

TWELVE READINGS ON THE LICHEN THALLUS

X. Homeostasis

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Figure 1. Fan Pelt (fungal partner: “*Peltigera*” *venosa*): probably not what you think. Photomontage by Tim Wheeler.

All models are wrong but some are useful.

George Box

THE MACROLICHEN THALLUS IS (I keep saying) *built*, not grown (Essay IX). It comes together more in the manner of a *relationship* – an episode from Days of our Lives – than anything you’d find diagrammed in a textbook on developmental biology.

To me it seems a minor miracle that the macrolichen thallus comes together at all. How indeed does a lichen, a composite organism (Essay IV), endowed with neither roots nor limbs nor waxy cutin nor efficient water storage, how does such an organism contrive not only to live in places where nothing else wants to, but also to there build itself an elaborate thallus of specific form?

This, you’ll grant, is a question. It’s a question I’ve asked before (Essay III), and it’s the question I want to dedicate this essay to answering. Rounded out, it comes to down to asking how macrolichens do it: how *do* macrolichens work, anyhow?

Obviously this is a vast and treacherous terrain. Doing it justice will absorb the final three essays in this series. Here I’ll focus mostly on the relation of lichen “structures” – soredia, rhizines, cortical vents, etc. – to the functioning of the lichen thallus. As always my vantage will remain on the far, emergent side of lichen systems, where once again I’ll draw inferences from outside in, rather than the other way around (Essay IV).

MACROLICHEN BASICS

First up, a short refresher on the macrolichen: its basic parts. There may not be too much here most enrichened readers don’t know already; but at least there’ll be some comfort knowing we’re all on the same page.

Stripped to its undershorts, the macrolichen thallus can be seen to consist of three basic parts: (1) the *lichen*

cortex, (2) the *lichen medulla*, and (3) the *lichen algae*. *Lichen bacteria* may also well belong in this line-up (Essay VIII); but we're not quite there yet.

1 **The lichen cortex** is a water-absorbent protective layer – a sort of exoskeleton – composed of indistinct, globular or sometimes elongate fungal hyphae all cemented together in a fungal matrix of varying thickness. Whether nature has invented a more responsive, highly versatile surface layer is doubtful. In some ways the cortex has the look of a cell wall (Essay VIII). Not only does it provide the lichen with structural support, it also oversees water and gas exchange, and controls the quantity and quality of light received into the thallus interior. Depending on species – and environmental conditions – the lichen cortex varies across a wide range of attributes: thickness, compaction, permeability, opacity, pigmentation, crystalline chemistry, hyphal alignment, surface texture. Sometimes it bears tiny hairs (tomentum, dew hairs), while other times it wears a coat of calcium oxalate crystals (pruina), dead cortical cells (epinecral layer) or, indeed, a see-through polysaccharide negligee (epicortex). No classification system will ever do justice to the synergistic complexity of the lichen cortex, which even across the length and breadth of a single thallus can vary in bewildering degree. This same variability in cortical structure must surely enforce differential rates of photosynthetic activity in different portions of the lichen thallus; and in so doing may well help to shape thallus morphology in ways as yet scarcely guessed at. Whether clothes really do make the man is questionable; but that the cortex really *does* make the lichen, or at any rate its outward form, seems fairly certain.

2 **The medulla** is the lichen's internal plumbing system, responsible for the transport of water, minerals and carbohydrates through all parts of the lichen thallus. Physically it's made up of loosely to compactly interwoven, partly anastomosing fungal hyphae connected at one end to the cortex (gateway to the external world) and at the other end to the lichen algae. Different from cortical hyphae, which are water-absorbent, medullary hyphae are thinly coated in hydrophobic rodlets. Any water entering the lichen medulla is therefore forced along the water-absorbent *inner* hyphal walls. Water movement is inwards toward the algae during periods of wetting, and outwards toward the cortex as the lichen dries out again. This to-ing and fro-ing

of solutes is a prerequisite to nutrient transport in macrolichens – though probably less so in microlichens – and is certainly one reason why macrolichens almost invariably colonize microsites subject to wetting and drying at frequent intervals.

