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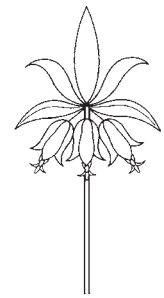

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# The inside story: A commentary on the study of lichen structure in the 18th and 19th centuries

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**Abstract**

Observations concerning the vegetative anatomy of lichens were first reported in 1784; these did little more than record the presence of green cells, and it was not until early in the 19th century that lichens were also shown to contain colorless filaments. Several studies undertaken in the first half of the 1820s established the basic features of lichen anatomy, but from then until mid-century the subject attracted scant attention; when work did resume, this involved macrolichen material in particular. Considerable histological detail was reported, and the cortical structures peculiar to lichens were thoroughly investigated. Despite a growing awareness of an affinity between the green cells of lichens and certain algae, it was not until the latter half of the 1860s that the thallus was understood to be a structure elaborated by fungal hyphae in combination with algae or blue-green algae (as cyanoprokaryotes were then known). Microlichen anatomy, which hitherto had received comparatively little attention, was well documented during the last three decades of the century. Over the years, terminology had kept pace with developments, and much the greater part of that currently used in the area of lichen structure was in place by the end of the 19th century.

## Introduction

Lichens are fungi growing in symbiotic association with photosynthetic microorganisms. This association generally exerts a profound morphogenetic effect on the fungal component, which, in consequence, forms a macroscopic structure that houses its nutritive partner. Since the morphology of this structure is determined by the particular species that constitute each association, and since close to 14,000 such are known (Sipman and Aptroot 2001), lichens display a wide range of variation;[1] for descriptive purposes, therefore, three principal growth forms are recognized: crustose, foliose and fruticose (Figs. 1–3).

For most of the period under consideration here, lichens were believed to be autonomous plants, related to, but distinct from algae and fungi. That belief was not contested until the late 1860s when, as a result of anatomical investigation, the hypothesis was advanced that lichens are fungi living parasitically on algae.[2] This insight created serious problems for those botanists who specialized in lichen taxonomy — it not alone undermined the independence of their subject but also seemed to call in question the validity of every binomial that had been applied to lichens. If these really were dual organisms, each component would have, or would have to receive, a binomial, and lichen names themselves would, it was feared, become redundant. No such jettisoning had, however, to be undertaken because, unlike the photosynthetic components, which also occur in the free-living state and have each a binomial, lichen fungi are not found other than in symbiotic association: lichen names therefore apply, strictly speaking, to the fungal component and not to the dual organism.[3]

## Internal investigations

The earliest anatomical study of lichens was undertaken by Pier Micheli (1679–1737),

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Figure 1. *Rhizocarpon concentricum* (Davies) Beltr., a crustose lichen. (From Hoffmann 1790–1801, 3: pl. 50, fig. 2.)

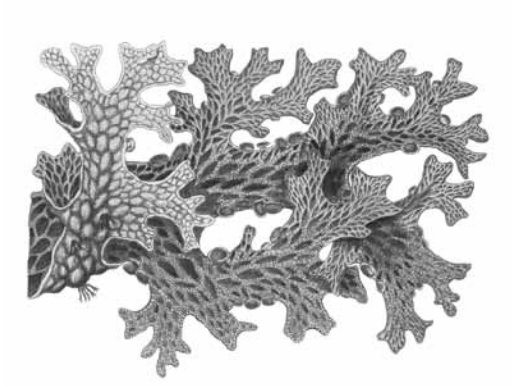

Figure 2. *Lobaria pulmonaria* (L.) Hoffm., a foliose lichen. (From Hoffmann 1790–1801, 1: pl. 1, fig. 2.)

superintendent of the Botanical Garden at Florence. He provided the first directions (1729, p. 74) for preparing sections of lichen reproductive bodies, and illustrated the procedure clearly (1729, pl. 52, fig. G), but did not apply his technique to the vegetative part of a lichen. The initiative in that regard was taken, though not until more than 40 years after Micheli's death, by Johann Hedwig (1730–1799). He was in medical practice at Chemnitz when the Imperial Academy of St. Petersburg announced in 1779 (Lütjeharms 1936, p. 107) that a prize was to be awarded in 1783 for a study of reproduction in cryptogamic plants; Hedwig submitted what proved to be the winning entry, which was published by the Academy under the title *Theoria Generationis et Fructificationis Plantarum Cryptogamicarum* (1784). The 37 plates that accompany Hedwig's report were described by Morton (1981, p. 322) as providing "the most accurate and beautiful figures of cryptogams yet produced by anyone,"[4] but the illustrations of lichens do not merit such commendation. One of these (see Fig. 4) is, however, of particular relevance to the present survey: in addition to being the first diagram of a section through the vegetative body of a lichen, it is the first attempt to depict the photosynthetic cells — Hedwig states (1784, p. 122, n. i) that, in this figure, the "darker islands represent particles of clustered, green parenchyma that often extend as far as the cuticle."[5]

By the end of the 18th century, the study of lichens had begun to emerge as a distinct discipline, a development largely attributable to the work of Erik Acharius (1757–1819). He had been in medical practice for nine years at Vadstena, southern Sweden, when his first major publication, *Lichenographiae Suecicae Prodromus* (1798), appeared. That work considerably facilitated identification by providing descriptions of about 400 species; Acharius accommodated all of these in the Linnaean genus *Lichen,* but five years later he replaced that genus with 25 new genera based on fruit–body morphology (Acharius 1803). He also helped underpin the independent status of the subject by coining a range of specialist terms, some of which soon found wider application: "apothecium," "perithecium," "soredium" and "thallus" are among his introductions (1803, pp. vii, ix, xviii, xxi).[6] At this stage, however, Acharius did not report any microscopical observations.

