

TWELVE READINGS ON THE LICHEN THALLUS

XI. Preassembly

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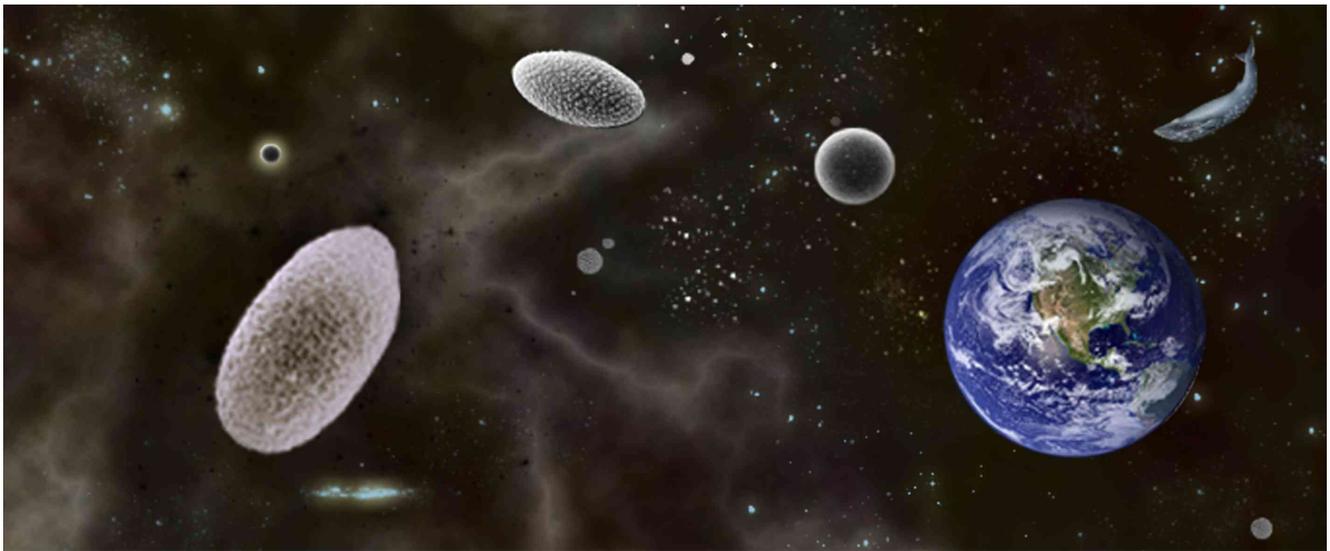


Figure 1. Why do lichens occur where they do? And furthermore, why **don't** lichens occur where they don't? Both these questions need to be answered if we're to understand the internal and external forces that shape lichen distribution in broad outline. Here notice the canny use of lichen spores in slow orbit. SEMs kindly provided by Christoph Scheidegger. Photomontage by Tim Wheeler.

The world is not to be narrowed till it will go into the understanding ... but the understanding is to be expanded and opened till it can take in the image of the world.

Francis Bacon

HOME, THEY SAY, IS WHERE YOU FIND IT. Where I find my home is in a green, mountain-flanked valley in southern inland British Columbia.

A century ago the Clearwater Valley would have resembled many valleys hereabouts. But not anymore. Nowadays only this valley of all the valleys around has been spared the ravages of industrial resource extraction.* If only by default, this makes the Clearwater Valley a special place: a wilderness tract half

again the size of Belgium: a place where the species of birds outnumber the human residents, and where the species of macrolichens, come to that, far outnumber the species of birds.

Odd thing about the Clearwater Valley, though. Fifteen thousand years ago it brimmed with glacial ice two kilometres thick. And yet today, a mere phyto-geographic eye blink later, it supports not simply an internationally significant macrolichen flora – which in a glaciated region would be remarkable in itself – but

* <http://waysofenlichenment.net/wells/chessboard>

by far the richest assemblage of macrolichens ever documented, at 424 species.*

Were this essay about flowering plants – or salamanders, or butterflies, or voles, or what have you – I'd surely be whistling a different tune. The Clearwater Valley holds little distinction for any of these. Only when you leave this valley, heading south, do these and other taxonomic groups really come into their own. Continue south far enough, beyond the limits of the Cordilleran Icesheet, and you enter a region – the American Pacific Northwest – where most of the species now resident in the Clearwater Valley waited out the Ice Age. And where a great many other species have lingered ever since, albeit obviously not the macrolichens.

Now it's one thing to infer that macrolichens must disperse and populate with comparative ease. But it's quite another to understand why exactly this should be. The question, to rephrase, is threefold. First, how *do* macrolichens get around, anyhow? Second, how do macrolichens, having gotten around, contrive to settle in, start up a viable population? And third what is it about the Clearwater Valley in particular that makes it such a macrolichen magnet – precisely in a region where on phytogeographic grounds you'd least expect it? These are the questions I want to examine in this essay; and tree-dwelling (epiphytic) macrolichens are the species that for convenience I'll adopt as my case study.†

SETTING THE STAGE: CLEARWATER VALLEY

Nowadays the valley of the Clearwater River supports 15 tree species – eight evergreen, seven deciduous – of which most are restricted, except as plantings, to western North America. Taken together these trees support 144 species of macrolichens. Only 41 of these

* <http://waysofenlichenment.net/wells/checklists/macrolichens>

† Epiphytic lichens have fascinated me as long as I remember. Many reasons, I suppose. Here are five. First, the branches of trees (and shrubs) renew themselves annually, hence partly circumvent the mathematical imponderables of competitive exclusion. Second, the arboreal life form has evolved in many unrelated groups which, when they grow side by side, can give rise to “found experiments” highly informative to a pattern-seeker like myself. Third, the increasing size of trees of increasing age creates ever more niches suited to ever more lichens. Fourth, the canopies of trees rise well into the air, hence are largely free of the confounding idiosyncrasies of climate near the ground. And fifth, lichens aren't the only things that grow on trees; so does money. The continued loss of oldgrowth forests makes it urgent to understand what ecosystem functions old trees perform. What better way, say I, to examine the ecology of trees than to study epiphytic lichens, for which trees are *alpha* and *omega*?

species, however, are endemic to the west (Table 1); the rest, or most of them, about half the total, turn up in suitable habitat around the world. To a birdwatcher or vascular botanist, such a statement could seem remarkable but the student of lichens knows it's actually pretty standard – for lichens. Head north, say, to the southern Yukon, and the incidence of circumpolar macrolichens will be even higher, around 70-80%. The take-home message is clear: a great many macrolichens have vast global ranges.

