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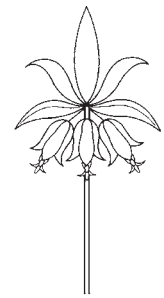

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"Function is smother'd in surmise": A survey of observations on the rôle of lichen conidia, 1850–2000

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Abstract

On close inspection, the upper surface of many lichens is seen to be liberally flecked with blackish dots, each the opening of a minute, flask-shaped receptacle. The first detailed study of those receptacles, early in the 1850s, showed them to contain a profusion of free, non-motile cells; the term "spermatia" was applied to those cells because they were perceived as possibly representing male gametes, while the receptacles, accordingly, became "spermogonia." That perception was taken as fact when, in 1874, evidence was provided that lichens possess a female reproductive apparatus and that spermatia regularly occur in contact with it. Two years later, however, spermatia of several non-lichenized fungi were germinated in vitro, a development that led some botanists to reject the received view of those cells — contending that a capacity to germinate precludes a capacity to fertilize, they declared the rôle of spermatia to be purely dispersive. These differing interpretations of spermatial function soon became part of a wider, and sometimes acerbic, debate on the subject of fungal reproduction. Germination of lichen spermatia under laboratory conditions was reported in the 1880s; this achievement strengthened the rejectionists' case and led to a proposal that the neutral terms "pycnidia" and "pycnoconidia" be used in preference to "spermogonia" and "spermatia." Others, however, continued to support the view that spermatia are male gametes, while a lone voice queried whether pycnoconidia/spermatia might not possess a dual capability. A considerable body of results was published by the opposing sides in the years to the end of the 19th century, but neither was able to carry the day. Interest in the topic declined during the first half of the 20th century, following which a consensus began to emerge that some, at least, of the non-motile cells now comprehensively described as "conidia," do, in fact, have the capacity to function as both asexual propagules and male gametes. Conclusive proof of this versatility has yet to be provided.

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Introduction

The first experimental evidence that flowering plants possess reproductive structures equivalent to those of animals was provided in 1694 by the German botanist Rudolph Camerarius (1665–1721). His discovery raised the question of whether comparable structures are produced by the flowerless plants, or cryptogams, a question that was to receive no early answer because few botanists of the day possessed either the equipment or the incentive to investigate it.[1]

In the case of lichens, it was not until almost a century later that sexual organs were first reported. Working with *Anaptychia ciliaris* (L.) Körber (as *Lichen ciliaris* L.), the Austrian bryologist Johann Hedwig (1730–1799) interpreted its fruit-bodies as "disci feminei," and described the dark spots commonly present on the cortex (Fig. 1) as "puncta floris masculi" (Hedwig 1784, p. 160).[2] Hedwig also attempted — somewhat ineffectively — to show one of the latter structures in vertical section (Fig. 2a); five years later, however, he published a more convincing illustration (Fig. 2b) of what he had by then come to term "mascula genitalia" (Hedwig 1787–1797, 2:6).

The lichen illustrations published by Hedwig in 1784 were reproduced, together with a translation of the corresponding text, by Withering (1787–1792, 3:29–31, pl. 16).[3] Information concerning sexual reproduction in lichens was now available to a considerably wider audience, though evidently to little effect since no further contemporary account

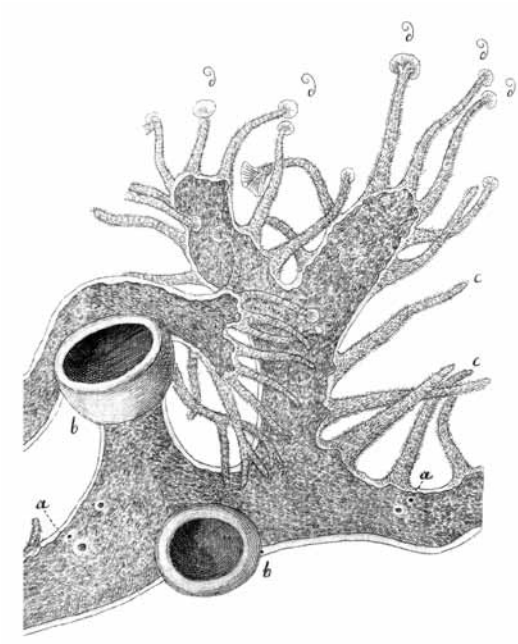

Figure 1. *Left, Anaptychia ciliaris* (L.) Körber, surface view of thallus showing pycnidia at *a* and apothecia at *b*. (From Hedwig 1784, pl. 30, fig. 176 (detail).)

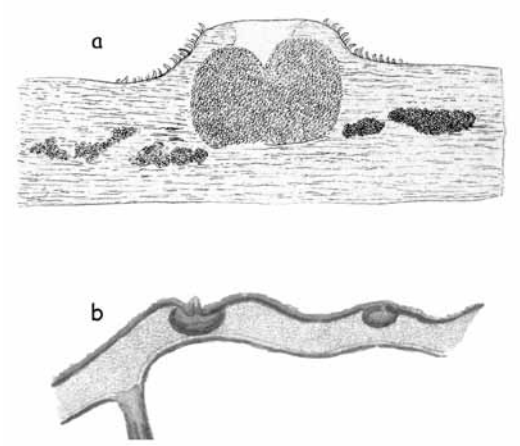

Figure 2. *Above, Anaptychia ciliaris*, *a*: vertical section through a lobe and pycnidium. (From Hedwig 1784, pl. 31, fig. 177); *b*: vertical section through a lobe and pycnidia. (From Hedwig 1787–1797, 2: pl. 1, fig. 3.)

of the subject appeared. This neglect, which continued until half a century after Hedwig's death, is attributable to the fact that the quality of most microscopes available before the 1830s did little to make lichen anatomy an attractive area of study, and also to the critical evaluation of Hedwig's findings published by the influential Swedish lichenologist Erik Acharius (1757–1819). In the course of an extended comment, Acharius (1810, pp. 1–3) rejected the concept of fertilization in lichens, and having declared, accordingly, that the structures interpreted as male organs by Hedwig had no such function, assigned them to the diverse group of cortical bodies for which he had introduced the term "cephalodia."[4]

The reproductive processes of cryptogams in general received scant attention during the first four decades of the 19th century, and the few observations that were reported had little impact.[5] The prominent German botanist Matthias Schleiden (1804–1881) could declare in 1842 that ferns and mosses do not reproduce sexually (Farley 1982, p. 84); similarly, Buhse (1846, pp. 321–322), echoing Acharius, dismissed Hedwig's results and stated that "lichens show no trace whatever of an organ about which there could, even for an instant, be any doubt as to whether or not it executed a fertilizing function."[6] Just before mid-century, however, the Leipzig music publisher and botanist Wilhelm Hofmeister (1824–1877) demonstrated not alone that bryophytes and vascular cryptogams reproduce sexually by means of gametes produced in antheridia and archegonia but also that those plants are characterized by an alternation of asexual and sexual generations (Hofmeister 1849).

