

The Role of Parasitism in the Co-development and Colonization of *Peltula euploca* and *Glyphopeltis ligustica*

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Abstract

The lichen *Peltula euploca* containing coccal cyanobacteria grows in arid and semi-arid localities in the Mediterranean. The lichen *Glyphopeltis ligustica* containing green algae often develops on the thalli of *Peltula*. Both lichens show different methods of reproduction and dispersal which, in connection with their type of growth and their strategies of colonization, are effective adaptations to the extreme conditions of the habitat. Principal aspects of mutualism and parasitism are discussed.

Keywords: mutualism, symbiosis, parasitism, development, colonization, *Peltula euploca*, *Glyphopeltis ligustica*, arid, semi-arid habitats

1. Introduction

One of the most important characteristics of lichens is their ability to colonize habitats unfavourable to most plants. That lichens are coevolved mutualistic organisms may be responsible for these special abilities, for it is well-known that both partners together can achieve a higher degree of adaptation to extreme environments than each of the partners alone.

The positive influence of the symbiosis on adaptability may be enhanced by contact with a third or even a fourth partner (Hawksworth, 1988). This secondary contact may take different forms such as undifferentiated contact with different kinds of algae (Jørgensen and Jahns, 1987), or the development of cephalodia (Ott, 1988). But there also exist special types of symbiotic interactions which help with the adaptation to environmental influences.

Many investigations have been conducted into the taxonomy of fungal parasites of lichens (Triebel, 1989), but rather few investigations on parasitic lichens and their distribution, and hardly anything on the biological significance of parasitism in lichens. Until now the most interesting and intensive research on parasitism in lichens has been undertaken in Poelt's laboratory (Poelt and Doppelbaur, 1956; Poelt, 1958, 1962; Poelt and Steiner, 1971; Zehetleitner, 1978). His observations principally deal with crustous lichens and/or crustous lichens parasitizing foliose lichens. Poelt classifies the parasitic associations as parasites of temporal nature, transient parasitism of young developmental stages, full parasites, and others (Poelt and Doppelbaur, 1956) and formulates some general rules for distinguishing between the different types (Poelt, 1958). The establishment of such a classification and general rules is logical and valuable as they help to explain and to clarify the numerous and heterogenous aspects of parasitism in lichens. The real problem with lichen parasitism is that it touches on the interpretation and concepts of lichen in general. Many authors have mentioned the problem (Smith, 1975; Smith and Douglas, 1987; Smith, Muscatine and Lewis, 1969; Ahmadjian, 1982), and Hawksworth (1988) in particular, has discussed it together with the numerous other types of multiple symbiosis. In connection with parasitism in the strict sense, the question arises as to whether these necessarily schematical categories are sufficient for the interpretation of the enormous diversity of parasitism in lichens. It was for this reason that Hawksworth referred to the range of symbiotic associations in terms of the number of bionts involved and avoided the need to use categories based on ill-defined or changing interactions. This problem was also recognized by Scheidegger (1987a,b) in his investigations on *Buellia*.

General aspects can not be discussed without continual reference to concrete examples of mutualistic or parasitic interactions, as all general interpretations must be tested against the existing associations. One interesting example of complex mutual relationships in lichens is the life-cycle of *Peltula euploca* and *Glyphopeltis ligustica*, described and discussed in this paper. Both lichens colonize arid and semi-arid habitats together, where *Glyphopeltis* always grows on thalli of *P. euploca* (Poelt, personal communication).

