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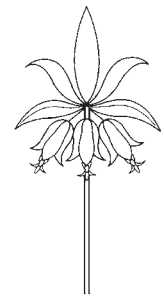

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Signposts to symbiosis: A review of early attempts to establish the constitution of lichens

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Abstract

Until the latter half of the 1860s, botanists had assumed that fungi growing in or on living plants behaved solely as parasites prospering at the expense of their hosts. Because host organisms are often characterized by conspicuous decline and early death, such associations were widely regarded as synonymous with disease and transience. Consequently, when the suggestion was advanced in 1866 that, rather than being the autonomous plants they seemed, lichens—long a symbol of vigor and durability—are the product of alliances between microscopic algae and fungi, few botanists were prepared to entertain the notion. But a presumption of algal and fungal participation in the composition of lichens was not, in fact, altogether new: 18th-century botanists had been aware of this possibility to the extent that some contemporary systematists had assigned lichens to the algae, others to the fungi. Early in the following century, however, that awareness had been rapidly eclipsed by a perception of lichens as plants distinct from either of those groups. Though results soon began to appear that were at odds with this view, these were either ignored or argued away. Evidence that algae and fungi do contribute to the formation of certain lichen thalli continued nonetheless to accumulate, until the concept of autonomy, which had prevailed for 50 years, eventually became no longer reasonably sustainable. This paper details the reporting of that evidence and reveals how a shadow that had flickered in the minds of botanists for over 150 years finally gained substance.

Introduction

When Joseph de Tournefort (1656–1708), professor of botany at the Jardin du Roi, came to prepare his *Elemens de Botanique* (1694), several quite unrelated plants had been categorized as lichens. That anomaly led Tournefort to attempt a scientific delimitation of the group: he created a genus *Lichen* (1:437–438) to accommodate such of the plants in question as exhibited similar fruit morphology.[1] Five years later, a corresponding category was introduced in the third volume of Robert Morison's *Plantarum Historiae Universalis Oxoniensis*; this volume was completed over an eight-year period following Morison's death in 1683 by Jacob Bobart (1641–1719), superintendent of the University's physic garden. While Bobart was aware of the generic name proposed by Tournefort, he chose not to use it, preferring to describe his 50-odd species (Morison 1680–1699, 3:631) as "Moss-Fungi" ("Musco-Fungos").[2] In the event, the name proposed by Bobart yielded to that of Tournefort, but its evocation of fungal affinity endured.

The first botanist to state that fungi and lichens are related was Antoine de Jussieu (1686–1758), a successor to Tournefort at the Jardin du Roi. In a paper presented to the Académie Royale des Sciences, Jussieu (1730, p. 377) remarked apropos of fungi that "if one looks in the classes of plants for a genus they resemble and to which they may be compared, the only one found is *Lichen*," and he further observed (p. 378) that fungi and lichens "show an almost identical method of producing their seed."[3] Jussieu's comments do not, however, appear to have at all attracted the attention of contemporary botanists[4]—when Linnaeus came to deal with the lichens, he assigned them not to his order Fungi but, with a few exceptions, to the Algae (1753, 2:1140–1156).

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After ten years in their Linnaean home, lichens were again on the move: the French botanist Michel Adanson (1727–1806) combined them with the fungi in his attempt at a natural classification (1763–1764, 2:6–7), but that bid to establish the systematic position of lichens found no immediate support. The Swiss polymath Albrecht von Haller (1708–1777) preferred to accommodate them in a distinct class "Lichenes," one subdivision of which he designated "Lichenes Gelatinosi. Nostoch" (1768, 3:94); Haller thus became the first to provide a collective name for that distinctive group of lichens and to associate them with an algal genus.[5] No further inklings of a relationship between lichens and either algae or fungi appear to have been reported until the late 1780s when the Austrian cryptogamist Johann Hedwig (1730–1799) referred (1787–1797, 2:[i]) to the bond ("nexum") that he considered to exist between fungi and lichens.[6] In the same work (p. 3) Hedwig reported his conviction, based on the internal structure of certain lichen fruit bodies, that there is "substantial correspondence between lichens and the Pezizas of Linnaeus or Elvelas of Gleditsch … certainly, everything properly considered, the complete conformity and affinity of all these is not to be denied — to the extent that if plants of this genus *[Lichen]* were to find a place among the fungi, then the fungi should in the same way be linked to lichens in the systematic arrangements of botanists."[7]

Evidence of such a link had likewise been observed by the mycologist Christiaan Persoon (1761–1836), a Capetonian of Dutch/German parentage. He commented (1794, p. 7) that "no plants have fruits more similar to those of fungi than lichens; if the crust is ignored, the scutellate [apotheciate] lichens can reasonably be viewed as a family of the cup fungi — the *Opegraphae* can be referred to the *Hysteriae*, while the *Endocarpa* and the *Verrucariae* can be taken for *Sphaeria*."[8] Also in the 1790s, the possibility was again raised that lichens are in some way related to algae: the French abbé and botanist Etienne Ventenat (1757–1808) — influenced perhaps by Haller — queried (1799, 2:36) whether "gelatinous lichens might not be instances of *Nostoc* having changed appearance."[9]

At the opening of the 19th century, therefore, botanists recognized that algae are somehow associated with the development of certain lichens, and fungi with that of others. Ten years later, however, in consequence of an uncompromising statement by the Swedish lichenologist Erik Acharius (1757–1819), botanists largely abandoned that view. In his authoritative *Lichenographia Universalis* (1810, p. 14), Acharius declared

> To summarize from a complete and careful examination of all the parts, I have concluded that lichens represent a special, natural, group separate from other cryptogamic plants and distinguished by the following arrangement: general receptacle (thallus) polymorphic, rootless, lacking a stem, perennating, with extremely small propagative bodies (gongyles) as much dispersed through all its substance — internally, externally and plentifully in cavities — as enclosed in distinct, colored, carpomorphic organs (partial receptacles or apothecia). It is evident from the arrangement indicated that, by their receptacles of double structure together with their different forms and nature, lichens remain quite distinct from algae, hepatics and fungi.[10]

This categoric statement from so influential a source was to cast a long shadow: for 50 years the concept of lichen autonomy led botanists to ignore growing evidence of algal and fungal participation in lichen development.

Findings incompatible with autonomy

The first intimation of a relationship between algae and lichens to appear after Acharius' pronouncement came from the French jurist

and botanist Henri Cassini (1781–1832). Having, as he wrote (1817, p. 396), "always been struck by the extreme analogy evident between common *Nostoc* and certain species of lichen that modern cryptogamists combine in the genus *Collema*"[11] (see Fig. 1), Cassini investigated both organisms in a mixed stand. He reported the *Collema* thalli occurring there as covered with loosely adhering "globules gélatineux" that, he claimed, either fixed themselves to the soil on becoming detached and gave rise to new *Collema* thalli or remained altogether free and developed into *Nostoc*. This belief led Cassini to conclude, in opposition to Ventenat, that *Nostoc* was nothing more than a "variété monstrueuse d'une espèce de colléma"; he did, however, stress that his conclusion was tentative and express the hope that others would repeat his investigation—a hope not early realized.

