

## TWELVE READINGS ON THE LICHEN THALLUS

### IX. Paralichens

TREVOR GOWARD

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



**Figure 1.** This even-aged lichen “bloom” marks the former presence of a paralichen, here involving *Usnea lapponica*. Ringlet Beard will have come later: the product of a lichen resynthesis event on the heels of an algal bloom involving the lichen alga *Trebouxia* cfr. *usneae*. Photo by Tim Wheeler.

*The implicit waits to be discovered, like a still-unstated theorem in geometry, hidden within the axioms.*

N. G. Charlton

**W**HEN SIMON SCHWENDENER famously announced, in 1867, that lichens are dual organisms, he can scarcely have imagined what powerfully divergent responses his short communication would excite.

Elsewhere I’ve considered what seems to have been the majority response of his lichenological peers: denial tempered with indignation (Essay II). Here I turn my attention to quite another species of response – curiosity born of amazement – which is, after all, more in keeping with the spirit of scientific inquiry.

Confronted with the dual nature of the lichen, many 19th century laboratory scientists will have found themselves asking two questions. First, if it’s true that lichens consist of two organisms, then might it be possible, in the lab, to culture the partners separately? And second, if the lichen partners can indeed be grown separately in culture, then might they further be persuaded to reunite in a new lichen?

Getting definitive answers to these questions has not been easy. Experience has taught that, yes, some lichen bionts *can* be grown in the laboratory, while

others not, or at least not yet. We also now know – which is crucial – that the lichen thallus doesn't grow the same way the lichen bionts grow. Lichens are *built*, not grown; and in this they have more in common with ecosystems, say, and enduring human relationships.

Learning routinely to build lichens in the lab needed about a century of dedicated effort. Notwithstanding some early breakthroughs in the decades immediately following Schwendener's announcement, it wasn't until 1970 that Ahmadjian and Heikkilä announced the first successful lichen resynthesis from spore to spore. The lichen in question was the soil-dwelling species Earthbound Stipplescale (fungal partner: *Endocarpon pusillum*). Since then, many additional lichens have been coaxed to rebuild from their member parts; though only in a few such cases have the resulting thalli yielded viable spores.

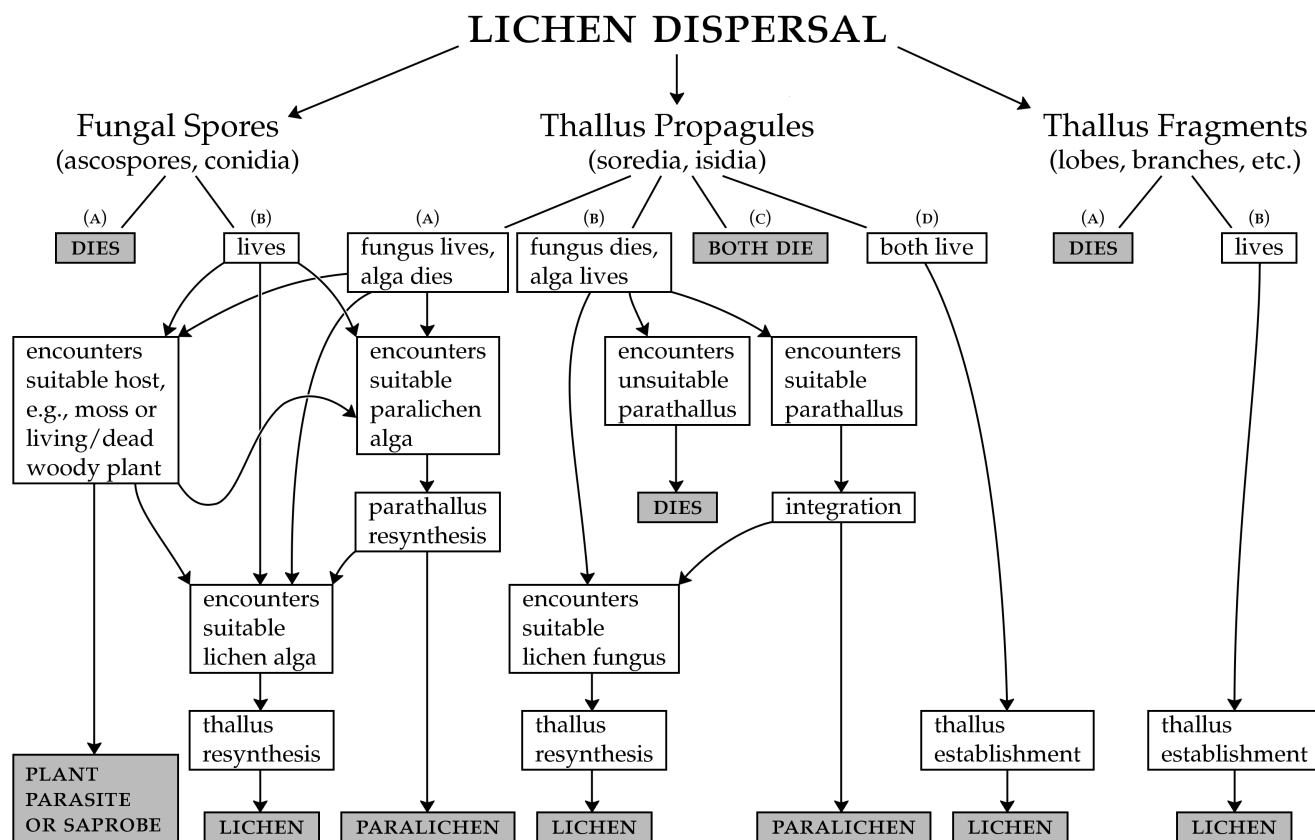
Resynthesis is to the lichen thallus basically what genetic recombination is to the lichen fungus and alga: a reshuffling of genetic material. How and where this reshuffling takes place differs according to case. In the case of the lichen bionts it occurs exclusively within the cell, while in that of the lichen it happens also one level up, in the thallus itself, through the periodic mixing and matching of bionts. In the end it is this repeated coming apart and coming together of the lichen system in potentially new combinations that enables the lichen to keep pace both with a changing environment and with slow genetic changes in its member parts. In short, to evolve.

