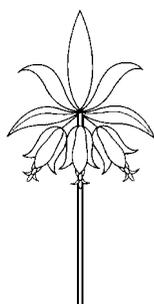


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Idée fixe: A commentary on the opposition in France to the theory of lichen duality, 1870 to 1900

M. E. Mitchell

Abstract

The discovery late in the 1860s that lichens are composed of microscopic algae and fungi left most botanists incredulous. Lichens had long been regarded as constituting an autonomous group of plants, and there was no known precedent for the existence of composite organisms. Fearful for their subject's survival, lichenologists went on the defensive. France led the way in what became a widespread effort to negate the discovery; this paper documents the campaign mounted in that country.

Early in 1857 the phycologist Gustave Thuret (1817–1875)—a man of independent means but fragile health—moved from Paris to the south of France where he settled at Cap d'Antibes, between Cannes and Nice. There he and his colleague Edouard Bornet (1828–1911; Fig. 1) established a marine research laboratory that quickly attracted postgraduate students from several European countries and North America, among them the Russian botanist Michael Woronin (1839–1903). Having spent several months at the lab in 1860, Woronin paid a return visit following a meeting of the Swiss Natural History Society at Rheinfelden, near Bâle, in September 1867. The speakers there included Simon Schwendener (1829–1919), professor of botany at the University of Bâle, who had stunned his audience by declaring that lichens are the product of a parasitic relationship between a fungus and an alga, not a discrete category of plants as was then almost universally believed (Anonymous 1867, pp. 88–91).

Woronin reported the news to Bornet, who, though anything but convinced, decided to investigate the claim. Believing at the time “that lichen gonidia¹... are the first stage of a lichen, [Bornet] set about examining the youngest specimens he could obtain in order to find the transition from a free to a lichenized alga. Within a week, however, he had reached the same conclusion as Schwendener” (Guignard 1912, p. 276, fn.);² that outcome decided Bornet to undertake a comprehensive investigation of lichen algae.

Dissent and denial

The first French response to the new theory was published by Casimir Roumeguère (1828–1892; Fig. 2), a Toulouse businessman for whom lichenology and mycology were a particular interest. He was in no doubt that “the curious notion promoted by a German [*sic*] physiologist, Schwendener, respecting the constitution of lichens” according to which “the fungi form the thallus and apothecia, the algae the gonidial layer... will, without doubt, be rejected by all physiologists” (Roumeguère 1870, p. 55).³ The theory was also dismissed in that year by William Nylander (1829–1899; Fig. 3), a Finnish botanist working independently for almost 20 years at the Muséum National d'Histoire Naturelle in Paris and recognized as the foremost lichen taxonomist of his time. He would have realized that were the theory to prevail, his widely used classificatory system would collapse and the hundreds of

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Figure 1. Edouard Bornet, photograph from Guignard (1912).

lichen names he had introduced over the years possibly become redundant.⁴ Faced with such an alarming prospect, Nylander (1870) attempted to argue that while “some lichen thalli entirely resemble those of algae (*Coenogonium* [*Cystocoleus*] similar to *Conferva* [*Trentepohlia*]),” they need not necessarily be the same because he saw no reason “why gonidia (and gonimidia) could not exhibit form and structure resembling, or indeed the same, as those of algae”;⁵ such fuzzy reasoning from a man of Nylander’s intellectual caliber may indicate the onset of denial.

Bornet concluded his investigations—which extended to species representative of 60 lichen genera—in 1872 and, early in the following year, published an extensive report that conclusively assigned the photosynthetic components of the species studied to seven algal genera, as then understood. He had also made the anatomical studies depicted in the 11 fine plates that accompany his report, work



Figure 2. Casimir Roumeguère, photograph courtesy of Bibliothèque Nationale de France.

that allowed him to state “under good optical conditions and trusting only to... clear and exact observations, one never sees gonidia develop from hyphae in any lichen or any indication that such could be the case” (Bornet 1873, p. 70).⁶

The first public discussion of Bornet’s results took place following a lecture delivered by Hugh Weddell (1819–1877; Fig. 4) at a meeting of the Société Botanique de France in Paris on 23 May 1873. Born in Gloucestershire, Weddell was brought while still a child to live with his father in France, where, in 1841, he qualified as a physician but never gainfully practised. Having become a French citizen (Lorch 1988, p. 31, n. 79), Weddell was appointed to an assistantship at the muséum in 1850 and soon found himself recruited for an expedition to Bolivia.⁷ When Weddell resumed his post, at the end of 1851, Nylander had begun his long association with the muséum and the two men formed a close, but fated, friendship.⁸



Figure 3. William Nylander, photograph from Norrlin (1913).

Weddell left Paris, for family reasons, towards the end of 1857 and had taken up permanent residence in Poitiers by the early 1860s. There he met Jules Richard (1836–1896; Fig. 5), a law graduate and municipal employee whose leisure hours were largely devoted to recording the local lichen flora. By late 1867 Richard had recruited Weddell to that pursuit (Weddell 1873, p. 145, n. 3), and the latter put Richard in contact with Nylander (Loynes 1896, p. 259), who was soon helping both men with the identification of their collections.

Weddell had developed a particular interest in the lichens of a granitic region south of Poitiers, and this was the subject of his May 1873 lecture. In reply to a question posed during the discussion that followed his paper, Weddell said “as matters stood, he did not believe the Schwendenerian hypothesis could



Figure 4. Hugh Weddell, photograph courtesy of Bibliothèque Nationale de France.

be considered a completely established and proven fact” (1873, p. 154).⁹ Joseph Decaisne (1807–1882), a professor at the muséum and the society’s president, replied that, “on the contrary, in his opinion Bornet’s recent memoir had given the question an altogether new direction and he considered lichen parasitism to have been conclusively demonstrated.”¹⁰ When Weddell explained that he had not seen Bornet’s report, which had only just appeared, Decaisne told him its publication “left no doubt that rather than constituting a special class, lichens were to be understood as representing a distinct group of thecosporous fungi.”¹¹

Though Weddell had not accepted the dual theory at the time of writing his paper, he did refer to it in the introduction: “recent observations introducing us to the curious



Figure 5. Olivier-Jules Richard, photograph from Loynes (1896).