An affinity between *Collema* and *Nostoc* was likewise accepted by the Swedish phycologist Carl Agardh (1785–1859), professor of botany at the University of Lund. He claimed to have seen his *N. muscorum* var. *lichenoides* develop into *C. limosum* (1820, p. 11), and he further stated that this was not the only instance of an alga developing into a lichen because some botanists had reported seeing the filamentous *Scytonema atrovirens* and *S. byssoideum* with apothecia.[12] The botanists Agardh had in mind would appear to have included his mycologist colleague Elias Fries (1794–1878) who based his lichen genera *Ephebe* and *Thermutis* on the *Scytonema* species in question.[13] Also at this time, Fée (1824, p. xxii) visualized the Nostocaceae as "evidently corresponding to incomplete *Collemata*."[14]

Despite this interest, *Collema* and the filamentous lichens were still a good deal less favored than their more conspicuous, non-gelatinous, relatives as subjects for investigation—particularly in the emerging field of lichen structure. Here Kurt Sprengel

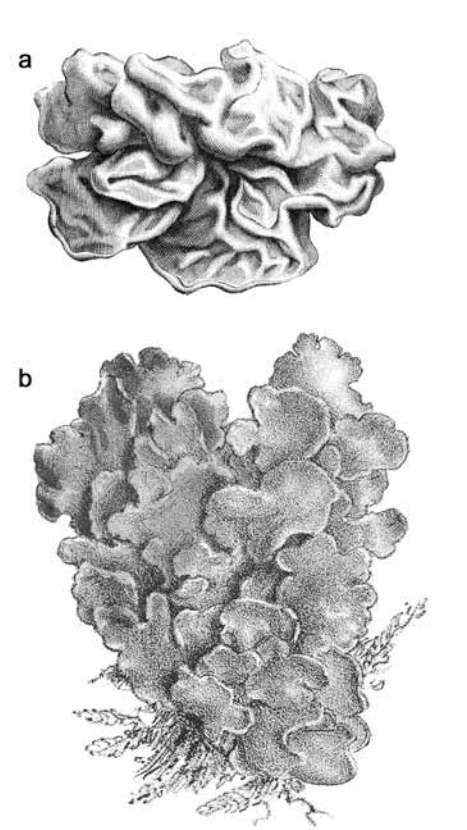

Figure 1. Gelatinous counterparts, *a*: *Nostoc* colony. (From Micheli 1729, pl. 67, fig. 1); *b*: sterile *Collema* thallus. (From Schaerer 1850, pl. 10, fig. 3.)

(1766–1833), professor of botany at the University of Halle, demonstrated (1802–1804, 3:325) the presence of a green, subcortical layer that was soon shown by a fellow German botanist, Heinrich Link (1767–1851), to consist of unicells; because he found these to be identical with the green constituents of soredia, Link (1807, p. 22) concluded that all those cells serve a purely reproductive function (1807, p. 22). This interpretation was enthusiastically promoted by Friedrich Wallroth (1792–1857), medical officer at

Nordhausen (North Thuringia): having applied the terms "Brutzellen" ("brood cells") to the unicells in general, "gonidium" to an individual cell and "stratum gonimon" to the entire green layer,[15] Wallroth (1825–1827, 1:40) declared

> in the whole economy of the lichen thallus we know of no component that has been so absurdly misunderstood, none to which Nature has assigned a purpose so important but at the same time so hidden, or given so versatile a power of development and metamorphosis, though one so carelessly observed by Acharius and, with the exception of Link, all other lichen specialists; we know of none that Nature later concealed so carefully, distributed so universally as that we have designated … by the name brood cells.[16]

Wallroth's endorsement of Link's misinterpretation lent credence to the doctrine of autonomy by appearing to establish that the green cells of lichens are endogenous asexual propagules.

The term "gonidium" won general acceptance following its use by Fries (1831). Though supportive of Link and Wallroth's contention that the green cells of lichens were to be understood as reproductive bodies, Fries was clearly aware of their algal nature, believing them to be representatives of the genus *Chlorococcum*, which he had introduced some years earlier (1825, p. 356); constrained, however, by the belief that lichens are independent plants, Fries wrongly interpreted his insight and concluded (1831, p. xx) that "*Chlorococcum* is a free, self-supporting, gonidium."[17]

The Austrian botanist Franz Unger (1800–1870) also recognized the algal nature of the green cells present in lichens. Until his appointment as professor of botany and zoology at the University of Graz in 1835, Unger was medical officer in Kitzbühel (Tirol), where he undertook a study of subaerial algae. While this led him to suppose (1833, p. 524–528) that multicellular algae could develop from the unicellular *Desmococcus olivaceus* (as *Protococcus viridis*), Unger did nonetheless accurately report the occurrence of algal unicells in the thallus of *Xanthoria parietina* (as *Parmelia parietina*); he recorded this in an imaginative diagram prepared to illustrate his presumed relationships (see Fig. 2). Unger's observations may have influenced the German phycologist Friedrich Kützing (1807–1893) who also entertained transfomationist notions at this time (Müller and Zaunick 1960, p. 15). An examination of corticolous *X. parietina* thalli convinced Kützing (1833, pp. 350–351) that their green constituents represent unicellular algae, which he assumed to be the same as those he had found growing adjacent to the thalli and which, in common with Unger, he labelled "*Protococcus viridis*." Kützing believed that, starting with *Protococcus*, he had followed "all stages in the growth of *Parmelia* from origin to complete development"[18] but was understandably non-committal as to the detail of those steps.

At this stage, it might reasonably have been expected that a lengthy dissertation on gonidia prepared at the University of Berlin in 1839 by Gustav Koerber (1817–1885) would have included consideration of the evidence linking gonidia with algae. But Koerber not alone omitted any mention of Fries' having equated *Chlorococcum* with liberated gonidia, he altogether ignored the views of Kützing, Unger and those who preceded them. Later, in a paper designed to expand on his 1839 work, Koerber (1841, p. 12) remarked that, given the structural similarity between *Collema* and *Nostoc*, "one could be tempted to number the gelatinous lichens among the algae, which, apart from their fruits, they so closely resemble"[19]; he did not, however, choose to pursue that resemblance.

On the other hand, when Kützing (1841, p. 83) came to report on plants belonging to

