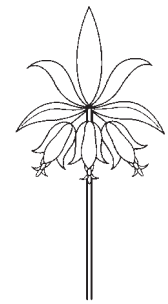
HUNTIA

A Journal of Botanical History



VOLUME 14 NUMBER 2
2011

Hunt Institute for Botanical Documentation
Carnegie Mellon University

Pittsburgh

The Hunt Institute for Botanical Documentation, a research division of Carnegie Mellon University, specializes in the history of botany and all aspects of plant science and serves the international scientific community through research and documentation. To this end, the Institute acquires and maintains authoritative collections of books, plant images, manuscripts, portraits and data files, and provides publications and other modes of information service. The Institute meets the reference needs of botanists, biologists, historians, conservationists, librarians, bibliographers and the public at large, especially those concerned with any aspect of the North American flora.

Huntia publishes articles on all aspects of the history of botany, including exploration, art, literature, biography, iconography and bibliography. The journal is published irregularly in one or more numbers per volume of approximately 200 pages by the Hunt Institute for Botanical Documentation. External contributions to *Huntia* are welcomed. Page charges have been eliminated. All manuscripts are subject to external peer review. Before submitting manuscripts for consideration, please review the "Guidelines for Contributors" on our Web site. Direct editorial correspondence to the Editor. Send books for announcement or review to the Book Reviews and Announcements Editor. The subscription rate is $60.00 per volume. Send orders for subscriptions and back issues to the Institute. Hunt Institute Associates may elect to receive *Huntia* as a benefit of membership; contact the Institute for more information.

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
Web site: http://huntbot.andrew.cmu.edu/HIBD/Publications/HI-Pubs/Pub-Huntia.shtml

Printed and bound by RR Donnelley, Hoechstetter Plant, Pittsburgh, Pennsylvania

ISSN 0073-4071

HUNTIA 14(2) 2011

"A somewhat esoteric pursuit": The course of lichenological inquiry from 1700 to 1950

M. E. Mitchell

Abstract

The practice of describing a diversity of non-vascular organisms as lichens came to an end late in the 17th century when *Lichen* was established as a genus to accommodate morphologically distinct thalli with concave fruit-bodies. The development of microscopy showed those bodies to have minute, simple or septate components, the function of which was variously interpreted. Consensus was also lacking as to the systematic position of lichens, with some authors believing them to constitute a distinct group and others assigning them to the algae or fungi. By the late 18th century, the number and diversity of lichen species described had become such that they could no longer reasonably be assigned to a single genus, and the task of delimiting new genera began. In the second decade of the 19th century, an assertion that lichens constitute an autonomous category comparable to algae and bryophytes became accepted as fact—a misconception that seriously hindered attempts to investigate their nutrition and systematic status. Work undertaken during the 1820s and 1830s in connection with the dyestuffs long sourced from lichens gave rise to a branch of chemical research that has, with few interruptions, prospered to the present day. With the slowly increasing availability of improved microscopes in the decades around mid-century, important anatomical and taxonomic advances were reported. Thallus physiology was little understood, however, and so it remained until the late 1860s when the proposition was advanced that lichens are the product of an association between a microalga and a microfungus. Initially, few botanists were prepared to endorse so unprecedented an alliance, but the fact that those who did were men of standing forced others to assess the basis of their scepticism. There remained, nonetheless, a core of uncompromising systematists who conducted a bitter and futile campaign in print against the new reading of lichen biology. Contrary to what might have been expected, there were no early attempts to explore the nature of the relationship between the thalline constituents: despite the widespread interest that lichens were now attracting, those seriously committed to their study remained few in number and, further, did not demonstrate any particular enthusiasm for experimental investigation. Some attempts were made to achieve artificial synthesis and when—with what can then only have been a rare measure of good luck—one of these was successful to the point of fruit-body production, the case for duality was finally made. Sporadic reports touching on gas exchange and water relations appeared from the 1870s to 1890s, but, in essence, knowledge of lichen physiology had advanced only minimally by the end of the century. Traditional floristics acquired a new dimension about this time with the emergence in North America of an ecological approach to field studies, an innovation soon adopted and further developed by European botanists. Important advances in lichen chemistry were reported, notably by German workers, in the years from 1890 to 1910. As was the case with biological science in general, lichenology marked time during World War I. The 1920s were charcterized by the publication of several authoritative reference works; the limited amount of original research undertaken related almost entirely to ecology and some aspects of physiology. This pattern—supplemented by taxonomy's increasing reliance on microchemical procedures—continued until 1939 when, once again, research came effectively to a halt. During the postwar years to 1950, lichenology began slowly to re-occupy its outposts, and so the ground was prepared for the discipline's striking progress over the following decades.

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

Introduction

The enduring notion of an equivalence between *Aspicilia esculenta* and the biblical manna that sustained the Israelites would, were it tenable, put the earliest datable link between humans and lichens at about 1300 B.C. That no such equivalence can plausibly be established emerges from a review of the literature by Crum (1993), who failed to find

any convincing data to support the contention; in his opinion (p. 295) "[t]he suggestion that unattached desert lichens may have been available to the Israelites as a miracle food is, in fact, no more than a pious conceit of Victorian times." The first real evidence of lichens having been used by humans actually dates from not much later than the Book of Exodus — material of *Pseudevernia furfuracea* is known to have been employed in the mummification of a 19th-dynasty pharaoh (Aufderheide 2003, p. 252; Lucas and Harris 1962, p. 312). Though lichens may well have had other contemporaneous uses, nothing was reported in this regard until about 1,000 years later; that Hippocrates recommended a lichen for the treatment of "uterine trouble" has been stated by Dugan (2008, p. 54), but the Hippocratic Corpus contains no such recommendation.

The earliest recorded description of a lichen dates from the 4th century B.C. when the Greek author Theophrastus (Amigues translation, 2003, p. 23) noted the occurrence on oak of a grey, pendulous growth that may reasonably be assigned to the genus *Usnea*; he called this epiphyte "phascon" not "lichen," which does, however, occur elsewhere in his writings with the specific meaning of an animal skin condition (Strömberg 1937, p. 192). The former term did not survive as such, and when the latter is next met with, in the 1st century A.D., it variously designates a bark exudate, a dermatosis and some plants of uncertain identity: in his *Natural History*, Pliny the Elder (A.D. 23–79) reported the occurrence "on wild and on cultivated plum trees" of "a gummy substance called lichen by the Greeks" (Jones translation, 1961, p. 505), but later applied the term to "a disfiguring … disease" for which he listed a number of treatments, and then stated "the plant lichen however is considered a better remedy than all these, a fact which has given the plant its name" (Jones translation, 1966, p. 281), though it is clear that the description he goes on to provide does not relate to a true lichen. In fact, when Pliny mentioned organisms that can with reasonable confidence be identified as lichens (Rackham translation, 1960, p. 77), he referred to them as moss ("sphagnos"). The Greek physician Dioscorides, Pliny's contemporary, was no more precise: "Lichen, that which grows upon rocks, but some call it Bryon, is a moss sticking to moist rocks. This being laid on doth … heal Lichenas" (Gunther edition, 1934, p. 444), while his account of "Bryon" begins "Muscus, but of somme it is called Splanchnon. Being found upon trees, as the Cedars, the white Poplars or the oakes … Of it that which smells sweetest & is white is the best" (p. 20).

It is evident then that, in antiquity, the term "lichen" was used indiscriminately for what came to be called cryptogams, and no serious attempt to differentiate between hepatics, lichens and mosses was made over the following 1,600 years. Indeed, the general European familiarity with lichens proper during much of this time was so limited that Fischer (1929) could document an awareness of no more than three (pp. 277, 285, 287), and only that described and illustrated by Anonymous (1485, cap. cccxiiii) can be identified — as *Lobaria pulmonaria* — with any confidence. In the 1530s, commentaries on materia medica published for the use of apothecaries and physicians underwent a transformation with the commissioning of naturalistic illustrations to replace the often primitive figures that had long been the norm. The earliest such herbal was the celebrated work compiled by Otto Brunfels (1488–1534); in this he sought "to identify his plants with those of Dioscorides" (Blunt and Raphael 1979, p. 120), a venture that led him to equate the latter's "lichen" with *Marchantia*, as Brunfels' text and corresponding figure clearly convey (1530, pp. clxxvii–clxxix). As a result of

Brunfels' equivalence, the term lichen became applied to liverworts, while lichens proper were combined with the mosses. Thus Turner (1538, unpaged) translated "lichen" as "Lyuer Wort," and Fuchs (1542) dealt with his hepatics under the heading "De Lichene" (p. 472). Where Fuchs mentioned a true lichen (p. 63), he opted for the early name Pulmonaria, which was subsequently employed by several botanists—notably Mattioli (1586, p. 783), who used it to categorize a number of figures referable to *Cetraria islandica*, *Cladonia* sp., *L. pulmonaria* and *Sticta* cf. *sylvatica*—but that trend did not continue, and over the following 100 years most new lichens were described as "Muscus." Not that there were many such: Krempelhuber (1867–1872, 1:19) put the total number of specific and infraspecific taxa recognized by the end of the 17th century at "circa 56."

Apart from their presumed therapeutic rôle, lichens remained the preserve of systematists, notably C. Bauhin (1623, p. 360–361), Parkinson (1640, pp. 1308–1314) and J. Bauhin (1650–1651, 2:759, 763–768), until the 1670s when they were first studied by other naturalists. In a paper on animal and vegetable dyes, Lister (1671, p. 2134) reported with regard to what can only have been *Cladonia* podetia that "[o]n the tops ... are certain red knots; these, upon the affusion of Lye [KOH], will strike a Purple, and stand"; this reaction involving rhodocladonic acid is familiar to all lichenologists, but only since it was again happened on some 200 years after Lister's original finding. Additionally, a close study of lichen morphology allowed Malpighi (1675–1679, pp. 63–64, pl. xxvii) to illustrate the structures now known as isidia and soralia on what was evidently a mixture of *Parmelia saxatilis* and *P. sulcata*. Malpighi also supplied the first closely observed illustration of lichen fruit-bodies, which he referred to as "fungi" (see Mitchell 2009); after a further period during which "lichen" continued to be applied to hepatics (e.g., Ray 1686–1704, 1:124–126), the structures depicted by Malpighi were eventually recognized as providing criteria for the designation of lichens proper.

Vistas and blind alleys

In 1683 Joseph Pitton de Tournefort (1656–1708) left his native Aix-en-Provence for Paris where he was appointed to a teaching post at the Jardin du Roi. There, building as he said on the work of his predecessors, Tournefort undertook a descriptive delimitation of plant genera. In the process, he combined hepatics and mosses in a single genus "*Muscus*" and reserved "*Lichen*" for "plants characterized by the production of basin- or cup-shaped fruit" (1694, 1:437–438); the latter genus runs to the names of just nine species, three of which—referable to *Anaptychia ciliaris*, *Cladonia* sp. and *Ramalina fraxinea*—are well illustrated. The favorable reception accorded his work in France decided Tournefort to make it available to an international readership by way of a Latin translation (1700; Fig. 1). He used that opportunity to make a number of revisions, one of which increased his lichen inventory fivefold (1:548–550).

Tournefort's innovation was a key contribution to the emergence of lichenology as an individual discipline, but there was a contender for his choice of generic name: the German Johann Dillenius (1684–1747) used "Lichenoides" ("lichen-like") in preference, while retaining "Lichen" for hepatics. When Dillenius produced the third edition of Ray's *Synopsis* (1724), "Lichenoides" appears as a category of "Musci," comprising 91 species categorized (p. 64) as "crustacea," "foliosa" and "caulifera." A work published five years later by Pier Micheli (1679–1737) ensured, however, that the rival generic names would not remain long in contention. Born in Florence to a family

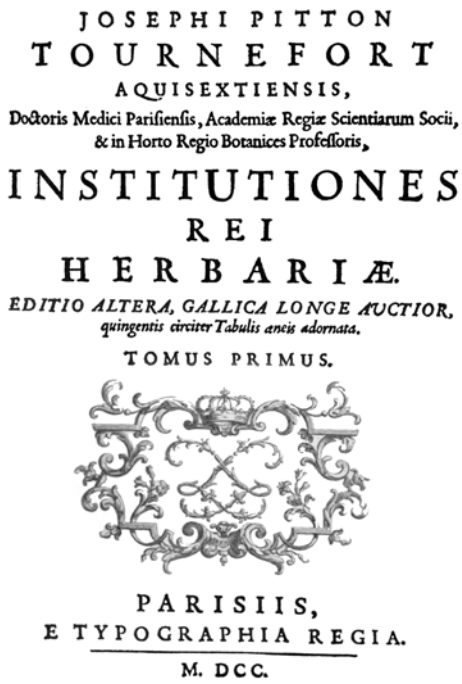

JOSEPHI PITTON
TOURNEFORT
AQUISEXTIENSIS,
Doctoris Medici Parisiensis, Academiæ Regiæ Scientiarum Socii,
& in Horto Regio Botanices Professoris,
INSTITUTIONES
REI
HERBARIÆ.
EDITIO ALTERA, GALLICA LONGE AUCTIOR,
quingentis circiter Tabulis æneis adornata.
TOMUS PRIMUS.
PARISIIS,
E TYPOGRAPHIA REGIA.
M. DCC.

Figure 1. Title page of Joseph Pitton de Tournefort *Institutiones Rei Herbariae*, 1700.


NOVA
PLANTARVM GENERA
IVXTA
TOVRNEFORTII METHODVM DISPOSITA
Quibus Plantæ MDCCCC recenſentur, ſcilicet fere MCCCC nondum obſervatæ, reliquæ ſuis ſedibus reſtitutæ; quarum vero figuram exhibere viſum fuit, eæ ad DL æneis Tabulis CVIII. graphice expreſſæ ſunt; Adnotationibus, atque Obſervationibus, præcipue Fungorum, Mucorum, affiniumque Plantarum ſationem, ortum, & incrementum ſpectantibus, interdum adiectis.
REGIAE CELSITVDINI
IOANNIS GASTONIS
MAGNI ETRVRIAE DVCIS.
AVCTORE
PETRO ANTONIO MICHELIO FLOR.
EIVSDEM R. C. BOTANICO.
FLORENTIÆ. MDCCXXVIIII.
Typis BERNARDI PAPERINII, Typographi R. C. MAGNÆ PRINCIPIS
VIDUÆ AB ETRURIA.
Propè Eccleſiam Sancti Apollinaris, ſub Signis Palladis, & Herculis.
SUPERIORUM PERMISSU.

Figure 2. Title page of Pier Antonio Micheli *Nova Plantarum Genera*, 1729.

of scant means, Micheli received little formal education. He did, on the other hand, have a particular aptitude for the study of plants, which he collected extensively, and in 1706 became assistant keeper of the Physic Garden at Pisa, with a subsequent appointment at Florence. Corrrespondents supplied him with a wide range of material, and this he described, together with his own collections, in a notable publication based on Tournefort's system (1729; Fig. 2). In that work Micheli raised awareness of the genus *Lichen* by extending its scope to almost 300 species distributed over 38 "orders," which he established to an extent on fruit-body morphology. Micheli was the first to investigate the anatomy of those bodies, having devised a method (p. 74) of preparing sections for microscopical study, an advance that allowed him to illustrate a variety of spore types; "flores" was his term for ascospores, and "receptacula florum" for ascomata.

