

LICHENS AND GALLS. TWO FAMILIES OF CHIMERAS IN THE SPACE OF FORM

Líquenes y agallas. Dos familias de quimeras en el espacio de la forma

Alessandro MINELLI
Università di Padova, Italia

Recibido: 19 de enero de 2017
Aceptado: 20 de octubre de 2017

ABSTRACT

Galls are produced by the interaction between a plant and a different kind of organism, commonly an insect. Many galls, especially those involving an insect, have a very specific and often complex shape, comparable to the specific and often complex shape of organisms capable of reproduction. Galls, however, do not reproduce –each individual gall takes origin from a new interaction between the plant and the external agent. To some extent, the same applies to lichens: the specific and sometimes complex structure of their thallus may have transgenerational continuity through fragmentation or another kind of vegetative reproduction, but gets completely disrupted by sexual reproduction, following which a new lichen is reconstructed by a newly established symbiosis between a fungus and an algal partner. How far is their form constrained by the structure of the two partners? How can natural selection act on their form?

Key words: Adaptation; Evolutionary Developmental Biology; Lichens; Plant Galls; Scaffolded Development.

RESUMEN

Las agallas se producen por la interacción entre una planta y un tipo diferente de organismo, comúnmente un insecto. Muchas agallas, especialmente

las que implican a un insecto, tienen una forma muy específica y a menudo compleja, comparable a la forma específica y a menudo compleja de los organismos capaces de reproducirse. Las agallas, sin embargo, no se reproducen—cada agalla individual proviene de una nueva interacción entre la planta y el agente externo—. Hasta cierto punto, lo mismo se aplica a los líquenes: la estructura específica y a veces compleja de su talo puede tener una continuidad transgeneracional a través de la fragmentación u otro tipo de reproducción vegetativa, pero se interrumpe completamente por la reproducción sexual, tras lo cual un nuevo líquen es reconstruido por una recién establecida simbiosis entre una pareja de hongos y algas. ¿Hasta qué punto su forma está limitada por la estructura de los dos socios? ¿Cómo puede actuar la selección natural en su forma?

Palabras clave: Adaptación; Biología Evolutiva del Desarrollo; Líquenes; Agallas vegetales.

1. LICHENS AND PLANT GALLS IN DEVELOPMENTAL BIOLOGY

Concepts, methods and research agenda of scientific disciplines depend to some extent on the criteria used to determine the set of objects that we regard as legitimately pertaining to each field. In this respect, disciplinary boundaries are usually revised when this is required by the discovery of new kinds of objects or phenomena, but the same does not happen regularly as a consequence of a revisitation of the properties of long-known systems that would deserve to be approached from a fresh perspective.

Paradigmatic in this respect is developmental biology. This discipline's tremendous advances in the last decades, especially at the frontier of the molecular mechanisms underlying the generation of living form, are not accompanied by an equally successful and universally agreed delimitation of its scope, not to mention by an explicit, fully articulated theory of development. The disparity of viewpoints expressed by the contributors to a recent volume on this subject¹ demonstrates (1) widespread disagreement on the inclusion of systems (e.g., unicellulars) and processes (e.g., regeneration and carcinogenesis) within the legitimate scope of this discipline, and (2) widely divergent opinions about a possible theory of development, ranging from denial of interest in establishing it to lack of agreement on its possible nature and contents.

1. Cfr., MINELLI, A./PRADEU, T. (eds.), *Towards a Theory of Development*, Oxford, Oxford University Press, 2014.

In this article I will discuss two kinds of biological systems, both of which deviate, in more or less important respects, from those on which developmental biology has been progressing thus far. In these systems, the lichens and the plant galls, we see form emerging at the interface between the tissues, the genes and the behaviour of two very distantly related partners: a fungus (the mycobiont) and an alga (the photobiont) in the case of lichens, a plant and an insect in the case of galls. (Galls are induced on plants by interactions with a diversity of organisms including insects, mites, nematodes, fungi, and also viruses, but in the following account I will restrict attention to those produced by the interaction of a plant with an insect, because of their distinct morphological properties: structural regularity, diversity, and species-specificity).

2. BAD TAXONOMY CAN KILL² (THOUGHT)

With the discovery of their symbiotic nature, lichens continued to be treated as natural systems articulated into species, diagnosable through morphological traits and/or the peculiar molecules they produce. There is nothing in nature like “pure mycobionts” corresponding to as many fungi associated with algae in lichenic symbioses. However, by realizing that the mycobionts of distinct lichenic taxa are in fact strictly associated with different lineages of non-lichenized fungi has eventually suggested to distribute the lichenized fungi across the system of the Ascomycetes and Basidiomycetes, following their phylogenetic relationships, rather than confining them to an artificial class of their own. This was a major reorganization of the fungal classification, although one that did not require a major conceptual revolution.

