TWELVE READINGS ON THE LICHEN THALLUS

VI. Reassembly

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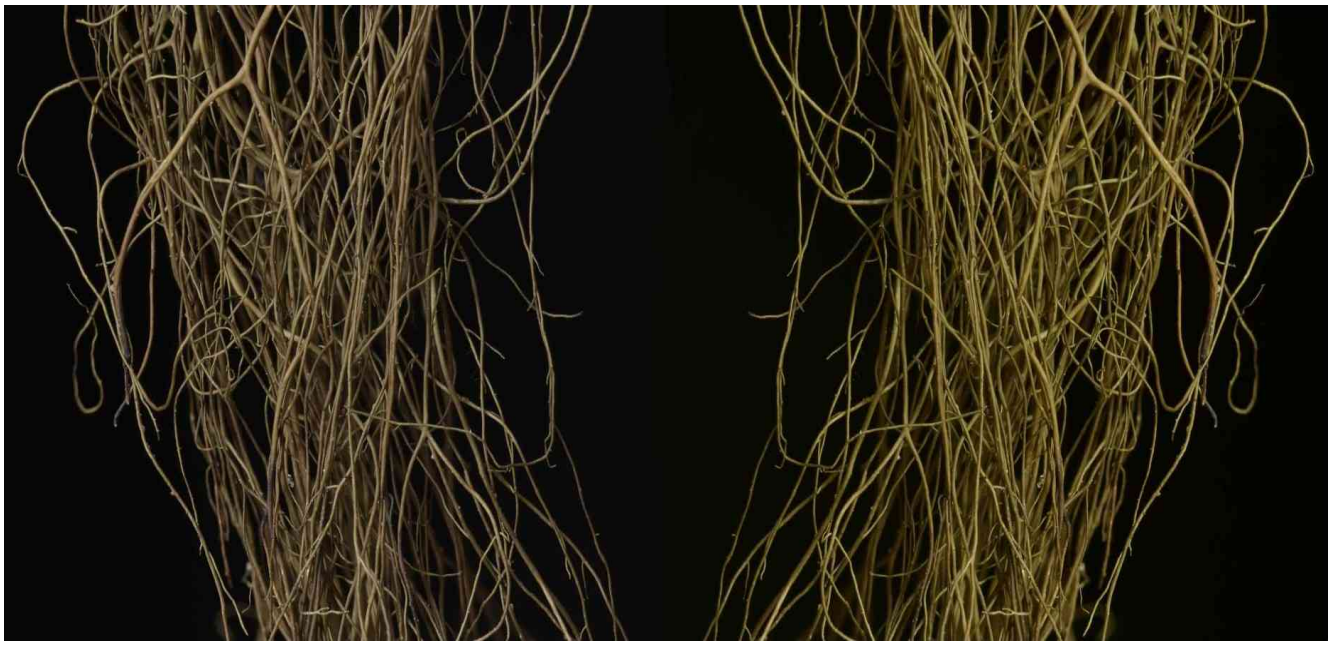


Figure 1. Edible Horsehair (left) and Inedible Horsehair: two lichens, one fungus: *Bryoria fremontii*. No? Photomontage by Tim Wheeler.

To become aware of the possibility of the search is to be onto something.

Walker Percy, *The Moviegoer*

In a world where lichens are routinely passed by with little regard and even less thought, it's refreshing to come upon a bona fide contender like Edible Horsehair. Here's a lichen that's been in the public eye a thousand years. That's how long, give or take, the indigenous peoples of western North America have been gathering it from the branches of trees, and pressing it into service as the matrix ingredient in a kind of vegetarian pemmican they once made, sometimes still do. Steam-cooked with tubers and bulbs and berries in season, these "black lichen cakes" stored well and long: proof against the dark hungry days of winter.*

Still one thing's for sure. There's no use going around looking for Edible Horsehair if you don't know how to tell it apart from *In*edible Horsehair. Fortunately distinguishing these two lichens is something the indigenous peoples of the region learned to do long ago – particularly the elder women of the tribe, sometimes called upon to evaluate, at distance, the culinary potential of some new collecting site. Handed a lichen fragment, grandma would first examine it for colour – dark and shiny was good, pale and dull not so

* Find out more about Edible Horsehair (alias Wila) at: http://en.wikipedia.org/wiki/wila_(lichen)

good – and then pop it in her mouth. Then she'd chew, consider, and finally pronounce the lichen edible or otherwise. Those early grandmothers were western North America's first practicing lichenologists.

