

# Chapter 4

## The Diversification of Bryophytes and Vascular Plants in Evolving Terrestrial Environments

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### Summary

This chapter covers the basic needs of plants and the constraints of the physical environment on a pioneer land flora, including acquisition of CO<sub>2</sub>, nutrients, and coping with the intermittent availability of water. The radiation climate, heat and mass transfer, laminar and turbulent boundary layers, heat budgets, and the control of evaporation and temperature are briefly discussed. The importance of scale is emphasized; the vascular-plant strategy is optimal at

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large scales (> a few cm), but the poikilohydric strategy is optimal at smaller scales. A scenario is envisaged for evolution of the “vascular-plant package”, allowing a transition from reliance on evaporative cooling close to the ground surface, to convective cooling of erect axes. The changing physical environment and vegetation through successive periods of geological time is briefly sketched in relation to the evolution of bryophyte diversity. Vascular plants have been an important part of the environment for bryophyte evolution since the early history of plant life on land.

## I. Introduction

All photosynthetic organisms need water, light, CO<sub>2</sub>, and other chemical elements that are essential for their structure and functioning – N, P, K, Mg, Ca, Fe and others (“micro-nutrients”) in smaller quantities. These all have to be acquired from the environment. The main challenge to an aquatic photosynthetic organism is remaining within the photic zone; other requirements are met from the surrounding water. On land, water is only locally and intermittently available. Above ground there is generally light, and atmospheric CO<sub>2</sub>, but other nutrients must come either from rain (or other airborne sources), or from the substratum. Resources from two different media have to be brought together. Furthermore, there are many problems associated with differences in interactions at the plant surface in water and in air.

That applies to all plants, however primitive or highly evolved, and we assume it has been true throughout geological time. Plants at every step in evolution change the habitat for organisms around them. Environments evolve hand-in-hand with the organisms that inhabit them; for any one species, all the other species in the same habitat are part of its environment. The complexity of modern forests with their multitude of ecological niches did not arise ready made; it evolved. “The past is a foreign country; they do things differently there” may apply to human behavior, but it is not a basis on which useful scientific work can be done. The basic principles of physics, and physiological and ecological knowledge from present-day plants and ecosystems, should inform our view of the geological past.

## II. Beginnings: The Transition from Water to Land

We can only conjecture when, and in what habitats, the first land-plants evolved. There must always have been an interface between water and land, both in the oceans and in rivers and lakes, and plants occupying that interface. The fossil evidence is sparse, and tantalizing (Chaps. 2 and 3). Of the diverse groups of photosynthesizing organisms in water, Chlorophyta (in the broad sense) are overwhelmingly predominant on land, with Cyanobacteria as a widely-pervasive poor second. The heterokont groups that are dominant in the sea, and prominent in freshwater aquatic habitats, probably evolved too late, and the land habitat was preempted by highly-evolved, green, land vegetation (Palmer et al. 2004).

This points to fresh (or brackish) water habitats, most probably wet mud on river banks or pool margins, as the likeliest origin of land vegetation as we know it. One of the first selection pressures at the land–water interface must have been for desiccation tolerance – manifested widely in different bacterial and algal groups, at least in desiccation-tolerant spores or resting stages. We can envisage the earliest land-plants forming a crust over the land surface, after the manner of “biological soil crusts” in present-day desert, polar and high-mountain environments, and as pioneer communities in all climates (Belnap and Lange 2001). As with present-day bryophytes and lichens, physical considerations would have limited their size to a few centimeters at the most – the *Racomitrium* mats of polar regions, and

the dense lichen growth in the coastal mist zone of the Namibian desert come to mind – so it would inevitably have been a Lilliputian world (Edwards 1996).

### III. Exchanges of Matter and Energy at the Earth's Surface

#### A. The Climate Near the Ground: Gradients at the Interface

The climate close to the ground surface can be very different from that of the air a meter or two above it. If the ground is wet the air in contact with it will be saturated with water vapour, with a gradient away from the surface to the concentration of water vapour in the ambient air. There will be lesser gradients of oxygen (O<sub>2</sub>) and carbon dioxide (CO<sub>2</sub>) due to the photosynthesis and respiration of the plants and soil. Under most conditions there will be temperature gradients too. On sunny days incoming solar radiation predominates, and the ground surface is warmer than the air. On clear nights, thermal infra-red radiation from the ground predominates, and the ground surface is cooler than the air: if the ground-surface temperature falls below freezing a ground-frost results.

#### B. Transfers of Heat and Matter to and from the Atmosphere

These temperature and concentration differences drive transfers of heat and gases between the ground (or plant) and the atmosphere. Temperature is a measure of the concentration of kinetic energy in the molecules in a gas, so transfers of heat and gases are analogous molecular diffusion processes. Rate of heat flow (J m<sup>-2</sup> s<sup>-1</sup>) is directly proportional to temperature difference (K), and inversely proportional to the diffusion resistance to heat transfer in air ( $r_H$ , units sm<sup>-1</sup>). The rate of diffusion of a gas (mol m<sup>-2</sup> s<sup>-1</sup>) is proportional to the concentration difference (mol m<sup>-3</sup>), and inversely proportional to the diffusion resistance ( $r_C$ , units sm<sup>-1</sup>). Light molecules diffuse

faster than heavy molecules, so each gas has its own characteristic diffusion resistance. In some simple situations the diffusion resistances can be calculated from relevant dimensions (m) and the thermal conductivity of air, or the diffusivity of the particular gas in air (Campbell and Norman 1998; Gates 1980; Jones 1992; Monteith and Unsworth 1990). In many cases the only recourse is to measure, e.g. water loss, under a particular set of conditions and to estimate diffusion resistances from the measurements.

When air flows past a solid object, the air in contact with the object is stationary, and there is a gradient of velocity away from the surface. Close to the surface viscous forces in the fluid predominate and the streamlines are parallel with the surface – *laminar* flow, which creates a laminar boundary-layer. Farther from the surface, or at higher wind-speeds, inertial forces become predominant, and the flow breaks up into eddies – leading to *turbulent* flow. The ratio of inertial to viscous forces is expressed by Reynold's Number (Re) =  $Vl/\nu$ , where  $V$  is the velocity of flow,  $l$  is a characteristic dimension (length or diameter for a flat plate, diameter for a rod or flow in a pipe), and  $\nu$  is the kinematic viscosity of air. In practical situations, if Re is much over 10,000 the flow is likely to generate turbulence, if less the flow is likely to be laminar. For a flat plate in laminar flow, the ratio of the effective (“displacement”) depth,  $\delta$ , of the laminar boundary-layer to  $l$  is approximated by  $\delta/l = 1.72/\sqrt{\text{Re}}$ ; thus the boundary layer depth is proportional to the square root of  $l$ , and inversely proportional to the square root of  $V$  (Monteith and Unsworth 1990). For a flat plate 5 cm wide in air flowing at 1 ms<sup>-1</sup>, the effective thickness of the laminar boundary layer is around 1.5–2 mm. At 0.1 ms<sup>-1</sup> (conventionally taken as “still air”), the thickness of the laminar boundary-layer will be c. 5–6 mm. Even if conditions are such that turbulence is being generated, there will always be a laminar sub-layer close to the surface.