2. “Bad taxonomy can kill” – with these words and a pertinent illustration, the cover of issue 6289 of *Nature* (13 September 1990) highlighted the important message conveyed by an article published in that issue (DAUGHERTY et al., 1990). The article provided a dramatic example of the potential consequences of an inadequate appreciation of the way nature is articulated, e.g., in species. Tuataras (genus *Sphenodon*) are rare and endangered lizard-like reptiles of New Zealand, the only living representatives of the Rhynchocephala. In 1877, the herpetologist BULLER described as *S. guntheri* what he regarded a species distinct from the already described *S. punctatus*, but his views were not accepted and *S. punctatus* continued to be regarded as the sole living rhynchocephalan. Since 1895 this animal is protected by law. But by 1990, when the taxonomic distinction between the two species was revisited and eventually confirmed, *S. guntheri* had long become extinct without notice. Bad taxonomy had caused it not be mentioned by national laws on nature conservation. Bad taxonomy had already killed it.

The new taxonomic approach allows for an easy accommodation of discoveries such as the existence of multiple lineages of delichenized fungi (i.e., non-symbiotic fungi derived from lichenized ones), or the possibility to cultivate a lichenic mycobiont in isolation from its natural algal partner.

The gall case is different. Galls are nearly universally regarded as pathological constructs of plants, produced under the influence of an external agent able to cause a local disruption of normal development. Insect-induced galls are often compared to the morphologically irregular tumours produced on plants by bacteria, only to remark the sometimes astonishing degree of morphological regularity (let's say: elegance) and repeatability of the former, contrasted with the accidental, unpredictable form of the latter. Besides the fact that the mechanisms underlying the regularity and repeatability of form of insect-induced plant galls are still unknown, this comparison (especially with the crown gall, caused by *Agrobacterium tumefaciens*, whose etiology is quite well known at the molecular level³) does not change the current description of both insect-induced galls and crown galls as pathological plant tissues. To some extent, this is justified because, at variance with the lichen case, galls exist in nature alongside the plant species on which, under appropriate circumstances, a gall may form. Thus, if the plant has its legitimate place in the classification, why should the gall also have one? To be sure, there is no place for "gall taxa" in the system (or the classification) of living beings. However, calling them simply, as we are accustomed to do, as, for example, the gall of *Andricus hungaricus* (a tiny wasp) on *Quercus robur* (the pedunculate oak), should not prevent us from studying these natural productions as legitimate and well-circumscribed developmental systems, within which specific and peculiar organic forms are generated.

3. LICHENS AND GALLS IN DEVELOPMENTAL BIOLOGY

To be sure, lichens have long found their little place in developmental biology. Different as they are, from minute, powdery (e.g., *Lepraria*) or endolithic (e.g., *Buellia*) blobs of living matter to foliose (e.g., *Lobaria*, *Parmelia*) or fruticose (e.g., *Ramalina*, *Usnea*) thalli, lichens exhibit shapes that are very different from those of non-lichenized fungi, still more from those of their algal partners, which are mostly unicellular, otherwise filamentous.

3. E.g., BINNS, A. N./THOMASHOW, M. F., "Cell Biology of *Agrobacterium* Infection and Transformation of Plants", *Annual Review of Microbiology*, 42 (1988), pp. 575-606.

This emergence of form has been studied both in terms of morphogenesis (how an individual lichen thallus takes its form⁴; and phylogenesis (from which morphological, genetic or developmental aspects of their non-lichenized ancestors did lichens eventually evolve their form; see below). On the other hand, plant galls have been always considered as abnormal products of plant development. Together with cancers and other pathologies accompanied by morphological change, galls have therefore a marginal place in respect to developmental biology: the place of systems to be explained by identifying the processes of normal development that have been troubled, and the nature of trouble, rather than the place of legitimate objects of the discipline, those that contribute, with others, to shape its basic concepts and perhaps its theory.

If a reliable production of form, often a complex one, accommunates lichens and galls, these two kinds of systems differ, however, in two important respects. The first is *adaptation*. Lichen symbiosis is largely acknowledged to be mutualistic, that is, to benefit both partners, the fungus as well as the alga. The mycobiont benefits from sugars and oxygen deriving from the metabolism of its partner, which apparently gets in turn a mechanical advantage in terms of availability of substrates and physical protection. On the other hand, the insect-plant relationship culminating in the production of a gall is a skewed one. The benefit to the insect is clear: nourishment and protection of the larva developing inside the gall. In the energetic budget of the plant, instead, the gall tissue is an unproductive burden that will turn into serious shortcoming if the gall's growth damages a flower or an inflorescence. That the production of a gall also represents a way to reduce the damage caused by an insect's attack is also probably true, but to limit the consequences of a potentially more serious damage caused by the interaction with the insect is not the same as obtaining instead an advantage from the insect-plant relationships. By analogy, a burst of fever can be a good strategy to kill the bacteria responsible for an attack to our health, but not suffering from any attack is better than releasing an adaptive response to an actual attack. Summing up: from the perspective of the plant, the production of galls is likely adaptive as a defensive strategy, but it is not adaptive per se, that is, with respect to the normal course of the plant's development.