Subsequently, Jussieu (1730) drew attention to the affinity betweeen fungi and lichens, which he described as showing "an almost identical method of producing their seed," and Neumann (1749–1755, 2(4):55–56) initiated the study of lichen chemistry by using alcohol to extract "resins" from *Lobaria pulmonaria*. However, those developments and the anatomical work of Micheli attracted little contemporary attention—it was not until the 1780s that the chemistry of lichens was further investigated and the microscope again employed to elucidate their anatomy. In the interim Dillenius published *Historia Muscorum* (1742), a work of prodigious industry that includes about 200 lichen descriptions, which he largely continued to accommodate

in "Lichenoides." The Dillenian perception of lichens as kin to bryophytes was not shared by Linnaeus (1753, 2:1140–1156), who assigned them almost exclusively to his order Algae, where they number less than a third of Micheli's total—Linnaeus never held lichens in particularly high regard. That grouping of lichens and algae did not go uncontested: Adanson (1763–1764, 2:6–7) transferred them to the fungi, Weis (1770, p. 12) queried whether certain algae might not be intrinsic to lichen thalli, and Hacquet (1777, p. 244) advanced the then idiosyncratic opinion that lichens, together with "molds, some filamentous organisms and fungi" do not belong in the plant kingdom. Meanwhile, the species count slowly grew with the appearance of regional floristic studies, mainly West European, among which may be mentioned that by Catharina Dörrien (1717–1795, see Viereck 2000) concerning the Nassau region (1777, pp. 295–303)—the earliest known feminine contribution to lichenology.

Fresh efforts to study the organic compounds produced by lichens were made by Georgi (1782), who succeeded in extracting what he termed "mucilages," "oils" and "resins" from five macrolichens. Micheli's sectioning procedure was taken up by Hagen (1782, p. viii), who evidently had difficulty interpreting his preparations. In the hands of a skilled microscopist, however, lichens soon began to reveal the basic features of their anatomy. A close study of sectioned *Anaptychia ciliaris* material enabled the Austrian physician Johann Hedwig (1730–1799) to include details and diagrams of lichen sexual and vegetative structures in a treatise on the reproduction of cryptogamic plants (1784); this work also contains the first mention of his finding that the cortex is underlain by "particles of clustered green parenchyma" (p. 122, n. 1), and an anatomical study of the structures that he termed (p. 160) "puncta floris mascula" (pycnidia). At heart a bryologist, Hedwig contributed little more to the study of lichens, though it is noteworthy that he regarded them as closely related to the fungi (see Mitchell 2007, p. 102).

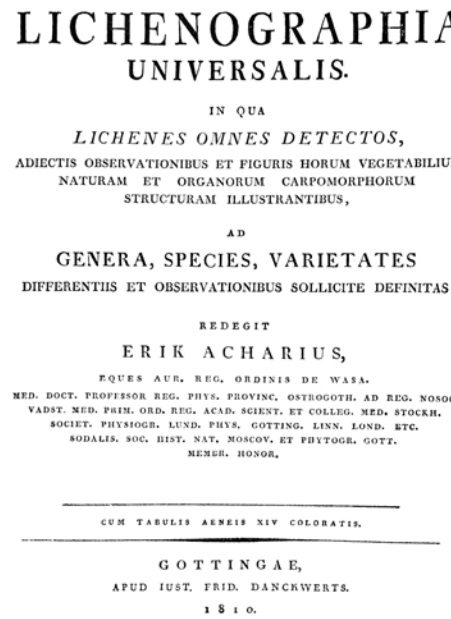
Those developments appear to have been virtually ignored by the few contemporary botanists whose interests ran to lichens. They concerned themselves almost exclusively with systematics and continued to accommodate new species in *Lichen*, though some recognized a need to create new genera: for example, *Umbilicaria* introduced by Hoffmann (1790–1801, 1:8), *Baeomyces*, *Calicium* and *Sphaerophorus* by Persoon (1794, pp. 19, 20, 23) and *Verrucaria* by Schrader (1794, p. 108). The status of those names was somewhat reduced, at least in the short term, by the Swedish lichenologist Erik Acharius (1757–1819), a Lund University medical graduate and longtime practitioner in Vadstena, Östergötland. Initially, Acharius (1799) followed his teacher Linnaeus in employing the single genus *Lichen*, though taking the step of grouping the species he treated into categories reflecting their relationships. His procedure was to organize the genus into families—crustose, foliose and fruticose—and further divide these, on the basis of fruit morphology, into 28 tribes, almost half of which received the names proposed for genera by Hoffmann, Persoon, Schrader and others. Subsequently, Acharius (1803) made the old, collective genus *Lichen* redundant by according generic status to most of his tribal names, an advance fundamental to the emergence of lichenology as an independent discipline. He further assisted in that regard by creating a terminology, still largely current, for the morphological features characteristic of lichens.

Those publications gave a significant stimulus to floristic activity in Europe and beyond; data relating to extra-European collections made during the late 18th and early

19th century by colonists, explorers and traders are documented for Australasia (Galloway 1985a), India (Awasthi 2000, pp. 1–2), Japan (Ikoma 1983, pp. 1–2), North America (Fink 1904, pp. 17–22), South Africa (Doidge 1950, pp. 18–28) and South America (Marcelli and Seaward 1998, *passim*). Such of the new material as reached Acharius was described in *Lichenographia Universalis* (1810; Fig. 3), a masterly survey of the world's then known species. That work won Acharius authoritative status as a systematist and simultaneously attracted widespread, though uncritical, acceptance of his view (p. 14) that lichens are "quite distinct from algae, hepatics and fungi," a circumstance to which the constructive misrepresentation of their constitution over the following 50 years is directly attributable; as has been observed in another context, a departure "whether felicitous in its consequences or otherwise, made by a man of genius will by and by be taken up and carried forward by the generations of his disciples and imitators" (Greene 1983, 2:933).

Three years before the *Lichenographia* appeared, Acharius' publisher had issued a work by Heinrich Link (1767–1851), then at the University of Rostock, that included an observation destined to compound the misconception introduced by Acharius; having remarked on the yellow medulla of *Pseudocyphellaria aurata*, which "careful examination shows to result from cells distributed in quantity through the white, filamentous tissue," Link (1807, p. 22) noted that corresponding cells occur in the soredia of that species and so proposed a propagative rôle for all such thalline cells. This notion did not attract any particular comment in the short term but would, when revived 20 years later, prove a serious hindrance to the study of lichen biology.

In addition to basic developments in systematics and anatomical investigation, the



LICHENOGRAPHIA
UNIVERSALIS.

IN QUA

LICHENES OMNES DETECTOS,

ADIECTIS OBSERVATIONIBUS ET FIGURIS HORUM VEGETABILIUM NATURAM ET ORGANORUM CARPOMORPHORUM STRUCTURAM ILLUSTRANTIBUS,

AD

GENERA, SPECIES, VARIETATES

DIFFERENTIIS ET OBSERVATIONIBUS SOLLICITE DEFINITAS

REDEGIT

ERIK ACHARIUS,

EQUES AUR. REG. ORDINIS DE WASA.
MED. DOCT. PROFESSOR REG. PHYS. PROVINC. OSTROGOTH. AD REG. NOSOC. VADST. MED. PRIM. ORD. REG. ACAD. SCIENT. ET COLLEG. MED. STOCKH. SOCIET. PHYSIOGR. LUND. PHYS. GOTTING. LINN. LOND. ETC. SODALIS. SOC. HIST. NAT. MOSCOV. ET PHYTOGR. GOTT. MEMBR. HONOR.

CUM TABULIS AENEIS XIV COLORATIS.

GOTTINGAE,
APUD IUST. FRID. DANCKWERTS.
1810.

Figure 3. Title page of Erik Acharius *Lichenographia Universalis*, 1810.

first decade of the 1800s brought a renewal of interest in the chemical constituents of thalli with the extraction by Berzelius (1808, p. 83) of what he termed "lichen starch" from *Cetraria islandica*. It was those three topics that received most of the meagre attention devoted to lichens in the years to mid-century. In systematics the first important advance was made by Eschweiler (1824, p. 14), who introduced the use of ascospore features as taxonomic criteria — his genus *Sclerophyton*, for example, is characterized by the production of "subclavate, 3–4 septate" spores. This innovation was endorsed by Georg Meyer (1782–1856), author of a wide-ranging survey of lichenology (1825) and subsequently professor of botany at the University of Göttingen, who recognized the diagnostic value of spore color (pp. 125–126), notably in connection with *Phaeographis* (as *Platygramma*). However, it is the case that some systematists chose not to engage with those developments;

descriptions in the widely used flora of Fries (1831), for instance, lack spore data. Their potential was not lost to view, however, and spore features were used to advantage by Fée (1824–1837, 2: *passim*) in the delimitation of exotic genera, while the diagnoses published by Notaris (1846) remain impressive for their detailed spore descriptions, which now included measurements (in "centimillimetri").

The study of lichen chemistry resumed towards the 1820s: Monkewitz (1817, p. 13) extracted chlorophyll as "phytochlorainon" from *Xanthoria parietina* with the latter term, abbreviated to "phytochlor," remaining in use for a good many years — e.g., Rabenhorst (1844–1848, 2(1):1) — as an alternative to Pelletier and Caventau's (1817) "chlorophyle." Braconnet (1825) reported the occurrence of calcium oxalate in a range of thalli, and Robiquet (1829) isolated several compounds from species then valued for their coloring properties. Over the following two decades the subject received a good deal of attention from workers in Austria, Britain, France, Germany, Ireland and the Netherlands: Heeren (1830, pp. 316–338) isolated erythrin from *Roccella tinctoria*; Guérin Varry introduced the term "lichenine" (Anonymous 1833, p. 102); Mulder (1838, pp. 600–601) separated lichenin into two components noting that one gives a blue reaction with iodine, closely followed by Dickie (1839, p. 166), who recorded "a substance which is tinged blue by iodine" in *Collema* and *Pertusaria* asci — 40 years were to pass before that substance was named "isolichenin" by Beilstein (1881–1883, 1:602); Kane (1840) reported on the composition of dyestuffs; Schunck (1842) isolated lecanoric acid, as lecanorin, from a mix of *Diploschistes*, *Lecanora* and *Pertusaria* material; Rochleder and Heldt (1843, p. 18) extracted usnic acid, as usnein, from *Ramalina* and *Usnea* spp.; Thomson (1844) introduced the term "parietin"; and Stenhouse (1849) isolated gyrophoric acid from *Lasallia pustulata*. A number of these publications were the subject of informed comment by Wiggers (1846, pp. 12–18).

The fact that lichen structure attracted no comparable level of attention until late in the same period is understandable given that microscopes remained optically flawed until the 1830s, and microscopical technique had progressed little since Hedwig's day. A glimpse of the constraints then prevailing is provided by Mohl (1863, p. 4): "the younger generation has no idea how matters stood at a time when interest in microscopy and possession of the requisite skills were a rarity. Though many students have use of a good microscope at present, there are still those who can remember when even a half-functional microscope was scarcely to be found in many German universities, and still less a person who would have known how to use it." Nevertheless Schärer (1820) managed to investigate the anatomy of species representing the principal lichen growth forms and, in addition to other features, was able to recognize vesicular (i.e., paraplectenchymatous) and filamentous tissue (see Mitchell 2005). Five years later the German physician Friederich Wallroth (1792–1857), then in practice at Nordhausen, published a flatulent text (1825) that requires mention for its introduction of three influential terms bearing on structure. Having identified a fundamental difference between gelatinous and other thalli as regards the relative position of their colored and colorless elements, Wallroth usefully described the unstratified arrangement seen in gelatinous material as "homoiomerous" and applied "heteromerous" to lichens whose green cells form a distinct, subcortical layer. The third anatomical term introduced by Wallroth — "gonidium" — also gained wide currency, but the rôle he attributed to the green cells so designated greatly hindered research on lichen physiology for well over 40 years: Wallroth (1825–1827, 1:40) had revived Link's

contention that because the green cells of soredia correspond to those within the parent thallus, all such cells were to be perceived as asexual propagules, an error unquestioningly accepted by virtually all botanists of that and the succeeding generation.

Meyer (1825) also contributed in the area of structure with a report (pp. 75–79) on fruit-body components, and in this connection attention may be drawn to his investigation of spore germination, which — given the reference to "filiform extensions" (pp. 175–176) — Meyer was evidently the first to observe. More than 20 years elapsed before the reproductive and vegetative anatomy of lichens was again investigated in detail. Friedrich Buhse (1821–1898), a Latvian naturalist, made a careful study of apothecial structure in about 20 species, the results of which included the observation (1846, p. 325) that paraphyses may be simple or branched. The same subject was reported on — at considerably greater length — in a doctoral dissertation presented three years later at the University of Göttingen by Gustav von Holle (1825–1893). Working with a single species, *Anaptychia ciliaris*, Holle carried out a thorough examination that enabled him to follow and illustrate apothecial development from late stages of the primordium onward; his work is noteworthy also for providing the first clear description of spore germination (1849, pp. 31–37).

Though still a predominantly European speciality, several contributions to lichenology had already appeared in North America when the Bostonian Edward Tuckerman (1817–1886) published the first detailed study devoted to east coast species (1847). Never one to embrace innovation, Tuckerman chose to omit spore characters, which made his work and that of Schaerer (1850) the last large-scale surveys prepared without use of the microscope. In the area of anatomy, that instrument was expertly employed by George Thwaites (1812–1882), though he failed to grasp the implications of what he saw. In a paper styling himself "Lecturer on Botany and Vegetable Physiology at the Bristol Medical School," Thwaites (1849) reported on a study of chlorophyllous cells from "a geat number of species" and concluded that those cells are not asexual propagules ("gemmae"), but "are in fact the *essential* part of the whole structure" (p. 220). In the case of *Collema* he found the cells to be "represented by the genus *Nostoc*," and by "*Pleurococcus*" in heteromerous material. Thwaites was not of course the first to have reported algal cells as components of lichen thalli, but no one had previously demonstrated the fact quite so explicitly. Since he also made several references to the green cells being surrounded by "anastomosing filaments," Thwaites was potentially in a position to controvert the notion of lichen autonomy but, in the event, did not question the prevailing orthodoxy — to the extent of providing an illustration "showing the arrangement of the cells and their attachment to the branched filaments." Thwaites' contemporaries also failed to grasp the implications of his research. The French mycologist Louis-René Tulasne (1815–1885), having promoted Acharius' dictum respecting autonomy (1852, p. 6), likewise convinced himself that the chlorophyllous cells of lichens originate from thalline filaments (p. 20). These failings apart, however, Tulasne's paper merits high commendation. He supplied copious anatomical data derived from a close study of the various growth forms and made available a multiplicity of observations concerning lichen conidia, which he tentatively labelled "spermaties" because of their possibly having a sexual function (see Mitchell 2006).

Around mid-century, then, a comprehensive system of generic description involving anatomical and morphological features was in place, floristic studies prospered, thallus structure had been reasonably well mapped

and a range of chemical constituents isolated, but lichen physiology was to remain a closed book for another 20 years.