Fertile pursuits

One result attributable to the appearance of Hofmeister's paper was a rekindling of interest in lichen reproduction. On this occasion,

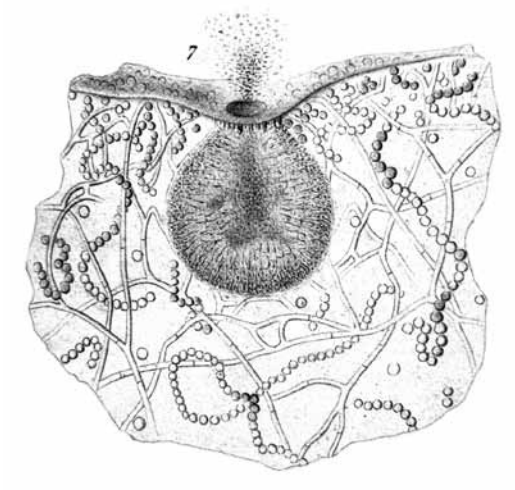

Figure 3. *Above, Collema* sp., vertical section through a lobe and pycnidium. (From Tulasne 1852a, pl. 6, fig. 7.)

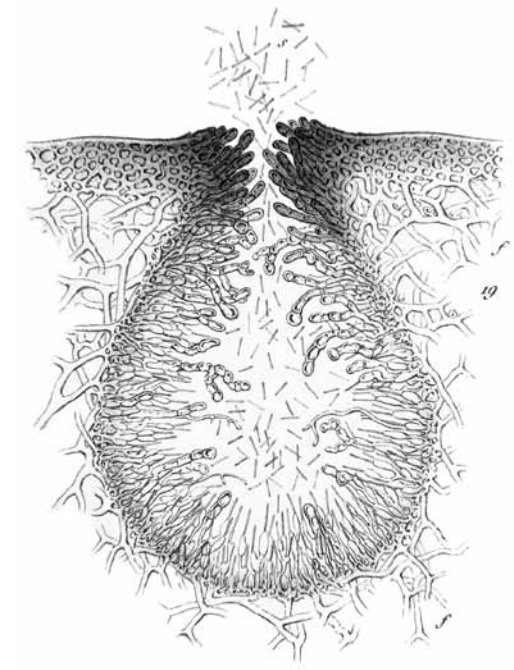

Figure 4. *Right, Hypogymnia physodes* (L.) Nyl., vertical section through a pycnidium containing small conidia ("spermatia"). (From Tulasne 1852a, pl. 14, fig, 19.)

results were first reported by Hermann Itzigsohn (1814–1879), a physician in practice at Neudamm, in the Prussian province of Brandenburg.[7] In an initial communication (1850a), which he introduced by stating that "the current physiological approach is to apply the term 'antheridium' only to an organ possessing internal spermatozoa,"[8] Itzigsohn claimed to have identified such organs on the thallus of *Anaptychia ciliaris* (as *Borrera ciliaris* (L.) Ach.) and to have seen them liberate spermatozoids ("Samenthierchen") similar to those of *Chara, Marchantia* and *Polytrichum*; in fact, the structures he interpreted as lichen antheridia were those investigated well over half a century earlier by Hedwig, whose work was evidently unknown to Itzigsohn. In a further paper, Itzigsohn (1850b, col. 917) noted that several botanists had queried his having seen motile cells within those structures, a difficulty he dealt with by alleging that motility becomes more evident in material macerated for some days, and is best seen "when maceration is continued to the onset of putrefaction."[9]

The novel results reported by Itzigsohn prompted the mycologist Louis-René Tulasne (1815–1885), then working at the Natural History Museum in Paris, to undertake a wide-ranging survey of the supposed antheridia. In a preliminary communication, Tulasne (1851) showed that the lichen bodies examined by Itzigsohn differ fundamentally in structure and content from bryophyte antheridia, but he was nonetheless prepared to entertain the possibility that they represent male organs; for this reason, he named those bodies "spermogonies" and applied the term "spermaties" to the minute, non-motile cells they contain (see Figs. 3 and 4).[10] In a further paper, Tulasne (1852a) provided details of the spermogonia and spermatia produced by over 100 lichens belonging to 31 genera, and again (p. 222) cautiously backed the perception of

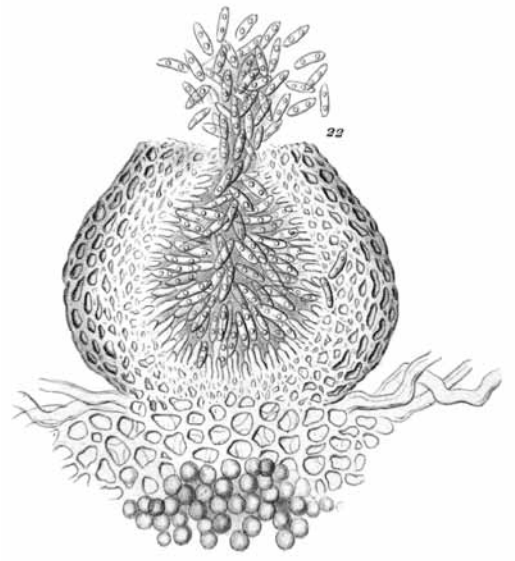

Figure 5. *Scutula miliaris* (Wallr.) Trevis., vertical section through a pycnidium containing large conidia ("stylospores"). (From Tulasne 1852a, pl. 14, fig 22.)

spermogonia as male organs: "in the matter of function, probably the better course at present is to compare the spermatia, or non-motile antherozoids, to mobile spermatozoids rather than to ordinary spores."[11] Tulasne also noted the occurrence in lichens of a spermogonium-like structure — for which he introduced the term "pycnide" (1852a, p. 108) — containing conspicuous objects that he had earlier (1851, p. 473) observed in fungal material and described as "stylospores" (see Fig. 5). He did not report any attempt to identify a specific female structure but, like Hedwig, assumed this to be associated with fruit-bodies: in an account of apothecia, Tulasne (1852a, p. 41) wrote, "certainly among lichens, the receptacles in which the female reproductive organs occur are most often disc-shaped."[12]

Though some understanding of the lichen sexual system might now seem to have been achieved, opinions differed as to how and where fertilization took place. The Scottish lichenologist William Lindsay (1829–1880) — later to add substantially to the number of species investigated by Tulasne — considered the function of spermatia (1856, p. 58) "to be the fertilization or fecundation of the spores," a notion also entertained by Berkeley (1857, p. 380) to whom it seemed that if spermatia "are really capable of impregnation, they probably act upon the sporidia [ascospores] when already formed, as the spermatozoids do on the spores of Algae." However, the fact that lichen spores are occasionally seen to germinate in the hymenium led Nylander (1858–1869, 1:40, n. 1) to reject the likelihood of spermatia being involved at this stage; on the other hand, his assertion that they exercise their fertilizing effect ("influence fécondante") on the lichen prothallus served only to cloud the issue further. Nylander's undocumented claim (pp. 41, 43) that the stylospores of lichens have the capacity to germinate while their spermatia do not, appeared to provide support for those committed to a sexual interpretation of the latter.[13]

An abundance of anatomical and morphological data relating to macrolichen pycnidia and spermogonia was made available in a lengthy paper by Lindsay (1859a),[14] but as to the rôle played by those bodies he could only say (p. 121),

> though I am inclined, so far as my own observations have gone, to the views regarding the functions of the spermogones and spermatia, pycnides and stylospores … taken by continental observers, — all that I feel warranted at present in advancing is, that I believe both spermogones and pycnides, in some way not yet fully established, to subserve the purposes of reproduction in lichens.[15]

When Tulasne had reported the occurrence of stylospores in lichens, he interpreted this finding (1852a, pp. 107–108) as proof "of the extreme affinity that exists between those plants and the ascophorous fungi, particularly in so far as the reproductive apparatus is concerned."[16] Here Tulasne had

glimpsed a fundamental truth, one not fully comprehended until late in the following decade, after the German botanist Anton de Bary (1831–1888) had introduced the concept of lichens as organisms composed of a fungus and a host alga (1866, p. 291). The gradual acceptance and expansion of that insight was achieved in the face of opposition from most lichenologists, whose reactionary stance also precluded their realizing that the search for evidence of fertilization in lichens could be meaningfully conducted only in the context of contemporary research on ascomycete reproduction.

