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INVITED REVIEW

Great Discoveries in Bryology and Lichenology

Simon Schwendener (1829–1919) and the Dual Hypothesis of Lichens

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On September 10, 1867, the Swiss Natural History Society held its annual general meeting in the small city of Rheinfelden. The botanical session was presided over by the taxonomist and palaeobotanist Oswald Heer, Professor of Botany at the University of Zürich. The first speaker was Simon Schwendener (Fig. 1), newly elected Professor of Botany at the University of Basel. Schwendener, a former student of Heer, had an astonishing career. Born on February 10, 1829 in Buchs at the Austrian border in northeasternmost Switzerland as the only son of a farmer, he was expected to take over the family farm. However, Simon proved to be an excellent student who became increasingly attracted to science rather than to farming. The financial situation of the family did not allow him to be sent to the university, as he desired. From age 18 onwards, Schwendener made a living as a school teacher, first at an elementary school near his home village and later in a private high school. In between, he went to the French speaking part of Switzerland and attended science classes at the University of Geneva where he met Alphonse de Candolle. A small inheritance and probably the ability to live on almost nothing allowed Schwendener to matriculate at Zürich University in 1853 where he studied science and wrote, under the auspices of Oswald Heer, a Ph.D. Dissertation on ''Periodic features in nature, especially in the plant kingdom'' that was completed in 1856; this topic was originally proposed by de Candolle.

From 1855–1857, Carl Wilhelm Nägeli had the chair of botany at the Polytechnic (now Swiss Federal Institute of Technology) and at the University of Zürich. Nägeli was an outstanding, multi-talented Swiss botanist with a strong interest in light microscopic research techniques. Under his guidance, Schwendener started microscopic studies. In 1857, Nägeli was nominated as a professor of botany at the University of Munich. He offered Schwendener a position as an assistant, which was gladly accepted. ''It was a beautiful time'' wrote Schwendener in a short autobiographic note (published in Zimmermann 1922), ''here (in Munich) I became a botanist in the strict sense.'' Schwendener greatly appreciated the contact and exchange of ideas with other young scientists. He had to work half time for Nägeli and the rest was devoted to his own projects. Already in Zürich he had decided to investigate lichens. Nägeli's herbarium and numerous specimens donated by Philipp Hepp (*Heppia* Nägeli ex A. Massal.), and careful light microscopic studies by Nägeli himself were the stimulus for Schwendener's own investigations on the functional anatomy, especially on growth and development of lichen thalli, which culminated in a series of publications (Schwendener 1860, 1862, 1863*a*,*b*, 1864, 1866, 1868*a*). These contain a wealth of interesting observations e.g., on cell and ''tissue'' dimensions in growing and mature thalline areas, intercalary (hyphal) growth as an important element in thallus development and the presence of a gas-filled zone in the thalline interior. The first publication on fruticose lichens was Schwendener's habilitation thesis; from 1860 onwards he was admitted as a so-called Privatdozent at the University of Munich and thus was eligible as a professor. In cooperation with Nägeli, Schwendener published two standard works on the theory and practice of the light microscope and their application in botany (Nägeli & Schwendener 1865, 1867), which were held in high esteem by Ernst Abbé, the world leading expert in optics in the company of Carl Zeiss, Jena. Nägeli and Schwendener were among the best microscopists of their time and thus had access to new dimensions. In early 1867 Schwendener was offered a chair in botany at the comparatively small University of Basel (founded 1460) in northern Switzerland, which he readily accepted.

On this memorable September 10, 1867, Heer was certainly interested to hear what his talented former student had to tell, and Schwendener, on the

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FIGURE 1. Simon Schwendener, in a low relief by R. Haberlandt. From: Berichte der Deutschen Botanischen Gesellschaft 41 (1922), no page number. With permission of the publisher, Gebrüder Bornträger Verlagsbuchhandlung, Berlin.

other hand, was probably curious to see the reaction of his presentation, since he planned to speak for the first time in public on a hypothesis that had crystallized during his extensive comparative light microscopic studies on lichens, algae, and fungi, but was not yet confirmed by experimental evidence. Extracts of the protocol (Verh. Schweiz. Naturf. Ges. 51: 88–90, 1867, often referred to as Schwendener's own publication), liberally translated, read as follows:

> ''Prof. Schwendener from Basel explains in his presentation, refering to his earlier publications on the anatomy of the lichen thallus, that during his recent investigations he became more and more convinced that . . . the gonidia and fibres of a large group of lichens were not genetically related; instead the latter had to be interpreted as growth of fungal hyphae on algae.''–''According to the current view of the speaker lichens have to be seen not as autonomous plants, but as fungi in connection with algae.''–''The president acknowledged the presentation of Prof. Schwendener but did not conceal his scepticism, which was primarily based on the wide distribution of crustose and foliose lichens and on their chemical composition (content of starch); the apothecia would have to be regarded as fungal fruit bodies.– This question was affirmed by Prof. Schwendener. He sees no contradiction to his findings in the wide distribution of crustose lichens since *Cystococcus* (= *Trebouxia*) is equally widespread and the nutritional situation of the fungus improves once the algal cells are overgrown by the mycelium. The chemical composition is not contradictory, but to the contrary supports his view since the membranes (= cell walls) of the gonidia react differently than the fibres, namely like algal membranes (= cell walls). There are no differences between ascomycetes and pyrenomycetes on the one and lichens on the other hand, except the presence of the green gonidia. Spermogonia . . . are exactly the same; for this reason lichens are considered by numerous authors as a group of the fungi.''

In tables and figures Schwendener listed lichens with either *Stigonema, Scytonema, Nostoc, Gloeocapsa,* or *Rivularia* and suggested that the ''common fruticose and foliose lichens contained *Cystococcus* (= *Trebouxia*) and the Graphidaceae had algae of the *Chroolepus*-group (= *Trentepohlia* spp.).'' A short summary of his findings which had spread among colleagues by oral communication was published in the following year (Schwendener 1868*b*) and a detailed publication with three excellent lithographs appeared in 1869 (see title page–Fig. 2 and Fig. 3).

Until the end of the 19th century Schwendener's dual lichen hypothesis was vigorously rejected by the majority of leading contemporary lichenologists (e.g., Crombie, Krempelhuber, Müller-Argoviensis, Nylander, and others), ''in part from reasons of common sense, in part because lichenology has always been a somewhat esoteric pursuit'' (Ainsworth 1976). The lack of scientific arguments led to some quite aggressive attacks (summaries: Ainsworth 1976; Hoppe 1987; Smith 1921). Schwendener replied in his last publication on lichens in 1872, where he once more explained the essence of his hypothesis. The last attempt to disprove the dual nature of lichens (Schmidt 1953) was published fourteen years after the first successful resynthesis of the symbiotic phenotype from aposymbiotically cultured *Cladonia pyxidata* and its green algal partner under sterile conditions by Thomas (1939) at the Swiss Federal Institute of Technology in Zürich.

Why then was it so difficult to revise the old view of lichens as one among other more or less independent groups of cryptogams or even as algae (as proposed by Linné), and of gonidia as reproductive organs that develop as outgrowths or buds on the fibres, as published by Wallroth (1825, 1827) and others? The similarity of the fibres with fungal hyphae and of gonidia with free-living algae had

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ALGENTYPEN

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FLECHTENGONIDIEN.

PROGRAMM FÜR DIE RECTORATSFEIER

DER UNIVERSITÆT

VON

S. SCHWENDENER.

BASEL MDCCCLXIX.

UNIVERSITÆTSBUCHDRUCKEREI VON C. SCHULTZE.

FIGURE 2. Title page of Schwendener's 1869 publication (42 pp., three lithographs) where he summarized his comparative studies of cyanobacterial and green algal photobionts of lichens and their free-living counterparts. Presented at the annual academic celebration (Rektoratsfeier) of the University of Basel and published by the Basel University Press of C. Schultze.

been recognized by various authors. Interestingly, Wallroth assumed free-living aerophilic algae to be brood-grains of lichens, which had failed to rebuild a thallus. As an outstanding microscopist, Schwendener critically investigated the gonidial layer and what nowadays is referred to as the mycobiont-photobiont interface and documented his findings in accurate line drawings. Already in his studies on fruticose and gelatinous lichens he (Schwendener 1860, 1863*b*) pointed out that he could hardly ever find early developmental stages of gonidia as outgrowths on fibres, but in those days he assumed the current opinion on the development of gonidia as outgrowths of fibres and their function as reproductive cells to be correct. Patterns of photobiont cell divisions were carefully documented in all of

