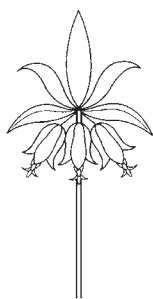


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“Such a strange theory”: Anglophone attitudes to the discovery that lichens are composite organisms, 1871–1890

M. E. Mitchell

Abstract

Until the 1860s lichens were generally considered to represent an independent group of plants. In 1866 Anton de Bary queried whether certain lichens might not be formed by a fungus growing parasitically on an alga, and, in the following year, Simon Schwendener advanced the view that all lichens could be considered the product of such an association. This revolutionary interpretation of lichen biology was welcomed by few botanists, regarded with scepticism by many, and summarily rejected by lichen taxonomists because of the threat it posed to their subject's autonomy. As experimentalists began to publish results that supported the dual theory and opinion shifted in its favor, the systematists responded with repetitious attacks that largely ignored those results. Hostilities between autonomists and dualists continued for over 20 years; the involvement of English-speaking botanists in the controversy is documented in this review.

Introduction

A lichen typically consists of a microfungus in association with a compatible microalga or cyanoprokaryote;¹ the macroscopic structure, or thallus, that results from this association is morphologically quite distinct from its individual components. Because their dual nature is not evident to the naked eye, lichens were long regarded as forming a discrete category of plants, comparable to the liverworts or mosses. That misperception became incorporated into botanical science when Tournefort (1694, 1:437–438) introduced the genus *Lichen*; this was adopted by Linnaeus (1753, 2:1140–1156) and remained in use until subdivided by the Swedish physician

Erik Acharius (1757–1819). His taxonomic system provided a scientific basis for the study of lichens, which, he stated (1810, p. 14), “form an autonomous natural order distinct from other cryptogamic plants”;² the fact that almost 60 years were to elapse before that pronouncement was questioned is largely due to a second error, relating, on this occasion, to structure and function.

In a lichen thallus, the photosynthetic cells generally occur as a conspicuous zone analogous to the palisade layer of a leaf. That zone first attracted close attention in the 1820s, notably from the German physician Friedrich Wallroth (1792–1857) whose observations led him to conclude that its constituent cells were reproductive bodies, which he named “gonidia” (1825–1827, 1: 40);³ his term gained wide currency following its adoption by Fries (1831, p. xix). Those cells were also studied by the German phycologist Friedrich Kützing (1807–1893); reporting on his work with *Xanthoria parietina* (L.) Th. Fr., which was then accommodated in the genus *Parmelia*, Kützing (1833, p. 350) remarked, “*Protococcus viridis* [*Desmococcus olivaceus* (Pers. ex Ach.) Laundon] is very often found on trees supporting the *Parmelia*. If the structure of this lichen is examined under the microscope, the same spherules of *Protococcus* are found in the thallus, and, indeed, this *Protococcus* is fundamental to the existence of *Parmelia parietina*.”⁴ Kützing's observations were disregarded, however, and Wallroth's misinterpretation of the cells' function prevailed until well into the latter half of the century.

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Figure 1. George Henry Kendrick Thwaites.

A second report that lichens contain algae attracted little more attention than the first: in an attempt to establish “the real character of those spherical or subspherical green bodies which are characteristic of true Lichens, and to which the name of *gonidia* has been given,” George Thwaites (1812–1882) (Fig. 1), a lecturer at the Bristol Medical School, examined (1849, p. 219) “a great number of species both of true Lichens and of the genus *Collema*”;⁵ with regard to the latter, he went on to remark

It is pretty generally known that the *thallus* of *Collema* consists of a number of moniliform filaments, and also of delicate anastomosing cylindrical filaments immersed in a more or less firm gelatine. When examined more carefully the structure is found to consist of numerous Nostoc-like vesicles closely cohering, and among which ramify the anastomosing filaments.

Thwaites, an “expert microscopist” (Boulger 1898), had observed the composite nature of his material — though he did not realize that the “anastomosing filaments” were fungal hyphae — and he commented (1849, p. 220), “[i]n the true Lichens is to be traced a very similar structure, only that instead of nostoc-vesicles we find groups of cells very nearly resembling those of the genus *Pleurococcus*.” Thwaites summarized his observations by stating (1849, p. 220), “between *Collema* and the true Lichens there subsists a close though not an immediate affinity, the essential part of the *former* being represented by the genus *Nostoc*, and of the *latter* by the genus *Pleurococcus*.” That Thwaites did not go on to investigate the relationship between the components of the thallus may be due, in part at least, to the fact that in the same month in which his paper appeared — March 1849 — he was appointed to a post in the present Sri Lanka; there his work dealt largely with aspects of the vascular flora, and though he maintained an interest in lichens he did not report any further microscopical investigation of them.⁶

Thwaites’ work received no mention in the substantial study of lichen anatomy published in 1852 by the French cryptogamist Louis-René Tulasne (1815–1885). The many original observations reported in that work, and the fine illustrations by his brother Charles (1816–1884) that accompany it, made it widely, if not always positively, influential: Tulasne accepted the contemporary perception of gonidia as propagative cells, which, he maintained (1852, p. 20), “develop directly from the medullary hyphae.”⁷ Those views were echoed in Britain by the Scottish physician William Lindsay (1829–1880), who stated (1856, p. 58) “the gonidium is a cellular bud, a reproductive cell ... destined to multiply the individual,” and by Miles Berkeley (1803–1889), a Church of England clergyman, for whom gonidia were (1857, p. 373) “globular bodies of a vegetable green produced from the threads of the thallus.”