The importance of these considerations in the present context is that exchange of heat and gases in the laminar boundary

layer is by molecular diffusion, which is slow. In turbulent air exchange processes are very much faster, in proportion to the size and vigour of the eddies – though of course the top of the laminar boundary-layer is not sharp but merges gradually with the turbulent air above. Bryophytes are often comparable in size to the laminar boundary layer of their substratum, and may be immersed within it, so molecular diffusion governs most exchange processes in their immediate environment. Vascular plants are generally much larger; exchange in the air spaces in the mesophyll and diffusion of water-vapour and gases through the stomata are governed by molecular diffusion, but exchange processes outside the leaves and stems mostly take place in turbulent air.

### C. The Heat Budget and Penman's Equation

The intensity of solar radiation reaching the earth's upper atmosphere is about 1,370 W per square meter ( $\text{Wm}^{-2}$ ); the peak energy of sunlight is at about 450 nm, in the middle of the visible spectrum. Some of this incoming radiation is absorbed by the atmosphere, and some is reflected back into space by clouds. On a clear day around 1,000  $\text{Wm}^{-2}$  reaches the ground. When sunlight is absorbed by a solid surface it is transformed into heat, which can leave the surface in only three ways. It may be *conducted* into the ground (or plant) raising its temperature, it may heat the air close to the surface and be *convected* away by gaseous diffusion and air currents, or it may be *re-radiated* back to the environment as thermal infrared radiation (with peak energy far outside the visible spectrum at a wavelength of around 10,000 nm).

The evaporation of water is driven by the concentration difference of water vapor between the air in contact with the wet surface (saturated) and the ambient air. For water to evaporate, the latent heat of evaporation must be supplied. The latent heat comes from some combination of radiative energy exchange at the surface, conduction from the substrate, and convective

transfer from the air (Campbell and Norman 1998; Gates 1980; Jones 1992; Monteith and Unsworth 1990). Penman (1948), making some simplifying assumptions, derived an equation to estimate the rate of evaporation from a wet surface:

$$\lambda E = [s(R_n - G) + \rho c_p (\chi_s - \chi) / r_H] / (\gamma^* + s)$$

where  $E$  is the rate of evaporation,  $\lambda$  is the latent heat of evaporation,  $R_n$  is the net radiation balance of the surface,  $G$  is storage of heat by the substratum,  $r_H$  is the diffusion resistance to heat transfer,  $s$  is the slope of the saturation vapor-density curve,  $\rho$  is the density of air,  $c_p$  is the specific heat of air,  $(\chi_s - \chi)$  is the saturation deficit of the ambient air, and  $\gamma^*$  is the apparent psychrometer constant. The quantities,  $\lambda$ ,  $\rho$ ,  $c_p$ ,  $s$  and  $\gamma^*$  are "constants" which vary somewhat with temperature and can be looked up in tables.  $R_n$ ,  $G$ ,  $(\chi_s - \chi)$  and  $r_H$  are variables, which can be measured or estimated.

The left-hand term in the numerator is the supply of heat by radiation or conduction. The right-hand term is the heat drawn by convective transfer from the air. If the net radiation income is small and heat cannot be drawn from the substratum, the rate of evaporation will be determined mainly by the saturation deficit of the air and the boundary layer diffusion resistance of the bryophyte. The latent heat of evaporation will be drawn mostly from the air, and the bryophyte surface will be cooler than air temperature. In a humid sheltered situation in sun the position is reversed. The right-hand term is now small, and evaporation is determined mainly by the net radiation income; the bryophyte will be warmer than the air. Evaporation will be at a minimum when net radiation income and saturation deficit are low, and boundary-layer resistances are high (implying low windspeed), as in sheltered, shady, humid forests. Evaporation will be maximal in full sun, in exposed situations, with dry air. Dry surfaces in full sun can easily reach 50–60 °C, and temperature can only be kept within tolerable limits for most life if evaporative cooling is added to the heat budget.

## IV. Selection Pressures on Early Land Plants

### A. Water Loss and CO<sub>2</sub> Uptake

A plant cannot acquire CO<sub>2</sub> from the atmosphere without at the same time losing water. However, the pathways for CO<sub>2</sub> acquisition and water loss are significantly different. Water is lost from the wet cell surfaces to the bulk atmosphere, so the diffusion resistance to water-loss is entirely in the gas phase (Nobel 1977; Jones 1992). Carbon dioxide is taken up through the wet walls of the photosynthesizing cells, and must then diffuse in the liquid phase from the absorbing cell surface to the chloroplasts. The CO<sub>2</sub> diffusion resistance in water is higher than that in air by a factor of around 10<sup>4</sup>; a diffusion barrier 1 μm of water is equivalent to about 10 mm of still air. This means that CO<sub>2</sub> acquisition is almost wholly diffusion-limited, and that a large part of the resistance to CO<sub>2</sub> uptake is in the liquid phase within the cell. The diffusion resistance of the air will still be an important factor affecting evaporation, but water loss is under more complex micro-meteorological control. Selection pressure will tend to increase area for CO<sub>2</sub> acquisition relative to projected area intercepting radiation and governing water loss. Hence selection pressures for maximizing CO<sub>2</sub> acquisition and for minimizing water loss are not diametrically opposed. The evolution of ventilated photosynthetic tissues (mesophyll and analogous structures), and probably of much of the diversity of bryophyte life-form, is driven by this difference.

### B. Desiccation Tolerance

Drying-out is an ever-present hazard on land, and desiccation-tolerance, the ability to lose most of the cell water without harm, suspend metabolism, and recover normal function on re-wetting (poikilohydry) is very common amongst small terrestrial plants including cyanobacteria, chlorophycean algae, bryophytes and lichens. Desiccation tolerance has a voluminous literature (Oliver et al.

2005; Alpert 2005, 2006; Proctor et al. 2007b), which will not be explored further here, beyond noting that in the dry state desiccation-tolerant organisms can tolerate far higher temperatures than when hydrated (Hearnshaw and Proctor 1982).