relations that appear to exist between lichens and algae, in particular, will, it must be hoped, provide a further inducement to the study of the first of those groups without in any way challenging its autonomy” (p. 143).¹² When Nylander, to whom Ahti (1990, p. xiv) attributed a “morbid hypersensitivity verging on paranoia,” read that innocuous sentence he chose to construe it as a betrayal. In a short, speedily produced, paper that quoted most of Weddell’s comment, Nylander (1874) declared “from this it would appear that the author, in his own way, assents to the Schwendenarian hypothesis,”¹³ and went on to disparage Weddell’s results. Weddell published a spirited response in which he said (1874, p. 182) that he could not “refrain from saying how deeply I regret that one whom I had been accustomed for so many years to consider as friend, and look up to as a master, should have thought it needful, on account of some variance of opinion on scientific matter, to treat me so

much like an enemy, and oblige me to act in self-defence.” By then, however, Weddell had come to accept Bornet’s evidence that a lichen’s green cells are algae as altogether correct: speaking at a meeting in Florence in May 1874 he said “like so many others, I was reluctant to accept such an extraordinary fact but, little by little, the various publications supporting it began to convince me, and that conviction became absolute the day, very recently, when I was able to examine microscopical preparations shown me by Dr. Bornet. I was able to compare these with the figures he has published and can guarantee that they agree perfectly” (1876, p. 66).¹⁴ Nylander, well realizing that those figures were fatal to his cause, appears to have made no published mention of either Bornet’s original paper or of his second report (1874).

Bornet’s academic colleagues, on the other hand, demonstrated their recognition of his achievements when, at a meeting in Paris on 11 April 1874, the Congrès des Sociétés Savantes recommended him for the award of its gold medal. In the address delivered on that occasion, Emile Blanchard (1819–1900), a professor of zoology at the muséum, described lichen duality as “a state of life that appears truly extraordinary” (1877, p. 57),¹⁵ which, taken with Weddell’s similar comment, helps convey just how difficult it was for contemporary naturalists to accept the discovery. The mycologist Maxime Cornu (1843–1901), then an assistant at the muséum, could write “lichens are nothing other than fungal parasites of algae, this has been put beyond doubt by the fine work of Schwendener, Reess [1872] and Bornet” (1876, p. 73),¹⁶ but lichenologists remained committed to the defence of their subject’s independence.

Théodore Brisson (1828–1897; Fig. 6), an insurance agent and enthusiastic field botanist in the Marne Département, northeastern France, was a dedicated autonomist. He had



Figure 6. Théodore Brisson, photograph from Brisson (1904), courtesy of Bibliothèque Nationale de France.

begun to catalogue the region's lichen flora in the late 1860s but was soon requesting help from Jean Müller (1828–1896), associate professor of botany at the University of Geneva and a prominent lichen taxonomist. Müller readily agreed to check his material and subsequently put him in touch with Nylander (Royer (1875, p. 124); aided by these able men, Brisson published *Lichens du Département de la Marne* (1875). Both of his mentors were resolutely opposed to the duality theory—Nylander for reasons already mentioned, Müller because of an obstinate belief in a delusory claim by Minks (1876) that lichens' colorless filaments contain chlorophyllous organelles and could not therefore be of fungal origin. That Müller and Nylander's hostility to Schwendenerism had communicated itself to Brisson was evident when, lecturing to his local scientific society, he assessed the views of over a dozen European authors on the subject of lichen

composition (1878a). Brisson divided those authors into three groups: a) advocates of duality (4), b) adversaries with reservations (2), and c) confirmed adversaries (8). Having made clear where his sympathies lay, Brisson believed the first group's evidence could be refuted by the specious assertion that “if lichen spores grown together with algae produce a lichen containing gonidia, it is certain that the algae have not been transformed into gonidia but that these develop from the actual fabric of the thallus” (p. 73).¹⁷ Brisson went on to review the adversaries' claims at considerable length before concluding with another ill-considered declaration: “for Schwendener's theory to be considered correct, it would be necessary to show that free-living gonidia occur in the vicinity of growing lichens and that these gonidia penetrate the thalli or that the first filaments of thalli go in search of them. That has not been shown, and cannot be shown because it does not happen” (p. 96).¹⁸

Schwendener's theory was also considered an aberration by Jules Richard whose legal career had prospered to the extent that, by the late 1860s, he had been appointed a public prosecutor. In December 1870, however, Richard was relieved of his duties by the newly established Provisional Government, after which he retired to the parental home, some 50 kilometers west of Poitiers, where he occupied himself with the preparation of a regional lichen flora. He would dedicate this, in fawning terms, to Nylander—only Latin sufficed—whom he further acknowledged in the preface for “advice and outstanding kindness in helping to resolve difficulties” (1878, pp. xiii–xiv).¹⁹ Richard dealt only briefly with the “algo-lichénique” theory, remarking that it “does not appear to me to have been proved” (pp. vii–viii);²⁰ he made no mention of Bornet's work.

The first conclusive proof that lichens are composite organisms came in the same

year when Ernst Stahl (1848–1919), a native of Alsace, reported the first spore-to-spore synthesis, an achievement realized while he was a postgraduate student at the University of Strasbourg (1877). His results and earlier work on the subject were reviewed by Gaston Bonnier (1851–1922), professor of botany at the École Normale Supérieure in Paris, who concluded that recent work had placed “the hypothesis advanced by Schwendener beyond doubt” (1877, p. 67).²¹ Bonnier’s declaration was, it may be assumed, read with approval by most of his academic colleagues, but it failed to influence the autonomists. Brisson, for example, (1878b) attempted to use Stahl’s findings to his own advantage by spuriously arguing that “a fungus lives parasitically because, lacking chlorophyll, it is obliged to live on organic matter... If it lived parasitically on algae it would destroy or weaken them, which does not happen because Stahl has established the contrary. Gonidia therefore are certainly not algae” (1878b, p. 275).²² Brisson concluded his polemic by quoting from a proof or preprint of a paper by Müller (1879) in support of Minks’ (1878) claim that gonidial primordia (“microgonidia”) originate in lichen hyphae and grow to normal size on release. He also printed a letter of 19 September 1878 in which Müller told him “I have now studied the more important details of Dr. Minks’ latest work [1878] and can declare Schwendener’s theory absolutely sunk.”²³

Another instance of a professional choosing to differ emerged during a meeting of the Association Française pour l’Avancement des Sciences in August 1878 at which Nylander presented a sadly discourteous paper. Harking back, for no evident reason, to the discussion that followed Weddell’s 1873 lecture, Nylander quoted Decaisne’s remark that “rather than constituting a special class, lichens were to be understood as representing a distinct group of thecosporous fungi,” and having repeated his

empty claim that “gonidia clearly originate from thalline cells,” saw fit to declare that, the now elderly, Decaisne “does not know what he is talking about” (Nylander 1879, p. 706).²⁴ There were two speakers to the paper—Maxime Cornu and Henri Baillon (1827–1895), professor of medical natural history at the Faculté de Médecine de Paris. Cornu stated bluntly that as far as he was concerned the “théorie algolichénique” had been conclusively proved, but Baillon claimed that a close study of microscopical preparations had enabled him to see gonidia emerge *in situ* and to follow their development, which made it impossible for him to accept Schwendener’s theory.