Figure 2. Simon Schwendener.

In 1857 the Swiss botanist Carl Nägeli (1817–1891) became professor of botany at Munich, where as assistant he had a compatriot, Simon Schwendener (1829–1919) (Fig. 2). During the ten years that he spent in Munich, Schwendener carried out a comprehensive investigation of lichen anatomy, the results of which appeared as three substantial papers in Nägeli's journal *Beiträge zur wissenschaftlichen Botanik*. At the outset, Schwendener did not question the accepted view of the origin and function of gonidia: his illustrations (1860, plate 6, figs. 3 and 5) of tissue from the thallus of *Rocella tinctoria* DC. represent the constituent alga (*Trentepohlia* sp.) as a lateral outgrowth from a hypha. Three years later, however, as noted by Hoppe (1987, p. 317), Schwendener (1863, p. 135) observed that

The gonidia correspond so strikingly in many ways to the lower algae, and particularly with

regard to their mode of reproduction, that it can be frankly stated that here Nature has brought a part of algal life into being for a second time. The blue-green gonidia correspond to the Chroococcaceae and Nostocaceae, the yellow-green to the Palmellaceae.⁸

This is essentially what Thwaites had reported 14 years earlier. Anton de Bary (1831–1888), professor of botany at Freiburg, took matters a stage further, however, and proposed (1866, p. 291) that gelatinous lichens are "either the fully developed, fruiting condition of plants whose immature states were included until now in the algae as Nostocaceae and Chroococcaceae, or those families are typical algae that assume the form of *Collema*, *Ephebe* etc. as a result of penetration by certain parasitic ascomycetes."⁹

At a meeting of the botanical section of the Schweizerische Naturforschende Gesellschaft held in Rheinfelden on 10 September 1867, Schwendener was recorded as having expressed the view that "in an entire group of lichens, gonidia and filaments are not in genetic connection, rather the latter are to be regarded as proliferations of fungal hyphae over algae," and as being of the opinion that "lichens may not be autonomous plants, but fungi in association with algae" (Anonymous 1867, pp. 88–89).¹⁰ Schwendener made the point more strongly in an addendum to his third paper on lichen anatomy (1868, pp. 195–200) and subsequently (1869, pp. 38–39) announced that "lichens do not, from my investigations, constitute a separate, higher division of cryptogams, but merely a subdivision of the great order of Fungi: they are ascomycetes parasitic on algae."¹¹

Reaction

Swendener's declaration sparked a controversy that lasted for almost a quarter of a century. The polarization that was to characterize it quickly became apparent: William Nylander (1822–1899) (Fig. 3), a Finnish botanist living in Paris — and foremost lichen taxonomist of his time — strongly



Figure 3. William Nylander.

attacked Schwendener's conclusions (Nylander 1870), while Julius Sachs (1832–1897), professor of botany at Würzburg and a leader in the field of experimental botany, did not hesitate to treat lichens as ascomycetes in his textbook (Sachs 1870, pp. 254–265). Outside continental Europe, the first published comment on Schwendener's findings was made by the American newspaper editor and lichenologist Henry Willey (1824–1907) (Fig. 4); in January 1871 he referred to the Swiss botanist as having “propounded the theory that they [lichens] are a compound plant, the thallus being a true alga, and the apothecium a fungus; but to this theory no true lichenist will be likely to assent” (p. 666). Though it may be assumed that Willey subsequently acquired a better understanding of the topic, he never came to accept that lichens are dual organisms.



Figure 4. Henry Willey.

Schwendener's discovery was next aired in the anglophone literature by the Irish phycologist William Archer (1830–1897) (Fig. 5). In a reference to observations concerning the dual theory, which he described as stating “that each [lichen] is to be regarded as some one or other Algal-type which has become, as it were, the home or residence of a parasitic growth,” Archer (1872, p. 22) described a statement by Schwendener in support of that view as seeming “sufficiently to convey its own refutation of the hypothesis, inasmuch as this assumed *parasitic fungus* does *not* destroy or live upon its assumed *algal-host*.” Here Archer was far from being alone: the general understanding that parasites weaken and ultimately kill their hosts left many botanists unable to reconcile Schwendener's contention with the vigor and longevity that are characteristic of lichens. That difficulty was not resolved until



Figure 5. William Archer.

the concepts of commensalism, mutualism and symbiosis emerged later in the decade. It is noteworthy that Thwaites had adumbrated those concepts in a letter read at a meeting of the Royal Horticultural Society on 1 October 1873 (Anonymous 1873):