Meanwhile the medulla itself remains dry even in the wettest weather, ever open to gas exchange.

3 **Lichen algae** are the photo-energetic engines of the lichen enterprise. In green algal macrolichens – my focus here – they're located by the many hundreds or thousands in a discrete layer just below the cortex. In common with medullary hyphae, lichen algae are coated in a hydrophobic layer that transmits light and gases, but prevents external wetting. Each algal cell is held in place by a short thumb-like or otherwise opposable outgrowth of some nearby medullary hypha. These hyphal outgrowths don't actually penetrate into the interior of the algal cells, rather they press against them – like stethoscopes – or sometimes slightly into them. Far from harming the algae, the outgrowths act as two-way feeding tubes, both furnishing them with water and dissolved nutrients, and at the same time siphoning off any excess carbohydrates. They even reposition the algae according to changing light conditions! Only in age are the contents of the algal cells finally "harvested." Whether the medullary hyphae cycle carbon back to the lichen algae in time of need is unknown and for practical purposes seemingly impossible (carbon withdrawn from the algae is converted by the lichen fungus to mannitol, no longer alga-accessible); though on theoretical grounds it must sometimes occur. Also unknown is by what means lichen algae by the hundreds or thousands communicate their innermost individual physiological needs to the ever-responsive lichen cortex.

Strictly speaking only the cortex, medulla and algal layer are required to make a workable macrolichen. So why then do all macrolichens maintain several structures additional to these, e.g., rhizines, rhizoids, soredia, pseudocyphellae, cilia, fibrils, marginal lobules, cortical hairs, papillae, maculae, and so on? And this is not even counting numerous thallus processes like cortical thinnings, cortical thickenings, cortical wrinkling and roughening, isotomic and anisotomic branching, programmed stress cracks, and the production of cortical and medullary compounds in tropical array. Clearly the existence of these and many other theoretically "extraneous" macrolichen

structures points to the elaboration, over evolutionary time, of numerous metabolic needs and niceties in whose service they are built anew at each successive generation. More on this in a moment.

MACROLICHEN CARBON ECONOMY: THEORY

Evolution moves forwards backwards. All attention is permanently focussed on what's come before, right up to this very instant, but with no attention whatsoever – not a single intent – on what lies ahead. What we term a species' or an organ's ecological or metabolic function always bears the imprint of earlier functions long since abandoned. We say things like "rhizines are holdfasts," "soredia are for dispersal"; but clearly it would be more accurate to say that these functions are in fact evolutionary hand-me-downs from earlier functions – each nested in a particular context – that in turn derive from earlier functions still. Go back far enough and eventually we're in plain view of the most basic function of all, the maintenance of carbon economy. The central importance of carbon economy resides in the sheer overwhelming dominance of carbon as an element of all living things, lichens not excepted. Though nowadays usually much obscured, this primary function of all biological function is necessarily still being served.

Carbon economy in lichens, as in plants, is helpfully thought of as a *dynamic balance* between two somewhat opposing forces: rates of carbon assimilation versus rates of carbon expenditure. Carbon gets used up partly in fuelling respiration by the lichen bionts, but mostly in sustaining thallus growth. What's important here is not the absolute *amount* of free carbon available, but rather how it balances against the potential for growth. This in turn is a function of several interactive factors including, on the inside, inherent variation in the capacity for photosynthesis and respiration, and, on the outside, temperature, illumination, moisture, and not least the availability of fixed nitrogen – which is needed for synthesis of the proteins needed for building cell walls needed for growth.