Up to this point, opinions concerning that theory had been confined, almost exclusively, to scientific journals. In 1878, however, Jules Gosselet (1828–1916), a professor at the University of Lille, published a school textbook from which the youth of France learned that “according to recent research, a lichen is to be understood as consisting of a fungus whose mycelium lives at the expense of an alga confined within its meshes” (p. 163).²⁵ Autonomists could never hope to reach such an audience, but they were presented with a means of making their case when Casimir Roumeguère founded the *Revue Mycologique*. His decision, announced in the first issue (November 1879), that the journal would accommodate contributions relating to lichenology did not mean that Roumeguère had come to accept that lichens are fungi. Quite the contrary: in the same issue he made favourable mention of Brisson’s last critique and declared his own unqualified belief in Minks’ imaginary microgonidia (1879, pp. 2, 4).

Jules Richard, meanwhile, had been compiling an inventory of the many substrates colonized by lichens—from bark and rock to bone and glass (1882a). That innovative study has an introduction conspicuous for the fact that half of its 38 pages have no bearing whatever on the

topic under consideration—their purpose was to promote opposition to the theory of duality by mounting a detailed attack on Bonnier’s 1878 paper. The fact that the introduction includes an acknowledgement of Nylander’s help (p. 223) may explain its anomalous content: as noted by Vitikainen (2001, p. 266), Nylander “provided his collaborators with short anti-Schwendenarian theses to be inserted in their publications as a return service for the identifications he made.”²⁶

Further opposition to the dual theory quickly followed. Camille Flagey (1834–1898), manager of a glassworks at Montferrand, south of Besançon, had undertaken the preparation of a regional lichen flora when, like Brisson, he found himself in difficulty and also turned to Jean Müller for help, which was again readily forthcoming. When Flagey visited Geneva with material for verification, Müller introduced him to the chimerical microgonidium; he returned home convinced of its reality and, in a section headed “De l’autonomie des lichens” in the introduction to his flora, declared that Müller’s microscopical observations had altogether invalidated any possibility of duality: “lichen autonomy is supported by the most eminent lichenologists... and it may be said that the Schwendenerian theory has had its day and that in a few years its ever having been accepted and discussed so seriously will be unimaginable” (1883, p. 313).²⁷

Conflict

In January 1884 the *Revue Scientifique de la France et de l’Etranger* published the text of a lecture delivered by Léo Errera (1858–1905), a lecturer at the University of Brussels, on old versus new approaches to plant classification. He devoted particular attention to “the epic struggle between lichenologists and laboratory botanists” (p. 67),²⁸ pointing out that in the light of synthesis experiments—particularly

those of Stahl—“it is clear that lichens as a class must disappear and the plants assigned to it be distributed among different groups of ascomycetes and basidiomycetes... a simple fact that would receive general acceptance were it not for conventional wisdom and the lichenologists” (p. 69).²⁹ Errera then hastened to say—tongue firmly in cheek—that he had the greatest respect for lichenologists, “those studious and zealous people who have undertaken the immense service of naming, ordering and describing legions of lichens,” adding that he readily understood how devoting oneself to such work left little time to study questions of physiology and microscopic anatomy in depth, a circumstance that put such people in danger of falling into error if they nonetheless venture to deal with them” (p. 69).³⁰ Giving a further twist to the knife, Errera then asked “how can one not be greatly amazed and a little amused on rereading the impassioned recriminations, the wailing with which lichenologists still respond to what was the algo-fungal theory but is now a fact experimentally established both by analysis and synthesis” (p. 69).³¹ Errera, however, ended his attack on a regrettably personal note by quoting what he termed “sterile speeches for the defence” (“plaidoyers steriles”) from several of Nylander’s publications. All of which drew a speedy response from Richard (1884a); borrowing Errera’s mock-serious style, Richard poked fun at him for presuming to criticize lichenologists when he lacked any first-hand experience of their work. The bantering ended, however, when Richard addressed the disrespect shown Nylander: this, Richard insisted, was “a distinguished scientist whose punishing workload, long residence among us and liberal sharing of his expertise entitled him to very different treatment” (p. 420).³²

The bit now firmly between his teeth, Richard set about preparing a substantial report that would, he believed, definitively

scuttle the duality theory. In short order, and almost certainly abetted by Nylander, Richard published a 56-page essay largely devoted to citing opinion supportive of his contention that Schwendenerism was “one of the strangest aberrations to emerge in a century so rich in marvels and absurdities of all kinds” (1884b, p. 99).³³ For Richard, a simple assertion by Nylander (1875, p. 303) that, in the thallus of *Lasallia pustulata* (L.) Mérat (as *Umbilicaria pustulata*), gonidia can be seen to develop in the lower part of the cortical-gonidial layer, was sufficient to exclude all possibility that they could originate externally. He therefore denounced the “importation of the German fable into France where, regrettably, it has taken root” (p. 111) but concluded by saying that he considered this “a passing crisis. Let it pass, we shall soon be done with it” (p. 155).³⁴

Roumeguère (1885, pp. 62–64) warmly welcomed Richard’s concoction, but it went unmentioned in the extensive reviews of current literature then appearing in the *Bulletin de la Société Botanique de France*. That omission may be attributable to the fact that Edouard Bornet had assumed overall responsibility for the journal’s bibliographical section in 1884 and would have avoided giving currency to Richard’s mistaken beliefs. Bornet was very likely responsible also for the rejection of a paper submitted to the *Bulletin* early in 1885 by Auguste Hue (1840–1917; Fig. 7). A native of Saint-Saëns, east of Caen, Hue took holy orders, but, “poor health having precluded his retaining a parochial ministry, he became tutor to one of the most distinguished families of... Canisy,”³⁵ also in northwestern France (Wuitner 1932, p. 26). Hue appears to have spent a good many years there, during which time he assembled an extensive herbarium of vascular plants. By 1881, however, he also had an address in Paris and had joined the Société Botanique de France. Nylander was likewise a member, and, whether at meetings

