Perspectives and comments

This is the twelvth of twelve invited essays by Trevor Goward concerning the lichenized condition.

Twelve readings on the lichen thallus
XII. Formal Propositions

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Figure 1. *Homo sapiens* isn't the only species to come in all shapes and sizes. So does Monk's Hood Lichen (fungal partner: *Hypogymnia physodes*). Lichens "learn" from their environment. The blackened thallus (top left) has learned what to do in case of too much light, while the rather pallid thallus below it what to do in response to too little light: thin its cortex. The top middle thallus is hunkered down for yet another bout of not enough nutrients in support of too much potential for growth, whereas the thallus below knows nothing of such things. Notice how the two thalli at right bear fungal reproductive structures: the top one peppered with pycnidia, the bottom one supporting a curious apothecial "fairy ring"[1]. There was a time when lichenologists paid real attention to such things. Maybe someday they'll do so again. Photo montage by Tim Wheeler.

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[1]The concentric "fairy ring" arrangement of the apothecia points to a brief coming into phase of physiologic "stress" that, rather than triggering soredia production, as is usual for this species, triggered apothecial production instead (for more on phenomena of this kind, see Essay VI). This thallus and the pycnidiate one above it were collected in central Canada (the others came from a small area in intermontane British Columbia); they could represent a separate species characterized, e.g., by the frequent presence of sexual and asexual fungal fruiting structures; but then again maybe not.

Shape. You have your reasons.
Dairyland milk carton (2%).

We who are born into a world brimming with shapely bodies can be forgiven for sometimes forgetting – or perhaps never knowing – that complex organic form, at least on this planet, is a relatively recent innovation.

Physics at the scale of the bacterium or other single-celled organism favours simple geometric shapes: spheres, ovoids, rods, and sometimes squiggles. Only at diameters larger than a few hundred microns do tensions between surface area and volume nudge living systems in the direction of morphologic complexity. Stromatolites aside, complex organic form on Earth had to await the evolution, about a billion years ago, of multicellular life.

Macrolichens illustrate the point nicely. At the scale of their member parts – ovoid algae, filamentous fungi – macrolichens provide a perfect case study in geometric form. View them, however, one level up, at the scale of the lichen thallus itself, and suddenly they rank with the most richly varied of terrestrial life forms.

The lichen thallus has evolved independently on several occasions, possibly seven times, or possibly more times than that (Essay VII). This observation, you'll grant, is bracing. It implies that the lichen thallus has had a really impressive number of runs starting at the beginning and evolving forward to now.

It seems fair to ask what this much-replicated experiment with lichen form, all this formal jiving about has come to. Also, I suppose one might like to know if whatever it's come to has anything interesting to tell us about the creativities, conservatisms and contingencies of evolutionary process. In effect these are the questions I want to consider in this essay which, accordingly, will be dedicated to what the scientist would call *morphology*, from the Greek *morphē*, form, shape.

FORMAL CONSIDERATIONS

Though we in our time, no less than the ancient Greeks in theirs, often use the terms *shape* and *form* as though they were interchangeable, in fact they are not. Shape is what the camera sees: a snapshot taken from a particular vantage at a particular time, the sun's rays slanting in just so. Form, or at any rate living form, is something more abstract and yet at the same time more alive than this, something more in the nature of a verb. Effectively living form is the species perceived at two time scales: first in *organismic time* – the individual at home in its own life history (Figure 1); and second in *evolutionary time* – the individual as participant in the billion-year stage play of life. Both subject areas are, of course, immense, would fill many football stadiums.

Here my approach will be the rather modest one of, first, teasing lichen form into its main "morphogroups" and, second, subjecting these to consideration from an evolutionary perspective. First up, however, I need to construct a few conceptual pathways ahead of the coming discussion. After that I'll briefly introduce various "formal elements" that taken together help make the lichen thallus what it is.

EVOLUTIONARY CONSIDERATIONS

PARTY TRICKS

One of the deep pleasures of biological classification, perhaps its greatest intellectual appeal, is the obvious fact that the people who practice it are really on to something. Inevitable messinesses aside, there really is something in the hierarchic structure of taxonomic classification – species into genera into families into orders and so on up – that answers to something else in the structure of living things. Thanks to Darwin, we can nowadays easily guess what that something must be: evolutionary exclamation marks. Every so often a population throws out a genotype that in its outward expression is so exceedingly well adapted to its time and place as henceforward to change the course of evolution, send it ramifying down some new corridor. The evolution of the eukaryotic cell is one such watershed (Essay VII). The evolution of multicellularity is another, and a very big one at that. But there are plenty of other evolutionary innovations that, though they never caught on in the manner of multicellularity, have nonetheless become embedded, often quite usefully, in a small number of species. Here I'm going to refer to such innovations as *party tricks*.

A party trick, of course, is the one neat thing somebody in the room can do that nobody else can quite manage. Touching one's ear lobe with the tip of one's tongue would be one example, though not a very useful one. In evolutionary terms, a party trick would be any attribute that having once arisen becomes conspicuously embedded in whatever lineage its having arisen occasions. Applied to lichens, it's the salient feature, technically a synapomorphy, that sets one group of lichens apart from its closest relatives. All diagnostic characters we use to tell lichens apart are effectively party tricks; and the higher up the taxonomic hierarchy they extend, the better party tricks they have proved to be. The evolution of the hydrophobic medulla is a good lichen party trick.

PHOTOCELLS

The great divide in lichen morphology is not to be found in the phylogenies of their fungal partners – whether Ascomycetes or Basidiomycetes – but rather in the identity of their photopartners, that is, whether cyanobacterial or algal. Lately it's become clear that lichen cyanobacteria and lichen algae differ markedly in their ability to tolerate high light: cyanobacteria do, algae don't. Now at first this could seem odd since of course it's the chlorolichen, not the cyanolichen, that we usually associate with open, sunlit places. But then that's precisely the point: to exist at all, algal-containing lichens had to evolve an array of light-quenching cortical pigments; and it's these that have subsequently led the chlorolichen out of the shadows and into the light. Cyanobacterial lichens, while adapted from the get-go for high light, nevertheless tolerate low light too. What's more, they also need liquid wetting ; so while chlorolichens function well on dew and even high atmospheric humidity, cyanobacterial lichens need to be thoroughly wetted and need to stay wet much longer than chlorolichens do; so it's this special requirement for water, not sensitivity to light, that prevents them from venturing out into open places where water evaporates too quickly. Some ecophysiologists suspect, and why not, that the thickish thalli of most cyanobacterial lichens are a special adaptation for retaining moisture.

Unfortunately these and other recent breakthroughs in our understanding of lichen photopartners haven't yet found their way into standard lichenological terminology. This makes it hard to talk on the subject without having to wave the arms around. Figure 2 points out some of the remaining terminological holes and makes some suggestions for filling them.

1a Thallus tri-partite (consisting of a fungus, a green alga and a cyanobacterium); cephalodia present ... **CEPHALOLICHENS*[1]** ...2
  2a Thallus entirely crustose ...Crustose cephalolichens (e.g., Almond Lichens [f.p.: *Amygdalaria*]).
  2b Thallus entirely foliose ...Foliose cephalolichens (e.g., Owl Lichens [f.p.: *Solorina*])
  2c Thallus fruticose, but arising from crustose, squamulose or rarely foliose basal portions ...Fruticose cephalolichens (e.g., Matchstick Lichens [f.p.: *Pilophorus*])
1b Thallus strictly bi-partite (consisting of a lichenized fungus and a lichenized green alga[2] or cyanobacterium but not both); cephalodia absent ...3
  3a Photopartner algal ...**CHLOROLICHENS**
  3b Photopartner cyanobacterial ...(**CYANOBACTERIAL LICHENS**) ...4
    4a Thallus stratified, white within ...**CYANOLICHENS**
    4b Thallus unstratified, dark throughout ...**HOMEOLICHENS***[3]

[1]In some cephalolichens, the fungal partner and the cephalodial cyanopartner sometimes form

independent, free-growing thalli. Such lichen consortia in effect consist of two lichens – one a cephalolichen, the other a cyanolichen – and are said to represent a **PHOTOMORPH PAIR**. Each member of which can be referred to as a **PHOTOSYMBIODEME** or, more specifically, as a **CHLOROMORPH/CYANOMORPH**, depending on the identity of the dominant photopartner**.** Lichen species that produce photomorph pairs can be termed **AMBILICHENS* -** a term applicable also at the genus level in the case e.g., of the Pelt Lichens (f.p.: *Peltigera*) which contain both cyanolichens and cephalolichens.

[2]In addition, a few crustose chlorolichens have photocells belonging to the yellow algae (*Heterococcus*) and brown algae (*Petroderma*) (Thüs et al. 2011: 399-415; Saunders et al. 2004: 511-522).

[3] Compare *homeostasis*, *homeotypic*. The terms *homoeolichens* and *homoiolichens* are etymologically acceptable alternatives, but less economic. Homeolichens are often described as *gelatinous* and may hence be informally termed *gel lichens*; see Tables 1, 2 and 3.

Figure 2. Towards a rationalized terminology for lichen functional groups emphasizing photocell identity and thallus organization. Terms accompanied by an asterisk are here proposed for the first time. Note that the terms *chlorolichen*, *cyanolichen* and *homeolichen* can be made more precise by specifying photopartner identity, e.g., *Chroococcalean cyanolichens*, *Trentepohlian* (or *Ulvophycean*) *chlorolichens*, etc. Genus names given here are those of the fungal partner alone.