This concept of dynamic balance is tidily captured for vascular plants in the following formulation: "if the ratio of carbon to nitrogen is too high, grow root; otherwise grow shoot." Of course lichens have neither roots nor shoots in the strict sense; but they do have algae (= carbon assimilation) and fungi (= carbon expenditure); and this provides at least a theoretical basis for introducing the root/shoot model to lichens. It was the

Swedish ecophysiological Kristen Palmqvist who saw this first; and in her classic paper, Carbon Economy in Lichens (Palmqvist 2000: 11-36) she proposed three lichen-based variants of the root/shoot model:

The first variant applies to lichens consorting with an algal partner, i.e., chlorolichens (the ones I'm focussed on in this essay):

*If carbon is limiting, grow algae; otherwise grow fungal hyphae.**

The second variant applies to lichens with a cyanobacterial partner, i.e., the cyanolichens):

*If carbon and/or nitrogen is limiting, grow algae; otherwise grow fungal hyphae.**

Though not explicitly formulated by Palmqvist, the third variant applies to lichens having both algal and cyanobacterial partners, i.e., cephalodial lichens: (Essay VII)

If carbon is limiting, grow algae; if nitrogen is limiting grow cephalodia.

Granted all this takes some thinking about. Yet there can be little doubt that the rewards are worth it: Kristen Palmqvist has taken a first large step toward "demystifying" the lichen thallus. Previously it seemed a kind of biological black box, but now it's more like hieroglyphics. The first question we should ask of a lichen thallus is how much of it is thalline (= "grow algae"), and how much strictly fungal (= "grow fungal hyphae"). Examine any two macrolichens of similar age growing side by side. How big or small they are, or what they look like doesn't matter. One will have copious soredia or lobules or fibrils or isidia, and the other not. These are thalline structures. Or again, one will probably have rhizines or cilia or papillae or apothecia, and the other not. These are strictly fungal structures. Whatever such differences you detect between your two lichens certainly bespeak carbon economies very differently adapted: the first more to carbon deficit, the second more to carbon surplus. I don't say this is all we need know about the workings of the lichen thallus; but

*Actually Palmqvist's original wording is: *if carbon is limiting, allow photobiont growth; otherwise grow hyphae and if carbon and/or nitrogen is limiting, allow photobiont growth, etc.* However, putting the matter like this implies that the lichen fungus is in charge of the alga – an instance of the mycological perspective (Essay IV). My own preference is for the ecosystemic perspective, wherein the notion of centralized control becomes meaningless. My apologies to Kristen.

at least we now have a framework within which seriously to think about – and experiment with – variations in thallus elaboration.

How about this? There are many more lichen fungi in the world than there are lichen algae – apparently at a ratio of 100:1, or even higher. From this it follows, or seems to, that a rather small number of algal “crops” are currently in cultivation by a much larger number of fungal “farmers.” What differs between two closely related lichens is thus not likely to be the crop, but rather the techniques being applied to its cultivation. Framing the lichen enterprise this way effectively focusses lichen field ecology around a single question, i.e., “How do we best interrogate the cultivation techniques being used by the lichen fungus?”

MACROLICHEN CARBON ECONOMY: APPLIED

Of course we shouldn't expect the root/shoot hypothesis to apply equally to all parts of every thallus. Each macrolichen species can be seen as a mixture of “stable” structures, which vary little from thallus to thallus, and of “unstable” structures, which can vary considerably, sometimes even within a single thallus (Essay VI). Not surprisingly the root/shoot hypothesis links most conspicuously to unstable structures, which now take on special importance in any attempt to “read” the thallus.

Which thallus structures can be judged stable, and which unstable, varies greatly from one lichen species to the next. Indeed most if not all structures are likely to be unstable in at least some lichen species. In the terminology of Essay VI, unstable structures have low to medium “bias settings.” The either/or structure of the root/shoot hypothesis implies two fundamentally unlike types of unstable structures in lichens. The first type initiates in response to carbon *undersupply* relative to growth potential, and consist mostly of thalline structures; these are the *carbon boosters*. The second type elaborates during periods of carbon *oversupply*, and is exclusively fungal; let's call these the *carbon sinks*. It seems clear, however, that both carbon boosters and carbon sinks, in order to exist, must be tied to – and linked by – some sort of carbon transport system serving the thallus as a whole. As mentioned, the medullary hyphae may themselves be adequate to perform this function; though additional conductive systems should probably be looked for in the case of the largest macrolichens. These can be referred to as *carbon distributors*. Table 1 provides

numerous examples of lichen structures that may be expected to function either as carbon boosters, sinks or distributors. Four subgroups within two of these functional groups are also designated.