Though no strictly mycological investigation of lichen sexuality was reported until the mid-1870s, mention may be made of three contributions touching on the question that appeared in the interim. Lindsay (1868, pp. 9–10) found "no reason to doubt the physiological relation of the Spermogonia to the Apothecia or perithecia — of the Spermatia to the Sporidia — save the circumstance that no act equivalent to impregnation has yet been actually observed." The same difficulty was noted by Bocquillon (1869, pp. 51–53) in a survey of published work on the reproductive structures of fungi and lichens. His account of lichen spermatia and stylospores took for granted Tulasne's belief that pycnidia are distinct from spermogonia, but within three years the tenability of that view had been called into question: following an extensive study of crustose taxa, Lindsay (1872, pp. 201–202) had become convinced "of the impossibility of drawing any scientific line of demarcation *between spermogones and pycnides* in lichens," and made clear that he had come to differ with those "continental authors, who have ventured to express decided opinions on the very difficult subject of the process of Lichen-reproduction. I am far from being prepared to accept their interpretations, preferring to hold the alleged functions of spermatia and stylospores in lichens simply as not yet established."

Similar reservations had already been voiced by Bary (1866, pp. 168–169), on which occasion he had also reminded his readers that "to date, no trace has been found of female sexual organs that could become fertilized by spermatia."[17] Seven years later, however, de Bary's student Ernst Stahl (1848–1919) undertook a search for such organs and was quickly successful: working with *Collema microphyllum* auct., Stahl (1874) observed that — arising from spirally-coiled, medullary hyphae, to which he applied de Bary's term "ascogonia" — septate filaments extended to the lichen surface and projected some little way beyond. Since Stahl frequently ("nicht selten") found spermatia attached to the tips of the ascogonial filaments, he concluded (col. 180) that "lichen spermatia are to be regarded as productions physiologically equivalent to the spermatozoids of other cryptogams. The projecting continuation of the ascogonium is to be seen as the female receptive organ; the fertilizing effect becomes transferred to the ascogonium through the multicellular tube."[18] Because Stahl believed that a correlation existed between his findings and the fertilization processes known to occur in red algae, he borrowed the phycological term "trichogyne" to designate the upward extension of the ascogonium.

Contentious findings

Stahl's results seemed to underpin the widespread perception of spermatia as male cells, but all was called into question when another French botanist, Maxime Cornu (1843–1901), an assistant — later professor — at the Natural History Museum in Paris, reported that he had germinated spermatia belonging to several non-lichenized ascomycetes. Cornu (1876, p. 100) claimed, therefore, that spermatia do not function as sexual cells but

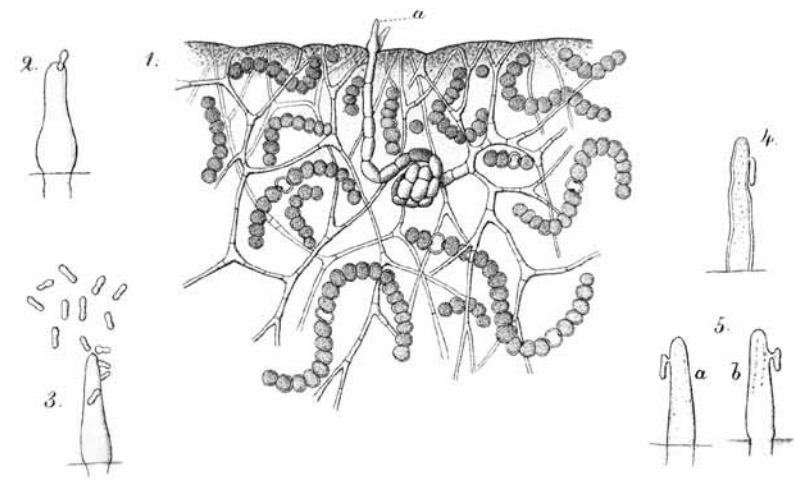

Figure 6. *Collema* sp., vertical section through a lobe and ascogonium showing projecting trichogyne at *a*; also shown are conidia adjacent to and in contact with trichogyne apices. (From Stahl 1877, 1: pl. 1, fig. 2; pl. 2, figs. 2–5.)

as propagules for the long-range dispersal of species; in his opinion (p. 55), spermatia belonged with the asexual ascomycete spores then recognized: stylospores produced in pycnidia and externally-occurring conidia. Though Cornu did not at all dismiss Stahl's results, he considered it strange ("singulier") that lichens should have a fertilization process distinct from that found in other ascomycetes. However, rather than venture a comment on this apparent anomaly, Cornu (p. 73) thought it best to wait "until M. Stahl had published figures and descriptions and fully demonstrated that the spermatia do indeed behave like non-motile floridean antherozoids."[19]

The first of Cornu's demands was quickly met. In the plates accompanying a much-expanded account of his work, Stahl (1877, pt. 1) provided illustrations of ascogonia, trichogynes and adhering spermatia (see Fig. 6). He sought to resolve the problem of germination by observing (p. 6) that

> although Cornu, on the basis of his investigations, is of the opinion that spermatia are nothing other than asexual propagules, he nonetheless believes that Tulasne's term "spermatium" must be retained for them, despite contending that they have no connection with fertilization; I cannot share this view … I propose, therefore, that the term introduced by Tulasne be used exclusively for those productions actually proved to be fertilizing agents, and, on the other hand, to employ the current terms stylospores, conidia, etc. for all those purely asexual propagules that have until now been wrongly described as spermatia.[20]

The only difficulty with Stahl's proposal was that spermatia had not, in fact, been proved to effect fertilization. However, on the strength of his observations, which included (p. 16) the occurrence of a spermatium joined to a trichogyne by a centrally-constricted bridge that appeared to bring the contents of the spermatium into contact with those of the trichogyne's apical cell, Stahl felt able to conclude (p. 45) that

> non-motile male cells, the spermatia, produced by abstriction in closed receptacles, travel passively by means of water to the female sex organs. The latter are divided into three different sections according to function: a unicellular organ to receive the male material, a multicellular conducting tube that mediates the fertilizing influence, and a similarly many-celled ascogonium, which, fertilized in this way, begins spore production.[21]

Any expectation that evidence would emerge to confirm the sequence of events outlined by Stahl, and possibly even demonstrate its

occurrence among lichens generally, began to recede early in the 1880s. First to voice opposition was the German mycologist Oscar Brefeld (1839–1925); a former student of de Bary's, Brefeld had come to differ bitterly with him on the question of fungal sexuality. In the course of a comment on the report of fertilization in lichens, Brefeld (1872–1881, 4:149–150) dismissed Stahl's conclusions as "mere interpretations" ("blosse Deutungen") and believed culture experiments would show that spermatia "have nothing to do with ascocarp development."[22] In the following year, Krabbe (1882) studied apothecial ontogeny in several species of the genera *Baeomyces* (as *Sphyridium*) and *Cladonia* and concluded (col. 82) that

> here, particularly, there can be no question of a fertilization process such as Stahl has described and illustrated for the Collemataceae. A carpogonium complete with ascogonium and trichogyne, as in the Collemataceae, is nowhere to be found; the earliest source of the ascogenous hyphae always occurs within the tissue of the lichen, and does not reach the upper surface either itself or by means of an extension.[23]

Soon afterwards, Fünfstück (1884) reported that a careful examination of fruiting material belonging to several species of *Peltigera* had revealed no trace of either spermogones or trichogynes.