CONSTRAINTS ON LICHEN FORM

Lichen thalli are organized around the need to display their photopartners to optimum photoenergetic advantage. This the lichen accomplishes – as most plants do, but very few animals – by arranging their photocells in little solar panels. This imposes certain constraints on thallus morphology, since much of the thallus area need to be accessible to light. Essentially the forms of lichens mirror those of plants, including graminoids, succulents and trees. However, the crustose growth form of lichens has no direct analogue in plants.

ELEMENTS OF FORM

MACROLICHENS, MESOLICHENS, MICROLICHENS

An obvious feature of the lichen thallus is its tremendous range in size, which can vary from species to species by roughly four orders of magnitude. How do we account for this? My guess – only that – is that the actively growing portions of the lichen thallus always operate within a specific ratio of surface area to volume. Surface area, recall, increases as the square, while volume increases as the cube. As the upper limits of the species-specific ratio are approached, the system would begin to withdraw available nutrients – carbon, nitrogen, phosphorus, etc. – and shunt them to thallus portions closer the low end of the range. In this view each lichen system comes with its own internal bias setting, specifying those thallus dimensions optimally suited to its particular portion of ecological – and vegetational – space. Something like that.

Reflecting this, it's helpful to arrange lichens – especially non-crustose lichens – into two size classes: mesolichens if they're small and macrolichens if they're larger. Setting the dividing line between these size classes at about 1 cm (as a measurement of maximum lobe or stem length) apparently corresponds with some real break point in the lichen architecture. At a guess, I'd say this must be the point below which passive diffusion plays a prominent role in lichen physiology, and above which some sort of definite transport system is needed for moving moisture and nutrients around. In this view the macrolichen would be characterized as a lichen that has evolved the capacity for an internal transport systems, whereas the mesolichen has not.

When I was in grade school, I remember learning that lichens don't have vascular systems, only plants and people do. I suppose this hinges on what is meant by "vascular". To me it seems clear that macrolichens could never have evolved complex form except by dint of having at least the equivalent of a vascular system. Likely candidates for lichen vasculature aren't hard to find. The veins of Pelt Lichens (f.p.: *Peltigera*), the reticulum of Lung Lichens, the brittle podetial walls of the Pixies (f.p.: *Cladonia*), the internal cartilaginous strands of Wolf Lichens or Beard Lichens (f.p.: *Letharia*, *Usnea*, respectively), the folds and plates in the lower surface of some Rocktripes and Wrinkle Lichens (f.p.: *Umbilicaria*, *Tuckermannopsis*), the lengthwise cortical tissues of the Centipede and some Rosette Lichens (f.p.: *Heterodermia, Physcia*): all of these structures, I'll wager, represent special accommodations for nutrient transport. More than that, they surely arise in the very act of being travelled along.

Consistent with this, it's worth noting that macrolichens grow, almost without exception, in places where there's plenty of moisture, even if only in the form of dewfall, and at least during critical times of the year when air temperatures are sufficiently cool to permit carbon fixation above carbon use or drawdown (Essay X). Mesolichen distribution, by contrast, is more hit and miss; but on average these species are characteristic of places where moisture is limiting – either because of too rapid evaporation, or because there's precious little moisture to evaporate in the first place. Their diminutive size probably allows them to get by without a well developed internal nutrient transport system, and this in turn caps maximum size, and so round and round.

WHY ARE SOME LICHENS SO VARIABLE, OTHERS NOT?

MODULARITY

To answer this question one needs to know a little about how lichens grow. Thallus development in most macrolichens and some mesolichens generally takes place in vaguely modular fashion, that is, through serial development and sometimes accumulation of one or a few repeating morphological units. Depending on the lichen species in question, the modules sooner (usually) or later lose their identity into the larger thallus system. In some lichens, however, the module closest to the general axis of growth generally takes over as the lobe tip, hence giving rise to elongate lobes. Rosette lichens are what result when this process operates more or less to the exclusion of secondary lobes. An interesting case is the Umbilicose growth form which, because the thallus grows outwards from the thallus centre rather than from the margins, seems not to have evolved modular growth. Scale Lichens have a colonial lifestyle (see below), and appear to shunt surplus carbon below ground; for this reason they either haven't evolved modular growth (e.g., the Groundscales (f.p.: *Psora*) or, as in many Pixie Lichens, often suppress it.

Repeating modular grows usually leads simply to an enlarging thallus, though in a few genera there's a definite "upgrade" to novel functional parts, albeit mostly not specifically thalline..
Of these, the Foam Lichens (f.p.: *Stereocaulon*) and some Pixie Lichens (*Cladonia*) with their shrubby habit and "leafy" stems are certainly the most familiar examples. The Thornbushes (f.p.: "*Dendriscocaulon*") also belong here. These are fruticose cyanolichens that start out as branching chlorophyllous shrubs with a dense "foliage" of granular isidia. In time, however, the branches lose their capacity for photosynthesis and become transformed into supporting stems and, in some cases, "trunks," hence calling to mind little oak trees.

DIFFERENTIAL GAS EXCHANGE

Differential gas exchange plays, I believe, a major role in determining the fine and sometimes coarse details of thallus form. Basically the idea is that increased gas exchange can accelerate thallus growth, while decreased gas exchange has the opposite effect. Elsewhere I called attention to the distinction between cortical macrovents or microvents (Essay X). Species endowed with microvents – Ruffle Lichens (f.p.: *Parmotrema*) and such – tend not to vary greatly in thallus form. By contrast species with macrovents – pseudocyphellae – sometimes do vary greatly and sometimes don't. Those that do tend to have what might be called "discretionary venting" in the sense that the vents are produced according to need, and can vary from absent to copious and from localized to widely scattered. Herein lies the difference, I believe, between the tremendous morphological diversity in Ragbag Lichen (f.p.: *Platismatia glauca*) compared with that in other members of its genus. Only in the well named Ragbag does the presence of discretionary venting make possible a varied and creative response to environmental perturbation.

ACCESSORY FEATURES

Other major contributors to thallus variation take the form of soredia, isidia, lobules, cilia and so forth – what I call "accessory features" (Essay X). Most lichens we'd wish to call "elegant" either lack accessory features or else acquire them late in development. To put this the other way round, the initiation of an accessory feature often seems to "deform" thallus growth. Or rather, lichen growth is more or less regular until the onset of physiologic imbalance within the system triggers a response – usually in the form of some accessory feature – that in effect activates a new lichen subsystem, and so sends the lichen, or a particular portion of it, into a new relation between carbon assimilation and thallus growth. This has the effect of creating thallus morphologies often at considerable variance from the strict specifications of the species blueprint.

ECOPHENOTYPIC CONVERGENCE AND DIVERGENCE

Lichens collected in one climatic region are often strikingly different from the same species collected elsewhere. In general terms the forces at work here directly relate to the lichen's rather unusual lifestyle. Animals respond to environmental adversity by moving elsewhere, plants are buffered by their root systems, bryophytes form dense colonies, mushrooms are evanescent. By contrast, most lichens are sessile, unrooted, non-colonial and perennial, hence such strategies are unavailable to them. Their most effective line of response to environmental perturbation is to modify their outward morphology in accordance. In a sense you might almost say that lichens, macrolichens in particular, are biology's answer to the snow crystal, each thallus recording a unique set of environmental input, no two thalli are exactly alike.

I think it's a safe bet that habitat-induced variation in lichen form generally trumps genotypically induced variation. A lichen is of course the outward manifestation of a *relationship* between two or more unrelated organisms; and though some variation in the genetic make-up of the partners is certainly tolerated – and even necessary for the purposes of evolution – yet too much fiddling around is likely to be detrimental to the relationship (Essay VIII). So far as I know, no similar strictures apply to lichen morphological response.

If macrolichen and mesolichen morphology is even half as responsive to environmental input as I'm suggesting, then lichen taxonomists have a problem. Just as similar environments can draw related lichens out to similar outward appearance, so dissimilar sets of conditions can have the opposite effect, tending to dissimilarity. Taken together these phenomena – ecophenotypic convergence and divergence respectively – raise an interesting question: How do we tell what a lichen "really" looks like? Put it this way: Do two related species look like what they look like when grown under similar conditions (convergence), or do they rather look like what they look like when grown under dissimilar conditions (divergence)? Of course there's no real answer to either question; or if there were, then it could only be that lichens, some more than others, look like where they grow.

Prior to the introduction of molecular systematics, lichenologists often classified such taxa as subspecies or varieties, the assumption being that their points of similarity in areas of overlap was a sure sign of introgression of one kind or another. Many plants and animals work this way, so why not lichens? Inward- Looking Rosette and Outward-Looking Rosette (f.p.: *Physcia aipolia* and *P. alnophila*) were for a long time classified as varieties, the latter placed within the former; yet under molecular scrutiny they proved to be distinct species – just hard to tell apart where their ranges overlap. Lately we've been hearing quite a lot about *cryptic species*. Quite probably ecophenotypic convergence is part of the reason. Such problems are inherent in the nature of the lichen thallus.

SO HOW *DO* LICHENS ACHIEVE SPECIFIC FORM ANYHOW?