CARBON BOOSTERS

Soredia are usually described as units of vegetative dispersal. Here I propose that these structures have actually arisen in a quite different context, as carbon boosters; and that at least during their early developmental stages, they continue to amplify carbon supply in specific areas of the lichen thallus (Essay V). There's plenty of circumstantial evidence that improved gas exchange into the thallus interior directly or indirectly enhances carbon assimilation in nearby lichen algae. Presumably this is the main physiological benefit conferred by cyphellae, pseudocyphellae, tubercles and other forms of cortical venting. Soredia perform a similar function – and go one better. As loose, non-corticate fungal-algal clusters directly exposed to the air, they are likely to assimilate carbon at rates far exceeding those achieved within the (more poorly ventilated) thallus itself.

A question. Why do soredia and isidia almost always remain minute so long as they're attached to the parent thallus? As dispersal units, both are clearly capable of enlarging into full-fledged lichens; yet generally this happens only once they become detached. The prevailing view seems to be that the lichen fungus exerts some sort of “control” on them – as indeed on everything else having to do with the lichen thallus. Outside lichenology such a view would by now be outdated. A more viable explanation – more in keeping with systems theory, and certainly with the concept of synchronicity – is that soredia and isidia simply fall in line with preexisting nutrient transport systems within the parent thallus. Instead of allocating any excess fixed carbon to their own growth, they shunt it back to the parent thallus – following the same conductive system that stimulated their growth in the first place; call it the line of least resistance. Such behaviour has nothing to do with fungal control; integrated biological systems don't work that way. A similar line of reasoning applies to other macrolichen structures of determinate size, including lobules, isidia, spinules and fibrils.

CARBON REDISTRIBUTORS

Lichens are said to have no specialized conductive tissues. But then neither, in the same sense, do mycorrhizae – notwithstanding their famed ability to

move nutrients around all over the place. I'd argue that the reason fungi, including lichen fungi, tend not to have obvious transport systems is simply because they don't need them; each fungal hypha is itself a ready-made conducting system. When we add together, for a single mature lichen, all the hyphal linkages – to the cells of the cortex at one end and to thousands of individual algal cells at the other end – what we've got, surely, is real conducting power. Now link these same hyphae together in an anastomosing system, and let some of them coalesce as water-absorbent central cords, stereomes and other internal cartilaginous structures, and surely what now emerges is functionally a "vascular system," albeit one built to fungal specs. Add to this, again, the probable conducting power of veins and cortical arterials and, indeed the prosoplectenchymatous cortex itself, and we've accounted for pretty well all lichen species of a size actually to require a vascular conducting system. Without which, I don't really see how outsized, rapidly growing foliose lichens like the Lungs (f.p.: *Lobaria*) or the Pelts (f.p.: *Peltigera*) could have evolved.

CARBON SINKS

Carbon sinks are rest homes for excess carbohydrates. Consider the rhizine. Rhizines of course are holdfasts; they keep the lichen in place – while in at least some lichens they also enhance the uptake of water and nutrients. These things granted, I can think of no reason why lichens should actually require holdfasts in the form of rhizines. The Bone Lichens (f.p.: *Hypogymnia*) get by without them, attaching instead by means of tiny hyphal outgrowths of the lower surface. Other macrolichens have either a single basal holdfast or, especially in foliose species, a more versatile, indeterminate attachment organ sometimes referred to as a hapter. From the perspective of carbon economics, I'd say rhizines are likely to function more after the fashion of stilts, that is, their primary role is to elevate the algal layer above the supporting surface, where improved air circulation presumably abets metabolic efficiency. Notice that the characteristically inflated lobes of the Bone Lichens surely perform a similar function, with only the strictly fungal portions of the lower surface in direct contact with the substrate.

