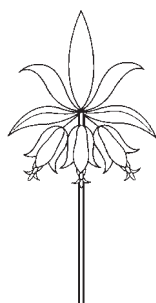


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Hunt Institute for Botanical Documentation  
Carnegie Mellon University  
5th Floor, Hunt Library  
4909 Frew Street  
Pittsburgh, PA 15213-3890  
Telephone: 412-268-2434  
Email: [huntinst@andrew.cmu.edu](mailto:huntinst@andrew.cmu.edu)  
Web site: <http://www.huntbotanical.org>

Editor and layout	Scarlett T. Townsend
Book Reviews and Announcements Editor	Charlotte A. Tancin
Associate Editors	Donald W. Brown Lugene B. Bruno T. D. Jacobsen J. Dustin Williams
Photographer	Frank A. Reynolds

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# Autonomy's long shadow: A report on issues concerning lichen classification, 1870 to 1981

M. E. Mitchell

## Abstract

The scientific study of lichens began early in the 1690s when they were presumed to constitute an independent systematic category. This supposition went virtually unchallenged until, 170 years later, a close study of lichen anatomy revealed that lichens are composite organisms. As a consequence, their perceived systematic status became open to question, and this proved an issue on which botanists found themselves in profound disagreement. Some few promptly recognized that lichens must now be classified as fungi. Others, mainly lichen taxonomists, sought to defend what they had come to regard as exclusive territory by attempting to discredit the unwelcome findings. The majority, however, while fully accepting that lichens incorporate algae and fungi, persisted in regarding them as an autonomous group because they differ in so many respects from their constituents. Most European lichenologists promoted the last approach; their American colleagues, on the other hand, mainly adopted the first.

A comprehensive system of classification that associated lichens with fungi, while also managing to portray them as autonomous, appeared serially in Germany during the first decade of the 20th century. Other systems came and went in the years between 1910 and 1950, but that promoted in the German publication continued to enjoy routine use among lichen taxonomists worldwide. In the latter year, however, a Swedish initiative refocused attention on the need to establish a system capable of accommodating lichenized and unlichenized fungi. That initiative got off to a rather slow start but was by the 1960s and 1970s receiving the active support of both American and German lichenologists. Soon the generality of botanists came to accept that the concept of autonomy was groundless and formally repudiated it in 1981.

## Introduction

The relationship between lichens and other organisms was first constructively

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Department of Botany, National University of Ireland, Galway, Ireland

addressed when Linnaeus (1753, 2:1140–1156) made them a subdivision of his order Algae. Adanson (1763[–1764], 2:6–7, 11), on the other hand, aimed to combine lichens with fungi, an objective ignored by Acharius (1810, p. 14), who held firmly to their purported, autonomous, standing.

The authors of the 30-odd systems of lichen classification published between 1810 and 1866 (Krempelhuber 1867–1872, 2:v–vi, 3:60) believed, with one exception, that lichens constituted a stand-alone group; the nonconformist was Jean-Baptiste Payer (1818–1860). When acting professor of botany at the Sorbonne in the 1840s, Payer prepared a second edition of Adanson's *Familles des Plantes* (printed 1847, published 1864) and also compiled a supplementary *Familles naturelles des Plantes ... Algues et Champignons* (1848). Taking his cue from Adanson, Payer merged fungi and lichens in a single system: he assigned gymnocarpic lichen genera to a "Famille Lichens" positioned between his "Pezizes" and "Hypoxylyons," the latter of which comprised both lichenized and unlichenized, angiocarpic and hemiangiocarpic, genera. Payer's 1848 work appears to have had only a very limited print run, but two years later he published an expanded version under the title *Botanique Cryptogamique*, which made his system widely available; to little avail, however, because Payer was well in advance of his time and the innovations he introduced were almost completely ignored.<sup>1</sup>

Throughout the following years lichenologists continued to believe implicitly in the integrity of their favorites. Consequently, when Simon Schwendener (1829–1919), professor of botany at the University of Basel, declared (1868, p. 291) that “rather than being autonomous plants, all lichens are fungi belonging to the ascomycetes, for which algae... serve as hosts,”<sup>2</sup> most of his contemporaries who interested themselves in floristic and nomenclatural matters were unable to concede that their secluded terrain was actually the property of mycologists. Some gradually learned to live with the unsettling evidence, but others actively contested it for decades. The most poignant dissenting voice was surely that of Krempelhuber (1867–1872, 3:185–186): “the prolific growth of lichens seen for example in mountain woodlands presents an endless number and variety of vivid, air- and light-loving forms that permanently cover the trees from foot to crown, and the rocks from valley to cloud-draped peak. Compare that scene with the growth of fungi—those gloomy, reclusive, suspect, transient companions of shade and damp, of death and decay—and then imagine both put together in a single class of the plant kingdom”; small wonder, Krempelhuber felt, that “the learned plant-anatomist proclaiming to the botanical world from behind his microscope that such unification was a necessity” should have encountered widespread and angry opposition.<sup>3</sup> Like Schwendener, physiologists had no territorial axe to grind, and one of their number was the first to publish an arrangement that situated lichens squarely among the fungi.

### Proposals for a unified classification

When Julius von Sachs (1832–1897) published the first edition of his *Lehrbuch der Botanik* in 1868, while professor of botany at the University of Freiburg, he treated



Figure 1. Title page of Julius Sachs *Lehrbuch der Botanik*, ed. 2, 1870.

algae, fungi and lichens as individual classes within the “Thallophyten” (p. v). Sachs was, however, aware that evidence incompatible with the concept of lichen autonomy had begun to accumulate. He made a point of mentioning (p. 257) “a verbal communication from Professor Schwendener, in summer 1867, relating to the algae of gelatinous lichens being infiltrated by external hyphae, these last being therefore parasites in the sense of de Bary’s second postulate<sup>4</sup>... I believe it correct to infer that Professor Schwendener is inclined to extend this opinion to all lichens.”<sup>5</sup> In the second edition of his textbook (1870; Fig. 1) Sachs unreservedly merged lichens with the fungi, having welcomed Schwendener’s (1869) data confirming the composite nature of lichens, which “henceforth ensured their

systematic position among the ascomycetes” (p. 265).<sup>6</sup> The translation of Sachs’ work into French (1874) and English (1875) revolutionized the teaching of botany in many countries, and, consequently, lichens gradually became accepted—though certainly not by all<sup>7</sup>—as organisms naturally assignable to the fungi; quite how they were to be accommodated there would prove an abiding and contentious issue.