Meanwhile features of the ascospore came increasingly to provide grist for the systematists' mill. Abramo Massalongo (1824–1860), a biology teacher in Verona, introduced more than 20 genera based primarily on such features in an impressive study of crustose lichens (1852); interestingly, he added conidial data for more than a quarter of the 80 genera surveyed in a further publication (1853; Fig. 4). This emphasis on the taxonomic importance of spore characters was quickly accepted by Gustav Koerber (1817–1885), professor of botany at the University of Breslau (now Wrocław), and used to effect in his new system of classification (1855). This comprised 24 families arranged in a series beginning with what he considered the "most advanced" thalli, exemplified by the Usneaceae, and continuing to his Lichineae. Also in the 1850s, William Nylander (1822–1899)—then in the process of quitting his native Finland for Paris, where space had been made available to him at the Museum of Natural History—began the single-minded work that would make his the dominant name in lichen taxonomy for the remainder of the century. Nylander was not, however, the most engaging of men: in a letter of 5 September 1858, at which time Nylander was aged 36, an acquaintance described him as "certainly not without ability, but such a porcupine and so cantankerous that nobody could get on with him" (Toni 1933, p. 55, n.). He was also a decidedly self-opinionated person and always ready to criticize those who did not see eye to eye with him. Having published his own system (1854) based on a hypothetical progression from the alga-like *Ephebe* to genera such as *Opegrapha* with evident fungal affinity, and making comparatively little use of spore characters, Nylander (1857, p. 252) saw fit to mock Koerber and Massalongo for

MEMORIE LICHENOGRAFICHE

CON UN' APPENDICE

ALLE

RICERCHE SULL' AUTONOMIA

DEI LICHENI CROSTOSI

DEL

D. A. PROF. MASSALONGO.

VERONA

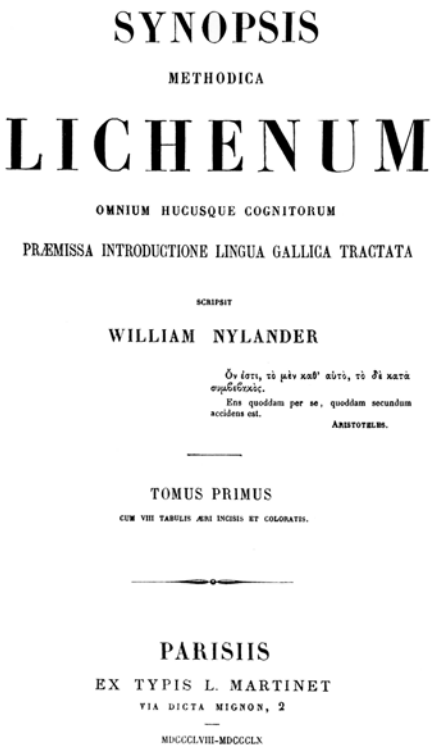
A spese di H. F. Münster

1853.

Figure 4. Title page of Abramo Massalongo *Memorie Lichenografiche*, 1853.

their work on delimiting genera and accuse them of introducing "minuscule, tiresome and repellent categories." Though both systems had their supporters (see Bentzel-Sternau 1859), that of Nylander became the more widely accepted; it gained currency with the publication of the first volume of his *Synopsis Methodica Lichenum* (1858–1869; Fig. 5), while the death of Massalongo in 1860, aged 36, and Koerber's limited taxonomic involvement after 1865 resulted in most of their genera being dropped—though not permanently, as time would prove.

Nylander's name became even more familiar to systematists when he reported on the use of reagents to elicit color reactions. Dickie's observation that the ascal tissue of some lichens


SYNOPSIS

METHODICA

LICHENUM

OMNIUM HUCUSQUE COGNITORUM

PRÆMISSA INTRODUCTIONE LINGUA GALLICA TRACTATA

SCRIPSIT

WILLIAM NYLANDER

Ὄν ἐστι, τὸ μὲν καθ' αὑτό, τὸ δὲ κατὰ συμβεβηκός.
Ens quoddam per se, quoddam secundum accidens est.
ARISTOTELES.

TOMUS PRIMUS

CUM VIII TABULIS ÆRI INCISIS ET COLORATIS.

PARISIIS

EX TYPIS L. MARTINET

VIA DICTA MIGNON, 2

MDCCCLVIII-MDCCCLX

Figure 5. Title page of William Nylander *Synopsis Methodica Lichenum*, 1858–1869.

turns blue when irrigated with an aqueous iodine solution had attracted no particular attention, but in the 1850s the taxonomic potential of the reaction was understood and promoted by Nylander (1853, pp. 153, 161–163; 1858–1869, 1:25–26). That development did not go unopposed: Fries (1861, p. 4) considered "reactions observed with the aid of iodine misleading and unreliable," a statement that evoked a derisive response from Nylander (1865), who, at the same time, provided the first extended account of iodine's use as a lichen reagent. That account was quickly followed by two seminal papers (Nylander 1866a; 1866b) detailing the use of $Ca(OCl)_2$ and KOH for the discrimination of species on the basis of color reactions speculatively linked to particular thalline products. As remarked by Vitikainen (2001, p. 263), "the 'spot test' method was launched"; it came too late for most of the 1860s floras but was used by Branth and Rostrup (1869).

Revolutionary developments

Nylander well recognized that gelatinous lichens display a clear affinity with algae, as the term was then understood, but he was not prepared to entertain a claim by the German physician Hermann Itzigsohn (1814–1879) that the chlorophyllous cells of *Collema* are "identical with *Nostoc*" (1854, col. 80). The Swiss botanist Simon Schwendener (1829–1919), working at the University of Munich, proved equally unreceptive, at least initially. In the second of his extensive reports on lichen structure (1860, 1863, 1868), Schwendener realized that some of the chlorophyllous cells he had seen were altogether comparable to "the lower algae" but chose to account for this by supposing "that here Nature has brought a part of algal life into being for a second time" (1863, p. 135). In a further paper, Itzigsohn (1863) drew "the attention not alone of lichenologists but also phycologists" to the filamentous lichen *Ephebe lanata* "because it has a very close, but far from obvious, connection and relationship with *Sirosiphon*, *Scytonema*, *Chroococcus*, *Gloeocapsa* etc." At this time the German mycologist Anton de Bary (1831–1888), then professor of botany at the University of Freiburg, was preparing his celebrated textbook (1866; Fig. 6). De Bary had come to regard the chlorophyllous cells of gelatinous lichens as actual algae and suggested two explanations (p. 291): either *Nostoc* and *Stigonema* represent no more than stages in the development of mature lichens, or those organisms develop into lichens as a result of infiltration by fungal hyphae. Two of de Bary's former students, the Russian Andrei Famintzin

MORPHOLOGIE UND PHYSIOLOGIE

DER

PILZE, FLECHTEN UND MYXOMYCETEN.

VON

DR. A. DE BARY,

PROFESSOR AN DER UNIVERSITÄT FREIBURG I. B.

MIT 101 HOLZSCHNITTEN UND EINER KUPFERTAFEL

LEIPZIG

VERLAG VON WILHELM ENGELMANN.

1866.

Figure 6. Title page of Anton de Bary *Morphologie und Physiologie der Pilze, Flechten und Myxomyceten*, 1866.

Protokoll

der

botanischen Sektion.

Sitzung: Dienstag den 10. September 1867.
Morgens 8 Uhr.

Die Sektion constituirt sich, indem sie zum Präsidenten Herrn Prof. Heer aus Zürich, zum Sekretär Herrn Rothenbach, Lehrer in Basel, wählt.

1. Herr Prof. Schwendener aus Basel begründet in einem längeren Vortrag, Bezug nehmend auf seine früheren Publikationen über den Bau des Flechtenthallus, die ihm in Folge neuer Untersuchungen zur Ueberzeugung gewordene Ansicht, dass bei einer ganzen Gruppe von Flechten Gonidien und Fasern nicht in einem genetischen Zusammenhange stehen, sondern dass letztere als Wucherungen von Pilzfaden auf Algenformen zu betrachten seien. Es wird an der Hand tabellarischer Abbildungen und kleinerer Farbenskizzen nachgewiesen:

1) dass der Flechtengattung Ephebe: eine Stigonema,
2) der Ephebella Hegetschweilerii: eine Scytonema,
3) den Collomaceen: Nostoc-Colonien,
4) den Omphalariaceen: Gloeocapsen,
5) den Racobloemaceen: Rivularien

zu Grunde liegen, und dass ferner ein Zusammenhang

Figure 7. Opening page of the report (1867) on Simon Schwendener's address to the Schweizerische Naturforschende Gesellschaft at Rheinfelden.

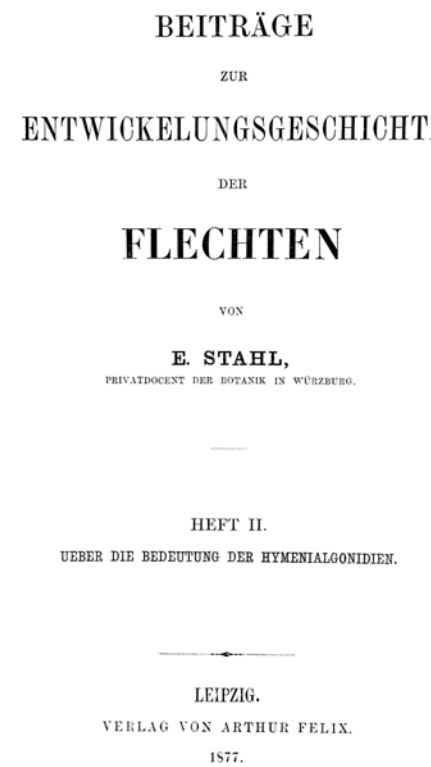
(1835–1918) and Ukrainian Josif Baranetzky (1843–1905), believed the former alternative confirmed when their cultures of green cells from *Cladonia*, *Evernia* and *Xanthoria* thalli were identified as *Cystococcus* (*Chlorococcum*) (1867). Schwendener, on the other hand, quickly realized the strength of de Bary's second explanation and proposed, accordingly, that all lichens be understood as associations of an alga and a fungus (Anonymous 1867; Fig. 7).

The twin illusions of autonomy and gonidial propagation were now dead, but few botanists were ready to admit as much because they knew of no precedent for regarding lichens as the product of an association between two altogether distinct micro-organisms. As remarked by Ainsworth (1976, p. 97), "Schwendener's 'dual hypothesis' excited much resistance, in part for reasons of 'common sense,' in part because lichenology has always been a somewhat esoteric pursuit." Schwendener, now professor of botany at the University of Basel, soon provided evidence to support his contention: having surveyed over a dozen homoiomerous and heteromerous genera, he described and illustrated their constituent algae (1869). This won some converts, but Nylander (1870) was not among them. He had too much invested in the status quo to countenance seeing it abandoned, being well aware that his system of classification depended on the assumption of autonomy and fearing, perhaps, for the survival of his nomenclatural work if the perception of lichens

as a combination of two distinct organisms were to gain ground (see Mitchell 2002). And gain ground it slowly did, thanks in large part to Julius Sachs (1832–1897), professor of botany at the University of Würzburg, who assigned lichens unequivocally to the ascomycetes in the second edition of his influential textbook (1870, pp. 254–265).

De Bary, having since moved to the University of Halle, aired the possibility of achieving artificial lichen synthesis by "inoculating free-living gonidia with spores of the species concerned" (1868). The practicability of such a procedure was soon investigated by his assistant Max Reess (1845–1901); he succeeded in germinating spores of a *Collema* species on *Nostoc* colonies and was able to follow events to the early stages of thallus development (Reess 1872). In the interim, several authors had sought to discredit the dual theory only to have their arguments decisively refuted by Schwendener (1872). When, in addition, Bornet (1873) provided abundant data to support his conclusion (p. 95) that "every lichen gonidium can be referred to a species of alga" and that "the relations between hypha and gonidia are such as to exclude any possibility of one being a product of the other," many previously sceptical of the new interpretation came to accept it. Nylander, however, was not for turning, and when the professor of botany at the Natural History Museum, Adolphe Brongniart (1801–1876), "demanded somewhat heatedly that he familiarize himself with Bornet's masterly study, Nylander replied that he did not read such absurdities, took his microscope and never again set foot in the Museum" (Boistel 1899, p. 227).

As Nylander made his dramatic exit, de Bary was adding distinction to a new academic posting. "Germany was on top of the world. They had won the Franco-Prussian war in 1871 and had annexed Alsace; Strasbourg became Strassburg and the university there was made into a showcase for German superiority" (Tanford and Reynolds 2001, p. 31). Here, with students from various European countries and the United States working under his direction, de Bary "made Strassburg the heart of German academic botany" (Drews 2000, p. 22). Those students included one native of Alsace, Ernst Stahl (1848–1919). He had moved with de Bary from Halle and soon announced his discovery of an ascogonial apparatus in *Collema* (1874), a development that gave new life to the question — still open — of whether the cells named spermatia by Tulasne have a fertilizing potential; some time later, using *Endocarpon pusillum*, Stahl (1877; Fig. 8) achieved the


BEITRÄGE

ZUR

ENTWICKELUNGSGESCHICHTE

DER

FLECHTEN

VON

E. STAHL,

PRIVATDOCENT DER BOTANIK IN WÜRZBURG.

HEFT II.

UEBER DIE BEDEUTUNG DER HYMENIALGONIDIEN.

LEIPZIG.

VERLAG VON ARTHUR FELIX.

1877.

Figure 8. Title page of Ernst Stahl *Beiträge zur Entwickelungsgeschichte der Flechten*, pt. I, 1877.

121

Professor de Bary aus Strassburg hielt hierauf den angekündigten Vortrag: „Ueber Symbiose."

Als ich einen Gegenstand für diesen Vortrag suchen sollte, war ich gerade mit der Untersuchung zweier Pflanzen beschäftigt, welche in einem eigenthümlichen Genossenschaftsverhältniss mit einander stehen. Die momentane Praeoccupation, nicht minder aber die Erwägung, dass ähnliche Genossenschaften, wie jene seit etwa 10 Jahren in sehr beachtenswerther Ausdehnung bekannt geworden und geeignet sind, allgemeines Interesse in Anspruch zu nehmen, bestimmte mich, eine Betrachtung der Erscheinungen des Zusammenlebens ungleichnamiger Organismen, der Symbiose, wie man kurz und allgemein sagen kann, zu wählen. Auch bei fernerer Ueberlegung blieb ich dabei; denn wenn es in diesen Versammlungen auch am nächsten liegt, Zeitfragen, Kritik und Geschichte der Methoden in Wissenschaft und Lehre zur Sprache zu bringen, so wird doch auch ein Bericht über concrete Forschungsergebnisse von allgemeinerem Interesse nicht unerwünscht sein.

Der erwähnten ersten Veranlassung entsprechend soll sich dieser Bericht vorwiegend mit Erscheinungen aus dem Pflanzenreiche beschäftigen. Einestheils weil hier bestimmte, vorzugsweise beachtenswerthe Verhältnisse am anschaulichsten hervortreten; anderntheils weil die verwandten Erscheinungen im Thierreiche den meisten hier Anwesenden bekannter und leicht erinnerlich sein werden, zumal an der Hand der reichen Zusammenstellung von Thatsachen, welche van Beneden kürzlich in seinem verbreiteten Parasitenbuche gegeben hat.

Der Hinweis auf letzteres genügt, um anzudeuten, dass es sich um ein höchst umfangreiches Material handelt, und dass die hier zugemessene Zeit nichts weniger als eine erschöpfende Behandlung desselben zulässt. Gestatten Sie mir daher nur die Hervorhebung der wesentlichsten Gesichtspunkte und ihre Erläuterung an einigen geeigneten Beispielen.