The first account of lichen structure to appear in the 19th century was published by Kurt Sprengel (1766–1833), professor of botany

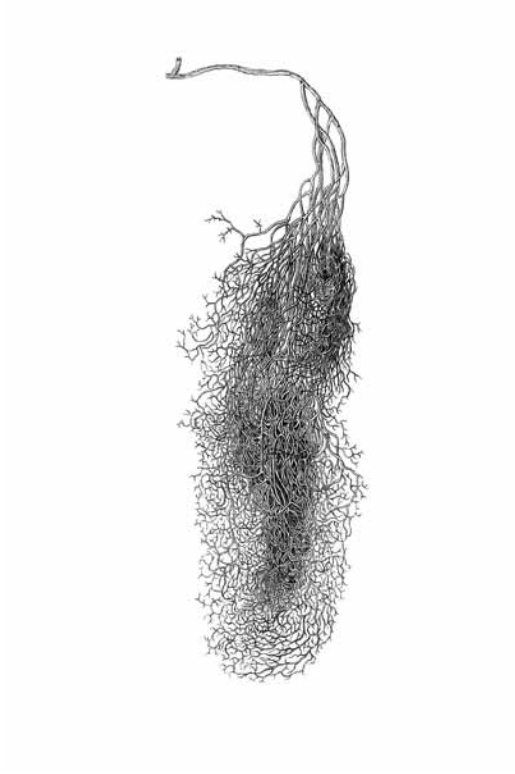

Figure 3. *Usnea* sp., a fruticose lichen. (From Hoffmann 1790–1801, 3: pl. 72, fig. 1.)

at the University of Halle. In a brief anatomical survey, Sprengel (1802–1804, 3:323–326) described lichens as "compact or gelatinous cryptogamic plants of filamentous rather than distinctly cellular structure" (p. 323).[7] His observations included (1804, pl. 10, fig. 104) the cortical layer underlying the apothecium in *Solorina saccata* (L.) Ach. (as *Peltidea saccata* (L.) Ach.) and (pl. 10, fig. 105) the concentric arrangement of tissues seen in sectioned axes of the genus *Usnea* Hill. Though he attached particular importance to his observation (p. 325) that the cortex is always ("alle Mahl") delimited by a green zone, Sprengel did not pursue this topic. He did, however, refer at some length to the occurrence of soredia, which, like earlier botanists, he recognized as having a reproductive function, and which he described (pp. 323, 326) as "germinative powder" ("Keimpulver").

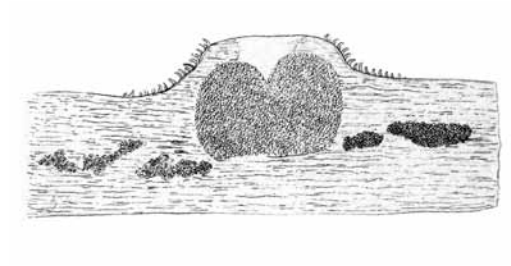

Figure 4. Vertical section through a lobe of *Anaptychia ciliaris* (L.) Körber; the drawing shows a reproductive structure (center) in addition to groups of algal cells. (From Hedwig 1784, pl. 31, fig. 177.)

Sprengel's conclusions were amplified by Heinrich Link (1767–1851), professor of botany at the University of Rostock. He described the lichen cortex (1807, p. 25) as composed of "vesicular tissue analogous to parenchyma,"[8] and the interior of the thallus as containing "filamentous tissue" ("fasrige Gewebe"), the individual filaments of which he found to be septate (p. 21). From a study involving *Pseudocyphellaria aurata* (Ach.) Vainio (as *Sticta aurata* (Ach.) Ach.), Link was able to establish that "granules" ("Körnern") corresponding to those present in soredia occur within the thallus; his illustration of the latter category (1807, pl. 1, fig. 10) may lack finesse, but it does have the merit of being the first attempt to show individual photobiont cells. Extrapolating from their occurrence in soredia, Link (p. 22) misinterpreted the function of those cells, which he described as gemmae ("Gemmen").

Acharius, meanwhile, had made substantial use of the microscope to investigate fruit-body anatomy and — though to a considerably lesser extent — vegetative structure; in consequence of his work in the latter area, he reported (1810, pp. 3–4) that

> "the substance of a thallus comprises two parts: one, namely the outer, is for the most part tougher, cartilaginous or crustaceous … termed *cortical* because it forms the upper and lower layer in most foliose lichens … the other constituent

> of the thallus, hidden below the cortex, is as a rule softer, tow-like, filamentous, containing vessels, sometimes rather hard, and this I call *medullary* … The compound microscope shows that the filaments forming the soft, silky, medullary material are not solid but tubular, and these may well serve as small ducts."[9]

The 14 plates that accompany Acharius' book were, presumably, his own work since he was at one time "employed as an illustrator … at the Royal Swedish Academy of Sciences" (Jørgensen 1999, p. 13). While most of the many sections depicted on those plates relate solely to fruit-body anatomy, 30 or so extend through the thallus, but, curiously, not one of these provides any indication that Acharius saw the green zone that occurs below the upper cortex, nor did he make any mention of it in his text.

A year after Acharius' death, the first report devoted specifically to lichen structure was published by the Swiss clergyman Ludwig Schaerer (1785–1853). His brief paper (Schärer 1820) advanced the view that "underlying the various external forms of the lichen thallus are just two basic structural types"[10]: one, according to Schaerer, was represented by crustose lichens and corresponded to Link's "vesicular tissue," the other, of which foliose, including gelatinous lichens, were representative, was interpreted as consisting of "filamentous tissue." It is indeed the case that two fundamental categories of thallus can be recognized, but Schaerer was wrong in equating these with Link's tissue types. Schaerer's assertion that a lichen's green cells, which he termed "globules" ("Kügelchen"), functioned individually as propagules ("Keime") gave further currency to Link's misinterpretation of the rôle played by those cells. Schaerer was correct, however, in noting that a lichen thallus can comprise "several superimposed layers."[11]

The findings of Link, Schaerer and Sprengel were extended by Friederich Wallroth (1792–1857), a medical officer at Nordhausen, between Göttingen and Halle. He produced the first textbook of lichenology (1825–1827), volume one of which — published in January 1825 (Stafleu and Cowan 1976–1988, 7:44) — includes several hundred pages on the subject of lichen structure. Those pages make tedious reading: Wallroth affected a highly periphrastic style and so encumbered his text with neologisms that Schleiden (1849–1850, 2:43) was provoked into describing the book as "altogether objectionable because of its barbarous terminology, which is as offensive as it is excessive."[12]

