

TWELVE READINGS ON THE LICHEN THALLUS

IV. Re-emergence

TREVOR GOWARD

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



Figure 1. Lichen as organism, lichen as ecosystem, lichen as construct of spatial scale. If we could visualize carbon cycling within the intact lichen thallus, we might find that it resembles the tracings of earth's own chaos-based weather systems. Note the Great Blue Whale, top right, falling to earth. Photomontage by Tim Wheeler.

PEOPLE OFTEN SAY THE KEY TO SUCCESS in science is asking the right questions. No use worrying about how many angels can dance on the head of a pin if, for example, there are no pins. But what people often neglect to say is that the key to asking the right questions is finding the right perspectives from which to conceive them.

People also like to point out that every story has two sides, and every triangle three. Macrolichens, for their part, have many sides – at least eight that I can think of. Why so many isn't hard to understand. Lichens, but especially macrolichens, exist at a kind of conceptual doorway, a portal. When we look out this portal in one direction, through the microscope, what we see is multiplicity: the lichen as its parts, as fungus, as alga, as symbiosis, as ecosystem. But when we peer through the same portal in the other direction, at

macroscale, what comes into focus now is unity: the lichen as emergent property, as physiologic entity, as organism.

Is it any wonder that lichen researchers have yet to achieve unanimity around how best to describe the lichen enterprise? Search through any ten review papers by any ten lichenologists and you'll certainly come across several widely differing interpretations. Think about these interpretations awhile and it may come to you that all are in fact resolvable to a finite number of underlying assumptions – call them perspectives – of which I think I discern, as I say, eight (Table 1). Working forwards again, I would argue that every shade and nuance of interpretation hitherto applied by lichenologists to the lichen consortium is ultimately an amalgam of two or more of these eight basic perspectives.

VANTAGE	PERSPECTIVE	FOCAL SCALE	RELATION TO ORGANISMIC PERSPECTIVES (7 & 8)	SAMPLE CORE HYPOTHESIS	RESEARCH TO DATE
CONSTITUENT	1 Mycocentric Perspective Lichens as fungus-induced constructs	Microscopic: cellular	Unhelpful (i.e., mistakes the part for the whole: misapplied metonymy). Forecloses on organismic perspectives, but provides critical background data.	"Lichens are <i>about</i> the fungal partner." (Unproductive)	Considerable
	2 Algocentric Perspective Lichens as alga-induced constructs	Microscopic: cellular	Unhelpful (i.e., mistakes the part for the whole: misapplied metonymy). Forecloses on organismic perspectives, but provides critical background data.	"Lichens are <i>about</i> the algal partner." (Unproductive)	Some
RELATIONAL	3 Symbiotic Perspective Lichens as fungal-algal constructs	Microscopic: "process"	Somewhat helpful (i.e., descriptive, but not explanatory; also promotes assumption that <i>symbiosis</i> is commensurate with eco-systemic process: "fallacy of misplaced concreteness"). Leaves open the possibility of organismic perspectives.	"Lichens are a consortium of differently named organisms." (Unproductive) "The lichen bionts are embedded in a cost-benefit relationship." (Unproductive)	Considerable
	4 Ecosystemic Perspective Lichens as miniature ecosystems	Microscopic: process	Supportive (i.e., the lichen bionts interact as complex systems, giving rise to non-linear relationships, feedback loops, and emergent properties). Links to organismic perspectives.	"Patterns of carbon cycling within the macrolichen thallus are likely to be most consistent with fractal geometry." (Productive)	Very little
EVOLUTIONARY/ CONSTITUENT	5 Phylogenetic Perspective Lichen fungi and lichen algae as evolutionary termini within their respective lineages	Microscopic: molecular	Somewhat helpful (e.g., modern lichens have arisen from two or more lichenization events), but promotes the assumption that lichen evolution is explicable independent of biont interaction. Discourages organismic perspectives.	"Lichens are about the bionts." (Unproductive) "Each independent lichen lineage may promote a different set of fungal-algal relationships." (Productive)	Fungal phylogeny: Considerable Algal phylogeny: Some
EVOLUTIONARY/ ORGANISMIC	6 Symbiogenetic Perspective Lichens as an emergent property of ancient fungal-algal "merger(s)"	Microscopic: cellular	Supportive (i.e., lichens are an unusual instance of <i>ectosymbiogenesis</i> , the partners having integrated without actually merging). Links directly to organismic perspectives.	"The lichen thallus is an emergent entity more helpfully understood in terms of biont interaction than of independent biont evolution." (Productive)	Very little
ORGANISMIC	7 Physiologic Perspective The lichen as a unit of <i>internal</i> , physiologic response to its environment	Macroscopic/ microscopic: process	Organismic (i.e., the lichen bionts operate within a single, unified, and hence unifying physiology). Complements Perspective 8.	"The relation between lichen form and lichen autecology can be empirically elucidated from the inside out." (Productive)	Considerable
	8 Morphologic Perspective The lichen as a unit of <i>external</i> , morphological response to its environment	Macroscopic: process	Organismic (i.e., lichen are self-sufficient, plant-like entities in which the algal biont functions as "chloroplast"). Complements Perspective 7.	"The relation between lichen form, function and distributional ecology can be inferred from the outside in." (Productive)	Very little