It wasn't until 1977, with the publication of Ernie Brodo and David Hawksworth's monograph "*Alectoria* and allied genera in North America," that a scientific explanation for grandma's taste test was finally forthcoming. In specifically targeting Edible Horsehair, the indigenous peoples had hit upon the one hair lichen – there are about a dozen others they might have chosen – that does *not* contain bitter chemical substances. In the case of Edible versus Inedible, the distinction turns on the amount (and apportioning) of a rather toxic, yet highly colourful substance that in concentration lends the thallus a yellowish hue. This is vulpinic acid, a byproduct of the shikimic acid pathway.

Edible Horsehair produces vulpinic acid only in the apothecia and soralia which, as these are usually lacking, means that vulpinic is also usually lacking. Inedible Horsehair, by contrast, accumulates vulpinic pretty much throughout the thallus: apothecia, soralia, cortical vents (pseudocyphellae), and, not least, the cortex itself. If you can think of Inedible Horsehair (Figure 1b) as Edible Horsehair (Figure 1a) with a more or less advanced case of infectious hepatitis, then you've got the general idea.

Edible Horsehair (fungal partner: *Bryoria fremontii*) and Inedible Horsehair (f.p.: *B. tortuosa*) were first formally described 150 and 100 years ago respectively. Since then both lichens have usually been regarded as "good" species – which in itself is a "good" thing since, as I say, indigenous peoples had already come to this about a thousand years earlier. Still there's reason to wonder aloud whether Edible and Inedible really *are* distinct lichens. The pros and cons of the case are multiple and mostly rather abstruse (see below); but finally they amount to the observation that many other lichen species are known to be chemically variable – some thalli contain such and such a substance, others lack it – so why should Edible and Inedible Horsehair be any different? Why couldn't they simply be chemical forms – chemotypes say – of one and the same species?

Well guess what. Just this year Saara Velmala, a PhD student at the University of Helsinki, published a paper (Lichenologist 41: 231-242) in which she shows – or rather her molecular data does – that Edible and Inedible contain one and the same fungus, *Bryoria fremontii*. And from what I understand from Saara, early molecular work on algal partners in Horsehair lichens in general suggests that a single algal species is likely involved here too. From this, two things: first, the name *Bryoria tortuosa* must now be relegated to the dust bin of lichen synonymy; and second, Edible Horsehair and Inedible Horsehair are to all intents one and the same lichen.

The case is sound, or seemingly so. According to current majority opinion – among professional lichenologists I mean – a lichen and its fungal partner are pretty much the same thing (Essay I). So much so that lichens don't even have their own scientific names (Essay II). In my view this is unfortunate, since it tends to get in the way of careful thinking about lichens as something *other* than their fungal partner (Essay IV). If only for this reason I think it's fair to ask whether sharing the same fungus *necessarily* means that Edible and Inedible Horsehair are also the same lichen. The same fungal identity, yes. But the same lichen? This is where the story starts to get interesting – and involved too, requiring at least two additional essays besides this one to relate. For now, however, I'll have to content myself with setting the stage and wading through some theoretical stuff it would be better not to clutter more than one essay with.