But here's something: When we examine how those vast global ranges sort out relative to lichen dispersal, we soon bump against a curious observation: macrolichens endemic to the west are twice as likely as their circumpolar counterparts (43% versus 21%) to reproduce via fungal spores; and hence twice as *unlikely* to bear soredia or isidia. This is not exactly what we'd expect. Surely fungal spores, which are microscopic, ought to travel much farther than vegetative diaspores more than 100 times larger; and in fact they certainly do. On the other hand, a spore is much less likely than a vegetative diaspore to establish a new lichen at the end of the trip. Partly this is because spores, precisely because they're so small, have almost no excess carbon for startup. Soredia, by contrast, are positively freighted with excess carbon; that's in large part what they're made of. So even if soredia don't get around quite as well, still they're much more likely to initiate a successful inoculation event. I'll have more to say about soredia as lichen dispersers later in this essay.

THALLUS INITIATION

Thallus initiation should be understood for what it is: a necessarily complex and presumably energy-expensive upgrade from two unrelated biological systems – those of the lichen fungus and the lichen alga – to a third entirely different system, a lichen. In most cases we should expect this process to require at least a certain amount of stored energy, e.g., for initiating lichen physiology and development, including start-up biosynthesis of secondary substances.

If so, then there's something about the lichen life cycle I've never quite understood, and has always felt a bit “off”. What happens in the case of all those innumerable lichen propagules – fungal spores, algal cells, soredia – that touch down in suitable habitat, start to grow, yet fail to form a lichen thallus prior to being shut down, e.g., by a change in the weather? Clearly it would be easy to suppose that nothing happens; they simply die. And yet it would be remarkable indeed if the lichen system in this one critical

DISTRIBUTIONAL TYPE (144 species)		Number of spp.	Apotheciate (% of distrib. type)	Sorediate/isidiate (% of distrib. type)
1	wNA	41 (28%)	18 (44%)	23 (56%)
2	wNA eEurasia	4 (3%)	2 (50%)	2 (50%)
3	wNA eNA	8 (6%)	5 (63%)	3 (38%)
4	wNA wEurasia	7 (5%)	2 (29%)	5 (71%)
5	wNA eEurasia eNA	3 (2%)	1 (33%)	2 (67%)
6	wNA eEurasia wEurasia	1 (1%)	0 (0%)	1 (100%)
7	wNA eNA wEurasia	9 (6%)	2 (22%)	7 (78%)
8	wNA eEurasia eNA wEurasia	71 (49%)	15 (21%)	56 (79%)
Total		144	45 (31% of total)	99 (69% of total)

Table 1. Global distribution types for 144 macrolichens of 15 major trees and shrubs in the Clearwater Valley, south-central British Columbia (52° N, 120° W). Eight distribution types are recognized: (1) endemic; (2) amphipacific; (3) amphi North American; (4) western North America – western Eurasia; (5) incompletely circumpolar, lacking in eastern Eurasia; (6) incompletely circumpolar, lacking in western Eurasia, (7) incompletely circumpolar, lacking in eastern North America, and (8) circumpolar. Note that half of the species have circumpolar distributions, attesting to the tremendous get-up-and-go of the lichen lifestyle. Also note, however, that the next largest group (28%) consists of macrolichens occurring only in western North America. Thus fully three-quarters of epiphytic macrolichens of the Clearwater Valley are shared between the narrowest (endemic) and the broadest (circumpolar) distribution classes. This could perhaps seem a little strange; see Table 2 and associated text for partial explanation.

function – thallus initiation – had not long since contrived to turn to reproductive advantage a die-off situation that otherwise would constitute a very great impediment to reproductive success. Here enter the *parathallus*, which in Essay IX I defined as a thin, persistent, often scurfy crust composed of one or more lichen-forming fungi and one or more non-lichenizing algae. As I’ve come to understand it, the parathallus is the one great escape clause in the lichen contract between the lichen fungus and its algal partner. Specifically it allows for the creation of who-knows-how-many different lichen fungal-algal systems that *need not immediately upgrade into a lichen*. My guess is that parathallus systems have quite a lot to do with the uncanny ability of lichens to colonize new territory rapidly and, at least in the Clearwater Valley, in great overall diversity. All of which comes under the rubric of what I’ll henceforth refer to as lichen “Preassembly Theory”.*

* In an earlier essay in this series (Essay VI: *Reassembly*), I discussed certain aspects of lichen systems theory viewed from the perspective of thallus initiation. Here, in Essay XI, my focus is on certain hypothetical unlichenized fungal-algal systems assumed to precede thallus initiation. My decision to gather the latter systems under the rubric *preassembly* is slightly problematic: first because not all such systems are likely to result in a lichen thallus (hence they really aren’t *pre-* anything); and second because they enforce a lichen-centric perspective on a much larger set of fungal-algal relationships

LICHEN PREASSEMBLY THEORY: FIRST BLUSH

Preassembly, as I conceive it, has its basis precisely in the dual nature of the lichen thallus – and hence in the absolute requirement on the part of the lichen fungus and the lichen alga periodically to exit the lichen system, reassert their independent existence as biologically, evolutionarily engaged organisms; and then, if and when the time is right, to renegotiate their respective terms of re-entry into a new lichen thallus constructed, as it were, from the ground up. Of course this disassembly-reassembly process could put one in mind of sexual reproduction expressed as meiosis and then mitosis; and this, by analogy, isn’t a bad way to think about it. At all events, thallus initiation is necessarily a two-step process, so it follows (or *could* follow) that these two steps – fungus first, then the alga – need not always be taken in rapid succession. In some paralichen systems, indeed, it’s conceivable they have become entirely uncoupled, and may operate quite independent of the great lichenological imperative to institute a thallus. What this comes to is the proposition that one or perhaps both members of some parathallus systems may well be present in a partic-

of which the lichen is simply the most conspicuous subset. My decision to adopt the term *preassembly* for the present purpose is in keeping with the primary subject of these essays, i.e., the “lichenized condition”.

ular region without, however, recording the fact (at least not yet) in the form of a lichen.

Having lived for some time with speculations of this kind, I find myself moving toward the view that thallus initiation may in some way be compared to the sudden popping up of a mushroom – which, depending on the year and the weather and maybe the phase of the moon, may seemingly come from nowhere. It will be an organizing principle for the remainder of this essay that lichen preassembly must provide at least part of the answer to my question concerning the rapid establishment, in remarkably short order, of 370 macrolichen species in my home valley.

But before we travel any further down this road, we'll first need to know something about the nature of the lichen fungus and the lichen alga in their capacity as microscopic organism – for it is precisely here, at the scale of microns, where both the parathallus and preassembly theory must operate.

THE WORLD OF THE VERY SMALL

If we could scale down to the size of a fungal spore or an algal cell, we'd experience a world teeming with particles in numbers astronomical (Figure 1). Scale back up again, and even a single deep breath in is likely to net you tens of thousands of particulates, whether pollen, algae, bacteria, heavy metals, dioxin, tobacco smoke, dandruff, comet dust – and maybe even lichen spores. At the scale of the very small, say less than about 25 μm , nothing that goes up really need ever come down again – except of course at the stochastic vagaries of rain, snow or downdraft. As Figure 2 makes clear, a great many lichen propagules must exist in a state, quite literally, of suspended animation, buoyed up and floating in the air with none of the (to us) usual tyrannies of gravity. And that a great many more propagules, though larger, must still buoy easily aloft even on the most gentle breeze. The only trick is to get successfully launched into the great rivers of wind and oceans of air in the first place. More about this in a bit.