I have been thinking a good deal over Schwendener's views as to the constitution of Lichens, and now there has just come into my hands the volume of the *Annales des Sciences Naturelles*, in which is M. Bornet's [Edouard Bornet (1828–1911)] article on this same subject, admirable so far as the analysis of the structures goes, but not at all convincing to me that Schwendener's views, which the author apparently adopts, are correct ones. According to our experience, I think parasitic fungi invariably produce a sad effect upon the tissues they fix themselves upon or in. These tissues become pale in colour, and in every respect sickly in appearance. But who has ever seen the gonidia of Lichens the worse for having the "hypha" growing amongst them? These gonidia are always

in the plumpest state, and with the freshest, healthiest colour possible. Cannot it enter into the heads of these most patient and excellent observers that a cryptogamic plant may have two kinds of tissue growing side by side without the necessity of one being parasitic upon the other ...?¹²

Bornet's paper was also commented on by Asa Gray (1810–1888), Fisher Professor of Natural History at Harvard University, who, unlike Thwaites, considered (Gray 1873) that "the presentation ... appears to be wholly convincing. The result is that Lichens of all sorts are composite; the green cells (*gonidia*) are *Algae*, of species which are of common independent occurrence; the filamentous tissues (*hypha* [*sic*]), which bear the fructification, belong to *Fungi*." However, Gray's friend Edward Tuckerman (1817–1886), the leading American lichenologist of the day, saw matters differently: in November 1874 he told Gray that he did "not at all agree to his [Sachs'] relegating the Lichens to the fungi..."¹³

The literature generated by Schwendener's discovery evidently held a particular interest for Archer, and since, in the early years at least, it was very largely the work of German-speaking botanists, he provided a valuable service by publishing two summaries in English. By way of introduction to the first, Archer (1873) remarked:

A novel hypothesis respecting the nature of Lichens, which was first propounded by Prof. Schwendener of Basel, and has since to a greater or less extent been adopted by other experienced observers, has for some time past been a subject of controversy between them and botanists of the older school. The "gonidia-question," as it is called, has been discussed in several of the continental journals, and a *résumé* of some of the papers on both sides will probably possess some interest for English readers.

A discursive précis of close to 20 publications follows, in the course of which Archer again adverts (p. 234) to the difficulty of accepting that lichen fungi behave as parasites.¹⁴ His second *résumé* (1874) is principally concerned with results reported by Melchior Treub (1851–1910),

then at the University of Leiden, of experiments designed to achieve lichen synthesis.¹⁵ Though many of the observations and opinions brought to the attention of English-speaking botanists by Archer's synopses were supportive of the dual theory, to the lichenologists among them it remained unacceptable; their attitude was well conveyed by the Anglican divine, William Leighton (1805–1889) when he observed (1874, p. 122)

Those whose studies are chiefly physiological maintain that the filamentous tissue of the thallus of lichens is a fungus which grows parasitically on an alga, which it envelopes and carries on with it in its growth so as to constitute the gonidia. On the other hand, true lichenologists, whilst admitting the apparent similarity of gonidia to certain algae, do not consider them as such, but as special organs of multiplication or propagation of lichens.

By far the most prominent anglophone rejectionist was, however, James Crombie (ca. 1831–1906), a Presbyterian minister who, in 1869, had begun to study the lichen collections in the British Museum; he was “an unflinching opponent of the Schwendenerian hypothesis,” upon which he “made three or four onslaughts” (Britten 1906). It is evident from the earliest of these (1874, pp. 260–261) that in undertaking the defence of his subject Crombie thought to an extent in terms of property and status:

... of late years ... the lichen territory has gradually been enlarged at the expense of its neighbours. Alike from the algae and the fungi it has made various important acquisitions, which of right belonged to it all along, though its title-deeds to them were written in characters so minute or obscure that it required both microscopical aid and keen research rightly to interpret them ... Very recently, however, a theory has been started, which, should it be accepted, would virtually deprive lichens of the position which had hitherto been assigned them in the vegetable kingdom.

Crombie listed a number of prominent lichenologists who had declared against the new doctrine, and remarked (p. 268)

Nor, indeed, was it to be expected that they would stand by *aequo animo* and see their favourite lichens ruthlessly deprived of their autonomous existence, and be converted, as if by the stroke of a magician's wand, into a ... master fungus, and an imprisoned algal slave. Surely it must have been the very novelty of such a strange theory much more than the apparently plausible arguments by which it was supported that has recommended it to the acceptance of any botanist of the so-called “new school.”

Crombie's allusion is, presumably, to the contemporary continental emphasis on anatomy and physiology, which Thomas Huxley (1825–1895) had recently introduced at the “Science Schools” in South Kensington. Here, between 1873 and 1876, responsibility for the botany courses was in the hands of William Dyer (1843–1928, Thiselton-Dyer from 1891¹⁶) (Fig. 6) and Sydney Vines (1849–1934); “it was these

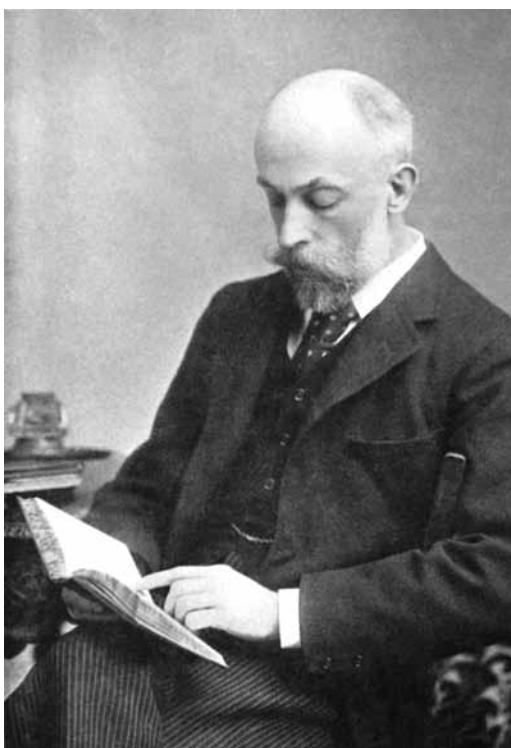


Figure 6. William Turner Thiselton-Dyer.