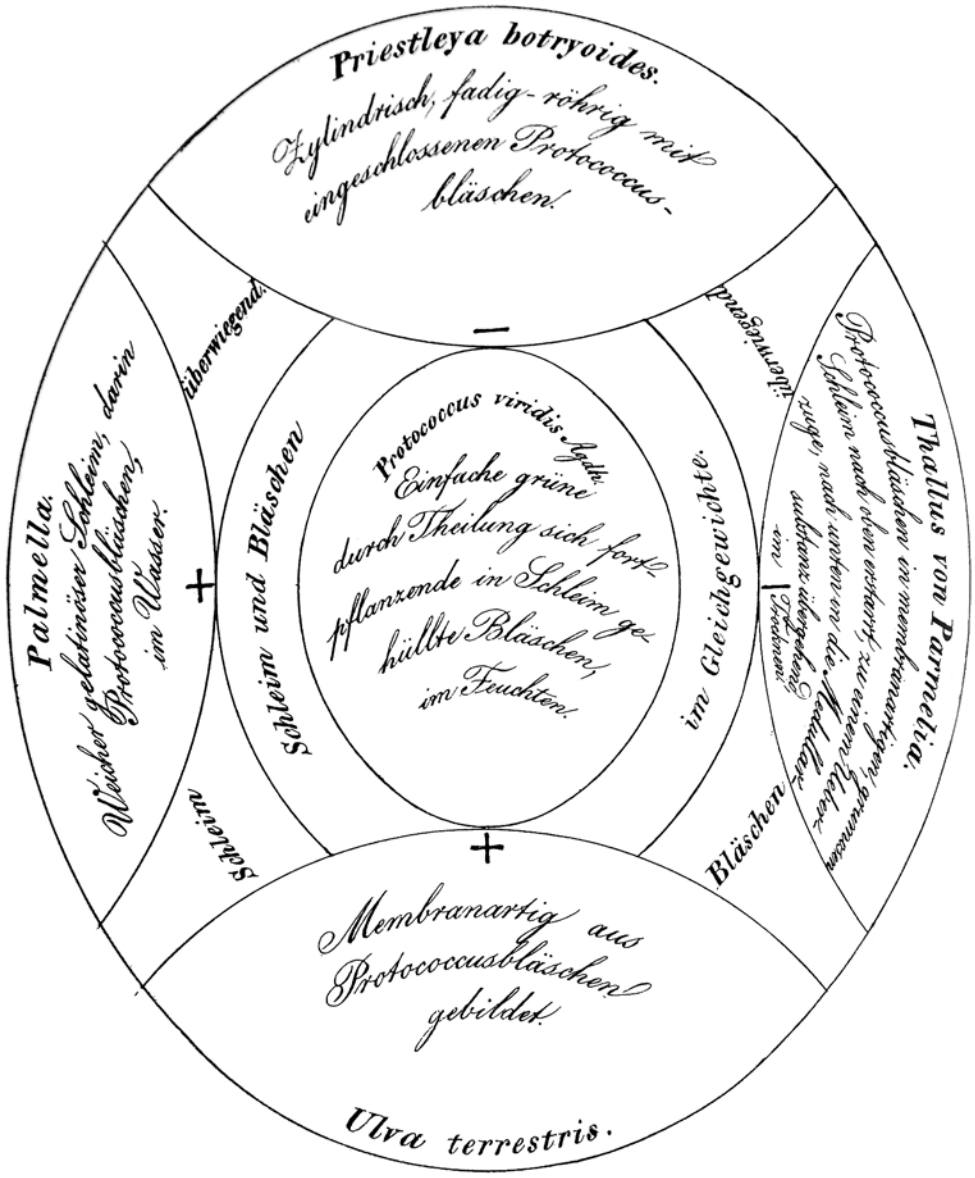

Figure 2. Green algal cells reported (right-hand segment) as lichen components. (From Unger 1833, p. 540.)

those same genera, he showed himself to be a good deal more insightful: an awareness of the fundamental rôle played by *Nostoc* filaments in the formation of *Collema* thalli is implicit in his statement that "as regards structure, the *Nostoc* stage of *Collema* development in no way differs from other *Nostoc* species."[20] Kützing also studied the structure of *Collema* fruit bodies, the asci of which led him to observe (1841, p. 85, fn.) "how remarkable the great similarity is, in this regard, with many *Pezizae*,"[21] and to report a tangle ("Gewirr") of moniliform and ramified filaments below the asci. This was the first clear demonstration that two types of filament are present in *Collema* thalli, but Kützing did not realize that they belong to separate organisms. In his view (1843, p. 204), the filaments were different manifestations of a single type: "in gelatinous lichens, moniliform texture is only found close to the surface; lower down the parts lengthen and thin out into very delicate filaments that, having altogether lost their moniliform appearance, extend beyond the covering of the thallus and form root fibrils."[22]

Kützing's observations were brought to the attention of a wide audience when Matthias Schleiden (1804–1881), professor of botany at the University of Jena, incorporated them in his celebrated textbook (1842–1843).[23] Having informed his readers (2:25) that "it is wholly impossible to distinguish *Undina [Nostoc]* (Algae) and *Collema* (Lichens)," Schleiden then went on to state (2:26), "[i]f we look, on the one hand, at the … fruits of the gelatinous Lichens and the species of *Peziza*, and on the other at the *Sphaeriae*, which agree with many of the Lichens, we soon see that no very marked difference can be established between Lichens and *Fungi* from their conditions of consistence and structure," and, accordingly, he assigned "the *Pyrenomycetes* and the *Discomycetes* to the Lichens, which, as far as regards the former of the two, appears in conformity with a natural arrangement, and is not very extravagant with respect to the latter." Schleiden further emphasized this point with the comment (2:39) that "[m]ost of the smaller species of *Peziza* are altogether deficient in any characteristic by which they may be distinguished from the apothecia of Lichens."[24] Though Morton (1981, p. 377) claimed that Schleiden's textbook "had a profound effect—acknowledged by all contemporary botanists—in stimulating a new outlook and direction in botany," there were some who did not respond quite so positively: while it is evident, at least with the benefit of hindsight, that the data set out by Schleiden presented a serious challenge to the continued acceptance of lichen autonomy, lichenologists of the day dealt with that problem by ignoring it.

Any data that conflicted with conventional wisdom were simply disregarded, as, for example, by the French cryptogamist Camille Montagne in his general survey of contemporary lichenology (1846); that lengthy article avoided any discussion of the ample evidence that by then pointed to an algal and fungal involvement in lichen formation. Koerber (1848) displayed an almost equally hidebound outlook; despite having commented, in what was the first textbook of cryptogamic botany, on the resemblance of fungal fruit bodies to those of lichens (p. 60) and noted that the chlorophyllous cells of *Collema* correspond to *Nostoc* filaments (p. 61), his commitment to the dogma of lichen autonomy remained complete. A striking instance of the extent to which contemporary botanists had become blinkered in this regard is provided by the work of the English botanist George Thwaites (1812–1882). While attached to the Bristol School of Pharmacy, Thwaites made a detailed anatomical study of material belonging to a variety of genera, which led him (1849a, p. 221) to recognize several types of thallus: "1. The *Lichens* proper;

2. *Collema*, *Leptogium*, &c.; 3. *Synalissa* and *Paulia*; 4. *Mastodia*; represented respectively, as regards their essential fundamental structure, by the genera *Pleurococcus*, *Nostoc*, *Coccochloris* and *Ulva*." Thwaites made no attempt to expand on that observation and was equally reserved when pointing out with regard to his new genus *Cystocoleus* (1849b, p. 242) that "[i]t is interesting to observe in these minute plants a parallel and simultaneous growth of an internal filament and an investing sheath, each in some measure independent of the other and representing separate systems of cellular development." As Smith (1921, p. 23) remarked, "Thwaites was on the threshold of the discovery as to the true nature of the relationship between the central filament and the investing sheath, but he failed to take the next forward step."[25] This threshold was again approached when Berkeley and Broome (1851, p. 188) reported that "Mr. Thwaites has found both *Stigonema atrovirens [Ephebe lanata]* and *mamillosum* in fruit, and in both instances perfect asci and sporidia exist. The genus then does not belong to *Algae*, but to *Collemals*. It appears that *Sp[haeria] affinis* is nothing more than the fruit of the *Stigonema*."[26] Though mistaken in those beliefs, Berkeley and Broome's construal of Thwaites' finding might nevertheless be expected to have given all concerned pause for thought as to the constitution of "Collemals," but this did not happen.

The fact that organisms far removed from Thwaites' *Cystocoleus* also possess "separate systems of cellular development" became known at this time: Cohn (1851, p. 264) noted the occurrence of green, algoid globules ("Kügelchen") in the protozoan *Paramecium bursaria*, and Milde (1851) reported the lobes of some hepatics as including concatenated, olive-green cells "that appear altogether similar to the corresponding structures in *Nostoc* and *Collema*,"[27] but no attempt was made to extrapolate from their findings. The French mycologist Louis-René Tulasne (1815–1885) appears to have been unaware of Thwaites' work when preparing his generally excellent study of lichen structure and function (1852). A man of his time, Tulasne endorsed the Acharian doctrine of autonomy (p. 6), rejected Schleiden's merging of fungi with lichens (p. 7) and dismissed Kützing's demonstration that some gonidia are of green algal origin (p. 102). Tulasne evidently had no difficulty in reconciling such attitudes with his comment (p. 36) that in the genera *Cladonia* (as *Cenomyce*) and *Peltigera* (as *Peltidea*) "the primitive hypothallus or *protothallus* of those lichens is identical to the *mycelium* of fungi," and the statement (p. 69) "I have seen from direct observation that as regards spore liberation, lichens correspond exactly to *Pezizae*, *Helvellae*, *Sphaeriae* and most of the ascophorous fungi belonging to the two tribes of Discomycetes and Pyrenomycetes."[28]

Other significant findings that went unremarked at the time were reported by Schacht (1852); he described a lichen thallus (p. 147) as comprising "two cell types: 1) filamentous, much-branched, anastomosing cells without chlorophyll and 2) small, round, chlorophyllous cells," with the walls of the latter type alone being found to contain cellulose (p. 395).[29] Despite having established this fundamental distinction, Schacht reported without comment that "[Johann] Bayrhoffer [1793–1868] has demonstrated the emergence of chlorophyllous cells (gonidia) from the filamentous tissue."[30] This is a telling instance of how the growing evidence of algal and fungal participation in thallus formation could continue to escape critical attention—botanists raised on the doctrine of autonomy felt, understandably enough, no compulsion to concern themselves with the unprecedented possibility of two quite dissimilar organisms combining to form a third.