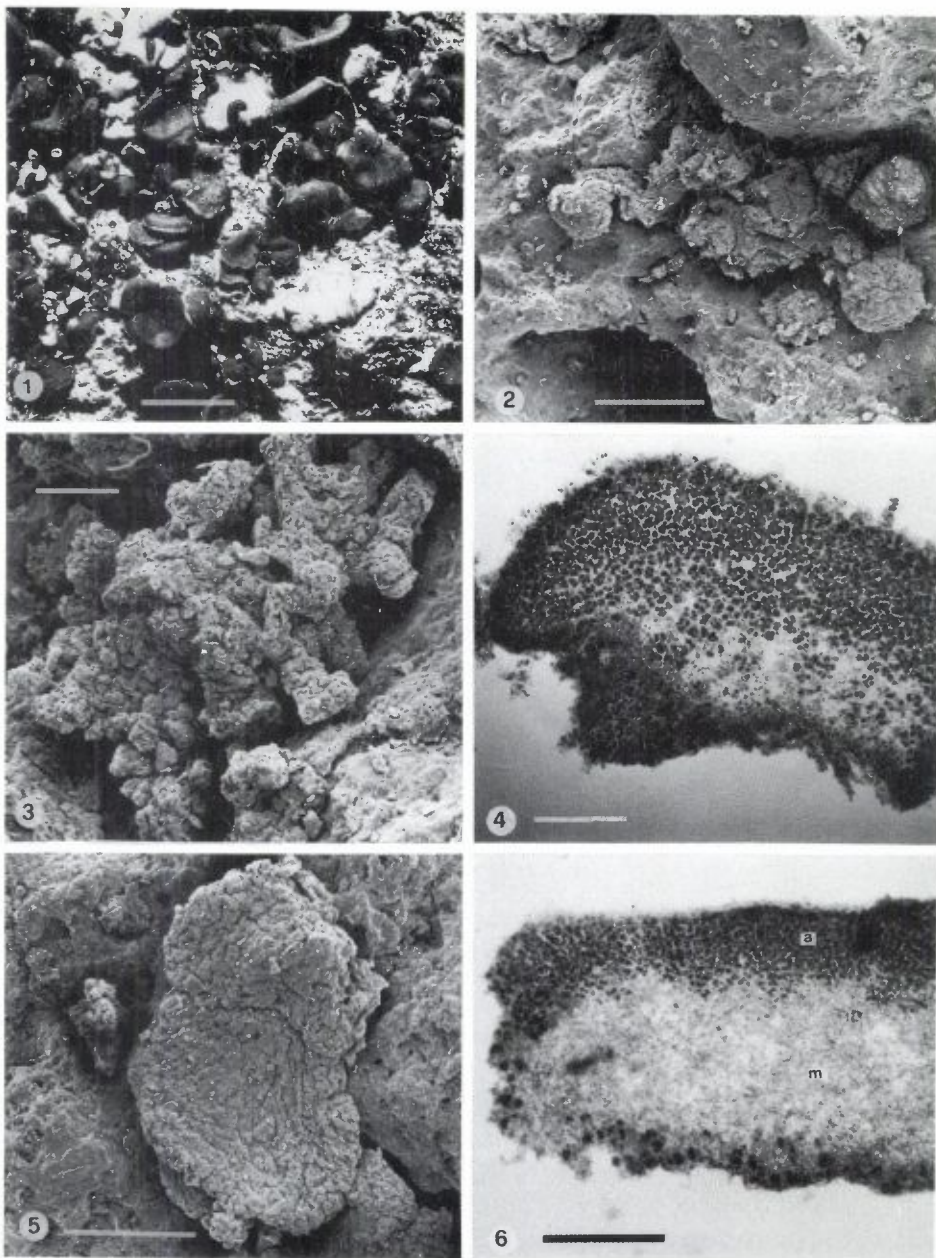
2. Materials and Methods

The samples of *Peltula euploca* (Ach.) Poelt ex Pisut and *Glyphopeltis ligustica* (B. de Lesd.) Timdal were collected on the western coast of the Mediterranean island of Sardinia (Italy). (Private herbarium Ott and Scheidegger.) The lichens grow on fully exposed rocks. Such world-wide habitats are characteristic of the genus *Peltula* (Büdel, 1987). Investigations were made with a light microscope (Leitz Dialux 20EB) and a scanning electron microscope (SEM). The material was air-dried or rehydrated, frozen and freeze-fractured and investigated in the frozen, partially freeze-dried state (Scheidegger et al., 1991).

3. Results

The peltate thalli of *Peltula euploca* are dark brown. Apothecia are immersed in the thallus surface which is also covered by some lateral and many marginal soralia (Büdel, 1987). The photobiont of *Peltula euploca* belongs to the coccal cyanobacteria. *Glyphopeltis ligustica* (syn. *Xanthopsorella llimonae*), which always grows on *Peltula* thalli in the Mediterranean (Nimis and Poelt, 1987), is easily distinguished from the dark brown *Peltula* because of its light-coloured cortex (Fig. 1). In contrast to *Peltula*, the photobiont of *Glyphopeltis* belongs to the coccal green algae. In the natural habitat one sometimes can get the impression that larger thalli of *Glyphopeltis* grow on the substrate and not on another lichen. But this impression is misleading as it is always possible to find remains of degenerated thalli of *Peltula* under these thalli of *Glyphopeltis*.