There are, nonetheless, several reasons why Wallroth's first volume warrants attention. He agreed with Schaerer that two principal categories of thallus can be recognized, but correctly based these on the manner in which the constituent colorless and green cells are arranged. In Wallroth's first category, represented by gelatinous lichens, the components occur intermingled, while the second, to which most other lichens belong, has the components arranged in discrete layers; Wallroth (1:23–24) applied the designation "homoeomeres" to the former category of thallus and "heteromeres" to the latter, terms that, variously modified according to language, remain in everyday use.[13] He investigated, in addition, the "green band" to which Sprengel, his botanical mentor, had drawn attention. Though evidently not a deft microscopist,[14] Wallroth succeeded in examining its constituent cells, to which — having followed Link and Schaerer in wrongly interpreting their function as reproductive rather than assimilative — he applied (1:40) the familiar, but now obsolete term "gonidia."[15] The general acceptance of that term, with its misleading connotation, impeded lichen research for over 40 years.[16] Wallroth made the first internal examination of the small, superficial growths to which

Acharius (1803, p. xix) had given the name "cephalodia" (Schneider 1897, p. 55; Smith 1921, p. 133).[17] These growths develop when cortical filaments react to the presence of cyanoprokaryote cells by proliferating to form a delimiting layer. Wallroth noted (1:678) that cephalodia ("phymata" in his terminology) "differ from the regular lichen not alone externally, but also internally in respect of color."[18]

Some months after Wallroth's first volume was published, another textbook of lichenology appeared. This was by Georg Meyer (1782–1856); described on the title page as "Physiographer to the Kingdom of Hanover" ("Physiographen des Königreiches Hannover"), Meyer subsequently became professor of botany at the University of Göttingen. He reported in connection with crustose thalli (1825, pp. 12–13) that

> the cortical layer forms the outer surface, but lacks an epidermis, which is not present in lichens. That layer consists of closely aggregated cells, which here and in foliose thalli are roundish; in the latter they become stretched owing to progressive growth, and assume an oblong shape … Immediately below the cortical layer there is a zone of round cells that differs from it only in being less compact. A double layer of cells can be distinguished in this zone: an upper, consisting of exposed, green cells, which is clearly distinguishable from the cortical layer by its differently aggregated cells and vivid green color, and a lower having the form of colorless loose cells.[19]

Meyer (p. 14) shared Wallroth's belief that the green cells had a reproductive function, and, since he found them to be a constant feature of lichens, concluded that the presence of those cells constituted "a definitive, natural, distinction between lichens and the closely related family of Fungi."[20] He also contributed the observation (p. 21) that gelatinous lichens possess articulated (i.e. cyanoprokaryote) filaments and applied (p. 22) the current term "rhizinae" to the outgrowths that secure thalli to the substratum.

Though the gist of Meyer and Wallroth's texts was quickly made available to the botanical community by Martius (1826), no one came forward to undertake further anatomical work. Certainly, the twin defects of chromatic and spherical aberration, to which microscope lenses of the day were subject, made structural research of limited appeal, but even after those difficulties had been resolved and better instruments became available, in the 1830s, lichen anatomy received little attention. This neglect is largely attributable to the works of Acharius: because these had considerably facilitated lichen identification, numerous regional studies were undertaken, and classification of the copious material that in consequence became available claimed the attention of the few botanists who interested themselves in lichens. The extent to which this was the case can be gauged from the comprehensive listings by Krempelhuber (1867–1872, 1:476–555, 574–575), which show that between 1825 and 1850, over 150 books and papers dealing, in whole or in part, with floristics and taxonomy were published, while lichen structure failed to attract any serious interest; the latter circumstance is further evident from the reviews of Buhse (1846) and Montagne (1846), which add nothing to what was known of lichen anatomy 20 years earlier.

The tide soon began to turn, but the prevailing belief that lichens were autonomous organisms caused students of structure to misinterpret the material they examined: they believed the colorless filaments and the green cells of the thallus to be congenetic and convinced themselves that their microscopes showed this. Thwaites (1849, pp. 220–221) remarked of *Synalissa symphorea* (Ach.) Nyl. (as *S. vulgaris* "Fr.") that "an examination of its internal substance … exhibits to us a structure very like that of the genus *Coccochloris* [*Aphanothece* Naeg.]: a number of single cells … are scattered throughout the gelatinous substance

of the plant … each cell is found, upon careful inspection, to be … situated at the extremity of an ultimate ramification of the numerous somewhat anastomosing filaments which pervade the whole mass of the plant." Thwaites (1849, pl. 8, fig. A 2) drew what he believed he had seen, and Bayrhoffer (1851, pl. 1, figs. 11–15) similarly depicted filaments producing globular cells — in his case both laterally and terminally. Those misrepresentations had the effect of strengthening received opinion concerning the constitution of lichens; consequently, the implications of contemporary observations by the German cytologist Hermann Schacht (1814–1864) that "there is no anatomical difference between fungal and lichen tissue" (1852, p. 134), that the "chlorophyllous cells correspond in shape and size to *Ulothrix* zoospores" (p. 149), and that "the wall of the green cells is distinguished from that of other lichen tissue by the blue color resulting from the application of iodine and sulphuric acid" (p. 395), went unremarked.[21]

In the same year that Schacht's book appeared, an extensive and lucid account of lichen biology was published by the French notary-turned-botanist, Louis-René Tulasne (1815–1885). This work, which made available a wealth of first-hand microscopical observation, reached a wide audience and was enthusiastically received.[22] Tulasne's thorough account of structure (1852, pp. 8–32) was based on a study of numerous specimens representing both heteromerous and homoiomerous thalli. The many details recorded by Tulasne include careful measurements of cortical cells and the extent to which their appearance is altered by gelatinization of the walls, together with the earliest data relating to hypophloeodal species (p. 9) and the first detailed examination of soredia (pp. 23–24); his reference (p. 20, n. 1) to the occurrence of "blackish-green clusters" ("agglomerats d'un vert noir") in

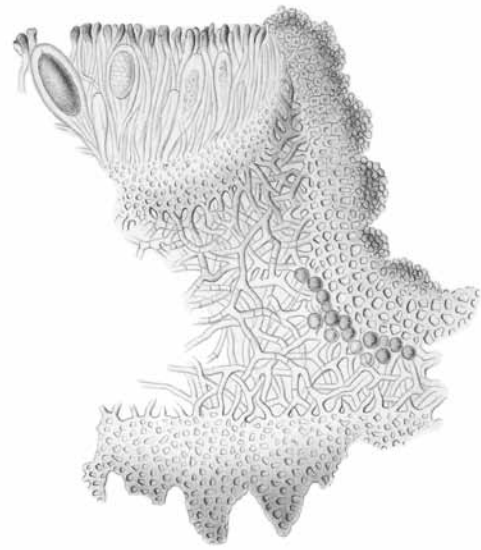

Figure 5. Vertical section through a lobe of *Lasallia pustulata* (L.) Mérat; the drawing shows apothecial anatomy and, lower right, the heteromerous structure of the thallus. (From Tulasne 1852, pl. 5, fig. 8.)

the thallus of *Solorina saccata* (L.) Ach. is the first observation of cyanoprokaryote cells forming internal cephalodia, though not then recognized as such. Tulasne's report was elegantly complemented by his brother Charles' (1816–1884) illustrations (see Figs. 5, 6).