Bottom-up lichen resynthesis used to be thought an exclusive attribute of apotheciate (or peritheciolate) lichens, in which reproduction depends on the production and dispersal of fungal spores. (To build a lichen, fungal spores need first to team up with their compatible lichen alga). Soredia and isidia, by contrast, come equipt with algae of their own, so have usually been viewed as clonal propagules, that is, they carry the lichen thallus forward to the next generation without modifying it. In fact the situation is not nearly so straightforward. For one thing, soredia during the establishment phase often fuse with other initiating soredia growing nearby. What results – or can result – is a genetically inhomogeneous lichen thallus made up of who knows how many discrete fungal and algal partners. And for another thing, soredia and sometimes even isidia are susceptible of a "dissolution" phase, during which they dissolve into a dark, lumpy mass. During this phase, they likely accept new algal partners and, for all we know, fungal partners too.

It seems a safe bet that lichens have been periodically resynthesizing from scratch ever since the lichen lifestyle arose 400 to 600 million years ago. Evolution being the endlessly inventive process it is, it would be strange if the lichen consortium in all this time had evolved only one protocol to self assembly. Admittedly the early stages in thallus elaboration itself do appear to follow one and the same set of instructions across all lichen groups and all lichen growth forms. Yet we still know very little, with few exceptions, about what happens during the period leading up to establishment, call it the "pre-establishment" phase. My own take is that lichen establishment, as currently understood, is only part of the story – and perhaps a rather small part at that.

As an evolutionary unit the lichen thallus is, as I say, very old. Down through geologic time it will have experienced environmental perturbation at scales we can scarcely imagine: the Permian extinction for one, the K-T event for another. That the lichen lifestyle somehow persisted in the face of environmental catastrophe sufficient to extinguish a majority of other life forms argues forcibly, I think, for the existence of some persistent, highly stable "resting phase" quite separate from the lichen thallus as currently understood. Such a structure seems to me actually *necessary* if we're to account for the present day distribution and population structure of lichens worldwide. So certain do I feel that some such entity must exist that I've lately opted to designate it in a name: the *parathallus* or, in the abstract, the *paralichen*, from the Greek prefix *para*, near, beside, parallel.