The development of *Peltula euploca* starts on the surface of the rock, especially in small cavities (Fig. 2). Here a blackish crust is formed by cyanobacteria, by hyphae and by some green algae as well (Fig. 3). From this undifferentiated mixture of bionts the thalli of *Peltula euploca* arise. In the beginning hyphae and cyanobacteria develop without any perceptible dominance of either one of the bionts, but after some time the growth rates of the partners diverges. In the early stages the growth and propagation of the photobiont is faster than that of the mycobiont and accordingly, in sections of this stage, a large number of algal cells can be seen, while the medulla is nearly absent (Figs. 4–5). It is obvious from Fig. 4 that in this early developmental stage the photobiont dominates morphologically. As the differentiation progresses, the relationship between fungus and the photobiont changes and the proportion of the fungal tissue increases. After this development, the thallus is divided into a well-delimited algal layer and a medulla (Fig. 6). The upper surface is closed by an epinecral layer and a thin phaenocortex in the sense of Poelt (1989). The



Figures 1-6. (1) *Peltula euploca* (dark coloured thalli) and *Glyphopeltis ligustica* (light coloured thalli) growing together at their natural habitat (bar: 4 mm).

(2) A typical cavity of the substrate with the first developmental stage of *P. euploca* (bar: 250 μ m).

(3) The blackish crust on the substrate formed by cyanobacteria, hyphae and some green algae as well (bar: 100 μ m).

(4) A very young squamule with a relatively thick algal layer and a thin medulla (bar: 100 μ m).

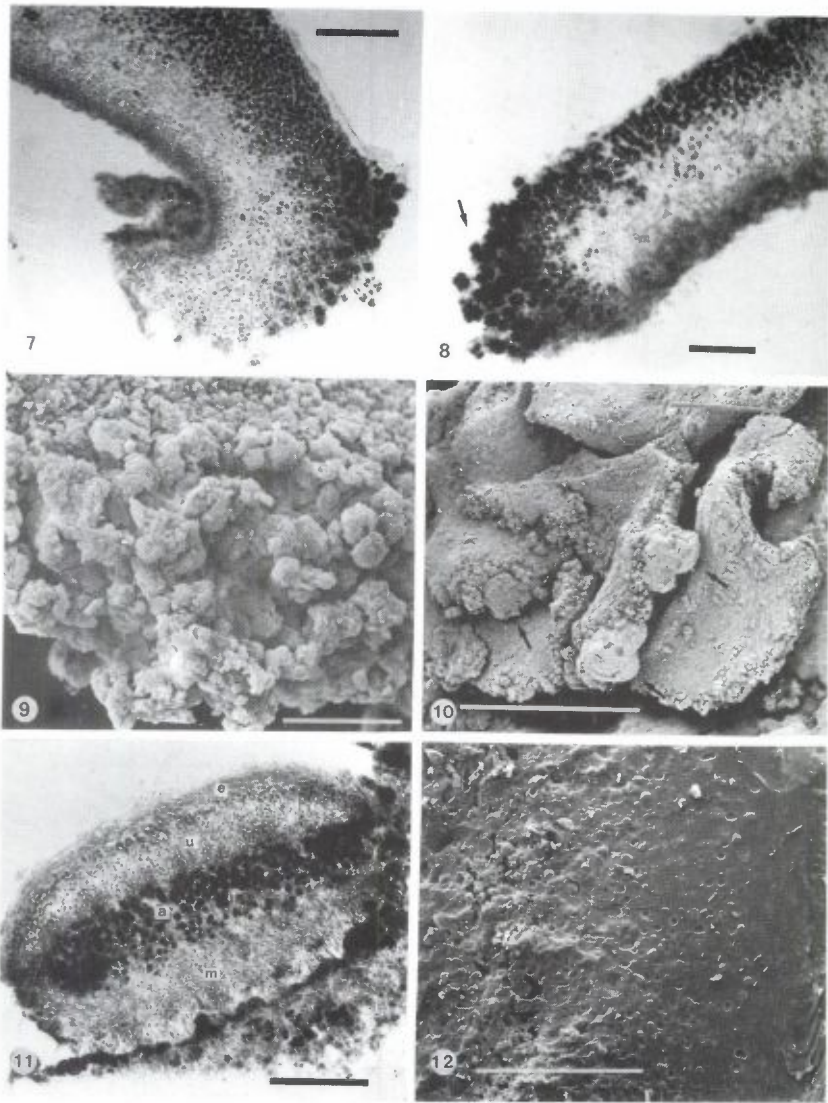
(5) The same stage of development as in Fig. 4 (bar: 250 μ m).

