

TWELVE READINGS ON THE LICHEN THALLUS

VII. Species

TREVOR GOWARD
Enrichened Consulting Ltd., Edgewood Blue, Box 131, Clearwater, BC, Canada V0E 1N0
email: tgoward@interchange.ubc.ca



Figure 1. How many lichen species do you see? Three? Four? Five? Clockwise from top left: 1A: Snow Pelt (fungal partner: *Peltigera chionophila*) with appressed, non-detachable cephalodia; 1B: Deciduous Pelt (f.p.: *P. britannica*), with loose, detachable cephalodia; 1C: lobe of Apple Pelt (f.p.: *P. malacea*); and 1D: lobe of Deciduous Pelt, sprinkled with tiny, unexpanded thalli of Panther Pelt (f.p.: *P. britannica*). Note: 1A and 1B are much enlarged. Photomontage by Tim Wheeler.

*Life don't clickity-clack down the straight-line track,
It comes together and it comes apart.*

Ferron

WE WERE TALKING, I believe, about species (Essay VI). More particularly we were talking about the fungal species *Bryoria fremontii*, whether it combines to form one lichen species, or two.

Even to ask such a question is already something. Basically it's to butt up hard against the lichenological orthodoxy according to which the lichen fungus and the lichen species are one and the same thing. This being the case, surely it's nonsensical to insist that a single lichen fungus might contribute to two lichen species. Actually I suppose the matter turns on what exactly we think a lichen is, and how exactly we define

species. These are the questions that will preoccupy me here. Even more, I will argue that it's scarcely possible even to *see* lichens without coming at them whole. Let's see how we go.

Homo sapiens is above all a narrative animal, a teller of tales, a relater of deeds. No other organism comes at existence this way, deconstructing it, annotating it, articulating it into concretions of thought enough to fill whole libraries. Words are the lens – narrative the frame – through which we peer out at the world. It's hard to get across a sense of how profoundly weird this is: our overwhelming allegiance to words. Often

it's as though we really believed words *were* the world. But of course they are not. The words by which we describe existence to ourselves can never actually contain it. Words are synaptic, catalytic, metaphoric: they signify, but they never *convey*. The map is not the territory, and neither is the word the thing. This is the first thing to understand about *species*.

The second thing to understand about *species* is that species are as much verb as noun. Beginning with the publication of Darwin's *origin*, 150 years ago, species once again became for the scientist what I suppose they have always been for most preliterate peoples: unpredictable, transformative, tricky. Gone are the days of Aristotelian yore when it was possible to think of species as the manifestation of a fixed, typological essence or idea. Nowadays most of us know we get much better traction when we think of species also from an evolutionary perspective: species as the distal end of process.

We are, as I say, a narrative species; we like a good story. The story encapsulated in Figure 2 is a good story indeed. It's the story of life on earth. Moving upwards from the bottom of the page to the horizontal line near the top nets you 3.5 billion years of evolutionary time. Study the lines and arrows a moment, and you'll easily make out the gist of the tale I'm about to tell. Keep in mind that I'm telling it from the perspective of a particular species of lichen: a lavishly leafy, freckly, emerald green, ground-hugging affair known to lichenologists by the name of its fungal partner, *Peltigera britannica* (Figure 1B, D). What's special about *P. britannica* is that it elaborates not one but to two very different lichens, here called Deciduous Pelt and Panther Pelt.

All of this – and more – is described step by step in the following 14 Waypoints, A through N.

A Life horizon. Our earliest undisputed evidence for life on Earth dates back 3.5 billion years. It's unlikely that life could have arisen much before this, since Earth itself had formed only about a billion years earlier, and had since then been absorbing meteoritic insult with a frequency scarcely conducive to life's tenuous beginnings. Around 3.8 billion years ago, however, the impacts let up; and life, seeing an opening, began (though whether it actually arose on Earth or was seeded here from elsewhere is another matter). No sooner did life begin on Earth than it began doing what non-life never does: evolving, diverging, exerting lineage, as shown.