In fact paralichens are already well known to lichenologists – though admittedly not quite in the way I have in mind. Here it helps to consider the full range of possible outcomes that await the dispersing lichen propagule after it touches down at some new locality (Figure 2). Should the propagule be a fungal spore, it will either (A) die or (B) go on to form (1) a parasitic or saprobic relationship with a living or dead plant, (2) a lichen, (3) a paralichen, or (4) first a paralichen and then a lichen. So far so good. However, if the propagule is a soredium or an isidium, the situation becomes more complex, as now there are four primary possible outcomes – A, B, C, and D – as well as several secondary and even tertiary ones. Still, note that only outcome D in Figure 2 leads *directly* to the establishment of a lichen thallus; the others get there, if at all, only indirectly, whether via resynthesis of a thallus or parathallus, or else by integrating with an existing paralichen.



**Figure 2.** Outcome Tree for three classes of lichen diaspores: fungal spores, thallus propagules and thallus fragments. Fourteen viable pathways are postulated. Two of these can potentially yield parasitic or saprobic relationships, while eight yield lichens, and four yield paralichens; see text. The lichen thallus is thus only one of three persistent outcomes of lichen dispersal. Shown here are outcomes for bi-membered lichens only. Design concept with Curtis Björk. Graphics by Jason Hollinger.

Providing a workable definition for the paralichen needs a bit of prep work, but is easily managed with the following thought experiment. First visualize an airborne lichen propagule, say a soredium. Now imagine that soredium alighting on (and fixing itself to) the slightly inclined trunk of an elm tree. Accept for a moment that environmental conditions here are beyond the ecological tolerance of the algal colony within the soredium. As the algae gradually die, they give up their stored carbon to the benefit of the lichen fungus. This buys the lichen fungus time to make contact either with a compatible lichen alga or, more probably, with one or more highly specific *non-lichenizing* algae; let's call them paralichen algae. Assuming the latter case, the paralichen hypothesis posits that the bionts now enter into a potentially stable *unlichenized* relationship of which the paralichen may be seen as an emergent property (Essay VIII). I say *unlichenized* because the resulting structure lacks a cortex at all stages of development, hence can't be

regarded as a lichen in the strict sense (Essay VIII). Similar unlichenized structures can also arise in other ways – isidia or fungal spores or even, indirectly, the death of the lichen fungus (Figure 2) – but whatever their origin, the end product comes to the same thing: a **Paralichen**. *n.* any persistent, thin, two-dimensional, non-corticate structure, usually scurfy in appearance, and arising as the emergent property of a complex relationship between one or more lichen-forming fungi and one or more **non-lichenizing** algae and/or cyanobacteria.

Back now to the elm tree. While initially inhospitable to our lichen alga, our patch of elm trunk needn't remain so indefinitely. Even the slightest shift in nutrient status or microclimatic expression may be sufficient to favour the alga's re-establishment here. Sooner or later a few of its cells, transported perhaps on the feet of a resident squirrel, get caught up in the parathallus. Re-inoculated, the lichen fungus responds to chemical signals released by the alga by attaching itself to its newfound partner, and then later more or

less enwrapping it. The alga, in turn, responds with yet more signals, and soon the two partners, reunited, are negotiating, first, the construction of certain non-thalline soredia-like structures characteristic of the prethallus\* and, later, the elaboration of a few small tentative thalline lobes, each bearing its hallmark lichen cortex.

Yngvar Gauslaa, the Norwegian ecophysiologist, recently recounted the following story. Once many years ago, he inoculated the trunk of an elm tree in his home garden, near Oslo, with the isidia of Peppered Moon (f.p.: *Sticta fuliginosa*) – a species not known to occur within 30 km. When Yngvar checked the tree the following year, he'd hoped to find a few small lobes of Peppered Moon; but in fact he found nothing. The following year he checked again. Still nothing. The year after that yielded the same result; and eventually Yngvar forgot about his failed inoculation experiment, and moved on to other things. Imagine, then, his surprise, more than a decade later, when he noticed 15 or 20 tiny, uniformly sized lobes of Peppered Moon growing in that very spot of elm trunk! Yngvar reports similar, albeit not quite so protracted experiences with Lungwort (f.p. *Lobaria pulmonaria*) and Old Smokey (f.p.: *Pleurosticta acetabulum*).