Die bekannteste und exquisiteste Erscheinung der Symbiose ist der vollständige Parasitismus, d. h. jene Einrichtung, bei welcher ein Thier oder eine Pflanze den ganzen Vegetationsprozess durchmacht. auf oder in einem anderen einer ungleichnamigen Species angehörigen Organismus. Letzterer dient jenem, dem Parasiten ausschliesslich als Wohnort und liefert ihm sein gesammtes Nährstoffmaterial, er ist im jeglichen Sinne des Wortes sein Wirth; und jener lebt auf Kosten des Wirthes, insofern sein Nährstoffmaterial die lebende Körpersubstanz oder die zur eigenen Ernährung aufgenommene Nahrung dieses ist.

Je nach den Einzelfällen sind die Beziehungen zwischen Parasit und Wirth in bekannter Weise höchst mannichfaltig verschieden. Einestheils bezüglich der Abhängigkeit jenes von letzterem. In dem einen extremen Falle ist der Parasit ohne den Wirth thatsächlich vollkommen existenzunfähig; sogar an ganz bestimmte, mit dem Entwicklungsstadium selbst wechselnde Wirthspecies gebunden, wie in den bekannten Fällen der Cestoden, der Rostpilze auf Berberis, Borragineen und Gräsern. Das andere Extrem weist Schmarotzer auf, welche nicht nur sehr verschiedenartige Wirthe aufsuchen, sondern auch, wenigstens in bestimmten Abschnitten ihres Lebens, ohne Wirth leben können, wie viele blutsaugende Epizoen, oder von Pilzen, manche Insektentödter. Der Muscardinpilz z. B. verschont kaum eine Insektenspecies, wenn er sie zur rechten Zeit findet; er vermag auch frei, ohne Wirth zu wachsen, Sporen zu bilden und mit diesen neue Opfer zu erreichen. Zwischen beiden Extremen finden sich alle erdenklichen Abstufungen.

Figure 9. Opening section of Anton de Bary's lecture (1878) to the Versammlung Deutscher Naturforscher und Ärzte in Cassel.

first artificial spore-to-spore synthesis. In the following year de Bary introduced the term "symbiose" at a meeting of the Gesellschaft Deutscher Naturforscher und Ärtzte in Cassel (Bary 1878; Fig. 9); an annotated version of his text appeared a year later. By replacing the then current assumption of parasitic dependence with a theory positing a mutually beneficial relationship between lichen components, de Bary removed the final major obstacle to what had come to be termed "Schwendenerism"; such prominent lichenologists as the Swiss Jean Müller "Argoviensis" (1828–1896) and Edward Tuckerman were, however, still unable to assimilate the new understanding and so marooned themselves in the past.

Anticlimax

The discovery of lichen duality might have been expected to focus attention on the nature of algal/fungal relationships within the thallus, but there was no early activity in this area. Schwendener published his last lichen paper in 1873 after which he worked mainly on aspects of vascular plant anatomy, Bornet became wholly occupied with marine phycology, and Stahl turned his attention to tropisms. Though Schwendener did supervise some postgraduate work in lichenology following his appointment to the chair of botany at the University of Berlin, this was restricted to apothecial ontogeny (Fünfstück 1884; Krabbe 1882; Lindau 1888; Wolff 1905).

Floristics and systematics remained the concern of most lichenologists during the closing decades of the century when important floras and monographs were published, notably by T. M. Fries (1871–1874), Harmand (1894–1899), Leighton (1871, 1879), Nylander (1888), Tuckerman (1882–1888) and Wainio (1887–1897, 1890). During the same period, the physiology of lichens understood as composite organisms was first investigated by Emil Godlewski (1847–1930), professor of botany at the University of Kraków. He reported (1874) on the effects of temperature and pressure on gas exchange by *Anaptychia ciliaris* in the absence of light. The fact that the results of this pioneering study were published in Polish meant, however, that workers in other countries remained virtually unaware of Godlewski's initiative — only Bonnier and Mangin (1884) seem to have mentioned it. Winter (1877), having promoted the interpretation of cephalodia formation as a reaction by cortical hyphae to the presence of a blue-green alga (cyanoprokaryote), aired the view (p. 200) that the parent thallus itself could be considered a morphogenetic response by its hyphae to their chlorophyllous associate; after being again touched on by Forssell (1884, pp. 180–181), this topic was shelved for 30 years.

Though algae had been isolated from several macrolichens by Famintzin and Baranetsky (1867), it was not until 20 years later that fungal components were successfully cultured. Credit for that achievement goes to the German mycologist Alfred Möller (1860–1922), who succeeded in germinating both conidia and spores from a range of crustose and foliose species (1887). In the area of chemistry, Paternò and Oglialoro (1877) isolated atranorin (as atranoric acid) from *Tephromela atra*, and Claëssen (1878, pp. 61–62) described lichenin (lichenan) as composed solely of dextrose, while Schwarz (1880) prepared crystals of several lichen products and reported on the color changes they exhibit when acted on by various reagents.

Factors influencing the distribution of saxicolous species were investigated at this stage by Hugh Weddell (1819–1877), a native of Gloucestershire and naturalized French citizen. Having taken up the study of lichens late in the 1860s, Weddell published a paper (1873) noteworthy in the main for its introduction of the terms "calcicole" and "calcifuge"; two years later he provided the first clear description of the zonation exhibited by lichens on rocky shores (1875, pp. 255–256). These promising investigations were cut short, however, by Weddell's death at the age of 58. The distribution of lichens in relation to rock type was further discussed by Richard (1883) in a contribution notable principally for its interesting lists of species reported from 40 substrata, natural and other (pp. 39–79). Substratum related studies were extended by Winter's (1875, 1876) work on the growth of saxicolous microlichens and that of Frank (1876) on the structure of hypophloeodal thalli. The latter's study features in the detailed review of lichen anatomy provided by de Bary in his *Comparative Morphology and Biology of the the Fungi, Mycetozoa and Bacteria* (Engl. transl. 1887, pp. 401–415), where he also touched on several unresolved topics that would, eventually, be the concern of others following de Bary's death, aged 57, in 1888.

Lichenological research was now largely restricted to the working-up of collections from Europe and elsewhere by such taxonomists as the Scot James Crombie (ca.1830–1906), the Bavarian August von Krempelhuber (1813–1882), Jean Müller, Nylander and another Finn, August Wainio (later Vainio) (1853–1929), with local botanists coming to the fore in Australia and New Zealand (see Filson 1976 and Galloway 1985b, pp. xix–xx). The presentation by Henri Jumelle (1866–1935) — a student at the University of Paris — of a

doctoral thesis detailing gas exchange by eleven macro- and eight microlichens in response to widely varying conditions of humidity and temperature was a welcome development. However, despite being awarded the Academy of Sciences' Prix Montagne for that investigation (1892), Jumelle made no further contribution to lichenology. The Austrian Hugo Zukal (1845–1900) drew to an extent on Jumelle's work in a perceptive commentary on the water relations of lichens representative of several foliose genera (1895, pp. 1333–1347) but did not extend that investigation.

The remark by George Massee (1850–1917), cryptogamist at the Royal Botanic Gardens, Kew, that "[w]e should be very pleased … to learn that a young lichenological student did actually exist in Great Britain" (1894, p. 81) applied more widely. Only in Germany, where Bachmann (1892) and Lindau (1895), for example, reported detailed observations on the anatomy of saxicolous and corticolous microspecies, respectively, was there now any significant amount of research activity. In an earlier publication, Bachmann (1886) had refocussed attention on the use of lichen chemistry as an aid to identification, a subject in which Wilhelm Zopf (1846–1909), then at the University of Halle, was to develop a particular interest. For most of his career Zopf worked with non-lichenized fungi, but evidently he also had a certain familiarity with lichen products because 19 of these, together with a table of species in which they occur and procedures for their extraction, appear in his mycological textbook (1890, pp. 131–138). Subsequently, Zopf made those products his special concern and, following a move from Halle to Münster, published (1895a) the first of an extensive series of papers on the subject, the second of which (1895b) is noteworthy for providing the first illustrations of crystals obtained by solvent extraction of specific products.

As the century drew to a close, Albert Schneider (1863–1928) published the doctoral thesis he had presented at Columbia University. In the first 100 pages of this substantial work (1897), Schneider "condensed practically all that was known about lichens at that time" (Plitt 1934). In anticipation, perhaps, of such criticism as made by Cummings (1898), who found the book overly technical and regretted "that it was not adapted for more general use," Schneider quickly produced a more accessible *Guide* (1898) but then decided to abandon lichenology for pharmacology. In 1899 the French botanist and cleric Auguste-Marie Hue (1840–1917) revived the study of thallus anatomy. Having already published the first section of a catalogue documenting collections recently acquired by the Paris Museum of Natural History (1898), Hue decided — in order to make his catalogue more than a mere inventory — that he would in future report fully on the anatomy and morphology of each taxon; the unprecedented range of detail thus recorded and illustrated is quite remarkable (1899–1901), and even more impressive is the fact that, this work completed, Hue went on to describe nearly 1,000 more taxa in like manner (1906–1910).

The last year of the century brought an end and a beginning. Nylander had continued his remarkable output of taxonomic papers into the 1890s, by which time, however, he had become seriously reclusive: Boistel (1899, p. 219) reported, from six months' personal experience, that gaining access to Nylander called for "diplomatic expertise beside which that of Richelieu and Mazarin was child's play"; death, on the other hand, did not have to negotiate, and Nylander passed away suddenly on 29 March 1899. The beginning concerned the subject of lichen ecology. "In 1893, a group of botanists meeting in Madison, Wisconsin, decided to adopt the word 'ecology' … that had been coined by Ernst Haeckel in 1866, but

XIX. CONTRIBUTIONS TO A KNOWLEDGE OF THE LICHENS OF MINNESOTA.—V. LICHENS OF THE MINNESOTA VALLEY AND SOUTHWESTERN MINNESOTA.

BRUCE FINK.

CONSIDERATIONS OF DISTRIBUTION AND HABITAT.

The area considered in this paper was selected with a view to obtaining as complete a knowledge as possible of the lichen flora of the Minnesota river valley and of that of southwestern Minnesota in general.

The upper portion of the valley near Minneapolis would, of course, give a flora essentially like that of Minneapolis and vicinity already studied. Hence, for the month's field work, it was thought best to begin operations at a locality a considerable distance from Minneapolis. As an initial place, Mankato, about 60 miles from Minneapolis, was selected. The location of this city is also advantageous in that it lies nearly midway between the Minneapolis and the northeastern Iowa areas compared carefully in the second paper of this series, thus forming a connecting link between the two areas previously studied. After a careful study of the lichens of the Mankato area both to gain a knowledge of the lichen flora of the region and for the sake of relationships with the areas indicated above, New Ulm was next selected as an area of special interest because of the exposures of Cretaceous sandstone and the most southeastward exposures of quartzite rocks in the valley. At New Ulm only these two rock formations were studied, as time spent on other substrata present would only be repaid for most part by a repetition of the species found upon the same substrata at Mankato, only 30 miles distant. Three days were next spent at Redwood Falls, Morton and North Redwood with a view to securing rare species and noting the southeastern extension of certain species in the valley. From here I proceeded to Granite Falls.

277

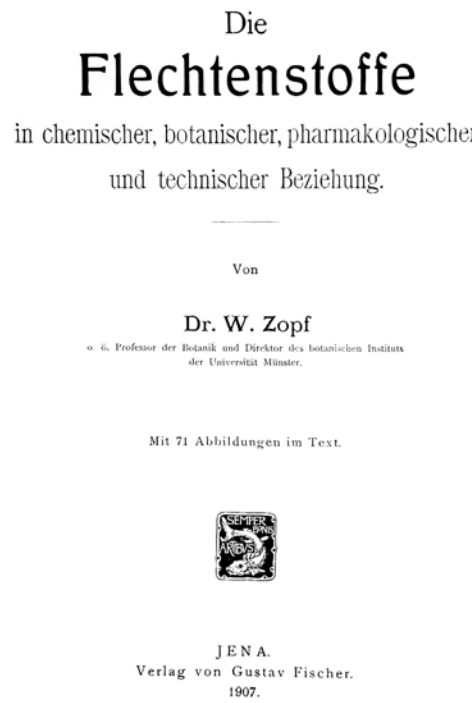
Figure 10. Opening page of Bruce Fink's landmark paper (1899) on lichen ecology.

had been used very little in either Europe or America since then" (Cittadino 1980, p. 171). Conway MacMillan (1867–1929), professor of botany at the University of Minnesota, was a member of that group, and while he was evidently the first to air the term, however marginally, in a context involving lichen distribution (1897, p. 951), it is correct to say that the study of lichen ecology was pioneered by Bruce Fink (1861–1927). MacMillan had sent his lichen collections to Fink, then at the University of Upper Iowa, for identification, and a list of the 60-odd taxa represented was published by the latter as the first in a series of "Contributions to a knowledge of the lichens of Minnesota" (1896). Three similar

listings based on Fink's own collections followed, but his fifth paper (1899; Fig. 10) was considerably more important. After a detailed introductory account headed "Considerations of distribution and habitat," Fink stated (p. 283), "I shall now pass to a consideration of the lichen formations of the region, causes of their peculiar make-up, and comparisons with similar formations within and outside the area under consideration." He reported a total of 25 corticolous, saxicolous and terricolous communities to which he applied such names as *Pyrenula lichen formation of trees with smooth bark*, comprising nineteen taxa, *Lecanora formation of exposed granite* with seventeen and a seven-strong *Endocarpon hepaticum formation of exposed earth*. Fink's discussion of his communities include the earliest serious attempt to assess the influence of environmental factors on lichen colonization; he was well aware of this achievement, stating (p. 308) "I know of no other paper which has dealt exclusively with lichen distribution as I have done herein, and surely this analysis must be helpful in the study of the lichen flora of other regions ... I hope that this paper may stimulate others to study the lichens from an ecologic point of view."

Challenging times

The lichenological studies that appeared during the opening decade of the 1900s dealt with lichen anatomy, chemistry, ecology and systematics, but it would be wrong to conclude from this list that there was widespread interest in the subject. In fact, most research involving lichens was confined to three German institutions. Schwendener's student Moritz Fünfstück (1856–1925) — mentioned earlier — became professor of botany at the Technische Hochschule, Stuttgart, where theses on the anatomy of saxicolous species were prepared under his direction by Friederich (1906), Lang (1906) and Stahlecker (1906). At the University of Kiel's Botanical Institute, Johannes Reinke (1849–1931) was known for his extensive observations on lichen morphology and systematics (1894–1896), though in the latter regard he promoted the reactionary notion (1895, p. 41) that "Acharius' perception of lichens as constituting a class of plants comparable to algae and fungi remains, for the most part, correct." The work of Baur (1901, 1904) and Darbishire (1900) on fruit-body development was carried out at Kiel under Reinke's supervision. Somewhat more innovative studies were undertaken and directed by Zopf at Münster where he continued to occupy himself with lichen chemistry, though now with a view to extending its taxonomic application. As an attempt "to evaluate the extent to which lichen acids can assist in the determination and classification of lichens," Zopf (1903, p. 95) undertook a "chemical-monographic treatment" (p. 99) of the genus *Evernia*. This, the first work of its kind, led Zopf to establish the new genus *Pseudevernia*; his chemotaxonomic studies subsequently extended to European *Cladonia* material (1908). In 1907 Zopf brought together the results of his research on secondary metabolites in what for long remained a standard work of reference (Fig. 11). A year after Zopf's death, Fischer and Freudenberg (1910, pp. 34–35) realized a synthesis involving two phenolic units and were confident that using their procedure "a large number of similar products may be obtained, and because many of these are likely to occur naturally — tannin apparently being an example — it may be appropriate to give them a collective name: we suggest the term 'depside' (from the Greek δεψειν, to tan). The nomenclature can then replicate that of polysaccharides and polypeptides, since di-, tri-, tetradepsides and so on can be distinguished depending on the number of phenol carbonic acids present in the


Die
Flechtenstoffe
in chemischer, botanischer, pharmakologischer
und technischer Beziehung.