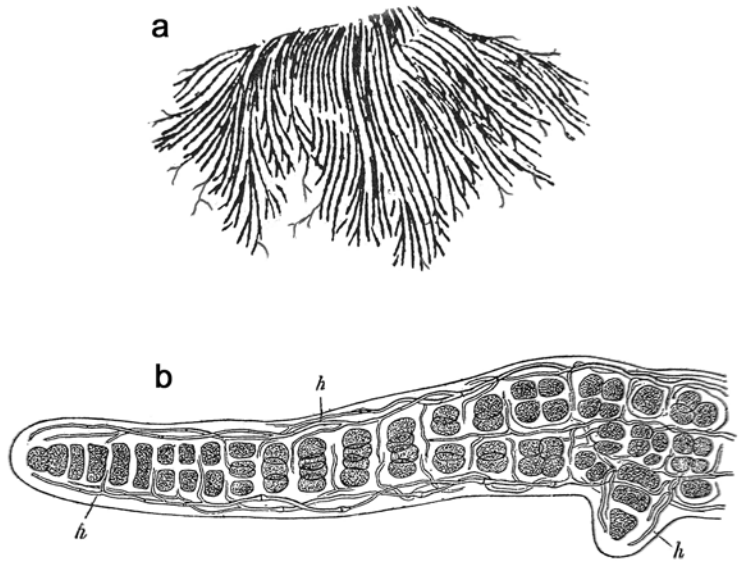

Figure 3. *Ephebe lanata*, *a*: habit ×3. (After M'Alpine 1883, 2: pl. 1, fig. 3); *b*: strand showing *Stigonema* filament and associated fungal hyphae *(h)* ×550. (From Sachs 1870, p. 258, fig. 191.)

Ephebe's evidence and journey's end

Despite further reports of a similarity between the chlorophyllous cells of lichens and commonly occurring algae from Flotow (1850, col. 363) and Kützing (1851–1852, 2:42–43), almost all botanists remained blind to the possibility that they could be one and the same. For example, in a detailed study of *Ephebe lanata* (as *E. pubescens*) — an inconspicuous, prostrate species occurring on wet, acidic rocks where it resembles a tuft of matted hair (Fig. 3a) — the French phycologist Edouard Bornet (1828–1911) noted (1852, p. 159) that its filaments could be taken for those of *Stigonema* if the apices alone are examined but claimed the two genera could be distinguished by the larger branches of both having their constituent cells differently arranged; Bornet did not, however, specify the nature of that difference. One of the few who saw matters more clearly was the German physician and botanist Hermann Itzigsohn (1814–1878). In a review of Bornet's paper, Itzigsohn (1854a, col. 473, fn.) declared "rather than there being merely a chance resemblance between the extremities of *Ephebe* branchlets and *Sirosiphon* (or *Stigonema*), the case is that the youngest developmental stages of *Ephebe* are nothing more or less than actual species of *Sirosiphon*," and he went on (col. 475) to equate "the *Stigonema* of Kützing and Agardh with the developmental stage attained by *Ephebe* when repeated transverse divisions have produced 4–8 rows of gonidial cells; a stiffening of those cells combined with the development of filamentous tissue results in the fruiting stage named *Ephebe*."[31] Itzigsohn (1854b, col. 80) had similarly realized that the moniliform filaments of *Collema* do not simply have a superficial resemblance to *Nostoc* but are entirely identical ("vollständig identisch") with it; and he further stated (1854c, col. 522) "it is well known that complete species of *Collema* can be distinguished from *Nostoc* globules by

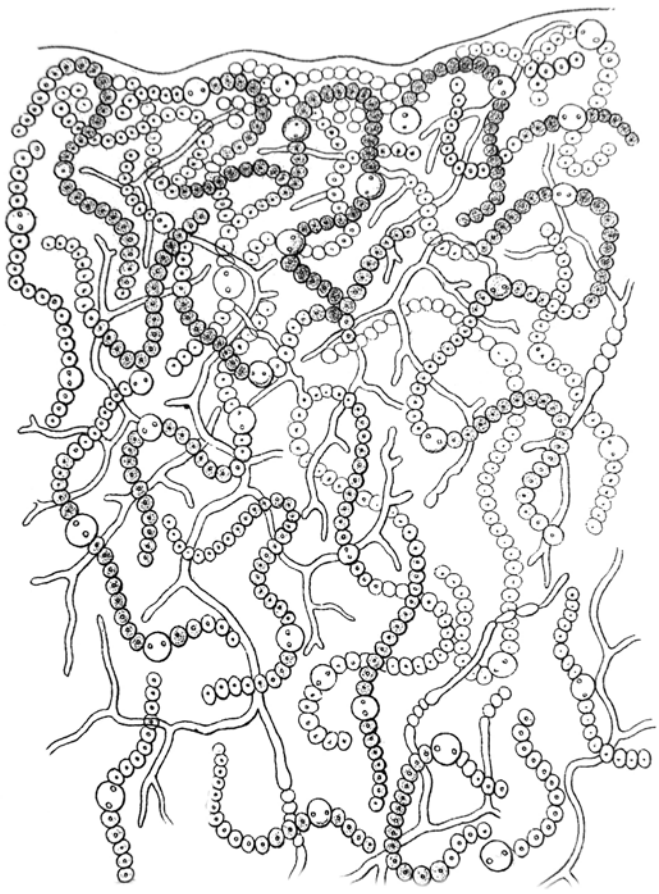

Figure 4. Vertical section of *Collema* thallus showing *Nostoc* chaplets and branched filaments later recognized as fungal hyphae ×300. (From Sachs 1855, pl. 1, fig. 6.)

the colorless filaments — corresponding to the filamentous layers of other lichens — that occur within the gelatinous body and ramify between the gonidial strands."[32] Itzigsohn did not speculate as to what the colorless filaments might be, but when Julius Sachs (1832–1897), then at the outset of a distinguished career, likewise saw them associated with *Nostoc* in a *Collema* thallus (see Fig. 4), he was reminded of fungal hyphae (1855, col. 3).[33] Though both Itzigsohn's and Sachs' papers appeared in the *Botanische Zeitung* — "one of the most famous periodicals of modern botany" (Klein 1974, p. 442) — their observations attracted no comment whatever, a fact that illustrates how effectively the doctrine of autonomy had closed botanists' minds to the possibility of a new organism emerging from the physiological union of an alga and a fungus. That doctrine was not, however, the sole obstacle to progress: elucidating the constitution of lichens was never going to be an easy matter at a time when the author of a textbook (Willkomm 1854, 1:159) could tell his readers "it may also be assumed that lichens form by spontaneous generation."[34]

The obvious resemblance between *Ephebe* and *Stigonema* continued, however, to interest several botanists, and it was their work in this regard that ultimately led to the overthrow of autonomy. The impetus came first from two German medical men: Philip Hepp (1797–1867), who practised in Neustadt an der Weinstrasse, southwest of Mannheim, until 1849 when he became a political refugee in Switzerland,[35] and Ernst Stizenberger (1827–1895), most of whose professional life was spent in his native Constance. Hepp settled near Zürich where he worked with the Swiss botanist Carl Nägeli (1817–1891)[36] and became acquainted with Stizenberger, now a not-too-distant neighbor. Hepp supplied Stizenberger, at the latter's request, with numerous specimens of *Ephebe lanata*, but when these all proved to lack fruits, Stizenberger (1858, p. 3) concluded that the plant was not a lichen but an alga whose supposed fruits were actually those of a parasitic fungus; he was supported in this conclusion by Hepp (1860, pl. 81, no. 712).[37]