Thallus anatomy was further investigated at this time by Julius Speerschneider (1825–1903), a German physician in practice at Schlotheim, northeast of Mülhausen. His investigation of five macrolichens was undertaken as a leisure interest, and it was only when encouraged by Schacht, whom Speerschneider had known while a student at the University of Jena, that he decided to publish his results (Möller 1957, p. 59). These appeared in a series of lengthy papers (Speerschneider 1853, 1854a, 1854b, 1854c, 1855, 1857), but, apart from observations on the mode of attachment of fruticose lichens to the substratum (1854a, col. 199) and the structure of rhizines (1854b, cols. 490, 505), Speerschneider added little of consequence to

Figure 6. Vertical section through a lobe of *Leptogium* sp.; the drawing shows apothecial anatomy and, lower right, the homoiomerous structure of the thallus. (From Tulasne 1852, pl. 6, fig. 11.)

what had been reported by Tulasne. One of his illustrations (see Fig. 7) shows Speerschneider following convention by representing the chlorophyllous cells as separable outgrowths from medullary filaments; he appears to have had some reservations in this regard, however, because he remarked (1854b, col. 486) that

> one is already led, a priori, to the gonimic [green] cell being formed from a filament cell, and to a connection between them. Because if, leaving aside the former, it is the latter in its various modifications that forms the whole thallus, where but from it can the free globular gonidia come? Can it somehow be an individual free product of the intercellular material, a secretion from the filament cell! This mode of origin and free development, independent of any cellular association, would be altogether without analogy in plant physiology.[23]

That the chlorophyllous cells and colorless filaments might be "independent of any cellular association" was also an inference to be drawn from an early paper by the German botanist Julius Sachs (1832–1897). His comparison (1855, col. 3) of sections from a *Nostoc* colony and an adjacent *Collema* thallus revealed that, while both preparations possessed moniliform filaments embedded in a transparent mucilage, the sections of *Collema* were characterized by the presence, in addition, of "very slender, hyaline filaments, as if a parasitic fungus had colonized the gelatin."[24] Sachs undertook no further work in lichenology, and his perceptive comment on the colorless filaments attracted no attention. Nor was there any response a year later when, commenting on "the very strange genus that [William] Nylander [1822–1899] has named *Gonionema* [*Thermutis* Fr.], the fructification of which is that of a lichen but whose thallus consists of filaments identical with those of *Scytonema,*" the French phycologist Edouard Bornet (1828–1911) remarked (1856, p. 225) that this was "an area in which discoveries awaited a careful and pertinacious investigator."[25]

It was another ten years before those discoveries were made. In the interim, the study of macrolichen structure was continued by the Swiss plant anatomist Simon Schwendener (1829–1919). He had begun to work with lichens in 1857 when attached to the University of Munich and, three years later, published an impressively detailed report on material representative of 13 fruticose genera (1860b). Schwendener provided extensive data relating to cell morphology in the cortical, green and medullary layers, and was able to show (p. 140) that some genera, notably *Roccella* DC., possess a distinctive type of cortex in which the constituent filaments curve outwards to meet the surface more or less at right angles.[26]

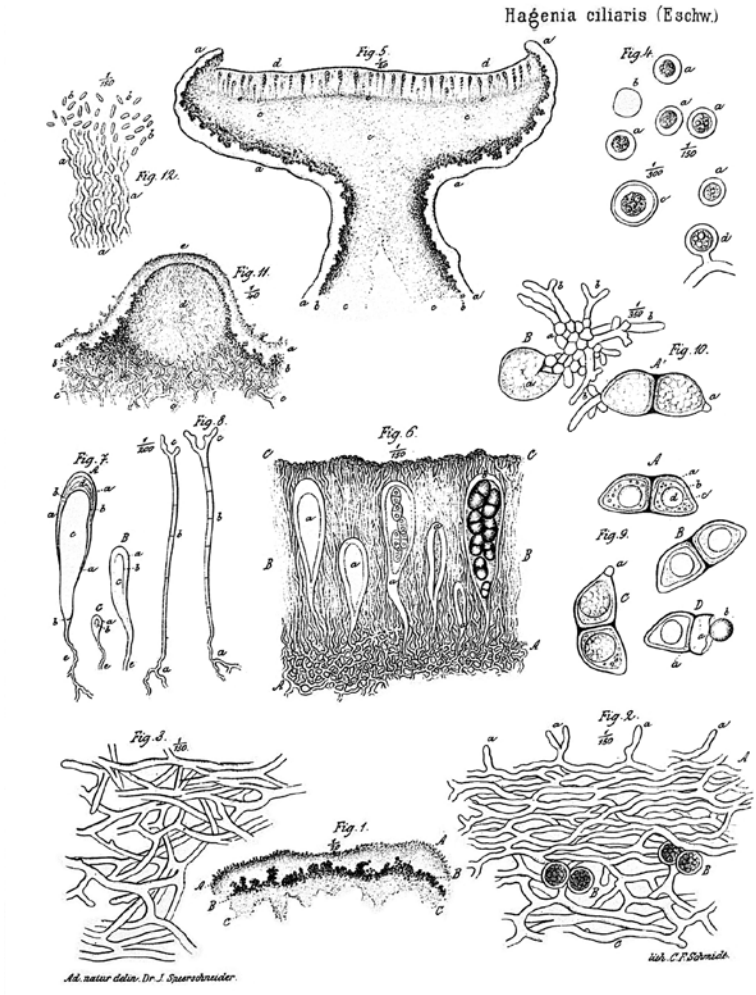


Figure 7. Anatomy of *Anaptychia ciliaris* (L.) Körber; a photosynthetic cell is represented as originating from a hypha at Fig. 4 d. (From Speerschneider 1854c, pl. 14.)