The second difference between lichens and galls is in their *replication*. This requires some explanation. Lichens reproduce in different ways, sexual and asexual. More precisely, it is the fungus that can reproduce either sexually

4. E.g., HONEGGER, R., "Morphogenesis", in: NASH, T.H. III (ed.), *Lichen Biology*, Cambridge, Cambridge University Press, 1996, pp. 65-87.

or asexually, whereas sexual reproduction of the algal symbiont has been reported only a couple of times⁵. The sexual reproduction (of the fungus) involves the dissolution of the symbiosis, followed by its reconstitution during the next generation. In asexual reproduction, instead, the continuity of the symbiosis is maintained. Multiplication can occasionally occur by simple fragmentation of the thallus into small portions containing both fungal hyphae and algal cells, but in most lichens fragments are not normally able to survive and to grow into a new thallus⁶. Much more frequent is the production of reproductive units, often suitable – due to their tiny size – for long dispersal, each of which contains, again, both fungal hyphae and algal cells. The cyclic dissociation and reconstitution of the symbiosis alongside the sexual cycle may suggest that the lichen as such cannot be regarded as an integrated reproducing unit and thus does not fully respond to the list of properties often declared to be foundational for organismicity (but see below).

The individuality of a lichen thallus is also often problematic. A lichen may have arisen from the coalescence of originally separate thalli eventually fusing together⁷ or as a mixture of separate propagules⁸. Sometimes, hyphae growing on the substrate get in touch, here and there, with scattered groups of compatible algal cells; as a consequence, separate patches of mycelium are initially lichenized and only subsequently will they grow to form a continuous thallus⁹.

Compound lichen thalli can even include different mycobiont genotypes and different photobionts¹⁰. As a consequence, what appears to be a single lichen is sometimes a mixture of genotypically distinct individuals, as documented

5. SANDERS, W., “In Situ Development of the Follicolous Lichen *Phyllophiale* (Trichotheliaceae) from Propagule Germination to Propagule Production”, *American Journal of Botany*, 89 (2002), pp. 1741-1746.

6. BÜDEL, B./SCHEIDEGGER, C., “Thallus Morphology and Anatomy”, In: NASH, T. H. III (ed.), *Lichen Biology*, Cambridge, Cambridge University Press, 1996, pp. 37-64.

7. HAWKSWORTH, D. L./CHATER, A. O., “Dynamism and Equilibrium in a Saxicolous Lichen Mosaic”, *Lichenologist*, 11 (1979), pp. 75-80.

8. E.g., SCHUSTER, G., “Die Jugendentwicklung von Flechten. Ein Indikator für Klimabedingungen und Umweltbelastung”, *Bibliotheca Lichenologica*, 20 (1985), pp. 1-206.

9. Cfr., LETROUT-GALINOÛ, M. A./ASTA, J., “Thallus Morphogenesis in Some Lichens”, *Cryptogamic Botany*, 4 (1994), pp. 274-282; SANDERS, W., “A Feeling for the Superorganism: Expression of Plant Form in the Lichen Thallus”, *Botanical Journal of the Linnean Society*, 150 (2006), pp. 89-99.

10. GRUBE, M./HAWKSWORTH, D. L., “Trouble with Lichen: the Reevaluation and Re-interpretation of Thallus Form and Fruit Body Types in the Molecular Era”, *Mycological Research*, 111 (2007), pp. 1116-1132.

by DePriest¹¹ in *Cladonia chlorophaea*. Lichens, by the way, are not alone in this condition. Even among animals there are species in which mosaicism (cells issued from different zygotes contributing to the body of one individual) is indeed the rule. In different forms, mosaicism is widespread among colonial animals such as sponges, cnidarians, bryozoans and tunicates. For example, fusion of larvae has been reported as a normal developmental process in freshwater sponges¹², whereas in a small freshwater fish (*Cynolebias*) one zygote often gives rise to two separate “twin embryos” that subsequently merge to reconstitute a single embryo¹³.

With respect to the recurrence of form, the case of galls is very different. In no sense can we speak of their “reproduction”. Even if a long-lived tree or shrub can host, over the years, galls produced by interactions with many generations of gall-inducing insects, there is no continuity between the plant cells forming a gall today and those that will form a new gall next year. Continuity goes only through the insect generations.