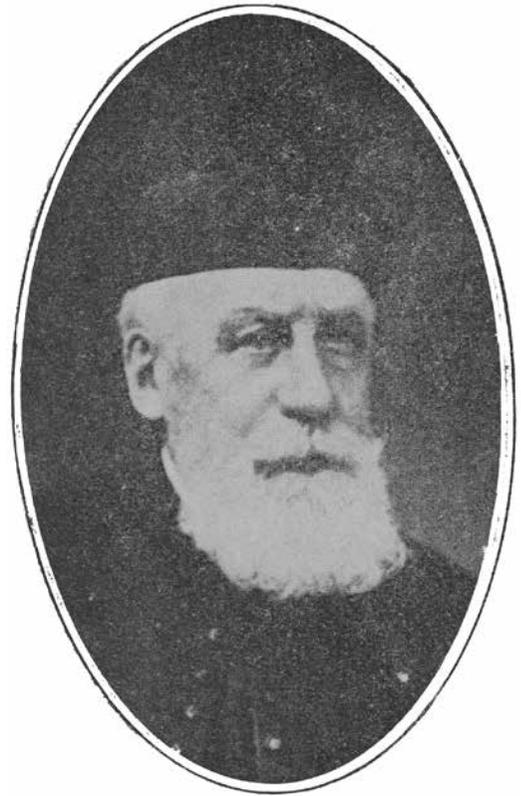


Figure 7. Auguste Hue, photograph from Wuitner [1932].

of the society or otherwise, the two men became acquainted. More than likely as a consequence, Hue developed an interest in lichen floristics and taxonomy that would lead to his publishing extensively in those areas over the years. Nylander proved supportive while Hue was finding his feet (Hue 1885a, p. c), and Nylander successfully recruited him to the autonomist cause. Early in the 1880s, Hue obtained permission to conduct independent research (“travaux personnels”) at the muséum, and Nylander—whose own association with that institution had ended, acrimoniously, in 1873—quickly found work for him.

Between 1865 and 1882 Nylander had published a series of almost 40 papers titled “Addenda nova ad lichenographiam

European,” and Hue was now tasked with assembling the descriptions of the more than 1,000 taxa involved and organizing them according to Nylander’s system of classification. While that work was in progress, Nylander received a specimen for identification that proved to be an undescribed species, which he named *Gyalecta lamprospora* (now *Bactrospora lamprospora* (Nyl.) Lendemer). When examining the material, Nylander convinced himself that he had seen hyphae develop from chlorophyllous cells within the thallus, which led him to ask, complacently, “what then becomes of the symbiosis fable, where now is the fungus, where the alga?”;³⁶ those remarks, which Nylander evidently regarded as delivering the *coup de grâce* to duality, appeared in the German journal *Flora* (1885, p. 313), but he also wanted them publicized in France. To that end, he had Hue reprint (not altogether verbatim) the description of the new species, together with a commentary, for the *Bulletin* of the Société Botanique de France; Hue dutifully submitted his work in April 1885 and immediately ran into trouble.

At this time, most French institutional botanists were dualists who simply ignored the naysayers.³⁷ When, therefore, the editor of the *Bulletin* read in Hue’s submission, titled “Note sur les gonidies d’un *Gyalecta*,” that the components of a lichen develop one from the other, he very likely referred it to Bornet. Whatever did happen behind the scenes, when receipt of Hue’s paper was recorded at a meeting of the society on 10 April 1885, a footnote read “The committee of the Bulletin has given Fr. Hue permission to withdraw his communication” (Anonymous 1885, p. 155).³⁸ Hue did so and sent it to Roumeguère for the *Revue Mycologique*, with an account of what had happened. Roumeguère, always ready to support the cause, published the paper accompanied by an editorial note berating the society for having “now become more Schwendenarian than the

initiator of the outlandish algo-lichen theory” (Hue 1885b, p. 1).³⁹

Jules Richard had also been engaged on an attempt to defend an unfortunate claim by Nylander. In a report on lichens collected in the Bolivian Andes, Nylander (1863, p. 244) had provided what he believed was the first description of fertile *Dictyonema glabratum* (Sprengel) D. Hawksw. (as *Cora pavonia*), having assumed that black ascocarps present on the specimens were the species’ fruit-bodies. However, Frederic Johow (1850–1933), a lecturer at the University of Bonn, was now insisting (1884, p. 400) that Nylander had erred—those ascocarps belonged to a fungus growing adventitiously on the species in question, whose fungal component is in fact an hymenium-forming basidiomycete. All of which was an abomination to Nylander, who, not wishing to become personally involved, supplied Richard with material from which to fashion a rebuttal. Richard (1886, p. 211) asked how Johow could have seen an hymenium on specimens of *Dictyonema*—naively arguing that “if indeed lichens, they cannot have an hymenium; on the other hand, if they do have an hymenium on the lower surface of the thallus they cannot have true apothecia on the upper surface of the same thallus. There is an absolute contradiction between these two classes of facts and, consequently, between the observations that concern them. But who could question the perfectly exact and full description provided by Dr. Nylander, the grand master of lichenography . . . He was the first to recognize the well-developed but hitherto unknown apothecia of these elegant plants . . . Obviously, therefore, Johow’s assertions are incorrect” (p. 211).⁴⁰ Having reached that conclusion, Richard declared “Schwendenerism is a joke, the muddled and fuzzy dream of a Germanic imagination—amplified and exaggerated in this country by a passion for novelty and the extraordinary” (p. 212).⁴¹

A report by Bonnier (1886) claiming *in vitro* synthesis of lichens had Nylander again reaching for his pen: he dismissed the possibility of a thallus being formed from a mixture of algal cells and spores because “the orderly arrangement evident in the structure of any lichen—with its gonidia and other anatomical parts jointly expressing their common nature—rebuts and utterly contradicts Schwendener” (1887, p. 272).⁴² Hue’s work on the *Addenda* project had progressed well by now, with the third and final section going to press in 1888. Nylander evidently kept a close eye on the undertaking because, when an opportunity presented, he inserted a further attack on Schwendener (Hue 1888, p. 110, fn).⁴³