Further, and what appeared to be decisive, evidence against Stahl's interpretation of spermatial function soon followed. In 1887 a student of Brefeld's at the Academy of Münster, Alfred Möller (1860–1922), made a fundamental contribution to the then still-contentious issue of lichen duality:[24] while algae from several species had been cultured by Famintzin and Baranetszky (1867),[25] and resynthesis of thalli had been detailed by Stahl (1877, pt. 2), growth of a lichen's fungal component in isolation had not been achieved. This was the work undertaken by Möller, and the fact that he was able to report successfully on it (1887) is directly attributable to his having had the benefit of Brefeld's direction. Over the years, Brefeld had developed a sophisticated "cultural methodology" (Dolman 1970, p. 438), and it is clear that Möller (e.g., pp. 5, 12, 34) fully availed himself of this. Though he worked with both micro- and macrolichen material, Möller (p. 18) chose to communicate only those of his results that concerned the former. He could have initiated his cultures using ascospores alone but, instead, painstakingly set about supplementing that source with the spermatia of nine species belonging to the genera *Arthonia, Buellia, Calicium* and *Opegrapha*. In this regard, he noted (p. 17),

> germination experiments carried out with lichen spermatia presented many initial difficulties, as was to be expected, but led ultimately to the anticipated results. A number of quite arbitrarily chosen lichen spermatia germinated … in the case of most, the development of a mycelium — soon followed in several instances by the formation of a thallus — could be exactly followed.[26]

He went on to say, "in the following account I shall not speak of lichen spermogonia and spermatia, but describe these structures instead as pycnidia and pycnoconidia," because "all the spermatia I have investigated proved to be true conidia."[27]

Möller's success in germinating lichen spermatia inevitably called into question the rôle accorded them by Stahl — such, indeed, may have been one of Möller's aims when he decided to include them in his investigation. Early in the 1860s, de Bary had demonstrated that ascomycetes reproduce sexually (Ainsworth 1976, pp. 117, 120), but Brefeld and Möller — blind to the confirmatory evidence that had since accumulated — refused to accept this fact, a stance that required them to rebut Stahl's conclusions; germinating

spermatia seemed to provide just the evidence they required, a point Möller (p. 17) did not fail to make. Brief reviews of Möller's work were published by two of de Bary's students. Büsgen (1888) commented that results obtained by culturing some crustose lichen spermatia might not necessarily apply to those of the Collemataceae and suggested that, before dismissing Stahl's results, Möller should consider extending his investigations to that family; Fischer (1888) took the view that Möller's findings were not necessarily in conflict with the sexual function attributed to spermatia because there was always the possibility that such cells had the capacity to behave as both conidia and gametes. Those points were taken up by Gustav Lindau (1866–1923) in a thesis prepared under the direction of Simon Schwendener (1829–1919) at the University of Berlin. Discussing what he described as "the burning question of lichen sexuality,"[28] Lindau (1888, p. 9) remarked that if spermatia of the Collemataceae were shown to be germinable, "the foundation of Stahl's hypothesis would be removed, as it would be altogether too surprising that spermatia could, at the same time, be asexual conidia and male fertilizing agents."[29]

Fischer's suggestion was rejected by Möller (1888), but Büsgen's criticism had led him to investigate what he termed the "so-called" ("sogenannten") spermatia of *Collema microphyllum*, the species — nominally at least — investigated by Stahl. As a result, Möller was able to report the germination of spermatia after a month in nutrient solution, and the development of branched filaments three months later. In Möller's opinion, there now existed sufficient evidence to justify discarding what he called (col. 423) "the illusion of sexually active ascomycete spermatia,"[30] and he advised any enduring sceptics to consult Brefeld (1884–1912, 7:57ff.). This reference includes Brefeld's assertion (p. 60) that "the sexuality elaborated for the fungi by de Bary, which has weighed like an Alp on the development of mycology … does not exist," and (pp. 60–61) the footnoted comment,

> Stahl mistakenly believed that he had shown lichen spermatia to be male cells. Culture of the so-called spermatia belonging to both free-living and lichen-forming ascomycetes proves, however, that they are nothing other than, as I have always assumed, asexual, perfectly usual but very small, almost rudimentary, conidia. This result effectively buries Stahl's contention, and extinguishes the glory of a discovery long proclaimed by de Bary and his school, and already accepted by every textbook.[31]

The first indication that interest in the "burning question" had spread beyond the European combat zone came when a graduate student at Harvard University, William Sturgis (1862–1942), published a study of apothecial development in over a dozen lichen species. With regard to the implications of Möller's work, Sturgis (1890, p. 18) remarked,

> [i]f it had not been definitely stated, it was at least tacitly assumed by most of the earlier mycologists, that lichens were sexual in their method of reproduction, and that the spermatia were the male organs. But we have seen that from these very spermatia Möller professes to have grown fully developed thalli, without the intervention of any female organ. If this is so, it is a fact which must militate very strongly against the view that the fruit of the corresponding lichens is in any respect sexual in its origin.

Sturgis investigated eight heteromerous species that he regarded as having a close relationship to the Collemataceae and five belonging to that family. In the former he had hoped to find the tripartite female apparatus described by Stahl but failed to do so. For the five homoiomerous species, on the other hand, he was able (p. 46) to establish "in all cases the essential point, — the existence within the thallus of a coiled ascogonium prolonged upwards in the form of a multicellular thread,

the trichogyne, whose tip appears above the surface of the thallus"; he made no mention, however, of having seen spermatia attached to a trichogyne.

A valuable précis of the principal contributions that had appeared on the subject of lichen spermatia up to the 1890s was provided by Fünfstück (1898, pp. 39–40, 42–44); this analysis of the published data convinced him (p. 44) of how "extremely likely it is that spermatia and carpogonia are no longer sexually functional."[32] Fünfstück's assertion might have been rather less sweeping had his literature survey not ended before Erwin Baur (1875–1933), a German physician and botanist, published the early results of a study involving a species of *Collema*. In four instances, Baur (1898) had successfully followed an entire trichogyne to its apex where he had seen adhering spermatia; his further observation that while free spermatia had richly-staining contents those attached to the trichogynes were empty, was advanced as evidence that gametogamy had occurred.[33] In the following year, trichogynes moved fleetingly center stage when Lindau (1899) returned to the subject of apothecial ontogeny; he was now fully committed to Möller's standpoint and altogether dismissive of any sexual rôle for the trichogyne.[34] The purpose of that filament, Lindau now contended, was to facilitate the emergence of young apothecia by boring ahead through the cortical plectenchyma, and he thought to win acceptance for this contention by proposing (p. 25) a new term, "terebrator," to replace "trichogyne." Lindau's proposal was quickly laid to rest by Darbishire (1900, pp. 342–343), whose studies involving trichogynes of *Physconia distorta* (With.) J. R. Laundon (as *Physcia pulverulenta* (Schreb.) Nyl.) had led him to conclude that such delicate structures (see Fig. 7) could not reasonably be construed as serving a mechanical function. In the course of his work, Darbishire (p. 337) had occasionally