According to the paralichen hypothesis, environmental conditions at the time of Yngvar's inoculation experiment must have been unsuited to establishment of a new lichen thallus. Presumably the isidia disintegrated when the lichen alga (actually a cyanobacterium: *Nostoc*) within them died. The lichen fungus itself, however, did not die, rather it must have gone on to form a stable parathallus with one or more paralichen cyanobacteria better suited to this particular microhabitat at this particular time. Once established, the parathallus persisted for more than a decade until conditions favoured re-establishment by the lichen-compatible cyanobacterium over the "germination bed" made available by the parathallus.

The paralichen is surely not some one-off bivouac, some emergency shelter erected in haste in time of duress. In my view it more likely represents a discrete evolutionary unit comparable in its way to the lichen thallus which, for that matter, it very likely predates;

---

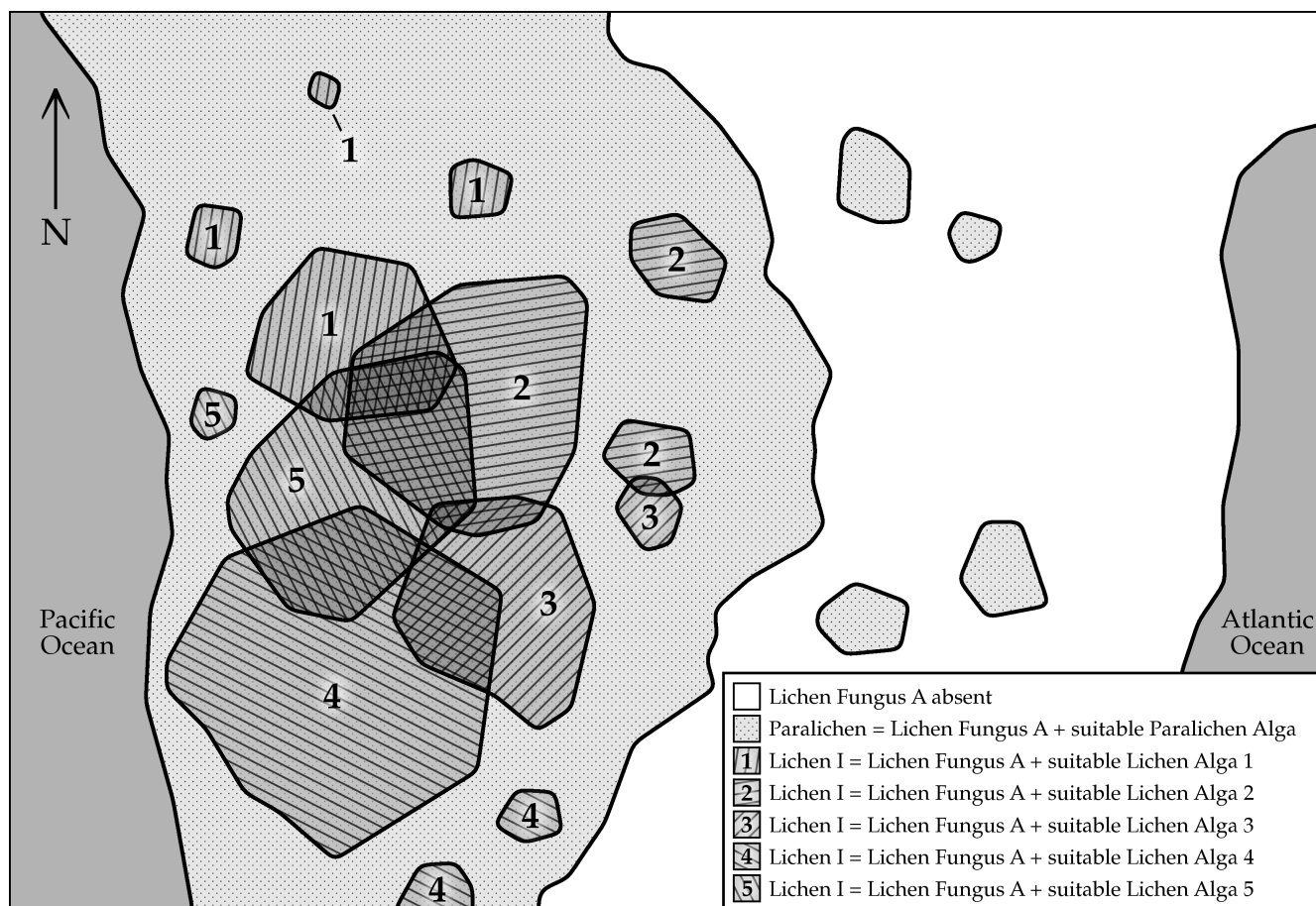
\*Some lichenologists circumscribe the prethallus to include the parathallus. This is not helpful. Etymologically, the term *prethallus* should designate the early, non-thalline phase of lichen resynthesis; it is presumably during this stage that the lichen-forming fungus and the lichen-forming alga gather resources preparatory to the coming systems upgrade to a fully corticate lichen (Essay VIII). The parathallus, unlike the prethallus, is not necessarily *pre-* anything; it *may* give rise to a lichen thallus, but more often it probably does not.