In 1857 Nägeli had been appointed professor of botany at the University of Munich where Simon Schwendener (1829–1919), also Swiss-born, became his assistant. There Schwendener had undertaken a survey of lichen structure that included *Ephebe lanata*, but the report containing his account of that species was still awaiting publication when Hepp and Stizenberger's observations appeared. Schwendener decided to issue a separate paper detailing only the results of his work with *E. lanata*, which he described (1863, p. 241) as "one of those plants that engage our interest because of the many misconceptions to which it has given rise"[38]; these, for Schwendener, included any perception of *E. lanata* as an alga supporting a parasitic fungus. It was, he argued, a lichen because the brown apical regions of the branches, which appear as no more than a single row of cells under moderate ("mässiger") magnification, are seen to have a covering of delicate, articulated, filaments when the brown pigment is removed by chemical treatment; the apices now exhibit (p. 243) "the same two cell types that generally characterize lichen tissue: filaments and gonidia."[39] Nevertheless, the possibility that the chlorophyllous cells of *Ephebe* and other gelatinous lichens are indeed algae remained a live issue: Itzigsohn (1863) "strongly recommended *Ephebe* … to the attention not alone of lichenologists but also phycologists because it has a very close, but far from obvious, connection and relationship with *Sirosiphon*, *Scytonema*, *Chroococcus*, *Gloeocapsa*, etc.,"[40] and Koerber (1864, p. 78) had come to regard "most species of the algal genera *Chroococcus*, *Gloeocapsa*, *Nostoc*, *Palmella*, among others, as nothing more than independent, degraded gonidia of some homoiomerous lichens; further the chlorophyllous gonidia of heteromerous lichens may under certain circumstances, perhaps as *Protococcus viridis*, etc., lead an alga-like existence."[41]

Those comments are likely to have been read with interest by Anton de Bary (1831–1888), professor of botany at the University of Freiburg, whose textbook devoted to fungi, lichens and myxomycetes was then in preparation. Having provided a detailed account of *E. lanata* and an assessment of the several views respecting its constitution (1866, pp. 268–269), de Bary advanced a choice of hypotheses (p. 291):

> Given all these facts, there can be no doubt that many of the Nostocaceae and Chroococcaceae are closely related to the gelatinous lichens, *Ephebe*, etc. In which way remains, however, to be investigated. If I may summarize my personal opinion — a full elucidation would be excessive — two suppositions are justified. Either the lichens in question are the fully developed, fruiting, condition of plants whose immature states were included until now in the algae as Nostocaceae and Chroococcaceae, or those families are typical algae that assume the form of *Collema*, *Ephebe*, etc. as a result of

> penetration by certain parasitic ascomycetes [see Fig. 3b], the mycelium of which proliferates in the growing thallus and frequently attaches itself to the phycochrome-containing cells *(Plectospora [Lempholemma], Omphalaria)*. In the latter event, the plants in question would be pseudolichens.[42]

Within a year of de Bary's communicating his speculative insight, empirical evidence of a link between lichen gonidia and algae began to emerge: Famintzin and Baranetzky (1867) reported the growth in culture of chlorophyllous cells from several macrolichen thalli and compared them to cells of the algal genus *Chlorococcum* (as *Cystococcus*),[43] while Askenazy (1867, pp. 234–236) described the occurrence in species belonging to *Collema*, *Peltigera* and the family Graphidaceae of pigments otherwise associated with certain familiar algae. De Bary did not initially visualize the scope of his algal/fungal hypothesis as extending beyond the gelatinous category, but Schwendener quickly realized that it could apply to all species (Anonymous 1867). With the promotion by Sachs (1870, pp. 254–265) of that inclusive interpretation, the concept of lichens as dual organisms began its chequered advance to universal acceptance.[44]

For 20 years, Milde's report of 1851 had remained almost the sole known example of endophytic algae. In the early 1870s, however, a number of botanists — alert to the new understanding of lichen composition — undertook investigations that revealed the widespread occurrence of such algae. These were first demonstrated in a vascular plant by Johannes Reinke (1849–1931), lecturer in botany at the University of Göttingen, who reported (1872a) the presence of what he took to be a species of *Scytonema* (actually *Nostoc*) in *Gunnera tinctoria* (as *G. scabra*) stems; because he believed that the endophyte lived parasitically, Reinke was led to conclude (col. 61) "if we consider this growth from the standpoint of de Bary and Schwendener's theory, the gonidia of *Gunnera* behave in quite the opposite way to those of lichens."[45] This was also the conclusion drawn by Janczewski (1872, p. 311) as a result of his work with the hepatic *Phaeoceros laevis* (as *Anthoceros laevis*): "from a physiological point of view, endophytic *Nostoc* is a chlorophyllous parasite that depends on the *Anthoceros* thallus for its raw nutrients. Its relationship to *Anthoceros* in no way resembles that of heteromerous lichen gonidia to their hyphae because *Anthoceros* has no need whatever of *Nostoc* and draws no nutrient, raw or combined, from it."[46]

The reality is of course that at the time no one knew anything of the physiological relationship between *Phaeoceros* and *Nostoc*. Strasburger, then at the University of Jena, was similarly disadvantaged when he reported *Anabaena* (as *Nostoc*) filaments in the aquatic fern *Azolla* (1872), but his attempt to explain their occurrence (p. 40) was rather more insightful than that of either Janczewski or Reinke: "the *Nostoc* filaments are almost to be thought of as contributing to the assimilatory work of *Azolla* leaves and, in a way, playing a similar rôle there to that in the lichen thallus."[47] Evidence of this being indeed the case did not emerge until almost 20 years later when Schloesing and Laurent (1892) discovered the nitrogen-fixing potential of *Nostoc*, by which time the concept of symbiosis had become a central element of biological thought.

Conclusion

The awareness that existed at the end of the 18th century of an algal and fungal involvement in the constitution of lichens was eclipsed little more than a decade later by an authoritatively promoted, and widely accepted, supposition that because lichens are in the main morphologically distinct from either of those groups, they were to be regarded as *sui generis*. This assumption acquired further plausibility

when the finding that soredia — whose propagative rôle had long been recognized — contain the same green cells as occur in the parent thallus caused all those cells to be viewed as vegetative propagules.

For 50 years these misconceptions precluded any serious attempt to establish the true nature of lichens. Time and again resemblances were reported between the chlorophyllous cells of lichens and known algae, but the twin illusions under which lichenologists were working forced them to dismiss or ignore all such claims. When, eventually, improvements in microscopy and microtechnique demonstrated unequivocally that a species familiar, under a variety of names, to generations of botanists actually consists of a multicellular alga surrounded by colorless, septate, filaments, a questioning of conventional wisdom became inevitable. Initially, this was restricted to querying whether gelatinous lichens might not be the product of a parasitic liason between microscopic fungi and algae. The subsequent extension of this hypothesis to lichens in general precipated a typically contentious paradigm shift that had repercussions far beyond the bounds of lichenology.