Schwendener next turned his attention to foliose and gelatinous lichens; the report of this investigation appeared in two sections, the first of which (1863) dealt with 18 foliose genera. This thorough account includes a study of the parenchyma-like cortical tissue formed when the constituent filaments retain a conspicuous lumen, and the contrasting appearance that such filaments present when their walls become substantially thickened. Schwendener noted (pp. 155–156) that both types of tissue occur in the thallus of *Physcia caesia* (Hoffm.) Fürnrohr (as *Parmelia propinqua* Laurer) and provided an illustration of this feature (see Fig. 8). He also made the first comprehensive examination (pp. 168–169) of the cortical pits that Acharius (1798, p. xvi) had termed "cyphellae"; this work led Schwendener to advance the view — still regarded as valid (see Jahns 1988, p. 108) — that those structures

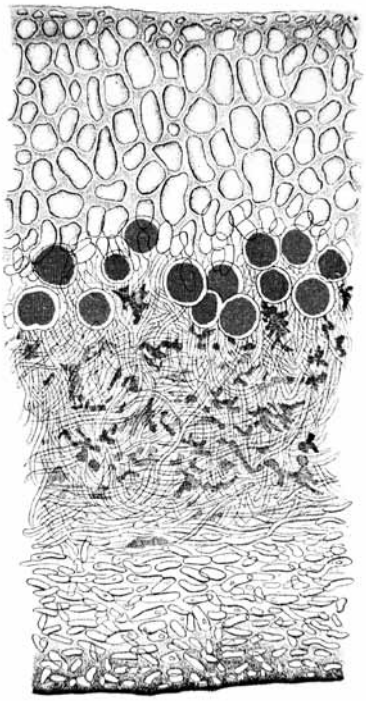

Figure 8. Upper and lower cortical structure in *Physcia caesia* (Hoffm.) Fürnrohr; the dark bodies are algal cells. (From Schwendener 1863, pl. 8, fig. 1.)

serve to facilitate aeration of the thallus. In common with Bayrhoffer, Speerschneider and Tulasne, Schwendener believed he had seen green cells develop from medullary filaments (1860a, p. 288; 1860b, p. 126; 1863, p. 133).

That the chlorophyllous cells did, in fact, originate in this way began to appear less certain when the German mycologist Anton de Bary (1831–1888) queried whether, in certain genera, the nature of those cells had been fundamentally misunderstood. De Bary began a review of lichen structure in his *Morphologie und Physiologie der Pilze, Flechten und Myxomyceten* (1866) with the observation (p. 241) that lichen fruit-bodies closely resemble those of ascomycetes, and he went on to signal the further resemblance between fungi and lichens seen in their common possession of vegetative bodies composed of interwoven hyphae.[27] Until this time, fenestrated fungal and lichen tissue was generally referred to as parenchyma; de Bary showed why such usage is wrong and explained (p. 2) that "it is therefore necessary, from an anatomical point of view, to distinguish clearly between true parenchyma and the parenchyma-like tissue of fungi, for which, if this is to be given a special name, the designation false parenchyma or pseudoparenchyma will be appropriate."[28] He followed convention in stating (p. 242) that the photosynthetic cells of a thallus develop from hyphae, but reported in his commentary on gelatinous lichens (p. 264) that, with one exception, he had never seen so much as a probable connection between chlorophyllous cells and hyphae. Doubts concerning such a connection were also aired in his comments (pp. 268–270) on the anatomy of *Ephebe lanata* (L.) Wainio (as *E. pubescens* auct.), a species that, as most contemporary botanists recognized, had clear affinities with a common blue-green alga. For some of those botanists, *E. lanata* was a lichen and not an alga because it possessed apothecia, while that same feature had led others (Stizenberger 1858, p. 1; Hepp 1860, pl. 81, no. 712) to conclude that it represented, in fact, two organisms: an alga parasitized by a fruiting fungus. Though the latter view had received little support, de Bary was careful to say (p. 269), "it must not, however, go unmentioned that while, at present, the parasitic point of view appears far less plausible, this cannot be altogether ruled out, because likewise the sterile *Ephebe* thallus could consist of a *Sirosiphon* with a fungus mycelium proliferating through its walls."[29] Towards the end of his survey, de Bary returned to the question of hyphal/photosynthetic cell relationships in *Ephebe,* and summarized (p. 291) his personal assessment ("meine subjektive Meinung") of the issue: either this genus and the Collemataceae represent the fruiting phase of plants that had, in their immature state, been regarded as blue-

algae, or *Ephebe* and the Collemataceae consist of blue-green algae that have been invaded by parasitic ascomycetes.

Schwendener supported the latter alternative in the concluding instalment of his second structural paper (1868, pp. 167, 171, 172, 181), but in an addendum (p. 195) he raised the possibility that de Bary's insight applied to all lichens and that "the green cells were everywhere to be regarded as typical algae and the colorless filaments as fungal hyphae, which the former provide with nutrients necessary for the construction of a thallus."[30]

Initially, this drastic reinterpretation of lichen form and function received only limited support; attitudes did, however, slowly begin to change following Sachs' endorsement of the hypothesis in his influential *Lehrbuch der Botanik* (1870, p. 255): "there can no longer be any doubt that the Lichens are true Fungi of the Section Ascomycetes, but distinguished by a singular parasitism. Their hosts are Algae … [t]he Fungi themselves (Lichen-forming Fungi) are not found in any other form than as parasites on Algae; while the Algae which are attacked by them … are known in the free condition without the Fungus."[31] Gradually, in the words of Lindau (1895, p. 1), the view "that the lichen is no single organism but an association of alga and fungus became a fundamental principle of lichenology, acceptance of which enlivened and gave new direction to a science mired in species mongering."[32]