see below. And while I grant that evidence for such a claim is at present a bit thin on the ground, yet I find Yngvar's experience compelling – the more so as I myself can report a similar experience with Lungwort. At the same time, I note that the only genetic study yet conducted on what I'm calling the paralichen detected a decided switching on and off of genes in both participant partners. I could be wrong, but to me the switching on and off of genes feels like something more than mere cohabitation. Very likely a second round of gene activation and suppression will some day be shown to coincide with the initiation of the lichen thallus itself.

Whatever its ontological status, the paralichen by its mere existence invites us to rethink our seeming majority assumption that the lichen thallus is the one and only steady state available to the lichen fungus. More likely the lichen thallus is simply one of at least two stable ecological units available to the lichen fungus. Taken together, these units – the lichen and the paralichen – doubtless confer upon their shared fungal partners an enhanced level of ecological and hence evolutionary fitness; they help to explain the otherwise seemingly unaccountable persistence of the lichen fungus over periods running to hundreds of millions of years. At the same time the lichen thallus itself begins to look like a kind of latter day evolutionary "upgrade": a luxuriating, basically 3-D variant of strictly 2-D fungal-algal systems presumably very much older.

The paralichen hypothesis also puts into new perspective our understanding of lichen distribution. Lichen range maps can now be seen to represent only a particular kind of intersection among the lichen bionts. In the case of most lichen fungi, actual distribution areas are likely to be much larger than those appearing, for example, in *Lichens of North America*. Precisely the opposite is true of most if not all lichen algae, in which individual clades doubtless occupy only a small portion of a lichen's range. Figure 3 presents a hypothetical range map for several lichen bionts both in their lichen form and as individual organisms in their own right. The take home message is that lichen distribution is probably defined less by the ecological limitations of the lichen fungus, and more by the number and ranges of the algal clades it can consort with. In its capacity as a paralichen, the same fungi doubtless occupy a much larger geographic range.

Substantiating – or refuting – these and other claims regarding the nature of paralichens is one among many intriguing tasks awaiting the application



**Figure 3.** Hypothetical distribution area of “Lichen Fungus A” in temperate North America. As portrayed here, Lichen Fungus A ranges across the western two-thirds of the map area, with four additional outlying populations. Over much of this range it occurs as a paralichen; see text. Lichen I is restricted to areas of overlap between Lichen Fungus A and Lichen Algae 1, 2, 3, 4, 5. Based loosely on the North American distribution of Timber Wolf (f.p.: *Letharia vulpina*) cunningly documented by Susanne Altermann: <http://bit.ly/4Izjtj>. Graphics by Jason Hollinger.

of molecular methods to lichen distributional ecology. The trouble with the paralichen is that it’s invisible, more or less, to the unaided human eye. Even when you think you’ve got one in focus in your hand lens, you still don’t know for sure what species you’re looking at – or whether in fact you might be looking at several species. In some ways the parathallus might be compared with the mycelium of a mushroom – no less difficult to recognize at sight. But whereas mushroom mycelia are usually parasitic on living organisms or saprobic on dead ones, paralichens are fuelled, at least in part, by photosynthates borrowed from their algal (including cyanobacterial) consorts.

The single most convincing indicator of the paralichen phenomenon is what I call the lichen “bloom”: the inexplicably copious occurrence, over uniform habitat, of lichen thalli belonging to a single species. Actually I seem to distinguish two kinds of

lichen blooms: those that develop gradually, as in the case of Edible Horsehair (f.p.: *Bryoria fremontii*) and Methuselah Beard (f.p.: *Usnea longissima*); and those that appear suddenly, seemingly “out of nowhere,” as the Timber Wolf (f.p.: *Letharia vulpina*), Antlered Oakmoss (f.p.: *Evernia prunastri*) and Holey Ribbon (f.p.: *Ramalina dilacerata*) sometimes do.