two men who, between them, were to change the face of British botany during the next few years" (Gilmour 1944, p. 44), and both supported the dual hypothesis. Dyer's influence is in large measure attributable to his having edited the English translation, published in 1875, of Sachs' *Lehrbuch der Botanik*, a text that inaugurated a new era in the teaching of botany by devoting detailed attention to anatomy, metabolism and non-vascular cryptogams.¹⁷ The approach to the dual theory adopted by Sachs is reflected in Dyer's statement (1875, p. 297) that "Lichens must ... be degraded from their position as a principal division of Thallophytes and be referred to ascomycetous Fungi as a characteristic group of parasitic forms." To some botanists, however, that opinion remained unacceptable: Thwaites (1877), despite his informed interest, declared

... in instances of real parasitism, as generally understood ... the parasite is observed to be nourished at the expense of the organism upon which it is growing, to be injurious to its health, and to impair its beauty and symmetry. But how different, in contradistinction to this, is the result brought about by the so-called *lichen-parasitism*! In this latter we observe that the intimate coalescence of the two ... organically adhering kinds of tissue ... eventuates in a most beautiful symmetrical structure — the perfect lichen, with its every part manifesting the possession of full health and vigour. In the presence of these last-mentioned circumstances it really seems to me that those who believe that the two kinds of tissue ... belong respectively to two totally distinct species of plants should, consistently with such belief, acknowledge that the phenomenon ought to be looked upon as an example of *commensalism* rather than one of parasitism ... But I will suppose, as I believe to be the case, and as was believed unreservedly in early times by botanists generally, that the lichen is a single autonomous organism, and not a compound of two distinct species of plants.

Other instances of botanists continuing to resist the view that lichens are the product of a parasitic association were reported in a continuation of Archer's summaries published by Vines (1878); by that time, however, the ground had been prepared

for a reassessment of the relationship between the components of the thallus.

In 1873, while attached to the University of Leipzig, Albert Frank (1839–1900) undertook an extensive study of hypophloedal lichens. His work led him to conclude that "the association between lichen hyphae and gonidia ... is something more than simple parasitism," and, he observed, "all instances of two different species living on or in one another must be brought together within a comprehensive concept that disregards the rôles played by the organisms, and is, in consequence, based solely on association; for this the term *Symbiotismus* may be recommended" (1876, pp. 190–191, 195).¹⁸ A move away from the notion of parasitism, as then understood, was also evident in a statement that brought official recognition for the dual theory in Britain: at the Anniversary Meeting of the Royal Society of London on 30 November 1878, Joseph Hooker (1817–1911) remarked (1878, p. 134a) that the theory

now ten years old, astonished botanists by boldly sweeping away the claims to autonomous recognition of a whole group of highly characteristic organisms — the lichens — and by affirming that these consist of ascomycetal fungi united in a commensal existence with algae ... [T]he advocates of the Schwendenerian view have gradually won their ground, and the success which has attended the experiments of Stahl¹⁹ in taking up the challenge of Schwendener's opponents, and manufacturing such lichens as *Endocarpon* and *Thelidium*, by the juxtaposition of the appropriate algae and fungi, may almost be regarded as deciding the question.²⁰

Some weeks after this endorsement, the theory was again aired in London: at a meeting of the Quekett Microscopical Club on 27 December, "Mr. Charles Stewart [1840–1907, then lecturer on comparative anatomy at St. Thomas' Hospital] made some highly interesting observations upon Lichens" (Anonymous 1879a, p. 186), in the course of which he promoted the composite interpretation of lichen structure. This brought him under fire from one member of the audience, the mycologist Mordecai Cooke (1825–1914)

— a rigid advocate of lichen autonomy.²¹ Further publicity came in the following month, January 1879, when an authoritative assessment of evidence corroborating the dual theory was published in the recently established *Nineteenth Century*, a monthly review. Its readers learned (Anonymous 1879b, p. 161) that

The Schwendenerian theory of the structure of lichens has probably been the exciting cause of more controversy of late years than any other subject in scientific botany. According to this bold and happy generalisation, for which we are indebted to De Bary and Schwendener, lichens are not autonomous organisms, forming a group intermediate between algae and fungi, but are true ascomycetous fungi, exhibiting the extraordinary peculiarity of being invariably parasitic upon, or rather commensal with, some species of alga.