First some notes on distribution. Actually this is more interesting than might at first appear, since our lichens exhibit two *kinds* of distribution. Edible is rather continuously distributed throughout the western cordillera, whereas Inedible turns up only here and there – as though it were always "just getting started." Only in summer-dry regions near the limits of Edible Horsehair does Inedible Horsehair really come into its own. By themselves these patterns don't tell us much: we could as easily be contemplating two lichens with different, albeit overlapping ecologies, or one lichen drawn out to two different chemical strains under different environmental conditions. More telling, I think, is the observation – confirmed in a five-year transplant experiment I once conducted – that these lichens don't actually intergrade, even if they sometimes seem to. So perhaps their distributional differences have something to do with dispersal and/or establishment.

Different from most hair lichens, Edible and Inedible occasionally produce apothecia and hence, by extension, fungal spores. Nobody really knows if the spores actually get around to resynthesizing – creating a new thallus from scratch – but if they do, which seems likely, then we're faced with two quite different scenarios: either Edible and Inedible are genetically distinct after all, their respective fungal spores resyn-

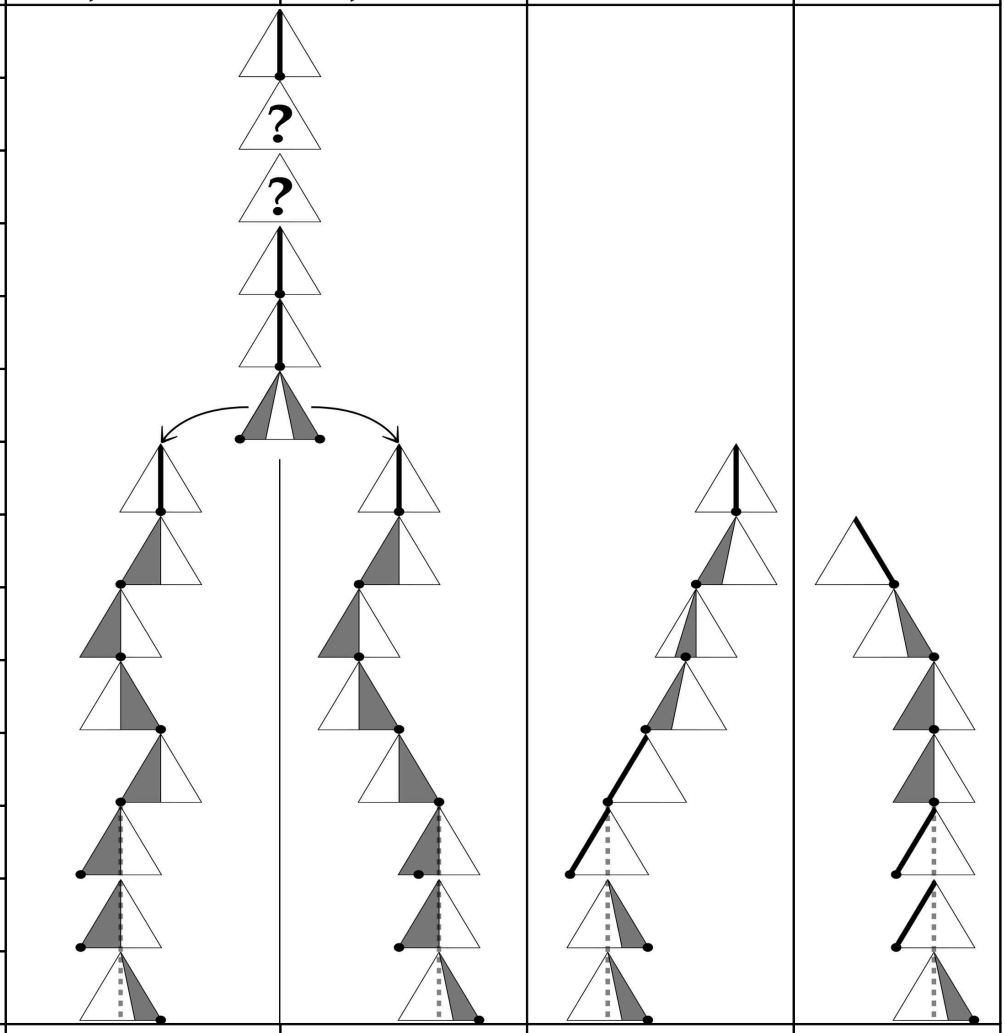
DECISION POINTS ↓		HORSEHAIR LICHENS (Fungal Partner: *Bryoria*)			
		EDIBLE (*fremontii*)	INEDIBLE (*fremontii*)	WOOLLY (*lanestris*)	ELECTRIC (*bicolor*)
1 ↓	fungal spore: strict				
2 ↓	incompatible alga: not known				
3 ↓	prethallus: not known				
4 ↓	compatible alga: strict				
5 ↓	thallus formation: strict				
6 ↓	2ndary chemistry: low, mod, high				
7 ↓	first branch: strict				
8 ↓	lateral branch: few, some, many				
9 ↓	terminal branch: none, weak, strong				
10 ↓	dominant branch: none, weak, strong				
11 ↓	cortical vents: none, some, many				
12A	apothecia (spores): none, some, many				
12B	soralia (soredia): none, some, many				
12C	thallus fragments: none, some, many				
13A ↑	spores return to 1:	rare	infrequent	N/A	N/A
13B ↑	soredia return to 7:	rare	rare	**frequent**	N/A
13C ↑	frags. return to 8:	**very frequent**	**very frequent**	**very frequent**	**very frequent**

