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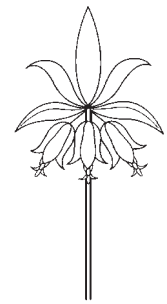
A Journal of Botanical History



VOLUME 15 NUMBER 1
2014

Hunt Institute for Botanical Documentation
Carnegie Mellon University

Pittsburgh

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Printed and bound by R.R. Donnelley,
Hoechstetter Plant, Pittsburgh, Pennsylvania



ISSN 0073-4071

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HUNTIA 15(1) 2014

# De Bary's legacy: The emergence of differing perspectives on lichen symbiosis

M. E. Mitchell

**Abstract**

Evidence that lichens exhibit algal and fungal characteristics had been reported intermittently from the 1760s onwards, but the significance of those observations was not grasped until a century later. This lapse is directly attributable to a blind endorsement by contemporary botanists of the prevailing belief that lichens constituted an autonomous category of plants. The composite nature of lichens was first posited in 1866 and 12 years later the term "Symbiose" was proposed for any union of dissimilar organisms; allegations that this term was an unacknowledged borrowing from an 1876 publication are shown to be groundless. The present paper surveys the — occasionally bizarre — attempts over the last 100 years to delimit categories of lichen symbiosis. Interpretations of biont interaction fluctuated primarily between mutualism and parasitism until the publication, early in the present century, of compelling evidence that non-photosynthetic bacteria are involved in the lichen symbiosis; this finding has made elucidation of the alliance a still more distant prospect.

The work of documenting the various postulated categories of symbosis had the unexpected result of turning up primary references for sundry other lichen-related terms. Since those references are widely dispersed across the literature, an attempt has been made to smooth the path of those wishing to source the names of specific features by preparing a documented inventory of all terms introduced in an exclusively lichen context and currently employed; the results of that attempt, chronologically and concisely presented, appear as an addendum to this paper.

## Introduction

The affinity between gelatinous lichens and the genus *Nostoc* was first remarked on late in the 18th century by Haller (1768, 3:94) and Ventenat (1799, 2:36), at which time the conformity between fungal and lichen fruit-bodies was also recognized by Hedwig (1787–1797, 2:3) and Persoon (1794a, p. 7). Those reports were underpinned in the opening decades of the following century by Cassini (1817, p. 396) in respect of *Nostoc*, by Fries (1831, p. lxiii) with regard to the structure of lichen sporocarps, and by Unger (1833, p. 540) who observed "*Protococcus*" unicells in thalli of *Xanthoria* (as *Parmelia*) *parietina*. Such findings did not, however, lead to any early understanding of lichen structure: by the 1840s virtually all botanists — hostages to "the paralysing influence of the preconceived idea" (Sprague 1933, p. 31) — endorsed the dictum of Acharius (1810, p. 14) that lichens represented an autonomous grouping distinct from either algae or fungi.

Despite the emergence of further evidence to the contrary, the Acharian view prevailed until Anton de Bary (1831–1888) — while professor of botany at the University of Freiburg — aired the possibility that some algae "assume the form of *Collema*, *Ephebe* etc. as a result of penetration by certain parasitic ascomycetes" (1866, p. 291).[1] Simon Schwendener (1829–1919), then at the University of Munich, was quick to grasp the significance of de Bary's intuition, which he realized could apply to all lichens (Anonymous 1867). Further development of this insight by Schwendener endorsed de Bary's parasitic assessment of the components' relationship, which the former vividly presented (1869, p. 3) as that of a fungal taskmaster exploiting colonies of algal slaves ("Sclaven"); Schwendener termed

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his interpretation "helotism" ("Helotenthum," p. 4). For most botanists, however, the notion that a parasitic relationship could generate a perennial organism was, at best, implausible, and there were widespread expressions of dissent (cf. Sapp 1994, p. 6). Though Schwendener (1872) addressed some of these, it was not until the concept of symbiosis was formulated later in the decade that a dual constitution of lichens came gradually to be accepted.

Perru (2006, p. 14) took the view that though "[Albert] Frank [1839–1900] and de Bary are the scientists whose names are commonly mentioned in connection with the origins of symbiosis … it appears more and more unlikely that de Bary and Frank coined the term symbiosis independently."[2] As his source for that contention, Perru cited Richardson (1999) where the relevant passage reads (pp. 641–642)

> It is most unlikely that de Bary and Frank independently invented the term symbiosis. They worked at universities only 35 km apart … and Frank not only used "symbiosis" first but also introduced other terms such as "mycorrhiza" (Frank, 1885). Hawksworth (1995a) believes that de Bary either heard a lecture by Frank on lichens, or a report of such a lecture, and then adopted and introduced the word "symbiosis" to his own audience a year later. There seems to be no documentation to show that they actually discussed "symbiosis" but it is clear that de Bary admired Frank's research. He is mentioned both in the preface of *Comparative Morphology of Fungi, Mycetozoa and Bacteria* and again several times in the text (de Bary, 1887). It is interesting, however, that de Bary does not, as far as I can see, use "symbiosis" anywhere in his book even though it contains a substantial section on lichens. This again suggests that he used the term in his lecture after listening to Frank's paper, talking or corresponding with him and that "symbiosis" was not a term that de Bary himself coined and of which he was proud.

Taking that final, gratuitous, comment first, it is incorrect to say that "de Bary does not … use 'symbiosis' anywhere in his book": the word is actually indexed in *Comparative Morphology* with reference to page 356 where de Bary wrote, "Fungi have long been divided into two main sections founded on their nutritive adaptation. Those which constitute the first category feed on living organisms whether plants or animals and are termed *parasites*. Their relationship with their hosts is that of a common life, a *symbiosis*. The others inhabit decaying bodies and feed on dead organic substances, and have been named therefore since 1866 [Bary, p. 205] *saprophytes*." As regards the statement that "[t]here seems to be no documentation to show that [de Bary and Frank] actually discussed symbiosis," a belief that they did so appears to be the reason for mentioning their having "worked at universities only 35 km apart [Halle and Leipzig]."[3] If any such local discussions did take place, they would necessarily have been before early 1872, when de Bary became professor of botany at Strasbourg (then Strassburg, which it remained until 1919), and would certainly not have found Frank in a position to contribute usefully to any discussion concerning lichen composition: as late as September 1873, when addressing the annual meeting of German Naturalists and Physicians, held that year at Wiesbaden, Frank (1873, p. 132) reported on an anatomical study of *Pertusaria pertusa* (as *Variolaria communis*) that, he claimed, demonstrated the production of green cells by colorless thalline filaments or, as he put it, "the development of gonidia from hyphae."[4] It is possible that de Bary attended Frank's lecture and later explained to him why he could not have made the observation in question; if symbiosis were mentioned during any such conversation, de Bary would have been the only one in a position to do so. In any event, three years later Frank (1876c) had not alone come to regard lichens as dual organisms but was proposing the term "Symbiotismus" (p. 195) to describe the component relationships.