The universe as known to us at human scale would seem a strange place indeed were we suddenly to experience it even a few orders of magnitude up or down (Figure 2) – a principle sometimes referred to, at least among the cognoscenti, as scale variance. And yet the macrolichen, for its part, experiences scale variance across as many as four orders of magnitude, that is, as measured from thallus initiation to the reproductively mature thallus. Obviously there must be some notable implications:

- ♦ The precise environmental conditions required at thallus start-up are by no means comparable to those needed for thallus maintenance later in life. In effect, this is the distinction between *potential* habitat and *realized* habitat. The microscale distribution of most macrolichens mirrors their ecological needs at establishment, often having little to do with any ecological limitations at thallus maturity. Failure to properly grasp this fundamental fact of scale-dependency has led to some pretty egregious claims regarding the ability of oldgrowth lichens, for example, to thrive in regenerating clearcuts. Nor should observed discrepancies between potential habitat and realized habitat really surprise us.
- ♦ The kinds of data provided by standard weather measurements are much less directly meaningful to life organized at the scale of microns than to its counterparts several orders of magnitude up. We know that some microscale habitats at arctic latitudes have close functional approximations to microscale habitats much farther south, even at tropical latitudes.
- ♦ The smaller the diaspore, the farther it is likely to travel. Below about 20 μm in diameter – the size of an average cloud droplet – lichen diaspores are for practical purposes “weightless,” that is, they remain suspended in the air indefinitely – or at any rate until carried to Earth by rain. Because weather systems need only about two weeks to circle the earth, it's certain that all lichen propagules – spores, algal cells, and smaller soredia – must also sometimes make it all the way around. On the other hand, the smaller the diaspore, the less likely it will successfully germinate and establish.
- ♦ Given the microscopic size of the distance-adapted lichen propagule (Figure 2), it seems fair to ask how long such a diaspore is likely to remain viable under standard conditions of the Earth's middle to upper atmosphere. In fact desiccation and UV radiation may well limit long distance dispersal in the case of certain cyanolichens of humid, warm-temperate climates; but for a majority epiphytic macrolichens adapted to high-stress conditions common in cool temperate and boreal latitudes, it seems unlikely to be limiting. In any event, the hundreds of thousands to possibly millions of years available for long distance dispersal – i.e., within the life span of a given species – effectively negates this and any other cautionary warnings concerning the improbability of successful circumpolar dispersal by lichen propagules.