At this time almost all of the lichenologists active in France had the distinction of being ecclesiastics—notably, in addition to Auguste Hue, Julien Harmand (1844–1915), Félix Hy (1853–1918; Fig. 8), Henry Olivier (1849–1922) and Gérard Parrique (also known as Brother Gasilien, 1851–1907)—all, then, with the exception of Hy, staunch Nylanderians.⁴⁴ Hy, professor of botany at the Université Catholique d’Angers, had endorsed the composite nature of lichens early in his career (1881, pp. 112–113), and it was on this topic that he lectured at a congress in Paris early in April 1888 (Hy 1889). Taking a carefully balanced approach, Hy assessed the contrasting opinions generated by Schwendener’s theory: “one maintaining that gonidia are discrete organisms within the thallus, the other that all parts of a lichen, having a common source, form a single entity... the nub of the matter is, crucially, the origin of the gonidium... does it arrive extraneously or is it produced by the germinating spore’s first hyphae?” (p. 469).⁴⁵ Hy rejected the latter alternative because it involved accepting that a chlorophyllous cell could emerge from an altogether alien tissue (p. 470). Later he addressed “the two principal assertions” that appear to contradict the dual



Figure 8. Félix Hy, photograph from Anonymous (1911).

theory: “gonidia are not true algae and lichen hyphae are altogether different from those of true fungi” (p. 473).⁴⁶ Taking the latter claim first, Hy pointed out that lichens must be considered true fungi since “their fundamental features correspond to those of the generality of that extensive class... their modes of reproduction are exactly comparable... their spermogonia agree in the most minute detail... The gonidia, also, differ so very little from ordinary algae that they can be assigned to the Cyanophyceae, Chlorosporeae...” (pp. 473–474).⁴⁷ Hy concluded with the insightful comment that “especially in the more highly organized lichens, the gonidium is a species of alga long adapted to a captive existence and no longer found in a free-living state” (pp. 477–478);⁴⁸ his paper would not be the last to deal with the issue of duality but would prove the most discerning of those published in the 19th century.

A study by one of Bonnier's students, Henri Jumelle (1866–1935), relating to gas exchange in lichens, now indirectly sparked renewed opposition to Schwendenerism. Prosper de Boutarel (1831–1908), science correspondent of a national daily, found Jumelle's work of sufficient interest to warrant the publication of a summary, in which he reminded his readers that lichens "are the product of an association between an alga and a fungus, the latter usually being the more conspicuous" (Boutarel 1891).⁴⁹ When, in due course, Jules Richard happened on the article he mounted what would prove his last defence of autonomy: "those lines give the impression that this extraordinary association is an actual, accepted fact, some sort of current doctrine, on which scientists have said the last word... But the alga and fungus theory—taken up in France when no more than outlined by Schwendener and promoted by laboratory experiments that have been repeatedly criticized and refuted by the most eminent specialists—is far from being an accepted belief, as is evident from its rejection by the authors of reputable floras, general and local" (1891, p. 182);⁵⁰ in support of that view, Richard drew attention to "a new and quite remarkable observation by Dr. Nylander that has provided a very strong argument against the Schwendenerian fable"⁵¹ and attached a long, translated extract from the publication in question (Nylander 1891). That extract, which concerned species of *Cladonia* and *Stereocaulon* with largely ecorticate podetia, included Nylander's simplistic argument (1891, p. 32) that the green cells seen in granules present on those podetia are generated there and could not be of external origin because he, Nylander, had not seen any such cells in the vicinity of those granules. Having added some personal observations of a similar nature, Richard concluded by lamenting that "an important newspaper, enjoying huge circulation, would proclaim *urbi et orbi* so bogus a topic as the

alliance between an alga and a fungus to form a lichen" (p. 188).⁵²

The topic soon received a further airing when Alexandre Acloque (1871–1941), a freelance writer previously unknown to lichenology, put together the first general survey of that subject published in France (1893). In his chapter on the composition of lichens (pp. 48–113), Acloque undertook an assessment of prevailing attitudes to the dual theory, an exercise that led him, with frequent resort to Nylander's assertions and flying in the face of 20 years' evidence, to maintain that "les gonidies ne sont pas des algues" (p. 65) and "les hyphes ne sont pas des champignons" (p. 72). Those conclusions were welcomed by Debat (1893) and Roumeguère (1893), both entrenched autonomists, but support for their stance was now dwindling, and nothing they or Acloque had to say would alter that.

Endgame

In 1895 Julien Harmand, chaplain to an institution for the deaf and dumb at Nancy, published the first part of a comprehensive *Flore des Lichens de la Lorraine*, which he dedicated to "M. l'abbé Hue, mon ami, mon collaborateur et mon guide." Harmand devoted pages 48–52 of his introduction to a digest of contemporaneous views on the nature of lichens and quoted several extracts from a paper by Hy (1892); these included the perceptive comment that "the remarkable association [of alga and fungus] benefits the constituents reciprocally since they exchange the products of their metabolism. A lichen is therefore seen to be, after all, no more than a singular fungus, remarkable for the fact that far from being a dangerous parasite of its nourisher, the fungus enters into partnership with it, such that both help one another to extend their growth in common" (pp. 339–340).⁵³ Harmand chose, however, not to adjudicate on the views he had

assembled, preferring to allow “the sufficiently informed reader to decide under which banner he should enlist;” his personal decision was to remain an autonomist because “I wonder how the *particular* gonidia materialize in the new lichen produced by spores. They certainly do not come from without... consequently they are produced by the young lichen. There is no way out of that” (p. 54).⁵⁴

Harmand’s friend, on the other hand, had come to see matters differently: since becoming Nylander’s protégé in the early 1880s, Hue had been convinced that the green and blue-green constituents of lichens develop from their associated hyphae, but, sometime in the mid-1890s, he realized that those chlorophyllous cells are in fact algae (as then understood).⁵⁵ That cost him his friendship with Nylander, who, following the death in January 1896 of his other key ally, Jules Richard, now had just three French contacts in the area of lichenology: Gérard Parrique (Br. Gasilien), a teacher at religious primary schools in central France, who for several years had known and been helped by Nylander,⁵⁶ Camille Flagey working as an engineer in Algeria since 1884 and—through the good offices of Parrique—benefiting from Nylander’s help with the preparation of a regional flora,⁵⁷ and Alphonse Boistel (1836–1908), professor of law at the Sorbonne. Field lichenology was Boistel’s leisure interest, and he was, again thanks to Parrique, fortunate to obtain Nylander’s help, though at arm’s length, when preparing an identification manual (1896).

During the 1880s Nylander had published lists of the lichens collected on the various excursions in which he had participated to localities around Paris, and in November 1896 he reissued these, systematically arranged, under the title *Les Lichens des Environs de Paris*. On the opening page of that work he returned defiantly to the issue of duality, stating “it is

quite clear today that the expression ‘lichens are fungi growing in symbiosis with algae’ is an absolute fantasy or a calumny. There is ample proof that lichens constitute a noble and venerable class of autonomous plants with little relationship to either fungi or algae.”⁵⁸ However, few were any longer prepared to listen, and Nylander’s was the last challenge to *Schwendenérisme* published in France.