Despite this fundamental difference between lichens and galls, there is nevertheless a common conceptual framework within which we can describe both lichens and galls as two kinds of developmental systems. This framework is the metaphor of the *scaffolded biological systems*.

4. SCAFFOLDED SYSTEMS

To raise a wall, or to build a house, we usually need a *scaffold*. As soon as the wall, or the house, is finished, the scaffold is dismantled. At no time is the scaffold a part of the wall or the house but, as long as building goes on, it takes part to the process. Of course, completing the building process does not necessarily imply the release of the scaffold. What characterizes the relationship between scaffold and scaffolded system is the functional role of the former, as a process relevant to the scaffolded system would not run (or at least would not run so expeditely and reliably) without its help.

A functional coupling between a scaffold and a scaffolded system is not limited to the products of human activity. To the contrary, many biological

11. Cfr., DEPRIEST, P. T., “Small subunit rDNA variation in a population of lichen fungi due to optional group-I introns”, *Gene*, 134 (1993), pp. 67-74.

12. BRIEN, P., “Les demosponges. Morphologie et reproduction”, in: GRASSÉ, P. P. (ed.), *Traité de Zoologie* (1973), Paris, Masson, Vol. 3, pp. 133-461.

13. CARTER, C. A./WOURMS, J. P., “Naturally Occurring Dibliostodermic Eggs in the Annual Fish *Cynolebias*: Implications for Developmental Regulation and Determination”, *Journal of Morphology*, 215 (1993), pp. 301-312.

phenomena can be described in these terms. Griesemer has recently provided examples¹⁴ of the new stimulating perspectives on reproduction and development that are disclosed when these processes are described as undergoing in unit systems representing *hybrids* between an organism and a living or non-living scaffold. An approach in terms of scaffolding has been suggested in many other sciences including neurosciences, cognitive sciences, cultural change, sociology, development of social systems and economics¹⁵.

As recently suggested¹⁶, we can define the scaffold as any resource used by the biological system without incorporating it as happens instead in the case of resources fuelling metabolism.

It will be important to take the following remarks into account. First, the relationships between scaffold and scaffolded system are often reciprocal. Second, reciprocity does not mean symmetry, that is, the relationship is often strongly skewed in favour of one of the partners. Third, scaffolding relationships can be temporary or permanent but even permanent associations can be occasionally terminated, sometimes with interesting results. Finally, the reciprocal association of two organisms as partners in a reciprocal scaffolding does not rule out the possibility for one of them (or for the whole hybrid system) to associate additionally to a non living scaffold.

In the following section I will describe the lichen symbiosis as an example of reciprocal scaffolding relationship between the fungus and the alga. In another paper¹⁷ I have already addressed, although briefly, the plant gall case, where the gall itself provides a indispensable although temporary scaffold to the development of the gall-inducing insect. Other metaphors or models may prove sensible here, especially *niche construction*¹⁸, as the gall can be

14. GRIESEMER, J. R., "Reproduction and Scaffolded Developmental Processes: an Integrated Evolutionary Perspective", in: MINELLI, A./PRADEU, T. (eds.), *Towards a Theory of Development*, Oxford, Oxford University Press, 2014, pp. 183-202; GRIESEMER, J. R., "Reproduction and the Scaffolded Development of Hybrids", in: CAPORAEL, L. R./GRIESEMER, J.R./WIMSATT, W. C. (eds.) *Developing Scaffolding in Evolution, Cognition and Culture*, Cambridge, MA, MIT Press, 2014, pp. 23-55.

15. Cfr., CAPORAEL, L. R./GRIESEMER, J. R./WIMSATT, W. C., *Developing Scaffolds in Evolution, Culture, and Cognition*, Cambridge, MA, MIT Press, 2014.

16. MINELLI, A., "Scaffolded Biology", *Theory in Biosciences*, 135 (2016), pp. 163-173.

17. *Ibid.*

18. *Sensu*: ODLING-SMEE, F. J., "Niche-Constructing Phenotypes", in: PLOTKIN, H. C. (ed.), *The Role of Behavior in Evolution*, Cambridge, MA, MIT Press, 1988, pp. 73-132; ODLING-SMEE, F. J./LALAND, K. N./FELDMAN, M. W., "Niche Construction", *American Naturalist*, 147 (1996), pp. 641-648; ODLING-SMEE, F. J./LALAND, K. N./FELDMAN, M. W., *Niche Construction: The Neglected Process in Evolution*, Princeton, N. J., Princeton University Press, 2003.

described as an adaptive modification of the proximate environment due to the insect's activity. We could otherwise describe galls as the insect's *extended phenotype*¹⁹. The latter language has been used, e.g., by Raman²⁰ who, for unclear reasons, applies it in the reverse, by describing galls as the plant's extended phenotype. While the following section is focussed on lichens as an interesting class of scaffolded relationships, I will return on galls later, to discuss their singular behaviour in respect to adaptation, with possibly far-reaching implications for the interpretation of their form in terms of evolutionary developmental biology.