B LUCA. So far as we know, all but one of life's early lineages are no longer with us: victims, perhaps, of some last great rendezvous with a planetoid. The sole survivor was LUCA: a single-celled creature whose perky acronymic name stands, reasonably, for Last Universal Common Ancestor. According to latest bookkeeping, LUCA lived between two and three billion years ago. Let's say three. Though no actual physical evidence of LUCA has come down to us, we can nevertheless infer many things about her – including, for example, her possession of most of the basic metabolic conveniences enjoyed by her modern descendents, including us: DNA, tRNA, lipid bimembranes, a full enzymatic quiver: not bad, really, for an organism supposedly only a half billion years out of the starting gate.

C Archaea and Bacteria are two of the three great domains of life (the third is Eukarya, next Waypoint). Neither is much to look at – think micro-microscopic rods, squiggles and spheres – yet taken together they encompass most of life's most impressive physiologic accomplishments, e.g., 20 metabolic pathways, as compared with only two in plants, one in animals. For the first 1.5 billion years after life got started on Earth, Archaea and Bacteria had the place to themselves, caking it with multicoloured crusts and slimes and flocs. These days, Archaeans keep mostly to themselves in sulphur hot springs and other out-of-the-way places. Bacteria, for their part, are pretty much everywhere. Many live “underground” – refugees from an oxygenated world – while others have turned to supporting macroscopic life, whose every nook and cranny they now inhabit in their untold billions. It is said, for example, that nine out of every ten cells in the human body are bacterial; only the tenth cell is “ours.”

D Eukarya, the third great domain of life, began simply enough. Around two billion years ago, an Archaean cell engulfed a Proteobacterian cell, but did not digest it. Instead the Proteobacterium took up residence inside its host: a loose association that in time gave rise to a partnership, then to a mutualism, and finally to a full-blown symbiogenetic merger. Symbiogenesis is the elaboration of new life forms from the metabolic integration of prior life forms. In principle it occurs when a biological system of relationship exceeds some critical level of complexity – the “tipping point” – beyond which the system converts to an entirely new system of “higher” order. This new system