Since Hue’s defection, Parrique and then Boistel had been the only lichenologists with the entrée to Nylander’s apartment in the passage (now rue) des Thermopyles; when Parrique also jumped ship, evidently late in 1896, Boistel became Nylander’s last personal link with his subject. Though he chose to be reclusive, Nylander was no hermit: early in 1897 he and Boistel joined a botanical excursion to a district south of Paris. Nylander’s health was, however, failing (Boistel 1899b, p. 224), and on the morning of 29 March 1899 the concierge of his apartment building found him dead at his desk.⁵⁹

With Brisson, Flagey, Richard and Roumeguère having predeceased Nylander, the autonomist campaign was now effectively over—whatever few diehards remained held their peace. A contemporary commentator had referred to “the much-debated Algo-Lichen hypothesis” (Williams 1889, p. 2), but in fact there was no debate, at least not in France. There academic and professional botanists had altogether ignored the oppositionists’ polemics, aware that little was to be gained from engaging in a dialogue with the deaf.

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Notes

1. The terms “gonidia” and “gonimia”—now obsolete, having been superseded by “photobiont”—are retained in the translations provided in this paper.
2. “disposé même à croire que les Algues, dont la ressemblance avec les gonidies des Lichens ne faisait aucun doute, n’étaient pas des Algues véritables, mais des ébauches de Lichens, il se mit à étudier les Lichens les plus jeunes qu’il put rencontrer, afin de trouver le passage de l’Algue pure à l’algue lichénisée. La semaine n’était pas écoulé qu’il était arrivé à la même conclusion que M. Schwendener.”
3. “La singulière opinion qu’un physiologiste allemand, M. Schwendener, a émise sur la constitution des Lichens [qui prétend que] les Champignons constituent le thalle et les apothécies et les Algues constituent la couche gonidiale des lichens... sera sans doute repoussée par tous les physiologistes.”
4. Nylander’s classification was abandoned, but his names have largely survived, though not as he would have wished. Once it was accepted that lichens’ green cells are algae, these either had or would have to receive names, and the same necessarily applied to their fungal associates. While work on naming lichen algae progressed slowly, lichen fungi—despite some attempts to find a solution—went nameless until 1950. In that year, delegates to the Seventh International Botanical Congress in Stockholm voted in favour of a proposal that lichen names should henceforth apply only to their fungal components. That decision had the unfortunate consequence of depriving actual lichen organisms of all but their vernacular names. The report by Spribille et al. (2016) that basidiomycetes in the form of yeasts are common lichen constituents has brought the issue of lichen nomenclature to renewed attention.
5. “quidem thallos Lichenum omnino thallos Algarum simulantes (*Coenogonia* similia *Confervis*...),” “Quid autem prohibet, quominus gonidia (et gonimia) Lichenum formas et structuram offerant subsimiles vel quidem similes Algis aut gonidiis Algarum?”
6. “dans de bonnes conditions optiques, en n’admettant... que des observations nettes et précises, on ne voit jamais dans aucun Lichen les gonidies naître de l’hypha, ni même aucun indice qu’il en puisse être ainsi.”
7. Weddell had already spent the years 1843–1848 in South America where the genus *Cinchona* was his particular concern (Leandri 1966).
8. Weddell (1869, p. 196) recorded his gratitude for the help he had received from “mon excellent ami M. le docteur W. Nylander.”
9. “il ne croit pas que dans l’état des choses l’hypothèse de M. Schwendener puisse être considérée comme un fait parfaitement établi et prouvé.”
10. “dit au contraire que, dans son opinion, le nouveau mémoire de M. Bornet fait entrer la question dans une voie toute nouvelle, et que le parasitisme des Lichens lui paraît un fait parfaitement démontré.”
11. “ne peut laisser aucun doute... que les Lichens ne doivent plus être considérés comme pouvant constituer une classe spéciale, mais comme représentant un groupe particulier des Champignons thécasporés.”
12. “Les observations récentes, en nous initiant aux relations singulières qui semble exister entre les Lichens et les Algues en particulier, donneront, il faut l’espérer, un attrait de plus à l’étude du premier de ces groupes, sans porter cependant aucune atteinte à son autonomie.”
13. Translation from Crombie (1874, pp. 145–146).
14. “j’ai bien éprouvé, comme tant d’autres, de la répugnance à admettre un fait aussi singulier; mais les travaux divers publiés en sa faveur ont apporté peu à peu la conviction dans mon esprit; et cette conviction est devenue entière le jour où j’ai pu, tout récemment, examiner la série des préparations que M. le docteur Bornet a fait passer sous mes yeux. J’ai pu comparer ces préparations avec les dessins qu’il en a publiés, et je puis attester leur parfaite conformité.”
15. “d’une condition d’existence qui semble vraiment extraordinaire.”
16. “Les Lichens ne sont pas autre chose que des Champignons parasites des algues; le fait est maintenant hors de doute depuis les beaux travaux de MM. Schwendener, Rees et Bornet.”
17. “Si les spores de Lichens cultivées simultanément avec les Algues, produisent un Lichen contenant des gonidies, il est certain que ce ne sont pas les Algues qui se transforment en gonidies; mais que celles-ci naissent de la substance même du thalle.”
18. “pour prouver que la théorie de M. Schwendener est vraie, il fallait démontrer que les gonidies vivent en liberté où germent les lichens, et que ces gonidies pénètrent dans les thalles, ou que les premiers filaments du thalle vont les chercher. Cela n’a pas été démontré, et ne peut pas être démontré, car cela n’existe pas.”
19. “m’a aidé de ses conseils et a mis une rare complaisance à dénouer les difficultés qui m’arrêtaient.”