5. SKEWED DEVELOPMENTAL SCAFFOLDING

The development of a lichen thallus can be described as the result of a reciprocal, but skewed scaffolding relationship. To some extent, the mycobiont provides a scaffold to the photobiont, and viceversa. In our context, scaffold should not intended in a purely spatial, mechanical sense but, following the definition of scaffolding relationship given above, as a set of resources used by the scaffolded partner. In the case of lichens, both components of the hybrid system are living organisms and their scaffolding relationship is a reciprocal one.

As mentioned above, there is no symmetry in this partnership: the lichen's phenotype is mainly fungal. However, the role of the two partners in the process through which a lichen's thallus takes its form is different in different lichen species.

In many crustose lichens, a mat of hyphae covers the symbiotic thallus: it will be progressively colonized by algal cells, but in the meantime the fungus will produce new hyphae projecting free from the surface²¹. A comparable uncoupling of the two partners has been observed in the fruticose lichen *Aspicilia californica* whose thallus is composed of branching axes with tapered tips. These axes have a central medulla of fungal cells covered by an algal layer which is in turn surrounded by a cortex of fungal cells. The tip of the branches, however, is formed exclusively of fungal tissue. Using the term in the original, purely mechanical sense, Sanders²² described this projecting fungal tissue as a

19. *Sensu*: DAWKINS, R., *The Extended Phenotype*, Oxford, WH Freeman, 1982.

20. RAMAN, A., "Morphogenesis of Insect-Induced Plant Galls: Facts and Questions", *Flora*, 206 (2011), pp. 517-533.

21. SANDERS, W. "A Feeling for the Superorganism: Expression of Plant Form in the Lichen Thallus", *Botanical Journal of the Linnean Society*, 150 (2006), pp. 89-99.

22. *Ibid.*

scaffolding over which the algal layer and cortex will advance and differentiate subsequently.

In other terms, in *A. californica* the different layers (fungal and algal) of the thallus do not differentiate simultaneously, but sequentially²³. Similar events have been observed in the lab in experiments of reconstitution of the lichenic symbiosis from previously separated mycobiont and photobiont of *Cladonia calycanthoides*²⁴. In other species of *Cladonia* the growing areas have also been reported to involve the fungal symbiont only²⁵.

To be sure, we cannot expect a substantial contribution of the photobiont to the overall morphogenesis, especially in the case of unicellular algae, which may be shifted about by the mycobiont, distributing the proliferating algal cells throughout the developing thallus. In other lichens the algal symbiont is filamentous, like the fungus, and the two symbionts often grow in parallel, unless the filamentous algal symbionts are broken up into individual cells or short segments by the push of the growing fungal hyphae.

But there are also examples of lichens where the photobiont seems to have the leading role in the morphogenesis of the thallus. This is the case of some lichens where the photobiont is a blue-green alga (that is, a cyanobacterium), whose spherical cells are embedded in a common sheath of gelatinous material emerging from the surface of the lichen almost independently of the fungus. These little branches will eventually become fully lichenized when the fungal hyphae will grow over the alga²⁶.

The degree of integration between the two partners of the lichenic symbiosis is sometime flexible along the development of an individual thallus²⁷. Moreover, differences between species are not simply expressed by the obvious differences in external form or in the spatial arrangement of fungal filaments and algal cells, but extend to the different degrees of “histological”

23. SANDERS W., “Thallus Organization and Development in the Fruticose Lichens *Aspicilia californica*, with Comparisons to Other Taxa”, *Lichenologist*, 31 (1999), pp. 149-162.

24. STOCKER-WÖRGÖTTER, E., “Experimental Studies of the Lichen Symbiosis: DNA-Analyses, Differentiation and Secondary Chemistry of Selected Mycobionts, Artificial Resynthesis of Two- and Tripartite Symbioses”, *Symbiosis*, 30 (2001), pp. 207-227.

25. HAMMER S., “Modular Growth in Verticillate Podetia of *Cladonia*”, *Mycologia*, 88 (1996), pp. 533-538; HAMMER S., “Developmental Variability in *Cladonia strepsilis*”, *Mycologia*, 91 (1999), pp. 334-342.

26. SANDERS, W. “A Feeling for the Superorganism: Expression of Plant Form in the Lichen Thallus”, *Botanical Journal of the Linnean Society*, 150 (2006), pp. 89-99.