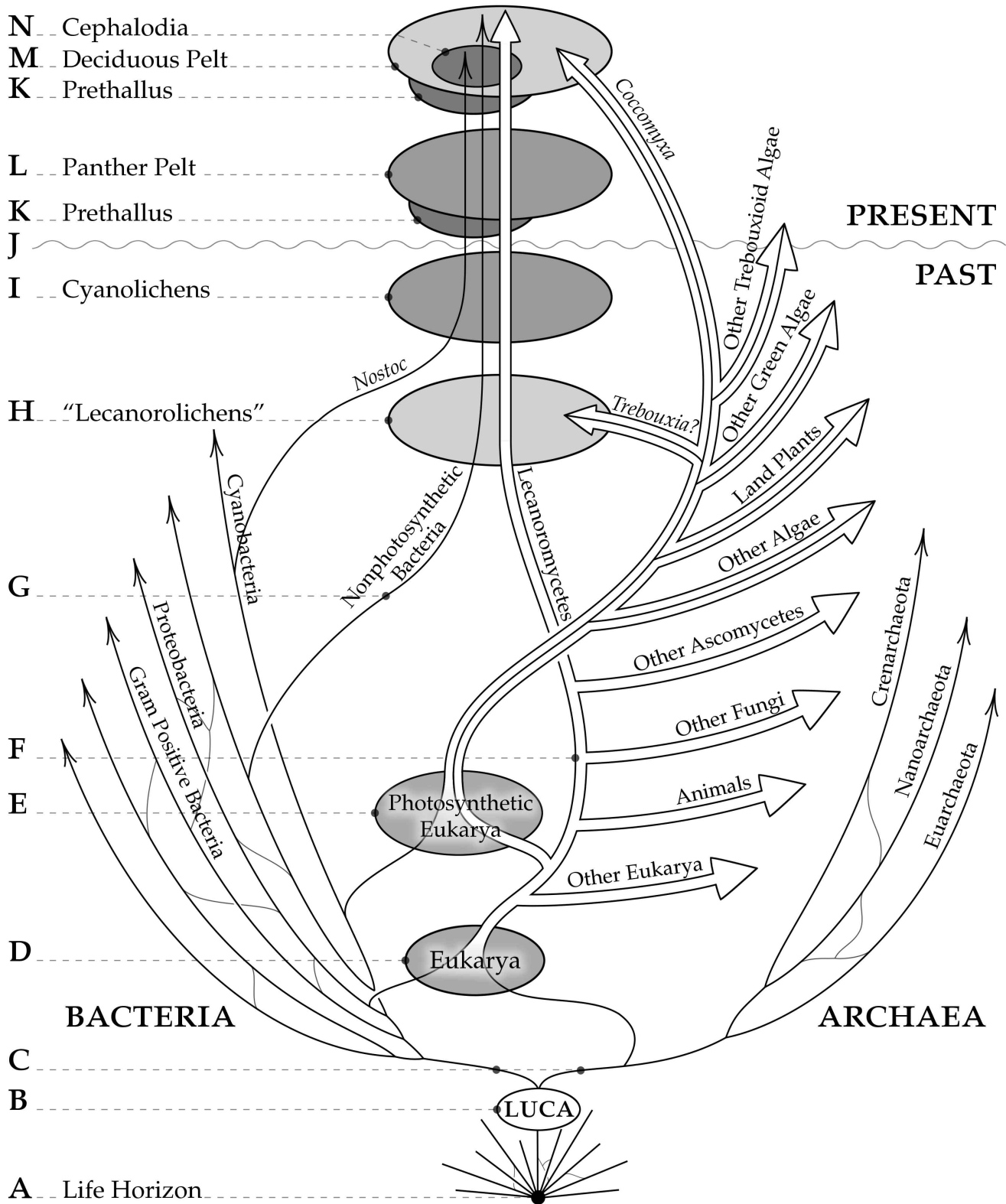


Figure 2. Evolution of life – and of two lichens: Deciduous Pelt and Panther Pelt (fungal partner: *Peltigera britannica*). Phylogenetic trees track one or a few genomes, and hence have an open, branching form. Here we track life itself, which has a closed, anastomosing form more like that of fungal hyphae. Eukarya encompasses two independent evolutionary lineages, and photosynthetic plants three. The original Lecanorolichens encompassed no fewer than six lineages, as shown. Design concept with Curtis Björk. Graphics by Jason Hollinger.

will have properties – termed “emergent” – that could not have been predicted from the properties of the system that came before (Essay v). In this sense, Eukarya is manifestly emergent. Where once we had two organisms – an Archaeon and a Proteobacterium – now we have one: the Eukaryotic cell: progenitor of every living thing big enough to be seen without a microscope. Embedded within this Eukaryotic cell, by the way, is our erstwhile Proteobacterium, now converted to energy-giving mitochondria. Notice the use of double lines, each denoting a separate evolutionary lineage.

E Photosynthetic Eukarya. Oxygenic photosynthesis was “invented” by Cyanobacteria about three billion years ago. Without exception, all photosynthetic macroorganisms alive today – including the photopartners of lichens – date from a symbiogenetic merger with cyanobacteria about 1.2-1.5 billion years ago. As with Eukarya, so with photosynthetic Eukarya: all have arisen from the failure of some carbon-hungry eukaryotic cell to digest a carbon-fixing cyanobacterium it had ingested. What started as a gesture of parasitism later strengthened into mutual dependence, and later still to full symbiogenetic merger. Photosynthetic Eukarya – apple trees, peat moss, bull kelp – are an emergent property of this merger, the original cyanobacterial cells having been long since converted to chloroplasts. Photosynthetic organisms thus encompass at least three evolutionary lineages, represented by the triple line.

F Fungi evolved – in water – as early as one billion years ago. Only much later, between about 540 and 490 million years ago, did they move onto land. Unlike plants, fungi lack chloroplasts. To live they must consume organic material derived ultimately from the photosynthetic activities of plants. And unlike animals, fungi absorb their food externally, through excretion of enzymes into the surrounding environment. This is why fungi – except when fruiting – are so seldom observed: they live hidden inside whatever it is they feed on. The major exception, of course, are lichen fungi, which “farm” photosynthetic algae and cyanobacteria inside living fungal “greenhouses” created by the interweavings of their own hyphae. As a result, lichen fungi alone hang out in the open air.