### C. Disseminule Dispersal

Spores (or other propagules) shed into a laminar boundary layer would almost certainly be deposited close to the point of release. To stand a chance of wide dispersal they need to be shed into air with at least a modest level of turbulence. The effect of this is easy to visualize when a moss such as *Mnium hornum* is fruiting in spring. The carpet of gametophyte leaves is photosynthesizing in relatively still air within a few millimeters of the ground, while the ripe sporophytes are dancing in the slightest wind on their wiry 5 cm-long setae. It is tempting to see spore dispersal in other groups of bryophytes too, as adaptations to get spores out of the relatively stagnant air close to the ground – the upstanding slender apically-dehiscing sporophytes of hornworts (Anthocerophyta), the dehiscence of *Sphagnum* (by whatever mechanism; Ingold 1965; Duckett et al. 2009; Whittaker and Edwards 2010), or the “catapult” mechanism of the elaters of liverworts (Marchantiophyta).

## V. The Evolution of Vascular Plants

It now seems to be the consensus that the liverworts (Marchantiophyta) are the sister group of all other archegoniate land plants (Edwards et al. 1995; Frey and Stech 2005; Qiu et al. 2006), and they probably originated in the mid to late Ordovician perhaps 450 million years ago (mya) (Chaps. 2 and 3). There is still doubt whether the Bryopsida or the Anthocerotopsida diverged next from the line leading to the vascular plants, but it seems certain that both groups were established by the end of the Ordovician. The fossil record over this period (c. 30–40 million years) is of dispersed (liverwort-like)

“cryptospores” and fragmentary plant remains. In the early Silurian, perhaps earlier in Gondwana, cryptospore abundance and diversity diminished as trilete spores appeared, became abundant, and underwent rapid diversification. This change coincides approximately with the appearance of vascular plant megafossils and probably represents the origin and adaptive radiation of vascular plants (Edwards et al. 1995, 1998b; Edwards 2000; Steemans et al. 2009).

#### A. The Evolution of Complexity of Form, and Conducting Systems

No doubt organisms competed from the start in the early land flora, and even at the relatively high levels of atmospheric CO<sub>2</sub> in the early Palaeozoic (Berner and Kothavala 2001; Bergman et al. 2004) complexity of form favoring CO<sub>2</sub> uptake relative to evaporation probably evolved early – branched filaments, multi-cellular plant bodies with air spaces (Raven 1996) or with filamentous, plate-like or leaf-like outgrowths. Modern terrestrial algae and bryophytes provide plenty of models, such as *Trentepohlia*, *Petalophyllum*, *Fossombronina*, the Marchantiales (Proctor 2010), *Crossidium*, *Aloina*, and the Polytrichales (Proctor 2005). Did an epidermis (with pores) arise first for mechanical protection of photosynthetic structures, which had to be thin walled to maximize CO<sub>2</sub> capture? Modern Marchantiales and Polytrichales provide two suggestive models in which protective layers (evolved in quite different ways) seem primarily to serve this function (Figs. 4.1 and 4.2).

Any organized multi-cellular plant body presupposes conduction of water, food materials and growth regulators (Raven 1977, 1984; Raven and Handley 1987). Extant bryophytes supplement diffusion through cell walls and general cell-to-cell transport of solutes (Proctor 1959; Pressel et al. 2010) by various specialized conducting systems. The water-conducting elements (hydroids) of mosses and similar water-conducting strands in Calobryales, Metzgeriales and *Takakia* probably all evolved independently, and none is homologous with the tracheids

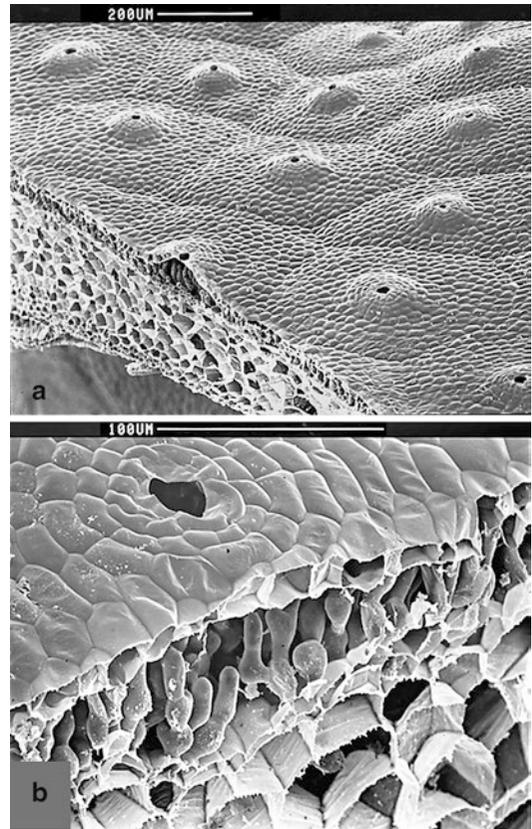


Fig. 4.1. Scanning electron micrographs of a vertical section of the thallus of the marchantial liverwort *Lumularia cruciata*. The Marchantiales typically have a ventilated photosynthetic tissue, a “pseudo-mesophyll”, analogous to a vascular-plant leaf, but evolved independently. The photosynthetic filaments occupy chambers within the upper surface of the thallus, protected from waterlogging and mechanical damage by an epidermis and opening to the exterior by pores. These allow access of CO<sub>2</sub> but not liquid water; they have sharp water-repellent margins but do not regulate water loss. Most of the thickness of the thallus is colorless parenchyma. (a) General view showing the pattern of air-chambers and pores on the surface of the thallus. (b) A closer view of an individual air-chamber and pore showing the photosynthetic filaments lining the chamber floor.

of vascular plants (Ligrone et al. 2000; Edwards et al. 2003). A polarized cytoplasmic organization with a distinctive axial system of microtubules characterizes the food-conducting cells of polytrichaceous mosses (Pressel et al. 2006). A similar organization probably with the same function occurs in other parts of the plant in mosses, including *Sphagnum*, and in thallus parenchyma of