27. GRUBE, M./HAWKSWORTH, D. L., “Trouble with Lichen: the Reevaluation and Re-interpretation of Thallus Form and Fruit Body Types in the Molecular Era”, *Mycological Research*, 111 (2007), pp. 1116-1132.

differentiation of the thallus, such that some loose symbioses have been described as “borderline lichens”. Examples are *Collemopsidium pelvetiae* and *Mastodia tessellata*, where the photobiont is enveloped by fungal tissue but without the differentiation of discrete layers²⁸.

6. EXAPTATION AND LOST SCAFFOLDS

The lichen symbiosis is very old: filamentous hyphae closely associated with cyanobacteria or algae have been found in rocks of the Doushantuo Formation (between 551 and 635 million years old) at Weng’an, South China²⁹. This discovery, and also the reconstruction of the phylogenetic relationships of lichenized and nonlichenized lineages of fungi³⁰, have shown that lichens evolved earlier than hitherto believed, whereas new events of lichenization have been infrequent during the evolution of the ascomycetes, the fungal lineages to which the large majority of lichens belongs. But the opposite trend, that is, the loss of the symbiosis with algae, has occurred multiple times independently³¹. As a consequence, major Ascomycota lineages of exclusively non-lichen-forming species are derived from lichenforming ancestors.

This temporal perspective is of great interest for the question of the evolution of complex structures both in lichens and in non-lichenized fungi. Lichen thalli, especially the most elaborate among the fruticose and foliose ones, are far more complex than a simple mat of hyphae; in the fungal morphology, complex structures are limited to the fruiting bodies (mushrooms and equivalents). Therefore, it has been suggested that the complex structure of lichen thallus evolved from reproductive tissue of the fungus³². However, if lichens are very old, as the above mentioned reports suggest, we should perhaps take also an opposite scenario into account. External inputs such as

28. KOHLMAYER, J./HAWKSWORTH, D.L./VOLKMANN-KOHLMEYER, B., “Observations on two Marine and Maritime ‘Borderline’ Lichens: *Mastodia tessellata* and *Collemopsidium pelvetiae*”, *Mycological Progress*, 3 (2004), pp. 51-56.

29. YUAN, X./XIAO, S./TAYLOR, T., “Lichen-like Symbiosis 600 Million Years Ago”, *Science*, 308 (2005), pp. 1017-1020.

30. E.g., LUTZONI, F./PAGEL, M./REEB, V., “Major Fungal Lineages are Derived from Lichen Symbiotic Ancestors”, *Nature*, 411 (2001), pp. 937-940.

31. *Ibid.*

32. DAL-FORNO, M./LAWREY, J. D./SIKAROODI, M./BHATTARAI, S./GILLEVET, P. M./SULZBACHER, M./LÜCKING, R., “Starting from Scratch: Evolution of the Lichen Thallus in the Basidiolichen *Dictyonema* (Agaricales: Hygrophoraceae)”, *Fungal Biology*, 117 (2013), pp. 584-598.

those deriving from algal cells already present on the substrate where fungal hyphae are growing may have been instrumental in stimulating the fungus to produce increasingly complex structures: these would have represented early forms of lichen thalli and their morphogenetic potential may have been retained by delichenized fungi and exapted as mechanism for the production of their fruiting bodies. Not being a specialist of lichens or fungi, I must leave to the specialists to evaluate this tentative hypothesis. What is clear, anyway, is that the contact with an appropriate photobiont causes in the fungus an alteration in gene expression patterns thus initiating a cascade of morphogenetic events leading to the expression of a mature thallus³³.

7. ADAPTATION AND ORGANISMALITY

Are lichens and plant galls organisms?

Despite the somehow loose degree of morphological and functional integration of its components, the organization of the lichen thallus is definitely adaptive, especially in the case of the more complex foliose and fruticose lichens, with their effectively displayed photosynthetic surfaces, with their marginal or apical zones of growth and branching that allow flexible proliferation in relation to the availability of light³⁴. The symbiosis between the two partners, the fungus and the alga, is mutualistic: that means that within the thallus there is more cooperation than conflict, thus showing what Queller and Strassmann describe as the key signature of any organism³⁵.

Plant galls are different. Galls are systems on which the widely accepted point, that the form of organisms, and their part reliably and consistently generated by developmental processes are adaptive, as a result of selection, is hard to apply. The gross features of gall morphology are quite probably adaptive from the perspective of the gall-inducing insect, although the sheer diversity of gall forms, including those generated by interactions of closely related insects (e.g., members of the same genus of cynipid wasps or cecidomyid midges) on closely related plant species, suggests that many peculiarities

33. TREMBLEY, M. L./RINGLI, C./HONEGGER, R., "Morphological and Molecular Analysis of Early Stages in the Resynthesis of the Lichen *Baeomyces rufus*", *Mycological Research*, 106 (2002), pp. 768-776.