IMPLICATIONS

So once again, our question: how do macrolichens do it? How do they manage, under highly unstable environmental conditions, to construct thalli of specific

morphology? Of course the answer, broadly speaking, is homeostasis. Homeostasis is the tendency of a system to "pull inwards," to achieve a kind of dynamic balance between energy input and output. All living things depend on homeostatic feedback loops (Essay v). Homeostasis in macrolichens appears to take the form of periodic metabolic readjustment effected by "indeterminate" structures including soredia, lobules, cilia, tubercles, etc. In keeping with the root/shoot hypothesis, these and other structures are likely to be triggered by physiological tensions which by their elaboration they help to resolve (Essay v). More specifically, carbon boosters arise during periods of carbon "draw down," whereas carbon sinks elaborate in response to excess carbon relative to growth potential. Given the architectural complexity of many macrolichens, both kinds of structures must often arise simultaneously in different portions of the same thallus.

Notice that carbon sinks are strictly fungal in nature (Table 1). Here belong dew hairs, rhizines, cilia, and water-absorptive cartilaginous strands. By contrast, carbon boosters can be either fungal or thalline. Many, including pseudocyphellae, fibrils and areoles remain permanently attached to the lichen thallus, whereas others, e.g., soredia, lobules and schizidia eventually become detached and then function as lichen vegetative propagules. What's striking about all of the above is that their contributions to the maintenance of the lichen consortium have usually been interpreted, if at all, in terms quite different from the root/shoot model taken up here. Yet biological function is, as I say, necessarily multivariate; so this is not really a contradiction, merely a shift in emphasis.

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So here's my pitch. Lichen field ecology as currently practiced might fairly be described as computer-assisted quantification uninformed, for the most part, by hypothesis. It's been that way, more or less, ever since the introduction of numerical approaches back in the 1960s. This is hardly the fault of numerical approaches. The problem seems rather to be on our side, that is, our analytic methods far outstrip our understanding of the lichen thallus, how it works, how effectively to think about lichen morphology, lichen dispersal, and indeed lichen distributional ecology. As things stand, it's as though we're asking the Hubble Telescope to tell us something interesting about a barn door. If ever field ecology as applied to lichens is to

attain the status of a mature science, we who practice it will first have to transact a major upgrade in our grasp of the lichen enterprise.

The time has come, I feel, finally to teach ourselves to “read” the macrolichen thallus. Lichens need no longer be construed as a biological “black box.” Thanks to the root/shoot model, the link between form and function in macrolichens is robust, certainly more so than in most other taxonomic groups. Yet learning to read the thallus does require effort and,

indeed, protracted apprenticeship. At base a thallus reading is a kind of exercise in hypothesis generation. It’s precisely what lichen field ecology in most applications has needed for a very long time.

To get things started, let me now undertake a thallus reading on Fan Pelt (fungal partner: “*Peltigera venosa*: Figure 1). The main objective of this exercise is to account for most or, if possible, all of the characteristics of Fan Pelt that, so far as we can tell, make it what it is. Let’s see how we go.

FAN PELT (“PELTIGERA” VENOSA): A THALLUS READING

Compared against other Pelt Lichens, Fan Pelt combines a great many curious morphological features. I count seven. First is the diminutive size, scarcely larger than a Canadian quarter. Second is the invariable presence of *copious* marginal apothecia. Third is the remarkable fidelity to freshly exposed soil. Fourth is the single marginal point of attachment, or *rhizopt*; there are no rhizines. Fifth is the presence of cephalodia on the *lower* surface of the lobes. Sixth is the tendency of the cephalodia to detach, fall to the ground, and grow out as tiny gel lichens in their own right. And seventh is the inevitable formation of well developed colonies consisting of numerous spatially distinct lobes. All these characteristics are surely related; but how?