Von

Dr. W. Zopf
o. ö. Professor der Botanik und Direktor des botanischen Instituts
der Universität Münster.

Mit 71 Abbildungen im Text.

JENA.
Verlag von Gustav Fischer.
1907.

Figure 11. Title page of Wilhelm Zopf *Die Flechtenstoffe*, 1907.

molecule"; aided by his son, Fischer went on to synthesize lecanoric acid (1913) and evernic acid (1914).

Lichen ecology still had its only serious student in Bruce Fink. Conscious of this fact, he sought (1902) to recruit floristic enthusiasts to the cause, urging "those who have or are able to acquire a knowledge of the lichens of a limited area to turn their attention to ecologic studies"; he further promoted that objective in "Some common types of lichen formations" (1903). Fink's papers were an important influence on the work of Olaf Galløe (1881–1965), a highschool teacher in Copenhagen, who published the first notable European study devoted to lichen ecology (1908). The subject soon became an almost exclusively European discipline, however, following a change of course by Fink that led to his devoting himself primarily to taxonomic research—a comprehensive treatment of Minnesota species appeared in 1910; elsewhere, important floras were published by Dalla Torre and Sarnthein (1902) and Jatta (1909–1911).

A report by Sernander (1912) on the colonization of nutrient-enriched habitats in eastern Sweden introduced (p. 805) the terms "coniophilous," for species favoring dusty, roadside substrates and "ornithocoprophilous," for those prospering in the presence of bird droppings. Thirty years after Weddell's report on the lichen zonation characteristic of rocky shores, Knowles (1913) returned to the subject in a study conducted on the east coast of Ireland. Preferring "to abstain from employing the terms 'formation' and 'association'" (p. 85), she elaborated on Warming's (1909, p. 224) recognition of coastal lichen "belts" and supplied carefully observed descriptions of five such, extending from a supralittoral characterized by *Ramalina* spp. to one comprising mainly marine *Verrucaria* spp. Darbishire (1914) also chose, without any mention of Fink or Galløe's work, to defer addressing the question of lichen associations: he took the view (p. 79) that "[a]t present the use of any such ecological terms in too definite a manner is to be deprecated. We should be grateful to those botanists who group all the rock lichens together in the one word 'lithophytes'."

One of the great taxonomic publishing ventures of the late 19th and early 20th century was *Die natürlichen Pflanzenfamilien* edited by Adolf Engler (1844–1930) and Karl Prantl (1849–1893). Over a ten-year time span, that work's serial appearance delivered five fascicles devoted to lichens: a survey of their biology by Fünfstück (1898) was followed in 1903, 1905, 1906 and 1908 by instalments of the taxonomic treatment assigned to Alexander Zahlbruckner

(1860–1938). A native of Jur near Bratislava (in the Austro-Hungarian Empire until 1918), Zahlbruckner joined Vienna's Natural History Museum in 1883 as herbarium curator; he began to publish on lichen taxonomy in the 1890s and was soon recruited to Engler's army of volunteers. Zahlbruckner's contributions, which are characterized by meticulous attention to detail, had, as remarked by Tehler and Wedin (2008, p. 398), "a huge impact on the classification of lichen fungi," but, as they also observe, "Zahlbruckner unfortunately chose the conservative view of his colleague Reinke ... that the 'lichens' were actually to be regarded as a systematic unit [Lichenes] ... a view [that] has prevailed during most of the twentieth century." The only contemporary dissenting voice appears to have been that of Fink (1913, p. 116), who insisted that lichens are to be understood as fungi and "should be distributed to the exclusion of the group Lichenes," though it is the case that Wainio had earlier declared (1890, p. xiii) "lichens differ from ascomycetes only in their biological attribute of *symbiosis with algae*. It is the *sole general characteristic* that distinguishes them from fungi."

Forty years after Bornet and Schwendener published their identifications of lichen algae, the Swiss botanist Robert Chodat (1865–1934) began an investigation of the physiological factors that influence the culturing of those organisms. Reporting on his work at the University of Geneva, Chodat (1913, p. 192) remarked with regard to earlier attempts at isolation, "it is extraordinary that so fascinating a subject as the nature of lichen gonidia should have occasioned no critical research" — a shortcoming also ably addressed by his students. A further welcome addition to the meagre literature on lichen physiology was produced under Stahl's direction at the University of Jena by Salomon (1914). He investigated the occurrence of Ca, K, Mg and P in a diversity of thalli and estimated their relative abundance in the components. Salomon did not, however, pursue this topic — as with other of the authors mentioned here whose dissertation proved to be their only lichenological publication, he had to find employment in a discipline that attracted funding.

Europe was now about to become a battlefield. During the calamitous years of the First World War and its immediate aftermath, publication of data relevant to the various areas reported on above came effectively to a standstill. Mention may be made, however, of an article by Moreau and Moreau (1918) claiming that, in their opinion, "a lichen owes its most characteristic features to the action of the alga on its associated hyphae. The greater part of the thallus presents, in this assessment, as the equivalent of a gall — it is a cecidium, an algocecidium, a generalized biomorphosis."

Revival

Though Annie Smith (1854–1937), a part-time assistant at the then British Museum (Natural History) had announced (1917) that "[a] general text-book on Lichenology is ready and awaits publication," it was not until 1921 that her excellent survey appeared. That comprehensive volume remains of service today, not least for the historical matter that introduces several of her chapters and sections. Also during the war years, Zahlbruckner in Vienna had set himself the task of assembling the published references to every infrafamilial lichen taxon. Beginning in 1916, with the services of one lady assistant (Riedl 1988, pp. 21–22), Zahlbruckner had the first volume of his *Catalogus Lichenum Universalis* (Fig. 12) ready for publication in 1922. That prodigious undertaking, which followed his Engler and Prantl arrangement and ultimately ran to some 7,000 pages in 10 volumes, remains an indispensible work of reference.


Catalogus
lichenum universalis

von

Dr. A. Zahlbruckner
Direktor der Botanischen Abteilung des Naturhistorischen
Museums in Wien

Band I

Leipzig
Verlag von Gebrüder Borntraeger
1922

Figure 12. Title page of Alexander Zahlbruckner *Catalogus Lichenum Universalis*, vol. 1, 1922.

Evidence that research activity had resumed postwar came first in the area of ecology. Results published by Einar Du Rietz (1895–1967), representing the Uppsala school of phytosociology (1921, pp. 164–172), and Eduard Frey (1888–1974), representing that of Zürich (1922, pp. 76–91), were the stimulus for painstaking studies by Hilitzer (1925) and Ochsner (1927), the first of whom applied the former school's methods, with the second employing those of the latter. While a substantial number of similarly oriented studies were carried out over the years in continental Europe (see Klement 1955, p. 5), anglophone lichenologists proved unreceptive to the new approaches until late in the century. Differing views also obtained as to the identity of the alga allegedly common to such genera as *Parmelia*, *Usnea* and *Xanthoria*. This occasioned much nomenclatural confusion, which was finally resolved by Puymaly (1924). Building on previous work by Octave Treboux (1876–ca.1940) at the University of Riga, Puymaly (p. 109) recognized that the photobiont of *X. parietina* belonged to an undescribed genus, which he mindfully named *Trebouxia*.

Though still comparatively few in number, lichenologists of the period were not without general surveys of their subject. In addition to Smith's text, the Swiss botanist Friederich Tobler (1879–1957), professor of botany at the University of Dresden, assessed the contemporary state of knowledge with particular regard to studies concerning symbiosis (1925); Nienburg (1926) provided a thorough review of structural investigation, which incidentally revealed how little attention lichen anatomy had attracted since the early years of the century; Moreau (1928) chose to emphasize reproduction and component interrelationships, while a second edition of Engler and Prantl's lichen section (1926) allowed Fünfstück to update his judicious first edition overview and gave Zahlbruckner the opportunity of making "small additions and modifications" to his system (Pišút 2002, p. 244). All those valuable texts do, however, have one failing in common: their dearth of experimental data. Lichenology's deficiencies in that regard were bluntly put by the German plant physiologist Otto Stocker (1888–1979) in the introduction to a lengthy and insightful paper (1927, p. 334): "Our current knowledge of lichen physiology presents a sad picture. To recognize this, one has only to glance for example at the summary given by Tobler in his recent and welcome book. In the two decades from 1870 to 1890, lichens were the focus of botanical attention … but subsequent years produced scarcely a dozen reports that, from a general point of view, have contributed

anything new or worthwhile." Stocker's paper, which principally concerns *Lasallia pustulata* and *Lobaria pulmonaria*, is in two parts: the first, and larger, presents his results bearing on water relations, photosynthesis and respiration, the second constitutes the earliest serious study devoted to physiological lichen ecology. Regrettably, that paper proved to be yet another lichenological only child: though Stocker retained a particular interest in water movement, his research on becoming professor of botany at the Technische Hochschule, Darmstadt, dealt almost exclusively with vascular plants. Ecophysiological issues also feature in the air pollution investigation carried out in Oslo by Haugsjå (1930) — "one of the earliest studies of its kind, which unfortunately was not followed up" (Jørgensen 2007, p. 57).

Physiological studies on *Teloschistes flavicans* undertaken by James Cuthbert (1908–1964) at the University of Capetown represent the earliest experimental work on lichens conducted in South Africa. Cuthbert reported first on the rate of water uptake and the amount absorbed by dried thalli "when allowed to reach a condition of equilibrium with (a) water-saturated air and (b) water" (1930, p. 44). In a subsequent paper, Cuthbert (1934) investigated relationships between respiration and water content; his finding that thalli remain "alive and respiring with a water content of only 0.4 per cent. of total saturation" led him to conclude (p. 53) that "even under the most adverse conditions extant in the Cape Peninsula, *T. flavicans* is living well within its powers of resistance." By the time Cuthbert's second paper appeared, he had exchanged lichenology for medical studies in Britain where he became a specialist in plastic surgery.

Demonstrating a welcome continuity in experimental lichen research, Smyth (1934) provided further data relating to respiration and water movement, derived on this occasion from two species of *Peltigera*. In addition to extensive laboratory work, Smyth carried out field studies involving atmospheric humidity, light and temperature measurements at sites ranging from exposed to sheltered; her results in this connection allowed, however, only somewhat general conclusions to be drawn (pp. 816–817). Because Smyth's findings differed from those of Stocker with regard to thallus hydration and rate of photosynthesis, Ellée (1939) re-investigated the subject. His findings confirmed Smyth's results but, as pointed out by Ahmadjian (1966, p. 63), the data reported by all three authors are in conformity with the use of compactly organized thalli by Stocker and more loosely structured material by Ellée and Smyth.

This spurt of physiological endeavor was brought to an end in the same year that Stålfelt (1939) produced a detailed report on factors influencing gas exchange in 11 macrolichens. That work represented a considerable advance over previous research in the area, indeed, Kershaw (1985, p. 173) believed Stålfelt to have been ahead of his time: "[a]lthough [he] carefully documented capacity changes in both respiration and net photosynthesis, surprisingly his work had little impact on the scientific community as a whole, probably because the results were difficult to interpret given the level of understanding at that time" — a more plausible explanation, however, is that Stålfelt's work appeared when the study of lichen biology, like so much else in the life sciences, was largely about to be shelved during a decade of war and privation. Similarly, when efforts to achieve the artificial synthesis of lichens were realized, with *Cladonia pyxidata*, by Thomas (1939) — inconclusive results having been reported by Werner (1931), Bartusch (1931) and Lange-de la Camp (1933) — there was no early attempt to build on his achievement; and his recommendation (p. 163) that the term "gonidia" be rejected was not acted on for nearly 20 years (Scott 1957).

Mikrochemischer Nachweis der Flechtenstoffe* (I)

von

Y. Asahina.

朝比奈泰彦： 地衣成分ノ顕微化學的證明法（其一）

Allgemeiner Teil

Die bisher zur Erkennung der Flechtenstoffe angewandten Reagentien sind keine spezifischen für bestimmte Substanzen, sondern stellen gemeinsame Gruppen-Reagentien für einige ähnlich konstruierte Stoffe dar. So färbt z. B. Alkalilauge das Atranorin und die Thamnolsäure gelb, was darauf zurückzuführen ist, dass sie ortho-Oxy-aldehyd-Gruppen enthalten. Stictinsäure und β-Methyläther-salazinsäure färben sich mit Alkali auch gelb. Obwohl diese beiden keine ortho-Oxy-, sondern ortho-Methoxyaldehyde sind, so doch enthalten sie in ihren Molekülen je eine meta-Oxy-aldehyd-Gruppe, die mit Alkali gelbe Färbung hervorrufen kann. Eine Ausnahme bilden Protocetrarsäure und Fumarprotocetrarsäure, die ortho-Oxy-aldehyd-Gruppe enthalten. Die Protocetrarsäure(=Caprarsäure) färbt sich nämlich beim Berühren mit Alkali anfangs gar nicht, erst nach einigen Minuten allmählich hell gelbbraun und endlich erzeugt eine braune Lösung, während die Fumarpro-

* Eine übersichtliche Tabelle der Flechtenstoffe befindet sich in Acta Phytochimica, VIII, 23–45 (1934).

— 66 —

Figure 13. Opening page of Yasuhiko Asahina's first paper (1936) on the application of microcrystallization procedures to lichen taxonomy.

Work on a second edition of Rabenhorst's *Kryptogamen-Flora* had been in progress for 50 years when, in 1930, the sections of that project devoted to lichens began to appear under the direction of, first, Zahlbruckner and then Karl von Keissler (1872–1965). Those sections, comprising volumes eight and nine in the series, provide admirably full descriptions of the species constituting many of the genera represented in Europe; prepared by leading taxonomists of the day and issued in parts, the work was, regrettably, never completed. Publication of lichen material ceased soon after the outbreak of war in 1939, though the series' lichen coverage did not actually end until almost 20 years later with the belated appearance of Keissler's Usneaceae. Outside Europe at this time, Chopra (1934) published on lichens of northern India, Fink's U.S. *Flora* (1935) appeared posthumously and Dodge and Baker (1938) issued an extensive report on Antarctic material.

Apart from ecological and taxonomic investigations, the only aspects of lichenology that continued to receive attention during the war years were chemistry and chemotaxonomy. Interest in lichen chemistry had been revived in the 1930s by Yasuhiko Asahina (1881–1975), professor of pharmacognosy at Tokyo University. In a report on the structure of salazinic acid, he and a co-worker proposed a formula for the acid founded on a conviction (Asahina and Asano 1933, p. 1216) that it is formed from "depsides of the thamnolic acid type by ether linkage"; subsequently, Asahina (1934a, p. 34) stated, "I propose to describe such compounds as *depsidones*." More or less contemporaneously, a school of lichen

chemistry established at University College Dublin by Thomas Nolan (1888–1945) had begun to report its results in a series of papers that continued to appear until 1948 (see Mitchell 1995, p. 148). Further work by Asahina (1934b, pp. 48–50) allowed him to demonstrate that depsidones produce distinctive color reactions in the presence of paraphynelenediamine (Pd), which then became a valuable addition to the reagents already in everyday use for spot testing. Asahina also developed — evidently unaware of Senft's (1908) work — the technique of depositing lichen products directly onto a microscope slide by solvent extraction of a thallus fragment. In a sequence of 11 papers (see Shibata 2000, p. 788) published between 1936 (Fig. 13) and 1940, Asahina showed that irrigating the slide deposits with various glycerol-based combinations allows readily identifiable microcrystals, characteristic of particular secondary metabolites, to form; this simple method proved a potent stimulus to taxonomic research.