34. SANDERS, W. "A Feeling for the Superorganism: Expression of Plant Form in the Lichen Thallus", *Botanical Journal of the Linnean Society*, 150 (2006). pp. 89-99.

35. QUELLER, D. C./STRASSMANN, J. E., "Beyond Society: The Evolution of Organismality", *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 364 (2009), pp. 3143-3155.

of gall morphology are probably neutral for the survival of the growing larva and the eventually reproductive success of the adult into which it will develop. What about the adaptive value of these peculiarities from the perspective of the plant? Arguably, none except for the different cost of producing larger or smaller galls, or different amounts of peculiar metabolites that the plant does not produce in normal tissues.

Summing up, there is probably no selection for many structural traits of the gall, and possibly of those that make it conspicuous and morphologically distinct not less than a biological species. On the other hand, plant and insect are both exposed to natural selection and this will be of consequence for the morphological properties of the gall. Intra- and especially interspecific variation in either partner will have an effect of gall morphology, witness the astonishing diversity of galls sometimes produced by conspecific insects on conspecific plants, as those of *Andricus* spp. on *Quercus* spp. On the other hand, if it seems hard to explain the morphological peculiarities of a given gall in terms of adaptation, the same peculiarities are likely caused by precise developmental constraints. As far as we know, this uncoupling of development (the arrival of the fittest) and evolution (the survival of the fittest) is very uncommon in nature, and perhaps unique among the forms exhibited by multicellular eukaryotes. For this reason, some plant galls deserve to find a place in the roster of model species in evolutionary developmental biology even if, to follow Queller and Strassmann definition³⁶, their nature as organisms can be questioned. But developmental systems they are nevertheless, although unconventional ones like the symbiotic lichens or the maladaptive and eventually self-destroying cancers.

8. BIBLIOGRAPHY

- BINNS, A. N./THOMASHOW, M. F., "Cell Biology of *Agrobacterium* Infection and Transformation of Plants", *Annual Review of Microbiology*, 42 (1988), pp. 575-606.
- BRIEN, P., "Les demosponges. Morphologie et reproduction", in GRASSÉ, P. P. (ed.), *Traité de Zoologie*, Paris, Masson, vol. 3, 1973, pp. 133-461.
- BÜDEL, B./SCHEIDEGGER, C., "Thallus Morphology and Anatomy", in: NASH, T. H. III (ed.), *Lichen Biology*, Cambridge, Cambridge University Press, 1996, pp. 37-64.
- BULLER, W. L., "Notes on the Tuatara Lizard (*Sphenodon punctatum*), with a Description of a Supposed New Species", *Transactions and Proceedings of the New Zealand Institute*, 9 (for 1876) (1877), pp. 317-325.