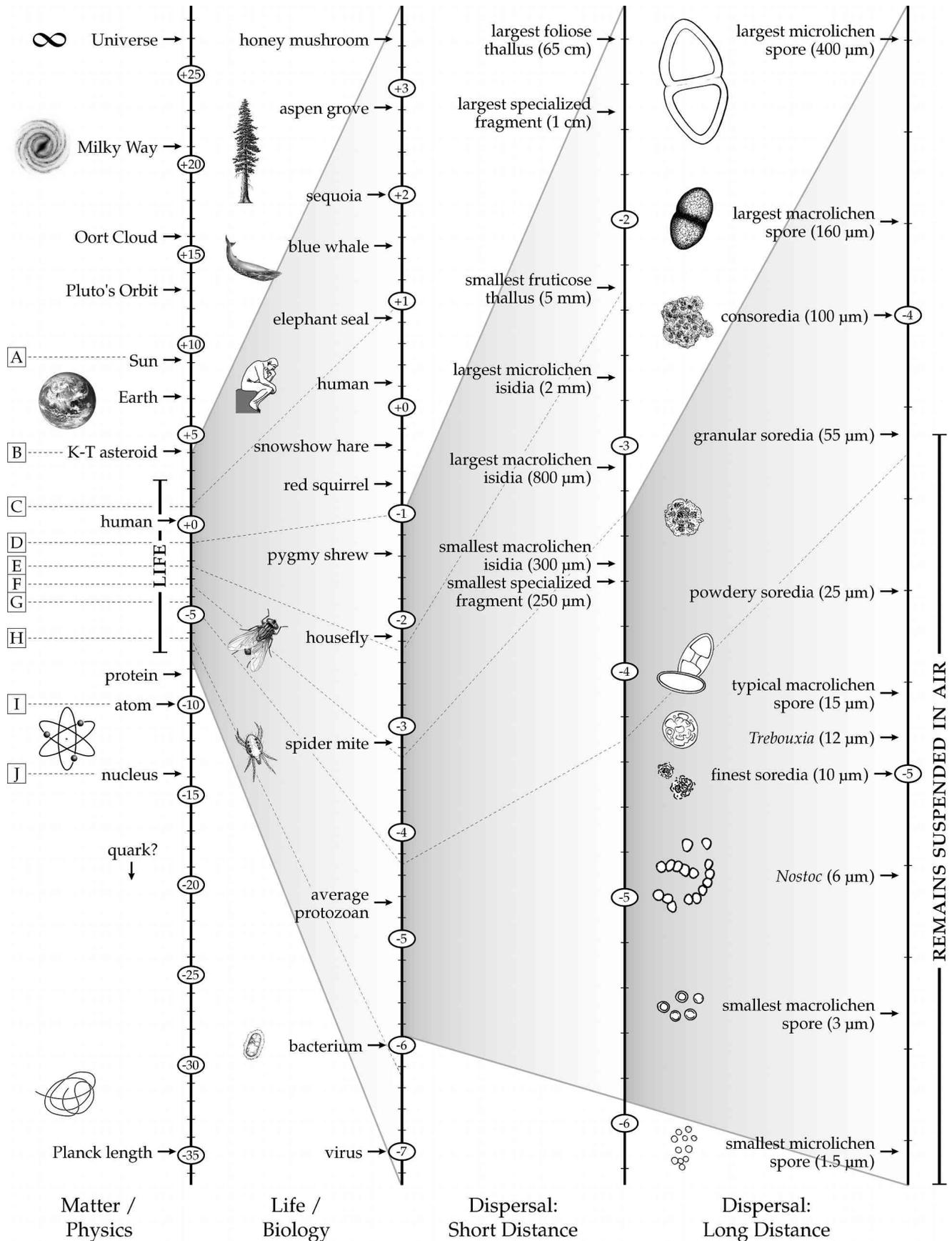


Figure 2. Except when we're seated before a microscope or telescope, the universe comes to us through the narrowest of spatiotemporal openings. True we easily speak of space and time in quantities measured from quarks to light years – our abstract arithmetic thinking makes this trivial – but in so doing we necessarily extrapolate outwards from direct human experience. On the whole our extrapolations work pretty well within a few orders of magnitude of the world as we experience it; but farther out the nature of things warps into unfamiliar relationships as the relative importance of gravity, electromagnetic force, strong force, etc. begins to reconfigure. Notice for instance that even the seeming mathematical certainties concerning the position of the planets and stars blur a few million years out, ultimately becoming probabilistic rather than deterministic. Space itself spans about 60 orders of magnitude from the Planck length ($= 3.6 \times 10^{-36}$ = the scale the scale below which string theory may paradoxically actually invert and behave as though getting bigger instead of smaller) up to the ever-expanding compass of the universe itself. Organismic life, nested within this, occupies roughly 11 orders of magnitude, ranging from a fraction of a micron (bacteria; viruses aren't usually thought of as alive) to tens of hectares, as in the rooting systems of clonal trees like Trembling Aspen (*Populus tremuloides*) or the (no doubt discontinuous) mycelial mats of the Honey Mushroom (*Armillaria ostoyae*). Measured along the time axis, life is bookended at the small end by *biochemical time* (measured in milliseconds or less) and at the large by *geologic time* (measured roughly in millions of years).

Macrolichens are unusual among terrestrial organisms in regularly encompassing up to four orders of magnitude from thallus initiation – a *fully external* process, notice – to full reproductive maturity. During its life cycle it therefore enlarges upwards through a succession of unlike operating environments that affect especially its relation to gravity, electromagnetic force, and surface-to-volume ratio. This in turn creates certain perceptual and conceptual difficulties for the lichenologist who, though operating at roughly five to six orders of magnitude

DISPERSAL VECTORS: LICHENS WITH WINGS

The spores of most lichen fungi launch directly into the air at time of release. A popgun mechanism within the ascus discharges them to distances that, while not impressive in terms of human ballistics – it's measured in millimeters – is nevertheless sufficient to elevate them above the laminar boundary layer and hence into the flow of wind.

Soredia, for their part, have no equivalent launch mechanism. Or rather, soredia have no *built-in* launch

above the lichen diaspore, may nevertheless wish to understand various physical and biochemical processes that taken together form the basis of lichen biology. Unfortunately such difficulties are likely to be most pronounced precisely during the processes of dispersal and establishment, these of course being processes of considerable importance in determining the specifics of lichen distribution at all spatial scales.

Two roughly mutually exclusive modes of lichen dispersal can be inferred from the physical size and structure of lichen dispersal propagules; and each, it would appear, performs a different function with respect to evolutionary fitness. Corticate propagules, including isidia, lobules, spinules and thallus fragments, are seemingly designed for short-range dispersal over distances measured in centimeters to scores of meters. These propagules obviously function in the maintenance of local populations. The other dispersal mode is achieved by spores, algal cells and, probably above all, soredia. Here the primary effect is dispersal over distance, and hence, with luck, the establishment of new populations or else the maintenance of gene flow between already-established populations at remove from one another. Maintenance of gene flow is particularly beneficial from the perspective of the species, since it puts the breaks on speciation, thereby tending to stabilize the species not only over space, but also time.

Points marked A, B, C etc. along the left hand scale bar are the approximate spatial scales at which a person, if expanded or shrunk, would (A) collapse into a black hole, (B) create her own gravity, (C) lose the ability to dissipate heat quickly enough to prevent lethal overheating, (D) survive a long fall, (E) walk on water, (F) stick to a wall, (G) float in air, (H) behave like a gas, (I) occupy multiple locations simultaneously, and (J) feel the strong force on her face. Size is measured as length for life forms but as diameter for heavenly bodies. A quark probably has no size; the size given is the current experimentally determined upper limit in the event that it does. Design by Trevor Goward and Jason Hollinger. Graphics by Jason Hollinger. Spore drawings by Curtis Björk.

mechanism; but this is only because they don't need one. Soredia are made to cling. Any forest bird that comes into contact with soredia is certain to accumulate them over its feet and feathers. When next this same bird takes flight, the drag created in so doing must soon overcome laminar resistance, hence releasing any number of soredia into the high, open air. This process, notice, puts an interesting shine on the lichen soredium, raising the question to what extent its repeated evolution in practically all lichen groups has been abetted by the activities of birds. The modern

distribution of forest lichens must certainly owe its overall shape to their migrations. Roughly put, wind disperses east to west, birds north and south.

LICHEN DISTRIBUTION: RELIC OF THE GEOLOGIC PAST?

There's no point arguing that lichens can't get around – that transcontinental and even transoceanic dispersal is impossible – when we know from the rich macro-lichen floras of far distant oceanic islands that macro-lichens get around very well indeed. Used to be that continental drift – a process whose discernible effects span millions of years – was invoked to explain some of the big-name patterns of modern lichen distribution, captured for example in the terms “Laurasian,” “Gondwanan,” “Madrean-Tethyan,” and so on. The concept of vicariance (disrupted remnant distributions of formerly more continuous ranges) has also loomed large in lichen phytogeography. Both of these approaches draw on the assumption that lichens don't get around very well. And while some modern large-scale distribution patterns – say between the northern and southern hemispheres – must certainly trace back to events in the far geologic past, yet increasingly I find myself coming to the view that the broad shape of lichen distribution as a whole is more felicitously explained in terms of habitat suitability than of geographic isolation imposed by dispersal limitation. Let me tell you one reason why.

Every thousand years or so, an asteroid 50 m across collides with Earth. Smaller impacts happen more often, roughly in inverse proportion to decreasing size. For sheer lichen propagule dispersal capacity, asteroid impacts shouldn't be underestimated. In 1908, a rather smallish asteroid, probably a few tens of metres across, exploded over Tunguska in Siberia, flattening some 80 million trees over a huge area. This single event must have sent trillions of lichen diaspores billowing up into the Earth's atmosphere, great numbers of them circling the planet before being rained out who knows where. Large or even small events of this kind needn't happen very often to effect lichen inoculation over vast spatial scales. An average species is said to persist maybe two million years (lichens probably longer) – an interval sufficiently long to bring about at least a few impact events at the 1 km scale, and hundreds more down to the size of the asteroid responsible for Tunguska. Repeated often enough, such lichen redistributive events might seriously compromise the ability of the lichen phytogeographer to infer, from existing lichen distribution, the geographic origins of most lichen

lineages. On the other hand, this impact approach to lichen dispersal and distribution could help to explain certain modern-day patterns that otherwise stare back at one rather in the manner of a smoking gun. One such pattern is the astonishing 40% overlap between arctic and antarctic lichens. Another is the roughly 20% overlap between the lichens of New Zealand and my own home province, British Columbia. In both cases, what strikes me most forcibly is not the number of lichen species shared between the Earth's antipodes – this is only a record of *successful* long distance inoculation events – rather it's the much greater number of species that by implication must have performed these same voyages, but that failed to establish at the other end – the *failed* long distance inoculation events.