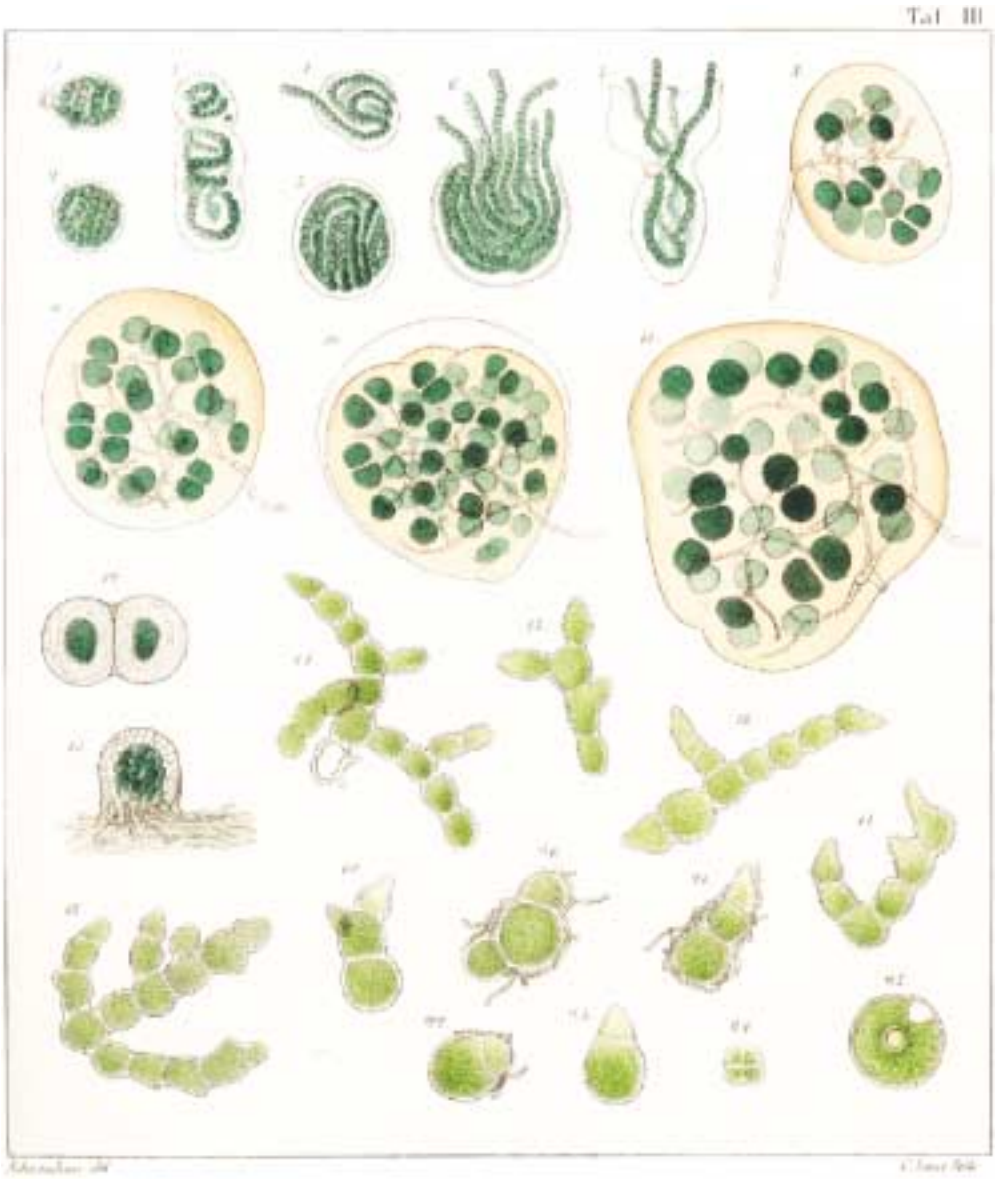

FIGURE 3. Tafel III (the third out of three lithographs) of the 1869 publication (see Fig. 1). The figure legend, liberally translated, reads as follows:
''Figs. 1–7. (× 500[1]) *Polycoccus punctiformis*[2]. Various developmental stages of the colonies. Figs. 8–11. (× 1000[1]) *Gloeocapsa*. Larger and smaller colonies being transformed to *Omphalaria*[3]-like tissues by invading fungal fibres[4]. Fig. 12. (× 500[1]) *Phylliscum endocarpoides*. A gonidium after division, identical with *Chroococcus turgidus* Kütz. fig. 13. (× 500[1]) *Pannaria triptophylla*. Corticate thallus squamule = overgrown algal group on the so-called prothallus of the lichen. figs. 14–19. (× 600[1]) *Roccella fuciformis*. Groups of gonidia, identical with *Chroolepus*[5]. Multicellular groups were preferentially drawn, although more simple ones, as shown in Fig. 19, are distinctly more common. Fig. 20–23. (× 500[1]) *Chroolepus umbrinum*[6]. More or less intensely overgrown cell groups. Drawn after an original specimen of Kützing. Fig. 24. (× 500[1]) *Pleurococcus vulgaris*[7] (× 500[1]) A group of four daughter cells. Fig. 25.(× 500[1]) *Cystococcus humicola*[8]. Single cell with nucleus and an excentric bright zone[9].''
Remarks: 1. slightly reduced; dimensions of the original plate are 19 × 16.4 cm (frame). 2. free-living *Nostoc punctiforme* (Kütz.) Hariot, known as the cyanobacterial photobiont of numerous lichen-forming fungi. 3. =*Thyrea*. 4. hyphae. 5. =*Trentepohlia*. 6. free-living *Trentepohlia umbrina* (Kütz.) Bornet, known as the photobiont of *Roccella* spp. and of a range of other lichen-forming ascomycetes. 7. common and widespread aerophilic green alga. 8. =*Trebouxia arboricola* De Puymaly. 9. Schwendener assumed the very conspicuous pyrenoid of the large, central chloroplast to be the nucleus; the latter is located at the cell periphery in the ''excentric bright zone'' as mentioned in the figure legend.

his publications and partly compared to free-living algae and cyanobacteria. The main problem of Schwendener's opponents was, with high probability, the holistic view of living beings in general which persisted far into the 19th century and even beyond. At the beginning of the 19th century, it was not known that different organisms may live in close connection or even one within the other. Microbial, plant, animal, and human pathogens were not recognized as such e.g., rust