That there was more to the association than parasitism became apparent when the anatomy of cephalodia came under close scrutiny. Schwendener's suggestion (1869, p. 18) that those structures develop when cortical hyphae react to the presence of a foreign alga was endorsed by the German mycologist Georg Winter (1848–1887). In a report on the cephalodia of *Lobaria linita* (Ach.) Rabenh. (as *Sticta linita* Ach.) and *Solorina octospora* Arnold, Winter (1877, p. 200) concluded that the foreign cells exert a stimulatory effect — "causing quite unusual and very active growth of the thallus hyphae" — and queried whether "the valid and proved relations between the algae of the cephalodia and their enveloping hyphae ought not be taken as applying to the thallus constituents also?!"[33]

The anatomical work of the 1850s and 1860s had not involved crustose lichens to any significant extent; Schwendener (1863, pp. 127, 138) had intended to include them in his survey but did not publish on the subject. Microlichens did receive detailed attention, however, when the German taxonomist Gustav Körber (1817–1885) stated (1874, p. 6) that though "almost all the younger botanists had immediately taken at face value, and further hawked about, the anatomical relationships described by Schwendener and Bornet [1873,]" lichens could not be fungi because "there are many species (almost all crustose) whose thallus contains no hyphae" (p. 11).[34] This claim was refuted by Winter (1875) in a study that dealt with several of the saxicolous species cited by Körber. Winter's anatomical examination of *Sarcogyne privigna* (Ach.) Massal. is particularly commendable given that this inconspicuous lichen grows on siliceous rock, which Winter carefully dissolved in order to trace the course of the hyphae. A further rebuttal of Körber's assertion was provided by Winter (1876) in a detailed report largely concerned with thallus organization in a range of calcicolous pyrenocarp material. Also at this time, a comprehensive account of thallus development in several corticolous microlichens was provided by the German botanist Albert Frank (1839–1900), who later worked principally as a plant pathologist and physiologist. He described (1876) the association that exists between algae and hyphae in hypophloeodal species, demonstrated the extent to which the components penetrate the periderm, and

observed that some species then regarded as lichens, e.g., *Arthonia excipienda* (Nyl.) Leighton (as *A. epipasta* (Ach.) Körber) and *Arthopyrenia rhyponta* (Ach.) Massal., lack algal cells.

Further elucidation of microlichen structure came with the work of the German botanists Ewald Bachmann (1850–1937) and Gustav Lindau (1866–1923). Bachmann, a high school teacher at Plauen, southwest of Chemnitz, made a thorough study of 18 species that grow within calcareous rock (1892a)[35] and successfully isolated thalli from their matrix. This led him to report (p. 5) that "in the thallus of all immersed, [36] calcareous lichens, three zones can be clearly distinguished: a gonidial layer between two zones formed only of hyphae," with "the boundaries separating the individual zones always so clearly drawn that the thallus of calcareous lichens can be as readily termed heteromerous as that of species growing on the surface."[37] Such zonation was not found in the corticolous counterparts of calcareous lichens: following an examination of over 30 epiphloeodal and hypophloeodal species, Lindau — a lecturer at the University of Berlin — considered (1895, p. 5) that "thalli of the latter type could almost be described as homoiomerous."[38] Also in that work, Lindau (pp. 48–60) provided the first comprehensive account of the attachment organs produced by corticolous macrolichens.

On 10 February 1899, Simon Schwendener celebrated his 70th birthday; to mark the occasion some of his former students produced a festschrift, the contributions to which included the last publication of relevance to the present survey. In that paper, which dealt with thallus structure in the genus *Umbilicaria* Hoffm. (as *Gyrophora* Ach.), Lindau (1899, p. 28) described de Bary's term "pseudoparenchyma" as too general for use in specific circumstances and proposed that any tissue composed of hyphae be designated "plectenchym," a term which could, as required, be given precision by the addition of an appropriate prefix: "previously it was not possible to distinguish the 'pseudoparenchyma' of the upper cortex, which has roundish apertures, from that of the medulla, and often the lower cortex, where those apertures are oblong. Now we can easily speak of a parenchymatic and prosenchymatic plectenchyma, or perhaps more concisely of 'para- and prosoplectenchyma.'"[39] Those coinages, which quickly found acceptance (Fünfstück 1902, p. 72), remain in everyday use.

## Conclusion

The few botanists who devoted their attention to lichens in the 18th and early 19th centuries were principally concerned with systematics, and those who did attempt anatomical work were badly hampered in their efforts by the poor quality of contemporary microscopes. Instruments with improved lenses became available from 1830 onwards, but most lichenologists continued to occupy themselves with floristics and taxonomy, and it was not until mid-century that anatomical observations came to be reported with any regularity. As earlier in the century, this work was largely undertaken by central-European botanists, most of whom were associated with German universities. Structural detail could now be readily observed, but not so readily interpreted: because workers were committed to the prevailing belief that lichens were autonomous organisms, they assumed that the green cells and colorless filaments evident in their sections actually developed one from the other — indeed the presence of appressoria and haustoria appeared to confirm that assumption. Though several anatomical observations reported in the 1850s had the potential of alerting contemporary botanists to the fact that there was more to lichens than met the eye, the significance of those findings

was not grasped until late in the following decade, when lichens were finally understood to be the product of an association between an alga and a fungus. While that discovery made the physiology of lichens an attractive research area, it had far less impact on the study of their anatomy, which remained very much a minority interest.

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The dates of birth and death cited for the lichenologists mentioned in this paper are derived from Grummann (1974).