In 1878, at Cassel, de Bary also addressed the meeting of German Naturalists and Physicians. He began by stating that he had chosen to speak on "the phenomena associated with the alliance of unrelated organisms — symbiosis, as it may be put concisely and in general," and later commented (p. 124; p. 21 in the 1879 reprint) "parasitism, mutualism, lichenism etc. are really at times special instances of that general associative arrangement for which the aforesaid term symbiosis may serve as a collective designation. If one wishes to differentiate between these main categories, two may be emphasized: one antagonistic with reciprocal conflict, and the other mutualistic, in the wide sense, with complementary betterment of the symbionts."[5] Hertig et al. (1937, p. 327) astutely remarked that "[t]he almost casual way in which the term was introduced" by de Bary "might give one the impression that it had been used previously in the biological literature" but "found no reference to it earlier than the symbiosis address"; they were, however, quite correct. When the Greek botanist Theophrastus (ca.370–ca.285 BC) described a particular instance of ivy growing on the olive in *Historia Plantarum* (2.1.2, Amigues translation, 2003, p. [44]), he applied the existing word "sumbiosai" ("συμβιωσάί") to the living together of those plants; the word also appears, in modified form though similar sense, in *De Causis Plantarum* (2.17.5, Einarson and Link translation, 1976, p. 338). Since we know that de Bary had read Theophrastus (Bary 1853, p. 103), it is reasonable to assume that memory served him well when circumstances required.

There remains the fact that de Bary made no mention of Frank's paper either in his lecture or the extensively annotated version published in the following year (1879), yet he could scarcely have been unaware of it because, in the summer of 1876, the then widely circulating journals *Flora* and *Hedwigia* carried a "Preliminary Communication" ("Vorläufige Mittheilung") of its content (Frank 1876a, 1876b). But if having seen one or other of these — both worded alike — de Bary deferred a reading of Frank's full 77-page report when it appeared late in 1876, he would not have met with Frank's "Symbiotismus" because the word does not appear in the "Preliminary Communication." The facts outlined above, together with the range of terms credited to de Bary by Wagenitz (2008), amply demonstrate that an attempt to portray him as reduced to cribbing is not rationally sustainable.[6]

## The word spreads and the concept broadens

At Strasbourg, de Bary created an outstanding research institute where many European and North American postgraduates enjoyed the privilege of working under his direction. Some of these men (all 68 of de Bary's Strasbourg postgrads were indeed male) later made the idea of symbiosis familiar to a wide public: among them, the German Georg Klebs (1857–1920) produced an exhaustive survey of the subject with reference to both plants and animals (1882), the Italian Oreste Mattirolo (1856–1947) produced a semi-popular account (1883) restricted to plants (then including fungi) and the Englishman Frederick Bower (1855–1948) paused in his study of vascular cryptogams to endorse the — then still contested — judgement "that lichens are not in themselves distinct plants, but are a compound of fungi and algae, living together in a relationship of mutual help called 'symbiosis,' (erroneously termed parasitism)" (1887, p. 38).

Among de Bary's peers, Eduard Strasburger (1844–1912), professor of botany at the University of Bonn, also helped popularize the concept. He believed that lichens depend for their existence on a mutualistic relationship and, in one of the earliest comments on lichen metabolism, personified them as "the

proletarians among plants" (1891, p. 199) because of the meager nutrient turnover available to them for survival and reproduction.[7] At this time, symbiosis already accommodated — in addition to mutualism — a ménage comprising commensalism,[8] consortism,[9] helotism, lichenism[10] and parasitism, but some believed still further categorization was needed. While attached to the Forestry Research Institute at the University of Munich, Karl von Tubeuf (1862–1941) published a plant pathology text (1895) that included a brief excursus on the lichen association; taking the view that mutualism did not adequately convey such "unification of two living beings into an individual whole," he proposed that the alliance be designated "Individualismus."[11]

Later in the decade Wilhelm Zopf (1846–1909), professor of botany at Münster and best remembered by lichenologists for his work on thallus chemistry, reported on a study involving several fungi that he regarded as lichen parasites. Zopf found that in some instances the hyphae of those fungi do not invade the host algae, a condition he termed "Parasymbiose" (1897).[12] Other instances of Zopf's tripartite associations were published by Alexandr Elenkin (1875–1942) while attached to the St. Petersburg Botanical Garden. His paper (1901) included the assertion that a mutualistic interpretation of component relations was incompatible with reports of dead algal cells within thalli, a view that led him to propose the jettisoning — in a lichen context — of "symbiosis" in favor of "endosaprophytism." Despite further advocacy in the following year, Elenkin failed to win support for that proposal, but his views did occasion debate at a time of particular Russian concern with the phenomenon of symbiosis (Khakhina 1992, pp. 51–54, 58, 90).

In 1905 Constantin Mereschkowsky (1855–1921), then lecturer in botany at Kazan University, published the now celebrated article in which he portrayed chloroplasts as symbiotically adapted cyanophytes (cyanoprokaryotes), and two years later Andrei Famintsin (1835–1919), professor of botany at the University of St. Petersburg, reported briefly on attempts to isolate and culture "a chlorophyllous structure from plants, lichen algae in particular" (1907, p. 355).[13] Mereschkowsky's revolutionary theorizing failed to attract any early attention outside Russia. It went unmentioned, for example, in a wide-ranging review (1910) of advances in the study of symbiosis by Zopf's assistant Friedrich Tobler (1879–1957). Mereschkowsky again aired his hypothesis in a comprehensive study that represented cell organelles as exogenous bodies, a concept he styled "Symbiogenesis" (1910, p. 279), but that paper too was ignored by most Western biologists for well over half a century.