Beyond Japan, Asahina's Pd test was first employed by Torrey (1935) in the United States, and his microchemical procedure by Duvigneaud (1939) in Belgium. The new chemotaxonomy was assiduously promoted by Alexander Evans (1868–1959). Following his retirement from the professorship of botany at Yale University in 1936, Evans transferred his research interest from hepaticae to the genus *Cladonia*. He soon came to rely on the use of Pd as a reagent, and his recognition of the support provided by microcrystallization led him to bring the details of that technique to general attention (1943). Evans also participated in an attempt, inspired by penicillin's contemporary impact, to establish the extent to which lichens possess antibiotic properties (Burkholder et al. 1944). Extracts of over 40 macrolichens were tested against 9 bacterial species, the most susceptible of which proved to be *Bacillus subtilis* and *Staphyloccocus aureus*. A further paper (Burkholder and Evans 1945) reported observations on the response of 16 bacteria to extracts from about 100 lichens. The results showed that lichen products inhibit Gram-positive species almost exclusively and that growth of *B. subtilis* was impeded by usnic acid in particular. The work of others who undertook research on this topic in the five years to the decade's end was reviewed by Bustinza (1951).

Despite the constraints of the war years, a certain amount of ecological and taxonomic research — the latter extending to material preserved in collections from around the globe — was published by such workers as V. Räsänen (Finland); H. des Abbayes, M. Bouly de Lesdain (France); C. F. E. Erichsen, J. Hillmann, G. Lettau, F. Mattick (Germany); R. G. Werner (Morocco); B. A. Lynge (Norway); C. N. Tavares (Portugal); S. Ahlner, O. Almborn, G. Degelius, T. E. Hasselrot, A. H. Magnusson, R. Santesson (Sweden); and A. W. Evans, A. W. Herre, J. W. Thomson (United States). Details of the relevant publications are provided in the comprehensive survey by Abbayes (1953).

The last innovative study dating to the period under consideration was carried out in the Netherlands, principally at the University of Leyden, by Anton Quispel (1917–2008). In an attempt to establish the nature of the association between lichen components, Quispel (1943–1945) undertook extensive laboratory work involving the isolated mycobiont of *Xanthoria parietina* and isolated photobionts of *Physconia distorta*, *Pleurosticta acetabulum* and *X. parietina*. His research included experiments concerned with resynthesis, growth requirements of the components, hydration and the influence of temperature on metabolism. Quispel concluded from his results that "the fungi use the products formed by the assimilating algae, live saprophytically from dead algae or

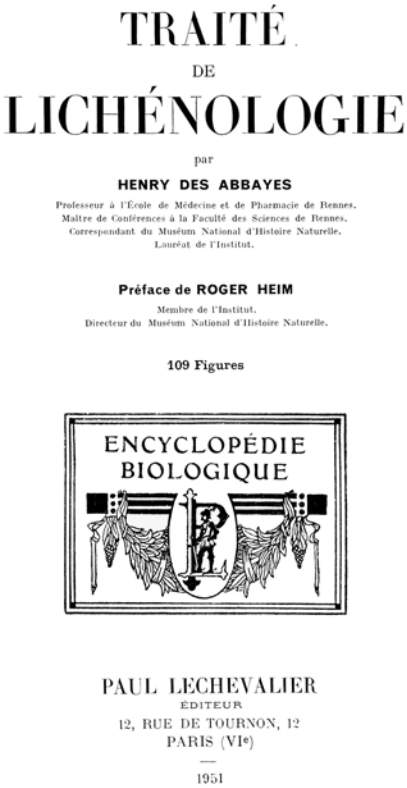

TRAITÉ
DE
LICHÉNOLOGIE
par
HENRY DES ABBAYES
Professeur à l'École de Médecine et de Pharmacie de Rennes,
Maître de Conférences à la Faculté des Sciences de Rennes,
Correspondant du Muséum National d'Histoire Naturelle,
Lauréat de l'Institut.
Préface de ROGER HEIM
Membre de l'Institut,
Directeur du Muséum National d'Histoire Naturelle.
109 Figures
ENCYCLOPÉDIE
BIOLOGIQUE
PAUL LECHEVALIER
ÉDITEUR
12, RUE DE TOURNON, 12
PARIS (VIe)
1951

Figure 14. Title page of Henry des Abbayes *Traité de Lichénologie*, 1951.

parasitically from cells attacked by haustoria. Moreover, the algae provide the fungi with a number of indispensible nutrilites [vitamins]. When the external situations are unfavourable the algae will live heterotrophically from the organic substances taken by the fungus from the substrate. Perhaps this heterotrophic metabolism of the gonidia is stimulated by certain nutrilites synthesized by the fungus. So we are certainly justified to consider this association as a mutualistic symbiosis" (pp. 525–526). Though not all would agree that we are in fact so justified, it is the case that Quispel's methodology proved quite influential.

The territory won by those botanists whose work has been reviewed here was ably assessed in the early postwar years by Henry des Abbayes (1898–1974), professor of botany at the Université de Rennes. His detailed, lucid and well-illustrated text (Fig. 14) helped in no small degree to set the stage for the remarkable surge in interest that lichenology came to attract in the decades after mid-century.

Acknowledgments

I am grateful in the first instance to Dr. A. Hanson, Harvard University, for valued guidance respecting the Hippocratic Corpus. Ms. I. Curlejova, Galway, obligingly undertook a translation of Riedl's (1988) article, and Dr. K. Grodziska, Kraków, generously provided a copy of the French translation of Godlewski's (1874) paper.

My best thanks go once again to Mr. T. Keady, Galway, for his attentive processing of the illustrations.

Requests for assistance were amiably and discerningly attended to by staff at the Bodleian Library, Oxford; British Library, London; Cambridge University Library; Department of Plant Sciences Library, Oxford; University of Cape Town Library and Archives; General Library, Natural History Museum, London; Göttingen University Library; James Hardiman Library, National University of Ireland, Galway; Liverpool University Library; Lund University Library; Municipal Library, Norrköping; National Library of Ireland, Dublin; National Library of Scotland, Edinburgh; Royal Botanic Gardens Library, Kew; Royal Irish Academy Library, Dublin; Utrecht University Library and Wageningen University Library.

Mention must also be made of my indebtedness to the reference works of Grummann (1974), Krempelhuber (1867–1872), Lindau and Sydow (1907–1917) and Stafleu and Cowan (1976–1988) and to the resources of the Internet.

References

Abbayes, H. des. 1951. Traité de Lichénologie. Paris: Lechevalier.

Abbayes, H. des. 1953. Travaux sur les lichens parus de 1939 à 1952. Bull. Soc. Bot. France 100: 83–123.

Acharius, E. 1799 (1798). Lichenographiae Suecicae Prodromus. Linköping: Björn.

Acharius, E. 1803. Methodus qua omnes detectos Lichenes. Stockholm: Ulrich.

Acharius, E. 1810. Lichenographia Universalis. Göttingen: Danckwerts.

Adanson, M. 1763[–1764]. Familles des Plantes. 2 vols. Paris: Vincent.
Ahmadjian, V. 1966. Lichens. In: S. M. Henry, ed. 1966–1967. Symbiosis. 2 vols. New York and London: Academic Press. Vol. 1. Pp. 35–97.
Ainsworth, G. C. 1976. Introduction to the History of Mycology. Cambridge: Cambridge University Press.
Anonymous. 1485. [Hortus Sanitatis. Deutsch]. Mainz: [Schöffer]. (Facsim. ed. 1966, München-Allach, Kölbl.)
Anonymous. 1833. Analyse d'un mémoire sur deux produits naturels de la végétation considérés comme des gommes, lu par M. Guérin Varry à l'Académie des Sciences de Paris, le 30 juillet 1833. Institut 1: 101–103.
Anonymous. 1867. Protokoll der botanischen Sektion. Verh. Schweiz. Naturf. Ges. 51: 88–91.
Asahina, Y. 1934a. Zur Systematik der Flechtenstoffe. Acta Phytochim. 8: 33–45.
Asahina Y. 1934b. Über die Reaktion von Flechten-Thallus. Acta Phytochim. 8: 47–64.
Asahina, Y. 1936. Mikrochemischer Nachweiss der Flechtenstoffe (I). J. Jap. Bot. 12: 516–525.
Asahina, Y. and J. Asano. 1933. Untersuchungen über Flechtenstoffe, XXIX. Mitteil.: Über Salazinsäure (III). Ber. Deutsch. Chem. Ges. Berlin 66: 1215–1217.
Aufderheide, A. C. 2003. The Scientific Study of Mummies. Cambridge: Cambridge University Press.
Awasthi, D. D. 2000. Lichenology in Indian Subcontinent. Dehra Dun: Singh.
Bachmann, E. 1886. Mikrochemische Reactionen auf Flechtenstoffe als Hülfsmittel zur Bestimmen von Flechten. Z. Wiss. Mikroskop. Mikroskop. Techn. 3: 216–219.
Bachmann, E. 1892. Der Thallus der Kalkflechten. Ber. Deutsch. Bot. Ges. 10: 30–37.
Bartusch, H. 1931. Beiträge zur Kenntnis der Lebensgeschichte des Xanthoriapilzes. Arch. Mikrobiol. 3: 122–157.
Bary, A. de. 1866. Morphologie und Physiologie der Pilze, Flechten und Myxomyceten. Leipzig: Engelmann.
Bary, A. de. 1868. Beitrag zur Kenntnis des selbständigen Lebens der Flechtengonidien. Von J. Boranetzky (*sic*). [Review.] Bot. Zeitung (Berlin) 26: 196–198.
Bary, A. de. 1878. Ueber Symbiose. Tagebl. Versamml. Deutsch. Naturf. Aerzte Cassel 1878: 121–126.
Bary, A. de. 1879. Die Erscheinung der Symbiose. Strassburg: Trübner.
Bary, A. de. 1887. Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria, transl. H. E. F. Garnsey and I. B. Balfour. Oxford: Clarendon Press.
Bauhin, C. 1623. Πίνάξ Theatri Botanici. Basel: King.
Bauhin, J. 1650–1651. Historia Plantarum Universalis. 3 vols. Yverson: N.p.
Baur, E. 1901. Die Anlage und Entwicklung einiger Flechtenapothecien. Flora 88: 319–332.
Baur, E. 1904. Untersuchungen über die Entwicklungsgeschichte der Flechtenapothecien. I. Bot. Zeitung, 2. Abt. 62: 21–43.
Beilstein, F. 1881–1883. Handbuch der organischen Chemie. 2 vols. Hamburg and Leipzig: Voss.
Bentzel-Sternau, A. von. 1859. Über die neueren Fortschritte der Lichenologie. Presburg: Wigand.
Berzelius, J. 1808. Undersökning af Islands-mossans sammansättning och dess användande såsom näringsmedel. Econ. Ann. 8: 53–94.
Blunt, W. and S. Raphael. [1979.] The Illustrated Herbal. London: Lincoln.
Boistel, A. 1899. Le Professeur William Nylander. Rev. Gén. Bot. 11: 218–238.
Bonnier, G. and L. Mangin. 1884. Sur les échanges gazeux entre les lichens et l'atmosphère. Bull. Soc. Bot. France, sér. 3. 31: 118–119.
Bornet, E. 1873. Recherches sur les gonidies des lichens. Ann. Sci. Nat., Bot., sér. 5. 17: 45–110.
Braconnet, H. 1825. De la présence de l'oxalate de chaux dans le règne minéral. Ann. Chim. Phys. 28: 318–322.
Branth, J. S. D. and E. Rostrup. 1869. Lichenes Daniae eller Danmarks laver. Bot. Tidsskr. 3: 127–275.
Brunfels, O. 1530. Herbarum Vivae Eicones. Strassburg: Schott.
Buhse, F. 1846. Ueber den Bau der Flechten. Correspondenzbl. Naturf. Vereins Riga 1: 158–163.
Burkholder, P. R. and A. W. Evans. 1945. Further studies on the antibiotic activity of lichens. Bull. Torrey Bot. Club 72: 157–164.
Burkholder, P. R., A. W. Evans, I. McVeigh and H. K. Thornton. 1944. Antibiotic activity of lichens. Proc. Natl. Acad. Sci. U.S.A. 30: 250–255.
Bustinza, F. 1951. Antibacterial substances from lichens. Endeavour 10: 95–99.
Chodat, R. 1913. Monographie d'algues en culture pure. Beitr. Kryptogamenfl. Schweiz 4(2): i–xii, 1–266.
Chopra, G. L. 1934. Lichens of the Himalayas. Part I. Lahore: University of the Punjab.
Cittadino, E. 1980. Ecology and the professionalization of botany in America, 1890–1905. Stud. Hist. Biol. 4: 171–198.
Claësson, P. 1878. Om de en- och flervärdiga alkoholernas jemte kolhydraternas sulfater. In: Anonymous, ed. 1878. Minnesskrift utgifven af Kongl[iga] Fysiografiska Sällskapet i Lund med Anledning af dess Hundraårsfest den 3 October 1878. Lund: Berling. Pp. 1–66.