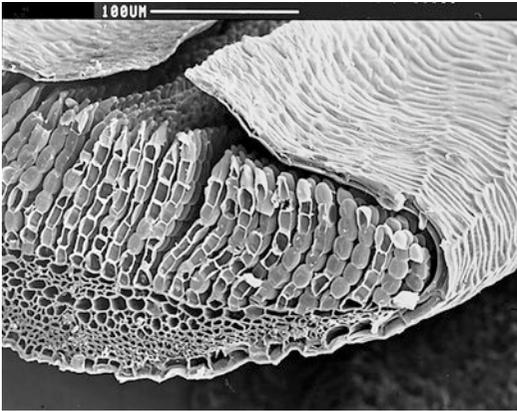


Fig. 4.2. Scanning electron micrograph of a leaf of the moss *Polytrichum piliferum*. Another “pseudomesophyll” of radically different structure and origin. In the Polytrichales the photosynthetic tissue consists of closely-spaced lamellae on the upper side of the midrib; the unistratose leaf lamina is reduced to a narrow colorless border. The marginal cells of the lamellae are thickened and water-repellent, and serve as a protective “epidermis”, in many species with prominent epicuticular wax. In this species and its close relatives the colorless leaf margins are inflexed over the lamellae adding still more protection to the photosynthetic lamellae.

liverworts. The distinctive structure of these food-conducting cells of bryophytes precludes any homology with the phloem of vascular plants (Ligrone et al. 2000). However, the apparent simplicity of the early land-plant fossils conceals a surprising diversity of structure in their conducting elements, as SEM studies of coalified fossils has shown (Edwards et al. 2003).

### B. The Importance of Scale

Modern bryophytes and vascular plants differ in size by around two orders of magnitude. This difference in scale brings with it major differences in physiology and responses to the environment; the scale-dependence of heat and mass transfer through the boundary-layer has been indicated already. Other things being equal, a plant a tenth of the linear dimensions of another has a hundredth of the surface area, and a thousandth of the volume and mass (and its root system, if it had one, could exploit a thousandth of the volume of soil).

The force of gravity depends on mass (proportional to volume), so it is important at our scale and a limiting factor for tall trees, but trivial for bryophytes. Surface tension, which works on linear interfaces, is trivial for us, but important physiologically for bryophytes, and life or death to small insects. The demands of tissues are proportional to volume, so the need of a plant for specialized transport systems increases with size. Volume is important in itself; there would simply not be room for the elaboration of vascular-plant structure in the bryophyte body. Particular scaling considerations apply to rates of uptake of nutrients by roots from soil, and rates of flow through water-conducting channels (Raven and Edwards 2001). The vascular pattern of adaptation is unquestionably optimal for a large plant, but there is much reason to believe that the poikilohydric strategy is optimal for one less than a few centimeters high (Proctor and Tuba 2002; Proctor 2009). The two strategies overlap, and both are viable, only in a limited “window” of scale from about 1 cm to about 10 cm, and it is in this size range that we should look for transitions between them – and for the earliest vascular plants.

Difference in scale brings profound differences in physiology between vascular plants and bryophytes, especially in relation to water (Proctor and Tuba 2002; Proctor 2009, 2011). Bryophytes are *poikilohydric*; vascular plants are *homoiohydric*. The basic cell biology of poikilohydric and homoiohydric plants is the same. Both need to be near full turgor for normal metabolism to take place. The difference is that the poikilohydric plant metabolizes when water is available, and goes into a state of suspended metabolism when it is not. In a Höfler diagram (Fig. 4.3), a vascular plant operates between about 30 % relative water content (RWC) and full turgor. Much of interest in the corresponding diagram for a poikilohydric plant lies in the regions below 30 % and above 100 % RWC (Proctor et al. 1998; Proctor 1999, 2009). Below c. 30 % RWC metabolism is slow or ceases altogether.

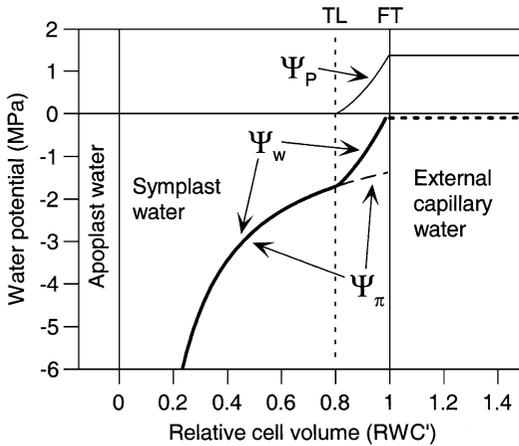


Fig. 4.3. Höfler diagram for a typical bryophyte, based on thermocouple psychrometer measurements on the leafy liverwort *Porella platyphylla* (Proctor 1999). The body of the diagram shows the relation of relative water content (RWC, strictly relative cell volume, RWC') to water potential ( $\Psi$ ), and its components:  $\Psi_w$  water potential of the cell,  $\Psi_\pi$  osmotic potential of the cell sap,  $\Psi_p$  turgor pressure. The water potential of the cell ( $\Psi_w$ ) is zero at full turgor (FT); the cell is in equilibrium with liquid water in its environment. As the cell loses water, turgor pressure ( $\Psi_p$ ) falls, and becomes zero at the point of turgor loss (TL). The tissue then becomes flaccid, and  $\Psi_w$  becomes equal to  $\Psi_\pi$ . Bryophytes share this much of the diagram with vascular plants. But in addition to water inside the cell, turgid metabolically-active bryophytes have *external capillary water* held in spaces at near-zero water-potential outside the cells, and this water is physiologically important too. The external capillary water is physically continuous with the *apoplast* water in the cell-walls, spanning a range of water potentials from zero to negative values far outside the limits of metabolism.

Most poikilohydric plants dry out to 5–10% RWC or less, and in the dry state they can survive for weeks or months, and revive when they are remoistened. Respiration recovers more rapidly than photosynthesis (Proctor et al. 2007a); it commonly takes from a few minutes to a few hours for the plant to return to a positive carbon balance. Vascular plants are also *endohydric* – their physiologically important free water is inside the plant's vascular system, separated from the surroundings by the cuticle and the stomata. Most poikilohydric plants are *ectohydric* – for them, the free water outside the plant body is physiologically important. Many bryophyte structures provide capillary

spaces in which water can be stored or moved freely from one part of the plant to another. The needs for water storage and movement may conflict with the needs of gas exchange. Bryophytes often have epicuticular waxes on the leaf surfaces; these usually have much more to do with controlling the distribution of water over the leaf surfaces than with reducing the rate of water loss (Proctor 1979a, b). The role of external water storage in bryophyte carbon balance is well illustrated by Alpert (1988), Zotz et al. (2000) and Zotz and Rottenberger (2001) and the data of Proctor (2004). Poikilohydry and desiccation tolerance is, in a sense, a drought avoidance strategy (Proctor 2000). For poikilohydric plants, partial hydration is a transient state between full turgor and desiccation, so they may spend less of their metabolically active time at sub-optimal RWC than drought-tolerant vascular plants.