Three public expressions of support for Schwendener in as many months brought Cooke into action: in a lecture to the Quekett Club on 28 March 1879 he attacked (1879, p. 125) what he called “this doomed hypothesis,” principally by drawing attention to the difficulties attendant on regarding lichens as the product of a parasitic association, and by attempting to show, despite all the evidence then available to the contrary, that lichen tissues were not formed by algae and fungi. Evidently he did not spare the author of the dual theory or its supporters — in the discussion that followed the lecture, Frank Crisp (1843–1919), solicitor and microscopist, deprecated “the way in which Dr. Cooke has spoken of such men as Stahl and Schwendener. They were men of great respect in their own country, and he thought it was hardly well for it to go forth that they had been referred to slightly by any one connected with the Quekett Club” (Anonymous 1879c, p. 207).²² Three other advocates of lichen autonomy reaffirmed their position that year: in the third edition of his *Lichen-Flora*, Leighton (1879, p. xvii) remarked, “I have purposely omitted any mention of the Schwendenerian Theory of Lichens, as I cannot but regard it as purely imaginary, ‘the

baseless fabric of a vision”;²³ Tuckerman (1879) advocated the fanciful claim by Arthur Minks (1846–1908) that lichen hyphae contain gonidial precursors;²⁴ and Crombie (1879), communicating extracts from an article by Nylander, considered the arguments it advanced “amply sufficient to show how untenable is the Schwendenerian hypothesis, which ... is thus ‘reduced to the nothingness from which it ought never to have emerged.’” But rhetoric could not halt the autonomists’ growing isolation. In Britain, a text as basic as William McNab’s *Botany: Outlines of Classification of Plants* (1878) treated the lichens “as ascomycetous fungi, parasitic on algae” (p. 54), while in the United States, Charles Bessey’s *Botany for High Schools and Colleges* (1880) would inform students that “there can no longer be shown any good reasons for not classifying them [lichens] ... under the Ascomycetes” (p. 295).

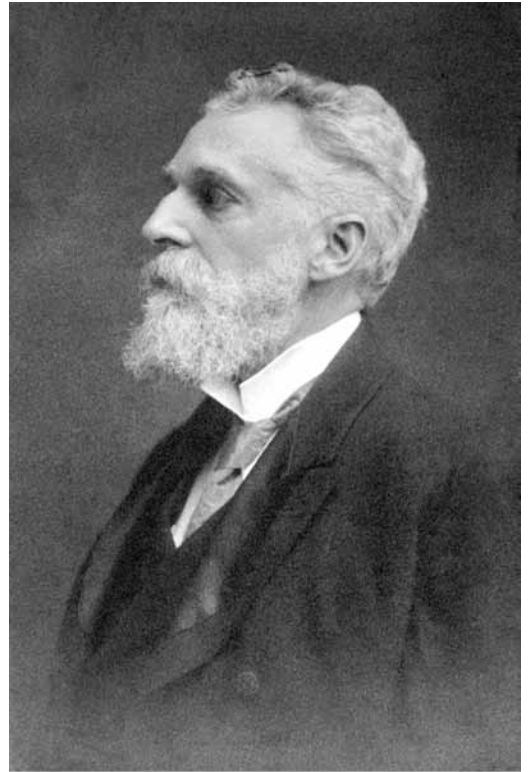
The dualist position was further advanced at the Jubilee Meeting of the British Association for the Advancement of Science held at York in August and September 1881; for his Presidential Address, delivered on 31 August, John Lubbock (1834–1913) chose the topic “Fifty years of science.” Referring to the progress made in certain areas of botany, Lubbock (1882, pp. 17–18) recorded that “Mr. Thiselton Dyer has been kind enough to assist me in endeavouring to place the principal facts before you,” one of these being “the startling theory, now however accepted by some of the highest authorities, that lichens are not autonomous organisms, but commensal associations of a fungus parasitic on an alga.”

A year later the autonomists retrieved some ground when Crombie contributed the article on lichens to the ninth edition of the *Encyclopaedia Britannica*. In a subsection devoted to “The origin of the gonidia,” he commented (Crombie 1882, p. 557), “Suffice it to state briefly that, according to Schwendenerism, a lichen is not an individual plant, but rather a community made up of two different kinds of individuals belonging to two different classes of cryptogams ... To such

a singular theory ... various *a priori* objections of great validity may be taken." The familiar arguments are then once again advanced, no reference is made to Stahl's successful synthesis, Nylander is invoked, and the author concludes, to his own satisfaction, that "as there is no algal in the lichen, so neither is there any fungus"; this biased account remained a source of misinformation until corrected in the 11th edition of the *Encyclopaedia* almost 30 years later (Crombie and Blackman 1911, p. 578). Crombie's article was the second of the "onslaughts" referred to in Britten's obituary — the third, and last, was delivered at a meeting of the Linnean Society of London on 17 April 1884.