Among the few prepared to keep an open mind on the subject was the American lichenologist Bruce Fink (1861–1927), professor of botany at Miami University, Ohio. During the years immediately following his appointment in 1906, Fink completed a study of Minnesota lichens on which he had been engaged for the previous ten years. The introduction to that work extends to a brief commentary on the topic of symbiosis in the course of which Fink (1910, p. 7) stated "we seem to have in lichens the highest expression, so far as is known, of mutualism." In November 1909, however, Fink had written to "75 American botanists and an equal number of foreign botanists asking for their views regarding the classification of lichens" (1911, p. 231); essentially he hoped to quantify the factions representing "those who believe that lichens should be regarded as fungi" and "those who think that these plants form a group entirely distinct from fungi" (p. 232). Of the 150 botanists circularized, 115 replied (Famintzin among them), and

some of their opinions evidently convinced Fink that symbiont relations should properly be interpreted as parasitic. In a further paper (1913), while accepting "that the chlorophyll granules of higher plants resemble certain algae and may be such" (p. 103), Fink now considered that even if proved this would not validate "the mutualism hypotheses, to one of which some of us had adhered for many years" (p. 117), and declared it was "time to be done with those unproved and hopeless hypotheses of mutualism, consortism and individualism" (p. 141). Such swaying between mutualistic and parasitic interpretations of the symbiosis became a lasting feature of the debate. A contemporary of Fink's, the German Wilhelm Nienburg (1882–1932)—subsequently author of the first work devoted to lichen anatomy—published an account of lichen symbiosis (1913) in which he too, harking back to Schwendener, visualized the fungus as surviving at the alga's expense: "the fungus can make subtle adjustments to its algal associate's metabolism with the result that the former is ultimately sustained by the latter's assimilates. Such dependency calls to mind a prudent master whose careful provision for his slaves enables him the better to exploit them" (p. 938).[14]

This return to a perception of lichen symbiosis as parasitism took a curious turn when Fernand and Valentine Moreau (1886–1980, 1886–1974), then working as assistants at the Sorbonne, published the results of an extensive anatomical study involving species of *Peltigera* and *Solorina* (1919). Their investigation of the cephalodia produced by, in particular, *P. aphthosa*, led them to interpret those structures as galls resulting from the stimulatory effect of airborne cyanoprokaryotes on cortical hyphae. The Moreaus then went further, to the extent of proposing that the entire thalli they had studied were a response of the component fungus to a biomorphogenetic stimulus delivered by the alga: "we have come to regard the *Peltigera* thallus as the equivalent of an organ deformed by a parasite … this concept should probably be broadened and extended to all lichens" (p. 125).[15] Their contemporaries were not particularly taken by such assertions, Nienburg (1926, p. 100) for example rejected them as "absurd," with Darbishire (1927, p. 222) similarly, if less bluntly, dismissive; despite Fernand Moreau's periodic championing of the gall concept in subsequent years, it never attracted serious support.

Another unorthodox take on lichen symbiosis was published early in the 1920s by Arthur Church (1865–1937), demonstrator in botany at Oxford University. His belief that fungi were "saprophytic and transmigrant derivatives of marine algae of higher grade" (1919, p. 63) led him to regard the lichen alliance as a "case of an algal race, deteriorating along the lines of a heterotrophic existence, yet arrested, as it were, on the somatic downgrade, by the adoption of intrusive algal units of lower degree to subserve photosynthesis" (1920, p. 267). If Church expected his brain-child to meet with general acclaim he was to be majorly disabused: principal among the very few contemporary lichenologists to comment on the theory were Darbishire (1924, p. 23; 1926, p. 753) and Smith (1921, pp. 421–422), neither of whom was unduly enthused. Though beyond question a very able botanist—his illustrations of floral anatomy are still widely admired—Church's engagement with symbiosis was not his finest hour.

A somewhat similar reception awaited the views of Ewald Bachmann (1850–1937), a retired German second-level biology teacher and author of numerous papers on lichenological topics. Observations made in the course of an anatomical study involving *Anaptychia*, *Cladonia*, *Schaereria* and *Umbilicaria* material led Bachmann (1923) to report a

marked increase in the number of algal cells at sites of incipient ascomatal and pycnidial formation, and their gradual disappearance as those structures matured. He consequently assumed that the algae had become a source of "nitrogen-rich material" ("sticksstoffreichen Baustuffe") for the fungal component (p. 239), an inference that pointed to a parasitic relationship and at odds, therefore, with Bachmann's firm conviction that symbiosis was essentially mutualistic. To overcome this problem, and influenced perhaps by Nienburg's (1913) analogy mentioned earlier, he contrived a decidedly anthropomorphic interpretation of his findings: "rather than indicating parasitism, the case of algal cells being completely resorbed during fruit development represents their 'sacrificial murder' ('Opfertod') for the benefit of the lichen fungus" (p, 253). He believed "the expression 'supportive slavery' might well be applied to lichen algae were it not that the fungal component suppresses their sexual reproduction. That stumbling block is removed, however, if the algae are compared to castrated farm animals, prized by their master as a highly valuable possession and treated accordingly" (p. 254).[16] Bachmann's arresting vision was at best coolly received by his peers and, apart from a mention by Wallert (1931, pp. 348–349), effectively forgotten.[17]

None of those who had so far concerned themselves with the interaction of lichen bionts doubted that they were dealing solely with algae and fungi. However, in the course of a study undertaken at the University of Urbino, Maria Cengia Sambo (1888–1939) noted that thalli of *Pannaria rubiginosa* and certain *Peltigera* species consistently harbor bacterial cells in the gelatinous sheaths surrounding their *Nostoc* photobiont. Having tentatively assigned those cells to the genus *Azotobacter*, she went on to suggest that they contribute to the lichens' metabolism by fixing atmospheric nitrogen, and introduced the term "polisimbiosi" for this tripartite association (1923, p. 236). Subsequently, after she had moved to the Plant Biology Laboratory at Florence, Cengia Sambo expressed herself satisfied that the *Nostoc*-associated bacterium did indeed represent a species of *Azotobacter* (1925, p. 194). In the short term, however, the concept of polysymbiosis attracted scant attention, to the extent that Friedrich Tobler, now director of the Dresden Botanical Garden, made no mention of it in the otherwise detailed review of symbiosis that constitutes the fourth section of his *Biologie der Flechten* (1925, pp. 167–216).[18]