It’s these latter blooms with their telltale even-sized thalli that seem to me to indicate the recent presence of a paralichen patch. Yngvar’s 20-odd thalli of Peppered Moon qualify as a small lichen bloom. Figure 1 pictures another bloom, here much denser and more extensive, at about 30 cm in length. While many macrolichens are capable of forming blooms, in practice they appear to do so only in “core” portions of their distribution area. Of course this leaves us without any convenient means of documenting the

presence of paralichens over large portions of their presumed range.

So, are paralichens really as widespread as I've indicated in Figure 3? I don't know. But I can tell you one thing. Beginning as of now, you'll find me following Yngvar's lead, inoculating the surfaces of rocks and trees hereabouts with lichen soredia, isidia and spores. I can think of worse pastimes. And besides, think of the pleasure, years from now, of coming upon a lichen bloom in some microsite all but forgotten. First a short pause; and then a sudden hearty shout of recognition: "Ah, so *there* you are!"

\* \* \* \* \*

Just for fun, let me bring this essay to a close with some quick and dirty observations and predictions concerning the paralichen, especially as it affects (or could affect) our current understanding of the lichen enterprise:

- ♦ Some lichens are still difficult to resynthesize in the laboratory. Many such species may prove more tractable once we get around to resynthesizing their respective parathalli. To accomplish this, however, we'd first need to figure out precisely which assemblages of paralichen fungi, algae, and perhaps bacteria are required for establishment by which assemblages of lichen fungi, algae, and perhaps bacteria. By no means a trivial undertaking.
  - ♦ To me it seems quite plausible that paralichens, being more robust than lichens, may have played a role – prominent I should think – in the original evolutionary expansion of lichens from terrestrial habitats onto the trunks and branches of trees and shrubs, that is, once trees and shrubs became available.
  - ♦ Some cyanolichens maintain both a cyanobacterial photopartner *and* an algal one (Essay VII). This has always struck me as a bit strange. One possible explanation is that nutrient-rich "germination beds" of the kind provided by the parathallus can, over evolutionary time, promote establishment by a wide range of photopartners. If so, then three-membered cyanolichens are most helpfully
- conceived as a kind of hand-me-down from systems upgrades that have occurred within the parathallus: the paralichen as facilitator. The same would be true of cyanomorphs and chloromorphs (Essay VII), alias photomorph pairs or lichen chimera.
  - ♦ Given that many lichens presumably nowadays arise from paralichens, it seems likely – ontogeny recapitulating phylogeny and all that – that paralichens must predate the lichen thallus: paralichens, in this view, are what there was long before there were lichens. If so, then the lichen thallus has arisen – multiple times – from a specific kind of systems upgrade on the part of the paralichen, giving rise to the metacell (Essay VIII). Other kinds of systems have doubtless arisen in like fashion, e.g., seemingly parasitic relations which may eventually be found, upon closer inspection, not to be parasitic after all.
  - ♦ We shouldn't be surprised if some lichens are eventually found to carry the parathallus, in one of its derivatives, forward long past the establishment phase. Lichens producing a thick, mat-like prothallus or hypothallus may qualify here, e.g., the Suede Lichens (f.p.: *Pannaria*) and, for that matter, the Map Lichens (f.p.: *Rhizocarpon*). Going the other way, both the Pixie Lichens (f.p.: *Cladonia*) and Stipplescale Lichens (f.p.: *Endocarpon*) grow a network of fungal hyphae downwards into the substrate. The parathallus underground?
  - ♦ If, as I suspect, paralichens supply nutrient-rich "germination beds" well suited to establishment by other lichens, then perhaps they can be seen in part as establishment boosters for lichens unlikely to colonize a particular substrate in their absence. Some such phenomenon may partly explain the curious lag in lichen colonization often observed, e.g., in young, regenerating forest stands.
  - ♦ Evolution being what it is, some paralichens may well have lost the ability to form lichens or, indeed, never possessed it. Should paralichens of the former kind ever be found, it's possible that a little clever laboratory manipulation may resurrect one or more lichen species not seen on Earth for a long while, perhaps millions of years. A bit like Jurassic Park, only smaller.