At one level the answer to this question seems obvious: the lichen fungus simply "knits" itself a lichen thallus much the way certain people knit beautiful sweaters of intricate design, that is, by following a pattern, here a genetic blueprint. But of course it's not that simple. Every detail of lichen growth needs to be coordinated between the lichen fungus and an algal colony consisting of thousands of cells, each one needing to behave in just such and such a way at just such and such a time. How coordination at this level is managed isn't yet known. One possibility – only that – is that lichen form is the outward manifestation of a cunningly choreographed dance routine in which nutrients and the differential potential for gas exchange move around within the thallus according to need. Differential rates of gas exchange can surely be easily moderated by effecting small variations in cortical thickness, compaction, porosity, etc. It may be something like this process that enables a thallus to accentuate coordinated growth in one portion while at the same time suppressing it in another. If so, then it's not hard to imagine how a lichen species might arrive at its characteristic form by, in a sense, "choreographing" a specific cortical development. There are of course other ways of thinking about this problem...

LICHEN MORPHOGROUPS

CRUSTOSE, FOLIOSE, FRUTICOSE

I've already given one man's take – that would be my own – on the question of mesolichens and macrolichens: what I think they're about, and what we might make of them. Now for a few words on the time-honoured *crustose – foliose - fruticose* classification of Erik Acharius.

Crustose lichens are not only ubiquitous and exceedingly numerous – three of every five lichen species in the world today are crustose lichens – they're also without doubt the original lichen growth form. It's not hard to guess their main evolutionary advantage. Being specially adapted to habitats where almost nothing else can grow has allowed them to evolve and trace their slow designs almost without impediment. Nobody knows how long crustose lichens have been around, but certainly it's in the many hundreds of millions of years: long enough, at any rate, to acquire a definite knack for living exclusively within the unventilated, thermally extreme boundary layer that covers the surface of all things.

Competition among crustose lichens being what it is, eventually some lichen somewhere must have "learned" that it could get a leg up on evolutionary persistence simply by rising a little above the surface of things, particularly other lichens, which it could then happily overgrow. The first lichen to adopt such an upside-downside form will effectively have invented lichen dorsiventrality. It's doubtful that such a lichen would have resembled a modern **foliose lichen** with all the usual accessory bells and whistles; probably it was more some placodioid crust tending, like Oopsy Daisy (f.p.: *Lobothallia alphoplaca*), toward thallus lift-off. Now two suppositions. The first supposition is that lichen dorsiventrality can have arisen only in places where rates of carbon fixation were consistently in excess of rates of carbon drawdown (Essay X); only in such places would it be possible to put that extra carbon to good use, come the right genotype, elevating the lichen thallus off its substrate, probably rock. The second supposition is that dorsiventrality, at least to begin with, is a by-product of top-down lighting. To me this seems a sound supposition for the very good reason that the lichen thallus is, as I say, really just a solar panel designed for optimum display of the lichen photocells within: no point displaying it suboptimally.

Not everywhere, however, does the sun's light reach the lichen surface in a steady stream from above. I suppose there have always been cloudy regions, foggy places, lands of mist and diffuse, scattered light. Here the sun's light arrives scattered, comes in at all angles. Such places, I suggest, if combined with excess carbon, would have been ideal venues for the evolution of **fruticose lichens**. In fruticose lichens the photocells are arranged radially around a stem or branch. Once the fruticose growth form gets going, the lichens that embody it can always find plenty of good selective reasons – physiological, reproductive, competitive – to elevate still more off the substrate; my only point is that in the beginning, to start things off, there must have been some other context for upward mobility. I believe scattered light to be as good as any, and perhaps better than most.

CUTTING THE LICHEN THALLUS ALONG ITS MORPHOLOGICAL JOINTS

The three lichen life forms bequeathed by Acharius have served us well as far as they go; but for present purposes they don't go far enough. It's not by abstracting lichen morphology to its broadest possible generalities that we gain insight into the workings of form. Instead it's by teasing lichen form apart, searching around for whatever repeating patterns are there to be found. The work of the taxonomist, so it has been said, is ultimately to carve up the living world along its evolutionary joints. This of course is true, but the point needs to be made that form doesn't always carve nicely along those self-same joints; sometimes the ecologically most meaningful groupings are simply where you find them. Clearly this doesn't make the study of morphology "unscientific," rather it reflects the obvious fact that form is as much about ecological context, in this case pertaining to the whole lichen, as it is about phylogenetic history, here pertaining only to the fungal consort. Lichen formal groupings are often by nature "multicultural" to an extent that lichen fungal phylogenies can never be. Except of course in cases of lateral gene transfer.

So now let's embark on an exercise in pattern seeking with a view to creating a rational system of lichen morphological groupings. Since my focus in these essays is on non-crustose lichens, we'll begin by assembling a list of all mesolichen and macrolichen genera so far reported from extra-tropical North America (our "study area").[2] Next we need to assess the genera – about 190 of them – for things like habit, size class, photocell identity, colour, internal structure, habitat and range. That done, the next step is to hunt around for any obvious morphological discontinuities, since it's here that we'll make our cuts. At this point we're presented with a decision. Do we insist that all morphogroups be defined strictly on thallus *form*? Or can we allow that from an ecological perspective, thallus form occasionally gets overridden by other thallus traits – cortical sunscreen for one, internal structure for another – not strictly speaking morphological? Maybe we need a system that incorporates both ways of thinking.

In the event our pattern-seeking exercise yielded more morphogroups that you might expect: 15 when the cuts are coarse, or 25 when they're made a little finer. For present purposes I've opted to go with 15 groups, since dealing with 25 morphogroups is just a bit too unwieldy. The remaining ten fine-scale morphogroups can be referred to as "subgroups"; see below. In Table 1, you'll see that only 11 of the 15 morphogroups are *morpho*groups in the strict sense; the remaining ones – Gel Lichens, Leather Lichens, Fire Lichens, Pixie Lichens – are defined, as already mentioned, on *functional* characters, as these seem a better fit with their respective ecological strategies. For purposes of analysis, however, I've made sure that the genera from each of these functional groups gets listed as appropriate in the eleven "true" morphogroups.

[2]Table 3 summarizes these genera. Note that the crustose genera, which fall outside the scope of these essays, are placed in a single group, the *Crust Lichens*. Call it a weakness.

Table 1. Fifteen lichen morphogroups in extra-tropical North America, including four functional groups (grey) and 11 groups defined strictly on morphological characters. The term *functional group* here refers to genera that respond to environmental stress in ways not expressed in outward thallus morphology *per se*; rather they are united by a common life strategy involving cortical pigmentation, internal anatomy, or handling of carbon. Macrolichens (macros) exceed 1 cm in longest dimension of the lobes or branches, while mesolichens (mesos) are 1 cm or less. Microlichens (micros) are equivalent to crustose lichens and, with the exception of the Dust Lichen category, are subdivided into morphogroups. For additional details, see Tables 2 and 3.

MORPHO-GROUPS	LIFEFORM	PLAN	CHARACTERIZATION
GELS	**Gelatinose** (mesos & macros)	various, but in the strict sense dorsiventral	dark, with dark mucella in place of white medulla; cyanobacterial
LEATHERS	**Foliose** (macros)	various	dark, white medulla present; algal

FIRES	**Igneose** (mesos & macros)	various	brilliant yellows, oranges; medulla white or coloured; algal
DUSTS	**Leprose** (micros)	2-dimensional	really crustose, but composed entirely of soredia
CRUSTS	**Crustose** (micros)	2-dimensional	various (not further elaborated); algal
SCALES	**Squamulose** (mesos)	dorsiventral	small overlapping scales, colonial; algal or cyanobacterial
NAVELS	**Umbilicose** (mesos & macros)	dorsiventral	attached by enlarged central holdfast; medulla present or absent; algal or cyanobacterial
LEAFS	**Foliose** (mesos & macros)	dorsiventral	pale, narrow to broadly lobed; medulla thick; attached by rhizines, basally attached, or loose; algal
MANTLES	**Foliose** (macros)	dorsiventral	pale or dark, broadly lobed; medulla present; loosely attached; cyanobacterial,
SUEDES	**Foliose** (mesos & macros)	dorsiventral	dark; mostly narrow-lobed; closely attached; medulla thin; often with hypothallus; cyanobacterial
STICKPINS	**Fruticose & Crustose or Squamulose** (mesos & macros)	2-dimensional, dorsiventral & 3-dimensional	basal thallus ever-present, supporting scattered, essentially unbranched, solid vertical stems; algal
PIXIES	**Fruticose & Squamulose** (mesos & macros)	dorsiventral & 3-dimensional	basal scales present at least when young, usually supporting hollow, unbranched or branched vertical stems; algal
SCRUBS	**Fruticose** (mesos & macros)	3-dimensional	basal thallus lacking or very evanescent; consisting of coarse branched or unbranched stems or stubs; algal or cyanobacterial
HAIRS	**Fruticose** (macros)	3-dimensional	basal thallus lacking or very evanescent; consisting of fine, hair-like, branching branches; medulla present; algal
SHAGS	**Fruticose** (mesos)	3-dimensional	branches fine, thallus structure formed around internal photocells; no medulla

SEVEN ORIGINS OF THE LICHEN THALLUS?

The lichen thallus has evolved independently several times, here let's say seven (Essay VII). Most of these "independent" lineages really do *feel* different from the others. The Lecanorolichens are masters of morphological complexity. The Arthoniolichens consort almost exclusively with *Trentepohlia* and, at least in the case of the non-crustose species, grow in foggy places. The Lichinolichens consort with a wide assortment of cyanobacterial genera and grow mostly on rock and soil. The Eurotiolichens consort with numerous algal photopartners and have dot-like perithecia in place of apothecial disks; most grow on rock. The Dothideolichens also have perithecia and grow in unusual habitats. This leaves only the Candelariolichens which in every regard except fungal phylogeny closely resemble the Lecanorolichens. More about that in a moment.