A report on the growth of a lichenicolous fungus within cephalodiate *Lobaria pulmonaria* thalli, prepared at the University of Strasbourg by Roger-Guy Werner (1901–1977), included a claim that the invasive hyphae exhibit a divergent response to contact with the chlorophyllous organisms present. Werner regarded the response he observed in hyphae associated with the host's algal cells as coming within the compass of parasymbiosis but chose to particularize the hyphal variation allegedly discernible in the vicinity of the secondary photobiont as "pseudoparasymbiose" (1928, p. 203). Such finespun discrimination appears to have been largely illusory, however, and Werner's coinage found no place in Abbayes' (1937) commentary on contemporary work in the area of lichen symbiosis. His review of that literature led him to conclude that the relationship definitely points—in the case of most thalli—to "the alga giving more than it receives,"[19] and, consequently, that the symbiosis concerned is, in effect, a parasitic association.

The question of bacterial involvement in thallus metabolism had hung fire for well over a decade when Pavel Henckel (1903–1985) communicated the results of a study undertaken at Perm State University. Having noted the presence of *Azotobacter* in material belonging to 11 micro- and macrolichen genera—a circumstance he referred to as

triple symbiosis — Henckel made "a special study of the question concerning the reciprocal relationships of the lichens' three components"; here he found that *Azotobacter* occurs in association with the algal cells, which supply the bacteria with nutrients that enhance their nitrogen-fixing capacity, and believed "in general, the fungus effects its nutrition osmotically at the expense of algal glucides and ammonia produced by *Azotobacter*" (1938, pp. 18–19).[20] Henckel seems to have been unaware of Cengia Sambo's work — there is no mention of his findings being at odds with her contention that symbiotic bacteria are restricted to thalli having a *Nostoc* photobiont; coincidentally, Cengia Sambo briefly revisited the topic of polysymbiosis in 1939, an occasion on which she somehow felt constrained to describe a loose arrangement of algae and fungi, allegedly characteristic of certain lichen species, as hemisymbiosis ("emisimbiosi").

A valuable appraisal of the more important literature on lichen biology published up to 1940 was provided by Reinhold Schaede (1887–ca.1965) while attached to the University of Breslau (Wrockław). His survey comprises ten sections ranging from algal components to water relations. The brevity of that devoted to symbiont interaction (1943, p. 97) reflects how few facts had then been established in this regard, with Schaede saying only that all intermediate stages exist from sustained parasitism (termed "Dyssymbiose"), involving death of the invaded cells, to compatibility ("Eusymbiose"). His review concluded with a line from Tobler (1934, p. 4): "lichen biology in general and physiology in particular are still almost untilled ground and call out for cultivation!"[21] Tobler's prayer was heard early in the the 1940s when Anton Quispel (1917–2008), a graduate student at Delft Technical College and, subsequently, at the Universities of Groningen and Leiden, undertook extensive experimental work on the nutrition and relationship of bionts isolated from several foliose species; his findings left him feeling "certainly justified to consider the association as mutualistic" (1943–1945, p. 525). Further results were, however, to prompt a reconsideration of that conclusion and occasion his observation (1951, pp. 69–70) that "[t]oo many biologists had failed to realize that two organisms don't enter into a symbiosis to give something to a partner, but in order to take as much advantage of the partner as possible." This view was endorsed by Mackenzie Lamb (1911–1990), who, during his tenure as director of the Farlow Herbarium, judged the partnership to be one of "controlled parasitism" (1959, p. 156), and by Mason Hale (1928–1990) at the Smithsonian Institution, employing the variant "balanced parasitism," (1961, p. 50). These further attempts to label a condition for which there existed no empirical data may have been the spark for Haynes' (1964, p. 79) quip that "[s]ince the initial discovery of the dual nature of the lichen thallus, the only relationship that has not been suggested between its components is one in which neither partner affects the other."

Interest in the physiology of lichen symbiosis received an important stimulus when Vernon Ahmadjian (1930–2012), professor of botany at Clark University, published the first book to deal solely with that subject (1967). The nature of the relationship between the bionts was not, however, discussed at length, with the author content to say only (p. 78) that the alliance could be expected to furnish instances of both mutualism and parasitism. Neither of these interpretations lacked for supporters, with those backing the former perhaps more numerous and imaginative: following a concise account of lichen ecology and physiology, the German plant physiologist Otto Stocker (1888–1979) stated that "in the final analysis, organization of the lichen symbiosis depends on the capacity of the heterotrophic fungus to direct its hyphae to

the construction of a 'house' for the storage of rainwater and the supply of resources promoting photosynthesis to the autotrophic tenant; some of the latter's metabolites go to pay the landlord's rent and so ensure survival of the fungus. That two such differently constituted partners should reach so successful a power balance represents a natural 'contrat social' to make politicians and sociologists die of envy."[22] This Rousseauvian parallel did not go untagged as Stocker, using the German word for "rent," proceeded to encumber the literature with the further notional category of "Mietsymbiose" (1975, p. 370).

The majority perception of lichen symbiosis as an essentially mutualistic union suffered a reverse early in the 1980s. Having noted the lack of any experimental evidence in its support, Ahmadjian and Jacobs (1981, p. 169) concluded from *in vitro* syntheses involving the mycobiont of *Cladonia cristatella* and various algae that "the relationship in this lichen is one of controlled parasitism." They subsequently proposed that the fungal component of a lichen be understood as a biotrophic parasite and the symbiosis as a balanced alliance, in the sense that "the percentage of cells killed is balanced by new cells added to the population by division of existing algal cells" (1983, p. 147).

Parasitism and several other postulates concerning lichen biont interactions were reviewed by Hale (1983, pp. 67–69) who concluded that "[a]ll proposed concepts of the relation between the fungus and alga in lichens contain some elements of truth, but no one theory can, in fact, embrace the complex physiological activities that make lichen symbiosis such a highly successful venture."[23] These wise words had, however, little impact in the short term: for example, Hawksworth (1988, p. 8) remained convinced that "the symbiosis has to be viewed as mutualistic," while Ahmadjian (1993, p. 3)—speaking now of "balanced" rather than "controlled" parasitism—described mutualism as a "myth."[24] In fact, the lichen symbiosis has to be regarded as just one among the many associations visualized by Saffo (1993, p. 23) as "too complex to pigeonhole into the simple categories of parasitism, mutualism and commensalism."