Figure 2: Reassembly Flowcharts for four Horsehair Lichens. Note that Edible Horsehair and Inedible Horsehair share the same fungal partner (*Bryoria fremontii*), and may also partner with one and the same alga, as reflected in decision points (DPs) 1-5. A hypothetical bifurcation at DP 6 initiates two developmental pathways marked by differing levels of metabolite production: negligible in Edible versus high in Inedible. DPs 8-10 are reiterated throughout the life of the thallus in all four lichens, with the likelihood that different portions of the same thallus will initiate under different sets of environmental conditions; presumably this accounts for observed discrepancies in subsequent thallus morphology through DPs 11-12. The total potential range of freedom for each DP is represented by a triangle, with the actual available portion (= "bias") indicated by the dark line or grey area. Areas darkened on the right represent a "high" bias setting (i.e., the designated feature arises readily), whereas those darkened on the left indicate a "low" setting (feature rarely produced). Some DPs are "strict" in the sense that they allow little or no freedom for innovation (dark line), while others are more or less "liberal," allowing a continuous range of options (broad grey area). Dots represent the most frequently encountered bias for thalli growing under optimum conditions. DP 6, with two discontinuous options, can be termed a "togglepoint"; see Figure 3. Graphics by Jason Hollinger.

thesizing true to the parent lichen; or else, which is much more probable, and certainly much more intriguing, resynthesis by *B. fremontii* opens up two quite different developmental potentials, one giving rise to Edible hair. In any event, this is hardly the whole story, since these lichens have two additional reproductive modes at their disposal: fragmentation and soredia. But these will have to wait another day.

Now for the theoretical stuff. I wouldn't obtrude these details upon the attention of my readers if I didn't think an informed reading of the lichen thallus depended on them: Edible and Inedible Horsehair for now, but also macrolichens in general. Here it helps to recall that lichens, though they look and behave like organisms, nevertheless operate as systems (Essay V). This means, for example, that it's not quite right to say that lichens "grow." As a matter of fact, plants and animals and fungal hyphae all grow; but lichen thalli "elaborate." Lichens are more like a good conversation, each following its own internal logic, no two thalli coming out quite the same. As *biological* systems, lichens do of course elaborate according to definite inherited "ground rules." But how these rules play out during thallus elaboration depends on a never-quite-predictable interplay between genetically specified internal feedback systems and more or less random external input from the environment.

Taken together these concepts suggest – at least to me – that lichen morphology needn't always be in a one-to-one relationship with the phylogeny of the lichen fungus. Examples aren't hard to come by, as for instance cephalodia and photomorph pairs (photosymbiodemes). Closer to home I'd say we have another example in Edible and Inedible Horsehair.