(6) After further differentiation the thallus develops a well-delimited algal layer (a) and medulla (m) (bar: 100 μ m).

lower surface is covered by a thick true cortex. The adult thallus continues to grow at the margin which often curves down a little (Fig. 7). In the margin, the cyanobacteria grow faster than the hyphae and are lying loosely at the surface. In Fig. 7 the loosely structured margin and the photobionts without a covering phaenocortex are shown, but an epinecral layer has not yet developed. The growing photobiont cells are enmeshed by hyphae and are excised as soredia (Figs. 8–9). The remaining parts of the loose tissue subsequently become covered by a phaenocortex and incorporated into the thallus.

Glyphopeltis ligustica, unlike *Peltula*, has no soredia and its propagation is exclusively by ascospores. Characteristically of *Glyphopeltis* is the marginal development of apothecia with multi-spored asci. The relichenization required by the distribution of the ascospores could theoretically occur on the substrate as the green algae – the necessary photobiont – can be present on the rock surface. As this does not happen in nature, there is reason to suppose that the conditions of this habitat are unsuitable for this process. The coccal green algae are not only found on the rock, but also in the marginal area of the *Peltula* thallus where they can be observed at nearly every developmental stage. They lie between the loosely interwoven hyphae and cyanobacteria of the growth zone. Some ejected ascospores of *Glyphopeltis* can be expected to reach the *Peltula* thallus surface. Here the conditions for lichenization seem to be perfect and consequently in this marginal zone the infection of *Peltula* by *Glyphopeltis* occurs. The youngest thalli of *Glyphopeltis* that can be found develop in this region (Figs. 7 and 10). On most thalli of *Peltula* several primordia of the *Glyphopeltis* can be observed. Young developmental stages of *Glyphopeltis* can be found on young thalli as well as on older specimens of *Peltula*.

Glyphopeltis differentiates an extremely thick upper cortex with a well-developed epinecral layer (Figs. 11–12). The material required for this process probably uses up much of the carbohydrates synthesized by the lichen and causes a relatively slow marginal growth of *Glyphopeltis*. The stages observed indicated that the rate of thalline growth is slower than in *Peltula*. This difference results in a change of position of the *Glyphopeltis* on the *Peltula* thallus. After some time the lichen with green algae no longer grows marginal on the lichen with cyanobacteria but is found in a lateral position (Figs. 13–14). Below the upper cortex is the algal layer, the coccal green algae being covered by matrix of fungal material (Fig. 15; Honegger, 1986). *Glyphopeltis ligustica* has no lower cortex and hyphae from the medulla penetrate the thallus of the *Peltula* (Fig. 16), although these are relatively few in number. This intrusion and the shading of the basal thallus by *Glyphopeltis* result in the degeneration of *Peltula*. This means that *Glyphopeltis* destroys its own substrate and



Figures 7-12. (7) An adult thallus with the typical loosely structured down curved margin of *P. euploca* (bar: 50 μ m).
 (8) The photobionts without a covering phaenocortex at the margin (arrow) (bar: 30 μ m).
 (9) The typical development of soredia by *P. euploca* (bar: 30 μ m).
 (10) Early stages of development of thalli of *Glyphopeltis ligustica* at the marginal zone of *P. euploca* (arrows) (bar: 1 mm).
 (11) A young, well-developed thallus of *G. ligustica* (e - epinecral layer, u - upper cortex, a - algal layer, m - medulla) (bar: 100 μ m).
 (12) The very compact upper cortex of *G. ligustica* (arrow) (bar: 100 μ m).