The first spore-to-spore synthesis of a lichen was achieved in 1876 by Ernst Stahl (1848–1919) at the University of Strasbourg. When, two years later, Stahl assumed responsibility for the report on lichen publications in the *Botanischer Jahresbericht*—a new journal surveying the botanical “Literatur aller Länder”—he used the opportunity to emphasize current thinking on the unity of lichens and fungi. Aware that “lichens, or better lichen fungi, are nothing other than ascomycetes” (1878, p. 70),<sup>8</sup> Stahl announced that effective with the next issue of the journal, reviews of lichen literature would no longer be grouped under the rubric “Flechten,” but would instead appear in the section devoted to fungi; for whatever reason, this did not happen, and lichens continued to enjoy separate status until the *Jahresbericht* became a casualty of World War II.

The failure to implement Stahl’s proposal is curious given that lichens were by then commonly regarded as parasitic ascomycetes. In a widely read, introductory text Bary (1878) located his account of lichens firmly in the chapter on fungi, pointing out (p. 122) that these organisms differ only to the extent that the former develop in association with algal cells. Luerssen (1879–1882, 1:175–207)—catering for more advanced students—presented lichens as an “Unterordnung” of the ascomycetes and provided an impressive survey of the facts as then established in relation to lichen biology; similar categorization appeared in the classificatory schemes elaborated by Winter

(1879, p. 9), Bennett (1880, p. 411), Gobi (1881, p. 515.) and Murray (1885, p. 834). Ferdinand Cohn (1828–1898) went further and attempted to position lichen families within the fungal system. Best remembered for his pioneering work on bacteria while professor of botany at the University of Wrocław (Breslau), Cohn (1880, p. 287) divided ascomycetes into five suborders and distributed the lichens among two of these: a) Discocarpi, which included the Graphideae, Lecideaceae, Collemaceae, Parmeliaceae and Usneaceae, and b) Porocarpi, containing Lichinaceae, Pertusariaceae and Verrucariaceae.

The case for integration was also forcefully made at this time by the Belgian plant physiologist Léo Errera (1858–1905). Following publication of his doctoral research—carried out under de Bary’s direction at the University of Strasbourg where his work with several ascomycete species produced the first evidence of glycogen in fungal tissue (1882)—Errera pointed out that “from a physiological point of view, there is really no great difference between a fungus such as the aecidium of barberry, which derives its organic nutrition from green cells of the host leaf, and a lichen whose sustenance is provided by the green cells of its associated alga. In short, *lichens are only a biological subdivision of the fungi*” (1883, p. 218); he also declared (p. 219) “it is clear that lichens as a class must disappear from systems of classification, and the plants so designated be distributed among various groups of ascomycetes and basidiomycetes.”<sup>9</sup> Errera did not further publicize his constructive observations, and the practice of treating lichens as a discrete category of ascomycetes continued (e.g., Goebel 1882, pp. 125–137; Tieghem 1884, pp. 1065, 1084–1173).

In North America the study of lichen systematics had been profoundly influenced for many years by the publications of Edward Tuckerman (1817–1886). Since these reflected

Tuckerman's unshakable belief in lichen autonomy, his colleagues in the United States were ill-equipped to deal with the issue of integration. In 1880, however, Charles Bessey (1848–1915) published a successful primer based to a considerable extent, as he made clear (p. iv), on Sachs' textbook; accordingly, lichens are unceremoniously assigned to the ascomycetes (p. 339), though without any attempt at actual distribution. Four years later Bessey was appointed professor of botany at the University of Nebraska, and there he made mycology one of his department's special interests. This soon led Herbert Webber (1865–1946), one of Bessey's students, to introduce a radical departure for North American lichenology in his catalog of the Nebraska flora (1890), where lichens were assigned to the orders Pyrenolichenes and Discolichenes,<sup>10</sup> positioned between the Pyrenomycetes and Discomycetes (pp. 52–59).

A fundamentally similar approach was taken by the Finnish botanist Edvard Vainio (1853–1929). During the tenure of a lectureship at the University of Helsinki, Vainio obtained funding in 1885 for a visit to southeastern Brazil, where he made extensive collections. In a report on that material, Vainio (1890; Fig. 2) introduced an ambitious classificatory scheme based on his recognition that lichens are polyphyletic and “do not form a distinct systematic group” (p. xiv).<sup>11</sup> Vainio knew that the ideal arrangement would have lichen genera positioned next to their nearest non-lichenized relatives, but all he could realistically do was assign lichens and “ascomycetes to one natural group, although lichenized taxa were kept in separate classes—Discolichenes and Pyrenolichenes” (Tibell 1998, p. 97).

Not everyone was prepared to go as far as Vainio and Webber. When Wilhelm Zopf (1846–1909), then attached to the University of Halle, published a treatise on the fungi in 1890, he made clear from the outset that

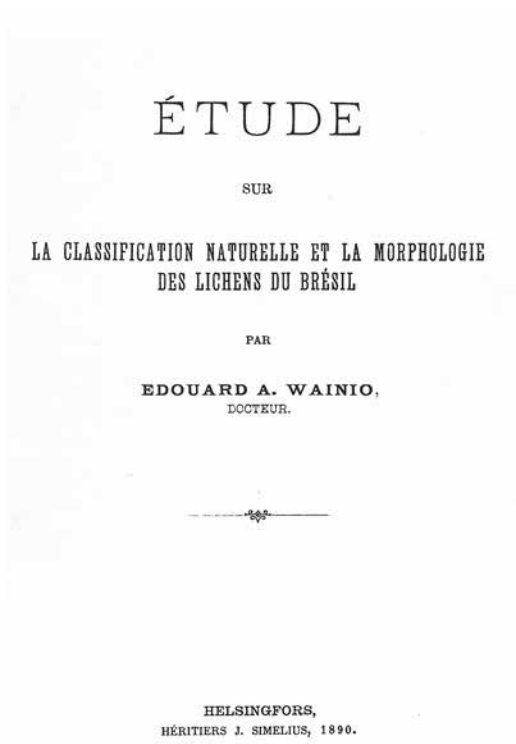


Figure 2. Title page of Edward Vainio (Vainio) *Étude sur la Classification naturelle et la Morphologie des Lichens du Brésil*, 1890.