or smut pustules were considered as ill outgrowths of the plant proper. The identification of pathogenic micro-organisms and the study of their life cycles and development on or within their hosts were among the most fascinating and important discoveries of the 19th century, with Anton de Bary being one of the most prominent investigators of plant and animal pathogenic fungi. From this background, the dual hypothesis of lichens arose. Schwendener (1869) considered lichen-forming fungi as ''parasites, although with the wisdom of statesmen,'' and their algal partners as ''helotes,'' the class of slaves in ancient Sparta. The term symbiosis was introduced by Frank (1877) in his study of crustose lichens and taken up by de Bary (1879) in the broadest sense as the ''living together of dissimilar organisms.'' The term mutualism was introduced by van Beneden (1875) for animal associations with mutual benefit.

While the dual hypothesis of lichens was rejected by leading lichenologists, it was readily accepted by many eminent contemporary biologists with an interest in lichens such as de Bary, the French algologists Thuret and Bornet, and the Russian Famintzin who later was among the first to suggest an endosymbiotic origin of chloroplasts (Famintzin 1907). De Bary (1866) had concluded that lichens were either the perfect fruiting form of ''Nostochaceae and Chroococcaceae,'' or the habit achieved by ''Nostochaceae and Chroococcaceae'' upon attack by parasitic fungi. In his 1867 lecture, Schwendener refered to the necessity of culturing experiments and pointed to the fact that no one had so far been able to grow lichens from either gonidia or ascospores alone and predicted better results may be possible by allowing ascospores to germinate on algal colonies. Such culturing experiments were set up in various laboratories and successful resyntheses under non-sterile conditions were reported by Reess (1872) for *Collema*, Stahl (1877, under the guidance of de Bary) for *Endocarpon*, and Bonnier (1886) for *Xanthoria.* The dual hypothesis of lichens opened the minds of scientists far beyond lichenology. Consequently numerous other mutualistic symbioses were discovered, such as zoochlorellae and zooxanthellae of invertebrates and protists (Brandt 1881, 1883), ectomycorrhiza (Frank 1885), and root nodules of Fabales (Hellriegel 1886). All of these investigators knew Schwendener personally and referred to his work.