As you'll notice in Table 2, each of the seven lineages divides up among the micros, mesos and macros in quite different ways. The Lecanorolichens are well distributed throughout, while the next most diverse group, the Lichinolichens, consist mostly of micros and mesos. The Arthoniolichens are overwhelmingly represented by mesos, but rather remarkably include a few well developed macros too. The remaining lineages are weighted heavily at the meso and especially micro end of the scale. To summarize: it's clear that evolutionary process, viewed from the perspective of thallus "size," has intersected with each of these lineages very differently.

Table 2. Thallus size class distribution in 4521 extra-tropical North American lichens arranged according to seven phylogenetic lineages assumed to represent an independent origin of the lichen thallus (Essay VII). Macrolichens are defined here as foliose or fruticose species in which the longest lobes or stems exceed 1 cm; mesolichens contain squamulose, foliose or fruticose thalli smaller than this. Microlichens are equivalent to crustose lichens. Cyanobacterial lichens are placed exclusively among the mesolichens and macrolichens; no cyanolichens are considered to be truly crustose. Genera containing species in two size classes are counted twice for completeness. Owing to phylogenetic uncertainty, 117 species in 15 genera had to be excluded from consideration. Data summary: Jason Hollinger. Data source: Esslinger 2011: (http://www.ndsu.edu/pubweb/~esslinge/chcklst/chcklst7.htm).

	MACROLICHENS (> 1 cm long)		**MESOLICHENS (< 1 cm long)**		**MICROLICHENS (= Crust Lichens)**	
	genera	**species**	**genera**	**species**	**genera**	**species**
Lecanorolichens	102	1106	43	271	221	2158
Arthoniolichens	4	8	1	1	26	243
Basidiolichens	0	0	2	5	2	8
Candelariolichens	0	0	1	2	3	34
Dothideolichens	0	0	2	2	16	81
Eurotiolichens	1	22	6	44	25	277
Lichinolichens	1	2	28	113	0	0
unplaced	0	0	0	0	29	144

Table 3 is an exercise in "what if". What if the lichen thallus really does trace back to seven independent origins? How do our 15 morphogroups sort out? Obviously there are no unequivocal answers here; but at least the patterns are suggestive. As Table 3 is necessarily a rather large and cumbersome one, I'll now briefly summarize some of the highlights.

- Only the Lecanorolichens have representation in all 15 morphogroups. The Lichinolichens and Arthoniolichens are represented in seven morphogroups, the Eurotiolichens in five, the Basidiolichens in three, and the Candelariolichens and Dothideolichens in two. Our seven lichens lineages thus exhibit an enormous range of repeating morphologic variation, with the Lecanorolichens standing out as exemplar.
- Only the Crust Lichens are represented in all seven lineages. The Scales are represented in five lineages, the Scrubs in four, the Fires, Navels and Shags in three, the Dusts, Leafs, Stickpins and Gels in two, and the Leathers, Mantles, Suedes, Pixies and Hairs are in one lineage each. Viewed this way, it's possible to discern a very general trend from higher lineage overlap among the structurally simple morphogroups to a lower overlap in the structurally more complex morphogroups.
- The primary nodes of morphological plasticity include the Gels (sensu lato, see Table 1), the Scrubs and to a lesser extent the Hairs. Taken together these encompass roughly half of all genera belonging to two or more morphogroups.
- Cyanobacterial lichens and chlorolichens are fairly evenly represented, with representation in 10 lineages in the first, and 14 in the second.
- Forty macrolichen and mesolichen genera span more than one morphogroup and hence effectively challenge the current classification.

Table 3. Morphogroup distribution in about 500 extra-tropical North American lichen genera across seven phylogenetic lineages hypothesized to represent independent origins of the lichen thallus (Essay VII). Four functionally based morphogroups are marked with a triple exclamation mark; see Table 1 for more detail. All genera included in these groups appear also in the remaining 11 "true" morphogroups, as appropriate. Note that Gel Lichens in the strict sense include only foliose homiomerous lichens, which thus appear only here. Genera accompanied by an asterisk include species in other morphogroups, while genera appearing in parentheses link back to the asterisked genera. A question mark indicates uncertainty around phylogenetic placement. Lichenicolous fungi are excluded. Genus names refer to the fungal partner only. Other conventions as noted.

↓ MORPHOGROUPS		
	↓ PUTATIVE INDEPENDENT ORIGINS OF THE LICHEN THALLUS	
	↓ 1: **Lecanorolichens**: e.g., *Parmelia*, *Peltigera*, *Xanthoria* and many others.	
		↓ 2-7: other putative origins
		2: Arthoniolichens: *Arthonia*, *Opegrapha*, *Bactrospora* and others. **3: Basidiolichens**: *Dictyonema*, *Lichenomphalia*, *Multiclavula*. **4: Candelariolichens**: *Candelaria*, *Candelariella.* **5: Dothideolichens**: *Arthopyrenia*, *Mycoporum*, *Trypethelium* and others. **6: Eurotiolichens**: *Catapyrenium*, *Pyrenula*, *Verrucaria* and others. **7: Lichinolichens**: *Lempholemma*, *Lichinella*, *Peltula* and others.
!!!**GELS:** Unstratified **cyanolichens**: white medulla lacking, i.e., dark on the outside and within (strictly speaking foliose, but more generally speaking also semi-crustose, squamulose, umbilicose, and fruticose, but not "shaggy" → SHAGS).		
	1: ***Collema***, ***Hydrothyria***, ***Leptochidium*****, ***Leptogidium***, ***Leptogium*****, ***Polychidium***, ***Santessoniella***, ***Spilonema***, ***Spilonemella.***	
		7: ***Anema***, ***Cryptothele***, ***Digitothyrea***, ***Euopsis*****, ***Gloeoheppia*****, ***Harpidium***, **(*Heppia*)**, ***Lemmopsis*****, ***Lempholemma*****, **(*Lichinella*)**, ***Lichinodium***, ***Paulia***, ***Peccania*****, ***Phloeopeccania*****, **(*Phylliscum*)**, ***Poroscyphus***, ***Pseudopeltula***, ***Psorotrichia***, ***Pterigiopsis***, ***Pyrenopsis*****, ***Stromatella***, ***Synalissa*****, ***Thallinocarpon***, ***Thelignya***, ***Thyrea***.
!!!**LEATHERS:** Stratified chlorolichens with flattened brown to black lobes, shiny toward the tips, and a white medulla (foliose but not umbilicose → NAVEL).		
	1: *Allantoparmelia*, (*Brodoa*), *Cetraria*, *Cornicularia**, *Kaernefeltia**, *Masonhalea*, *Melanelia*, *Melanelixia*, *Melanohalea*, *Neofuscelia*, (*Phaeophyscia*), (*Pseudephebe*), *Tuckermanella*, *Tuckermannopsis.*	
		None.
!!!**FIRES:** Igneose chlorolichens: brilliant orange or yellow in thalline portions (crustose, squamulose, umbilicose, foliose, fruticose).		
	1: (*Acarospora*), (*Arthrorhaphis*), (*Calicium*), (*Caloplaca*), *Candelina*, *Catolechia*, (*Chaenotheca*), (*Cyphelium*), *Edrudia*, *Fulgensia*, (*Ionaspis*), (*Lasallia*), (*Lecidea*), *Letharia*, *Pleopsidium*, (*Porpidia*), (*Psilolechia*), (*Rhizocarpon*), *Teloschistes*, *Tremolecia*, *Vulpicida*, *Xanthoria**.	
		2: see Dusts: *Chrysothrix.*
		4: *Candelaria*, *Candelariella.*
DUSTS: Leprose and continuously sorediate crustose chlorolichens & **cyanolichens**: more or less entirely covered in soredia; apothecia lacking or rare.		
	1: *Botryolepraria*, (?*Chaenotheca*), (***Fuscopannaria***), (*Lecanora*), *Lepraria*, (*Psilolechia*).	
		2: *Chrysothrix*.*
CRUSTS: Crustose chlorolichens: intimately attached, sometimes with elongate lobes.		
	1: *Absconditella*, *Acanthothecis*, *Adelolecia*, *Agyrium*, *Amandinea*, *Amygdalaria*, etc. See also Flames: *Acarospora*, *Arthrorhaphis*, *Caloplaca*, *Candelina*, *Ionaspis*, *Lecidea*, *Pleopsidium*, *Porpidia*, *Rhizocarpon.*	
		2: *Arthonia**, *Arthothelium*, *Bactrospora*, *Chiodecton*, etc.