For that address, Crombie drew extensively on his 1874 paper, incorporated material from his *Encyclopaedia Britannica* article and, as always, took his lead from Nylander. On this occasion he gave a brief account of Stahl's work, which, however, he dismissed (1884, p. 266) as having "been imagined in some quarters to supply 'the missing link' in the chain of evidence by which the Schwendenerian hypothesis can be demonstrated"; he also attempted to explain away the established fact that algae are present in lichen thalli by stating (p. 271), "with respect to the gonidia, notwithstanding their general resemblance to certain of the lower algals, it by no means follows that similarity is identity — the two things being logically very different." There were two published responses to Crombie's paper. The 19 February 1885 issue of *Nature* carried a letter from Marcus Hartog (1851–1924), professor of natural history at Queen's College, Cork, that did not spare Crombie for his errors and omissions; Hartog concluded by expressing — perhaps a shade patronizingly — the hope that he had "not exceeded the bounds set by the respect all must feel towards his honest and arduous work on the classification of so difficult a group."²⁵ On the other hand, in a paper read to the Washington Microscopical Society on 11 May 1886 and published in June of that year, Frank Knowlton

(1860–1926), best known as a paleobotanist, could still express support for Crombie; however, Knowlton's statement (p. 103b) that "the gonidia are principally stimulating in their effect, the real organs of nutrition being the cortical layers" shows that he was not particularly well qualified to pronounce on the topic. *The American Monthly Microscopical Journal*, in which Knowlton's paper had appeared, redressed the balance some months later when it carried an article by Frederick Sargent (1863–1928) (Fig. 7), professor of botany at the University of Wisconsin, in support of the dual theory (Sargent 1887).



Faithfully yours
Frederick LeRoy Sargent.

Figure 7. Frederick LeRoy Sargent.

Though the controversy occasioned by Schwendener's discovery was now drawing to a close, it had not lost the potential to generate acrimony. A work on freshwater algae published by the versatile Cooke in 1890 contains a chapter titled "The dual hypothesis," in which no mention whatever is made of the results that had accumulated over 20 years in support of the hypothesis. Instead, Cooke sought to promote Minks' discredited views and went on to assert (p. 181), "[i]t can be clearly demonstrated that the gonidia are developed within the substance of the lichen." That chapter was the subject of particular comment by George Murray (1858–1911), phycologist at the then British Museum (Natural History), in a withering review of the book (Murray 1890):

Most reasonable people have spontaneously remarked that in the controversy, while it lasted, on the subject of the dual nature of lichens, the systematic lichenologists were ranged on one side, and the morphologists pitched over against (and into) them. It was further noted that the question was really one for morphologists to settle ... and it was not decided in favour of the systematists, headed by Nylander. Mr. Cooke, however, digs up the hatchet, and goes for de Bary, Schwendener, and the rest, just as if there were some novelty left in his proceedings ... It is difficult to take seriously the work of any man on Fresh-water Algae who describes, in this year of grace 1890, the symbiosis of lichens as a "hallucination" ... [W]hen an author presents to the public a book which professes to teach the form and structure of Fresh-water Algae, it might surely be expected that he should leave this matter alone or take a reasonable view of it.

This dismissal of Cooke's attempt to breathe life into a moribund theory effectively ended the dispute concerning the origin of gonidia.²⁶

That term continued, however, to be applied to the photosynthetic cells of lichens until the latter half of the last century when, in response to "an ever-increasing awareness of the insufficiency and ambiguity of the term," Scott (1957) proposed that it be replaced by "phycobiont," applicable to an alga in association with a fungus in the

formation of a lichen." That proposal quickly gained acceptance, though the subsequent transfer of the blue-green algae to the bacteria necessitated a refinement of Scott's term, which came with Ahmadjian's (1982) recommendation that "phycobiont" be reserved for eukaryotic algal symbionts, with "cyanobiont" being applied to their cyanobacterial counterparts.

Conclusion

When Simon Schwendener announced in the late 1860s that lichens are the product of a parasitic association between a fungus and an alga, the small number of botanists actively interested in the group were mainly taxonomists. They expressed uncompromising opposition to Schwendener's view because they knew that, if accepted, theirs would cease to be an independent discipline. Initially, the taxonomists received general support because many botanists were reluctant to abandon the time-honored belief in lichen autonomy and the reproductive role of gonidia, and equally reluctant to accept a theory that interpreted the lichen thallus as a structure elaborated by a parasitic fungus.

Schwendener's theory was, however, promoted by the physiologist Julius Sachs. When an English translation of his authoritative *Lehrbuch der Botanik* appeared in 1875 it had a profound effect on the teaching of botany in Britain and the United States; it was soon followed by indigenous texts that reflected Sachs' influence, and, in consequence, Schwendener's opponents lost ground in those countries. They found themselves further marginalized following Ernst Stahl's report of lichen synthesis, and when their core contention — that the vitality manifested by lichens precluded the possibility of parasitic involvement — was made irrelevant by Anton de Bary's development of the concept of symbiosis, the advocates of lichen autonomy became defenders of a lost cause. Their refusal to accept that fact, coupled with a continued disregard of evidence in support of

the dual theory, exposed them to due criticism. When this they similarly ignored, the autonomists could no longer command the attention of the botanical community, and, by the early 1890s, the controversy had run its course.

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Notes

1. Also termed "blue-green alga", "cyanobacterium" or "cyanophyte."
2. "Lichenes Ordinem Naturalem peculiarem et a reliquis Plantis Cryptogamis distinctum constituere ..."