In open, sun-exposed situations not only is there full exposure to near-UV, but diffusion limitation of CO<sub>2</sub> uptake may mean that there is an excess of excitation energy, with the attendant hazard of generating damaging reactive oxygen species (ROS; Smirnov 2005; Chapter 7). For a poikilohydric plant, the periods of drying out and recovering from desiccation are particularly hazardous. This leads to strong selection pressure for photoprotection (Heber et al. 2006). The xanthophyll cycle is typically very active in these plants; chlorophyll fluorescence generally shows high, but fast-relaxing, non-photochemical quenching (Marschall and Proctor 1999, 2004; Proctor MCF and Smirnov N, unpublished data). In mosses that have been investigated, CO<sub>2</sub> and O<sub>2</sub> act as alternative electron sinks (Proctor and Smirnov 2011), probably by the Mehler reaction (Asada 1999, 2006).

### C. The Vascular-Plant Package

It is inconceivable that a vascular plant could have evolved *de novo* as an integrated whole (Raven 1984). All the ingredients of the “vascular-plant package” exist in small poikilohydric modern plants, as models of

potential Palaeozoic precursors, but never all together. Which part of the vascular-plant package evolved first, roots, a vascular system, ventilated photosynthetic tissue, a waterproof cuticle, or stomata? All of the major extant groups adopted a different course.

The liverworts (Marchantiophyta) remained faithful to the gametophyte, and the limitations of boundary-layer life. The sporophyte passes most of its existence protected by gametophyte structures (involucre, perianth, perichaetial leaves) until the spores are mature, when rapid elongation of the seta, capsule dehiscence and spore liberation and dispersal, all generally take place within a day or two. Seta elongation occurs only if the plant is turgid, and capsule dehiscence takes place only if the air is dry. The sporophyte confines its venture into the dangerous world away from its substratum and protective gametophyte to a sacrificial few hours before shedding its spores and dying. The liverwort life-cycle seems to offer no insights into the origin of vascular plants.

Mosses (Bryophyta *sensu stricto*) have coped better with evolving a long-lived sporophyte capable of life outside the boundary layer, but have failed to make the critical breakthrough to full independence of the sporophyte. The embryonic sporophyte develops an apical cell at both ends (Campbell 1918; Smith 1938), the growing apex at the lower end forming the bottom part of the seta and the foot, that at the top end forming the upper part of the seta and the capsule. The developing sporophyte depends entirely on the gametophyte for water and mineral nutrients, and to a large but varying extent for photosynthate as well (Proctor 1977). By its small diameter and by growing away from the surface it speeds convective heat transfer with the surrounding air. Moss capsules are typically cuticularized and resistant to water loss but, in species with sporophyte development spanning a dry summer period, probably less *desiccation* tolerant than the gametophyte (Stark et al. 2007). The moss sporophyte has solved part of the heat-balance problem, and possesses ventilated photosynthetic tissue

with cuticle and stomata, and a conducting strand in the seta. It lacks one crucial ingredient of the vascular-plant package. It has no root system, and it is probably not nearly big enough to develop one that is viable. So it remains locked into dependence on the gametophyte. Nevertheless, moss (and hornwort) sporophytes do provide (small scale) models for a credible stage in the evolution of the first vascular plants (Ligrone et al. 2012).

#### *D. Possible Scenarios for the Evolution of Vascular Plants*

An impermeable cuticle would make no sense for a liverwort or moss growing on the ground; when hydrated and photosynthesizing in bright sun they would need to absorb CO<sub>2</sub> freely, and they would need evaporative cooling to keep temperature within tolerable limits. There are no obvious preconditions (apart from a multicellular plant body) for the evolution of a conducting system. Stomata only make sense in the context of a cutinized epidermis and ventilated photosynthetic tissue, and an efficient conducting system to support a transpiration stream, so the ventilated photosynthetic tissue has to come first (Edwards et al. 1998a). Roots, or parts of the shoot system serving the same function, are the last crucial innovation that made independent orthotropic growth possible, and paved the way for exploitation by plants of the third dimension – height. Roots with an anatomy distinct from stems, appear in the fossil record some 15 million years after the first evidence of vascular plants. The evolution of true roots heralded the increasingly rapid escalation of plant size, diversity and complexity from herbaceous dimensions to tall forest trees during the Devonian.

Early fossil vascular-plant floras are all from low (palaeo)latitudes, so they were probably all from environments free from seasonal extremes. As a possible place of origin of homoiohydric vascular plants, we may consider a constantly-watered spot, with rainfall distributed round the year and comfortably exceeding annual evapo-transpiration. Nowadays

such a place can support communities of bryophytes, in which gametophytes make up the bulk of the plant cover. Some species grow to a few centimeters above the general level and are able to maintain turgor at their apices by either external capillary or internal conduction. Sufficient heat is lost by the latent heat of evaporation and keeps the temperature well within tolerable limits. Sporophytes of mosses and hornworts grow a few centimeters taller and both have air spaces and stomata. A modern marsh of this kind often includes rushes (*Juncus* spp.), or other plants of similar erect terete growth form. These have roots, ventilated photosynthetic tissue, cuticle and stomata. They also have a morphology which offers a small target for solar radiation, a large area in contact with air and a small diameter perpendicular to the airflow, hence thin boundary-layers, low resistance to heat transfer, and close coupling to air temperature. Rushes can close their stomata and still have enough convective cooling to keep their temperature from rising to lethal levels. This is an environment in which we can visualize the evolution of first, air spaces in the photosynthetic tissue, then cuticle and stomata evolving hand in hand, and simultaneously with these, basal parts of the shoot system increasingly devoted to uptake of water and nutrients. “Roots” no doubt evolved more than once, and various lines of evidence suggest roots evolved at least two and possibly three times (Raven and Edwards 2001).

Fossil cooksonioid axes span a range of diameters from slender examples with conducting strands, which could have borne aloft sporangia but could not have been photosynthetically self-supporting (much like modern moss setae), to axes wide enough to have contained not only a conducting strand, but sufficient photosynthetic tissue to be self-sufficient for carbon nutrition (Boyce 2008). Modern hornwort sporophytes (Anthocerophyta) provide suggestive models of a transitional stage – with a slender conducting strand, ventilated photosynthetic tissue, and stomata. But any successful breakthrough into homoiohydry

would be expected soon to have been massively outnumbered in the fossil record by diverse and numerous fast-evolving progeny – a besetting problem of the search for “missing links”!