While there had been sporadic comment during the latter half of the 20th century respecting the claim that bacteria contribute to the lichen symbiosis, most of this was uncompromisingly dismissive, e.g., Millbank and Kershaw (1974, p. 298). Some years into the new millenium, however, well substantiated results demonstrating that non-photosynthetic bacteria would have to be factored into the lichen equation began to appear (Cardinale et al. 2006, Hodkinson et al. 2006 and Bates et al. 2011). This development has exposed the mutualism versus parasitism debate as simplistic and further deferred an understanding of the metabolic commerce that sustains lichen growth.

## Addendum: The naming of parts

Preparation of the above report on symbiotic categories had the incidental result of bringing to light the first appearance of various other lichenological terms. As the corresponding literature sources are nothing if not diverse, it is hoped that the following attempt to provide a brief but comprehensive itemizing of the current lichen vocabulary will be of benefit. General mycological terms pressed into service by lichenologists over the years are not considered here; only such designations as were introduced with specific reference to lichenized fungi are documented in the following account.

The first feature of a lichen to be individually characterized was the concave structure produced by certain *Cladonia* species for the deployment of their fruit-bodies. That structure was termed an "acetabulum" by the Swiss physician Jean Bauhin (1541–1612) in *Historia Plantarum Universalis* (posthumously

published 1650–1651, 3:767). His lead in this regard was followed by Tournefort (1700, 1:549) and Micheli (1729, p. 82), but the German botanist Johann Dillenius (1687–1747) preferred the word *scyphus* (1742, p. 75)[25]; endorsement of this alternative by Linnaeus (1753, 2:1151) ensured that it prevailed. No further labelling occurred until the 1790s. When Adanson (1763–1764, 2:11) established the genus *Graphis*, he described the fruit-bodies as furrows ("sillons"), a view endorsed by the South African mycologist Christiaan Persoon (1761–1836) in his statement that "this very variable structure may be named a *lirella*" (1794a, p. 3).[26] Since just two lichen-related terms were current at the end of the 18th century, contemporary mention of other thalline features showed little consistency — a shortcoming that would soon be addressed.

The emergence of lichenology as a distinct discipline is largely attributable to the industry of Erik Acharius (1757–1819), a native of Gävle, eastern Sweden. Of Acharius' many publications, those that appeared in 1803, 1810 and 1814 amply justify his portrayal as "the founder of the systematic study of lichenology" (Arvidson 1999, p. 25). Acharius' first contributions to terminology came in *Lichenographia Suecicae* (1799), where, together with nine now obsolete designations, he described the pits occurring on the lower cortex of *Sticta* species as *cyphellae* (p. xvi). This was followed by a suite of terms that have been familiar to lichenologists ever since: *apothecium*,[27] *cephalodium*,[28] *podetium*, *proper margin*, *soredium*, *thallus* (1803, pp. ix, xix, xxii, xvi, xxi, vii, respectively); Acharius subsequently added *thalline margin* (1810, p. 6) and *mazaedium* (1817, p. 224). A selection of his introductions was glossed for British botanists by Gray (1821, 1:223–224), and in the case of proper and thalline margin, the Swedish mycologist Elias Fries (1794–1878) changed the noun to *exciple* (1825, pp. 230) — all four of which renderings remain current.

Primarily, of course, Acharius was the author of many new genera, and one of these, *Isidium*, was designed to accommodate species characterized by the production of distinctive, cortical, outgrowths. That genus was later recognized as representing a quite artificial assemblage, at which stage its name was applied to a single such outgrowth by Georg Meyer (1782–1856). Before his appointment to a professorship at the University of Göttingen, Meyer was "Economic Counsellor of the British Crown in Hanover," as rather grandly stated on the title page of his *Entwicklung, Metamorphose und Fortpflanzung der Flechten* (1825).[29] The appearance in that work of such expressions as "development of *isidia*" ("Isidienbildung," pp. 201, 207), "tops of isidia" ("Isidienköpfe," p. 204) and "shape of isidia" ("Isidienform," p. 206) made the new usage familiar to a specialist readership that soon gave it currency (e.g., Fries 1831, p. lxxiv). Meyer was furthermore responsible for *prothallus*, introduced in a discussion of lichen growth (pp. 315–316).

Also in 1825, the German physician Friedrich Wallroth (1792–1857) published the first volume of *Naturgeschichte der Flechten* (1825–1827). An able though self-opinionated botanist, Wallroth was particularly critical of Acharius, to the extent that he prepared an alternative, largely Greek-based, terminology. This would have presented little difficulty to so accomplished a classicist,[30] but given Wallroth's addiction to periphrasis, the results were so long-winded that he was publicly censured (e.g., Martius 1826, pp. 209–210; Fée 1826, p. 362). Wallroth is now remembered only for the designations *epi-* and *hypophloeodal* (1825–1827, 1:141–142), the thalline categories *hetero-* and *homoiomerous* (1:23–24) and the word "gonidium" (1:40), which last continued in everyday use until supplanted in the 1960s (see Scott 1957 below).

Wallroth's critic Carl von Martius (1794–1868), professor of botany at the University of

Munich, had spent the years 1817 to 1820 on fieldwork in Brazil and reported on some of the lichens collected there in the first part of *Icones Plantarum Cryptogamicarum* (1828–1834). Here, on the basis of painstaking microscopical investigation involving *Cladonia*, *Collema*, *Lecidea* and *Parmelia* material, he described and illustrated the *hypothecium* (pp. 23–30, pls. 23–24). *Hypothallus* also dates from this time and is attributable to Fries (1831, p. xxix) who, though happy as we have seen to endorse Meyer's use of isidium, sought to replace his prothallus with this new term. In the event, both designations came to be used and have proved a recurrent source of confusion (see Hannemann 1973 below). By the early 1830s the number of thalline features whose names remain in current use had reached 21, and there the figure remained for the following 20 years.