4. Discussion

The morphological and anatomical structures of *Peltula euploca* and *Glyphopeltis ligustica* and the manner of their co-development point to interesting adaptations of both lichens to their arid environment. Probably, the special type of mutual interactions observed here is important for the colonization of the extreme habitat. It is remarkable, that the two species, while they are exposed to the same extreme conditions, differ significantly in their anatomy, morphology and colonization strategy.

It is well known that mucilagenous layers of cyanobacteria often dominate in an extreme environment and obviously this holds true for the first stages of *Peltula*. *Peltula euploca* has a very thin phaenocortex together with an epinecral layer followed by the algal layer of cyanobacteria and a relatively loose-structured medulla. The lower side of this lichen is covered by a well-developed true cortex. The loose structure of the marginal zone of the thallus has two different functions. On one hand, it is the growth zone of the thallus, and on the other hand, serves as a sororium. Additionally, the loose structure of the marginal area is very important for the development and growth of *Glyphopeltis ligustica*.

According to the results of Büdel (1990), these characteristic features seem to adapt *Peltula euploca* very well to the environmental conditions of arid and semi-arid habitats. The peltate thallus enables the lichen to gather capillary water beneath its lower side and thereby ensures an optimal water uptake. Furthermore, *P. euploca* as a species of the genus *Peltula*, has the ability to absorb 2.5 times the amount of water in relation to its dry weight (Büdel, 1990), and this in addition to the water gathered between the thallus and the substratum. The structure of the medulla, with numerous airspaces between interwoven hyphae, does not explain the high water storage capacity, as more structurally complex lichens do not store water in these cavities but only in the cell walls of the fungi and in gelatinous substances (Honegger, 1986). This makes the high water storage capacity of *Peltula* remarkable, and it must be regarded as an excellent adaptation to the dry habitat. The thin phaenocortex and the epinecral layer are no protection against water loss, but their structure enables the lichen to profit immediately from liquid water in the form of rain or dew (Lange et al., 1989). The epinecral layer, together with the pigmentation of the phaenocortex, probably provide protection of the cyanobacteria from the high insolation typical of the habitat. Büdel (1990) considers these layers as providing protection against photosynthetic damage.

In contrast to *Peltula*, *Glyphopeltis* develops a completely different anatomical structure which nevertheless is also effective as an adaptation to the same

habitat. *Glyphopeltis* has a true thick upper cortex which obviously is necessary for the protection of the well-developed algal layer of coccal green algae. The same is true in the thallus structure of *Buellia lactea* (Scheidegger, 1987b). The green algae are evidently sensitive to high light intensities, and the absence of pigmentation seems to be compensated for a development of an especially thick upper cortex. Ertl (1951) investigated the permeability of cortices of lichens with green algal photobionts to light and found values of 48–73%. This contrasts with *Peltula euploca* where Büdel (1987) only found a permeability of 7%. Therefore, in contrast to *Peltula* with its pigmentation, the unpigmented thick upper cortex of *Glyphopeltis* may be necessary as a protection against the high insolation. Though several reports exist about the significance of thickening of the cortices or epinecral layers as a protective device against high insolation (Galun, 1963; Follmann, 1965; Poelt and Wirth, 1968; Rogers, 1977), caution is required in this interpretation as there is no clear evidence as to the damaging effects of high light intensity on the photosynthetic activities of lichen photobionts (Kappen, 1974). Recent investigations point to an inhibiting effect of high light intensity on the photosynthesis (Büdel, personal communication).

Apart from the question of light intensity, a thick cortex is bound to be of significance in respect to water relations. Imbibition of water can be facilitated, and because of the compactness of the cortex, a high water storage capacity is probable. This also applies to the medulla of *Glyphopeltis*, which is nearly twice as thick as the medulla of *Peltula* and much more compact. *Glyphopeltis* lacks a lower cortex. This is very important with respect to the ability of colonization of *Peltula* as it enables hyphae from the medulla of *Glyphopeltis* to penetrate *Peltula*.

Both lichens are consequently successfully adapted to the same habitat by their anatomy, even though the means of adaptation is completely different. This is a very interesting example for the variability of adaptation which can be achieved when different bionts are paired, each possible combination of partners finding their own solution to the same problem. The range of mechanisms which are possible in the mutual relations of the lichen symbiosis is notable. Though both lichens are exposed to the same conditions in this habitat, they have developed two completely different sets of adaptational characteristics.