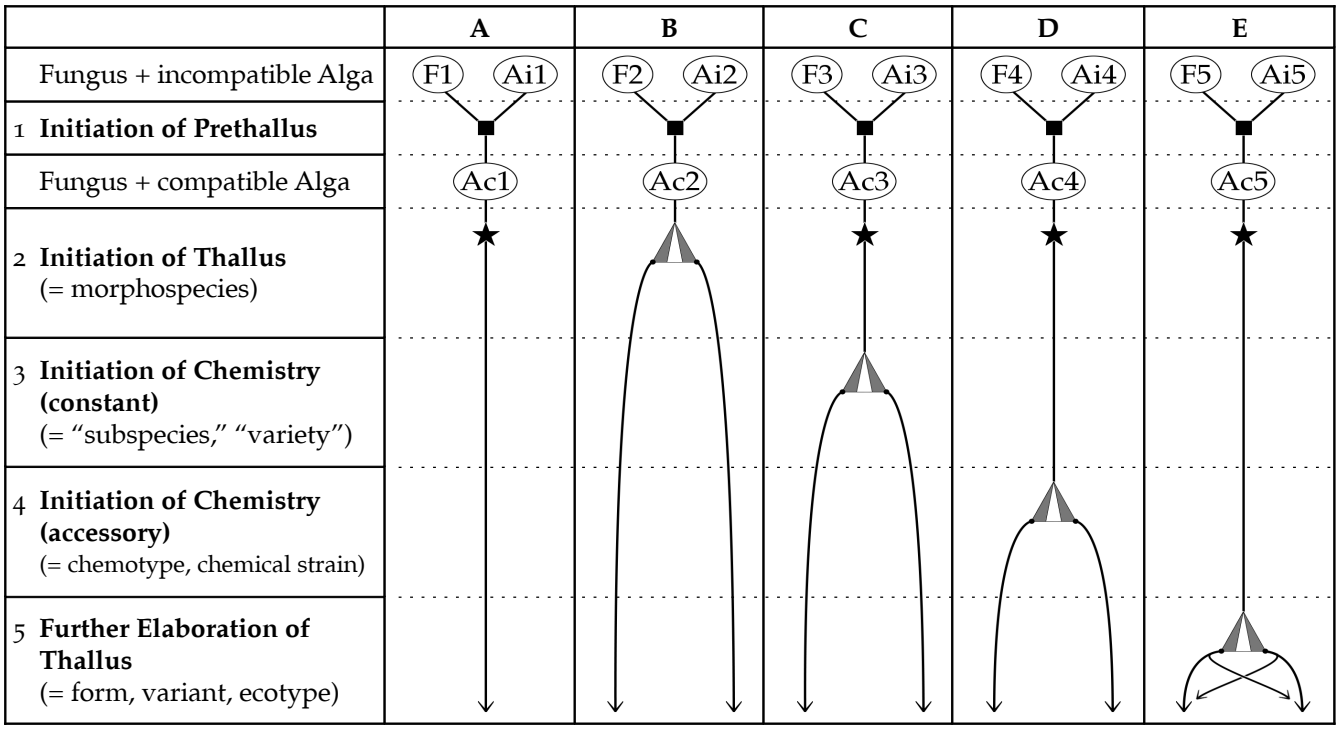


Figure 3. Thallus Reassembly Hypothesis: The Togglepoint Principle, applied to four hypothetical chlorolichens, with suggestions for a phylogenetically uncoupled taxonomy of whole lichens. Note: A togglepoint is defined as any developmental decision point presenting a *discontinuous* range of options; see Figure 2.

From left to right: (A) Togglepoint absent (1 phylospecies, 1 morphospecies); (B) Togglepoint encountered during thallus initiation (1 phylospecies, 2 morphospecies); (C) Togglepoint encountered during initiation of constant chemistry (1 phylospecies, 1 morphospecies including 2 subspecies or varieties); (D) Togglepoint encountered during establishment of accessory chemistry (1 phylospecies, 1 morphospecies including 2 intergrading chemotypes or chemical strains); and (E) Togglepoint encountered during subsequent thallus elaboration (1 phylospecies, 2 intergrading forms, variants or ecotypes).