Towards mid-century, good quality microscopes were in the hands of a privileged few, among them Julius von Flotow (1788–1856), a Prussian army officer, who expressively described how the acquisition of a Schiek instrument had furthered his researches (1850, p. 361). Flotow paid special attention to crustose lichens, work on one of which — *Rimularia* (as *Mosigia*) *gibbosa* — led to his recognizing the *epithecium* (1851, p. 776). In the area of lichen anatomy the most accomplished microscopist of the period was, however, Louis-René Tulasne (1815–1885). Beginning in 1842, Tulasne spent 30 years as an assistant at the Natural History Museum in Paris where his work earned him renown as a mycologist. Initially he took a particular interest in lichens, and in 1852 published an innovative anatomical and morphological study of the group, which included his description and naming of the *pycnidium* (p. 108). For much of the period from 1850 to the early 1870s, Tulasne had the expatriate Finn William Nylander (1822–1899) as an unofficial colleague at the Museum. Nylander's unremitting nomenclatural drive was not reflected, fortunately perhaps, in his engagement with terminology: here his contributions numbered just four, the earliest of which were *hymenial algae* (as "gonidia") and the use of *thecium* as an alternative to "hymenium" (1853, p. 158, fn.).

The first relevant contribution from a British lichenologist appeared about this time. In a prefatory comment to his survey of the genus *Arthonia*, the clergyman William Leighton (1805–1889) drew attention to the fact that when Acharius introduced that generic name, he wished to convey his perception of the fruit-bodies as sprinkled over the thallus but, in the process, had somehow used "artho" instead of "ardo." Consequently, when Leighton decided there was need, he chose "to designate the [*Arthonia*] apothecium by the term *ardella*, significant of its appearance as a sprinkled spot" (1854, p. 437).[31] With microscopes becoming more readily available, spore morphology began to receive close attention as a source of generic criteria. One advocate of this approach was Wilhelm Koerber (1817–1885), professor of botany at the University of Breslau (Wrockław); he described the distinctive spores of *Rhizocarpon* and *Umbilicaria*, for example, as *muriform* (1855, p. 443) and those of *Xanthoria* as "polari-dyblastae" (p. 91; anglicized to "polari-bilocular" by Mudd (1861, p. 11) and abbreviated by the French abbé Henri Olivier (1849–1923) to *polarilocular* (1882–1884, 1:14)). Koerber also coined *amphithecium* (1855, p. 321), which, being of obscure application, was soon lost to view and so remained until reintroduced some 40 years later (see Darbishire 1898 below). Activity in the 1850s concluded with, first, Nylander's remaining contributions, viz. *chondroid axis* and *pseudocyphella* (1858–1869, 1:266, 333), and, secondly, the publication by Theodor Fries (1832–1913) — son of Elias Fries and also, eventually, professor at Uppsala — of a commentary on the genus *Stereocaulon* in

which he added *phyllocladium* to the growing tally, though clearly with reluctance (1858, p. 315, fn.).

The three decades following the 1850s proved a good deal less productive. *Goniocyst* was introduced by Johannes Norman (1823–1903), a Norwegian forester (1872, p. 10),[32] *campylidium* by Johannes Müller (1828–1896), professor of botany at the University of Geneva (1881, p. 111), and *pseudopodetium* by Gustav Krabbe (1855–1895) while a research student at the University of Berlin (1882, p. 108).[33] The years to century's end brought a return to form with the emphasis on anatomical attributes. First, however, Vainio (1890, p. xxiii) proposed the use of *pseudostroma* in the case of lichenized fungi. Then in an extensive study of cortical structure and its bearing on water relations, Hugo Zukal (1845–1900) — working at a teacher training institute in Vienna — identified the *pallisade hyphae* that characterize the *Roccella* cortex (1895, p. 1306). As originally conceived by Acharius in 1803, the soredium denoted a specific cortical area, but later the word also became applied to an individual diaspore produced in such areas; this dual usage continued until Johannes Reinke, professor of botany at the University of Kiel, proposed that the diaspore-producing areas be named *soralia* (1895, p. 380, n. 1). At the same time, Otto Darbishire (1870–1934) — Reinke's Welsh assistant — was engaged on a monograph of the genus *Roccella*, work that led to his designating the amphithecium and *parathecium* (1898, p. 7).[34] The 1890s ended with a proposal by Gustav Lindau (1866–1923), then at the University of Berlin, that the vague term "pseudoparenchyma" be replaced by *plechtenchyma*, to which the prefixes *para-* and *proso-* could be appended as required (1899, p. 7); this initiative quickly won general support.

The opening decade of the new century produced three additions: Arthur Minks (1846–1908), in medical practice at Stettin, published a revision of the genus *Umbilicaria* in which an unreported propagule became a *thyllale* (1900, p. 17), Elenkin (1902, pp. 75, 83) reported a *necral layer* in certain crustose thalli, and the French abbé Auguste-Marie Hue (1840–1917) labelled the *fastigiate cortex* (1906, p. 243). There then followed a period of almost 40 years during which no currently employed additions were made to the terminological inventory.

Postwar, a return to the logging of thalline features was initiated by two Swedish workers. Einar Du Rietz (1895–1967), professor of plant ecology at the University of Uppsala, suggested replacing epi- and hypothecium with *epi-* and *subhymenium* (Nannfeldt and Du Rietz 1945, p. 86); this did not happen, however, and all four terms have so far stayed the course. Gunnar Degelius (1903–1993), then also at Uppsala, described a new asexual propagule observed on *Lempholemma cladodes* material as a *hormocyst*, produced within a *hormocystangium* (1945). Monographic studies of, first, *Umbilicaria* by George Llano (1910–2003), working at the Smithsonian Institution, introduced *gyro-*, *leio-* and *omphalodisc* (1950, p. 5), while Degelius (1954, p. 56) distinguished between the *eu-* and *pseudocortex* in *Collema*. Also in that work (p. 50, fn.), Degelius revived earlier objections to the practice of describing the chlorophyllous cells of lichens as "gonidia," and three years later George Scott (1927–), at the University of Glasgow, proposed that lichen components be known as *mycobionts* and *phycobionts*.[35]