3. From γωνη, offspring + diminutive suffix -ιδιον.
4. "... sehr häufig an den Bäumen, wo dieselbe [*Parmelia parietina*] sitzt, sich auch *Protococcus viridis* befindet. Untersucht man die Structur dieser Flechte mit dem Microscop, so findet man, dass ganz dieselben *Protococcus*-Kügelchen mit in die Substanz des Laubes verwebt sind, und in der That ist auch dieser *Protococcus* die erste Veranlassung zur Erzeugung der *Parmelia parietina*." In fact, the alga in *Xanthoria parietina* is *trebouxioid* rather than *pleurococcoid*.
5. Thwaites followed Fries (1831, pp. xxix–xxxii) in segregating the gelatinous Collemataceae from other lichens.
6. "At the time when Thwaites was pursuing his researches cryptogamic botany was little studied in this country, and the value of Thwaites' discoveries was by no means generally appreciated. By the few, however, who devoted themselves to this most important branch of science Thwaites and his work received every sympathy and encouragement. It was a matter of regret to them when in 1849 Thwaites accepted the post of Director of the Botanic Garden, Peradenya, and in spite of the excellent work done there by him we are not sure that his removal from England was not a distinct loss to science. Thwaites was peculiarly qualified for microscopic research, while, on the other hand, the kind of work that it fell to his lot to accomplish in Ceylon might have been done by someone else destitute of his special powers" (Anonymous 1882).
7. "... il est manifeste que ces cellules naissent directement des filaments de la médulle ..."
8. "Die Gonidien stimmen in mancher Beziehung und namentlich auch mit Rücksicht auf die Vermehrungsweise so auffallend mit den niederen Algen überein, dass man geradezu sagen kann, die Natur habe hier ein Stück Algenleben zum zweiten Mal zur Erscheinung gebracht. Die blau-grünen Gonidien entsprechen den Chroococcaceen und Nostochaceen, die gelb-grünen den Palmellaceen."
9. "Entweder sind die in Rede stehenden Lichenen die vollkommen entwickelten, fructificirenden Zustände von Gewächsen, deren unvollständig entwickelte Formen als Nostocaceen, Chroococcaceen bisher unter den Algen standen. Oder die Nostocaceen und Chroococcaceen sind typische Algen; sie nehmen die Form der Collemen, Epheben u.s.f. an, dadurch, dass gewisse parasitische Ascomyceten in sie eindringen ..."
10. "... bei einer ganzen Gruppe von Flechten Gonidien und Fasern nicht in einem genetischen Zusammenhange stehen, sondern dass letztere als Wucherungen von Pilzfäden auf Algenformen zu betrachten seien ... Die jetzige Ansicht des Dozenten geht also dahin, dass die Flechten nicht selbstständige

- Pflanzen, sondern Pilze in Verbindung mit Algen seien ...” For an account of the Rheinfelden meeting, see Honegger (2000).
11. “... bilden die Flechten, meinen Untersuchungen zufolge, keine besondere Hauptabtheilung der Kryptogamen, sondern nur eine Unterabtheilung in der grossen Reihe der Pilze: es sind Ascomyceten, die auf Algen schmarotzen.”
 12. Thwaites’ letter was read to the meeting by Berkeley who, earlier in the proceedings, had expressed similar sentiments: having “alluded to certain views as to the nature of Lichens propounded by Schwendener and supported by Bornet ... Mr. Berkeley dissented from these views, and referred to his introduction to *Cryptogamic Botany*, wherein is mentioned a case where, in the cells of some driftwood, he had found Lichen threads giving rise to gonidia.” Bornet (1873) greatly strengthened Schwendener’s position by establishing, to generic level, the identity of the algal component in species belonging to 60 lichen genera; a synopsis of Bornet’s paper was published by Archer (1874, pp. 117–120) and Phillips (1873).
 13. Quoted in Rodgers (1944, p. 89); until the end of his life, “[t]he Schwendenerian theory of the lichen ... found no support in Edward Tuckerman” (Culberson 1964, 1: xiv).
 14. Smith (1921, p. 28) states that “Archer welcomed the new views on lichens, and attempted [synthetic] cultures but with very little success.” In fact, Archer is little forthcoming as to his personal stance, and he nowhere mentions having attempted cultures; indeed, as far as can be established, the only attempt at synthesis outside continental Europe during the 19th century was the primitive experiment reported by Richard Croft (1843–1912) to a meeting of the Hertfordshire Natural History Society on 25 January 1881 (Croft 1882).
 15. Lorch (1988, p. 31, n. 61) erroneously remarks of Archer’s 1874 paper that “many of the statements there attributed to Treub, such as his view about Müller, do not occur in the original article!” Archer (1874, p. 122, n. 1) refers to two publications by Treub — the first (1873a) is brief, the second (1873b) runs to 80 pages — but evidently Lorch saw only the first, while Archer’s résumé concerns the other, where the reference to Müller appears on pages 43–44. Werner (1927, p. 4) had also misread Archer’s résumé and, like Smith (n. 14 above), credited him with culture experiments that Archer made clear were actually carried out by Treub (1873b, pp. 60–63).
 16. *Fide* English (1987, p. 207).
 17. For the reform of botanical education in Britain and North America consequent on the publication of Sachs’ *Text-Book*, see Bower (1938, *passim*), Farlow (1913, p. 84), Green (1914, p. 534) and Rodgers (1944, p. 230).
 18. “... die Beziehung der Flechtenhyphen zu den Gonidien...ist doch etwas mehr als blosser Parasitismus”; “Wir müssen sämtliche Fälle, wo überhaupt ein Auf- oder Ineinanderwohnen zweier verschiedener Species stattfindet, unter einen weitesten Begriff bringen, welcher die Rolle, die beide Wesen dabei spielen, noch nicht berücksichtigt, also auf das blosses Zusammenleben begründet ist, und wofür sich die Bezeichnung Symbiotismus empfehlen dürfte.” Two years after the publication of Frank’s paper, de Bary used the term “Symbiose” in a lecture to a meeting of German naturalists and physicians at Cassel (Bary 1878); that lecture was reprinted, with notes (Bary 1879), but though neither version made any mention of Frank’s “Symbiotismus,” there is a belief that de Bary had been aware of it at the time of his address. In a study devoted to the history of symbiosis, Sapp (1994, p. 132) considered that de Bary had not “originated the term,” an opinion supported by Hawksworth (1995), in a review of Sapp’s book, on the grounds that de Bary and Frank were “once based in universities 35 km apart (Halle and Leipzig)” and “must have discussed such issues.” However, any discussions that de Bary and Frank may have had would not have extended to the latter’s “Symbiotismus”: the detailed investigations that led Frank to propose the term were undertaken from 1873 onwards (Frank 1876, p. 128), and, therefore, at a time when de Bary was no longer in Halle — he had moved to the University of Strasbourg in spring 1872 as professor of botany. The alternative view — that de Bary had not seen Frank’s paper before delivering his 1878 address — can be more plausibly advanced. Max Reess (1845–1901), professor of botany at Erlangen, was a former student of de Bary’s and a contributor to the experimental work that helped validate Schwendener’s theory. Reess was familiar with Frank’s paper (Reess 1879, p. 46) but made no mention of it in the comment relating to “Symbiose” in his obituary of de Bary (Reess 1888, p. xiv), to whom alone credit for introducing that term is given: “Under this happily chosen expression, de Bary was able to bring together all examples of the regular association of two different organisms in the areas of botany and zoology” (“Unter diesem glücklich gewählten Schlagwort konnte de Bary sämtliche Erscheinungen des gesetzmässigen Zusammenlebens zweier verschiedener Organismen auf botanischem und zoologischem Gebiete vereinigen”). What, however, constitutes the most compelling argument in favor of de Bary’s term having been an independent coinage is the fact that,