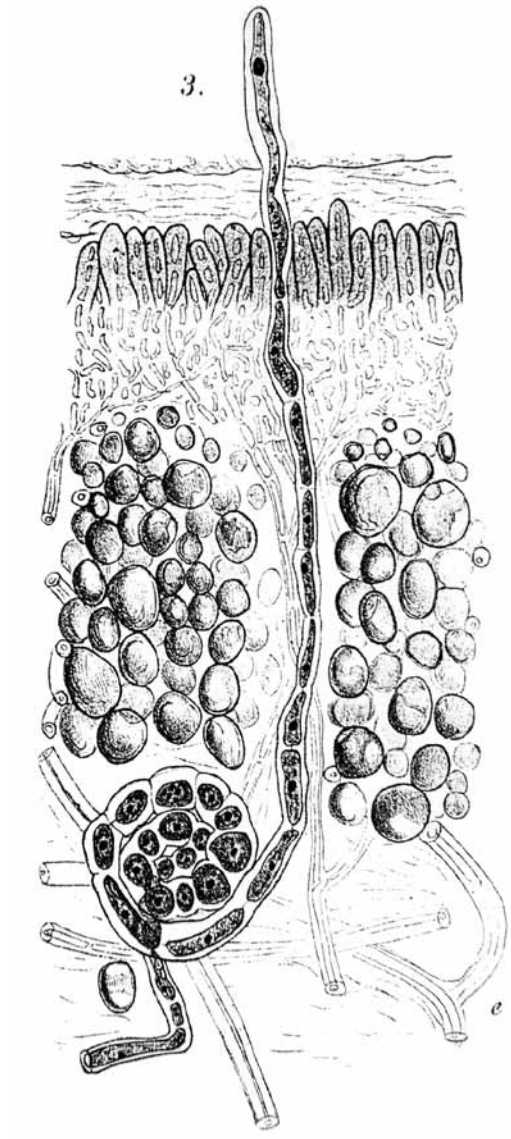

Figure 7. *Physconia distorta* (With.) J. R. Laundon, vertical section through a lobe and ascogonium with trichogyne. (From Darbishire 1900, pl. 11, fig. 3.)

seen spermatia attached to trichogyne apices, from which—though no fusion of contents was noted—he, like Baur and Stahl, inferred that trichogynes are receptive organs fertilized by spermatia.

At the close of the 19th century, therefore — after 50 years of investigation — no consensus had emerged as to why lichens devote resources to producing spermatia. Breaking more than a decade's silence on the subject, Möller now re-entered the debate with an outspoken attack (1901, p. 44) on Baur's results: "it seems almost unbelievable that in 1898 the 'question concerning sexuality of the Collemataceae' could still be raised in its old sense in the Berichte der deutschen botanischen Gesellschaft (p. 363), and that discredited and irrational views could once again be trotted out there without any adequate extent of essential supporting evidence having since been provided."[35] Evidence was, however, available: Baur (1901, p. 329) had found

> spermatia with discharged contents inseparably attached to the apices of all trichogynes whose associated ascogonia give rise to apothecia. Such does not occur in the case of the many carpogonia that degenerate without developing further. Every unprejudiced person must therefore draw the conclusion that the stimulus for further development of the carpogonium can be nothing other than fusion with a spermatium.[36]

Baur then went on to query whether the results of Möller's (1888) work with *Collema* spermatia did, in fact, amount to germination and to argue that, in any event, the "stunted outgrowth" ("kümmerliches Auswachsen") it had taken Möller four months to produce did not invalidate a perception of spermatia as male cells.

Two further contributions to the debate appeared in 1901. Julius Steiner (1844–1918), an Austrian high school teacher, published an assessment of the findings reported during the previous quarter century on the subject of conidial function. In his opinion (p. 130), the accumulated evidence — including that newly advanced by Baur — did not support a sexual rôle for spermatia, or pycnoconidia in the terminology preferred by Steiner.[37] The second contribution was provided by the German lichenologist Georg Bitter (1873–1927) whose observation that many richly spermogoniferous species of *Hypogymnia* produce very few apothecia led him (1901, p. 217, n. 1) to interpret the spermatia of such species as conidia with a "dispersive capacity" ("Fortpflanzungsfähigkeit"). Bitter did, nonetheless, accept that spermatia are associated with fertilization in some lichens and, in an attempt to account for this dual capability, aired anew "the possibility, though of course unsupported by evidence, that the same spermatia are, depending on circumstances, able to perform both functions."[38]

At this point, perhaps the sole detail on which all involved in the debate on lichen sexuality would have agreed was that pycnoconidia/spermatia are extruded from receptacles located in or on the upper surface of a thallus. An exception to this seemingly established fact was, however, reported in the following decade by Freda Bachmann (1878–1961), a graduate student at the University of Wisconsin.[39] Working with a species of *Collema*, Bachmann (1912) discovered that, unassociated with any receptacle, clusters of what she considered spermatia occur as (p. 753) "scattered groups embedded in the thallus," where "[t]hey arise by what appears to be a process of budding from certain slender lightly staining hyphae."[40] The ascogonia of the species also differed from those of other lichens in that their trichogynes did "not grow vertically upwards to the surface" but extended laterally, and "[i]f we follow them in their course the striking fact is at once noted that they grow towards the groups of spermatia." She further recorded (p. 754) that "[t]he end of the trichogyne becomes closely appressed to and flattened against the wall of the spermatium," and referred to an "opening" between the cells in question. Though Bachmann made no mention of any observations respecting

plasmogamy or karyogamy, she nonetheless did not hesitate to declare (p. 757) that the findings she had reported gave "a final and complete demonstration that the spermatia of the Lichens are male gametes and not asexual conidia."[41] Bachmann's results were dismissed, though for no valid reason, by the French husband and wife team, Fernand and Valentine Moreau (1886–1980, 1886–1974)[42]: having failed to find internal spermatia or trichogynes in material of the genus *Solorina*, which is quite unrelated to *Collema*, they (1916) took this as sufficient reason to "reject the theory proposed by Miss Bachman [*sic*]."[43]

With any meeting of minds on the subject of spermatial function now evidently as far away as ever, the time was ripe for an updated appraisal of the literature. In fact, several such reviews appeared in the 1920s. The first was provided by Smith (1921, pp. 160–166, 192–207) who, in summing up, largely restricted herself to saying (p. 206), "[m]any modern lichenologists reject the view that they [spermogonia] are sexual; they regard them as secondary organs of fructification analogous to the pycnidia so abundant in the related groups of fungi." Nienburg (1926, p. 127) also provided a useful evaluation of the relevant data and though, like Smith, wary of making a definitive statement, did venture the opinion that "spermogonia were, at least originally, male organs, though now, perhaps, no longer functional."[44] Fünfstück (1926) listed the principal contributions that had appeared since his previous summary; these had not led him to alter his earlier perception of spermatia as vestigial bodies—indeed, he commented (p. 55) "the fact that they are germinable, as A. Möller has shown, does not rule out their having originally been active in a reproductive capacity, given that germination of sexual energids is known among algae."[45] The possibility that spermatia are capable of acting in a dual capacity was also entertained by the German mycologist Hans Kniep (1881–1930). He believed (1928, p. 385) that Stahl's reports had firmly established the existence of sexual reproduction in lichens, which led him to pose the question (p. 387) of whether spermatia produced by species that lack trichogynes have switched rôles and become adapted predominantly to vegetative reproduction, or whether their potential in this regard is attributable to spermogones having originally been wholly asexual pycnidia that only subsequently acquired a sexual function also? A clash of publication dates precluded any mention of Kniep's work by Moreau and Moreau (1928), but even had they known of it, their response to his speculations would scarcely have been supportive: wide-ranging ascogonial studies had convinced them (p. 27) that "spermatia have nothing whatever to do with apothecial development, and the trichogyne is to be regarded merely as a terminal filament of the ascogonium … not as an organ in any way concerned with the capture of spermatia, either external or internal."[46]