## Notes

1. Though a separate species of fungus (mycobiont) is involved in each association, this is not the case with the photosynthetic component (photobiont)—only about 20 cyanoprokaryotes (cyanobacteria) and 80 algae have so far been identified from lichens, but "this is probably a small percentage of the number … actually present" (Tschermak-Woess 1988, p. 5).
2. Cyanoprokaryotes were not separated from the algae until the 1970s.
3. Tehler (1996, p. 217) makes the point that "[l]ichens are not organisms. Lichens are small ecosystems, associations with two or more components: an algal producer and a fungal consumer"; nor, it can be contended, are they plants, since one of the components is always a fungus. In practice, however, the words organism and plant continue to be used in reference to lichens.
4. The figures were drawn by Hedwig and engraved by Johann Capieux (1748–1813). According to Florschütz (1960, p. vii), Hedwig used "a simple 'Rheinthaler'"—a Cuff-type microscope—that he modified "in the course of the years and at last he used a 170–290× magnification."
5. "… ubi insulae opaciores, particulas grumosi viridantis parenchymatis denotant, subinde ad cuticulam usque extendendas."
6. Soredium, as currently employed, is "a non-corticate combination of phycobiont cells and fungal hyphae having the appearance of a powdery granule, and capable of reproducing a lichen vegetatively" (Kirk et al. 2001, p. 487); as originally employed by Acharius, however, a soredium was the area of a cortex in which such granules are produced. The term was used in both senses until Reinke (1895, p. 380, n. 1) proposed that "such clearly characterized breeding places of soredia be called soralia" ("Solche scharf abgesetzte Brutstätten von Soredien … könnte man Sorale nennen"). The statement by Ramsbottom (1941, p. 352) that "C. A. Agardh had introduced the term thallus for the vegetative parts of lichens" is incorrect.
7. "Kryptogamische Gewächse, von einem nicht deutlich zelligen, sondern faserigen, gedrängten oder gallertartigen Bau." Gelatinous lichens, which have cyanoprokaryotes as photobionts, were grouped by Acharius (1803, p. 221) in the subdivision *Collema* of his genus *Parmelia*; he subsequently gave that subdivision generic status (Acharius 1810, p. 129).
8. "Wir haben … das *blasenförmige Gewebe* … in der äussern Haut der Lichenen … Es ist dem Parenchym analog."
9. "Thallus … e duplici substantia compositus est: una scilicet exteriori, utplurimum duriori, cartilaginea vel crustacea … Hanc *corticalem* dixi, nam stratum et supremum et infimum thalli efficit in plerisque Lichenibus foliaceis … Altera pars substantialis thalli intra corticalem recondita, quae mollior plerumque est, stuppea, fibrosa, vasculosa, interdum duriuscula, *medullaris* a me appellatur … Fibras, substantiam hanc mollem bombycinam medullarem constituentes, non solidas sed tubulosas esse, ope vitrorum compositorum detegere successit et ductulorum munere fungi probabile est." There appears to be no record of the type of microscope used by Acharius, but it may be concluded that it was not of the best: an illustration of sectioned material (1810, pl. 9, fig. 6 E) described (p. 95) as "greatly increased in size" ("m[agnitudine] valde a[ucta]") is actually at about ×40 magnification.
10. "… den mannigfaltigen äussern Formen des Thallus der Flechten nur zwey Urformen innerer Bildung zum Grunde liegen."

11. "Gewöhnlich liegt ein solcher Thallus in mehrern Schichten übereinander."
12. "*Wallroth* durch eine ebenso überflüssige als ekelhaft barbarische Terminologie sein Werk völlig ungeniessbar gemacht hat." Grummann (1941, p. 127) described Wallroth's work as "scarcely usable owing to the opacity of the text" ("Wegen der Unverständlichkeit des Textes kaum benutzbar").
13. "Heteromeres" was coined by Wallroth as an antonym of "homoeomeres," which has a pedigree extending at least as far back as Theophrastus (1916, 1:14). Wallroth was an able classicist (Osswald 1896, pp. 24–25), and could have met the word in any of several editions of the Greek text, but there is an alternative source, with which he, like Fries (1831, p. liii), would certainly have been familiar: the *De Rerum Natura* of Lucretius, in which lines 830–832 of Book 1 read, "Let us now look at Anaxagoras / And his theory of 'equalpartedness,' / Or 'homoeomeria,' as Greeks call it" (Lucretius 1974, p. 37); the terms were evidently first anglicized by Tuckerman (1872, p. 44). Of Wallroth's many other introductions, the only survivors are "epiphlöodisch" and "hypophlöodisch" (1825–1827, 1:141–142), which—applicable, respectively, to lichens growing on and within bark—were first used in English by Leighton (1871, p. 362).
14. Wallroth's friend the phycologist Friedrich Kützing (1807–1893) later wrote of him, "he is not altogether at ease with matters relating to the microscope because he lacks skill in dissection" ("…mit mikroskopischen Sachen kann er nicht immer fertig werden, weil ihm die Geschicklichkeit im Präpariren abgeht") (Müller and Zaunick 1960, p. 233).
15. Wallroth deliberately coined "gonidium" (literally "little offspring") as a near homonym (1825–1827, 1:47) of the term "conidium," which had been introduced by Link (1807, p. 22).
16. Bary (1866, p. 294) remarked, "in my opinion, Wallroth's 'Naturgeschichte' has, for all its merit, been a serious hindrance to lichenology" ("Wallroth's 'Naturgeschichte' ist meines Erachtens, bei allem Verdienst, ein arger Hemmschuh für die Flechtenkunde gewesen").
17. As first employed, "cephalodium" encompassed a range of cortical bodies; Acharius (1810) maintained this broad usage, but the term subsequently came to retain only the sense in which he had applied it (pp. 99–100) when describing features of *Peltigera aphthosa* (L.) Willd. (as *Peltidea aphthosa* (L.) Ach).
18. "…weichen nicht allein äusserlich von der lichenischen Typosis sondern auch innerlich von dem morphologischen Verhältnisse der Grundformen, selbst in Hinsicht der Färbung ab."
19. "Die Kortikallage bildet die äussere Fläche ohne durch eine besondere Epidermis, die man bey keiner Flechte antrifft, bekleidet zu seyn. Sie besteht aus dicht vereinigten … Zellen. Die Form dieser ist rundlich, sowohl hier als auch im enstehenden laubartigen Lager, in welchem sie durch fortschreitenden Wachstum gedehnt wird, und dann in die längliche übergeht … Unmittelbar unter dieser Rindenschict liegt die rundzellige Schicht, die im wesentlichen von jener nur durch die nicht verwachsenen locker aggregirten Zellen abweicht. Man kann in ihr eine doppelte Lage von Zellen unterscheiden, eine obere und eine untere. Die obere besteht aus frey liegenden grün gefärbten Zellenkörnern. Sie ist von der sie deckenden Kortikalschicht durch den verschiedenen Aggregatzustand und die lebhaft grüne Färbung bestimmt gesondert; in den unter ihr liegenden ungefärbten Theil der lockern Zellen geht sie dagegen allmälig über"; Harris (1999, p. 86) has noted that "[i]t is difficult to establish the exact connotations of 'Zelle' and 'Körnchen' for scientists in the first half of the nineteenth century."
20. "In ihr glaube ich daher denn auch einen … durchgreifenden natürlichen Unterschied zwischen den Flechten und der so verwandten Familie der Pilze gefunden zu haben."
21. "Das Gewebe der Pilze und Flechten lässt sich anatomisch nicht von einander trennen"; "…ihre [die Chlorophyllzellen] Gestalt und Grösse entspricht den Schwärmsporen der Ulothrix"; "…ihre [die Chlorophyllzellen] Zellwand unterscheidet sich von der Zellwand des übrigen Flechtengewebes durch seine blaue Färbung vermittelst Jod und Schwefelsäure." As noted by Smith (1915, p. 97), "Schleiden in 1838 and von Mohl in 1840 showed that after treating the cell wall with sulphuric acid, iodine caused a blue coloration of the cellulose."
22. For Duby (1853, p. 190) it was "ce beau travail," Lindsay (1856, p. 28) declared it "the most important monograph ever published on this subject," and Stizenberger (1862, p. 401) spoke of Tulasne's "epochemachende Arbeit."
23. "Ausserdem wird man schon a priori auf eine Entstehung und einen Zusammenhang der gonimischen Zelle mit der Fadenzelle geführt. Denn wenn ausser der ersteren die letztere in allerdings verschiedenen Modifikationen die