it would not deal with lichens: for them, Zopf (p. iii) envisaged a companion volume because his current text dealt solely with what he described as “true” (“eigentlich”) fungi (p. 1).<sup>12</sup> Zopf's reactionary stance—which would have a baleful influence on some in his circle—was countered in the short term by another mycological author, the Swiss Franz von Tavel (1863–1941), whose doctoral research had been carried out in de Bary's Institute at Strasbourg. Von Tavel's was an altogether more enlightened approach, which dispensed with the categories Discolichens and Pyrenolichens despite admitting that full integration was not then achievable “because they [lichenized fungi] have until now been placed in untenable lichen systems, and their release must await the



# VERGLEICHENDE MORPHOLOGIE DER PILZE

VON

DR. F. VON TAVEL,

DOZENT DER BOTANIK AM HOHEN POLYTECHNIKUM IN ZÜRICH.

MIT 90 HOLZSCHNITTEN.

JENA,  
VERLAG VON GUSTAV FISCHER  
1892.

Figure 3. Title page of Franz von Tavel *Vergleichende Morphologie der Pilze*, 1892.

task of positioning them in the system of fungi” (1892, p. 94; Fig. 3).<sup>13</sup> Regretably, von Tavel abandoned mycology four years later on joining the Salvation Army, in which he served until the end of his life (Blumer and Müller 1971, p. 103). Though von Tavel’s perspective on lichen systematics attracted no comment in reviews of his book (e.g., Ludwig 1893; Smith 1894), it did not escape attention elsewhere.

Johannes Reinke (1849–1931) was professor of botany at the University of Kiel from 1885 to 1921 and, for almost 25 years, that university’s delegate to the Prussian parliament. His research interests were largely in the area of marine phycology (see Wynne 2004), but von Tavel’s forceful rejection of autonomy appears to have spurred Reinke into resuming a

previous, brief, involvement with lichens, and he set about acquiring material by “purchase, exchange and personal collecting” (Reinke 1925, p. 134).<sup>14</sup> This led to the publication of five, rather long-winded, papers (1894–1896), two of which were specifically concerned with classification. Reinke strongly contested the reasoning behind attempts to merge lichens with fungi and had so little time for von Tavel’s views that he summarily dismissed his “establishment of an affinity between typical ascomycetes and Pertusariae... Lichenaceae as failing at every essential point... For me there can be no doubt that lichens have undergone their phylogeny as consortia, not as fungi” (1894, pp. 532–533).<sup>15</sup> Hence Reinke’s subsequent declaration that “while so-called modern botany cannot sufficiently emphasize that lichens are true fungi, in the preceding paper I have aligned myself squarely with old Acharius” (1895, p. 39).<sup>16</sup>

Reinke’s pronouncements quickly attracted both criticism and support. Gustav Lindau (1866–1923), a German mycologist well qualified to comment on the subject of lichens, published a balanced and detailed response in which he stressed that there could be no justification for maintaining lichens as a distinct category “because they always remain, in fact, just fungi growing on algae” (1895, p. 202).<sup>17</sup> Albert Schneider (1863–1928), working at Columbia University, was, however, wholly supportive of Reinke’s position, to which he devoted several reports (1896–1897); readers of his *Text-Book* (1897, p. 29) learned that “Reinke has proposed a system... which, when more perfected, will form the first approximately natural system of classification for lichens.”

## Continental divide

Those contrasting observations on Reinke’s theorizing could be taken to indicate an emerging European partiality for fungal/

lichen unification, and a North American preference for separate categorization, but much the opposite proved to be the case. In 1894 Reinke had recruited the Welsh-born Otto Darbishire (1870–1934) as his assistant, an appointment that also secured him a keen apologist. During the four years that he spent at Kiel, Darbishire prepared his inaugural dissertation, *Monographia Rocelleorum* (1898), in which he declared, “Reinke has therefore correctly decided recently that lichens must be treated as a distinct realm, despite their dual nature” (p. 6).<sup>18</sup> That endorsement of autonomy was welcomed by the Slovakian Alexander Zahlbruckner (1869–1938), most of whose working life was spent at Vienna’s Natural History Museum. In 1885 Zahlbruckner had succeeded Stahl as reviewer for the *Botanische Jahresbericht*—a load he would shoulder for more than 50 years—and in that capacity Darbishire’s monograph duly reached him; Zahlbruckner’s assessment included the judgement that “the author has hit the mark and taken an important step towards the establishment of a natural system (in the sense of Reinke)” (1900, p. 271).<sup>19</sup> This was shortly after Zahlbruckner had provided the outlines of a new system, derived from Reinke, for Engler’s *Syllabus der Pflanzenfamilien* (1898, pp. 42–46). Here a category Lichenes—described as an ancillary class (“Nebenklasse”) to Ascomycetes and Basidiomycetes—contains the series (“Reihe”) Basidiolichenes and Ascolichenes, the first of which is represented by a single subseries, Hymenolichenes, and the second by four: Coniocarpineae, Graphidineae, Discocarpineae and Pyrenocarpineae. That sketch constituted the first stage of what became the detailed survey of families and genera published by Zahlbruckner (1903–1907) in Engler and Prantl’s *Die natürlichen Pflanzenfamilien* (Fig. 4). Despite being speculative in many regards, Zahlbruckner’s achievement represented the only functional,



Figure 4. Cover of last fascicle (1907) of the lichen system published by Alexander Zahlbruckner in Adolf Engler and Karl Prantl *Die Pflanzenfamilien*.

comprehensive, system then available and, in Europe at least, won broad acceptance—it saved the appearances.<sup>20</sup>

In North America, on the other hand, a fresh drive was underway to merge lichens unequivocally with fungi. Lucien Underwood (1853–1907), a cryptogamist and professor of botany at Columbia University, bluntly declared that “lichens are distinctively fungi and there is no more real reason for holding them apart from the fungous orders with which they intergrade than there would be in separating other parasitic forms in distinct series because of some supposed mutualism between the parasite and its host” (1896, p. 532). The point was soon made again by Frederic Clements (1874–1945), another of

THE  
 GENERA OF FUNGI

FREDERIC EDWARD CLEMENTS, PH. D.  
 Professor of Botany and Head of the Department of Botany  
 in the University of Minnesota

MINNEAPOLIS  
 THE H. W. WILSON COMPANY  
 1909

Figure 5. Title page of Frederic Clements *The Genera of Fungi*, 1909.