Scott's recommendations soon became generally accepted, as for example by the German specialist on fruit-body development, Aino Henssen (1925–2011), in the work that contributed *pycnoascocarp* (1963, p. 20). Shortly afterwards, her compatriot Josef Poelt (1924–1995), whose career began at the Botanische Staatssammlung in Munich, gave the first evidence of his terminological flair with the coining of *schizidium* (1965, p. 581) and *epipsamma* (1969, p. (32)). In the following

decade, Poelt's former student Brigitte Hannemann (ca.1940–) distinguished the *rhizinomorph* of *Umbilicaria* and, in connection with *Anzia*, proposed that *spongiostratum* replace hypothallus, which "is used for very different things" (1973, pp. 8–9).[36] The other 1970s introductions were reported by the Czech Antonín Vězda (1920–2008) for *hyphophore* (1973, p. 82), the Norwegians Eilif Dahl (1916–1993) and Hildur Krog (1922–2014) for *pseudoisidium* (1973, p. 13),[37] Henssen and Jahns (1973, p. 99) for *thallinocarp*, Poelt (1974, p. 107) for *phyllidium*, the British physician Dougal Swinscow (1917–1992) and Hildur Krog for *dactyl* (1978, p. 162), and Hasenhüttl and Poelt (1978, p. 276) for *thalloconidium*. The following decade was equally fruitful, with the asexual diaspores *blastidium* and *thlassidium* being named by Poelt (1980, p. 23; 1986, p. 16), *polysidium* by Kalb (1987, p. 18) and *parasoredium* by Poelt in collaboration with Codogno et al. (1989, p. 67, fn.); new thalline features were also distinguished at this time under the names *paracephalodium* (Poelt and Mayrhofer 1988, p. 279) and *phenocortex* (Poelt 1989, p. 67, fn.).

This survey ends with the year 2000, which leaves just two coinages to be accounted for: that by Tor Tønsberg (1948–), University of Bergen, in respect of *consoredium* (1992, p. 34), and *photomorph* introduced by Jack Laundon (1934–), long associated with the Natural History Museum, London, to impose order on a ravelled synonymy (1995).

**Acknowledgments**

I wish to record my deep indebtedness to the following colleagues: Professor R. Piervittori, University of Turin, for generously providing a photocopy of Oreste Mattirolo's 1883 publication; the ILL team at the Library, National University of Ireland, Galway, for their unfailing help; and the members of staff who obligingly supplied copies of material in their care at the British Library, Cambridge University Library, Natural History Museum, London and Royal Botanic Gardens Library, Kew.

My frequent and helpful visits to the internet have also to be gratefully recorded.

## Notes

1. "…sie nehmen die Form der Collemen, Epheben u. s. f. an, dadurch, dass gewisse parasitische Ascomyceten in sie eindringen."
2. "Frank et de Bary sont les deux savants dont le nom est généralement invoqué lorsqu'il est question des origines de la symbiose … il paraît de plus en plus improbable que de Bary et Frank aient inventé le terme de symbiose indépendamment l'un de l'autre."
3. De Bary had moved to Halle in 1867.
4. "…die Gonidien von den Hyphen abstammen."
5. "…eine Betrachtung der Erscheinungen des Zusammenlebens ungleichnamiger Organismen, der Symbiose, wie man kurz und und allgemein sagen kann, zu wählen"; "Parasitismus, Mutualismus, Lichenismus u. s. w. sind eben jeweils bestimmte Specialfälle jener allgemeinen Associationseinrichtung, für welche der vorangestellte Ausdruck Symbiose als Collectivbezeichnung dienen mag. Will man unter dieser Hauptkategorien unterscheiden, so dürften sich deren zwei herausstellen, die antagonistische mit gegenseitiger Bekämpfung und die in weiterem Sinne mutualistische mit gegenseitiger Förderung der Symbionten."
6. In the interests of historical accuracy, the opening sentence of the entry for symbiosis in Kirk et al. *Dictionary of the Fungi* (2008) needs to be revised.
7. "Sie sind die Proletarier unter den Pflanzen, müssen sich mit schlechter Nahrung begnügen und oft am Hungertuche nagen."
8. The concepts of commensalism and mutualism were introduced by Van Beneden (1873, pp. 785, 790).
9. The term "consortium," mentioned in passing by de Bary in his 1878 lecture, has been widely attributed to Johannes Reinke (1849–1931), lecturer in botany at the University of Göttingen and subsequently professor at Kiel. In a report on the occurrence of *Nostoc* cells in stems of *Gunnera tinctoria*, Reinke (1872, p. 108) described the association as a consortium, stating that the word had been suggested by his colleague August Grisebach (1814–1879); he subsequently recorded (1894, pp. 525–526) that the suggestion was made in the summer of 1872. As luck would have it, that venerable Latin word had already been chosen by Ferdinand Cohn (1828–1898), professor of botany at the University of Breslau (Wrocław), in January 1872 to describe the lichen association (1873, p. 69). Reinke (1894, p. 529) expressed keen resentment at de Bary's not having cited his paper when mentioning "Flechtenconsortium" (1878, p. 126 ; 1879 reprint, p. 29), but de Bary's silence in this regard

may reasonably be attributed to his having been aware that the word's use in a biological sense did not originate with Reinke.