Crum, H. 1993. A lichenologist's view of lichen manna. Contr. Univ. Michigan Herb. 19: 293–306.
Cummings, C. 1898. Text-book of Lichenology. [Review.] Bot. Gaz. 25: 284–286.
Cuthbert, J. B. 1930. Some notes on the physiology of *Teloschistes flavicans*. Trans. Roy. Soc. South Africa 19: 27–44.
Cuthbert, J. B. 1934. Further notes on the physiology of *Teloschistes flavicans*. Trans. Roy. Soc. South Africa 22: 35–54.
Dalla Torre, K. W. von and L. Sarntheim. 1902. Die Flechten (Lichenes) von Tirol, Vorarlberg und Liechtenstein. Innsbruck: Wagner.
Darbishire, O. V. 1900. Ueber die Apothecienentwicklung der Flechte *Physcia pulverulenta* (Schreb.) Nyl. Jahrb. Wiss. Bot. 34: 329–345.
Darbishire, O. V. 1914. Some remarks on the ecology of lichens. J. Ecol. 2: 71–82.
Dickie, G. 1839. Remarks on the reproductive organs of lichens. Ann. Nat. Hist. 3: 165–167.
Dillenius, J. J. 1742 (1741). Historia Muscorum. Oxford: Sheldonian Theatre.
Dioscorides. 1934. The Greek Herbal of Dioscorides Illustrated by a Byzantine A.D. 512, Englished by John Goodyer A.D. 1655, ed. R. T. Gunther. Oxford: For the author.
Dodge, C. W. and G. E. Baker. 1938. Botany of the Second Byrd Antarctic Expedition. II. Lichens and lichen parasites. Ann. Missouri Bot. Gard. 25: 515–718.
Doidge, E. M. 1950. The South African fungi and lichens to the end of 1945. Bothalia 5: 1–1094.
Dörrien, C. H. 1777. Verzeichniss und Beschreibung der sämtlichen in den Fürstlich Oranien-Nassauischen Landen wildwachsenden Gewächse. Herborn: Academic Press.
Drews, G. 2000. Anton de Bary, ein bedeutender Biologe, lehrte in Freiburg, Halle und Strassburg. Freiburger Universitätsblätter 149: 5–25.
Dugan, F. M. 2008. Fungi in the Ancient World. St. Paul, Minn.: American Phytopathological Society.
Du Rietz, G. E. 1921. Zur methodologischen Grundlage der modernen Pflanzensoziologie. Uppsala: For the author.
Duvigneaud, P. 1939. Notes de microchimie lichénique. Bull. Soc. Roy. Bot. Belgique 71: 192–198.
Ellée, O. 1939. Über die Kohlensäureassimilation von Flechten. Beitr. Biol. Pflanzen 26: 250–288.
Eschweiler, F. G. 1824. Systema Lichenum. Nuremberg: Schrag.
Evans, A. W. 1943. Asahina's microchemical studies on the Cladoniae. Bull. Torrey Bot. Club 70: 139–151.
Famintzin, A. and J. Baranetzky. 1867. Sur le changement des gonidies en zoospores. Ann. Sci. Nat., Bot., sér. 5. 8: 137–144.
Fée, A.-L.-A. 1824–1837. Essai sur les Cryptogames des Écorces Exotiques Officinales. 2 vols. Paris: Didot (vol.1); Paris and Strasbourg: Didot and Levrault (vol. 2).
Filson, R. B. 1976. Australian lichenology: A brief history. Muelleria 3: 183–190.
Fink, B. 1896. Contributions to a knowledge of the lichens of Minnesota.—I. Lichens of the Lake of the Woods. Minnesota Bot. Stud. 1: 693–701.
Fink, B. 1899. Contributions to a knowledge of the lichens of Minnesota.—V. Lichens of the Minnesota Valley and southwestern Minnesota. Minnesota Bot. Stud. 2: 277–329.
Fink, B. 1902. Ecologic distribution an incentive to the study of lichens. Bryologist 5: 39–40.
Fink, B. 1903. Some common types of lichen formations. Bull. Torrey Bot. Club 30: 412–418.
Fink, B. 1904. Two centuries of North American lichenology. Proc. Iowa Acad. Sci. 11: 11–38.
Fink, B. 1910. The lichens of Minnesota. Contr. U.S. Natl. Herb. 14: i–viii, 1–269, ix–xvii.
Fink, B. 1913. The nature and classification of lichens—II. The lichen and its algal host. Mycologia 5: 97–166.
Fink, B. 1935. The Lichen Flora of the United States. Ann Arbor: University of Michigan Press.
Fischer, E. and H. O. L. Fischer. 1913. Über die Carbomethoxy-derivate der Phenol-carbonsäuren und ihre Verwendung für Synthesen. VIII. Derivate der Orsellinsäure und α-Resorcylsäure. Ber. Deutsch. Chem. Ges. Berlin 46: 1138–1148.
Fischer, E. and H. O. L. Fischer. 1914. Synthese der o-Diorsellinsäure und Struktur der Evernsäure. Ber. Deutsch. Chem. Ges. Berlin 47: 505–512.
Fischer, E. and K. Freudenberg. 1910. Ueber die Carbomethoxyderivate der Phenolcarbonsäure und ihre Verwendung für Synthesen. IV. Justus Liebigs Ann. Chem. 372: 32–68.
Fischer, H. 1929. Mittelalterliche Pflanzenkunde. Munich: Münchner Drucke.
Forssell, K. B. J. 1884. Lichenologische Untersuchungen. Flora 67: 1–8, 33–46, 58–63, 177–193.
Frank, A. B. 1876. Ueber die biologischen Verhältnisse des Thallus einiger Krustenflechten. Beitr. Biol. Pflanzen 2: 123–200.
Frey, E. 1922. Die Vegetationsverhältnisse der Grimselgegend im Gebiet der zukünftigen Stauseen. Mitth. Naturf. Ges. Bern 6: i–iv, 1–195.
Friederich, A. 1906. Beiträge zur Anatomie der Silikatflechten. Beitr. Wiss. Bot. (Stuttgart) 5: 377–404.

Fries, E. 1831. Lichenographia Europaea Reformata. Lund: Berling.
Fries, T. M. 1861. Genera Heterolichenum Europaea Recognita. Uppsala: Edquist.
Fries, T. M. 1871–1874. Lichenographia Scandinavica. 2 vols. Uppsala: Berling.
Fuchs, L. 1542. De Historia Stirpium. Basel: Isingrin.
Fünfstück, M. 1884. Beiträge zur Entwickelungsgeschichte der Lichenen. Jahrb. Königl. Bot. Gart. Berlin 3: 155–174.
Fünfstück, M. 1898. Lichenes (Flechten). A. Allgemeiner Teil. In: A. Engler and K. Prantl, eds. 1887–1915. Die natürlichen Pflanzenfamilien. 244 fascs. Leipzig: Engelmann. Sect. 1. pt. 1*, fasc. 180. Pp. 1–48.
Fünfstück, M. 1926. Lichenes (Flechten). A. Allgemeiner Teil. In: A. Engler et al., eds. 1924+. Die natürlichen Pflanzenfamilien, ed. 2. 26 vols. Leipzig and Berlin: Engelmann. Vol. 8. Pp. 1–60.
Galløe, O. 1908. Danske likeners økologie. Bot. Tidsskr. 28: 285–372.
Galloway, D. J. 1985a. Lichenology in the South Pacific, 1790–1840. In: A. Wheeler and J. H. Price, eds. 1985. From Linnaeus to Darwin. London: Society for the History of Natural History. Pp. 205–214.
Galloway, D. J. 1985b. Flora of New Zealand: Lichens. Wellington: Hasselberg.
Georgi, I. G. 1782. Scrutamen chemicum lichenum parasiticorum. Acta Acad. Sci. Imp. Petrop. 6: 282–292.
Godlewski, E. 1874. Some experiments on lichen respiration (original title in Polish). Rozpr. Spraw. Posiedzeń Wydz. Mat.-Przyr. Akad. Umiejetn. 1: 247–256. [French translation published in Anonymous, ed. 1930. Oeuvres d'Emile Godlewski. Kraków: Academy of Sciences. Vol. 1. Pp. 209–216.]
Greene, E. L. 1983. Landmarks of Botanical History, ed. F. N. Egerton. 2 vols. Stanford: Stanford University Press.
Grummann, V. 1974. Biographisch-bibliographisches Handbuch der Lichenologie. Lehre: Cramer.
Hacquet, B. 1777. Beschreibung und Abbildung einer zweifelhaften Pflanze. Beschäft. Berlin. Ges. Naturf. Freunde 3: 241–252.
Hagen, C. G. 1782. Tentamen Historiae Lichenum. Königsberg: Hartung.
Harmand, J. 1894–1899. Catalogue descriptif des lichens observés dans la Lorraine. Bull. Soc. Sci. Nancy 29: 43–115, 30: 307–397, 31: 194–273, 32: 162–259, 33: 33–121, 34: 46–124. [Also issued as a 513 p. separate, with t. p. dated 1894, by Berger-Levrault, Nancy.]
Haugsjå, P. 1930. Über den Einfluss der Stadt Oslo auf die Flechtenvegetation der Bäume. Nyt Mag. Naturvidensk. 68: 1–116.
Hedwig, J. 1784. Theoria Generationis et Fructificationis Plantarum Cryptogamicarum Linnaei. St. Petersburg: Academia Imperialis Scientiarum.
Heeren, F. 1830. Untersuchungen über die Bildung des Flechtenrothes. J. Chem. Phys. (Nuremberg) 29: 313–355.
Hilitzer, A. 1925. Étude sur la végétation épiphyte de la Bohême. Prague: Faculty of Sciences.
Hoffmann, G. F. 1790–1801. Descriptio et Adumbratio Plantarum e Classe Cryptogamica Linnaei quae Lichenes dicuntur. 3 vols. Leipzig: Crusius.
Holle, G. von. 1849. Zur Entwicklungsgeschichte von *Borrera ciliaris*. Göttingen: Huth.
Hue, A.-M. 1898–1901. Lichenes Extra-Europaei a pluribus collectoribus ad Museum Parisiense missi. Nouv. Arch. Mus. Hist. Nat., sér. 3. 10: 213–280; sér. 4. 1: 27–220, 2: 49–122, 3: 21–146.
Hue, A.-M. 1906–1910. Lichenes morphologice et anatomice disposuit. Nouv. Arch. Mus. Hist. Nat., sér. 4. 8: 237–272, 10: 169–224; sér. 5. 1: 110–166, 2: 1–119.
Ikoma, Y. 1983. Macrolichens of Japan and Adjacent Regions. Tottori City: For the author.
Itzigsohn, H. 1854. Wie verhält sich *Collema* zu *Nostoc* und den Nostochineen? Bot. Zeitung (Berlin) 12: 521–527.
Itzigsohn, H. 1863. Bitte an die Herren Lichenologen wegen *Ephebe pubescens* Fries. Bot. Zeitung (Berlin) 21: 147–148.
Jatta, A. 1909–1911. Lichenes. In: Società Botanica Italiana, ed. 1905–1916. Flora Italica Cryptogama. 3 pts. Rocca San Casciano: Cappelli. Pt. 3. Pp. 1–958.
Jørgensen, P. M. 2007. History of lichenology in Norway up to 1973. In: I. Kärnefelt and A. Thell, eds. 2007. Lichenological Contributions in Honour of David Galloway. Berlin and Stuttgart: Borntraeger. Pp. 41–61.
Jumelle, H. 1892. Recherches physiologiques sur les lichens. Rev. Gén. Bot. 4: 49–64, 103–121, 159–175, 220–231, 259–272, 305–320. [Also issued as a 92 p. separate by Klincksieck, Paris.]
Jussieu, A. de. 1730. De la nécessité d'établir dans la méthode nouvelle des plantes, une classe particulière pour les fungus. Hist. Acad. Roy. Sci. Mém. Math. Phys. (Paris, 4to) 1730: 377–383.
Kane, R. 1840. Contributions to the chemical history of archil and of litmus. Philos. Trans. Roy. Soc. London 130: 273–324.

Kershaw, K. A. 1985. Physiological Ecology of Lichens. Cambridge: Cambridge University Press.
Klement, O. 1955. Prodromus der mitteleuropäischen Flechtengesellschaften. Feddes Repert. Spec. Nov. Regni Veg., Beih. 135: 5–194.
Knowles, M. C. 1913. The maritime and marine lichens of Howth. Sci. Proc. Roy. Dublin Soc., n.s. 14: 79–143.
Koerber, G. W. 1855. Systema Lichenum Germaniae. Breslau: Trewendt and Granier.
Krabbe, G. 1882. Entwickelung, Sprossung und Theilung einiger Flechtenapothecien. Bot. Zeitung (Berlin) 40: Cols. 66–83.
Krempelhuber, A. von. 1867–1872. Geschichte und Litteratur der Lichenologie. 3 vols. Munich: For the author.
Lang, E. 1906. Beiträge zur Anatomie der Krustenflechten. Beitr. Wiss. Bot. (Stuttgart) 5: 162–188.
Lange-de la Camp, M. 1933. Kulturversuche mit Flechtenpilzen (*Xanthoria parietina*). Arch. Mikrobiol. 4: 379–393.
Leighton, W. A. 1871. The Lichen-Flora of Great Britain, Ireland and the Channel Islands. Shrewsbury: For the author.
Leighton, W. A. 1879. The Lichen-Flora of Great Britain, Ireland, and the Channel Islands, ed. 3. Shrewsbury: For the author.
Lindau, G. 1888. Über die Anlage und Entwicklung einiger Flechtenapothecien. Flora 71: 451–489.
Lindau, G. 1895. Lichenologische Untersuchungen. I. Ueber Wachstum und Anheftungsweise der Rindenflechten. Dresden: Heinrich.
Lindau, G. and P. Sydow. 1908–1917. Thesaurus Litteraturae Mycologicae et Lichenologicae. 5 vols. Leipzig: Borntraeger.
Link, D. H. F. 1807. Grundlehren der Anatomie und Physiologie der Pflanzen. Göttingen: Danckwerts.
Linnaeus, C. 1753. Species Plantarum. 2 vols. Stockholm: Salvius.
Lister, M. 1671. Some observations, touching colours, in order to the increase of dyes, and the fixation of colours. Philos. Trans. 6: 2132–2136.
Lucas, A. and J. R. Harris. 1962. Ancient Egyptian Materials and Industries, ed. 4. London: Arnold.
MacMillan, C. 1897. Observations on the distribution of plants along shore at Lake of the Woods. Minnesota Bot. Stud. 1: 949–1023.
Malpighi, M. 1675–1679. Anatome Plantarum. 2 vols. London: Martyn.
Marcelli, M. P. and M. R. D. Seaward. 1998. Lichenology in Latin America: History, Current Knowledge and Application. São Paulo: Cetesb.
Massalongo, A. 1852. Ricerche sull'Autonomia dei Licheni Crostosi e Materiali pella loro Naturale Ordinazione. Verona: Frizierio.
Massalongo, A. 1853. Memorie Lichenografiche con un Appendice alle Ricerche sull'Autonomia dei Licheni Crostosi. Verona: Münster.
[Massee, G.] 1894. Bibliography. Grevillea 22: 79–82.
Mattioli, P. A. 1586. De Plantis Epitome. Frankfurt: N.p.
Meyer, G. F. W. 1825. Die Entwickelung, Metamorphose und Fortpflanzung der Flechten. Göttingen: Vandenhoeck and Ruprecht.
Micheli, P. A. 1729. Nova Plantarum Genera iuxta Tournefortii Methodum disposita. Florence: Paperini.
Mitchell, M. E. 1995. 150 years of Irish lichenology: A concise survey. Glasra, n.s. 2: 139–155.
Mitchell, M. E. 2002. "Such a strange theory": Anglophone attitudes to the discovery that lichens are composite organisms, 1871–1890. Huntia 11(2): 193–207.
Mitchell, M. E. 2005. The inside story: A commentary on the study of lichen structure in the 18th and 19th centuries. Huntia 12(1): 13–29.
Mitchell, M. E. 2006. "Function is smother'd in surmise": A survey of observations on the rôle of lichen conidia, 1850–2000. Huntia 12(2): 149–167.
Mitchell, M. E. 2007. Signposts to symbiosis: A review of early attempts to establish the constitution of lichens. Huntia 13(1): 101–120.
Mitchell, M. E. 2009. Graphic developments: Lichen illustration in scientific publications, 1679–1900. Huntia 14(1): 5–22.
Möller, A. 1887. Ueber die Cultur flechtenbildender Ascomyceten ohne Algen. Münster: Coppenrath.
M[ohl], H. [von] 1863. Giambattista Amici. Bot. Zeitung (Berlin) 21: Beilage, pp. 1–8.
Monkewitz, J. H. 1817. Chemisch-medicinische Untersuchung über die Wandflechte. Dorpat: Schünmann.
Moreau, F. and [V.] Moreau. 1918. La biomorphogénèse chez les lichens. Bull. Trimestriel Soc. Mycol. France 34: 84–85.
Moreau, F. 1928. Les Lichens. Paris: Lechevalier.
Mulder, G. J. 1838. Over de Zamenstelling van … Ijslandsche Mosmeel en Atlantsmeel. Natuur- Scheik. Arch. 5: 546–605.
Neumann, C. 1749–1755. Chymiae Medicae Dogmatico-Experimentalis, ed. C. H. Kessell. 4 vols. in 10 pts. Züllichau: Dendeler. Vol. 2, pt. 4, pp. 55–56.
Nienburg, W. 1926. Anatomie der Flechten. Berlin: Borntraeger.
Notaris, G. De. 1846. Frammenti lichenografici di un lavoro inedito. Giorn. Bot. Ital. 2: 174–224.
Nylander, W. 1853. Collectanea lichenologica in Gallia meridionali et Pyrenaeis. Nya Bot. Not. 1853: 151–165.
Nylander, W. 1854. Essai d'une nouvelle classification des lichens. Mém. Soc. Sci. Nat. Cherbourg 2: 5–16.