Bessey's team at the University of Nebraska. In a thorough review of Reinke's essays, which he described as "the rallying ground of all those fearful of the degradation of the autonomous dignity of the lichens" (1897, p. 278), Clements dismissed Reinke's criticism of von Tavel as "essentially puerile" (p. 280) and rounded off his analysis by declaring "Reinke's conclusion that lichens are physiologically and morphologically distinct from fungi is untrue, and his statement that it is impossible, on account of certain physiological characters, to distribute them among fungi is equally unwarranted" (p. 284). That judgement may be assumed to reflect precepts learned from Bessey whose own scheme of distribution, published some years

later, had the Order Pyrenomycetales followed by the Pyrenolichenes comprising 13 families, which he described as accommodating "[l]ichen-forming fungi allied to the preceding families, with which they may eventually be merged" (1907, pp. 297–298); similar wording accompanied his Order Discolichenes, with 29 families (pp. 300–303). In that paper Bessey chose to avoid any mention of Zahlbruckner's system, three fascicles of which had already appeared (1903, 1905, 1906).

Clements (1909; Fig. 5) took this issue further. Similarly distancing himself from Zahlbruckner's system, and making clear (p. [iii]) that his own "distribution of lichens is original," Clements amalgamated lichen and fungal genera as best he could. His efforts were criticized, rather harshly, by Bruce Fink (1861–1927), professor of botany at Miami University, Ohio, who nonetheless considered "that the distribution of lichens in some such manner as that proposed by Dr. Clements is the only proper treatment of those plants and that the only question that remains is the manner of distribution. We can not hope for a very satisfactory solution until further studies of *Ascomycetes* give us a more thorough knowledge of the relationships of these plants, but Dr. Clements' treatment furnishes a working basis and appears to be better than retaining the artificial group *Lichenes*" (1910, p. 83). Soon after making that last comment, Fink set about assessing the level of support among botanists for the conflicting perspectives on lichen classification. In November 1909 he sent a circular to 75 American and 75 European colleagues, whose specialties ranged from anatomy to mycology to systematics, inviting replies to the question "[s]hould the lichens be maintained as a distinct class of plants, or should they be distributed among the fungi?" (1911, p. 231). Fink received 115 replies, 96 of which supported autonomy, with just 17 (all evidently American) recommending

THE ASCOMYCETES OF OHIO.—I  
PRELIMINARY CONSIDERATION OF CLASSIFICATION\*

BRUCE FINK

All classifications of ascomycetes hitherto followed have been highly artificial, nor are the data for a satisfactory disposition at hand. Hitherto, these fungi, except for lists from two states and certain works mentioned in this paper, have been placed in two groups. In the work to follow, all the ascomycetes of Ohio will be treated as a single class of fungi, and some defense of this method is in order.

The reasons for treating ascomycetous lichens and other ascomycetes together involve mainly the following three considerations: first, the nature of the lichen in general; second, a review of the similarity of lichens and other ascomycetes; third, a discussion of the origin of all ascomycetes, with a view to showing relationships within the group. These three matters will be treated in order and as briefly as is consistent with clearness. Frequent reference will be made to other papers where more lengthy discussions of certain phases of the problem may be found.

Until the time of Schwendener (57), it was generally believed that the chlorophyllous cells found in lichens were the chloroplasts of these plants. Bornet (12) grew lichens from spores in cultures and saw them attack algae. Bonnier (11), by similar methods, obtained mature fruited plants of *Xanthoria parietina* and *Rinodina sophodes*. Möller (47) followed by growing *Calicium parietinum* in cultures without algae and obtained plants that produced spermatogonia and probably archicarpas as well. Fink (31) has reported on the frequent growing of various algal hosts in the same habitats with lichens.

Had it not been for clinging to erroneous tradition, the researches referred to above and others like them would have convinced all botanists that the lichen is a fungus living in some peculiar relation with an alga. Unfortunately, Reinke (53), Schneider (55), and others have aided in retarding progress, and a considerable number of botanists still cling to some modification of the early view. Peirce (52), Elenkin (25), and Danilov (20), with their researches which greatly strengthen belief in the parasitism or the saprophytism of lichens on algae, have succeeded in turning the attention of botanists toward more plausible conclusions.

We need only to advance definitely to the widely but rather hazily understood idea that the lichen is a fungus, the alga being its host and

\* Contributions from the Botanical Laboratory of Miami University—XI.

Figure 6. Opening page of Bruce Fink *The Ascomycetes of Ohio*, pt. 1, 1915.

distribution “to the exclusion of the class Lichenes” (p. 234). Fink, if he voted, would certainly have been of the minority group because he went on to publish an outline arrangement of the “Class Ascomycetae” (1915, pp. 21–25; Fig. 6) comprising 16 orders, three of which—sequentially Lecanorales, Caliciales and Pyrenulales—are entirely devoted to lichens. This initiative was largely dismissed or ignored by Fink’s European colleagues; Smith (1915, p. 296), for example, remarked that while “some writers have suggested distributing lichens amongst fungal families according to affinities ... [i]t seems to us that on account of their structure and physiology, the lichens are just as natural a class as are their nearest relatives the fungi and the algae.”