GEOGRAPHIC STRUCTURE IN LICHEN FUNGI AND LICHEN ALGAE

Some of the most compelling work on the molecular nature of lichen distribution – or rather that of its fungal and algal partners – appears in a wonderful PhD thesis by Susanne Altermann. Susi studied the lichen fungus *Letharia lupina* sp. nov. and its algal consort *Trebouxia jamesii* s. lat., these together comprising the coarse, shrubby, isidiate, citron yellow, toxic, epiphytic lichen sometimes called Mountain Wolf. Mountain Wolf (or rather its fungal partner) has yet to be formally described, but occurs both in western North America, where it's widespread and common, and in Europe, where it's otherwise. The American fungal partner resolves into six genetic units (curious in a species that almost never produces viable spores), while its algal consort sorts into nine independent lineages. Figure 3 shows how the algae sort out in space.

Notice how nicely the areas covered by Susi's algal lineages (circles and ellipses) overlap with what's referred to on the map as “Lichen Population Pools” (polygons). I should explain here that these LPPs are part of a lichen mapping exercise I'm involved in. In principle each LPP is supposed to circumscribe a unique, regionally uniform assemblage of macro-lichens. To judge from the considerable correspondence between the algal “principalities” and the LPPs, it seems fair to conclude that their respective geographic extent must in some way be shaped by something like the same set of environmental factors. At first this could seem surprising. After all, individual algal cells experience the world at a spatial scale measured in microns. Why would we expect their macroscale distribution to mesh so well with the kinds

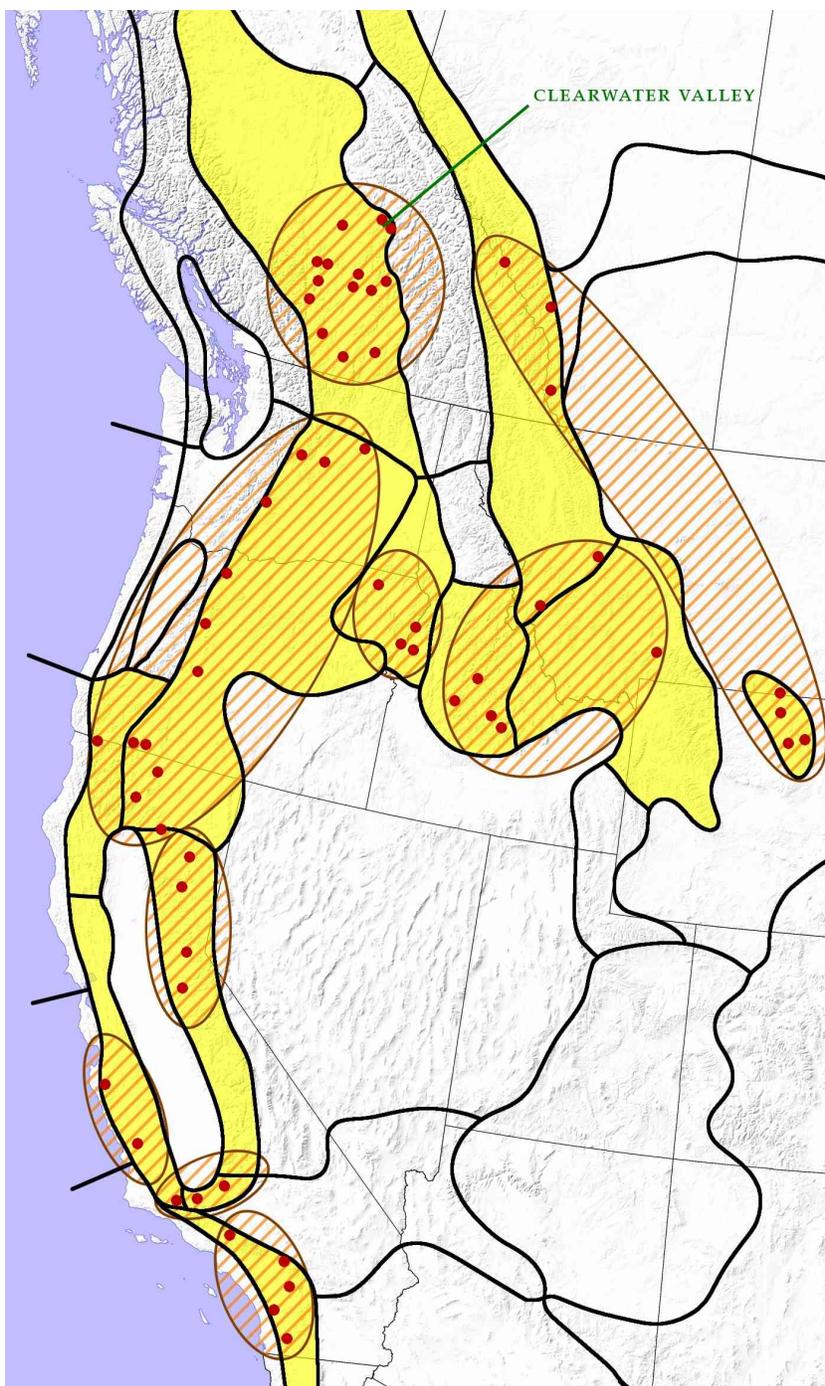


Figure 3. Partial North American distributions for nine algal lineages currently attributed to *Trebouxia jamesii*, based on collections and laboratory work by Susanne Altermann. *Trebouxia jamesii* s. lat. consorts with the lichen fungus *Letharia lupina*, together forming the brightly coloured Mountain Wolf Lichen. Dots mark collecting localities. Each circle or ellipse represents a discrete algal lineage, as shown by molecular markers. The black lines enclose areas understood to support repeating macrolichen assemblages (Lichen Population Pools: LPPs) conceived as topographically variable, but nevertheless taxonomically uniform within each LPP. Note the remarkable level of agreement between each algal lineage and a unique LPP. Coloured LPPs hypothesize full potential distribution area for each algal lineage. The arrow points to the position of the Clearwater Valley, global macrolichen hotspot. Map design by Trevor Goward and Jason Hollinger. Data on distribution of *Trebouxia jamesii* s. lat. derived from Altermann, S. 2009. Geographic structure in a symbiotic mutualism. PhD. Thesis. University of California, Santa Cruz: http://waysofenlichenment.net/ways/resources/susi_alterman_thesis.

of patterns visible to ourselves so many orders of magnitude up? Of course the answer is that LPPs are after all *lichen* distributional units; hence whatever factors control the spatial occurrence of lichen alga are likely also to be reflected, several orders of magnitude up, in the spatial apportioning of the lichens those algae eventually become. Summing up, I guess you could say that Mountain Wolf provides a kind of macroscale window through which we can easily peer, if we wish, into the microscale operating environment of the vanishingly small. Multiply this observation by hundreds of macrolichen species, and you've got yourself a Lichen Population Pool, an LPP.