This schema does not consider potential morphological influence by the bacterial partners (bacteriobionts). Ac = compatible algal partner, Ai = incompatible algal partner, F = fungal partner, star = lichenization event, triangle = togglepoint.

Far from representing an isolated case, these lichens will eventually be shown, I believe, to belong to a whole class of one-fungus-two-lichens phenomena expressed across a wide array of lichen systems, particularly among fruticose genera like *Cladina*, *Cladonia*, *Stereocaulon*, *Usnea*. Anticipating this, it might be helpful here to introduce the "Thallus Reassembly Hypothesis," or TRH. TRH visualizes the lichen as an integrative system shaped by a more or less sequential series of decision points. Fifteen such decision points are given for Edible and Inedible Horsehair in Figure 2, though this is in fact an arbitrary number; many additional decision points might have been included. What is important here is that these so-called "decision points" are really the physical outward manifestation of internal feedback systems otherwise hidden from view (Essay V). The relation of the thallus to a particular decision point is referred to as its "bias." The caption in Figure 2 discusses bias in relation to other associated terms.

By far the great majority of decision points encountered during thallus elaboration are likely to take the form of a narrow to wide array of continuous, interconnected options (Figure 2). Occasionally, however, a *dis*continuous range of options is presented instead, in which case the decision point in question qualifies as a "togglepoint." Togglepoints present pairs of options opening out on mutually exclusive opportunities for thallus development. Which option a young, elaborating thallus actually takes is doubtless determined by a complex of environmental cues about which very little or perhaps really nothing is as yet known; but clearly this one decision will have a profound effect on future thallus development. It is for this reason that togglepoints form a cornerstone of the TRH, as indicated in Figure 3.

How togglepoints arise is impossible to know, but fairly easy to imagine. At a running guess, I'd say they develop when a pre-existing feedback system within the lichen begins to compete with some alternate system newly arisen in response to some new environmental exigency. Usually the competing systems will eventually merge (= broad amplitude), or else one will prevail at the expense of the other (= broad or narrow amplitude). Under certain circumstances, however, what results must be a kind of Mexican standoff whereby both systems "win" simply because neither loses. What is "won" here is an increase in overall fitness for the lichen system as a whole. Because there are now two alternative systems in place of one, the lichen partners are able to occupy much broader range of environmental conditions than would have been available to it prior to the evolution of that particular togglepoint.

Butterfly effects being what they are, you might expect the placement of a togglepoint (i.e., relative to thallus development) to correlate with the strength of its subsequent impact on thallus development. In principle an early intersection should affect thallus development much more profoundly than a later one. Follow the reassembly process backward far enough, and the subsequent pairs of thalli begin to look like separate species. And so, in a sense, they are – at least inasmuch as they represent two discrete lichen systems unlikely to converge on a single outward morphology. I play around with this idea a bit in Figure 3, where I attempt to show how the TRH might eventually be gentled into a workable taxonomic system capable of accommodating two fundamentally different, yet largely overlapping species concepts: one a phylospecies concept based on fungal phylogeny, and pertinent to the lichen fungus alone; the other a morphospecies concept relevant only to the whole lichen.

In the end it comes to this: Whether Edible and Inedible Horsehair warrant separate taxonomic status *as lichens* is less a matter of scientific "fact" and more a question of definition and perspective (Essay IV). Yet when we come to contemplate lichens as complex, highly integrated, self-corrective systems, we find ourselves confronted with the considerable likelihood that thallus form may sometimes align more closely with thallus function than with the genetic identity of the constituent members. The indigenous peoples of western North America have been differentiating between Edible Horsehair and Inedible Horsehair for a very long while. I personally think they're on to something, and would like to see professional lichenologists continue to follow suit – even if doing so requires recognition of two taxonomic systems. A lot to hope for no doubt, but surely not too much to ask.

