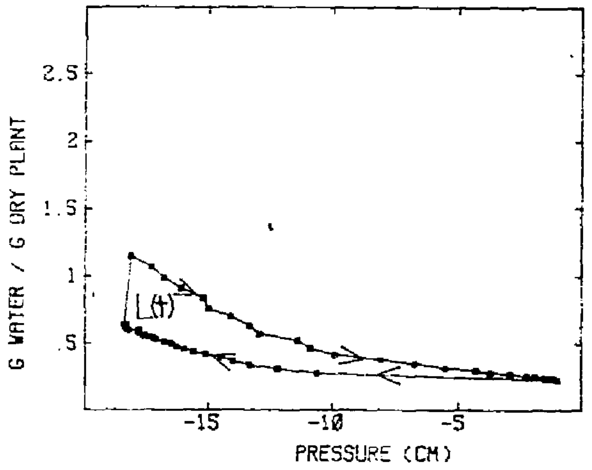
G WATER / G DRY PLANT
2.5
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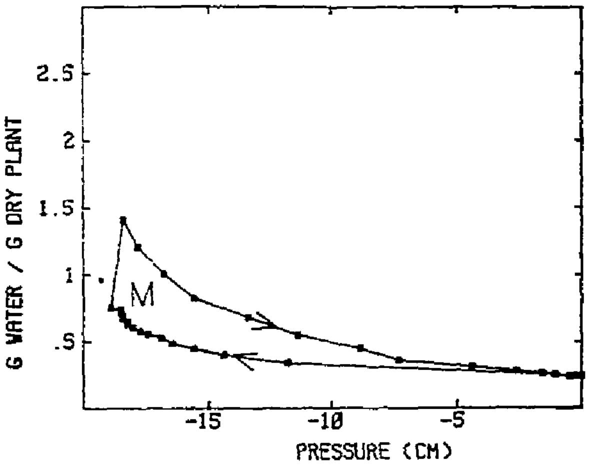
PRESSURE (CM)


G WATER / G DRY PLANT
2.5
2
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.5
M
-15
-10
-5
PRESSURE (CM)

Rather elegant earlier methods measured water content and water potential in the laboratory (Bushby and Whitfield, 1978). The present apparatus can measure both simultaneously in the field. Beyond this innovation, the generality of these results is extensive. The curves generated indicate how the pressure generating spaces within the exoapoplast, the external capillary conducting systems of these diminutive land plants fits a hydric milieu or water table varying from the presence of surface water to a water table separated from the surface by 20 cm of distance. These reciprocal relations between apoplastic external capillary conducting spaces and a varying water table indicate that roots are not an immediate necessity for inhabiting the surface of the terrestrial landscape. Capillary fringe or the remains of plants could conduct water from the water table to the base of the plant itself. From there, the configuration of the proteinaceous-cellulosic apoplast could act as primitive regulator of water balance near the substratum of the earth.

Conclusion

The land plants inhabit the interface between earth and atmosphere, hospitable to life only in the presence of the mutual interface between the plant body, liquid water, the substratum, and the atmosphere. The structural feature of the embryophytes which guarantees the interfacial presence of water is the proteinaceous cellulosic cell wall, the primary apoplastic water conducting pathway of all terrestrial plants. At the same time, however, there are two essential limits to this guarantee: the maximal evaporative rates of the turbulent atmosphere; and, the minimal evaporative rates at the laminar surface boundary layer of the substratum. Exchange of carbon dioxide can only occur through evaporative surfaces. Where evaporation rates are too high, all liquid water may be lost, and this excludes the requisite exchange of the living state. Where rates are vanishingly small, concomitant carbon gain is similarly diminished. These studies indicate that the edge of the laminar flow boundary layer serves to divide two fundamentally different strategies of water conduction in the land plants, together with the functional morphologies characteristic of these strategies.

Small scale plants utilize their proteinaceous-cellulosic cell walls to move apoplastic water in low resistance external capillary conducting systems. Beyond a limiting height depending on wind speed, temperature, and relative humidity, on the order of 5 cm, evaporation rates become exceedingly high. Here the tracheophyte strategy becomes tenable, utilizing high resistance to water movement, internal conduits, stomates, paraffin seals, the biopolyesters of cutin and suberin, and other mechanisms to regulate water movement. These larger land plants may control a continuous stream of water from root hair and casparian strip to stomate across negative pressures in the hundreds of atmospheres. Their origin, however, in an ontogenetic or phylogenetic sense, was necessarily at the smaller scale. At the magnitude of millimeters to centimeters, the apoplastic surfaces of cells, organs, and axes may fill their external conducting spaces from the capillary fringe of the substratum, the circadian arrival of dew or mist, or the free surfaces of pond, stream or rain drop. There is not one but several habitats within the small scale spaces near the substratum, and a considerable variety of arrangements of these apoplastic surfaces is possible at this small scale. The result of some of these arrangements may be seen in the characteristic emptying and refilling curves, specific solutions to water balance problems using the generalized strategy of low resistance external capillary water conduction. While the growth forms of bryophyte colonies are in need of more extensive study in this regard, these initial investigations indicate that colony forms exemplify variations on the theme of low resistance external capillary apoplastic water conduction. Any land plant ancestor at the same scale likely utilized a similar system.

Diminutive beginnings apparently led to greater things for the land plants. By the mid Devonian, plants at the scale of trees had appeared. But this cannot be explained by the constraints of fluid dynamics, only by the potentials of morphogenetic mechanisms. What forms of developmental control of branching and the disposition of organs could provide the apoplastic variations that opened the landscape to the embryophytes? One answer to this question is phylogenetic, but the other might be stated in the form that only developing variants with high resistance to the flow of water, and with largely internal apoplastic water conduction could survive atmsopheres of less than 90% humidity. This is not tautology, but, by the comparative method, in part, an empirical question.

What were the original structures of internal support? Were such structures involved in maintaining form through wetting and drying cycles? Internal differentiation of support tissue may have provided the theme for the next variation, as internal support structures became coupled with apoplastic conduction. How large may a hydrated apoplastic system become before the forces and weight of water begin to deform it? Does gravity inform developmental systems? From the work of Lintilhac (1974) and Jaffe (1966), inter alia, the answer appears to be yes. But then as now, the smaller terrestrial plants encounter gravity as the lesser force to that of the surface tension of water. Does this parameter inform the developmental system? The answer must be affirmative, but at present, no one knows how. At what scale do gravitational and surface tension forces become equal? While these questions await answers, for the present, if there are laws of form governing the shape of terrestrial plants, the properties of water are amongst these.

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