There's something else worth mentioning, too. The sharply demarcated geographic structure mapped for Mountain Wolf's algal lineages in Figure 3 is nowhere to be found in the distribution of its fungal partner. In fact *Letharia lupina* manifests approximately the same range of genetic structure from one end of its range to the other. Such marked discrepancy in the geographic behaviour of two consorting lichen partners makes it pretty clear they must play very different roles in maintaining the lichen system. To revert to the old agricultural model (Essay 1), we may say of the fungal partner that when viewed at the scale of the lichen thallus it behaves like a true "farmer," always acting in the service of its one and only algal crop; but that when viewed from farther away, at the scale of western North America, it behaves not like a farmer at all, but more like a hunter-gatherer. Apparently the fungus gets around fairly easily throughout its range, no doubt carried here and there by birds. What's fascinating, though, is that the algal lineages, though they too must get carried around (they're encapsulated in the isidia the birds transport) seldom consort with their erstwhile lichen partner once outside their home range. This implies that a newly transported lichen isidium must somehow "relinquish" its former algal partner at time of establishment, taking on a new one more at home in the new environment.

How exactly this might happen, nobody's yet dared to guess. Obviously we're not used to thinking of lichen algae this way, as forming little principalities, I mean. At first view it could seem that each algal lineage must be specially adapted to some overall suite of environmental conditions specific to its particular LPP. But this seems unlikely in the case of a microscopic organism like *Trebouxia*, in which the world is experienced at a scale only microns across. In fact it's frankly impossible that any particular region within the distribution area of Mountain Wolf could uniform-

ly provide conditions conducive only to a particular algal lineage. Something else must be going on, possibly some sort of competitive exclusion mechanism. In this scenario Susi's various algal lineages would sort themselves out spatially according to prevailing conditions during establishment. Once established, however, any given population would effectively prevent encroachment of later-arriving lineages through simple numerical superiority.

POPULATION ESTABLISHMENT AND MAINTENANCE

Population establishment = successful inoculation event + stabilizing mechanisms + time.

The ecological distance between successful inoculation of a single lichen thallus and its eventual establishment as an enduring population is vast. I suppose it must occasionally happen that a population gets established simply because local environmental conditions remain favorable for colonization over long periods. This permits a gradual buildup of population levels until, some magic threshold finally crossed, it becomes proof against the kinds of stochastic attrition peculiar to its habitat. But such lichenological success stories, I'll wager, must be infrequent; and even when an establishment event does seem to play out this way, I'll also wager it's in large part owing to certain invisible "stabilizing mechanisms" operating behind the scenes. Several such mechanisms doubtless exist – ecosystems simply wouldn't be ecosystems in the absence of centripetal forces operating to hold them together – but here I'll focus on only four obvious ones: source populations, host tree specificity, genetic amplification, and the parathallus. As I'll now try to show, most of these mechanisms are inherent in the structure both of the lichen consortium and of the larger ecosystems in which they find themselves embedded.

Source Populations

Have you ever wondered, as I have, what makes some lichen species common at a particular locality, others less so? The answer's not simple, and I don't pretend really to understand it in any detail. But surely in part it has to do with feedback mechanisms operating across spatial scales much larger than any particular patch of forest. Just as weather is mostly about air moving from areas of higher pressure to areas of lower pressure, so lichen frequency (for any given species) is about dispersal from higher density populations outward to populations at relatively lower concentra-

tion. Abstracting a bit, this comes out as a net movement from “source” populations to “sink” populations.

But how do source populations arise in the first place? In a sense this is easy: rates of thallus recruitment exceed, over extended periods, rates of thallus attrition. The kinds of operating environments under which this can occur vary from one lichen species to another, but at a minimum they should entail favorable branch chemistry and lighting in combination with periodic runs of cool, often humid weather. Sink populations, for their part, can form under numerous sets of conditions, for example: (1) not enough diaspores produced to offset background attrition; (2) plenty of propagules, but low establishment rates; (3) plenty of propagules and high rates of establishment to boot, but die-back events at too frequent intervals; (4) insufficient recruitment from nearby source populations; (5) any combination of the above operating at different times and in various complex combinations. Notice that this account of frequency status isn't quite the same thing as saying some species reproduce rapidly, other more slowly; rather, we're allowing for a highly complex sharing around between thallus-rich source populations and surrounding thallus-poor sink populations. The net result is a general trend toward lichen populations much more stable than would be possible in the absence of their periodic recruitment.

Host Tree Specificity

One clearly important promoter of lichen source populations – and hence of population stabilization – is the close association of certain epiphytic macrolichens with one or a small number of host trees or shrubs. Table 2 lists eleven epiphytic macrolichen species that, in the Clearwater Valley, are demonstrably host specific. What is interesting here is: first, that all but one of these lichens are apotheciate, implying a requirement to resynthesize a new thallus at each generation; and second, that the kinds of lichen systems included in this roster are certainly heterogeneous, perhaps sorting into as many as seven functional groups. Three of these groups (designated as groups A, B and C) are tied to members of the Pinaceae, in which bark chemistry and/or texture can be assumed to promote periodic mass establishment of their respective algal partners, and hence to favour thallus initiation from the fungal spore. Groups D and E are linked at establishment to the (mostly young) stems of deciduous shrubs, which they appear for a time to parasitize; see below. Group E consists of two species (one has not yet

been described, hence is excluded in the table) that in both cases are probably parasitic on their respective host shrubs, yet exhibit no signs of such behaviour when colonizing other host species. Finally Ringed Beard (f.p. *Usnea lapponica*), in Group G, appears to arise from some sort of parathallus arrangement, about which more in Essay IX. Notice that all but two of these species are endemic – or essentially endemic in the case of Flattened Thornbush (f.p., *Kaernefeltia merrillii*) – to western North America. Each of these species appears to owe this status to a strict requirement for a specific algal partner which in turn is highly adapted to the bark chemistry and/or textural properties of trees and shrubs likewise endemic to the region. In this view, a great number of the western endemic epiphytic macrolichens of the Clearwater Valley are ultimately restricted to this region in consequence of its specialized arboreal flora; see Table 1. The only seeming exception to this one-alga rule is Flattened Thornbush which, besides varying greatly in appearance from one portion of its range to another, also has a comparatively broad ecological amplitude – indeed, it actually occurs outside of North America in a small portion of Spain.

Two of the lichens in Table 2 – Eyed Chestnut and Mountain Shrublover – are remarkable among epiphytic macrolichens in their ability to withstand prolonged burial by the winter snow. Mountain Shrublover in particular seems actually to *need* prolonged burial under snow; and to be sure, I have seen this species emerging from snow patches in early August! For most lichens, prolonged burial by snow means death, presumably by starvation when the physiologically active fungus runs out of stored sugar (most lichen algae can't photosynthesize in the dark). One possibility is that the lichen fungus takes nourishment from its host shrub, e.g., accounting for Mountain Shrublover's otherwise peculiar fidelity to the bark of huckleberry bushes (*Vaccinium*) at startup. Eyed Chestnut is not quite so host specific, occurring equally on Bog Birch (*Betula glandulosa*) and Soopallie (*Shepherdia canadensis*). One wonders whether this strange occurrence on two unrelated host shrubs may not point to the existence here of two lichens, not one. If so, they will clearly have to be regarded as cryptic species.