G Bacteria have almost certainly been integral to the lichen enterprise from the start. They may not actually run the place – who can say? – but clearly Bacteria are more than just happy campers. Witness their ubiquitous presence as “biofilms” over fungal

hyphae. These biofilms appear to support the lichen enterprise in several ways, whether as nitrogen boosters, as nutrient mobilizers, or, indeed, as *de facto* immune systems. It’s a safe bet that lichenologists will sooner or later recognize Bacteria as the third prime member of the lichen consortium – the invisible “ghost in the machine” – largely responsible not only for the astonishing morphological plasticity of lichens, but also for their ability to occupy habitats well beyond the ecological tolerance of the lichen photopartner or, indeed, the lichen fungus. All of this, however, is for the future. For now I find myself constrained to indicate only a single indefinite joining Bacterial lineage, as shown.

H Lichenizing event: Lecanorolichens. According to fossil evidence, lichens have been around a very long time, 600 million years for the trusting, 480 million years for the skeptic. Not that all lichens – if indeed any – have necessarily come down to us from those distant days. According to recent estimates, lichens originated on at least nine to twelve different occasions, each an independent lichenizing event. Four to seven of these origins involved cup fungi (Ascomycota), the remaining ones “mushroom fungi” (Basidiomycota). Going partly on intuition (and for convenience collapsing the Basidiolichens to a single origin), I myself posit seven such events (Figure 3). The one we’re most interested in here is the Lecanorolichen event, since that’s the one that ultimately gave rise to Deciduous Pelt and Panther Pelt.

What’s particularly intriguing about the origin of lichens is how each independent origin must have followed the same basic storyline already outlined for Eukarya, and then later for plants. First we have a failed attempt by a carbon-hungry consumer (fungus) to suck dry a carbon-producing producer (alga); then a gradual transition from association to co-dependence to full-bodied mutualism; and finally the inevitable symbiogenetic upgrade to an entirely new system of relationship: here a self-sufficient, metabolically integrated, self-replicating organism: a lichen thallus. Evolution may not exactly repeat itself, but certainly it rhymes.

There is, however, this one important difference: that whereas symbiogenesis in the case of Eukarya and plants involved a process of internalization – resulting in mitochondria and chloroplasts – yet in lichens the bionts remain mutually external to one another: the fungus external to the alga external to the fungus. Might this not, asks the skeptic, be