Much of the argument of the preceding paragraphs could be read as favoring the *antithetic* or “rise of the sporophyte” model of vascular plant evolution first suggested in the 1870s (Bower 1890, 1935; Hemsley 1994), which saw the sporophyte as an intercalation into a basically haploid life-cycle. An alternative *homologous* model, also dating from the 1870s, saw the origins of the gametophyte and sporophyte as the two phases of an isomorphic alternation of generations, exemplified by some marine algae (Eames 1936; John 1994). The finding of gametophyte axes apparently anatomically similar to known fossil sporophytes in the Rhynie Chert (Remy et al. 1993; Remy and Hass 1996), seem to support the homologous model (Kenrick 1994; Taylor et al. 2005). With the discovery of apospory and diploid gametophytes, and developing concepts in genetics, morphological differences between the generations of the life cycle can now be seen as less fundamental than they were perceived to be a century ago. The scenario sketched above need not have been a unique event; different groups of vascular plants may well have evolved independently, many lineages sooner or later becoming extinct (Crane et al. 2004; Palmer et al. 2004).

#### *E. Why Did Vascular Plants Not Supersede Bryophytes?*

In the favourable habitats just envisaged for the origin of vascular plants, vascular plants may have superseded bryophytes. However, wide expanses of the Earth’s surface must have been less favourable. There would always have been rocky places impenetrable to roots, and places intermittently too dry. At high latitudes and altitudes conditions would have been too cool for growth except close the ground during the day, especially in sunshine; Davey and Rothery (1997)

measured midday temperatures up to 11–12 °C at 10 mm depth on Signy Island in the sub-Antarctic. In cold climates, the temperature gradients at the surface of the Earth would have been not a potential hazard, but a prerequisite of plant growth. At the present day we take for granted a low vegetation, in which bryophytes and lichens are prominent, in polar regions and on high mountains.

Vascular plants opened up a new dimension. They did not simply replace the smaller poikilohydric plants. Rather, they created their own new ecological niches, and by increasing the complexity of the landscape created a new range of microhabitats for smaller plants to colonize. The small poikilohydric plants continued to evolve *at their own scale*. And who would argue that the bryophytes were unsuccessful with around 20,000 species distributed in almost every habitat from the Equator to the Polar regions?

#### *F. Physiological Consequences of the “Vascular-Plant Package”*

This had physiological consequences for the vascular plants themselves. The mesophyll cells found themselves in a constantly-humid environment with a regular water supply, relieved of the selection-pressure to tolerate intermittent desiccation. Growth to overtop neighbors was the new imperative. There was still a need for desiccation tolerance at particular points in the life cycle; almost all vascular plants have desiccation-tolerant spores or pollen grains, and many have desiccation-tolerant seeds. Accordingly vascular plants have retained genes for desiccation tolerance, but they are only switched on during sporogenesis and seed development, and vegetative tissues are generally sensitive to desiccation.

The vascular-plant package also had implications for photoprotection. As we have already seen, poikilohydry and CO<sub>2</sub> limitation both tend to lead to intermittent production of excess excitation energy, which needs to be degraded harmlessly to

heat if it is not to generate damaging free-radicals. Vascular-plant leaves have a larger, and more constant, photosynthetic capacity. They have less need for photoprotection; glycolate photorespiration can be seen as the principal vascular-plant answer to what need they have. Vascular plants, with their large complex bodies and conducting systems, also have the option of exporting excess photosynthetic products to non-photosynthesizing storage organs.

We take these vascular-plant traits for granted, and tend to regard them as fundamental, but they are derived consequences of the evolution of the vascular-plant package.

## **VI. The Post-palaeozoic Scene: Complex Habitats**

### *A. The Close of the Palaeozoic Era*

In the earlier part of the Palaeozoic temperatures were c. 4–6 °C higher, and atmospheric CO<sub>2</sub> levels some 15 times higher than at the present day. By the late Devonian (c. 360 mya) lycophytes, ferns, Equisetales and pteridosperms were in existence, some of them large trees; atmospheric CO<sub>2</sub> had declined to around five times present levels, and temperature was falling too. By the close of the Carboniferous period (300 mya), complex phyletically-rich tropical forests had been in existence for 50 million years, with considerable habitat and regional diversification. Atmospheric CO<sub>2</sub> had dropped to no more than 500–600 ppm (some measurements put it lower than that), the concentration of oxygen in the air was about 30 %, and temperatures were similar to the present day. The evolution of large (megaphyll) leaves probably had more to with mutual shelter as vegetation increased in height and closure than with declining CO<sub>2</sub> in the air, despite the arguments of Beerling et al. (2001). It is more likely that the scale of photosynthesis, which large leaves made possible, drove the fall in atmospheric CO<sub>2</sub> than vice versa. The rise in O<sub>2</sub> was reflected by the increasing

frequency of fire in the later Palaeozoic (Scott and Glasspool 2006).

Ecologically, in the course of 150 million years, the Earth had become an incomparably richer, more complex and more diverse place. Forests created a whole new set of niches for bryophytes, on the shady forest floor, on fallen wood, and probably as epiphytes on trunks and branches. The shade meant that light, not CO<sub>2</sub>, became the limiting factor for growth. This was less of a constraint on bryophytes, with their largely unistratose leaves and poikilohydric habit, than on vascular plants. Bryophytes could draw nutrients from throughfall, the rain penetrating the canopy, and dripping from the leaves, and from stemflow, the rainwater running down the trunks. Microhabitats on bark were largely inaccessible to vascular plants because there was nowhere for roots to penetrate.

The great Carboniferous coal-forming rainforests declined abruptly (within a few thousand years) to a fraction of their former extent about 315 mya. The causes of this (geologically) sudden collapse are not certain, but probably the onset of a cycle of glaciations, coupled with a long-term trend to drier climate, was a major factor (Montañez et al. 2007; DiMichelle et al. 2010). The tall lycophytes that had dominated the rainforests declined with them and became extinct by the end of the Permian, and the tree-ferns and pteridosperms declined with them. Cordaitales and ferns had long occupied the drier uplands, and had spread into the lowlands during drier climatic phases. These, together with early conifers, expanded to dominate the increasingly dry and continental landscape, until by the end of the Permian (250 mya) primitive conifers and the maidenhair trees (Ginkgoales) were the predominant trees.

From the evidence of molecular phylogenies, combined with such fossil evidence as we have, all the major backbone lineages of bryophytes were in place by the end of the Palaeozoic. The Marchantiopsida (complex thalloid liverworts) had probably split from the remaining liverworts (Jugermanniopsida)

in the late Devonian (c. 370 mya), and the simple thalloid and leafy liverworts probably diverged in the late Carboniferous (c. 310 mya; Heinrichs et al. 2007). The split of the line leading to Porellineae, Radulineae and Lepidolaeninae (all largely epiphytic) from the remaining leafy liverworts is dated by Heinrichs et al. at about 280 mya in the Permian. Among the mosses, *Takakia*, *Sphagnum*, and *Andreaea* diverged earliest, and the Oedopodiaceae, Tetraphidaceae, Polytrichaceae, Buxbaumiaceae, Diphysciaceae, Timmiaceae and the Funariidae, Dicranidae and the Bryidae/Hypnidae lineages were probably in place by the opening of the Mesozoic (Goffinet and Buck 2004; Bell and Newton 2004; Newton et al. 2007), having evolved in the late Devonian and Permo-Carboniferous forests.