A novel system based on thallus structure, proposed by Hue (1915), presented no serious challenge to the prevailing orthodoxy, which now went almost unquestioned.<sup>21</sup>

Two papers by Fink and his assistant Sylvia Fuson (1895–1990) on the ascomycetes of Indiana (1919, 1921) were the last to publicize his attempt at integration. Fink was already working on a lichen flora of North America, later restricted to the United States, and it is more than likely that he intended to structure the flora along the lines of his 1915 arrangement, but evidently that had not been worked out at the time of his sudden death in 1927. Consequently, when another of his assistants, Joyce Hedrick (1897–1980), undertook to complete and prepare the manuscript for publication—a labor of eight years—she had little option other than to employ Zahlbruckner’s system (Fink 1935). By this time Zahlbruckner had acquired further status with the publication of his *Catalogus Lichenum Universalis*, the first volume of which appeared in 1922; this and subsequent volumes quickly came to be relied on by lichen taxonomists worldwide, and the fact that the *Catalogus* was structured on his Engler and Prantl system further publicized the notion of autonomy.

### The triumph of integration

In the 1930s, however, several botanists made proposals for a truly natural system of lichen classification. Following an ill-conceived attempt by Wirsching (1931) to construct a system involving pycnidial anatomy, Frederic Clements, then attached to the Carnegie Institute, and Cornelius Shear (1865–1956), a Bessey-trained mycologist at the United States Department of Agriculture, produced an extensive, but uncritical, revision (1931) of the former’s 1909 *Genera*. Their 500–page volume was essentially a compilation

of data culled from published sources, and reviewers did not spare it: Sydow (1931, p. 418) described the authors' attempts at establishing synonymy as a "complete shambles" ("wüstes Durcheinander"), and Seaver (1932) damned their book as "the largest volume of misinformation, inconsistencies, and contradictions which the writer has ever encountered" (p. 262), though he did note "that the lichen genera have been interspersed with those of other fungi" (pp. 249–250). That interspersed involved assigning the several hundred genera recognized by Zahlbruckner (1926) to one Basidiomycete and 10 Ascomycete families.<sup>22</sup> Despite its dire reception, "Clements and Shear" went on to become—*faute de mieux*—a widely used work of reference and must be saluted for its commitment to integration.

In 1932 the Swedish mycologist John Nannfeldt (1904–1985) reported, in what was quickly recognized as a major contribution to fungal systematics (Fig. 7), that ascomata exhibit two ontogenetically distinct lines of development—these he termed ascohymental and ascolocular. Nannfeldt's study included discussion of a natural lichen system, which he proclaimed to be "*that of the fungal components*" (1932, p. 47).<sup>23</sup> Though his new categories were to prove less clear-cut than originally thought, Nannfeldt's work was the first in a distinguished and continuing Swedish commitment to the pursuit of integration. Elsewhere, however, conventional wisdom continued to prevail. The Swiss Friedrich Tobler (1879–1957) was recruited as an assistant by Wilhelm Zopf soon after the latter's 1899 move from Halle to Münster, where, according to Ulbricht (1957, p. (44)), Zopf significantly influenced the direction of Tobler's work. As mentioned earlier, Zopf differentiated between lichens and what he called "true fungi," a point of view unreservedly accepted by Tobler and consistently promoted by him on becoming

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STUDIEN ÜBER DIE MORPHOLOGIE UND  
SYSTEMATIK DER NICHT-LICHENISIERTEN  
INOPERCULATEN DISCOMYCETEN

VON

J. A. NANNFELDT

DER KÖNIGL. SOCIETÄT DER WISSENSCHAFTEN ZU UPPSALA  
MITGETEILT AM 5. FEBRUAR 1932

UPPSALA 1932  
ALMQVIST & WIKSELLS BOKTRYCKERI-A.-B.

Figure 7. Title page of John Nannfeldt *Studien über die Morphologie und Systematik der nicht-lichenisierten inoperculaten Discomyceten*, 1932.

professor of botany at the Dresden Technical Institute in 1924. In a paper devoted to lichen systematics Tobler (1933) made no reference to the work of Clements and Shear or Nannfeldt but clearly conveyed his—and no doubt many of his contemporaries'—thinking on the subject with the ringing declaration that "we ... stand by the enduring autonomy of the lichen group" (p. 176).<sup>24</sup>

Another Swiss, Eugen Thomas (1912–1986), did understand the significance of Nannfeldt's views and was the first to bring them to the attention of lichenologists. An assistant at the Confederate Technical Highschool in Zürich from 1937 to 1939, Thomas isolated and grew the components of nearly 20 lichen species, one of which he resynthesized. As



a consequence of that work, Thomas (1939) raised the question of how a lichen and its fungal component should be named—the algal partner being, presumably, assignable to a recognized taxon. He was familiar with Nannfeldt’s observation (1932, p. 44) that the discovery of lichens’ composite nature had left their fungal components nameless since each lichen binomial continued to designate the organism as a whole. Developing this point, Thomas (p. 169) first stated “like every other fungus, that occurring in a lichen requires a name under which it can be positioned in the natural system of fungi,” and then suggested (p. 170) that the requirement be met by adding the suffix “-myces” to the ‘generic names’ of lichens and putting their ‘specific names’ in the genitive”;<sup>25</sup> *Xanthoriomyces parietinae* was the example chosen to illustrate his proposal (p. 170).

Nannfeldt and Thomas’ concerns were slow to be addressed. Räsänen (1943) drew on the work of neither in his ambitious attempt to frame a new system based on those of Vainio and Zahlbruckner. Räsänen’s declared aim was “to focus the attention of the researcher on new standpoints that would lead to the development of a natural system” (p. 7);<sup>26</sup> a failure to present any really new perspective resulted in his elaborate effort being largely ignored. A similar fate befell the scheme advanced by Choisy (1945, 1949), which also relied on dated principles.

While most European botanists continued to believe in a class Lichenes, the North American commitment to integration remained firm. In a posthumously published entry on lichens for the *Encyclopedia Americana*, Frederic Clements (1947, p. 362) made plain the thinking of his country’s mycologists on the question of maintaining lichens as a distinct group. He described such a group as “highly artificial, containing representatives of two distinct classes of fungi” [“Ascomycetae” and

“Basidiomycetae”]... lichens have not arisen from a single point, as members or offshoots of one line of development... [i]n ascolichens the form of the sporocarp indicates the main places of origin: the *Verrucariaceae*, with perithecia, are *Pyrenomycetales*; the *Graphidaceae*, which show the hysterothecium, belong to the *Hysteriales*; the remaining families, *Caliciaceae*, *Collemaaceae*, *Parmeliaceae*, etc., belong to the *Pezizales*.” A comparable arrangement would soon be independently promoted by several Swedish lichenologists.