When starting his teaching and research activities as the only professor in general botany at the University of Basel in spring 1867, Schwendener decided to finish his investigations on lichen anatomy, although as an assistant in Munich, he had planned to continue with crustose taxa. This decision was made prior to the presentation of the dual lichen hypothesis and thus was not born out of frustration about its perception. Instead he focused on the correlations of plant form and function with physiology. Much to his excitement, Schwendener, an admirer of elegant contemporary iron constructions such as large bridges and halls of train stations, discovered that the ''mechanical system'' of plants almost perfectly followed the laws of physics. During his long and fruitful professional life he became a leading and internationally honored expert in physiological plant anatomy (reviews: Haberlandt 1919; Tschirch 1919; Zimmermann 1922, with bibliography). This reflects Schwendener's very broad interests and multiple talents. However, some of Schwendener's students continued lichenological research.

According to his autobiographic notes (published in Zimmermann 1922) Schwendener felt quite isolated at the small University of Basel and thus was pleased to accept a call from the renowned University of Tübingen, in Germany in 1877 as successor of Wilhelm Hofmeister. Here ''I had the pleasure to welcome a talented young botanist . . . it was the Viennese doctor G(ottlieb) Haberlandt . . . ever since my faithful combatant'' (Schwendener in Zimmermann 1922—in 1910 Haberlandt became Schwendener's successor in Berlin). Only a few months later and very much to his surprise he was offered a chair at the University of Berlin, which he accepted after some hesitation. In those days Berlin was one the most important places for botanical research in German-speaking countries, and with the numerous institutions of applied research in and around the imperial capital, probably the most stimulating one. His colleagues in Berlin were, among many others, the botanists Pringsheim (reproductive biology) and Engler (''Pflanzenreich''), the plant pathologist Sorauer (''Handbuch der Pflanzenkrankheiten''), the forest pathologist Frank (crustose lichens, ectomycorrhiza, commemorated in the actinorhizal genus *Frankia*), but also the medical microbiologist Koch (''Koch's postulates,'' Noble prize 1905).

According to Zimmermann (1922) the respected scientist Schwendener was a modest person who avoided the elegant social events of the imperial capital unless on duty as dean of the faculty or as

rector (1887) of the University, but he greatly enjoyed the regular contact with professional and amateur botanists. He was a founding member of the German Botanical Society, which he presided over from 1895 to 1909. According to his former students and collaborators, Tschirch (1919) and Zimmermann (1922), Schwendener was a patient and most amiable professor who introduced his students with utmost care to the beauty of functional plant anatomy. The excellent working atmosphere of the institute is mentioned. Lichenological studies were carried out by Fünfstück, Krabbe, and Lindau, but also by Baur, a former medical doctor, who published three interesting studies on apothecial development in lichens before he became a leading expert in plant genetics. Schwendener's field trips to the surroundings of Berlin were primarily social events, with interesting discussions on sciences, arts, and politics, and were joyfully remembered by all participants. In Berlin, Schwendener had at least one female post-doc, Grace D. Chester, who worked with him on stomata on petals and anthers. Three out of the five female members of the German Botanical Society in its first fifteen years of existence were recommended by Schwendener. This is noteworthy in times when other science professors at the University of Berlin, upon spotting a female student in the audience, personally escorted the ''respected Miss'' (gnädiges Fräulein) out of the lecture hall before starting their lecture.

Schwendener was never married. In his home at Matthäikirchstrasse 28 in Berlin he wrote poems, mostly in praise of nature, which were published in 1912 (''Stimmungen und Erinnerungen,'' Vita, Deutsches Verlagshaus, Berlin). Few tender and rather shy love poems refer to a sensitive man who, considering his economic situation, did not dare to hope for long-lasting marital happiness. In his younger years, his financial situation would not have permitted him to support a family and to continue his work as a scientist; thus he had to make the most difficult decision of his life, as confessed to Haberlandt (1919). When he became professor at Basel University and, for the first time, had an adequate income, he was already 38.

According to Zimmermann (1922), Schwendener was remembered as a benefactor by innumerable less privileged people. He provided generous financial support even to recipients who, in the eyes of some of his contemporaries, did not at all merit this favor. Schwendener retired in 1910 at the age of 81 and died on May 27, 1919 in Berlin. He was an honorary doctor of the Universities of Leipzig and Bologna, and corresponding or honorary member of numerous academies and learned societies throughout Europe from London to Moscow. Remembering what a privilege it was in his youth to attend higher education (only elementary school being free of costs in those days) Schwendener testamentarily donated all his possessions to the school of his former home village of Buchs where he is commemorated in an inscription at the fountain of the city hall (Professor Simon Schwendener-Brunnen) as a great son of his home county (Lippuner 1995). In science his name stands primarily for the discovery of lichen symbiosis.

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