20. "cette théorie à laquelle on a donné le nom d'algolichénique... ne me paraît pas démontrée."
21. "Des travaux plus récents ont achevé la démonstration; l'hypothèse émise par M. Schwendener est maintenant hors de doute."
22. "Le Champignon, au contraire est dépourvu de chlorophylle, ce qui explique son parasitisme. Il est donc condamné à se nourrir exclusivement des substances organique... S'il était parasite des Algues, il les détruirait ou les affaiblirait, ce qui n'a pas lieu, puisque M. Stahl a constaté le contraire. Donc les gonidies ne sont point des Algues."
23. "J'ai maintenant examiné les détails les plus importants du dernier travail du docteur Minks, et je puis affirmer que maintenant la théorie de Schwendener est absolument coulée."
24. "gonidia manifeste in cellulis thalli Lichenum oriri"; "de rebus loquitur sibi minime familiaribus."
25. "D'après des observations récentes, un lichen serait un champignon dont le mycelium vivrait au dépens d'une algue qu'il enveloppe et enferme dans les mailles de son mycelium."
26. In addition to preparing his inventory, Richard found time to pen a 120-line ode to lichens (1882b) in which they became, rather fetchingly, "ces fragiles merveilles"; nor was this the muse's first such visit to France—Lirou (1844) had managed 90 lines.
27. "La théorie de l'autonomie des lichens a, du reste, pour elle les lichénologues les plus éminents... et il est permis de dire que le système de Schwendener a fait son temps et que dans quelques années on ne supposera même pas qu'il ai pu être admis et discuté aussi sérieusement."
28. "la lutte épique des lichénologues contre les botanistes de laboratoire."
29. "Mais il est évident que la classe des lichens doit disparaître des classifications: les végétaux qu'on y rangeait doivent être répartis parmi divers groupes de champignons ascomycètes et basidiomycètes... Cette vérité si simple serait admise universellement sans la routine et les lichénologues."
30. "Ce sont des gens studieux et zélés qui ont rendu à la science l'immense service de classer avec ordre, de nommer et de décrire la légions des lichens... C'est là un travail considérable et nous concevons volontiers qu'on y consacrant sa vie on n'ait pas le temps d'approfondir les questions de physiologie et d'anatomie microscopique et qu'on s'expose à se fourvoyer si on les aborde quand même."
31. "comment ne pas s'étonner beaucoup et sourire un peu en relisant les récriminations passionnées, les lamentations avec lesquelles les lichénologues n'ont cessé d'accueillir ce qui était jadis la théorie algo-fongique des lichens et ce qui est devenu aujourd'hui une vérité expérimentale, établie à la fois par l'analyse et par la synthèse?"
32. "c'est un savant illustre entre tous, succombant presque sous le poids d'un labeur incessant, établi depuis des longues années parmi nous, et qui, prodiguant, à tous, les trésors de ses lumières, devait s'attendre à être traité d'une toute autre manière."
33. "une des plus étrange aberrations qu'aura produit ce siècle si fécond en merveilles et en folies de toutes sortes."
34. "la fable allemande fut importée en France où, malheureusement, elle s'est implantée."; "C'est une crise qui passe. Laissons-là passer, nous en verrons bientôt la fin."
35. "son état de santé ne lui permit pas de continuer pendant longtemps son ministère paroissial, et il devint précepteur dans unes des plus illustres familles... de Canisy (Manche)."
36. "Quid tum evenit fabula symbioseos, nam ubi hic "fungus" vel ubi hic "alga."
37. There is, for example, no mention whatever of autonomist dissent in the comprehensive textbook published in 1884 by Phillippe Van Tieghem (1839–1914), professor of botany at the muséum.
38. "M. l'abbé Hue a été autorisé par la Commission du Bulletin à retirer cette communication."
39. "la société botanique est paraît-il devenue à cette heure plus schwendénérienne que le chef lui même de la singulière théorie." Roumeguère soon published another repudiation of the dual theory: in an expanded version of his 1883 account, Flagey (1886) undertook an extensive survey of the claims then in contention respecting the origin of lichens' chlorophyllous cells. Since Flagey still believed in the existence of microgonidia, he inevitably concluded (p. 132) that "lichens must be seen as perfectly distinct, autonomous plants related to algae by *Collema*, and still more closely to thecosporous fungi by the Verrucariaceae, but always distinguished by their chlorophyll-containing hyphae" ("les lichens doivent être regardés comme formant des plantes autonomes et parfaitement distinctes touchant aux algues par les *Collema*, plus encore aux champignons thécasporés par les Verrucariacées, mais pouvant toujours être distinguées de ceux-ci par la chlorophylle contenue dans leurs hyphes."
40. "s'ils ont cet hyménium à la partie inférieure du thalle, ils ne peuvent avoir, à la partie supérieure de ce même thalle, de vraies apothécies lichéniques. Il y a une contradiction absolue entre ces deux ordres de faits et, par conséquent,