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Notes

1. "Lichen" had earlier been used as a collective term by Bauhin (1623, p. 362) for a number of plants — seemingly all bryophytes — that he believed, citing several classical authors, to be effective in treating the skin conditions that still share this plant name.
2. The observations attributed to Morison by Krempelhuber (1867–1872, 1:17) and Smith (1921, p. 155) are clearly the work of Bobart — Tournefort's *Elemens* did not appear until 11 years after Morison's death.
3. "En effet, si l'on cherche dans les Classes des Plantes un genre avec lequel ils ayent quelque ressemblance, & auquel on puisse les comparer, il ne s'en trouve guere d'autres que les *Lichen*"; "il y a enfin entre les uns & les autres une manière presque uniforme de produire leur graine."
4. His paper, read on 28 July 1728 but not published until 2 years later, was forgotten for over 200 years — attention was first drawn to it by Lütjeharms (1936, pp. 131, 219).
5. Throughout the period under review, the term "alga" included the organisms currently known as "cyanobacteria" or "cyanoprokaryotes"; in order to avoid repeated qualification, "alga" in the present paper is to be understood in that early, inclusive, sense.
6. When making that reference, Hedwig alluded to his new genus *Octospora* whose second element he had evidently already settled on as a suitable name for fungal reproductive bodies; a further ten years went by, however, before he set that element on the road to universal acceptance as a biological term. Because a degree of confusion exists regarding this development, a fresh look at the facts may not come amiss. The first reference to the origin of "spora" was made by Lütjeharms (1936, p. 172) citing Hedwig (1798, p. 146). This was developed by Ramsbottom (1941, pp. 338–339) whose comments were drawn on by Ainsworth (1976, p. 62), though he mistook the Hedwig publication in question. But Lütjeharm's citation did not represent the whole story. "Spora" was actually introduced, complete with derivation, by Hedwig (1798, p. 64, fn.): "Because of men's former unfamiliarity with matters concerning the organization of nature,

the same word has been used to indicate quite different things. In now dispelling obscurity, no ambiguity of names can properly have a place, particularly where those relate to science. The Romans used semen both for the impregnating substance of male animals and plant embryos, the Germans likewise; but the Greeks used two words to describe them, viz. τό σπόρα (the seed) and τό σπερμα (the germ) … And certainly I believe it more in accordance with the greater clarity of our times to use sperm for the fertilizing principle derived from male genitalia, and seed or, idiomatically from the Greek, spore for the product arising from this fertilization" ("Antiqua hominum inscitia in rebus institutisque Naturae effecit, vt res plane diuersas vno eodemque vocabulo indigitarent. Discussis nunc tenebris, et inprimis quidem, vbi illae scientifice tractantur, certe ne vocabulorum ambiguitas decenter locum habet. Romani et animalium masculum impraegnantricem massam et partus vegetabiles semen dixerunt. Idem Germani. Sed Graeci ad horum indicationem duplici vsi sunt vocabulo, scilicet τό σπόρα et τό σπερμα … Et ego quidem crediderim, magis conuenire dilucidioribus nostris temporibus, id sperma dicere, quod genitale masculum excernit foecundans principium; ab hoc foecundatum autem, indeque in prolem viuificatum, Semen vel graeco idiomate Spora"). "Spore" appears to have been first employed in English by Gray (1821, 1:220).

7. " … denique etiam structurae internae haud exigua conuenientia Lichenes inter atque illas Linnaei Pezizas aut Eluelas Gleditschii … certe, cunctis rite perpensis, neganda non est summa harum cum illis convenientia, atque propinquitas. Vt adeo, si vegetabilia huius generis, porro inter Fungos locum obtineant, per eadem ipsa Fungi Lichenibus forent adnectendi in systematibus Botanicorum."
8. "Endlich haben keine Pflanzen in ihrer Frucht so viele Aehnlichkeit mit den Schwämmen als die Flechten; denn wenn man auf die *Kruste* … nicht Rüksicht nahm, so könnte man die Lichenes scutellatos nicht unschiklich als eine Familie der Schuselschwämme ansehen. Die Opegraphos zu den Hysteriis bringen, und die Endocarpa und Verrucarias für Sphaerias halten."
9. "Les Lichens gélatineux ne seroient-ils pas des individus de *Nostoc* qui auroient changé de forme?"
10. " … propriaque mea experientia et examine omnium partium summa cum sollertia instituto colligere potui, uti ratum habeo: Lichenes Ordinem Naturalem peculiarem et a reliquis Plantis Cryptogamis distinctum constituere, charactere sequenti notabilem: Receptaculum universale (thallus) polymorphum arhizum, acaule, perennans, corpusculis minutissimis (Gongylis) propagationi inservientibus, tam in tota sua substantia, extus intusque dispersis ac nidulantibus scatens, quam in organis propriis carpomorphis, coloratisque (Receptaculis partialibus seu Apotheciis) inclusis, instructum. E charactere dato patet, Lichenes et Receptaculis duplicis structurae et uniuscujusque horum diversa forma ac indole ab Algis, Hepaticis et Fungis satis distinctos manere."
11. " … j'ai toujours été frappé de l'extrême analogie qui m'a paru exister entre le nostoc commun et certaines espèces de lichens réunies par les cryptogamistes modernes dans le genre *colléma*." This was not Cassini's sole contribution to lichenology—in an interesting study (1820) of *Physcia tenella* (as *Borrera tenella*), he provided the earliest detailed account of soralia formation.
12. This was the first occasion on which lichens were equated with apothecia-bearing algae. Agardh's view was shared by Hooker (1821, 2:78): in an account also concerned with *S. atrovirens* he commented "[i]t seems doubtful whether this should be arranged with the *Lichens* or *Confervae*. External swellings (tubercles or apothecia?) have been observed upon them; but whether actual fructification or not, future observations must determine." Subsequently, Agardh (1824, p. 42) transferred *Scytonema atrovirens* to his new algal genus *Stigonema*.
13. Fries (1825, pp. 256, 302) cited them by the synonyms *Conferva atrovirens* and *Collema velutinum*, respectively. When introducing the generic name *Thermutis*, Fries did not supply its derivation, an omission that put Feige (1998, p. 59) in the position of having to speculate; in a later publication, however, Fries (1846–1849, 1:122) provided the requisite gloss: "Nomen filiae Pharaonis, Mosen ex aqua tollens."
14. " … qui semblent être des *collema* imparfaits"; the relationship between *Collema* and *Nostoc* is represented diagrammatically in Fée's Plate 4, a reproduction of which appears in Dörfelt and Heklau (1998, p. 139).
15. This was not one of Wallroth's many coinages—"gonimon," meaning "productive," had been used in a biological context by at least one classical Greek author (Wit 1992–1994, 1:15).
16. "Wir kennen … in der ganzen Oekonomie des Flechtenlagers keinen Theil, dem die Natur eine so erhabene, aber zugleich auch verschleyerte Bestimmungserreichung angewiesen oder eine

so vielseitige Bildungs- und Umbildungs-Kraft verliehen hätte, der so leichtsinnig von Acharius und mit Link's Ausnahme von allen andern Flechtenkundigern beachtet, so widersinnig verkannt wäre; wir kennen keinen, den die Natur späterhin so sorgfältig verhüllt, so allgemein verbreitet hätte, als denjenigen, den wir nach Maassgabe seiner primitiven Entstehung, seiner Form und seines Zweckes, mit dem Namen Brutzelle belegt haben."