From the 1930s to the 1950s, lichen conidia received little attention. Fink (1935, p. 11), Stevens (1941, p. 66) and Johnson (1954, p. 343) took them to be essentially male gametes, while des Abbayes (1951, pp. 65, 69) denied them any such rôle and insisted that they served solely as vegetative propagules. Most botanists of the time, however, would likely have agreed with Santesson (1952, p. 28): "The function of the lichen conidia is still an open question in spite of various hypotheses."

Reconciling the results

Renewed interest in the topic began to emerge early in the 1960s: Ahmadjian (1964, p. 96) suggested that the purpose of "pycniospores or spermatia is to provide a nucleus of opposite mating type as well as to retain the capacity

to function as asexual spores," and Culberson and Culberson (1968, p. 463), commenting on species in which there is a plentiful production of both apothecia and pycnidia, remarked, "[i]f pycnidia and conidia (the pycniospores) which they produce were functioning here in sexual reproduction, then the high frequency of pycnidia in plants also bearing apothecia would be explained." This interest gathered momentum in subsequent years. Having studied 35 species belonging to 17 genera, Jahns (1970, p. 115) reported that "cytological investigations and other observations seem to make it probable that a fertilization of the ascogon occurs from the outside of the thallus by the nucleus of a conidium migrating through the trichogyne." A few years later, Henssen and Jahns (1973, p. 79) considered it "altogether likely that somatogamy and fertilization by conidia occur in lichens"[47]; Poelt (1974, p. 101) took the view that pycnospores (his preferred term) "function normally as spermatia because of their small size, the very small amount of protoplasm, and their occurrence on trichogynes." All these observations and opinions helped reinforce the perception of conidia as agents of spermatization, but evidence to the contrary was soon to emerge: Vobis (1977) reported the germination of conidia belonging to three crustose species, an achievement specifically adverted to by Kärnefelt (1979, pp. 23–24) when reminding lichenologists that "[t]here is no actual proof that pycnoconidia (or microconidia) function as spermatia, and a nucleus has never been seen to pass from a pycnoconidium into the cytoplasm of a trichogyne."

Nonetheless, in a summary of the evidence available at the close of the 1970s, Culberson and Culberson (1980, pp. 133–134) continued to make the case for lichen sexuality:

> There has long been controversy over the biological role of microconidia in the lichens. Are they asexual propagules or spermatia? … The high correlation of apotheciate thalli with the presence of pycnidia bearing microconidia—a frequently made observation by lichen taxonomists—would point to a sexual function for these structures … In the most recent experimental work (Vobis, 1977), the microconidia of 13 species failed to germinate but those of *Calicium adspersum* Pers. and *Opegrapha vermicellifera* (Kunze) Laund. did germinate. In *Lecanactis abietina* (Ach.) Körb., which produces both microconidia and macroconidia [stylospores], peculiar asexual spores produced in a few lichen genera, the former did not germinate but the latter did. It therefore seems that microconidia probably serve primarily a sexual function and only secondarily an asexual one.[48]

The plausibility of that interpretation was considerably strengthened by the work of Honegger (1984); SEM preparations of material belonging to *Cladonia furcata* (Huds.) Schaerer enabled her not alone to see and illustrate points of fusion between conidia and trichogynes but also to demonstrate that perforation of the trichogyne occurs at those points. Though karyogamy was not reported, Honegger (p. 17) believed her data could "be interpreted with reference to spermatial function." She also pointed out (p. 18) that "[s]permatial function and an ability to germinate are not necessarily exclusive properties as has been demonstrated in some non-lichenized ascomycetes." The possibility that lichen conidia have the potential to behave as both gametes and diaspores—originally suggested, as referenced above, by Eduard Fischer (1861–1939)—has also been supported by Hawksworth (1988, pp. 181, 186) and Tibell (1993, p. 335).

At the beginning of the 20th century, Fünfstück (1902, p. 62) wrote, "though a whole series of works aimed at resolving the sexual question has been undertaken since Stahl's well-known investigation, it nonetheless remains open"[49]; 100 years later it still does.

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Dates accompanying the names of lichenologists referred to in this paper are cited on the authority of Grummann (1974), except where otherwise stated.

Notes

1. The latter deficiency may reflect an initial reluctance to follow Camerarius when, having searched unavailingly for female structures corresponding to the "pollen" producing organs of club mosses and horsetails, he envisaged (1694, p. 77) a class of incomplete plants comprising those without, or possessing only indistinct, flowers. The term "Cryptogamia" was introduced by Linnaeus (1735, p. [5]) to designate the 24th class of his "Clavis systematis sexualis."
2. The existence of these bodies had already been reported by Johann Dillenius (1684–1747) under the general term "verrucae"; though he illustrated only their superficial appearance (1742, e.g., pl. 20, figs. 45b–c), Dillenius had attempted an internal examination—he noted (p. 150) that "in transverse section, these verrucae show only some spongy material" ("Hae verrucae transversim sectae nihil nisi fungosam quandam substantiam visui exhibent").
3. Of the 214 figures published by Hedwig, Withering reproduced a total of 90, which included all 7 of those relating to lichens. Regarding his incorporation of Hedwig's material, Withering remarked (3:10) "in bringing my readers to an acquaintance with this Class [Cryptogamia], it would be unpardonable to make no mention of the illustrious HEDWIG, who has immortalized his name by the accuracy of his researches, and the splendor of his discoveries, in these obscure families of plants. He communicated the result of his observations to the Academy of Sciences at Petersburgh, in the year 1783. As this work is but little known to the English Botanist, I shall subjoin the following compendious view of the subject, confining myself principally to the discoveries more immediately relating to the parts of fructification. Those who wish for further information, cannot fail of being highly gratified by an examination of the original work, and by a perusal of this very ingenious author's subsequent publications." Withering's "compendious view" of Hedwig's text comprised a translation, with occasional additions, of passages principally concerning bryophytes, ferns, fungi and lichens, together with copies of the illustrations referred to in those passages. Withering did not, however, adequately convey that all his illustrations of cryptogams, which occupy plates 13–16, are borrowed from Hedwig—the title page of volume 3 refers only to "figures, partly by the author, and partly by Jonathan Stokes, M.D."; this omission has misled commentators (e.g., Henrey 1975, 2:124) into assuming that Stokes and Withering were responsible for the illustrations on all 16 plates.
4. Acharius did, nonetheless, investigate the structures described by Hedwig and appears to have been the first to record that they contain discrete particles: one of his illustrations (pl. 9, fig. 6E) shows "in vertical section, two cephalodia whose somewhat dense, subgelatinous contents include gongyles [corpuscles] assembled in glomerules" ("Thalli pars una cum duobus Cephalodiis … perpendiculari sectione, quorum substantia intus solidiuscula subgelatinosa, gongylos in massulas congestos continet" (p. 95)); in current usage, the term "cephalodium" is reserved for a cortical outgrowth consisting of hyphae and cyanoprokaryote cells.
5. For details of those observations, see Johnson (1915, pp. 387–388) and Leroy (1960, pp. 17–18).
6. "Bei den Flechten vollends fehlt jede Spur eines Organ's, bei dem man auch nur für einen Augenblick in Zweifel sein könnte, ob es einer befruchtenden Function vorstehe oder nicht."
7. Now Depno in northwestern Poland, about 15 km north of Kostrzyn. Grummann (1974) does not have an entry for Itzigsohn—his dates as given above are those cited by Möbius (1937, p. 75).
8. "Nach dem gegenwärtigen Standpunkte der Physiologie hat kein Organ Anspruch, Antheridium genannt zu werden, als dasjenige, das in seinem Inneren Spermatozoen zeigt"; Goebel (1926, p. 124) observed, "[i]n the middle of the nineteenth century everything was designated as Physiology that was not System."