The importance of host trees as anchors of epiphytic macrolichen community structure has received little attention. In a sense this is curious. While most other lichen habitats are widely distributed, usually circum-polar, yet many tree species have much smaller, more

FUNCTIONAL GROUP	LICHEN NAME (Essay II)	LICHEN FUNGAL PARTNER	PRIMARY HOST (LOCAL)	SECONDARY HOSTS (LOCAL)
A	Twig Bishop*	<i>"Ahtiana" pallidula</i>	<i>Pseudotsuga menziesii</i>	other conifers
A	Idaho Tatter*	<i>Esslingeriana idahoensis</i>	<i>Pseudotsuga menziesii</i>	other conifers?
A	Forking Bone*	<i>Hypogymnia imshaugii</i>	<i>Pseudotsuga menziesii</i>	other conifers, shrubs
A	Deflated Bone*	<i>Hypogymnia wilfiana</i>	<i>Pseudotsuga menziesii</i>	no
B	Mountain Candlewax*	<i>Ahtiana sphaerosporella</i>	<i>Pinus albicaulis</i>	no
C	Flattened Thornbush*	<i>Kaernefelia merrillii</i>	<i>Pinus contorta</i>	other conifers
C	Brown-eyed Sunshine*	<i>Vulpicida canadensis</i>	<i>Pinus contorta</i>	other conifers
D	Eyed Chestnut	<i>"Cetraria" sepincola</i>	<i>Betula glandulosa</i>	<i>Shepherdia canadensis</i>
E	Mountain Shrublover*	<i>Cetraria subalpina</i>	<i>Vaccinium membranaceum</i>	no
F	Punctured Ribbon	<i>Ramalina dilacerata</i>	<i>Cornus stolonifera</i>	other conifers, shrubs
G	Ringed Beard	<i>Usnea lapponica</i>	<i>Alnus incana</i>	other conifers, shrubs

Table 2. Host specificity among epiphytic macrolichens in the valley of the Clearwater River, south-central British Columbia, arranged by "functional groups". See text for details. Lichens accompanied by an asterisk are endemic to western North America. Trees and shrubs in bold periodically host dense, even-aged populations, or "blooms," of the species indicated (Essay IX). Many of the macrolichens listed here are specific to other host trees elsewhere. All species associate with *Trebouxia*, and with the exception of Ringed Beard all reproduce via fungal spores, hence need to re-instate the lichen thallus at each generation.

region-specific distributions. To me it seems entirely plausible that tree host specificity may eventually be found to enforce distributional patterns at far larger spatial scales than the ones I've outlined here. Taking my cue from the powerful stabilizing effects of source populations, I hereby wonder out loud to what extent the dominance of low pH conifers in cool regions of the northern hemisphere has favoured the evolution of an acidophytic chlorolichen flora (photopartner = alga) – and, conversely, to what opposing extent the general dominance of trees with a higher bark pH in critical portions of the southern hemisphere may have favoured the evolution of a basophytic cyanolichen flora (photopartner = cyanobacteria). Thus, I guess I'm asking whether a key point of distinction between the epiphytic macrolichens of the northern versus the southern hemispheres might not have at its base the global distribution of trees.

Soredia: Algal Gangplanks?

If the thallus can be regarded as the first and defining marvel of the lichen enterprise (Essay VIII), then the soredium is certainly its second and supporting marvel. Soredia have evolved time and again across almost the entire panoply of lichen systems. In Essay X, I argued that soredia arise, day to day, in response to certain kinds of physiological stress within the lichen

thallus – which in the act of becoming they help to resolve. Here I suggest that soredia may further constitute a kind of portal – a gangplank – to what is increasingly being understood as the Noah's ark of the lichen thallus. That the thalli of some sorediate lichens harbor more than one algal lineage – in some cases several – is already well documented. We've also lately become aware that other lichens – Deciduous Pelt (f.p. *Peltigera britannica*) comes to mind: Essay VII – basically "grab" cyanobacteria out of the air, coaxing them into separate colonies that live over the lichen surface.

Within the compass of the lichen thallus, the presence of multiple algal lineages might be expected to increase ecological fitness for the thallus as a whole. One imagines, for instance, how different lineages might come into numerical dominance at different seasons (in response, say, to varying light), thereby bolstering the ability of a thallus to thrive under conditions that might cause a younger, less biodiverse thallus of the same species considerable stress. Seen in this light, soredia might well be said to perform a stabilizing function in the maintenance of older, well established populations. Often it's assumed that whatever level of fungal and algal diversity a lichen encompasses is acquired at the outset; and in the case of non-sorediate species, this may well be so. But it's

hard to believe that soredia, at least in some cases, don't confer an alternate window for increasing intrathalline biodiversity.

The Parathallus (and Other Preassembly Systems)

It's never easy to write convincingly about a phenomenon you haven't seen with your own eyes. This is certainly true of the parathallus, as indeed for the concept of preassembly in general. That said, I've already given my reasons for feeling pretty certain the parathallus must exist; but for convenience here they are again in summary form: (a) lichen establishment is necessarily a two-step process; (b) the vagaries of microclimatic expression exerts continuous adaptive pressure on the establishing lichen consortium to uncouple these steps, permit them to take place over indefinite periods; and (c) evolutionary process is all but infinitely inventive. How all this plays out against a background of lichen dispersal and establishment is, of course, hard to know. Even so, Table 3 summarizes several hypothetical parathallus and other preassembly systems expected eventually to be detected in epiphytic macrolichens. While some such systems seem specially adapted to a short parathallus interval followed by thallus initiation, others – especially some

cyanolichen species – delay thallus initiation by as much as a decade, presumably pending build-up of sufficient carbon to carry it rapidly through to completion.

Note that the parathallus is only one of several non-lichenizing preassembly systems potentially available to the macrolichen fungus. Another possibility is raised in Tables 2 and 3, where Eyed Chestnut and Mountain Shrublover are postulated to enter into an obligate parasitic relationship with their host shrub. Other potential preassembly relationships include saprobism, e.g., involving forest duff, as in Bighorn Pixie (f.p.: *C. cornuta*) or decaying bark and wood, as in Singing Pixie (f.p.: *C. cenotea*), and minerotrophism, involving calcium-rich soil, as in Lesser Rib-pixie (f.p.: *C. cariosa*). In all such cases, the alternate substrate would both physically support the lichen fungus and nutritionally sustain it, i.e., at least until such time as a compatible lichen alga entered the system. In Essay x, I described a somewhat similar preassembly relationship for Fan Pelt (f.p. *Peltigera venosa*).