Table 1. Eight perspectives relative to the proposition that lichens exist independent of their constituent parts. Future essays in this series will focus primarily on Perspective 8.

The most basic lichenological perspective – that lichens are organisms – has been around since long before the days of the first practicing lichenologist. By contrast, the opposing perspective – that lichens are *not* organisms – is a much more recent proposition, dating from Simon Schwendener's epoch-making

deconstruction of the lichen thallus into its component parts: fungus and alga/cyanobacterium (henceforth alga). That was back in the 1860s. Since then our understanding of the lichen bionts and, indeed, of the lichen consortium has benefitted enormously from the recruitment into lichenology of several new perspec-

tives, most on the heels of technological and theoretical advance in other scientific disciplines, and all within the past 40 or 50 years.

In principle the emergence of each new perspective has required – or ought to have required – a careful rethinking of the perspectives that preceded it, with a view to their reinterpretation. Of course this revaluation process is likely to be successful only insofar as lichenologists are prepared to set aside those portions of their “traditional” perspectives incommensurate with the latest, expanded insights. This is what Simon Schwendener effectively asked of lichenologists in the late 19th century (Essay II), and I think this is what’s required of us today, as recent findings in bacteriology, systems ecology, molecular biology, phylogenetics, and endosymbiotic theory begin to propel lichenology into the coming “post-Swendenerian” era.

First up is the **mycocentric** perspective. Mycologists, of course, study fungi. I’m guessing that to a mycologist a lichen is apt to look like a fungal initiative: a stroma say, an ascomycetous elaboration built on the diffused photosynthetic energy of a thousand algal cells. In this view a lichen comes across as a kind of mycological party trick, something certain fungi have learned how to do – rather like the juggler’s art of keeping several balls in the air at once. Lichen algae, in this view, are merely the balls the lichen fungus has learned how to juggle. Notice that lichenologists effectively espouse this perspective when they describe lichens as a dietary strategy of certain fungi or, indeed, as an instance of fungal parasitism, controlled or otherwise. Actually I myself once encapsulated the same perspective in my assertion that “lichens are fungi that have discovered agriculture” (see Essay I).