In July 1950 the Seventh International Botanical Congress was held, following a 15-year hiatus, in Stockholm. The participants included 20 lichenologists (Abbeyes 1952), 10 of whom delivered papers; that read by Rolf Santesson included the uncompromising statement “‘Lichen systematics’ based on algal characters is as unnatural as, e.g., a system of Uredinales based on characters from the host plants” and—drawing on the work of Nannfeldt (1932)—outlined a “scheme of the taxonomical position of the Lichenized ascomycetes” (Fig. 8). Santesson’s presentation was promptly supported by Tavares (1950, p. 7), but another participant, Fritz Mattick (1901–1984), based at the Berlin Botanical Garden and Museum, was almost as quick to voice opposition (1951, 96). Mattick had been a student at the Dresden Technical Institute in the mid-1920s when he attended Friedrich Tobler’s lectures and evidently took the latter’s conservatism entirely to heart: 20 years later he could describe Zahlbruckner’s system as grounded “on modern views” (“nach modernen Gesichtspunkte”; 1943, p. 1).

As the case for the “new systematics” was again being made by Santesson (1952, pp. 42–46), Mattick was at work on an assignment that would bring autonomy to renewed attention. In 1949 the publishers of Engler’s *Syllabus der Pflanzenfamilien* commissioned a new, 12th, edition under the editorship

54 The new systematics of lichenized fungi.

by

R. Santesson  
Stockholm 1950

It is remarkable that in most plant systems lichens are still treated as a separate class, sometimes named a form class, comparable with Fungi Imperfecti. Not even practical reasons can be stated for the preservation of such a lichen class. From a taxonomical point of view we have <sup>deal</sup> with lichenized fungi, not with lichens. The concept of lichen is a biological one. "Lichen systematics" based on algal characters is unnatural as, e.g., a system of Uredinales based on characters from the host plants.

The "anobolases" Ascolichenes and Eudolichenes must axiomatically be rejected. Corn is to be referred to Rhizoporceae and is probably to be included in some already existent fungus genus.

As stated by WANNFELDT (1932), lichenized ascomycetes are found in Ascoloculares as well as in Ascolymeniales. In ZÄHRGRIKNER's system members of these two groups have been <sup>X</sup> fungi, "Pycnolichenes" as well as "Piscolichenes" belong to Ascolymeniales. and are to be referred to the orders Sphaeriales and Lecanorales, respectively. (Even the latter comprises a number of non-lichenized fungi.) The following is a very preliminary scheme of the taxonomical position of the lichenized ascomycetes:

Ascoloculares.

Pseudosphaeriales. Pleosporaceae (e.g. Arthopyrenia), "Dothideales" (e.g. Dermatisma Almq.), Hyeteriaceae (e.g. Opegrapha), Arthoniaceae, Roccellaceae.

Hemisphaeriales. Microthelopsis, and some others, are probably referable to this order.

Ascolymeniales.

Sphaeriales. Verrucariaceae, Pyrenulaceae (emend. excl. Forkin, Arthopyrenia a.o.), etc.

Lecanorales. Graphidaceae (emend. excl. Opegrapha a.o.) Thelotremaceae, Asterothyriaceae (emend) Ogalactaceae, Lecidaceae, Teloschistaceae, and others.

Caliciales? Probably forming a separate order, but must be studied more carefully.

Most of the lichen families, as hitherto delimited, should be revised, and a number of them are to be rejected. E.g.: Coenogoniaceae is to be included in Graphidaceae, and Striguladene in Verrucariaceae, as <sup>gonidial</sup> united, e.g. in the families Graphidaceae and Pyrenulaceae. Most lichenized...

- 2 -

families" only. Pyrenulaceae (emend) is not characterized by its gonidia but mainly by its spore type (spore cells lentiform), like that of Graphidaceae and Thelotremaceae. Pycnolicheniaceae and Dermatocarpaceae should be included in Verrucariaceae, as they are distinguished by a better developed thallus only. Byssolecaniaceae is to be referred to Lecidaceae (their ecological differences of less importance).

The delimitations of lichen genera are now very often unnatural. "gonidial genera" such as Phylloporina, Paraphysothelia, Allothoria, Arthoniopsis, Fungiopsis, Lecanopsis, etc., must be rejected. Most genera of crustaceous lichens are very schematically based on the spore separation only. For practical reasons we have to accept some of them provisionally until they have been treated monographically, but we must always try to find the natural delimitation of the genera. E.g.: Macoma (sp. HEDLUND 1892) seems to be a good autonomous genus. Certain species of Bacidia and of Logpidium (Sporopodium) have to be united in the genus Tapellaria. Species with spores only transversally separated as well as such with muriform spores must be included in the genera Trichothelium and Tricharia Ré.

Figure 8. Précis of Rolf Santesson's paper as circulated at the 7th International Botanical Congress; it differs in some respects from that subsequently published (Santesson 1953).

of Hans Melchior (1894–1984) and Erich Werdermann (1892–1959), both attached to the Berlin Botanic Garden; they, perhaps understandably, delegated responsibility for the lichens to their colleague Mattick. In a foreword to the first volume (1954), the editors stated that the advances made in all areas of systematic botany since the work's previous appearance (1936) had necessitated the new edition. Mattick, however, evidently felt that no significant advances had been made in systematic lichenology during that period: his survey includes the statement (1954, p. 208) "the system accepted here is that established by Zahlbruckner (1907) in conformity with the investigations of Reinke (1894–1896)."<sup>27</sup>