		3: *Dictyonema*, *Lichenomphalia**, *Multiclavula.*
		4: see Flames: *Candelariella.*
		5: *Arthopyrenia*, *Astrothelium*, *Bathelium*, *Eopyrenula*, etc.
		6: *Anthracothecium*, *Bagliettoa*, *Celothelium*, *Distopyrenis*, etc.
		7: see Gels: (***Lemmopsis***), ***(Leprocollema***), (***Lichinella***), etc.
SCALES: Squamulose chlorolichens, **cyanolichens**, **cephalolichens** & ambilichens, scale-like, forming more or less overlapping colonies.		
	1: (***Arctomia***), (*Baeomyces*), (*Cladonia*), (*Fuscopannaria*), *Gypsoplaca*, *Hypocenomyce*, ***Leciophysma***, (***Massalongia***), (***Placynthium***), ***Protopannaria***, *Psora*, *Psorinia*, ***Psoroma***, *Psorula*, *Solenopsora*, *Toninia*, ***Vahliella***, *Waynea.* See also Flames: *Catolechia*, (*Fulgensia*), (*Xanthoria*).	
		2: (*Arthonia*).
		3: (*Lichenomphalia*).
		6: *Agonimia*, *Anthrococarpon*, *Catapyrenium*, *Clavascidium*, (*Dermatocarpon*), *Endocarpon**, (*Henrica*), (*Heteroplacidium*), *Involucropyrenium*, *Neocatapyrenium*, *Normandina*, *Placidium. Placidiopsis.*
		7: ***Heppia****, (***Peltula*).** **7:** see also Gels: (***Euopsis***), (***Gloeoheppia*). (*Phloeopeccania***).
NAVELS: Umbilicose chlorolichens & **cyanolichens** with lobes attached at a single point, also with a white medulla.		
	1: *Glypholecia*, *Lasallia*, *Omphalora*, *Rhizoplaca*, *Umbilicaria.*	
		6: *Dermatocarpon.*
		7: (*Heppia*), ***Peltula*.*** **7:** also see Gels: (***Euopsis***), (***Peccania***), ***Phylliscum****, (***Phloeopeccania***), (***Pseudopeltula*).**
LEAFS: Foliose chlorolichens with mostly pale (where sheltered) but not brilliant lobes and a white (or rarely coloured) medulla; except medulla lacking in *Flakea*.		
	1: *Ahtiana*, *Anaptychia*, *Anzia*, *Arctoparmelia*, *Asahinea*, (*Baeomyces*), *Brodoa**, *Bulbothrix*, *Canomaculina*, *Canoparmelia*, *Cavernularia*, *Cetradonia*, *Cetrelia*, *Culbersonia*, *Dirinaria*, *Esslingeriana*, *Flavocetraria*, *Flavoparmelia*, *Flavopunctelia*, *Heterodermia*, *Hyperphyscia*, *Hypogymnia*, *Hypotrachyna*, *Imshaugia*, *Lobothallia**, *Menegazzia*, *Myelochroa*, *Parmelia*, *Parmelina*, *Parmelinopsis*, *Parmeliopsis*, *Parmotrema*, *Phaeophyscia*, *Physcia*, *Physciella*, *Physconia*, *Platismatia*, *Pseudevernia*, *Pseudoparmelia*, *Punctelia*, *Pyxine*, *Relicina*, *Rimelia*, *Speerschneidera*, *Squamarina*, *Usnocetraria*, *Xanthoparmelia.* See also Leathers: *Allantoparmelia*, *Cetraria*, *Cornicularia**, *Kaernefeltia**, *Masonhalea*, *Melanelia*, *Melanelixia*, *Melanohalea*, *Neofuscelia*, *Tuckermanella*, *Tuckermannopsis.* See also Flames: *Vulpicida*, (*Xanthoria*).	
		6: *Flakea.*
MANTLES: Foliose **cyanolichens &** ambilichens with broad, rounded, loosely attached lobes and a white medulla.		
	1: *Erioderma*, *Leioderma*, (*Leptochidium*), *Lobaria*, *Nephroma*, *Peltigera*, *Pseudocyphellaria*, *Solorina**, *Sticta.*	
		None.
SUEDES: Foliose **cyanolichens**, **cephalolichens** & ambilichens with mostly narrow or at any rate closely attached lobes and a white medulla, also (especially when young) with a black prothallus.		
	1: *Coccocarpia*, ***Degelia***, *Fuscopannaria**, ***Koerberia***, ***Massalongia****, *Pannaria*, ***Parmeliella***, ***Placynthium****, ***Vestergrenopsis***.	
		None.
STICKPINS: Crustose & squamulose chlorolichens and **cephalolichens** with scattered, upright, thin-stalked fruiting structures powdery or not at the tips.		
	1: *Baeomyces*, *Calicium*, ?*Chaenotheca*, *Dibaeis*, *Gomphillus*, *Gyalideopsis*, (*Micarea*), ?*Microcalicium*, ***Pilophorus***, *Pycnothelia*, ?*Sclerophora*, (*Sphinctrina*), (***Stereocaulon***),	

		Szczawinskia.
		2: *Lichenomphalia**, *Multiclavula.*
[!!!]**PIXIES:** Squamulose chlorolichens usually bearing upright, hollow, coarse-stalked fruiting structures sometimes with compact apothecia at the tips.		
	1: *Cladonia*.*	
		None.
SCRUBS: Fruticose chlorolichens, **cyanolichens** & **cephalolichens**, with clustered upright, prostrate or pendent, coarse branches and white medulla; habitat various.		
	1: *Acroscyphus*, *Allocetraria*, (*Bryocaulon*), *Bunodophoron*, *Cladina*, (*Cladonia*), *Coelocaulon*, *Cornicularia**, *Dactylina*, ***Dendriscocaulon***, *Evernia**, *Everniastrum*, (*Kaernefeltia*), *Leprocaulon*, *Loxosporopsis**, *Niebla*, (*Nodobryoria*), (*Pertusaria*), (*Pseudephebe*). *Ramalina**, *Siphula*, *Sphaerophorus*, ***Stereocaulon****, *Thamnolia*, *Tholurna**, *Tornabea*, (*Usnea*). See also Gels (but then with mucella in place of white medulla): **(*Lempholemma*)**, ***Leptogidium***, **(*Leptogium*)**, ***Polychidium***, ***Spilonema***, ***Spilonemella.*** See also Flames: (*Caloplaca*), *Edrudia*, *Letharia*, *Teloschistes*, (*Xanthoria*).	
		2: *Dendrographa*, *Hubbsia*, *Roccella*, *Schizopelte.*
		6: (*Endocarpon*).
		7: see Gels: ***Lichinella****, (***Peccania***), (***Peltula***), (***Pyrenopsis***), (***Synalissa***)**.**
HAIRS: Fruticose chlorolichens with hairlike branches > 1 cm long and with a white medulla.		
	1: *Alectoria*, *Bryocaulon**, *Bryoria*, *Gowardia*, *Nodobryoria**, *Oropogon*, *Pseudephebe**, (*Ramalina*), *Sulcaria*, *Usnea*.*	
		None.
SHAGS: Fruticose chlorolichens & **cyanolichens** with pendent, cobwebby or somewhat coarse branches mostly < 1 cm long , the shape determined by the photocells; dark within or too small to tell.		
	1: *Coenogonium*.*	
		5: *Cystocoleus*, *Racodium.*
		7: ***Ephebe***, ***Lichina***, ***Thermutis***, ***Zahlbrucknerella***.

ENHANCED EVOLVABILITY?

An interesting pattern brought into focus in Table 3 is the extent to which certain lichen lineages act as crucibles of morphological complexity, while other lineages clearly do not. Why the difference? One possibility is that rates of evolution can be enhanced in groups that "learn" to build serially on their past "breakthroughs". If so, then it seems clear that the Lecanorolichens must have undergone such an upgrade. In Figure 3, I follow up on this thought by presenting several "party tricks" – saprophytism, modularity, mucilarity, medullarity, vascularity, etc. – that may well have contributed to enhanced evolvability in the Lecanorolichens. At the same time I attempt an overview of its morphogroup evolution.

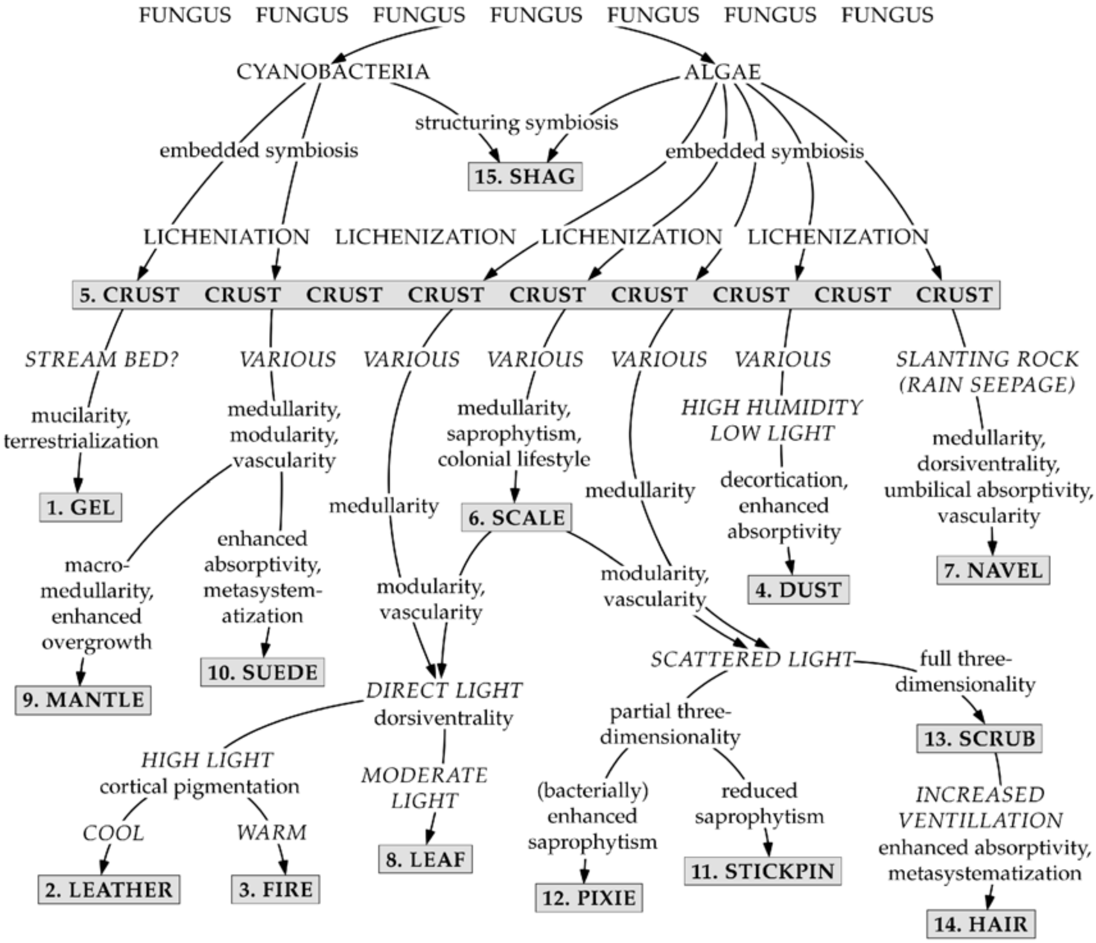

Figure 3. Flow chart showing the hypothetical elaboration of 15 Lecanoralean lichen morphogroups in extra-tropical North America. The schema is presented for illustrative purposes only and is intentionally uncoupled from known or suspected phylogenetic history. Items appearing in upper case italics represent putative selective pressures, whereas items in lower case are highly successful "party tricks" in the evolution of thallus form. Boxed items represent morphogroups in the order given below in the "morphogroup line-up". Design concept with Jason Hollinger. Graphics by Jason Hollinger.