17. "*Chlorococcum* … est gonidium liberatum, per se vegetans."
18. "Ich konnte hier schon alle beliebigen Stufen verfolgen, welche die *Parmelia* von ihrem Entstehen an bis zur Ausbildung durchlief." For additional detail of Kützing's observations in this regard, see Mitchell (2002, p. 193).
19. "… man könnte in Versuchung kommen, die Gallertflechten desshalb zu den Algen zu zählen, denen sie auch äusserlich, mit Ausnahme ihrer Fructificationsorgane, so ähnlich sind."
20. "… die nostochinische Stufe der Collemabildungen sich durchaus nicht von den andern Nostocarten, ihrem Bau nach, unterscheidet."
21. "Es ist merkwürdig wie sich hierdurch eine grosse Aehnlichkeit mit der Structur mancher Pezizae ausspricht."
22. "Bei den Gallertflechten zeigt sich nämlich die perlschnurartige Structur nur in der Nähe der Oberfläche; weiter nach unten verlängern und verdünnen sich die Glieder zu sehr feinen Fäden, bei denen sich die perlschnurartige Bildung zuletzt ganz verliert; ja diese Fäden verlängern sich unterwärts noch über die Ueberhaut des Thallus hinaus und bilden Wurzelfasern."
23. Three editions, with an English translation of the second, appeared in seven years.
24. The versions of the three passages quoted above—virtually unchanged in all German editions—come from the English translation (1849, pp. 144, 145, 157).
25. There are, it would appear, no actual instances to warrant the statement by Boulger and Grout (2004, p. 734) that "many of his [Thwaites'] discoveries were overlooked and subsequently attributed to later continental workers."
26. *Sphaeria (Paranectria) affinis* was described by Greville (1823–1828, 4: pl. 186) from material parasitic on *Ephebe lanata* (as *Bangia atrovirens*).
27. "… welche den entsprechenden Gebilden bei *Nostoc* und *Collema* ganz ähnlich sehen."
28. "L'hypothalle primitif ou *protothallus* de ces Lichens imite entièrement le *mycelium* des Champignons"; "L'observation directe des faits m'a montré que les Lichens, dans l'émission de leurs spores, imitent entièrement les Pézizes, les Helvelles, les Sphéries et le plus grand nombre des Champignons ascophores que renferment les deux tribus des Discomycètes et des Pyrénomycètes." According to Tulasne (1852, p. 42, n. 2), Ambroise de Beauvois (1752–1820) was credited by Bosc (1817) with having—in a communication of 1780 to the Académie des Sciences—first demonstrated the structural equivalence between lichen fruit bodies and those of *Peziza*; in fact, Bosc's article on lichens makes no mention of de Beauvois, though the latter did read a paper on fungi (never published) to meetings of the Académie in April and May of that year.
29. "… zweierlei Zellenarten: 1) aus fadenartig an einander gereihten, vielfach verzweigten, Zellen, die kein Chlorophyll führen und 2) aus kleinen, runden, mit Chlorophyll erfüllten Zellen"; further information concerning Schacht's observations can be found in Mitchell (2005, p. 18).
30. "Bayrhoffer … hat das Entstehen der Chlorophyllzellen (Gonidia) aus dem Filzgewebe nachgewiesen"; Bayrhoffer's claim to have observed this circumstance (1851, p. 4) was echoed by Tulasne (1852, pp. 18, 20), but the truth is, as Hugo von Mohl (1805–1872) remarked in another context, that both men "blinded by their preconceptions, believed that they saw what they could not have seen" (quoted in Krikorian (1975, p. 19)).
31. "… zwischen den Endspitzen der Ephebeästchen und den Sirosiphonen (respekt. Stigonemen) nicht blos eine zufällige Aehnlichkeit stattfindet, sondern dass die jüngsten Entwickelungszustände der Ephebe nicht mehr und nicht weniger, als wirkliche Sirosiphonen sind"; "Die jüngsten Zustände von *Ephebe* sind auf das Allerbestimmteste ein *Sirosiphon*; tritt in diesen eine wiederholte Quertheilung der Gonidien ein, so dass diese 4-8reihig liegen, so ist diese Entwickelungsstufe Kützing's und Agardh's *Stigonema*; verholzen diese, und tritt die Bildung von Fasergewebe hinzu, so ist der Zustand, den man *Ephebe* nennt, und welche der Fruktifikation fähig ist." For Bary (1879a, col. 80) most of Itzigsohn's publications were characterized by "a certain agitation and eccentricity" ("eine gewisse Unruhe und Excentricität"), but he acknowledged contemporary appreciation of their "valuable stimulus" ("werthvolle Anregung"). One of Itzigsohn's observations that appears to have gone altogether unremarked requires mention. In connection with a *Nostoc*-containing species of *Peltigera*, Itzigsohn (1868, col. 188) reported that

if a number of chlorophyllous cells are isolated from the thallus "a property immediately becomes apparent that, apart from their blue-green color, at once entirely separates them from lichens with green gonidia (*Parmelia*, *Lecanora*, *Evernia*, *Cenomyce [Cladonia]*, *Pertusaria*, etc.). This is *the absence of any cell nucleus*. An examination of green gonidia, for example from the soredia of *Parmelia conspersa*, *[Physcia] stellaris*, etc. … shows that even when quite young they have a well-defined *nucleus* … The cells of all Chroococcaceae and Collemataceae (at least in their normal state) lack nuclei. I have never seen a true nucleus in the thousands of species of *Oscillaria*, *Scytonema*, *Collema*, etc. that I have studied over the years" ("Sind … eine Anzahl Gonidien … ins Freie gefördert, so tritt, abgesehen von ihrer blaugrünen Farbung, eine Eigenschaft an den Gonidien sofort ins Auge, welche sie sofort von den Gonidien chlorogonimischer Flechten (Parmelia, Lecanora, Evernia, Cenomyce, Pertusaria etc.) weit entfernt. Es ist dies *der Mangel jedes Zellkernes*. Untersucht man nämlich Chlorogonidien, z. B. aus den Soredien der *Parmel. conspersa*, *stellaris* etc. … so sieht man, dass sie schon in ganz jungen Zuständen einen deutlichen *Zellkern* haben … Ein Zellkern fehlt den Zellen aller Chroococcaceen und Collemaceen (im normalen Zustande wenigstens). Bei den Tausenden von Oscillarien, Rivularien, Scytonemen, Collemen etc., die ich in einer grossen Reihe von Jahren studirt, habe ich nie einen wahren Zellkern gesehen").

32. "Da sich aber bekanntlich vollständige Collemen von Nostockugeln durch das Vorkommen von farblosen Fasern untersheiden, die sich innerhalb des Gallertstockes zwischen die Gonidialschnüre hindurch winden."
33. Hauptfleisch (1898, p. 265) made the unrealistic claim that Sachs had here recognized "the symbiotic connection" ("dass symbiotische Verhältniss") between algae and fungi, but it is not surprising that, when the time came, Sachs (1870, pp. 254–265) was among the first to promote the new interpretation of lichen structure.
34. "Auch bei den Flechten ist eine Urzeugung anzunehmen."
35. Hepp's involvement in the Rhineland-Palatinate uprising of 1849 earned him the death penalty; he was pardoned in 1865 (Grummann 1974, p. 18).
36. Their collaboration is recorded by Hepp (1853, pl. 1).
37. Hepp and Stizenberger were quite correct in believing the ascomata described for *Ephebe lanata* by Bornet to be those of a parasite, but their contention was ignored and the wrong fruits continued to be ascribed to *E. lanata* until a century later when the position was clarified by Henssen (1963, pp. 37–38).
38. "*Ephebe pubescens* ist eine jener Pflanzen, welche schon durch die vielfachen Täuschungen, zu denen sie Veranlassung gegeben, unser Interesse erregen."
39. "… den nämlichen zwei Zellformen, welche überhaupt das Flechtengewebe characterisiren: den Fasern und Gonidien."
40. "Ueberhaupt empfehle ich *Ephebe* … sehr der Aufmerksamkeit, nicht nur der Lichenologen, sondern auch der Algologen, da dieselben in einem sehr engen, wenn auch noch gar nicht gelichteten Verhältnisse und Zusammenhange mit den Sirosiphonen, Scytonemen, Chroococcen, Gloeocapsen etc. stehen."
41. "… die meisten Species der Algengattungen: *Chroococcus*, *Gloeocapsa*, *Nostoc*, *Palmella* u. A. nichts anderes sind, als selbständige, in ihrer weiteren Entwickelung fehlschlagende Flechtengonidien irgend welcher homoeomerischer Flechten. Aber auch die Chlorophyllgonidien der heteromerischen Lichenen können unter Umständen, etwa als *Protococcus viridis* u.s.w., ein scheinbares Algendasein leben." Views similar to Koerber's had already been expressed by the Finnish lichenologist William Nylander (1822–1899); because these appeared in Swedish (1856) they remained known to few other than Scandinavian botanists until a translation appeared almost a decade later (Nylander 1864). With reference to the similarity between certain algae and the genera *Ephebe* and *Thermutis* (as *Gonionema*), Nylander suggested (1864, p. 418) that some forms of *Sirosiphon* and *Scytonema* "may perhaps rightly be regarded as imperfect species, developmental stages or degenerations of the two lichen genera" ("mit Recht für unvollständige Arten der genannten zwei Flechtengattungen, für dazu gehörige Entwicklungszustände oder Degenerationen angesehen werden"). Though Koerber and Nylander clearly recognized an affinity between algae and the chlorophyllous cells of lichens, neither ever accepted that they are in fact such: in an obituary, Cohn (1885) described Koerber as having resolutely adhered to a belief in autonomy, and the American lichenologist Bruce Fink (1861–1927) recorded (1904, p. 23) that when in 1895 he sent Nylander—then long resident in Paris—a paper in which he mentioned the dual nature of lichens, he received a reply telling him that, in addition to being wrong, this perception constituted "une calomnie."
42. "Nach allen diesen Daten ist es wohl nicht zu bezweifeln, dass ein grosser Theil der Nostocaceen und Chroococcaceen zu den