einzige und alleinige ist, die den ganzen Thallus zusammensetzt, woher kann denn das freie kugelige Gonidium wohl anders kommen als von ihr? Sollte es etwa ein eigenes, freies Gebilde des Zwischenzellenstoffes, der Absonderung der Fadenzelle sein! Diese Entstehungsweise, so wie die ganz freie Entwickelung ausserhalb jedes Zellenverbandes stände wirklich ganz ohne ein weiteres Analogon in der Pflanzenphysiologie."

24. "… wurden ausserdem durchsichtige sehr dünne Fäden bemerkbar, als ob sich ein parasitischer Pilz in der Gallerte angesiedelt hätte."
25. "… le genre si curieux que M. Nylander a nommé *Gonionema* … dont la fructification est celle d'un lichen, mais dont le thallus est composé de filaments identiques à ceux des *Scytonema*. Nul doute qu'il n'y ait là un champ fertile en découvertes pour un observateur attentif et persévérant." There was an increasing awareness about this time of how closely fungi and lichens are related: Payer (1850, pp. 87–93) treated lichens as just one of several families in a fungal order "Thécasporées," and was followed by Berkeley (1857, p. 81), who proposed a category "Mycetales" comprising "Fungales" and "Lichenales."
26. For a detailed account of Schwendener's work on cortical structure, see Nienburg (1926, pp. 56–61).
27. De Bary appears to have been the first to employ the term "hypha" in a lichenological context.
28. "Es ist daher vom anatomischen Gesichtspunkte aus nothwendig, die parenchymähnlichen Gewebe der Pilze von dem eigentlichen Parenchym wohl zu unterscheiden, und will man für sie einen besonderen Namen haben, so wird die Bezeichnung als Scheinparenchym oder Pseudoparenchym passend sein."
29. "Es darf übrigens nicht verschwiegen werden, dass die Parasitenansicht zur Zeit zwar minder wahrscheinlich, aber keineswegs völlig ausgeschlossen ist, indem auch der sterile Thallus von Ephebe gebildet sein könnte aus einem Sirosiphon und einem die Zellwandungen dieses durchwuchernden Pilzmycelium"; *Sirosiphon* Kützing is a synonym of *Stigonema* C. A. Agardh.
30. "… drängt sich jetzt schon die Frage auf, ob nicht vielleicht sämmtliche Flechten in dieser nämlichen Weise entstehen: ob die Gonidien nicht durchgehends als typische Algen und die farblosen Zellfaden als Pilzhyphen zu betrachten seien."
31. Quoted from Sachs (1875, pp. 262–263).
32. "Die Erkenntnis, dass die Flechte kein einfacher, sondern ein aus Pilz und Alge zusammengesetzter Organismus ist, wurde ein Fundamentalsatz der Lichenologie, der berufen war, dieser in Specieskrämerei versunkenen Wissenschaft neues Leben einzuhauchen und sie in neue Bahnen zu lenken."
33. "Die Algen in den Cephalodien von *Sticta* und *Solorina* veranlassen die Thallus-Hyphen zu einem ganz ungewöhnlichen äusserst lebhaften Wachsthum"; "Und dürfen diese für die Algen der Cephalodien und die sie umschliessenden Hyphen gültigen und erwiesenen Beziehungen nicht auch für die Bestandtheile des Flechtenthallus als richtig angenommen werden?!"
34. "… die von Schwendener und Bornet dargestellten anatomischen Verhältnisse … von fast allen jüngeren Botaniker sofort als baare Münze aufgenommen und weiter colportirt wurden"; " … es viele (indess fast nur Krusten-) Flechten giebt, die in der That in ihrem Thallus keine Hyphen besitzen."
35. Little had been added to the knowledge of such lichens by Steiner (1881), most of whose observations were wrongly interpreted owing to his belief in the spurious "microgonidium" concept of Arthur Minks (1846–1908).
36. The terms "endolithisch" and "epilithisch" were introduced by Bachmann (1892b, p. 30) and evidently first used in English by Schneider (1897, p. 29).
37. "Im Thallus aller unterirdischen Kalkflechten lassen sich deutlich drei Zonen unterscheiden, von denen die mittelste Gonidien führt … Ausserhalb und innerhalb der Gonidienschicht liegen zwei nur aus Hyphen zusammengesetzte Zonen"; "… die Grenze zwischen den einzelnen Thalluszonen immer so deutlich gezogen [ist], dass das Lager der Kalkflechten mit demselben Rechte heteromer genannt werden kann, wie das verwandter oberirdischer Lichenen."
38. "… wir können den Thallus beinahe als homoeomer bezeichnen."
39. "Vor allen Dingen war es früher nicht möglich, durch einen scharfen Ausdruck das 'Pseudoparenchym' der oberen Rinde mit seinen mehr rundlichen Öffnungen von dem des Markes (und oft auch der unteren Rinde) mit mehr länglichen zu unterscheiden. Jetzt können wir ohne Zwang von einem parenchymatischen und prosenchymatischen Plectenchym sprechen, wenn man nicht vielleicht noch kürzer 'Para- und Prosoplectenchym' sagen will."

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