In principle, parathalli ought to accumulate within a landscape over time, hence we'd expect them to be much more ubiquitous in older ecosystems than in younger counterparts. Should environmental con-

FUNGUS	PRECURSOR TO	DESCRIPTION OF PARATHALLUS AND/OR PREASSEMBLY SYSTEM
<i>Hypogymnia imshaugii</i>	Forking Bone	Bark chemistry promotes patchy establishment of compatible algal partner, hence promoting establishment of lichen fungus, hence favoring establishment of lichen.
<i>Cetraria subalpina</i>	Mountain Shrublover	Obligate juvenile saprobe: invariably absorbs at least some carbohydrates from host shrub during early developmental stages.
<i>Ramalina dilacerata</i>	Punctured Ribbon	Facultative juvenile saprobe: may or may not absorb carbohydrates from host shrub during early developmental stages.
<i>Usnea lapponica</i>	Ringed Beard	Enters into parathallus relationship with compatible lichen alga; forms diffuse but often continuous parathallus; environmental triggers cause rapid upgrade to lichen thallus.
<i>Letharia vulpina</i>	Timber Wolf	Enters into parathallus relationship with compatible lichen alga and/or possibly incompatible unlichenizing alga; environmental triggers may or may not cause upgrade to lichen thallus.
<i>Sticta fuliginosa</i>	Peppered Moon	Enters into parathallus relationship with compatible lichen cyanobacterium; upgrades to lichen thallus only upon acquisition of sufficient stored carbon, often only after many years: Essay IX.
unknown fungi	unknown lichens	additional unknown systems

Table 3. Working behind the scenes. There is growing evidence that lichen fungi at the early establishment phase may enter into any of several categories of temporary and/or possibly permanent nonlichenizing relationships with an assortment of algae, cyanobacteria and, in some cases, lichen substrates, including the living bark of various host shrubs; see also Table 2. The hypothetical cases summarized here are drawn from examples discussed in the present essay, as well as in Essays IX and X.

ditions at some point favor thallus initiation by the partners of a parathallus system already in place and well established, the result is likely to its broad-based and hence comparatively rapid establishment as a viable *lichen* population. Once established as a lichen, various stabilizing mechanisms come into play; and taken together, these bolster its status still further. Seen from this perspective, lichen establishment is rapid because much of the necessary groundwork gets performed behind the scenes, i.e., through the prior establishment of fungal-algal (and other) systems that, besides being easier to start up, are continuously restocked by diaspores blown in from outside the region.

LICHEN POPULATION POOLS (LPPS)

A Lichen Population Pool (LPP) can be defined as a geographically delimited, regionally uniform lichen population visualized across a wide array of repeating landforms, geology and climatic expression (Figure 3). Owing to ecological disconformities at its periphery, LPPs tend more successfully to disperse their constituent lichen species internally within the unit than externally outside of it. At first view a LPP might be regarded as merely a snapshot in time: a temporary species assemblage likely to be significantly altered, e.g., by future climate change. The preassembly theory, however, would dispute this: first, because most lichen species, once established in a given region, are subject to various stabilizing mechanisms that tend to keep them in place; and second, for some arcane theoretical considerations probably better handled in a footnote.*

* Lichens, in common with all other living organisms, occupy n -dimensional ecological space. This being so, it's easy to imagine how some habitats, depending on the spatial scale they're examined at, must constantly come in and out of focus with respect to the establishment capacities of whatever lichen propagules happen to be floating by at any particular time. To put this another way, the specific mix of lichen fungi present within an LPP at time x will be determined (at least probabilistically) by the duration, geographic extent and degree of its ecological "visibility" to potential colonization events. But because this is an n -dimensional function, there's no simple way to predict which LPP ecogeographic elements at time x are most visible to innovative colonization. One thing we can say, I think, is that only a portion of the lichen fungi actually present within a LPP occur in lichen form; the remainder exist only in preassembly form. The point to be made here is that any future lichen "additions" to the lichen flora of any particular LPP are much more likely to be drawn from its extant preassembly pool than from one-time diaspore inoculation events by diaspores derived from outside the LPP. This observation, notice, must apply with much greater predictive force in older ecosystems than in young ones, owing to both the longer time

In principle, most if not all LPPs should include at least a small number of localities with a distinctly elevated level of lichen species richness. Depending on the areal extent of such "hotspots," they may act as a major source population for the ongoing replenishment of surrounding areas less suited the long term maintenance of some elements of the LPP lichen flora. Such hotspots thus help to support regional biodiversity far outside their actual boundaries, hence certainly qualify as areas of high ecosystem value at a regional or even higher level. In British Columbia, the Clearwater Valley clearly represents a major macrolichen hotspot for the Southern Inland LPP.

PREASSEMBLY THEORY

Finally I return to the question I posed in the opening pages of this essay: How on Earth did the Clearwater Valley accumulate, seemingly in short order, the largest macrolichen flora ever documented? My answer, the one I'll now attempt to give, encompasses the several elements of this essay, plus a few more: clean, unpolluted air, fresh off the Pacific; a wild, prominently undisturbed landscape; a presumed continual drizzle of lichen propagules from who knows where; 15 species of host trees; plenty of undisturbed oldgrowth forest around, those ports of entry for prethalli and hence lichen novelty; an ample sprinkling of enrichment nodes; some base-rich dust wafted in from time to time; a stopping place on the great cordilleran migratory flyway; and of course the lichenologist effect: the homely fact that I myself, a lichenologist, happen to live here.

These, I think, are the main elements, presented here as a list of ingredients. And yet I'm bound to say it's not the ingredients *per se* that sustains within the Clearwater Valley a macrolichen flora of world-class proportion. Resident lichenologist aside, the same list of ingredients might be drawn up for any number of places, none of which would ever, I think, yield an assemblage of 370 macrolichens. For that, something else is needed. Happily for this essay, I think I know what that something else is. It's cold air drainage.

It so happens that the eastern flank of the Clearwater Valley levels off near treeline in a broad rolling upland, a plateau. At night, when the wind is still, a dome of cold air builds over the surface of this plateau. Some of this cold air spills off the plateau and collects in the valley below. In my view it's this dependable

spans involved (= more time for parathallus accumulation) and to more diverse opportunities for establishment (= more niches).

nighttime pool of cold air – and more particularly the dews and morning mist it triggers – that nourishes lichen magic in this valley. It prompts the lichen spores and soredia to germinate, primps the lichen algae, sparks thallus initiation. Repeated night after night, year in and year out, it sustains this Guinness book of world lichen floras, the Clearwater Valley.

There's more, much more, I'd like to tell you about the morning mists, the nighttime dew, and how and where the macrolichens sort themselves out in this most licheniferous of valleys I happen to call my home; but alas, I see I've now run out of space. And come to that, I see I'm about to run out of essays, too. Next up, in the closing essay in this series, I hope you'll join me for a good long look at lichen form, or better, its beautiful, its most wonderful dance with lichen function.