9. "… wenn man die Maceration bis zur beginnenden Putrescenz fortsetzt."
10. He subsequently (1852b, p. 842) reported the occurrence of those bodies in non-lichenized fungi. Lichen reproduction was also investigated at this time by Johann Bayrhoffer (1793–1868), an artist and one-time printer. His conclusions appeared in an elaborate, but quite fanciful, publication (1851) that did nothing to advance the subject; Kützing (1851–1852, 2:309) found the work "quite unintelligible" ("sehr unverständlich"), an assessment equally applicable to most of Bayrhoffer's many illustrations.
11. "… il vaut mieux sans doute aujourd'hui assimiler, quant aux fonctions, les spermaties ou anthérozoïdes immobiles avec les spermatozoïdes doués de motilité, plutôt qu'avec les spores ordinaires."
12. "La forme, sans contredit, la plus générale qu'affectent chez les Lichens les réceptacles où sont placés les organes femelles de la reproduction, est celle d'un disque."
13. A perceptive account of the views held by early students of lichen reproduction may be found in Krempelhuber (1867–1872, 1:382–388, 3:48–49)
14. An abstract of that paper was published by Lindsay (1859b).
15. Nothing further had been established four years later when the topic was briefly reviewed by Vaillant (1863, pp. 54–57).
16. "La présence de ces organes [stylospores] dans les Lichens fournira une nouvelle preuve de l'extrême affinité qui existe entre ces végétaux et les Champignons ascophores, pour tout ce qui touche à l'appareil reproducteur."
17. "Es ist ferner bis jetzt immer noch keine Spur von weiblichen Geschlechtsorganen gefunden worden, die etwa durch Spermatien befruchtet würden."
18. "… die Spermatien der Flechten als den Spermatozoïden anderer Kryptogamen physiologisch gleichwerthige Gebilde zu betrachten sind. Als weibliches Empfängnissorgan ist der nach aussen tretende Fortsatz des Ascogons anzusehen: die befruchtende Einwirkung wird zu dem letzteren durch den mehrzelligen Schlauch übertragen." A contemporary comment well illustrates the confusion of those botanists who refused to accept that lichens are associations of fungi and, mostly, green algae: Leighton (1874, p. 124) believed it "worthy of consideration" that "zoospores in lichens do possibly fertilize, by their movements and contact, one or more gonidial cells, and that the gonidia so fertilized give birth to the asci and paraphyses of the hymenium."
19. "… il faut attendre que M. Stahl ait publié des figures et des descriptions et qu'il ait pleinement démontré que les spermaties agissent bien comme les anthérozoïdes immobiles des Floridées."
20. "Wenn auch Cornu auf Grund seiner Untersuchungen der Ansicht ist, dass die Spermatien nichts anderes sind als ungeschlechtliche Vermehrungszellen, so glaubt er nichts desto weniger den von Tulasne geschaffenen Namen Spermatium für diese nach ihm mit keiner Befruchtungserscheinung in Beziehung stehenden Gebilde beibehalten zu müssen. Ich kann diese Ansicht nicht theilen … Ich schlage deshalb vor, den von Tulasne geschaffenen Namen ausschliesslich für diejenigen Gebilde zu gebrauchen, für welche es thatsächlich erwiesen ist, dass sie die befruchtenden Organe sind; dagegen für alle die, bis jetzt fälschlich als Spermatien bezeichneten, Zellen, welche nur ungeschlechtliche Vermehrungszellen sind, die für diese letzteren gebräuchlichen Ausdrücke Stylosporen, Conidien u.s.w. anzuwenden."
21. "Die in geschlossenen Behältern, durch Abschnürung erzeugten, bewegungslosen, männlichen Zellen, die Spermatien, gelangen passiv durch Vermittelung des Wassers zu den weiblichen Geschlechtsorganen. Diese letzteren sind in drei nach ihrer Function verschiedene Theile gegliedert: in ein einzelliges Conceptionsorgan, welches den männlichen Stoff aufnimmt, in einen mehrzelligen Leitungsschlauch, welcher die befruchtende Einwirkung vermittelt und in ein ebenfalls mehrzelliges Ascogon, welches auf diesem Wege befruchtet, die Sporenbildung übernimmt." Stahl's conclusions were made available to a wider audience by Vines (1878), not all of whom proved receptive: Crombie (1882, p. 555), who believed that the function of spermatia was "the fertilization or fecundation of the spores," charged Stahl with having "supposed that he had detected sexual organs in the shape of an *ascogonium* and a *trichogyne*, regarded by him as a type of *carpogonium*. These observations, however, have not been confirmed by subsequent researches … while his attributing to the hyphae a faculty of 'contortion' or spirally coiling themselves, which from their nature they do not and cannot possess, is calculated to invalidate all that he otherwise observed and depicted"; Tuckerman (1882–1888, 1:xi–xii) went even further by making no mention whatever of Stahl's work in his treatment of spermatia.