#### *B. The Mesozoic Era: Continuing Evolution of Bryophytes*

About 250 mya there was the greatest mass extinction in the history of the planet; 96 % of marine species died out. The extinction bore less heavily on land life, some 50 % of plant species may have become extinct, but this figure is very uncertain (McElwain and Punyasena 2007). The tree lycophytes and sphenophytes and the Cordaitales disappeared from the fossil record at the end of the Permian, as did most of the Palaeozoic families of ferns. The Permian–Triassic boundary marks a dramatic change from a primitive Palaeozoic flora and vegetation to one of essentially modern aspect in the Mesozoic. The causes of the extinction are obscure, but vulcanism, the releasing of methane clathrates, ‘greenhouse’ warming, and anoxia in the oceans with emission of hydrogen sulfide, may all have played a part.

It appears to have taken some millions of years before a substantial forest cover was regained. How the extinction affected bryophytes we can only conjecture. Heinrichs et al. (2007) locate two dated nodes of their phylogeny in the Permian, two in the Triassic, and four in the Jurassic – periods of roughly

equal length. Evidently the Triassic was not a period of very active radiation in liverworts. The early Triassic climate was warm and arid, becoming cooler towards the end of the period. Atmospheric CO<sub>2</sub> was some six times and O<sub>2</sub> rather below present atmospheric levels. Recognizably modern conifers and the cycads and cycad-like plants that were to be so characteristic of Mesozoic vegetation began to appear in the Upper Triassic, joining the still-abundant Ginkgoales. Liverworts continued to differentiate, though slowly. The Triassic–Jurassic boundary was marked by another major extinction event, probably caused by widespread flood-basalt eruptions associated with the imminent break-up of Pangaea (McElwain et al. 1999; Whiteside et al. 2010).

The ensuing Jurassic period (c. 200–146 mya) was a time of rising temperature, rising O<sub>2</sub> levels (~25 %), high CO<sub>2</sub> (peaking at ~2,000 vpm) – and renewed evolution. Pangaea broke up, the northern continents (Laurasia) separating from the southern continents (Gondwana), and Laurasia itself began to break up before the end of the period. Gymnosperms dominated the forests. They included cycads and the cycad-like Bennettitales, Ginkgoales (especially in temperate northern latitudes), and varied conifers including Pinaceae, Taxaceae, Taxodiaceae and Podocarpaceae (the last particularly in the southern hemisphere). Some of the conifers had broad leaves, as does the extant *Phyllocladus* (the celery-top pine of Tasmania, and the toatoa and tanekaha of New Zealand) and the Ginkgoales, so the Mesozoic forests would have been more varied than their modern coniferous counterparts. A few modern bryophyte families seem to go back to the Jurassic, Frullaniaceae, Radulaceae, Porellaceae and Metzgeriaceae among them. The pleurocarpous mosses first appeared early in the Jurassic and the major pleurocarpous families diverged later in this period or early in the Cretaceous (Newton et al. 2007).

The Cretaceous Period (c.146–66 mya) followed on from the Jurassic, and was the longest period of the Mesozoic. The break-

up of Laurasia continued, but what were to become North America, Greenland and northern Europe remained close together, with the North Atlantic a broadening triangle between and south of them. Gondwana broke up during the Cretaceous, South America, Africa, Madagascar/India, Australia and Antarctica becoming discrete continents. The last links between the southern continents, between Antarctica and Australia and between Antarctica and South America, were not broken until the Cenozoic. Climatically, the trends set in the Jurassic continued. Temperature continued to rise, approaching early Triassic levels. Carbon dioxide remained high (~2,000 ppm) declining toward the end of the period, and oxygen peaked at levels (~30 %) not reached since the Carboniferous. Vegetationally, the early part of the period was essentially a continuation of the Jurassic, dominated by conifers, Ginkgoales, cycads and Bennettitales; these last became extinct in the mid-Cretaceous. The fossil record shows that coniferous forests extended to both northern and southern polar regions in the Mesozoic (Beerling and Osborne 2002). Dinosaurs peaked in diversity in the mid-Cretaceous. Flowering plants (Angiosperms) first appeared as pollen early in the Cretaceous (Soltis and Soltis 2004). At first they expanded slowly, but in the mid-Cretaceous (Albian–Cenomanian) they diversified rapidly, and by the end of the period 70 % of known terrestrial plant species were angiosperms. They seem to have evolved in open upland situations, and they may not have been generally dominant until the Cenozoic (Wing and Boucher 1998).

The Cretaceous was also a time of active diversification amongst bryophytes. Many of the major bryophyte families (at least in a broad sense) trace their origins back to the Cretaceous, including Scapaniaceae, Lophocoleaceae, Plagiochilaceae, and Lepidoziaceae amongst liverworts. Many of the better-circumscribed genera are of similar age.

The close of the Cretaceous was marked by a mass extinction (the “K–T boundary”), probably primarily due to an asteroid impact

66.5 mya, though the eruption of the Deccan Traps (flood basalts) which spanned the same period may have contributed. Groups becoming extinct included the dinosaurs (except the ancestral birds), plesiosaurs, pterosaurs, ammonites and belemnites. Corals, coccolithophorids and foraminifera suffered heavy losses, but fish, amphibians, turtles and crocodiles were relatively unaffected. There was major global disruption in terrestrial vegetation at the K–T boundary. In North America (relatively close to the postulated impact site) more than half the plant species became extinct, but in New Zealand and Antarctica the mass death of vegetation seems to have caused no significant turnover in species. In the immediate aftermath, open habitats seem to have been widely colonized by ferns, leading to a brief ‘fern spike’ in the geological record before closed forests re-established (Nichols and Johnson 2008).