Second we have the **algocentric** perspective. This is simply the mycocentric perspective made to stand on its head. From this vantage the lichen enterprise now looks much less like a fungal initiative, and much more like an algal one: lichens as alga-induced galls, call them fungal greenhouses, each elaborated to algal specifications, and all promoting the propagation and long-term well-being of the algal colonies within. And why not? Whereas practically all lichen fungi depend utterly on the lichen consortium – they can persist nowhere else in nature – yet many lichen algae are quite capable of living apart from it, either as a participant in some other symbiotic association – with water ferns, cycads, hepatics and *Gunnera* – on their own. Likewise lichen morphology, the way lichens are put together: here too it’s the alga’s requirements for

light, moisture, nutrients, etc. that determines, in general outline, what a lichen will look like. The alga as operations manager, as architect, as CEO.

Strange thing, though, about the algocentric perspective: one almost never hears it advanced as a valid way of thinking about the lichen enterprise. Not even the good people who study lichen algae seem inclined to cleave to it. One wonders about this. Naturally there are plenty of good *nomenclatural* reasons why lichenologists have opted to emphasize the lichen fungus over the lichen alga. That said, this convention does have at least one serious drawback, in that it tends to structure the lichenological dialogue around the assumption that lichen fungi must somehow be what lichens are *for*. The point here, I hasten to add, is not that lichens are in fact *for* anything; but that if they were, then logically they would have to be at least as much *for* the lichen alga as *for* the lichen fungus. But this is merely Escher all over again (Essay III): the metonymic price we pay for conflating the parts of the lichen with the whole.

Third is the **symbiotic** perspective. Symbiosis is the living together of differently named organisms in prolonged or permanent physical association. If the mycocentric perspective can be thought of as *thesis*, and the algocentric perspective as *antithesis*, then the symbiotic perspective would have to be *synthesis*, inasmuch as it accords equal weight to both lichen bionts. Or does it? Actually I suspect that the widespread currency of the symbiotic perspective in lichenological circles has to do with its being rather noncommittal on this point. That is, everybody readily agrees that the lichen bionts are in *some kind of* symbiotic relationship, so we sidle up to the symbiotic perspective as a convenient catch-all for our conscious and unconscious preconceptions concerning its nature – without the inconvenience of having to consider the matter further. No wonder *symbiosis* has proved so tricky to tie down to a single meaning.

Given the enormous sway the symbiotic perspective has held over lichenology for more than a century, it’s easy to forget that *symbiosis* is, after all, an abstraction, a construct of human perception. Though it clearly has descriptive power when applied to lichens – lichens really *are* a form of symbiosis – the question seems rarely to have been asked whether it has explanatory power as well. I would argue that it does not, as witness my own failed attempt to link *symbiosis* to a single important testable hypothesis (Table 1). Helpful though *symbiosis* may be in describing the nature of a wide range of associations

of the cost-benefit kind – bees and flowers say – it seems to me to shed little light on the integrative essence of lichens; see below. Indeed, with its seeming implication that knowing much about the fungus and the alga is tantamount to knowing much about the relationship between them, the symbiotic perspective has on balance done nearly as much in the 20th century to impede lichenology as it did in the 19th century to advance it.

The fourth perspective is what I call **ecosystemic**. An ecosystem, of course, is a community of organisms in dynamic interaction – both with one another and with their immediate environment. Key to the ecosystemic perspective is a temporal focus, the concept of process. True, not all ecologists see the world in four dimensions, yet those who do would be apt, I'm guessing, to think of lichens as miniature ecosystems. And surely they would not be wrong to do so, inasmuch as lichens, after all, qualify as ecosystems on all the usual criteria. Not only do they embody the requisite level of biotic diversity – particularly when we include their various bacterial and fungal parasymbionts – they also exhibit definite trophic structure in the form of producers (algae), consumers (fungi) and decomposers (presumably fungi and bacteria). Only in freeze-frame is it really helpful to think of lichens as fungi and algae; living lichens are much more helpfully conceived of as compact, interactive, fully-functioning ecosystems complete, more or less, unto themselves.