- when introducing it, he made no reference whatever to Franks' "Symbiotismus." The *Oxford English Dictionary*, ed. 2 (1989, vol. 17, p. 451) dates the appearance of "symbiosis" to 1877 with a supporting quotation from the sixth English edition of Otto Thomé's *Text-Book of Structural and Physiological Botany*; in fact, that edition was not published until 1887, and the earliest occurrence in print of "symbiosis" appears to have been in the caption to an account of endozoic algae in the 16 February 1882 issue of *Nature* (25: 377b).
19. Ernst Stahl (1848–1919), who had studied under de Bary, reported (1877) the synthesis of three lichens under laboratory conditions. His publication attracted widespread attention because of its bearing on the dual theory; in Britain a summary was provided by Vines (1878, pp. 153–157), and in the United States it was enthusiastically reviewed by Farlow (1878).
 20. Hooker had commented on the dual theory some years previously in a note on pages 946–947 of his wife's translation of Le Maout and Decaisne (1873). The passage quoted above may, however, owe something to Dyer, who had joined Hooker at Kew as assistant director in 1875: on 14 December 1878 Hooker told Charles Darwin, "I am immensely gratified with your praise of the Address, which I was most anxious about, and feared would be a failure ... Dyer gave me great help in vegetable Physiology" (Huxley 1918, 2:141).
 21. He had rejected Schwendenerism some years earlier (Cooke 1875, pp. 10–16), and he accommodated like-minded contributors in his journal *Grevillea* during the 20 years (1872–1892) that he remained its editor.
 22. This was not the first such attack in Britain: Lindsay (1876) declared "My opinion of the speculations of Schwendener and his followers has all along been, and still is, that so far from 'clearing up' the 'the true nature of Lichens,' they introduce elements of very decided confusion; and that they are to be regarded merely as illustrations of German transcendentalism."
 23. Leighton went on to quote an extract critical of Schwendenerism from the Presidential Address delivered to the Linnean Society of London on 24 March 1872 by George Bentham (1800–1884); evidently Leighton was not aware that by 1874 Bentham had come to accept the dual theory (Lorch 1988, p. 22).
 24. Minks, a German physician, had attempted to refute Schwendener's conclusions by claiming that the photosynthetic cells of lichens develop from "microgonidia" formed in the hyphae (Minks 1879). This spurious assertion remained vaguely in contention until finally disposed of by Darbishire (1895).
 25. Hartog, whose interest in lichenology may have dated from the years 1874 to 1877 when he worked with Thwaites at Peradeniya, failed to influence Crombie: some months after the criticisms appeared, Crombie, on the basis of an observation by Nylander, asserted that "'symbiosis' is seen to be but a mere fable" (Crombie 1885).
 26. Cooke, like Crombie, would seem to have lost sight of reality as far as Schwendenerism was concerned: he saw fit to reprint (1893, pp. 73–79) a good deal of what he had written in 1890 relating to the dual theory, and to make the irrational statement (p. 73) that the theory had "created some excitement twenty-five years ago, but has at length almost subsided into oblivion."

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