### *C. The Cenozoic Era: The Modern World*

The Cenozoic era (66 mya onwards) brings us to the modern world. From the outset, plant cover was predominantly of angiosperms, mostly belonging to modern genera, or to closely related taxa. In the Paleocene and Eocene dense tropical, sub-tropical and deciduous forests covered the globe; polar regions were ice-free, and occupied by temperate forest of deciduous and coniferous trees. Average global temperature peaked at c. 6 °C above present levels around the opening of the Eocene, a little over 55 mya, but (as in the Jurassic and Cretaceous) the difference between equatorial and polar regions was only half that at the present day, so the tropical regions were little or no warmer than now. By the Eocene, the mammals had evolved to occupy most of the ecological niches left vacant by the demise of the dinosaurs. From mid-Eocene onwards temperature had begun the slow decline that was to culminate in the Pleistocene glaciations, and by the end of the period (34 mya) Antarctica was an expanse of tundra fringed by deciduous forests. Collisions between tectonic plates following the fragmentation of

Pangaea led to mountain-building in western North America, Asia (Himalayas etc.) and Europe (Alps etc.) that was to continue into the following Oligocene and Miocene periods and beyond; the Andes came later starting in the Miocene. Early in the Oligocene the first permanent ice-sheets appeared in Antarctica. A trend towards cooler and drier climate, coupled with continuing evolution of grazing mammals, saw an expansion of grasslands at the expense of forest, trends continued in the Miocene (23–5.3 mya) and Pliocene (5.3–2.6 mya). Declining temperatures and atmospheric CO<sub>2</sub> levels culminated in the Pleistocene glaciations, which are still with us in Greenland and Antarctica.

The Cenozoic has been an eventful period, of mountain building, climatic change, and vigorous evolutionary radiation of angiosperms, mammals, birds and insects. It has also been an eventful period for bryophyte evolution. We know that the Cenozoic has been a time of active speciation in both mosses and liverworts, in response to the diversity of angiosperm forests and the mountain building that has characterized the era. The polar-alpine bryoflora is a creation of Cenozoic evolution as surely as the angiosperm arctic-alpine flora (Hultén 1937).

### *D. Phyletic Conservatism and Life-Strategy Correlations*

Evolution has left us with four major clades of plants whose fossil record goes back to the Paleozoic; from molecular evidence they have been independent lines at least since that time. Two of these are of large vascular plants; the Lycophyta, once prominent as large trees in Palaeozoic forests but since reduced to a minor role, and the fern–horsetail–pteridosperm line with its later offshoots the conifers and flowering plants. Two groups, the mosses and liverworts, are of small poikilohydric plants; these we traditionally lump together as “bryophytes”. A third bryophyte group, the hornworts (Anthocerophyta) of which the fossil record is sparse, must from molecular evidence be equally old. These taxonomic groups have retained their

phyletic independence, and their characteristic ecophysiological adaptation, since those early days.

There are evidently just two basic strategies of adaptation for plant life on land, each optimal at a particular scale. They overlap at the scale of the largest bryophytes, and the smallest vascular plants, around 1–10 cm. It is in this range that the earliest vascular plants probably arose. Crossovers between the two strategies seem to be very rare. The filmy ferns are one of the few examples. Their sporophytes function ecologically as “bryophytes”; they are the right size, they are poikilohydric, and they grow in company with mosses and liverworts in shady humid situations (Proctor 2012). The ferns in fact have a foot in both camps. Their sporophytes are in general unequivocal vascular plants, but their gametophytes share the “bryophyte” strategy of adaptation (Watkins et al. 2007; Proctor 2007). “Why are desiccation-tolerant organisms so small or rare?” (Alpert 2006). Small poikilohydric plants are numerous, because they are optimal at that scale. Large desiccation-tolerant plants are rare because they are basically mainstream vascular plants, which only later evolved (or re-evolved) desiccation tolerance in response to seasonally-desiccated habitats which, globally, are themselves rare. The molecular evidence speaks for a common origin for bryophytes and vascular plants. However, it is clear that the vascular plants, and the bryophytes have evolved independently, facing different selection pressures at the cellular level, since the mid-Palaeozoic – in round figures some 400 million years.

## VII. Overview

Bryophytes thus have a long evolutionary history of era-by-era diversification. The major divisions into mosses (Bryophyta), liverworts (Marchantiophyta) and hornworts (Anthocerotophyta) were probably in place by the end of the Ordovician, and these (and perhaps other bryophyte groups) took their place alongside early vascular plants. Since

then bryophytes have evolved with vascular plants as part of their environment. The main backbone lineages of both the mosses and the liverworts probably diverged in the late Devonian and Carboniferous landscape, which must have included many habitats for (and some dominated by) small poikilohydric plants, in addition to the forests of which we are most aware from palaeobotany. Cladistic analyses of molecular data give every reason to suppose that Andreaeales, Sphagnales, Polytrichales, Dicranales, Grimmiiales and others go back to the Palaeozoic. The Sphagnales are a particularly interesting case; presumably their limited but important ecological niche has existed since that time. The Carboniferous forests would have provided terrestrial habitats for a range of acrocarpous mosses and thalloid liverworts, but many of the dominant vascular plants might not have provided extensive habitat for epiphytes. Nevertheless, the “leafy l” clade of liverworts (Davis 2004), which now include many epiphytes, appears to have diverged in the late Palaeozoic. I have emphasized forests because these provide a wide range of ecological niches for bryophytes; it is noteworthy that most of the largest bryophytes grow in the shade and shelter of forests. The dendroid life-form, surely a response to conditions on the forest floor, has evolved repeatedly amongst unrelated mosses, e.g. *Dendroligotrichum*, Hypnodendraceae, Climaciaceae, *Thamnobryum*. Many of our modern families and genera diverged and diversified in the Mesozoic, in the gymnosperm-dominated Jurassic and (especially) Cretaceous periods. The major diversification of modern families and genera, such as the majority of the leafy liverworts (Davis 2004; Heinrichs et al. 2007) and pleurocarpous mosses (Bell and Newton 2004; Newton et al. 2007) which are so prominent in the present-day world came, along with the flowering plants, in the late Mesozoic and Cenozoic. Forests have been important in the evolution of bryophytes, but we should never forget that non-forested habitats have been ever present and important too.

Some genera and many species date from the Cenozoic, and active speciation (Shaw 2009) has been going on throughout the Cenozoic and still continues in “difficult” groups (*Calypogeia*, Lejeuneaceae, *Marchantia*, *Pellia endiviifolia* complex, *Bryum*, *Philonotis*, *Plagiothecium*, *Schistidium*, *Sphagnum*, and many others). As we approach the present day we are most aware of speciation. That is a consequence of the limited time frame afforded by the human life-span! Were we able to go back and bryologize the Mesozoic or Palaeozoic world, we should encounter a diverse and fascinating bryoflora, of which we might be able to assign a proportion to families (and even genera) we knew, but the species would be different – and evolving. The “present” is merely the point at which we step into the “river of time”.

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