10. The first appearance of this term has not been located.
11. The English translation is from Tubeuf (1897, pp. 86–87).
12. This relationship was interpreted as "commensalistic" by Rambold and Triebel (1992, p. 18) on the grounds that both fungi "share one and the same nutritive source, the photobiont of the host."
13. "…habe ich fortwährend, an die Flechtenfrage anknüpfend, mich bemüht, aus Pflanzen, den Gonidien entsprechend, einen chlorophyllhaltigen Organismus auszuscheiden und ihm zum selbständigen Leben zu zwingen."
14. "…weiß der Pilz die Entwickelung der Algen ganz genau seinem eigenen Wachstum anzupassen, so dass schließlich alle ihre Assimilate ihm wieder zugute kommen. Er gleicht einem klugen Herren, der seine Sklaven gut füttert, damit er sie dann um so besser ausnutzen kann." This interpretation was further promoted by Nienburg (1917, pp. 543–544).
15. "…nous avons considéré le thalle aérien d'une Peltigéracée comme l'équivalent d'un organe déformé par un parasite…[c]ette notion doit sans doute être élargie et étendue aux Lichens en général."
16. "Der Fall, daß bei der Fruchtentwickelung Gonidien gänzlich resorbiert werden, ist kein Anzeichen von Parasitismus, sondern ein 'Opfertod' zum Besten des Flechtenpilzes." "Deshalb würde auf sie der Ausdruck 'wohlwollende Sklaverei' viel besser anwendbar sein, wenn die Gonidien durch den Flechtenpilz nicht an der geschtlechtlichen Vermehrung gehindert würden. Aber auch diese Klippe wird umschifft, wenn man die Gonidien mit kastrierten Haustieren vergleicht, die von ihrem Herrn, dem Flechtenpilz, als wertvollstes Besitzum geschätzt und dementsprechend behandelt werden."
17. Eventually, however, its second element would be formulated anew to become "the common model of the lichen symbiosis as a 'domestication' of photosynthetic algae by heterotrophic fungi" (Piercey-Normore and DePriest 2001, p. 1496).
18. Any incidental standing that Cengia Sambo's work did enjoy would have suffered by association when the *Rhodobacterium* cells reported from *Herpothallon* (as *Chiodecton*) *sanguineum* by Uphof (1925) proved to be crystals of chiodectonic acid (Kolumbe 1927).
19. "…l'Algue donnant plus qu'elle ne reçoit."
20. "L'auteur…examine spécialement la question concernant les rapports réciproques entre les trois components du lichen"; "en général la nutrition du champignon s'effectue osmotiquement aux dépens des glucides de l'algue et de l'ammoniaque de l'Azotobacter." Other Russian work of the period on lichen bacteria is discussed by Khakhina (1992, pp. 92–93) where the transliteration "Genkel`" is used as an alternative to "Henckel."
21. "Flechtenbiologie im allgemeinen, Physiologie im besonderen sind noch fast unbeackerte Gebiete und rufen nach Bestellung!"
22. "Letzten Endes beruht also die Organisation der Flechtensymbiose darauf, daß der heterotrophe Pilz konstitutionell befähigt ist, seine Hyphenstruktur zu einem den atmosphärischen Niederschlag sammelnden "Haus" auszubauen, in welchem der autotrophe Mieter die Arbeitsbedingungen für eine photosynthetische Produktion findet und aus ihr dem Hausbesitzer eine Miete bezahlt, die dem Pilz seinen Lebensunterhalt sichert. Zwei Partner so verschiedener Konstitution zu einem so erfolgreichen Gleichgewicht der Kräfte zusammenzubringen, is ein "contrat social" der Natur, vor dem Soziologen und Politiker vor Neid nur erblassen können."
23. The case for regarding symbiosis as solely a collective term was cogently put at this time by Lewis (1985).
24. Ahmadjian's pronouncement was not widely influential: 17 years later Chapman and Chapman (2010) still had reason "to attack the very common misconception that lichens are a classic example of mutualistic symbiosis between an alga and a fungus" (p. 549) and to declare "the simple and incorrect notion that lichens are examples of a mutualistic ('stress-free') symbiosis really must be put to rest!" (p. 554).
25. All current lichenological terms are italicized on first citation here.
26. "Dieser sehr abweichenden Bildung könnte man den Namen Lirella geben."
27. Some confusion surrounds this term and "perithecium." The latter has been attributed to Acharius (e.g., Ainsworth 1976, p. 96) but was, in fact, coined by Persoon (1794b, p. 64) who used it to indicate a tissue enclosing the "actual seed capsules" ("die eigentlichen Saamenkapseln") in certain non-lichenized fungi. Those capsules—today's asci—were then also known as thecae, which Persoon described as sometimes forming a continuous layer or "hymenium" (p. 65); he did not use thecium as an individual term and neither, it seems, did any one else until Nylander

more than 50 years later. Acharius' apothecium has been stated to derive from "apo- away + Gr. thēkē case or cup" (Snell and Dick 1957, p. 10), but Acharius made quite clear that he was using, in its sense of "repository," an existing word common to Greek and Latin. Perithecium was first applied to lichen fruit-bodies by Fries (1831, pp. lxvii, 8).

28. Here Acharius restricted the term to several types of fruit-body, and others followed suit for a good many years, despite his later having also applied it to the cortical productions characteristic of *Peltigera aphthosa* (1810, p. 517).
29. "Königlich Grossbritannisch Hannoverschem Oekonomie-Rathe."
30. Wallroth practised in the town of Nordhausen, where he had the phycologist Friedrich Kützing (1807–1893) as a colleague. When the first volume of *Tabulae Phycologicae* appeared in 1845, a friend expressed astonishment at the elegant Latin of the Introduction, to which Kützing replied, "Wallroth hat's geschrieben" (Osswald 1896, p. 25).
31. The mistake was first pointed out by Fée (1824, p. xxxi).
32. The status of the terms goniocyst and *goniocystangium* (Santesson 1968, p. 181) has been reviewed by Sérusiaux (1985, pp. 2–13) and Sérusiaux et al. (2006, pp. 118–119).
33. Krabbe believed that his new type of secondary thallus was peculiar to just one member of the Cladoniaceae — *Pycnothelia* (as *Cladonia*) *papillaria*. The Finnish *Cladonia* monographer Edvard Vainio (1853–1929) soon showed that the development of *P. papillaria* podetia does not, in fact, exhibit the features claimed by Krabbe, but at the same time ensured the survival of "pseudopodetium" by applying that designation to the secondary thallus of *Stereocaulon* (1887, pp. 53–54).
34. Darbishire was very likely unaware of Koerber's priority in respect of amphithecium — an understandable lapse given that only Tuckerman (1872, p. 245) and Vainio (1890, p. xxiii, n. 2) appear to have mentioned the word.
35. Schneider (1895, p. 497, fn.) had declared that "[g]onidia and related terms as 'gonimia,' 'gonidimia,' etc., are meaningless in modern lichenology, and should therefore be rejected," a view echoed by Fink (1922, p. 116) and Thomas (1939, p. 163). When what had been known as blue-green algae came to be recognized as prokaryotes, Ahmadjian (1982) recommended that the "[p]hotosynthetic symbionts of lichens should together be referred to as *photobionts*," while also introducing *cyanobiont* and recycling phycobiont to designate lichens' blue-green and green cells, respectively.
36. "… der für verschiedenste Dinge benutzt wird."
37. Unaware of this report, Awasthi (1975, p. 13) and Vězda (1979, p. 48) applied the term to different structures. In the same decade, Hale (1973, p. 3) used the term *epicortex* in the belief that this was a fresh coinage, but it had already been introduced in a mycological context by Lohwag (1941, p. 122).

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