Gallertflechten, Ephebe u.s.f. in naher genetischer Beziehung steht. In welcher? das bleibt zu untersuchen. Darf ich meine subjective Meinung, deren ausführliche Motivirung zu weit führen würde, hier kurz andeuten, so scheinen mir zwei Vermuthungen berechtigt zu sein: Entweder sind die in Rede stehenden Lichenen die vollkommen entwickelten, fructificirenden Zustände von Gewächsen, deren unvollständig entwickelte Formen als Nostocaceen, Chroococcaceen bisher unter den Algen standen. Oder die Nostocaceen und Chroococcaceen sind typische Algen; sie nehmen die Form der Collemen, Epheben u.s.f. an, dadurch, dass gewisse parasitische Ascomyceten in sie eindringen, ihr Mycelium in dem fortwachsenden Thallus ausbreiten und an dessen phycochromhaltige Zellen öfters befestigen (Plectospora, Omphalarieen). In letzterem Falle würden die in Rede stehenden Gewächse Pseudolichenen sein."

43. Famintzin and Baranetzky misconstrued their results, however, and concluded—like Fries 30 years earlier—that the algal genus corresponding to their isolated cells was merely a name that had been applied to gonidia growing outside the confines of a thallus.
44. In a comment on these developments de Bary (1879b, p. 17, fn.), having referred to the long-standing perception of lichens as an independent group occupying a position between algae and fungi, declared "this belief to have been very strongly supported by Schwendener's detailed studies of lichen structure, from which it appeared to follow that gonidia originate as branchlets or branch endings from filaments lacking chlorophyll. Nonetheless much remained obscure … Because of these and related considerations, I first speculated in 1866 (on the basis of extensive, unpublished, research) that certain lichens result, perhaps, from the association of a specific fungus with an alga; the studies then available, particularly those of Schwendener, did not warrant extending this speculation to all lichens. Later, and then largely as a result of Famintzin and Baranetzky's work, the probability of the so-called gonidia being identical to independently occurring algae increased to the extent that new investigations enabled Schwendener to formulate the theory summarized above." ("Diese Anschauungen fanden eine besonders feste Begründung durch Schwendeners eingehende Studien über den Bau des Flechtenthallus, aus welchen hervorzugehen schien, das die Gonidien als kleine Zweige oder Zweigenden der chlorophyllfreien Fäden selbst entstehen. Immerhin blieb noch manches unklar … Auf Grund dieser und ähnlicher Bedenken sprach ich 1866 zuerst für bestimmte Flechten die (auf ausgedehnte, nicht publicirte Untersuchungen gegründete) Vermuthung aus, sie möchten vielleicht aus der Vereinigung eines jedesmal bestimmten Pilzes mit einer Alge hervorgehen. Die Ausdehnung dieser Vermuthung auf alle Flechten gestatteten die damals vorliegenden, insbesondere Schwenderers Untersuchungen nicht. Nachdem nun in der Folge, zumal durch Famintzins und Baranetzkis Arbeiten, die Wahrscheinlichkeit immer mehr hervorgetreten war, dass die sogennanten Gonidien mit selbständig vorkommenden Algen identisch sein, gelangte Schwendener, in Folge neuer Untersuchungen, zur Aufstellung der im Texte resumirten Theorie"). Eduard Strasburger (1844–1912), professor of botany at the University of Bonn, also commented on this topic (1895, p. 201): "[i]n 1860 and 1868, in the first two parts of his researches into the lichen thallus, Schwendener declared the gonidia to be the terminal cells of short lateral branches of the hyphae. In 1866 de Bary led up to the true idea of the lichen thallus in the gelatinous lichens, and spoke the words which solved the whole problem and brought about the right conception of all lichens. This final step was taken by Schwendener in the supplement to the last part of his 'Flechtenstudien,' and was repeated still more decisively in his 'Algentypen der Flechtengonidien,' published in 1869." On the other hand, in an autobiographical sketch written in 1900 and first published in full by Zimmermann (1922, pp. 54–59), Schwendener made no mention of the advance for which he was then, and remains, best known.
45. "Betrachten wir diese Bildung unter dem Gesichtspunkte der neueren, durch de Bary und Schwendener begründeten Theorie des Flechtenthallus, so verhalten sich die Gonidien von *Gunnera* genau umgekehrt, wie die der Flechten." Sapp (1994, p. 6) states that in 1873 Reinke suggested "consortium" as an appropriate term for the algal/fungal association characteristic of lichens. In fact, it is not at all clear who first proposed the term, though we can be sure that it was not Reinke: in a further report on *Gunnera* (1872b, p. 108) he thanked a colleague, August Grisebach (1814–1879), for having communicated the term to him verbally ("mündlich") but without any indication of when. Coincidentally, on 18 January 1872 the German microbiologist Ferdinand Cohn (1828–1898), professor of botany

at the University of Breslau (Wrocław), referred to the "alliance or consortium of a fungus and an alga" ("Verbindung oder Consortium eines Pilzes und einer Alge") in an address to the Schlesische Gesellschaft für Vaterländische Cultur (1873, p. 69). It is noteworthy that while Cohn was prepared to accept that members of the Collemataceae are the product of algal/fungal relationships, he could not then (1872, p. 19) bring himself to regard heteromerous lichens in the same light: "I am not aware of any alga that could be transformed into *Usnea*, *Cladonia*, *Cetraria*, etc. by the influence of a fungus" ("Mir sind keine Algen bekannt, die sich durch den Einfluss eines Pilzes in Usneen, Cladonien, Cetrarien etc. verwandeln könnten.")

46. "Considéré au point de vue physiologique, le Nostoc entophyte est un parasite renfermant de la chlorophylle, mais ne pouvant puiser ses aliments bruts que dans la fronde de l'*Anthoceros*. Cependant il n'est nullement possible de comparer sa relation avec l'*Anthoceros* à celle des gonidies des Lichens héteromères envers leurs hyphes, car l'*Anthoceros* n'a nullement besoin du Nostoc et n'en tire aucun aliment brut ou élaboré."
47. "Man sollte fast glauben, dass die Nostocschnüre den Blättern der Azolla in ihrer Assimilationsarbeit behülflich sind, und somit in gewisser Weise eine ähnliche Rolle in denselben, wie im Innern des Flechtenthallus spielen."

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