TWELVE READINGS ON THE LICHEN THALLUS

III. Credo

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Figure 1. Lichens as emergent property? Photo by Tim Wheeler.

IT'S NOT EASY BEING GREEN, said Kermit the frog, and he ought to know. Nor, I might add, is it particularly easy being a green naturalist who likes to think holistically about lichens.

Two reasons. First, lichens are basically dual affairs. Part fungus, part alga, they occupy a kind of conceptual no-man's land between "organism" on the one hand and "ecosystem" on the other. Or better, lichens can rightly be said to qualify as organisms *and* ecosystems – an existential status admittedly easier to put into words than to get one's head around. In a degree the problem with seeing lichens whole is not unlike a certain more famous problem in physics, the one Einstein solved when he posited the space-time continuum. To think seriously about whole lichens is, I submit, fundamentally to move outside the comfort zone of "common sense."

The second impediment to holistic thinking rises like a blue haze around the best efforts of lichenologists to come to terms with the first impediment. Basically it amounts to the proposition that lichens don't really exist. In practice, of course, few lichenologists would take the matter this far; but there can be no mistaking the official catechism, which has two parts, and goes something like this: (1) lichens aren't really organisms, therefore the ultimate reality of the lichen enterprise must reside in its component parts; and (2) the fungal partner is the quantitatively dominant component part, therefore lichens must perforce be fungi. What *d*o exist, in this view, are *lichenize*d *fung*i, by which lichenologists mean fungi that in the process of entering an obligate dietary relationship with certain microscopic algae and/or cyanobacteria, have learned to become transformed into elaborate gall-like "growth

chambers" known correctly to lichenologists as thalli, but to the uninitiated not quite correctly as lichens.

Here, then, is the lichen community's majority interpretation of the lichen consortium. And a finely reasoned, nicely tuned, fully self-consistent interpretation it is, too. But whether it constitutes the only *valid* interpretation is of course another matter.

Biology, it has been observed, amounts to something more than applied chemistry, just as chemistry is something more than applied quantum mechanics. In similar fashion, it is my view that the lichen thallus is something other than the mere sum of its component parts. It is, I submit, an emergent property, say the emergent property of lichenization. Admittedly the concept of emergence is troubling to some reductionist thinkers; but I nevertheless think it is a useful concept – how else do we account for the existence of life, if not as an emergent property of DNA, RNA, lipid bimembranes and the like? Emergence, says the physicist, is what happens when a system exceeds some critical threshold of internal complexity, and suddenly reconfigures to a wholly new level of organization. To qualify as emergent in biology, this new level of organization should at once be radically novel, fully integrated, self-sustaining, and capable of evolving. Its functionality, moreover, should be based less on any specific attributes of the component parts and more on the particular nature of their relationship. That the lichen thallus meets all of these criteria seems to me self-evident; accordingly I henceforward give myself permission to return to the original use of *lichen* as a synonym of *lichen thallus* (Figure 1).

Not that lichens, as I say, are necessarily easy to think about this way – as whole entities I mean (Figure 2). In some ways lichen thalli are actually more readily conceived in terms of their parts which of course are what most catch the eye under a micrscope. To a eukaryotic life form like ourselves, who store the basic machinery of life hidden neatly away inside our cells (as mitochondria for example), the internal anatomy of the lichen thallus is bound to seem a bit haphazard: a few tufts of fungal hyphae, some

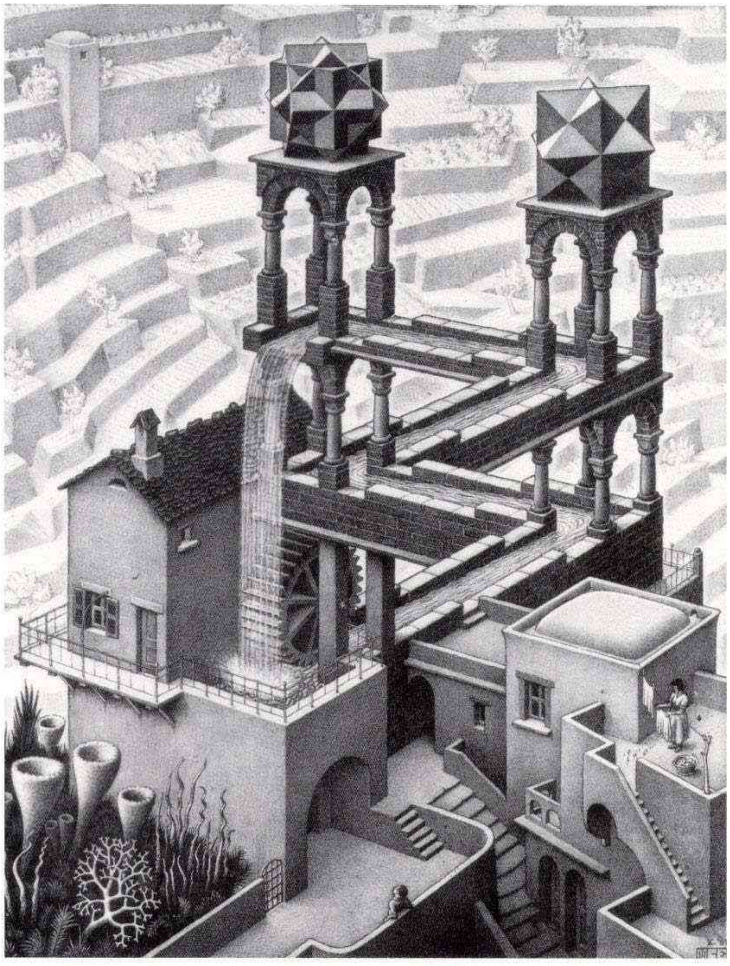

Figure 2. Thinking about whole lichens isn't always easy. "Waterfall" lithograph by Cornelis Escher