Nylander, W. 1857. Prodromus lichenographiae Galliae et Algeriae. Actes Soc. Linn. Bordeaux 21: 249–467.
Nylander, W. 1858–1869. Synopsis Methodica Lichenum. 2 vols. Paris: Martinet.
Nylander, W. 1865. Ad historiam reactionis iodi apud lichenes et fungos notula. Flora 48: 465–468.
Nylander, W. 1866a. Circa novum in studio lichenum criterium chemicum. Flora 49: 198–201.
Nylander, W. 1866b. Quaedam addenda ad nova criteria chemica in studio lichenum. Flora 49: 233–234.
Nylander, W. 1870. Animadversio de theoria gonidiorum algologica. Flora 53: 52–53.
Nylander, W. 1888. Lichenes Novae Zelandiae. Paris: Schmidt.
Ochsner, F. 1927. Studien über die Epiphyten-Vegetation der Schweiz. Jahrb. St. Gallischen Naturwiss. Ges. 63: Beilage, pp. 1–108.
Parkinson, J. 1640. Theatrum Botanicum. London: Cotes.
Paternò, [E.] and [A.] Oglialoro. 1877. Sopra un nuovo acido estratto dalla *Lecanora atra*. Atti Reale Accad. Lincei, ser. 3. Transunti 1: 145–147.
Pelletier, P. J. and J. Caventau. 1817. Sur la matière verte des feuilles. J. Pharm. Sci. Accessoires 3: 486–491.
Persoon, C. H. 1794. Einige Bemerkungen über die Flechten. Ann. Bot. (Usteri) 7: 1–32, 155–158.
Pišút, I. 2002. Alexander Zahlbruckner (1860–1938): The author of two historical milestones in lichenology. Bryologist 105: 243–245.
Pliny. 1960. Natural History, vol. 4, bks. 12–16, transl. H. Rackham. Cambridge, Mass.: Harvard University Press; London: Heinemann.
Pliny. 1961. Natural History, vol. 7, bks. 24–27, transl. W. H. S. Jones. Cambridge, Mass.: Harvard University Press; London: Heinemann.
Pliny. 1966. Natural History, vol. 6, bks. 20–23, transl. W. H. S. Jones. Cambridge, Mass.: Harvard University Press; London: Heinemann.
Plitt, C. C. 1934. Albert Schneider. Bryologist 37: 5–8.
Puymaly, A. de. 1924. Le *Chlorococcum humicola* (Naeg.) Rabenh. Rev. Algol. 1: 107–114.
Quispel, A. 1943–1945. The mutual relations between algae and fungi in lichens. Recueil Trav. Bot. Néerl. 40: 413–541.
Rabenhorst, L. 1844–1848. Deutschlands Kryptogamen-Flora. 2 vols. in 3 sections. Leipzig: Kummer. Vol. 2. Sect. 1.
Rabenhorst, L. 1884–1966. Kryptogamen-Flora von Deutschland, Österreich und der Schweiz, ed. 2. 14 vols. Leipzig: Akademische Verlagsgesellschaft. Vols. 8 and 9.
Ray, J. 1686–1704. Historia Plantarum. 3 vols. London: Clark (vols. 1 and 2), Smith and Walford (vol. 3).
Ray, J. 1724. Synopsis Methodica Stirpium Britannicarum, ed. 3. London: Innys.
Reess, M. 1872. Über die Entstehung der Flechte *Collema glaucescens* Hoffm. durch Aussaat der Sporen derselben auf *Nostoc lichenoides*. Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1872: 523–533.
Reinke, J. 1894–1896. Abhandlungen über Flechten. Jahrb. Wiss. Bot. 26: 495–542; 28: 39–150, 359–486; 29: 171–236.
Richard, O. J. 1883. Étude sur les substratums des lichens. Actes Soc. Linn. Bordeaux, sér. 4. 37: 1–88.
Riedl, H. 1988. Alexander Zahlbruckner and the Science Museum in Vienna (original title in Slovak). In: A. Lackovičová, ed. 1988. Alexander Zahlbruckner (1860–1938). Bratislava: Múzeum Petra Jilemnického. Pp. 17–24.
Robiquet, [P.-J.] 1829. Essai analytique des lichens de l'orseille. Ann. Chim. Phys. 42: 236–257.
Rochleder, F. and W. Heldt. 1843. Untersuchungen einiger Flechtenarten. Ann. Chem. Pharm. 48: 1–18.
Sachs, J. 1870. Lehrbuch der Botanik, ed. 2. Leipzig: Engelmann.
Salomon, H. 1914. Über das Vorkommen und die Aufnahme einiger wichtiger Nährsalze bei den Flechten. Jahrb. Wiss. Bot. 54: 309–347.
Schärer, L. E. 1820. Ueber den Bau des Thallus der Flechten. Naturwiss. Anz. Allg. Schweiz. Ges. Gesammten Naturwiss. 5: 67–69.
Schaerer, L. E. 1850. Enumeratio critica Lichenum Europaeorum. Bern: For the author.
Schneider, A. 1897. A Text-Book of General Lichenology. Binghamton, N.Y.: Clute.
Schneider, A. 1898. A Guide to the Study of Lichens. Boston: Whidden.
Schrader, H. A. 1794. Spicilegium Florae Germanicae. Hanover: Ritsdher.
Schunck, E. 1842. On some of the substances contained in the lichens employed for the preparations of archil and cudbear. London Edinburgh Dublin Philos. Mag. & J. Sci. 20: 495–500.
Schwarz, F. 1880. Chemisch-botanische Studien über die in den Flechten vorkommenden Flechtensäuren. Beitr. Biol. Pflanzen 3: 249–265.
Schwendener, S. 1860. Untersuchungen über den Flechtenthallus. Beitr. Wiss. Bot. (Leipzig) 2: 109–186.
Schwendener, S. 1863. Untersuchungen über den Flechtenthallus. II. Beitr. Wiss. Bot. (Leipzig) 3: 127–198.
Schwendener, S. 1868. Untersuchungen über den Flechtenthallus. II. Schluss. Beitr. Wiss. Bot. (Leipzig) 4: 161–202.

Schwendener, S. 1869. Die Algentypen der Flechtengonidien. Basel: Schultze.
Schwendener, S. 1872. Erörterungen zur Gonidienfrage. Flora 55: 161–176, 177–183, 193–202, 225–234.
Schwendener, S. 1873. Die Flechten als Parasiten der Algen. Verh. Naturf. Ges. Basel 5: 527–550.
Scott, G. D. 1957. Lichen terminology. Nature 179: 486–487.
Senft, E. 1908. Über ein neues Verfahren zum mikrochemischen Nachweiss von Flechtensäuren. Verh. Ges. Deutsch. Naturf. 79: 161–164.
Sernander, R. 1912. Studier öfver lafvarnes biologi. I. Nitrofila lafvar. Svensk Bot. Tidskr. 6: 803–883.
Shibata, S. 2000. Yasuhiko Asahina (1880–1975) and his studies on lichenology and chemistry of lichen metabolites. Bryologist 103: 710–719.
Smith, A. L. 1917. Lichenology, a new departure. Trans. British Mycol. Soc. 6: 32.
Smith, A. L. 1921. Lichens. Cambridge: Cambridge University Press.
Smyth, E. S. 1934. A contribution to the physiology and ecology of *Peltigera canina* and *P. polydactyla*. Ann. Bot. (Oxford) 48: 781–818.
Stålfelt, M. G. 1939. Der Gasaustausch der Flechten. Planta 29: 11–31.
Stafleu, F. A. and R. S. Cowan. 1976–1988. Taxonomic Literature, ed. 2. 7 vols. Utrecht: Bohn, Scheltema and Holkema.
Stahl, E. 1874. Beiträge zur Entwickelungsgeschichte der Flechten. Bot. Zeitung (Berlin) 32: 177–180.
Stahl, E. 1877. Beiträge zur Entwickelungsgeschichte der Flechten. 2 pts. Leipzig: Felix.
Stahlecker, E. 1906. Untersuchungen über Thallusbildung und Thallusbau in ihren Beziehungen zum Substrat bei siliciseden Krustenflechten. Beitr. Wiss. Bot. (Stuttgart) 5: 405–451.
Stenhouse. J. 1849. Examination of the proximate principles of some of the lichens. Part II. Philos. Trans. Roy. Soc. London 139: 393–401.
Stocker, O. 1927. Physiologische und ökologische Untersuchungen an Laub- und Strauchflechten. Flora 121: 334–415.
Strömberg, R. 1937. Theophrastea: Studien zur botanischen Begriffsbildung. Göteborgs Kungl. Vetensk. Samhälles Handl., ser. A. 6: 1–234.
Tanford, C. and J. Reynolds. 2001. Nature's Robots: A History of Proteins. Oxford: Oxford University Press.
Tehler, A. and M. Wedin. 2008. Systematics of lichenized fungi. In: T. H. Nash, ed. 2008. Lichen Biology, ed. 2. Cambridge: Cambridge University Press. Pp. 336–352.
Theophrastus. 2003. Théophraste: Recherches sur les Plantes, vol. 2, bks. 3 and 4, ed. and transl. S. Amigues. Paris: Les Belles Lettres.
Thomas, E. A. 1939. Über die Biologie von Flechtenbildnern. Beitr. Kryptogamenfl. Schweiz 9: 1–208.
Thomson, R. D. 1844. On parietin, a yellow colouring matter, and on the inorganic constituents of lichens. London Edinburgh Dublin Philos. Mag. & J. Sci. 25: 39–49.
Thwaites, G. H. K. 1849. On the gonidia of lichens. Ann. Mag. Nat. Hist., ser. 2. 3: 219–222.
Tobler, F. 1925. Biologie der Flechten. Berlin: Borntraeger.
Toni, G. B. De. 1933. L'Opera Lichenologica di Abramo Massalongo. Verona: Tipografica Veronese.
Torrey, R. H. 1935. Paraphenylenediamine, a new color test for lichens. Torreya 35: 110–112.
Tournefort, J. P. de. 1694. Elemens de Botanique. 3 vols. Paris: Imprimerie Royale.
Tournefort, J. P. de. 1700. Institutiones Rei Herbariae. 3 vols. Paris: Typographia Regia.
Tuckerman, E. 1847. A synopsis of the lichenes of the northern United States and British America. Proc. Amer. Acad. Arts 1: 195–285.
Tuckerman, E. 1882–1888. A Synopsis of North American Lichens. 2 vols. Boston: Cassino (vol. 1); New Bedford, Mass.: Anthony (vol. 2).
Tulasne, L.–R. 1852. Mémoire pour servir à l'histoire organographique et physiologique des lichens. Ann. Sci. Nat., Bot., sér. 3. 17: 5–128, 153–225.
Turner, W. 1538. Libellus de Re Herbaria. London. (Facsim. ed., 1965, W. T. Stearn, ed., London, Ray Society, pp. 41–60.)
Viereck, R. 2000. "Zwar sind es weibliche Hände": Die Botanikerin und Pädagogin Catharina Helena Dörrien (1717–1795). Frankfurt and New York: Campus.
Vitikainen, O. 2001. William Nylander (1822–1899) and lichen chemotaxonomy. Bryologist 104: 263–267.
Wainio, E. [A.] 1887–1897. Monographia Cladoniarum universalis. Acta Soc. Fauna Fl. Fenn. 4: 1–509, 10: 1–498, 14: 1–268.
Wainio, E. A. 1890. Étude sur la Classification Naturelle et la Morphologie des Lichens du Brésil. Helsinki: Simelius.
Wallroth, F. W. 1825–1827. Naturgeschichte der Flechten. 2 vols. Frankfurt: Wilmans.
Warming, E. 1909. Oecology of Plants, transl. P. Groom and I. B. Balfour. Oxford: Clarendon Press.
Weddell, [H. A.] 1873. Sur le rôle du substratum dans la distribution des lichens saxicoles. Compt. Rend. Hebd. Séances Acad. Sci. 77: 1247–1249.

Weddell, H. A. 1875. Excursion lichénologique dans l'Ile d'Yeu, sur la côte de la Vendée. Mém. Soc. Natl. Sci. Nat. Cherbourg 19: 251–316.
Weis, F. W. 1770. Plantae Cryptogamicae Florae Gottingensis. Göttingen: Vandenhoeck.
Werner, R.-G. 1931. Histoire de la synthèse lichénique. Mém. Soc. Sci. Nat. Maroc 27: 7–44.
Wiggers, H. 1846. Bericht über die Fortschritte der Pharmacognosie und Pharmacie. Jahresbericht über die Fortschritte in der Heilkunde 4: 1–204.
Winter, G. 1875. Zur Anatomie einiger Krustenflechten. Flora 58: 129–139.
Winter, G. 1876. Ueber die Gattung *Sphaeromphale* und Verwandte. Jahrb. Wiss. Bot. 10: 245–275.
Winter, G. 1877. Lichenologische Notizen I. Cephalodien von *Sticta* und *Solorina*. Flora 60: 177–184, 193–203.
Wolff, G. P. 1905. Beiträge zur Entwicklungsgeschichte der Flechtenapothecien. Flora 95: 31–57.
Zahlbruckner, A. 1903–1908. Lichenes (Flechten). B. Spezieller Teil. In: A. Engler and K. Prantl, eds. 1887–1915. Die natürlichen Pflanzenfamilien. 244 fascs. Leipzig: Engelmann. Sect. 1, pt. 1*, fasc. 217, pp. 49–96; fasc. 221, pp. 97–144; fasc. 225, pp. 145–192; fasc. 23, pp. 193–249.
Zahlbruckner, A. 1926. Lichenes (Flechten). B. Spezieller Teil. In: A. Engler et al., eds. 1924+. Die natürlichen Pflanzenfamilien, ed. 2. 26 vols. Leipzig: Engelmann. Vol. 8. Pp. 61–270.
Zahlbruckner, A. 1922–1940. Catalogus Lichenum Universalis. 10 vols. Leipzig: Borntraeger.
Zopf, W. 1890. Die Pilze. Breslau: Trewendt.
Zopf, W. 1895a. Zur Kenntnis der Flechtenstoffe. Justus Liebigs Ann. Chem. 284: 107–132.
Zopf, W. 1895b. Zur Kenntnis der Flechtenstoffe. Ueber Atranorsäure und ihre Begleitstoffe. Justus Liebigs Ann. Chem. 288: 38–74.
Zopf, W. 1903. Vergleichende Untersuchungen über Flechten in Bezug auf ihre Stoffwechselprodukte. Beih. Bot. Centralbl. 14: 95–126.
Zopf, W. 1907. Die Flechtenstoffe. Jena: Fischer.
Zopf, W. 1908. Beiträge zu einer chemischen Monographie der Cladoniaceen. Ber. Deutsch. Bot. Ges. 26: 51–113.
Zukal, H. 1895. Morphologische und biologische Untersuchungen über die Flechten (II. Abhandlung). Sitzungsber. Kaiserl. Akad. Wiss., Wien, Math.-Naturwiss. Cl., Abt. 1. 104: 1303–1395.