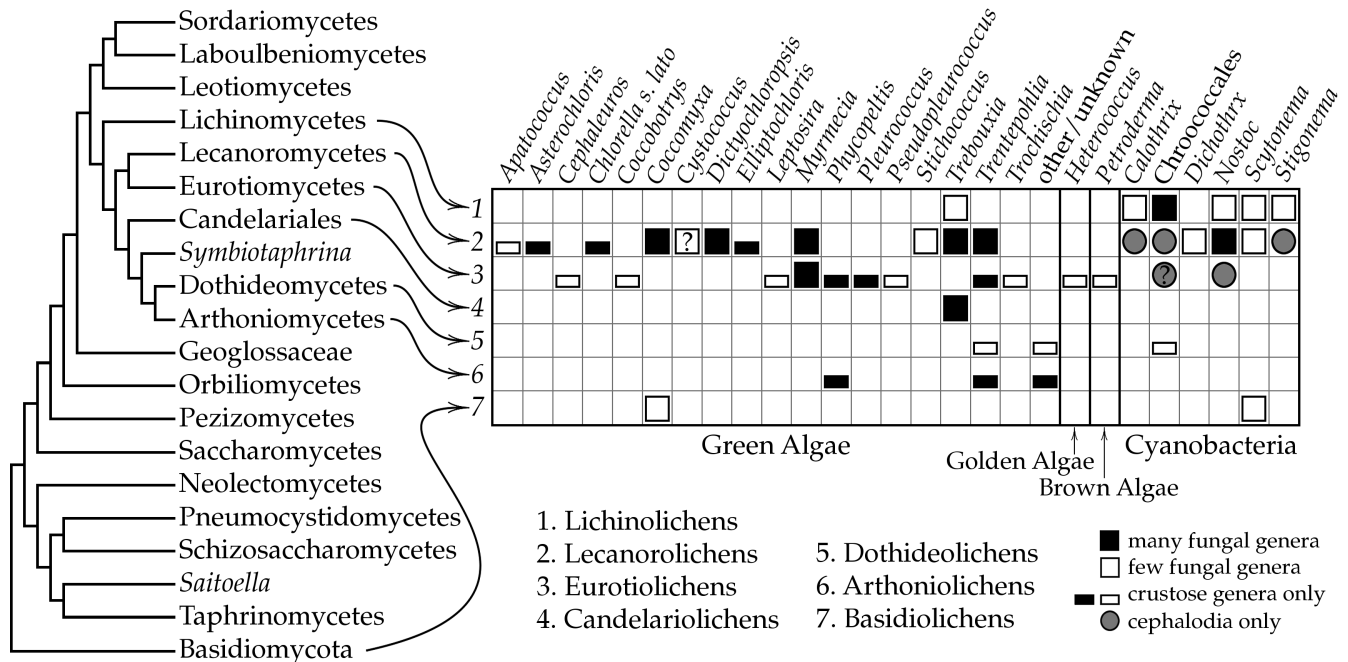


Figure 3. The lichen lifestyle has evolved independently on several occasions, here represented as six origins involving Ascomycota and one involving Basidiomycota. The following list documents all North American macrolichen genera and representative *mesolichen* and (*crustose lichen*) genera occurring in each of these “independent” lineages: (1) *Lempholemma*, *Thyrea*, *Thallinocarpon*, *Peltula*, etc.; (2) all macrolichen genera except those listed at (1), (3), (6) and (7), also *Polychidium*, *Protopannaria*, *Psora*, (*Caloplaca*), (*Lecanora*), (*Lecidea*), (*Rhizocarpon*), etc.; (3) *Dermatocarpon*, *Agonimia*, *Endocarpon*, *Placidium*, (*Verrucaria*), etc.; (4) *Candelaria*, (*Candelariella*); (5) (*Arthopyrenia*); (6) *Dendrographa*, *Hubbsia*, *Roccella*, *Schizopelte*, (*Arthonia*), (*Lecanactis*), (*Opegrapha*), etc.; (7) *Dictyonema*, *Lichenomphalia*, (*Multiclavula*), etc.

Sources: Peršoh et al. 2004 (*Mycological Progress* 3:103-121); Miadlikowska et al. 2006 (*Mycologia* 98:1088-1103); Ertz et al. 2008 (*American Journal of Botany* 95:1548-1556); Schoch et al. 2009 (*Systematic Biology* 58:224-239). Design concept with Curtis Björk. Graphics by Jason Hollinger.

taken as evidence of an integrative process not yet brought to term? Frankly I doubt it. Retention of biont identity is surely what you’d expect in a biological system involving a fungal partner specialized in acquiring carbon externally (through absorption) rather than internally (through digestion). The cellularly diffuse nature of the *Pelt* Lichen in our hand shouldn’t fool us into believing it’s not an organism. What, indeed, is the lichen photopartner if not an externally positioned chloroplast (Essay IV)?

- l **Relichenization: Cyanolichens.** Think of cyanolichens as simply foliose lichens powered in part or in whole by the photochemical energy of cyanobacteria. It is by no means clear how the cyanolichen lifestyle came about. Waypoint l assumes it arose via photocell replacement from a *Trebouxia*-containing forebear. It is also possible, I suppose, that cyanolichens hale from an independent

lichenizing event; but such speculation is best left to others. What’s important here is: first, that seemingly most if not all cyanolichens have gone through a period of complete dependence on cyanobacteria, i.e., to the exclusion of algal photopartners; and second that at least some of these exclusively cyanobacterial cyanolichens now consort once again with green algae – just like the very old days, only different. More on this at Waypoint m.