MORPHOGROUP LINE-UP

No system of biological classification based on outward form can ever be fully consistent, and this one is no exception. Even so, it may be useful to flesh out the 15 morphogroups just now outlined with some commentary on their main party tricks and other features. To keep things lively, I'll include a liberal sprinkling of inferences and, in some cases, some wild hunches thrown in. Use of asterisks, small case bolding, and underlining follows Table 3. Genera classified in the four functional groups (Gels, Leathers, Fires and Pixies) appear also in the subgroup listings as appropriate. As you work your way through the line-up, you may wish to link to one of many excellent online lichen photogalleries. The one I'm most familiar with links here: http://www.waysofenlichenment.net/lichens

1: GEL LICHENS*

FAMILIAR GENERA: *Collema*, *Lempholemma*, *Leptogium*, *Phylliscum*, *Polychidium*.
LINEAGES: Lecanorolichens, Lichinolichens.
SUBGROUPS: Divides nicely and for the most part phylogenetically and ecologically into the:

- **LECANORALEAN GELS**, mostly with *Nostoc* as photopartner; see under Lecanorolichens in Table 3.
- **LICHINALEAN GELS**, with photopartners belonging to other cyanobacterial genera; see under Lichinolichens in Table 3. (Note: *Lempholemma* is a Lichinolichen genus that nevertheless contains *Nostoc*).

DEFINING PARTY TRICK: The namesake mucilage both prolongs water retention compared with other lichen morphogroups and acts as a major carbon depot against periods of prolonged carbon drawdown during warm wet weather.
EVOLUTIONARY ADVANTAGE: Some gel lichen groups, especially in the Lichinolichens, withstand prolonged periods without liquid wetting. This ability enables colonization of arid habitats not available to most other non-crustose lichens. The presence of cyanobacterial photopartners permits most gels to fix atmospheric nitrogen.
LIMITATIONS: Nitrogenase activity within the cyanobacterial photopartner requires nutrient-rich microhabitats with pH higher than about 5.
NOTES: *For convenience (but probably not clarity), the term *Gel Lichens* is accepted here in two extensions. In the broad sense it includes all unstratified lichen genera endowed with a hydrophilic mucella in place of a hydrophobic medulla. More narrowly defined, however, it includes only those unstratified genera consisting primarily of foliose and, to a limited extent, squamulose lichens: ***Collema***, ***Hydrothyria***, ***Leptochidium****, **(*Lempholemma*)**, ***Leptogium****. *Leptochidium*, with a partly stratified thallus, is accepted as a "honorary gel". Here note that many Gel Lichens s. lat. in their present circumscriptions encompass an extraordinarily wide range of morphological variation. As this phenomenon occurs in both the Lecanorolichens (*Collema*, *Leptogium*) and the Lichinolichens (*Lempholemma*), it's tempting to conclude that Gel Lichens have considerable morphological plasticity at evolutionary timescales.

2. LEATHER LICHENS

FAMILIAR GENERA: *Allantoparmelia*, *Cetraria*, *Melanelia*, *Tuckermannopsis*.
LINEAGES: Lecanorolichens only.
SUBGROUPS: No clearly defined subgroups.
DEFINING PARTY TRICK: Brown or black cortical melanins shelter the algal cells from excessive illumination and at the same time warm the thallus during cool weather in autumn, winter and spring; this greatly extends the period of physiologic activity.
EVOLUTIONARY ADVANTAGE: Specially adapted to northern climates, particularly in continental regions where winters are cold.
LIMITATIONS: Poorly represented in warm or humid climates.
NOTES: Many otherwise pale Leaf and Scrub lichens bear melanins at the extreme tips of the lobes and branches. In many cases these melanins are soon reabsorbed by the thallus. It seems likely that Leather Lichens can likewise vary melanin concentration in response to changing light, as has been shown for some Orange Lichens; see below.

3. FIRE LICHENS

FAMILIAR GENERA: *Letharia*, *Teloschistes*, *Vulpicida*, *Xanthoria*.
LINEAGES: Lecanorolichens, (Arthoniolichens), Candelariolichens.

SUBGROUPS: Genera with a distinct orange hue (parietin present) form a distinct if not entirely phylogenetically unified group handily termed the **ORANGES**: *Caloplaca*, *Edrudia*, *Fulgensia*, *Teloschistes*, *Xanthoria*. The remaining genera are a hodgepodge.
DEFINING PARTY TRICK: The brilliant colours of the Fire Lichens are in a sense the sun's light shone back at itself. The pigments that produce them provide the photocells with powerful protection from excessive illumination.
EVOLUTIONARY ADVANTAGE: Having an effective sunscreen in the form of cortical pigments has enabled these lichens to evolve into dry, sunlit places where the main source of moisture often comes in the form of nighttime dew. The Oranges (see above) appear to be unusually tolerant of bird droppings, presumably indicating a long evolutionary association with cliff nesting seabirds, for example.
LIMITATIONS: Most Fire Lichens do poorly in shady places and cloudy climates.
NOTES: The Candelariolichens seem likely to have arisen independent of the Lecanorolichens. Even so there are sufficient similarities between the two groups to raise an eyebrow, if not suspicions.

4. DUST LICHENS
FAMILIAR GENERA: *Chrysothrix*, *Lepraria*.
LINEAGES: Lecanorolichens, Arthoniolichens.
SUBGROUPS: None.
DEFINING PARTY TRICK: Having a fully sorediate surface greatly increases the capacity for moisture absorption directly from the air, favouring colonization of rain-sheltered microhabitats shunned by most other potential competitors for space.
EVOLUTIONARY ADVANTAGE: In principle the absence of a cortex should permit a constant repositioning of the lichen algae according to changing light: close to the surface in low light, deeper into the thallus during periods of high illumination. Hence Dust Lichens are well suited to low-light habitats.
LIMITATIONS: The requirement for high humidity combined with minimal wetting limits the range of habitats available for colonization. Such habitats become highly localized in arid climates.
NOTES: All Dust Lichens are derived from corticate lichens through the loss of the cortex.

5. CRUST LICHENS
FAMILIAR GENERA: *Arthonia*, *Arthopyrenia*, *Lecanora*, *Verrucaria*.
LINEAGES: All seven lineages are represented here!
SUBGROUPS: As a rule, Crust Lichens group much more tidily on sexual fruiting structures than on thalline characters.
DEFINING PARTY TRICK: Crust lichens form thin living "scabs" over the surfaces of things. The crustose habit approximates the minimum possible ratio of surface area to volume. This together with their exceedingly slow growth rates enables crust lichens to exert maximum control of their internal physiology with a minimum expenditure in energy.
EVOLUTIONARY ADVANTAGE: Crust Lichens alone have evolved to establish and live out their lives entirely within the boundary layer, the special zone of no air movement that covers the surfaces of all things. As few other life forms are specifically adapted to this lifestyle, the Crust Lichens have had enormous ecological amplitude essentially to themselves.
LIMITATIONS: Only Crust Lichens are, in most cases, readily overgrown by species in other lichen morphogroups.
NOTES: That Crust Lichens are the only morphogroup represented in all seven lineages is consistent with the hypothesis that they constitute the original lichen life form. As a group they are most at home in habitats for which few species of any kind are well adapted.

6. SCALE LICHENS

FAMILIAR GENERA: *Catapyrenium*, *Hypocenomyce*, *Psora*, *Toninia*.
LINEAGES: Lecanorolichens, Basidiolichens, Eurotiolichens, Lichinolichens.
SUBGROUPS: None come to mind.
DEFINING PARTY TRICK: All scale lichens are likely colonial, the squamules being linked to one another through hyphal "pipelines" that run through the supporting surface and in some, perhaps all cases absorb nutrients on behalf of the colony. Seen from the perspective of the lichen fungus, scale lichens are possibly only small carbon assimilating solar panels sent above ground in support of a saprophytic lifestyle; though of course from the perspective of the scale lichens themselves, it's quite the other way around: it's they who benefit from nutrients absorbed from within the substrate. At the same time I feel persuaded that carbon and other nutrients get passed around not only from the above-ground lichen solar panels to the below-ground fungus, but also, via the fungal hyphae, between individual squamules according to need. This is what I mean by "colonial lifestyle".
EVOLUTIONARY ADVANTAGE: As I've just mentioned, the same fungal hyphae that hypothetically link the squamules to one another probably look after the interests of the entire colony by passing around fixed carbon and other nutrients along nutrient gradients, and hence as needed.
LIMITATIONS: None I can think of.
NOTES: Scale lichens are crustose lichens "on tiptoe". Lacking a cortex on the underside, they can be described as semi-open lichen systems, in which the lichen alga is only moderately protected from environmental extremes.