36. *Ibid.*

- CAPORAEL, L. R./GRIESEMER, J. R./WIMSATT, W. C. (eds.), *Developing Scaffolds in Evolution, Culture, and Cognition*, Cambridge, MA, MIT Press, 2014.
- CARTER, C. A./WOURMS, J. P., "Naturally Occurring Diblastodermic Eggs in the Annual Fish *Cynolebias*: Implications for Developmental Regulation and Determination", *Journal of Morphology*, 215 (1993), pp. 301-312.
- DAL-FORNO, M./LAWREY, J. D./SIKAROODI, M./BHATTARAI, S./GILLEVET, P. M./SULZBACHER, M./LÜCKING, R., "Starting from Scratch: Evolution of the Lichen Thallus in the Basidiolichen *Dictyonema* (Agaricales: Hygrophoraceae)", *Fungal Biology*, 117 (2013), pp. 584-598.
- DAUGHERTY, C. H./CREE, A./HAY, J. M./THOMPSON, M. B., "Neglected Taxonomy and Continuing Extinctions of Tuatara (*Sphenodon*)", *Nature*, 347 (1990), pp. 177-179.
- DAWKINS, R., *The Extended Phenotype*, Oxford, WH Freeman, 1982.
- DEPRIEST, P. T., "Small subunit rDNA variation in a population of lichen fungi due to optional group-I introns", *Gene*, 134 (1993), pp. 67-74.
- GRIESEMER, J. R., "Reproduction and Scaffolded Developmental Processes: an Integrated Evolutionary Perspective", in: MINELLI, A. and PRADEU, T. (eds.), *Towards a Theory of Development*, Oxford, Oxford University Press, 2014, pp. 183-202.
- GRIESEMER, J.R., "Reproduction and the Scaffolded Development of Hybrids", in: CAPORAEL, L. R., GRIESEMER, J.R. and WIMSATT, W. C. (eds.) *Developing Scaffolding in Evolution, Cognition and Culture*, Cambridge, MA, MIT Press, 2014, pp. 23-55.
- GRUBE, M./HAWKSWORTH, D. L., "Trouble with Lichen: the Reevaluation and Reinterpretation of Thallus Form and Fruit Body Types in the Molecular Era", *Mycological Research*, 111 (2007), pp. 1116-1132.
- HAMMER S., "Modular Growth in Verticillate Podetia of *Cladonia*", *Mycologia*, 88 (1996), pp. 533-538.
- HAMMER S., "Developmental Variability in *Cladonia strepsilis*", *Mycologia*, 91 (1999), pp. 334-342.
- HAWKSWORTH, D. L., CHATER, A. O., "Dynamism and Equilibrium in a Saxicolous Lichen Mosaic", *Lichenologist*, 11 (1979), pp. 75-80.
- HONEGGER, R., "Developmental Biology of Lichens", *New Phytologist*, 125 (1993), pp. 659-677.
- HONEGGER, R., "Morphogenesis", in: NASH, T.H. III (ed.), *Lichen Biology* (1996), Cambridge, Cambridge University Press, pp. 65-87.
- KOHLMEYER, J./HAWKSWORTH, D.L./VOLKMANN-KOHLMEYER, B., "Observations on two Marine and Maritime 'Borderline' Lichens: *Mastodia tessellata* and *Collempsidium pelvetiae*", *Mycological Progress*, 3 (2004), pp. 51-56.
- LETROUT-GALINO, M. A., ASTA, J., "Thallus Morphogenesis in Some Lichens", *Cryptogamic Botany*, 4 (1994), pp. 274-282.
- LUTZONI, F./PAGEL, M./REEB, V., "Major Fungal Lineages are Derived from Lichen Symbiotic Ancestors", *Nature*, 411 (2001), pp. 937-940.

- MINELLI, A./PRADEU, T. (eds.), *Towards a Theory of Development*, Oxford, Oxford University Press, 2014.
- MINELLI, A., “Scaffolded Biology”, *Theory in Biosciences*, 135 (2016), pp. 163-173.
- ODLING-SMEE, F. J., “Niche-Constructing Phenotypes”, in: PLOTKIN, H. C. (ed.), *The Role of Behavior in Evolution* (1988), Cambridge, MA, MIT Press, pp. 73-132.
- ODLING-SMEE, F. J., LALAND, K. N. and FELDMAN, M. W., “Niche Construction”, *American Naturalist*, 147 (1996), pp. 641-648.
- ODLING-SMEE, F. J., LALAND, K. N. and FELDMAN, M. W., *Niche Construction: The Neglected Process in Evolution*, Princeton, N. J., Princeton University Press, 2003.
- QUELLER, D. C./STRASSMANN, J. E., “Beyond Society: The Evolution of Organismality”, *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 364 (2009), pp. 3143-3155.
- RAMAN, A., “Morphogenesis of Insect-Induced Plant Galls: Facts and Questions”, *Flora*, 206 (2011), pp. 517-533.
- SANDERS W., “Thallus Organization and Development in the Fruticose Lichens *Aspicilia californica*, with Comparisons to Other Taxa”, *Lichenologist*, 31 (1999), pp. 149-162.
- SANDERS, W. “A Feeling for the Superorganism: Expression of Plant Form in the Lichen Thallus”, *Botanical Journal of the Linnean Society*, 150 (2006). pp. 89-99.
- SANDERS, W., “In Situ Development of the Foliicolous Lichen *Phyllophiale* (Trichotheliaceae) from Propagule Germination to Propagule Production”, *American Journal of Botany*, 89 (2002), pp. 1741-1746.
- SCHUSTER, G., “Die Jugendentwicklung von Flechten. Ein Indikator für Klimabedingungen und Umweltbelastung”, *Bibliotheca Lichenologica*, 20 (1985), pp. 1-206.
- STOCKER-WÖRGÖTTER, E., “Experimental Studies of the Lichen Symbiosis: DNA-Analyses, Differentiation and Secondary Chemistry of Selected Mycobionts, Artificial Resynthesis of Two- and Tripartite Symbioses”, *Symbiosis*, 30 (2001), pp. 207-227.
- TREMBLEY, M. L./RINGLI, C./HONEGGER, R., “Morphological and Molecular Analysis of Early Stages in the Resynthesis of the Lichen *Baeomyces rufus*”, *Mycological Research*, 106 (2002), pp. 768-776.
- YUAN, X./XIAO, S./TAYLOR, T., “Lichen-like Symbiosis 600 Million Years Ago”, *Science*, 308 (2005), pp. 1017-1020.