- j Here we cross the indefinite divide from an impossibly abbreviated **Past** to a more detail-heavy **Present**. Be prepared for heavy sledding.
- k **Prethallus.** A prethallus is hardly more than a nameless photosynthetic smudge: what happens when a newly germinated lichen fungus teams up with a photopartner not quite adequate to its needs. At the same time the prethallus is also doubtless a necessary first step in the creation of a lichen: a

lichen in the process of becoming. Not only does it sustain the young fungus until it can make contact with a more “compatible” photopartner, it also provides an energy store the fungus can tap into when the time to build a full-fledged lichen finally comes. For simplicity, I’ve indicated the prethallus and the mature lichen thallus as having one and the same *Nostoc* strain, though different strains are almost certainly involved here.

L **Panther Pelt** is a ground-dwelling lichen similar in appearance to Apple Pelt (Figure 1C). Panther Pelt is much better known to lichenologists by the name of its fungal partner, *Peltigera britannica*. What’s “special” about *P. britannica* – I mentioned this earlier – is that it contributes to two quite different lichens. One of these is Panther Pelt, wherein the photopartner is a cyanobacterium (*Nostoc*). The other is Deciduous Pelt (Waypoint N), in which the dominant – but not exclusive – photopartner is an alga (*Coccomyxa*). Most or all lichenologists regard Panther Pelt and Deciduous Pelt as two forms of one and the same lichen: the first they refer to as the cyanomorph or cyanotype of the second, and the second as the chloromorph or chlorotype of the first. Still, the extent to which this assessment of equivalence is accurate, or at any rate helpful, must ultimately depend on the extent to which the lichen fungus and the lichen really are one and the same thing.

M **Algal Acquisition: Deciduous Pelt.** Viewed at evolutionary time scales, lichens are continually changing partners: a kind of biological square dance (Figure 3). Pelt Lichens illustrate this partner swapping capacity of lichens in real time. At some point in the evolution of Lecanorolichens (Waypoint H), or perhaps earlier, there must have been an alga-powered lichen that learned – or possibly simply “remembered” – how to build a new kind of lichen photopowered by cyanobacteria. The resulting cyanolichen will have been suited to cool, humid habitats not accessible to its precursors. Thriving, it eventually giving rise to all the many hundreds of cyanolichens that exist in the world today. Along the way, however, an interesting thing happened: some members of certain strictly cyanolichen genera – *Lobaria*, *Peltigera*, *Pseudocyphellaria*, *Sticta* – reverted once again to algal mode, that is, they “traded in” their cyanobacterial partner for an alga. What is particularly interesting here is that these lichens didn’t simply go back to their old ancestral

morphologies. Instead they created whole new lineages of highly distinctive “green cyanolichens,” each with its own little nitrogen factories (Waypoint N). Such is the power of partner switches in the elaboration of lichen diversity.

N **Cephalodia.** Actually the cyanobacterial precursors of green cyanolichens are still with us. Nowadays they take the form of cephalodia. Cephalodia (Figure 1A, B, D) are small wartlike incrustations – actually little cyanobacterial colonies – borne on, in, or under the thalli of all green cyanolichens. Besides fixing carbon via photosynthesis, cephalodia also fix atmospheric nitrogen which, released to the host lichen, enables it to grow rapidly and large: a big help, no doubt, in the case of ground-dwelling lichens faced with heavy competition from ground-dwelling plants, especially bryophytes. Cephalodia have also arisen – independently – in certain green fruticose and crustose lichens of moss and rock.

Not all cephalodia are always small and crust-like. In a few green Pelt Lichens, including Deciduous Pelt (Figure 1B, D), cephalodia can sometimes grow outwards into foliose lichens in their own right. Such lichens – Panther Pelt is one – invariably bear a close resemblance to Apple Pelt (Figure 1C), itself a member of a lineage ancestral to Deciduous Pelt and its green relatives. Lichenologists usually refer to foliose cephalodia as “cyanomorphs” of the “parent” lichen, though from an evolutionary perspective they are probably better thought of as reversions to the cephalodia’s ancestral form. The cephalodia of Pelt Lichens can thus be seen as miniaturized lichens nowadays growing epiphytically on evolutionarily derived green pelt lichens.