Given its status as a colonial lichen, Fan Pelt is probably best approached at the level of the colony viewed as a single interactive system. The fact that its cephalodia (a reliable source of fixed nitrogen) grow on the lower surface tells us right off there must occasionally be liquid water down there, since water vapour alone isn’t sufficient to sustain them. From this we can already advance the following four testable hypotheses: (1) water must sometimes wick upward along the veins from the rhizopts to the lobe tips; (2) since the cephalodia grow attached to the veins, any excess nitrogen they produce is probably leached out and carried forward to the tips; (3) having a ready and reliable supply of nitrogen must contribute to Fan Pelt’s ability to bear numerous apothecia; and (4) the diminutive lobes possibly reflect the average maximum wicking distance achieved by the nitrogen-laden water.

Take a look at Figure 1 and you’ll notice that the lobes of Fan Pelt actually more closely resemble a partly rolled funnel than a fan. Such lobes doubtless guide rainwater (laden with carbohydrates released through the upper

cortex) first downward to the rhizopt, and then via capillary action up the veins to the lobe tips. Because apothecia in the Pelt Lichens lack algal cells, the energetic cost of their production has to be offset by nutrients supplied by the thallus. If only for this reason it seems reasonable to infer that the rhizopt is not merely a holdfast, but also a powerful nutrient distributor – as suggested, for example, by its comparatively large diameter. Notice how the Tudor-style veins are beautifully set off by dark pigments presumably acting as sinks for excess carbon.

Now to reflect a bit on Fan Pelt’s status as a colonial lichen. Once again the cyanobacterial partner provides a good starting point – here in the form of tiny terrestrial gel lichens scattered around the rhizopt (not shown). In common with the cephalodia, these gel lichens need periodic wetting. They also doubtless periodically release fixed nitrogen, in this case into the soil. Given Fan Pelt’s strict occurrence on soil, we can reasonably hypothesize the existence of an underground hyphal web emanating outward from the rhizopt. These hyphae must absorb much of the released nitrogen, some of which gets cycled back to the parent lichen, and the rest to other nearby thalli early in the establishment phase. At the same time, growth of the parent lobe ceases soon after initiation of the apothecia – after which point any excess carbon is probably also dispersed to other colony members.

One likely consequence of such a system is a gradual build-up of fixed carbon and nitrogen, both continuously recycled through the expanding colony. When at length, however, mosses overtake the last of the bare soil, Fan Pelt is no longer able to establish, and soon the entire system goes into decline. Yet by then it has doubtless produced hundreds of thousand of spores – sufficient, in any event, to ensure colonization of some soil bank newly exposed.

Other explanation threads are feasible, but seemingly less parsimonious.

THALLUS PARTS ↓	CARBON BOOSTERS (Fixed vs <i>Detachable</i>)	CARBON DISTRIBUTORS	CARBON SINKS (Permanent vs <i>Redeemable</i>)
SPORE PRODUCERS			apothecia [†] , perithecia, pycnidia
UPPER CORTEX	cortical cracks (programmed), cortical thinnings, cortical vents*, cyphellae, isidalia*, micropores*, pseudocyphellae, rain cups*, rugae, soralia, tartaria*	prosoplectenchyma (cortical hyphae in parallel)	<i>cortical thickenings</i> , <i>melanins</i> (in part), papillae, scabrosities, scleridia*, <i>secondary substances</i> (in part), verrucae
BRANCHES & STEMS	adventitious branching (early)	podetia, pseudopodetia	isotomic branching
LAMINAL & MARGINAL FEATURES	areoles, <i>blastidia</i> , cavernulae, fibrils, <i>isidia</i> , <i>isidiomorphs</i> , <i>lobules</i> , <i>microsquamules</i> , <i>phyllidia</i> , phyllocladia, <i>polysidia</i> , pustules, <i>schizidia</i> , <i>soredia</i> , <i>sorsidia</i> *, spinules, <i>squamules</i> , tubercles, <i>undulidia</i> *		cilia, dew hairs*, marginal projections [‡] , pseudoisidia, tomentum
THALLUS INTERIOR		cartilaginous strands, central cords, medullary hyphae, stereomes	
LOWER SURFACE OR CORTEX	cyphellae, cortical thinnings, decortications, pilema, pseudocyphellae	arterials*, basal holdfasts, hapters (in part), lamellae, prosoplectenchyma (cortical hyphae in parallel), rhizines (in part), rhizino-se strands, rhizopts, trabeculae, umbilicus, veins	basal holdfasts (in part), hypothallus, melanins, papillae, rhizines (in part), rhizinomorphs, rhizoids, thallospores [§]