Another flawed classificatory scheme was published about this time by Rafaele Ciferri (1897–1964) and Rugiero Tomaselli (1920–1982), both working at the University of Pavia. Having argued, to their own satisfaction at least (1952, p. 26), that lichens and unlichenized fungi could not be accommodated in the same system, Ciferri and Tomaselli introduced — autonomy redux — "an independent systematic of the genera of fungi found in Lichens" (p. 81). Those authors gave effect to their misconception by reviving Eugen Thomas' suggestion that a lichen fungus be designated by appending "myces" to the generic name of the lichen concerned; they thus concocted over 150 new names, which included the honorific *Mattickiomyces* and *Santessoniomyces*. Ciferri and Tomaselli next decided that an amendment to the International Code of Botanical Nomenclature was called for in light of their publication. The Stockholm Section on Nomenclature had accepted "that the name given to a lichen should apply to its fungal component" (Rogers 1955)—leaving, as a consequence, the composite organism nameless—and Ciferri and Tomaselli now proposed that the Eighth International

Congress, scheduled for July 1954 in Paris, agree "to modify the present nomenclatural precept and to accept the newly proposed systematics and the respective nomenclature of the fungal components as distinct from the lichenic complex" (1953, p. 196). This move provoked Santesson into publishing a swingeing rejection of Ciferri and Tomaselli's proposal, which he alleged was intended "to make fun of lichenology" (1954a, p. 148); the bruised authors issued a dignified, if somewhat hollow, response (1954). At the July meeting in Paris, Ciferri and Tomaselli's motion to amend Article 76 was rejected (Pichon and Stafleu 1955, p. 158), and a paper by Santesson (1954b) on the systematics of lichen fungi received only a lukewarm reception (Anonymous 1956, pp. 5–6)—possibly because it added little to what had been said four years previously.

The American Mason Hale (1928–1990) took the next step towards integration. Aware that "[t]he assimilation of lichens into a fungal classification... is not as easy as one might expect" (1961, p. 99), Hale soldiered on to produce what he called "a speculative integration" (pp. 100–102) derived to an extent from the phylogenetic diagrams of Luttrell (1955, pp. 513–514).<sup>28</sup> The publication of several integrative systems by lichenologists in the early 1970s (Henssen and Jahns 1973, pp. 263–265; Hale 1974, pp. 150–154; Poelt 1974, pp. 605–630) confirmed a general awareness that the time had come to jettison the category "Lichenes," which served only to impede the work of establishing relationships between lichenized and other fungi.<sup>29</sup> The term made its last official appearance in Article 13 of the Leningrad International Code of Botanical Nomenclature (Stafleu et al. 1978, p. 11). There the starting dates are laid down for groups ranging from "(a) Spermatophyta and Pteridophyta" to "(h) Myxomycetes"; "Lichenes" formed group (d), a proposition deemed obsolete at the 1977 International



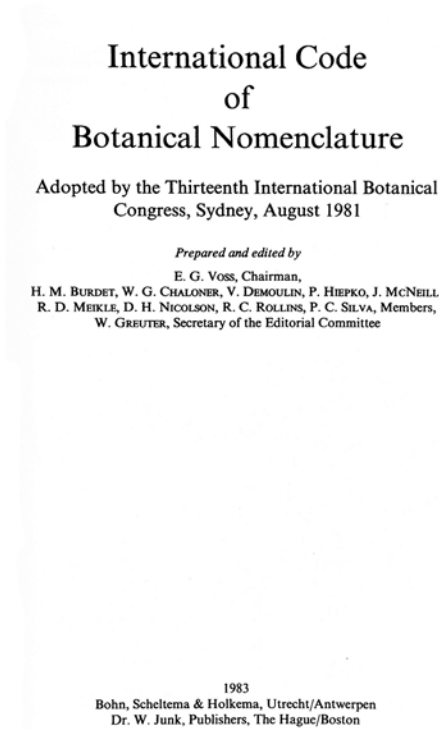


Figure 9. Title page of Edward Voss et al. *International Code of Botanical Nomenclature Adopted by the Thirteenth International Botanical Congress*, 1983.

Mycological Congress in Tampa, Florida. Accordingly, a decision was taken there to table a proposal at the 1981 International Botanical Congress in Sydney that would have the (d) entry become “Fungi (including lichen-forming fungi) ...” (Warmello 1979, p. 430); that proposal — amended to read “Fungi (including Myxomycetes and lichen-forming fungi ...” — was in due course adopted (Voss et al. 1983, p. 12; Fig. 9).

The illusion of lichen autonomy had now been laid to rest, as three years later would be Fritz Mattick, its last protagonist.

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I have also gratefully to record many rewarding visits to the Biodiversity Heritage Library and other online sites.

The illustrations were once again prepared by Mr. T. Keady, Galway, to whom my best thanks are due.

#### Notes

1. They were known to Berkeley (1857), who noted Payer’s work (p. 570), and may have influenced the organization of his “Lichenales” (pp. 372, 389).
2. “... dass die Flechten sammt und sonders keine selbständigen Pflanzen seien, sondern Pilze aus der Abtheilung der Ascomyceten, denen ... Algen ... als Nährpflanzen dienen.”
3. “Betrachtet man z.B. in einem Gebirgswalde die reiche Flechten-Vegetation, wie da ihre charakteristischen, heiteren, Luft und Licht liebenden Gestalten in unendlicher Mannigfaltigkeit und Anzahl, langlebend die Bäume vom Fuss bis zum Wipfel, die Felsen vom Thal bis zu den höchsten, in die Wolken sich tauchenden Gipfel bedeckt, vergleicht dann mit diesem Bilde die Vegetation der Pilze, dieser düsteren, einsamen, verdächtigen, meist schnell vergänglichen Gesellen des Schattens und der Feuchtigkeit, des Todes und der Verwesung: und denkt sich nun beide unter eine Klasse des Pflanzenreiches vereinigt” ... “der gelehrte Pflanzen-Anatom hinter seinem Mikroskop die Nothwendigkeit jener Vereinigung der botanischen Welt verkündet.”
4. The German botanist Anton de Bary (1831–1888), professor of botany at the University of Halle and then Strasbourg, had proposed alternative interpretations of the chlorophyllous cells found in lichens, the second of which equated them with algae subject to fungal parasitism (Bary 1866, p. 291).
5. “Im Interesse der Sache halte ich es hier nöthig, eine mir mündlich von Herrn Prof. Schwendener im Sommer 1867 gemachte Mittheilung über diese Frage zu erwähnen; ihm ist es gelungen,