The relation of green Pelt Lichens to cephalodia varies from species to species. The cephalodia of Snow Pelt (Figure 1A), for example, are now entirely subordinate to the green “host” lichen, having long since lost their ability to revert to their foliose past. By contrast, the cephalodia of Deciduous Pelt (Figure 1B, D) still retain, in a degree, their original identity as foliose lichens; they support their green “host” lichen, but are not entirely subordinate to it. These same cephalodia, moreover, are detachable (“deciduous”), hence do double duty as reproductive propagules not only for their green host, but also – and this is important – for Panther Pelt. Thus from a systems perspective, Deciduous Pelt and Panther Pelt can be thought of as two separate

enterprises. Though “joined at the hip,” they occupy very different portions of ecological space, so warrant recognition as separate taxonomic entities (Table 1).

* * * * *

Of course there remains the question – subject of this essay – how best to apply what we think *species* are to what we think lichens are. Lichens, for their part, are a kind of paradox. One the one hand they qualify as organisms: self-sufficient, self-replicating, and visible to evolution in roughly, but not precisely, the same ways as their fungal partner (Table 1). Yet on the other hand lichens are certainly also ecosystems: diffuse, externally integrated, composed of exchangeable parts (Figure 3). Thus lichens exist not so much in their member parts as in the systems that holds their member parts together (Essay v). It is above all the system, not so much the parts, that remains constant from one thallus to the next, from one generation to the next and, in a degree, over evolutionary time.

Now the punch line: lichens need to be thought of as systems to be meaningfully thought of at all. To see lichens as fungi – even as a “dietary strategy of fungi” – is to miss seeing lichens altogether. The proof of this is that lichens, like systems, have histories, yet they

have no phylogenies; only their member parts do (Essay iv). The fact, moreover, that lichens are not necessarily reconcilable with the identity of their fungal partner (Table 1) makes it pretty clear that the identity of the lichen fungus need not be integral to the identity of the lichen system. In the end, we need two kinds of species concepts here: a phylogenetic one applicable to the member parts of lichens, and a morphological one uncoupled from the member parts, but tied instead to the thallus as outward manifestation of system. Thus seen, a lichen “species” is pretty much what it used to be back in the days of Acharius: a population of thalli bounded by discontinuities coincident across any of several possible sets of independent characters: chemistry, morphology, anatomy, reproduction, ecology, distribution.

Defining lichen “species” this way makes it feasible, once again, for one fungal phylogenetic species to be involved in two lichen “species” – or indeed, for two fungal phylogenetic species to sustain one and the same lichen “species” (Table 1). In the coming Post-Schwendenerian era (Essay iv), we will be free once again to celebrate the full morphological, ecological and, indeed, evolutionary “reality” of whole lichens. Without symbiology, there is no biology.

PHYLOGENETIC PERSPECTIVE		SYSTEMS PERSPECTIVE	
FUNGUS NAME	TAXONOMIC RANK: FUNGUS	LICHEN NAME	TAXONOMIC RANK: LICHEN
<i>Bryoria fremontii</i> <i>Bryoria tortuosa</i>	One species: synonyms	Edible Horsehair Inedible Horsehair	Two “subspecies”
<i>Letharia lupina</i> <i>Letharia vulpina</i>	Two distinct species	Mountain Wolf Timber Wolf	One “species” with two “forms”
<i>Lobaria amplissima</i> “ <i>Dendriscoaulon</i> ” sp.	One species: synonyms	Arbuscular Lung Baby Brier	Two “genera”
<i>Lobaria oregana</i> <i>Lobaria silvae-veteris</i>	?One species: synonyms	1. Lettuce Lung 2. Oldgrowth Lung 3. Solarpanel Lung	Three taxa: 1 + 2 = “species” 2 + 3 = “subspecies”
<i>Peltigera britannica</i>	One species	Deciduous Pelt Panther Pelt	Two “subspecies”
<i>Peltigera chionophila</i>	One species	Snow Pelt	One “species”
<i>Peltigera venosa</i>	?One species	Fan Pelt Pelt “Vinyl”	Two “genera”

Table 1. Lichens have histories but not phylogenies, so are not susceptible of phylogenetic reconstruction. To be seen at all, lichens – as *lichens* – need to be seen as systems. The phylogenetic perspective (based on the fungal partner) and the systems perspective (based on all partners) are not always commensurate, as shown in the examples below. The taxonomic ranking suggested for whole lichens is loosely based on the schema presented in Essay vi.