7. NAVEL LICHENS

FAMILIAR GENERA: *Phylliscum*, *Rhizoplaca*, *Umbilicaria*.
LINEAGES: Lecanorolichens, Eurotiolichens, Lichinolichens.
SUBGROUPS: The Navels divide rather evenly into two largely natural groupings:

- **UMBILICATES** consist mostly of macrolichens with a white medulla and an algal photopartner: *Dermatocarpon*, *Glypholecia*, *Lasallia*, *Omphalora*, *Rhizoplaca*, *Umbilicaria*.
- **PELTATES** are mesolichens, mostly lack a white medulla and have a cyanobacterial photopartner: (***Euopsis***), (***Heppia***), ***Peltula***, (***Peccania***), ***Phylliscum***, (***Phloeopeccania***), (***Pseudopeltula***)**.**

DEFINING PARTY TRICK: The presence of a centrally positioned umbilicus combines with the radially expanding foliose "umbrella" to create a zone of delayed evaporation after rain. Hence rainwater delivered by gravity on a characteristically slanting rock surface can be absorbed gradually by the umbilicus and wicked upwards to the central portions of the thallus – here the most actively growing portions. Those navel lichens that have adapted to growing on more level rock surfaces absorb water also from above and, in such cases only, grow outwards primarily from the lobe margins, hence taking on a more "polyphyllous" appearance.
EVOLUTIONARY ADVANTAGE: Having a single point of establishment improves the chances of establishment and maintenance in microsites subject to competitive pressure from other lichens. The elaboration of a foliose "umbrella" outward from the umbilicus tends to exclude underlying Crust Lichens.
LIMITATIONS: A requirement for hard rock, usually acidic.
NOTES: Occurrence in physiologically dry environments is supported by highly moisture-absorbent pruina that accumulates in actively growing portions of the thallus.

8. LEAF LICHENS

FAMILIAR GENERA: *Cavernularia*, *Flavocetraria*, *Parmelia*, *Physcia*, *Platismatia*.
LINEAGES: Lecanorolichens, Eurotiolichens.
SUBGROUPS: Two largely phylogenetic groups can be distinguished here:

- **PHYSCIOIDS** have narrow, elongate lobes that are dull and/or distinctly frosted toward the tips: *Anaptychia*, *Dirinaria*, *Heterodermia*, *Hyperphyscia*, (*Lobothallia*), *Phaeophyscia*, *Physcia*, *Physciella*, *Physconia*, *Pyxine*, *Speerschneidera*,
- **PARMELIOIDS** encompasses the remaining genera, and have narrow to broad lobes generally shiny toward the tips.

DEFINING PARTY TRICK: Having a distinct upper surface is an adaptation to habitats subject mostly to top lighting, while having a distinct and slightly elevated lower surface confers considerable evolutionary advantage as a carbon depot (or carbon sink) during prolonged periods of surplus carbon production. The presence of rhizines doubtless serves a similar carbon function; and by acting as "stilts" should also enable the thallus to elevate the algal layer to the optimum physiologic height above the boundary layer.

EVOLUTIONARY ADVANTAGE: The ability of Leaf Lichens to overgrow Crust Lichens seems likely to have conferred a major competitive advantage in the early days of lichen evolution, and may have been a major driving force in the evolution of the Leaf morphogroup.

LIMITATIONS: Parmelioids are not well suited to extreme environments, partly owing to relative exposure of the internal portions as noted above. By contrast many Physcioids are well adapted to dry conditions, apparently owing, first, to closer attachment to the supporting surface and, second, to the frequent presence of moisture-absorbent pruina over the lobe tips.

NOTES: Generalist group, containing many subgroups, each adapted to a different set of environmental conditions. Overall, leaf lichens are present across all mesic environments, with some adapted outwards into subarid, but not usually arid climates, unless supported by frequent dew or fog.

9. MANTLE LICHENS

FAMILIAR GENERA: *Erioderma*, *Lobaria*, *Peltigera*, *Sticta*.

LINEAGES: Lecanorolichens only.

SUBGROUPS: Each genus is distinguished by a unique set of several characters.

DEFINING PARTY TRICK: The large, loose, leafy lobes and rapid growth enable Mantle Lichens to readily overgrow bryophytes competing for space in the humid, nutrient-rich habitats characteristic of the group.

EVOLUTIONARY ADVANTAGE: Whether cyanobacterial or cephalodial, these lichens come equipped with their own "nitrogen factories" – clearly a special adaptation for rainy climates where nitrogen is often limiting.

LIMITATIONS: Mantle Lichens need prolonged wetting for positive net carbon assimilation, hence tend to be restricted mostly to rainy climates.

NOTES: The proportionately thick medulla characteristic of Mantle Lichens probably prolongs moisture retention after rain – a great benefit to the cyanobacterial photopartner – and provides an ample carbon reserve for use in times of prolonged carbon drawdown.

10. SUEDE LICHENS

FAMILIAR GENERA: *Coccocarpia*, *Massalongia*, *Parmeliella*, *Vestergrenopsis*.

LINEAGES: Lecanorolichens only.

SUBGROUPS: No large subgroups are present.

DEFINING PARTY TRICK: Most Suede Lichens are more or less closely appressed over a fungal hypothallus/prothallus that especially in early developmental stages extends ahead of the lobe tips and likely absorbs nutrients, including canopy throughfall, from the immediate environment. At the same time the hypothallus doubtless absorbs and recycles any assimilated nitrogen or carbon that would otherwise be lost to the system, e.g., by leaching from rain. This has the effect of creating within this morphogroup a "metasystem" in which the entire thallus functions as an emergent property of its parts.

EVOLUTIONARY ADVANTAGE: Most Suede Lichens establish early in succession – no doubt partly owing to the "ram scoop" function of the fungal hypothallus – hence complete their life cycle on newly available substrates prior to the establishment, e.g., of competing bryophytes.
LIMITATIONS: The requirement for high nutrient status coupled with mostly cool rainy climates – where nutrient tend to be leached in rainwater – doubtless accelerates establishment, but at the same time greatly limits the occurrence of Suede Lichens in most regions.
NOTES: The presence of cyanobacterial photocells permits growth in rather poorly lit habitats. The name "Suede" takes its origin from the rather soft appearance of the upper cortex.

11. STICKPIN LICHENS

FAMILIAR GENERA: *Baeomyces*, *Calicium*, *Gyalideopsis*, *Pilophorus*.
LINEAGES: Lecanorolichens only.
SUBGROUPS: Divides cleanly if not entirely phylogenetically into:

- **STICKS** have coarse fruiting stems: *Baeomyces*, *Dibaeis*, *Pilophorus*, *Pycnothelia*, (***Stereocaulon***).
- **CALICIOIDS** have hair-stalked apothecia bearing dark spores in a powdery mass: *Calicium*, *Chaenotheca*, *Microcalicium*, *Sclerophora*, *Sphinctrina*. (Note: Traditionally the Calicioids also include various unlichenized fungi similar in appearance and ecology: *Chaenothecopsis*, *Mycocalicium*, *Phaeocalicium*, *Stenocybe*).
- **TICOIDS** have hair-stalked pycnidia bearing pale conidia rather more "isidioid" or droplet-like than powdery: *Gomphillus*, *Gyalideopsis*, (*Micarea*), *Szczawinskia*. (Note: Actually these genera have exclusively non-thalline fruiting stems, hence are strictly speaking crustose. Ditto the Calicioids).

DEFINING PARTY TRICK: Having a basal thallus permits the accumulation of carbon reserves preparatory to initiating the upright fruiting stalks characteristic of the group.
EVOLUTIONARY ADVANTAGE: Elevating the apothecia and other fruiting structures above the boundary layer greatly improves the chances of successful dispersal of the spores.
LIMITATIONS: Some cosmopolitan groups are included here, suggesting no inherent limitations on the members of this morphogroup *per se*.
NOTES: The basal thallus is remarkably variable in this group, in some cases ranging from crustose to scale-like to foliose within a single genus. The Calicioids and Ticoids actually bear non-thalline fruiting stems, hence strictly speaking are crust lichens. Their inclusion with the Stickpins reflects the part played by the basal crust in gathering and storing carbon preparatory to development of the fruiting stems. Basidiolichens like *Lichenomphalia* and *Multiclavula* could also be placed here but have evanescent fruiting structures ("mushrooms"). In the case of sexually reproducing Stickpin Lichens, it's worth noting that the apothecia at the stem tips invariably lack photosynthetically supportive photocells, hence depend for their development on carbon carried upwards from the basal thallus.

12. PIXIE LICHENS

FAMILIAR GENERA: *Cladonia*.
LINEAGES: Lecanorolichens only.
SUBGROUPS: No subgroups.
DEFINING PARTY TRICK: *Cladonia* combines the advantages of a colonial squamulose lifestyle (see Scale Lichens, above) with the dispersal efficiencies of the Stickpin Lichens (also see above), whose development is supported by carbon accumulated by the basal thallus.
EVOLUTIONARY ADVANTAGE: The fruiting stalks usually either bear terminal apothecia or else they are covered in powdery soredia: in both cases they are well equipped to release their diaspores into the circulating air well above the boundary layer. The stems and scales are brittle and are readily caught in the fur or feet of passing animals, which therefore act as vectors of dispersal.