scattered algal cells: little wonder if it puts us in mind of some quaint, imperfect hand-me-down from a bygone age: a biological model T Ford say. Yet we forget, or neglect to remember, that the lichen ectosystem has been in place for hundreds of millions of years. Let's not be too astonished if it turns out, as I think it's beginning to do, that the fungi and algae of at least some lichen lineages have achieved a level of physiological integration and sophistication scarcely less "perfect" than that within our own cells.

Reductionist approaches have contributed much concerning the identities of the lichen partners, and not a little regarding how the lichen partners conspire to produce a lichen; but there are still many details the lichen ecologist would need to know – especially concerning the workings of whole lichen thalli – in order to answer the ultimate question regarding the relationship between lichen form and lichen function: in what ways do how lichens "look" relate to where they grow? If I have insisted upon the emergent nature of the lichen enterprise, it is precisely to suggest the very high probability that the internal, physiological "reality" of the lichen bionts and the external, ecological "reality" of the lichen system itself are for all practical purposes incommensurate. This is by no means to say I reject the existence of a quantifiable causal relationship between these two levels of organization. Rather it is to say I have too much respect for the sophistication of the lichen enterprise to believe that a satisfactory elucidation of its innermost workings will soon be forthcoming.

Meanwhile, there is of course much that can still be learned about lichen field ecology. As a pattern ecologist, I have long been in the habit of examining lichens for recurring correspondences in their morphology, behaviour, and spatial distribution. Over the years I think I have learned to discern scores of such patterns, most of which seem to have escaped notice in the literature. It is my view that these patterns, read carefully, can yield crucial insights into the workings of the lichen system. My approach for now will be to turn scientific protocol, so to speak, on its head, attempting to infer from the outside the existence of certain key mechanisms on the inside, rather than the other way around. Admittedly this approach is more suited to hypothesis generation than to "proof." But then proofs, I believe, needn't always come looking like the punch line to a good joke. I heartily accept Henry Thoreau's dictum that some circumstantial evidence can be very strong, "as when you find a trout in the milk." What counts here is the elaboration of lines of evidence that sooner or later tend to converge on a single large conclusion. Nothing *proved*, perhaps, but much suggested.

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The 12 essays in this series have as their primary focus the distributional ecology of foliose and fruticose lichens, collectively macrolichens. Many of the ideas I wish to develop here require the acceptance of certain key assumptions, most of which are supported by recent findings in lichen physiology, though some unfortunately still lack corroborating evidence:

- Macrolichens are the evolutionary hand-me-downs of crustose forebears.
- The crustose forebears of macrolichens represent several independent origins of the lichen thallus, each embodying a unique set of relationships between the lichen partners.
- The transition from the two-dimensional crustose growth form to three-dimensional macrolichen growth forms was made possible through efficiencies in the handling of organic carbon, particularly its transport and storage within the thallus.
- Macrolichen haustoria and appressoria (points of contact between the fungus and the photopartner) function in part as feeding tubes for the periodic provision of nutrients to the photocells.
- Some lichen metabolites function in part as temporary carbon depots, from time to time releasing nutrients to the benefit of one or possibly both lichen partners.
- Many macrolichens require or at least benefit from the metabolic byproducts of bacteria of various kinds, in some cases including nitrogen from nitrogen-fixing bacteria other than cyanobacteria.
- Sexual reproduction aside, the macrolichen thallus is divisible into two basic systems, one involved in the assimilation of carbon, the other in its temporary or permanent storage.
- The details of thallus growth and morphology are ultimately controlled via the maintenance of a specific relationship between these two systems, each lichen according to its kind.

I suppose it goes without saying that macrolichens ought not to be viewed merely as assemblages of thallus parts the primary value of which is to serve as "characters" for reliable identification. When in a dichotomous key we distinguish between 1a and 1b, we are drawing attention to something that ultimately

has its basis in the deep inner workings of the lichen thallus. Better to think of macrolichens, I believe, as self-sustaining ecosystems composed of numerous working parts that taken together enable the successful functioning of the whole.

For me it is an article of faith that most if not all the parts of the lichen thallus perform multiple functions, the most fundamental of which pertain to carbon. The most fundamental question regarding soredia and isidia, for instance, is not to what extent these structures serve as agents of dispersal, but rather in what ways they relate to the assimilation and/or storage of carbon; for it is surely in this context, not dispersal, that they will have evolved in the first place. Similar questions are fairly asked of other lichen parts, including cilia, fibrils, lobules, papillae, spinules, veins, cortical hairs, cortical vents, cortical roughenings, cortical thickenings, cortical thinnings, and so forth.

Here then is my creed: that whatever supplementary roles the various parts of the lichen thallus perform in the operation of the lichen system, it is to their role as carbon boosters, carbon quenchers, carbon conductors, carbon sinks, and carbon depots that we must look if we really wish to understand how the lichen consortium, in the face of environmental inconstancy, contrives nonetheless to elaborate a complex thallus of specific form.