22. "… nichts mit der Bildung der Ascusfrüchte zu thun haben"; Brefeld continued his criticism of Stahl on pp. 159–160.
23. "Hier kann nun vor Allem an einen solchen Befruchtungsvorgang, wie er von Stahl bei den Collemaceen beschrieben und abgebildet worden ist, nicht wohl gedacht werden. Ein so beschaffenes Carpogon mit Ascogon und Trichogyn, wie bei den Collemaceen, ist hier nirgend zu finden; die ersten Anfänge der Schlauchfasern liegen stets im Innern des Gewebes und treten weder selbst noch vermittelst eines Fortsatzes an die Oberfläche."
24. Möller's work in this area has largely been forgotten, to the extent that it went unmentioned by Peveling (1987).
25. In fact, Famintzin and Baranetzky failed to understand what they had achieved: having observed that green cells ("gonidies") from a variety of lichen thalli produce zoospores in culture and that these appeared to be representative of the algal genus *Cystococcus*, they grasped the wrong end of the stick and concluded that such genera represent nothing more than chlorophyllous lichen cells growing independently of their parent thalli. Famintzin and Baranetzky's misinterpretation was corrected by Woronine (1872).
26. "Es wurden Keimversuche mit Flechtenspermatien angestellt, die zwar zunächst, wie es nicht anders zu erwarten war, erheblichen Schwierigkeiten begegneten, endlich aber doch zu dem ewarteten Resultate führten. Eine Anzahl ganz beliebig herausgegriffener Flechtenspermatien keimten … bei den meisten konnte die Entwicklung eines Mycels, demnächst in einer Reihe von Fällen die Bildung eines Thalluskörpers genau verfolgt werden." Some of the spermatia he investigated took weeks to germinate in nutrient solution, and on occasion months elapsed before any semblance of a mycelium became visible (p. 31); Möller did not include any illustrations of his cultures.
27. "Ich werde im folgenden nicht von Spermogonien und Spermatien der Flechten sprechen, sondern diese Gebilde als Pycniden und Pycnoconidien bezeichnen, und zwar aus folgenden Gründen. Alle von mir untersuchten Spermatien erwiesen sich als echte Conidien."
28. "… die brennende Frage nach der Sexualität der Flechten."
29. "Sollte allerdings auch bei den *Collemaceen* das Auswachsen der Spermatien zum Thallus erfolgen, so wäre damit der Stahl'chen Hypothese der feste Boden entzogen, denn es erschiene doch zu wunderbar, wenn die Spermatien zu gleicher Zeit asexuelle Conidien und männliche Befruchtungsorgane wären." Though Lindau did not defend his thesis until November 1888, he had evidently completed work on it before July of that year when Möller (as referenced in text) responded to Büsgen and Fischer's reviews.
30. "… das Trugbild der sexuellthätigen Ascomycetenspermatien."
31. "Die von *de Bary* für die Ascomyceten construirte Sexualität, die wie ein Alp die Entwicklung der Mycologie bedrückt ... besteht in Wirklichkeit nicht"; "Von den Spermatien der Flechten glaubte irrthümlich *Stahl* nachgewiesen zu haben, dass sie männliche Geschlechtszellen seien. (Beiträge zur Entwicklungsgeschichte der Flechten 1877, I. Heft). Mit der Cultur der sogenannten Spermatien von gewöhnlichen wie flechtenbildenden Ascomyceten, welche erweist, dass sie nichts anderes sind wie das, was ich stets angenommen habe (Schimmelpilze, IV. Heft p. 158–160 Anmerkung), nämlich ungeschlechtliche ganz gewöhnliche, aber sehr kleine, fast rudimentäre Conidien, gehen die unbegründeten Behauptungen *Stahl's* zu Grabe und die Herrlichkeit einer Entdeckung hat ein Ende, die von *de Bary* und seiner Schule seit Jahren verkündet und bereits in alle Lehrbücher aufgenommen ist."
32. "… im höchsten Grade wahrscheinlich ist, dass die Spermatien und Carpogone nicht mehr sexuell funkionieren."
33. Baur's paper was evidently not known to Glück (1899) when compiling the useful literature survey that accompanies his substantial memoir. Glück was concerned almost exclusively with the comparative morphology of lichen spermogonia and commented only briefly (p. 86) on their spermatia, which he regarded as asexual cells.
34. This uncompromising view may have owed something to Brefeld, with whom Lindau worked when volume nine of the *Untersuchungen* … (1891) was in preparation.
35. "… erscheint es fast unglaublich, dass noch im Jahre 1898 in den Berichten der deutschen botanischen Gesellschaft (S. 363) die 'Frage nach der Sexualität der Collemaceen' im alten Sinne wieder auftauchen konnte, dass dort die alten, so gründlich widerlegten und ad absurdum geführten Anschauungen wieder vorgetragen werden, ohne dass der zu ihrer Stütze nun doch wohl sicher nothwendige Beweis in irgend ausreichendem Maasse geliefert würde"; in his only published reference to those remarks, Baur (1904, p. 24) described Möller's stance as

altogether partisan and declared that taking the trouble to counter his criticisms would be a waste of time ("Zeitverschwendung").

36. "… finden wir an allen Trichogynspitzen, deren zugehöriges Ascogon die Apotheciumbildung beginnt, ein untrennbar fest anhaftendes Spermatium, das seinen Inhalt entleert hat. An allen den vielen Carpogonen, die der Rückbildung anheimfallen, ohne sich weiter zu entwickeln, ist dies nie der Fall. Jeder Unbefangene muss daraus den Schluss ziehen, dass der für die Weiterentwickelung eines Carpogons nöthige Reiz nichts anderes sein kann, als die Copulation mit einem Spermatium."
37. Steiner proposed (p. 119) that use of the term pycnoconidia be extended to include stylospores.
38. "Es bleibt ja sogar die allerdings durch nichts bewiesene Möglichkeit offen, dass die gleichen Spermatien zu beiden Funktionen, je nach den Umständen, befähigt sind."
39. The date of Freda Bachmann's death was kindly provided by the Bureau of Vital Statistics, Toledo, Ohio.
40. Bachmann identified her material as a "form of *C. pulposum*" (p. 750), but Fink (1918) considered it sufficiently distinct to merit not alone independent specific but also generic status; accordingly, he introduced the name *Collemodes bachmanianum*, which, however, became *Collema bachmanianum* (Fink) Degel. following the rejection of Fink's genus by Degelius (1954, p. 102).
41. In a second paper, Bachmann (1913) supplemented her account with extensive anatomical and cytological detail; that paper also includes a comprehensive "Historical Sketch" (pp. 370–383) of the literature relating to spermatia and apothecial ontogeny that had appeared up to the time of her own research.
42. Fernand and Valentine Moreau's dates of death are cited, respectively, from Letrouit (1980) and courtesy of Service de l'État Civil, Oradour-sur-Vayres, Haute-Vienne.
43. "… nous rejetons donc la théorie suggérée par Miss Bachman"; but Bachmann was correct, and nearly forty years later internal conidia were reported from another species of *Collema* (Degelius 1954, p. 98).
44. "… daß die Spermogonien wenigstens ursprünglich männliche Sexualorgane waren, wenn sie auch jetzt vielleicht funktionslos geworden sind."
45. "Daß die Spermatien keimfähig sind, wie A. Möller gezeigt hat … kann nicht als Argument gegen die ursprünglich sexuelle Natur dieser Gebilde gelten, da Keimung sexueller Energiten bei Algen bekannt ist."
46. "… les spermaties ne jouent aucun rôle dans le développement de l'apothécie et nous présentons le trichogyne comme un simple filament terminal de l'ascogone … nous ne reconnaissons nullement en lui un organe capteur de spermaties, tant internes qu'externes"; those views were further promoted in the textbook of lichenology published by Moreau (1928).
47. "… ist es durchaus wahrscheinlich, daß bei den Flechten Somatogamie und eine Befruchtung durch Conidien nebeneinander vorkommen."
48. Coppins (1983, p. 67) and Sipman (1983, p. 35) also tended to accept that conidia can effect fertilization. At the same time, Coppins reported (p. 67) that, in addition to apothecia, several species of the genus *Micarea* produce three types of conidium; he designated these micro-, meso- and macroconidia, while accepting that their rôle "is as yet unknown." However, in the case of lichens known to produce only pycnidia, e.g., *Cheiromycina flabelliformis* B. Sutton, conidia evidently serve a purely dispersive function.
49. "Obwohl seit den bekannten Stahl'schen Untersuchungen eine ganze Reihe Arbeiten das Ziel verfolgten, die Sexualitätsfrage zur Entscheidung zu bringen, so ist letztere trotzdem heutigen Tages noch offen."

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