LIMITATIONS: This is a highly versatile, virtually cosmopolitan genus with no obvious ecological limitations. *Cladonia* does, however, seem to need soft substrates – soft bark, decayed wood, moss, duff, soil – presumably in keeping with a requirement for fungally derived nutrient supplement.
NOTES: Some *Cladonia* species withstand warm, humid conditions to a remarkable degree, perhaps hinting at a symbiotic relation with substrate-inhabiting bacteria that in some way operate similar to our own intestinal flora operates, that is, in the breakdown of carbon sources otherwise unavailable. Among the stratified lichens, *Cladonia* is morphologically by far the most diverse genus; it fits comfortably nowhere else than within a morphogroup dedicated to it alone. *Cladina*, by contrast, is unequivocally a Scrub Lichen, while *Pycnothelia* is a Stickpin Lichen.

13. SCRUB LICHENS

FAMILIAR GENERA: *Cladina*, *Dendrographa*, *Evernia*, (*Polychidium*), *Thamnolia*.
LINEAGES: Lecanorolichens, Arthoniolichens, Eurotiolichens, (Lichinolichens).
SUBGROUPS: This is an extremely heterogeneous group united by the presence of coarse, radial, unbranched to more often branching stems. The only subgroups one could recognize would cut first along thallus size and, after that, degree of branching:

- **STUB LICHENS** contain all coarsely fruticose mesolichens less than about 1 cm tall: (*Caloplaca*), *Edrudia*, (*Endocarpon*), *Leprocaulon*, *Loxosporopsis*, (*Pertusaria*), (*Teloschistes*), *Tholurna*, (*Xanthoria*).
- **CLUB LICHENS** include all unbranched or sparsely branched fruticose macrolichens with rather coarse branches: *Hubbsia, Niebla**, *Siphula*, (*Sphaerophorus*), (***Stereocaulon***), *Thamnolia*, *Tholurna*.
- **SHRUB LICHENS** encompass all similar macrolichens, but much-branched:. *Acroscyphus*, *Allocetraria*, (*Bryocaulon*), *Bunodophoron*, *Cladina*, (*Cladonia*), *Coelocaulon*, *Dactylina*, ***Dendriscocaulon***, *Dendrographa*, *Evernia**, *Everniastrum*, (*Kaernefeltia*), (*Niebla*), (*Pseudephebe*), *Ramalina**, *Roccella, Schizopelte*, *Sphaerophorus**, ***Stereocaulon****, *Teloschistes** *Tornabea*, (*Usnea*).

DEFINING PARTY TRICK: Radial stems and branches likely represent a special adaptation for foggy and/or cloudy climates where light is reflected and hence received from all directions.
EVOLUTIONARY ADVANTAGE: Various. Many species are conspicuously brittle, hence readily fragment into large, physiologically robust propagules readily transported by passing birds or mammals. Some branchy Shrub Lichens form well established, self-sufficient metasystems that create their own internal microclimates and enhance nutrient recycling without loss to the system.
LIMITATIONS: Resynthesis is probably a rare event in many habitats, owing to the difficulty of gathering sufficient carbon reserves to fuel upward growth from the boundary layer.
NOTES: Most ground-dwelling scrub lichens have distinctly brittle thalli, whereas the thalli of most tree-dwelling species are normally pliant.

14. HAIR LICHENS

FAMILIAR GENERA: *Alectoria*, *Bryoria*, *Usnea*.
LINEAGES: Lecanorolichens only.
SUBGROUPS: A mildly informative subgroup would be the **USNEOIDS** (*Alectoria*, *Ramalina thrausta*, *Usnea*), all of which are green (usnic acid) and hence respond differently to microclimatic gradients than the remaining species which contain cortical melanins, and hence are brownish or blackish. I'll have more to say on this subject in Essay XIV.
DEFINING PARTY TRICK: Having a very large surface area relative to volume enhances the ability of this morphogroup to absorb moisture and nutrients directly from the air and rainwater.
EVOLUTIONARY ADVANTAGE: The lengthwise orientation of the cortex presumably shunts water (and nutrients) in the direction of negative osmotic gradients, while the creation in the mature thallus of an intricate, self-sufficient lichen "metasystem" that enhances retention of leached

nutrients at each wet-dry cycle, and at the same time captures canopy throughfall that would otherwise be lost to the system.

LIMITATIONS: Most members of this group are clearly disadvantaged in warm, humid climates, presumably owing to an inability to store sufficient carbon within the capillary branches to see the thallus through periods of carbon drawdown. The sole exception to this rule is *Usnea*, which has numerous likely carbon depots including papillae, fibrils and the dense cartilaginous strand at the core of the thallus.

NOTES: That hair lichens have evolved in the Lecanorolichens alone is noteworthy. It is tempting to speculate that this morphogroup may have arisen in the canopies of trees, e.g., in response to rapid drying in the wind.

15. SHAG LICHENS

FAMILIAR GENERA: *Coenogonium* (in part), *Cystocoleus*, *Ephebe, Thermutis*.

LINEAGES: Lecanorolichens, Dothideolichens, (Lichinolichens).

SUBGROUPS: Divides cleanly, phylogenetically and probably ecologically into the:

- **CHLOROSHAGS** have an algal photopartner: *Coenogonium*, *Cystocoleus*, *Racodium*.
- **CYANOSHAGS** have a cyanobacterial photopartner: ***Ephebe***, ***Lichina***, ***Thermutis***, ***Zahlbrucknerella***.

DEFINING PARTY TRICK: This morphogroup contains very few species, at least in North America. Its party trick may perhaps be said to reside with the photopartner, which in this group alone determines the shape of the thallus, rather than with the lichen itself.

EVOLUTIONARY ADVANTAGE: At least some Shag Lichens appear to tolerate low illumination, suiting them to microhabitats with little competition from other lichens.

LIMITATIONS: The photopartners in this group appear to receive only scant fungal buffering against climatic extremes, an observation consistent with a general requirement for cool, humid, rather sheltered microsites.

NOTES: The exceedingly low species richness in this group across all three independent origins is perhaps not surprising given the scant ability (or inclination) of lichen photocells to co-evolve with their fungal consort.

SUMMING UP

Stephen J. Gould once famously suggested a thought experiment in which the "tape of life" is replayed to find out how a second run would compare to the first. Gould's assumption was, of course, that it would not compare; that each run would give rise to profoundly different life forms. Now this is interesting; because if it's really the case, as posited here, that the lichen thallus has several times evolved from scratch, then in some measure we can say that Gould's thought experiment has actually already been tried; and that the results are, in fact, right there in front of us, staring us in the face.

The question is what, if anything, can we conclude from those results?

Two things actually. First, we can conclude that most of our seven independent lineages are in fact unique, that is, most have a very different "feel"; see above. Partly this has to do, I should think, with their status as separate runs; but partly it must also have to do with the very different sets of photopartners involved. The evidence for this latter conclusion is, I think, compelling. In two instances where the same photopartners – *Trebouxia* in one case, *Nostoc* in the other – are shared between two lineages, the resulting lichens actually do overlap quite significantly in outward appearance. Thus the Yolk Lichens (*Candelaria*: Candelariolichens) really do resemble certain brightly coloured Lecanorolichens, just as Mourning Phlegm (f.p.: *Lempholemma polyanthes*: Lichinolichens) really does seem to have more in common with the Vinyl Lichens (f.p.: *Leptogium*: Lecanorolichens) than the letter "L".

Second, we can also conclude that our lineages are in fact highly similar. Take another look through Table 3 and you'll be struck, if you haven't already been, by how much morphological overlap there really is among the lineages. Based on existing evidence, one can easily imagine the overlap would be greater still if only the Eurotiolichens and the Candelariolichens had travelled a little further down the road to enhanced evolvability. The conclusion seems inescapable that the lichen thallus in all cases except perhaps the Dothideolichens has tended to converge on a specific number of general forms; and that these would likely arise regardless how often the tape of lichens, if not necessarily of life, is replayed.

I guess there are only so many ways you can orient a solar panel.

POSTSCRIPT

I was pleased the other day to learn that some of the morphotypes pictured in Figure 1 may actually have published names – even if according to the Botanical Code they really shouldn't have. There was a time, not long ago, when lichenologists paid real attention to morphological variation, whence names like *Hypogymnia physodes* f. *cassidiformis*, "helmet-shaped" (= top middle thallus), and f. *vittatoides*, "resembling *H. vittata*" (= bottom middle). Other form names have also been assigned – *elegans, epiphylla, foraminifera, granulosa, isidiosa, labrosa, maculans, minor, pinnata, platyphylla, stigmatea, subcrustacea, sublugubris, subtubulosa* – and for these I'm glad. Even if such names harken to morphological variation rather than genetic identity, well what then? At worst they become a small nuisance: little plastic bottles of spring water strewn across the Death Valley of lichen synonymy.

Whenever we apply a name to a lichen variant, we open a little window. Through that window we can, if we wish, contemplate the ever-shifting response of the lichen thallus to place. Mapping the distributions of lichens is well and good, but it doesn't tell us much about *how* lichens live where they do. For that we need to pay attention less to the map and more to the lichen itself. The project ahead of us, I should say, is to learn to read the lichen thallus as a surrogate for place. Giving names, even informal names to lichen variants is a good first step forward.

Now take another look at Figure 1 and let me know what you see.

FINIS