Table 1. Hypothetical roles of selected lichen structures and processes in macrolichen carbon economy. Structures designated as “carbon boosters” are expected to enhance carbon assimilation, whereas “carbon sinks” provide storage sites for excess carbon. Some carbon sinks may be “redeemable,” i.e., susceptible of cycling back into the lichen system. Carbon transport within the thallus is presumably accomplished by “carbon distributors.” Notes:

- ♦ In addition to the three functional groups outlined here, a fourth group can be posited, i.e., the “carbon quenchers,” consisting of structures and processes likely to reduce or offset carbon fixation. Possibly belonging here are: algal clustering, biont respiration, cortical thickening, the epicortex, the epinecral layer, heteroderms, the phenocortex, the polysaccharide layer, and perhaps the production of specific secondary substances, e.g., usnic acid.
- ♦ Some thallus “structures” (e.g., foveoles, maculae) may not be directly related to carbon economy, and are excluded from Table 1.

* See note on the following page for definition of these terms.

† Biatiorine and lecideine apothecia only; lecanorine apothecia have amphithecial algae, doubtless somewhat offsetting the energetic costs of apothecia production.

‡ Present in *Cetraria*, *Coelocaulon*.

§ Also termed thalloconidia.

- ♦ Also excluded are carbon efficiencies achieved via thallus form and metastructure, e.g., through nutrient recycling in colonial lichens.
- ♦ Ten previously undesignated macrolichen structures seemingly integral to macrolichen carbon economy are proposed:
 1. **arterials**: irregular, narrowly raised cortical networks, often developing in older thalli of some foliose lichens, e.g., Crinkled Wrinkle (f.p.: *Tuckermannopsis platyphylla*).
 2. **cortical vents**: general term for well delimited openings into the thallus interior; includes cyphelloids (cyphellae and pseudocyphellae), isidalia, micropores (epicortex only), perforations (hollow lobes or branches only), soralia.
 3. **dew hairs**: tiny erect hairs, usually positioned at lobe tips, common in foliose lichens of semi-arid climates.
 4. **isidalia**: isidia-bearing counterpart of soralia, e.g., Oldgrowth Specklebelly (f.p.: *Pseudocyphellaria rainierensis*).
 5. **micropores**: microscopic openings of the epicortex.
 6. **rain cups**: water-collecting depressions in the upper surface, e.g., some Lung Lichens (f.p.: *Lobaria*).
 7. **scleridia**: hardened, rounded, translucent inclusions of the upper cortex, presumably aborted pycnidia, acting as carbon sinks, e.g., some Rockfrog Lichens (f.p.: *Xanthoparmelia*).
 8. **sorsidia** (also “isidioid soredia,” “soredioid isidia”): cortical outgrowths structurally intermediate between soredia and isidia, e.g., Granulating Crottle (f.p.: *Parmelia hygrophila*).
 9. **tartaria**: diffuse, crumbly regions of the (upper) cortex, often giving rise to isidia, soredia, schizidia; sometimes termed “diffuse soralia.”
 10. **undulidia**: the undulating, often friable margins of some foliose lichens, e.g., Ruffled Pelt (f.p.: *Peltigera leucophlebia*).
- ♦ For definitions of other terms included in Table 1, see: Goward (1999: 1-319) and/or Brodo, Sharnoff & Sharnoff (2001: 1-795) and/or Ryan et al. (2001: 8-23) and/or Büdel & Scheidegger (2008: 40-68).