- entre les observations qui s’y rapportent. Or qui pourrait mettre en doute le diagnostic si précis et si complet du D^r Nylander, le grand maître de la Lichénographie... il a pu admirer, pour la première fois, les apothécies bien développées, mais jusqu’alors inconnues de ces gracieuses plantes... Les observations de M. Johow sont donc évidemment erronées.”
41. “Le Schwendenérisme n’est pas sérieux. C’est le rêve incohérent et nébuleux d’une imagination germanique, mais encore amplifié et exagéré chez nous par le besoin de faire du nouveau et de l’extraordinaire.”
 42. “Congruentia systematica, quae semper adest in textura thallina Lichenis cujuscumque inter gonidia et cetera elementa anatomica eusdem, communem suum in serie systematica junctim exprimens, omnem schwenderiam repudiat absoluteque refellit.” In a letter of 4 May 1887 to Júlio Henriques (1838–1928), professor of botany at the University of Coimbra, Nylander articulated the frustration that had provoked this swipe at Schwendener. On Henriques’ recommendation, Nylander had been awarded the Portuguese Cross of St. James for his contribution to lichenology, an honor that, he made clear, was all the more appreciated because “most countries having now been invaded by Schwendenerism, my position as principal opponent of a false, ridiculous and fateful dogma has brought me nothing but the enmity and scorn of many botanists” (“après l’invasion du schwenderisme dans la plupart des pays, ma situation comme le principal opposant à une doctrine fautive, ridicule et funeste m’a valu des inimitiés et dédains de nombreux botanistes.” Available online and last accessed 31 October 2016 at <http://bibdigital.bot.uc.pt/obras/UCFCTBt-JH-MeN769-NYL-W31/UCFCTBt-JH-Me>).
 43. Having remarked in relation to *Verrucaria aquatilis* Mudd (as *V. vitricola*) that “with light shining through the transparent substratum of this species, complete development of the thallus and the emergence of gonidia from its tissues can be seen,” Nylander asked “what more stupid than the Schwendenerian fantasy asserting that lichen hyphae seize (*greifen* in German) locally occurring algae, something no one has ever seen or can see.” (“Per substratum pellucidum, luce pemeante, omnem evolutionem thalli et gonidimia nascentia in textura ejusdem observare licet. Quid stultius quam inventio schwendeneriana licheno-hyphis narrans arripi (germanice *greifen*) algas circum errantes, quod nemo unquam vidit nec videre potest.”) Mägdefrau (1973, p. 146) stated, without citing a source, that Nylander used the expression “stultitia Schwendeneriana,” which has been quoted on Mägdefrau’s authority by several authors, but there does not appear to be any actual evidence of Nylander having done so.
 44. Others were Théodore Barbiche (1840–1901), Jean Calumel (1841–1917), Jules Dominique (1838–1902), Jean Fuzet (?–1895), André de la Godelinai (?–1889), Jean-Jacques Kiefer (1857–1925), Louis Ravaut (1822–1898); in a lichenological glossary published by Olivier (1888), the entry for “Schwendenerisme” reads “A fictitious theory first published in 1868 by its author Dr. Schwendener, according to which lichens are no more than the product of an alga and a fungus. No lichenologist worthy of the name has ever taken that theory seriously” (“Fausse théorie publiée pour la première fois en 1868 par son auteur, le D^r Schwendener, d’après laquelle les Lichens ne seraient qu’une production d’une algue et d’un champignon. Aucun lichénologue digne de ce nom n’a jamais pris cette théorie au sérieux.”)
 45. “l’une tenant les gonidies pour des organismes distincts du Lichen; l’autre admettant que les unes et les autres, issues d’une origine commune, constituent un seul et même être... le noeud de la question repose sur ce fait capital: quelle est l’origine de la gonidie... vient-elle du dehors? ou bien nâit-elle à la suite des premières hyphes, de la germination de la spore?” Hy’s paper was reviewed by Edouard Tison (1848–1924), professor of botany at the Université Catholique de Paris. Admitting to no specialist knowledge of the subject, Tison (1888) was content to devote most of his space to an extract from a brochure produced by Nylander (1888). Evidently pleased with his work, Tison—clearly aided by Nylander—published an expanded version as a newspaper article (1889); authorship of that article is misattributed to an “A. Tison” by Grummann (1974, p. 353).
 46. “Les gonidies ne sont pas de vraies algues;—les hyphes des lichens diffèrent complètement de ceux des vrais Champignons.”
 47. “leurs propriétés essentielles concord avec celles de l’ensemble de cette vaste classe... leurs modes divers de reproduction les assimilent exactement... la multiplication par spermogonies se retrouve identique dans les plus minutieux détails. Les gonidies, de même, diffèrent bien un tant soit peu des Algues ordinaires, tout en conservant des analogies assez précises pour permettre de rattachar les unes aux Cyanophycées, d’autres aux Chlorosporées...”
 48. “dans certain cas, spécialement celui des Lichens les plus élevés en organisation, la gonidie est une

- Algue dont l'espèce, depuis longtemps adaptée à une existence captive, a cessé d'exister à l'état habituel de liberté."
49. "sont produits par l'association d'une algue et d'un champignon, et le champignon y prédomine la plupart du temps."
 50. "Il semblerait, en lisant ces lignes, que cette extraordinaire association est un fait tout simple, nullement contesté, une sorte de doctrine courante sur laquelle les savants ont dit leur dernier mot... Mais la théorie de l'Algue et du Champignon, — à peine ébauchée par Schwendener, reprise et préconisée en France, au moyen d'expériences de laboratoire qui ont été constamment critiquées et réfutées par les spécialistes les plus éminents, — cette théorie loin d'être une doctrine courante, n'est admise par aucun des lichénologues de flores ou de florules un peu en renom."
 51. "une nouvelle et très remarquable observation du D^r Nylander est venue apporter un argument d'une grande force contre la fable schwendenerienne."
 52. "Mais il est bien regrettable que, dans un grand journal dont la publicité est énorme, on vienne affirmer *urbi et orbi* un fait aussi controvérsé que l'union d'une Algue et d'un Champignon pour former un Lichen"
 53. "L'association remarquable qui en résulte se traduit par un bénéfice réciproque pour les deux conjoints, qui se communiquent mutuellement les produits de leur activité propre. Le Lichen ainsi ne se trouve être, en définitive qu'un Champignon particulier, très remarquable en ce que, loin d'être pour sa nourrice un parasite dangereux, il l'associe à sa propre existence, de telle sorte que l'un et l'autre s'aident à prolonger leur végétation commune."
 54. "Le lecteur suffisamment renseigné pourra s'enrôler, s'il le veut, sous l'une ou l'autre bannière"; "je me demande de quelle manière les gonidies *propres* apparaissent dans le nouvel individu produit par spores. Elles ne sont pas certainement prises au dehors... par conséquent elles sont produites dans ou par le jeune Lichen. Il n'y a pas moyen de sortir de là." That Harmand eventually came to accept the dual theory is evident from the introduction to volume 1 of his *Lichens de France* (1905, p. ix).
 55. Hue (1894) provided a brief account of structure in which (p. 117) he described the chlorophyllous layer as "formée de hyphes et de gonidies" — there was no mention of algae. Two years later, however, when Hue (1896, p. 8) published the new species *Psorotichia allobrogensis*, he assigned its blue-green cells to the genus *Gloeocapsa*.
 56. There are profuse expressions of thanks to Nylander in, for example, Gasilien (1891, p. 390, 1898, p. 40).
 57. In addition to recording his appreciation of Nylander's help (p. xi), Flagey included a rejection of "la théorie Schwendenerienne" (p. 120) that was almost certainly supplied by his benefactor.
 58. "On sait bien aujourd'hui que la formule 'les Lichens sont des champignons vivant en symbiose avec des algues est une assertion de pure fantaisie ou une calomnie. Il est abondamment prouvé que les Lichens constituent une noble et vénérable classe autonome de végétaux n'ayant rien de sérieusement commun ni avec les Champignons ni avec les Algues.'"
 59. Nylander's death was first publicly reported by Boistel (1899a) in a brief tribute that provides a unique glimpse of Nylander *chez lui*: from "the accumulation of pamphlets, letters, herbarium specimens that covered his tables, his mantlepiece, all his furniture and even the floors of his two rooms to hand height, there emerged, here and there, his microscope, phials for reagents, a few bottles of good wine and a jar of cherries in brandy with which he rounded off his simple meals" ("l'amoncellement de brochures, de lettres, échantillons, cartons d'herbier qui couvraient ses tables, sa cheminée et, jusqu'à hauteur de la main, le plancher même de ses deux chambres, d'où émergeaient de ci, et de là, son microscope, ses fioles à réactifs, quelques bouteilles de bon vin, et un bocal de cerises à l'eau-de-vie, par lesquels il complétait ses modestes repas.")

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