The ecosystemic perspective has, I think, much to recommend it. For one thing it confers upon the lichen bionts a kind of Marxist cogs-in-the-wheel equality: comrades in the great lichen enterprise. And for another thing, its modular structure ensures plenty of conceptual *Lebensraum* for whatever discoveries still lie ahead concerning the good and necessary works performed by the above-mentioned parasymbionts. Best of all – or so it seems to me – the ecosystemic perspective invites the lichenological community finally to leave off its century-plus debate concerning the nature of the lichen symbiosis, i.e., whether parasitic, controlled parasitic, or what have you. Seen from the ecosystemic perspective, such labels are misleading. It is in the nature of ecosystems not to have a “nature”: they either fire away interactively on all cylinders, or they don't exist. If the internal workings of the lichen ecosystem could somehow be visualized the way the Earth's weather systems can (Figure 1), I suspect we'd see more points of similarity between them than points of difference. Both are

nonlinear, essentially chaos-based enterprises: to attempt to shoehorn the constituent parts of either into a static one-size-fits-all relationship is, I think, entirely to miss the point.

Fifth, the **phylogenetic** perspective. Phylogenetics is defined as the study of evolutionary relatedness among species and populations. Its most characteristic activity is the construction of evolutionary “trees” which, nowadays, are usually built around molecular data gleaned from mitochondrial, plastid and nuclear DNA. In point of fact, lichens don't actually have molecular phylogenies, only their bionts do. This is not to say, however, that lichens don't have evolutionary histories. Here it helps to recall that natural selection exerts its feedback loops not only on the genomes of the fungus and the alga, but also on the *relationship* (or “conversation”) between them. Given that these two feedback processes are to a large extent independent of one another, it follows that a lichen thallus can with only slight exaggeration be thought of as the latest outward manifestation of one such “conversation” – which itself has been going on ever since the lichen enterprise began. That said, we probably shouldn't expect to reconstruct lichen conversations by means of molecular markers any time soon. Molecular symbiology is, I believe, a science whose day is still to come.

Most of the “lichen” phylogenies generated to date are fungal phylogenies; and most accord pretty well with earlier taxonomic inferences of lichenologists working from lichen morphology, anatomy, chemistry, and so forth. Each lichen fungus, that is to say, seems to be exclusive to one and only one lichen. On the surface this would appear to be good news all around. Not only does it vindicate the long lichenological practice of according the lichen fungus nomenclatural pride of place over the lichen alga (Essay 11), it also suggests that for now, at least, we can probably safely allow the fungal phylogeny to stand in for the lichen “phylogeny” as a whole. There remains, however, one minor downside, insofar as these early successes seem likely to confirm mainstream lichenology in its assumption that lichen fungi must be what the lichen consortium is *for* – a prolongation of the mycocentric perspective.

Sixth up is the **symbiogenetic** perspective. Symbiogenesis is sometimes defined as the inheritance of acquired genomes. Less telescopically, it can also be described as the evolution of long-term biological fusions that begin as symbiosis – unlike organisms living together – and that often end as something

fundamentally *other*: an emergent structure. From the symbiogenetic perspective, the lichen thallus is a classic example of emergence. Emergence is a tricky concept to get one's head around. Cast, however, in reductionist terms, it comes to the quite sensible proposition that the lichen examined at the scale of its parts is not fully reconcilable with the lichen viewed several orders of magnitude up, at the scale of the whole. Not that the perspectives invoked by these two scales of perception *can't* be reconciled; but rather that they *won't* be, at least not us, and not any time soon – any more than we are likely any time soon to trace the little ripples of air created by the butterfly's wing outward to the eye of Hurricane Katrina.