It is clear that both lichens have individual strategies for the colonization of the same habitat, one (*Glyphopeltis ligustica*) being completely dependent on the other (*Peltula euploca*). This leads to the question of the type of relationship between the two organisms and how this relation can be defined. In this context, an important aspect is the very thin phaenocortex of *Peltula* and the lack of a lower cortex in *Glyphopeltis*. Therefore the penetration of

the phaenocortex of *Peltula* by the hyphae of *Glyphopeltis* is very easy. These hyphae continue to grow into the algal layer but hardly at all into the medulla of the *Peltula* (Fig. 14). As most of the penetrating hyphae end in the algal layer, *Glyphopeltis* perhaps acquires substances from the algae and profits from the ability of the cyanobacterial photobionts to fix nitrogen. This connection, and the possible transfer of nutrients, resembles that of cephalodia of lichens with green photobionts. Cephalodia have occasionally been discussed as a kind of gall caused by parasitism (Ozenda, 1963; Henssen and Jahns, 1973). *Peltula*, is no cephalodium, but perhaps its thallus fulfills the same function for *Glyphopeltis*.

The second striking aspect of the relation between the two lichens is the colonization of one thallus by a second. Here, a good water supply for *Glyphopeltis* can be postulated, creating for *Glyphopeltis* a favourable microclimatic environment. The interconnection of water relations in the two lichens is an important feature as *Peltula*, a lichen with cyanobacteria, is dependent on liquid water and therefore mainly colonizes small depressions while the water evaporated from *Peltula* and the substratum is an acceptable water source for *Glyphopeltis* and its green algae.

These remarks show several types of mutual interactions which are known from other plants and which have been described by different terms, such as mutualism, parasitism, etc. It can be argued whether *Peltula* and *Glyphopeltis* share a mutualistic or an antagonistic relationship, after the definition of Hawksworth (1988). All observations point to an antagonistic contact, as no evidence could be found that the fitness of survival of the thallus of *Peltula* is enhanced by contact with *Glyphopeltis*. Hawksworth further divides the antagonistic system into parasitic and necrotrophic relations. Probably both types are present in these two lichens as *Glyphopeltis* at first grows on the living *Peltula* as a parasite, later on destroys the host-lichen and lives on the remaining debris; this latter part of the life-cycle can be interpreted as necrotroph. Another example for necrotrophic behaviour was observed by Zehetleitner (1978) in *Verrucaria insularis* and *V. aspiciliae* on *Aspicilia calcarea*. Both *Verrucaria* species had "taken over" the thallus of their host after having killed it before, and then spreading centrifugally in the thallus of the host.

The first steps of the ontogeny and establishment of *Glyphopeltis* suggest a transient parasitism of young developmental stages. Such an interpretation is supported by *Glyphopeltis* having a completely developed thallus with full photosynthetic capability. Such a thallus may kill its host without destroying itself at the same time (Poelt and Doppelbaur, 1956). If the thallus of *Glyphopeltis* exists for a time after the death of *Peltula*, the parasitism can

be seen as a transient stage. Poelt and Steiner (1971) describe this type of parasitism for a species of *Acarospora*, which start their juvenile development normally on a specific host, and finally developing substantial thalli of their own. These results correspond with our observations on *Glyphopeltis*. At least the growth on *Peltula* gives *Glyphopeltis* an ecological advantage, which might be called spatial parasitism, even if in most examples of this type, the parasite does not impair or kill the host. As *Glyphopeltis* causes the death of *Peltula*, the term of obligately parasitism would perhaps be suitable. But Poelt and Doppelbaur (1956) explained that usually parasites of this type show definite reductions of the thallus, a feature completely absent in *Glyphopeltis*.

On the whole, it can be said that the relation of *Peltula* and *Glyphopeltis* resembles several types of parasitism, but fits no definition completely. Exact definitions of symbiosis, mutualism and parasitism (Lewin, 1982; Goff, 1982; Scott, 1969; Ahmadjian and Paracer, 1986; Poelt and Doppelbaur, 1956; Smith and Douglas, 1987) are certainly necessary and valuable but it should be remembered that they are sometimes insufficient to describe the complex examples of mutualistic relationships in nature. The complexity of the individual relation defies the application of suitable labels and neutral terms such as "lichenicolous lichen" clearly have this advantage as a general one to discuss lichen dependent on others where the biology is uncertain.

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