- direct zu beobachten, dass die Hyphen der Gallertflechten von aussen her in die betreffenden Gallertalgen eindringen, also Parasiten im Sinne der zweiten Vermuthung de Bary's sind... Ich glaube nicht zu irren, wenn ich annehme, dass Prof. Schwendener geneigt ist, diese Ansicht auf alle Flechten zu übertragen."
6. "... welche den Flechten fortan ihre systematische Stellung unter den Ascomyceten sichert."
  7. Arthur Minks (1846–1908), a German physician in practice at Szezecin (Stettin), for example, persuaded himself that the filaments of lichen tissue are distinguishable from fungal hyphae because the former produce minute, green, internal bodies—"microgonidia"—that, on release, become typical, chlorophyllous, thalline cells. Though Minks' papers (1878) came in for some harsh criticism, two prominent systematists did not hesitate when presented with the alternative of deluding themselves or adjusting their mindset: Tuckerman (1879, p. 256) lauded "the sufficient microscope and the patient skill of Dr. Minks," while his papers constituted a "splendide ouvrage" for Müller (1881, p. 372). The illusory microgonidia remained a comfort to some until late in the century.
  8. "... die Flechten, oder besser Flechtenpilze nichts anderes sind als Ascomyceten."
  9. "Et même au point de vue physiologique, la différence n'est certes pas énorme entre un Champignon comme l'Accidium de l'Épinevinette, qui tire ses aliments organiques des cellules vertes de la feuille dans laquelle il niche, et le Lichen qui se les fait fournir par les cellules vertes de l'Algue qu'il héberge. En résumé, *les Lichens ne sont qu'une subdivision biologique des Champignons*"; "... 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."
  10. These categories appear to have been first employed by Masee (1887, p. 309); the "Gasterolichenes" of his paper's title was quickly shown to be a spurious taxon (Fischer 1890).
  11. "... *les Lichens ne forment pas un groupe systématique distinct.*"
  12. The companion volume was not published.
  13. "Da sie bisher nur in die unhaltbaren Flechtensysteme gebracht sind, während die Aufgabe, sie in das Pilzsystem einzureihen, ihrer Lösung noch harrt, müssen sie hier gesondert angeführt werden."
  14. "... durch Kauf, Tausch und Selbstsammeln."
  15. "... während es für die Pertusarien, Lecanoreen, Pannarien, Umbilicarien, Peltideaceen, Parmeliaceen, Usneaceen, Cladoniaceen, Sphaerophoreen, Epebeen und Lichineen zur Feststellung ihrer Verwandtschaft mit typischen Ascomyceten an jedem Anhaltspunkte fehlt"... "Für mich unterliegt es keinem Zweifel, dass die Flechten ihre Phylogenie nicht als Pilze, sondern als Consortien durchgemacht haben." For particulars of the term "consortium," see Mitchell (2014, p. 16, note 9).
  16. "Während die sogenannte moderne Botanik gar nicht emphatisch genug verkündigen kann, dass die Flechten echte Pilze sind, habe ich mich... ganz auf den Standpunkt des alten Acharius gestellt."
  17. "... denn sie bleiben eben immer nur Pilze, die auf Algen leben."
  18. "Neuerdings ist jedoch Reinke, entschieden mit Recht, dafür eingetreten, dass die Flechten als eigenes Reich behandelt werden müssen trotz ihrer zweifachen Natur."
  19. "Nach der Anschauung des Referenten hat Verf. das Richtige getroffen und für den Ausbau eines natürlichen Flechtensystems (im Sinne Reinke's) einen wichtigen Schritt nach vorwärts gethan."
  20. Some few Europeans, among them Richard von Wettstein (1863–1931), professor of botany at the University of Vienna, understood however that Zahlbruckner's system represented no more than an interim solution. Wettstein made quite clear that, ideally, lichens should be assigned their due position in the fungal system (1901–1908, 1:182), but he had to concede that such a course was not then possible. Reinke (1908, p. 98) on the other hand—sticking to his guns—complained that Zahlbruckner had gone too far because in Reinke's opinion lichens "must never be treated as an adjunct to the ascomycetes" ("dürfen nicht etwa als ein Anhängsel der Schlauchpilze behandelt werden").
  21. Zahlbruckner (1926) made minor revisions to his system, and Watson (1929) added to these.
  22. These families appear in the sequence Verrucariaceae, Mycoporaceae, Graphidaceae, Caliciaceae, Collemaceae, Cladoniaceae, Physciaceae, Peltigeraceae, Lecideaceae, Parmeliaceae (pp. 25–27) and Theleporaceae (p. 28).
  23. "*Das System der Flechten ist dasjenige ihrer Pilzkomponenten*"; Nannfeldt's pronouncement would be ably developed by his student Rolf Santesson (1916–2013).
  24. "Wir halten... an der unerschütterten Selbständigkeit der Gruppe Flechten im System fest."

25. "Gleich jedem anderen Pilz beansprucht der Flechtenpilz einen Namen, unter dem er in das natürliche Pilzsystem einzureihen ist" ... "die 'Gattungsnamen' der Flechten mit der Endsilbe '-myces' zu versehen und die 'Artnamen' der Flechten in den Genetiv zu setzen."
26. "... die Aufmerksamkeit der Forscher auf neue Gesichtspunkte zu lenken, auf welchen dann das natürliche System künftig gebaut werden kann."
27. "Das hier zugrunde gelegte System ist von Zahlbruckner (1907) im Anschluß an die Untersuchungen von Reinke (1894–96) aufgestellt." Mattick was severely taken to task by Henssen and Jahns (1973, p. 254) for having used the influential *Syllabus* to promote antiquated concepts.
28. Both Hale's outline and its revision (1967, pp. 148–154) were evidently unknown to the German mycologist Hanns Kreisel (1931–) when he attempted a merger of lichenized and other fungi, "probably for the first time in a German textbook" ("wohl erstmalig in einem deutschsprachigen Lehrbuch"; Kreisel 1969, p. 6). The author's regrettable failure to familiarize himself with the work of contemporary lichenologists resulted in their ignoring his text — apart that is from Mattick (1969), who used the opportunity of a review to recite his familiar separatist arguments.
29. The extent to which those relationships have since been established is summarized by Beck and Peršoh (2009, pp. 18–21).

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