We talk about economies of scale, so why not ecologies of scale? We are mistaken if we think we can shift across whole orders of magnitude without experiencing a corresponding shift in the kinds of interpretations we are entitled to make. The mere fact that surface area varies as the square, volume as the cube means the world experienced at different spatial scales is necessarily a very disparate, effectively incommensurate place. We don't move from higher orders of perception to lower ones by simply drawing nearer to the thing observed, even less by merely magnifying it. Such shifts require, I think, that we ourselves effectively grow smaller, miniaturize: a process perhaps akin to a slow falling to earth, the small blue ball in space gradually growing larger, the great blue whale in *Hitchhikers' Guide to the Galaxy* growing proportionately smaller, exclaiming all the while at the sheer wonder of it (Figure 1). The microscopist at her work bench may be convinced she accomplishes any number of such transformative journeys each day before coffee break; but I have my doubts.

Last up, seventh and eighth, are the **physiologic** and the **morphologic** perspectives. I discuss these together because they seem to me variants of a single overarching assumption: that lichens operate as discrete systems sufficiently integrated to possess a unified, and hence unifying physiology. For convenience, I define the physiologic perspective as the vantage of those who attempt quantitatively to deduce lichen physiology from the inside out: the business of researchers working with laboratory support. By contrast, those who adopt the morphologic perspective approach lichens the other way around, from the outside in. This is purview of naturalists and lichen field ecologists, who attempt to infer the inner workings of whole lichens from a consideration of

thallus form, function and distributional ecology. I'll have much more to say about these two perspectives in future essays. For now the main point is that both open out on similar kinds of questions, albeit from very different, yet complementary perspectives; and that when both approaches tend toward the same answers, what we have is real explanatory power.

But are lichens truly organisms? Given our growing awareness of the biological significance of symbiogenesis, not to mention lateral gene transfer, this question is no longer so easy to answer as it once was. Everything hinges on what an organism *is* exactly. Certainly animals qualify, and so, albeit more diffusely, do plants. In my view lichens qualify as organisms inasmuch as they satisfy roughly the same set of criteria as plants do. Thus they grow in coordinated fashion, differentiate several tissue types, and pass through a succession of developmental stages culminating sooner or later in a reproductive phase. Lichens also "feel" like organisms – or why else would the words we call them by in all the world's languages – *lav*, *huidmos*, *porost*, *mareru*, *cen*, *gil-i-sang* – denote the macroscopic whole, rather than the microscopic parts?

About the only thing that could reasonably count against according organismic status to lichens is their admittedly composite nature. Sticklers will insist that lichen algae are external, not internal, to the lichen fungus, and hence by no means to be compared to the chloroplasts of plants. But external chloroplasts are surely what one would expect given that fungi are, after all, the world's consummate absorbers; no need to internalize carbohydrate resources so readily accessible from without. And besides, the so-called externality of the lichen alga disappears utterly when we examine lichens at macroscale, peering in under the cortex.

I for one look forward to a time when lichenologists once again unanimously embrace a certain key assumption too long relegated to the periphery of their discipline. This assumption is, of course, that lichens *exist* – independent of their constituent parts, I mean. Reaffirming the organismic status of lichens would seem to me automatically to release lichens to their rightful place as poster children for the ultimate nature of all eukaryotic life which, as we know, is itself an evolutionary hand-me-down from (= emergent property of) symbiogenetic mergers of long ago. Far from being existentially orthogonal to other macroscopic organisms, the lichen enterprise would now simply represent the next tier up in the symbiogenetic

enterprise: organisms composed of organisms composed of organisms.

The re-emergence of whole lichens, in the coming post-Schwendenerian era, is likely to feel to its participants like a kind of lichenological homecoming. Once again we will find ourselves gentling into perspectives that would have been familiar, in a degree, to Acharius, Fries, Nylander and our other great pre-Schwendenerian forebears. Free once more to contemplate lichens as organisms – the same way we

look at most other forms of macroscopic life – we will learn to “read” certain broadly repeating patterns of lichen form, pigmentation and distributional ecology. In time it will come to us that these patterns have of course always been there; but that for more than a century they have been opaque to our discipline in its constituent perspectives. Picking out, holding up, and commenting on some of the more interesting of these patterns will occupy me in the remaining essays in this series.