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Nils Svedelius

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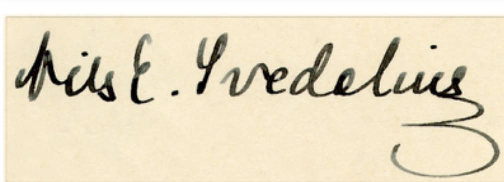
Although two detailed biographical sketches have already been published on the life and accomplishments of Nils Eberhard Svedlius (Skottsberg,1961; Papenfuss, 1961), he was such a significant person in terms of achievements in the first half of the 20th century that his inclusion in this series of essays seems fully justified. Nils Svedelius was born in Stockholm on the 5th of August, 1873. He received his education at the University of Uppsala under the tutelage of another eminent Swedish phycologist, F. R. Kjellman (Svedelius, 1908a). With Kjellman's permission, Svedelius carried out his Ph.D. research on the algal flora along the southern part of the east coast of Sweden, that is, the Baltic Sea, a then-neglected region with low salinity and a reduced number of species. But the uniqueness of the region enabled Svedelius to recognize the inherent ecological and morphological problems offered. He defended his thesis ["Studies in the marine algae of the Baltic Sea", 1901) in May 1901. The fact that he had earned his doctorate with distinction resulted in his being appointed to the position of docent in October, 1902 (Skottsberg, 1961).

Nils Svedelius, In Woods Hole, MA, 1926



A year after earning his doctorate, docent Svedelius received a traveling scholarship, enabling him to spend almost a full year (1902-1903) primarily in Sri Lanka [Ceylon] but also with side trips to Singapore and Java. In the latter he spent some time in the Dutch administered botanical garden in Buitenzorg. During his extended stay in Sri Lanka, he was based in the coastal town of Galle, the site of the Ceylon Marine Laboratory and in close proximity to the splendid coral reefs that lie just beyond the ramparts of the old town. Svedelius made excursions to other sites along the coast, going by railroad to Colombo, on the west coast, and eastward to Weligama, Matara, Tangalla, and Pamban, and to Jaffna in the north. Interestingly, W. H. Harvey had collected at some of these same sites 50 years earlier. Svedelius collected marine algae in Sri Lanka intensively, paying close attention to their detailed distribution and time of occurrence. These studies resulted in his monograph (1906a) (Fig. 1) of *Caulerpa*, in which he gave his observations on a total of 21 species of the genus in Ceylon, including two newly described ones (*C. dichotoma* and *C. parvula*). Svedelius (1906b) also published a paper on the phenology of the benthic algal flora present on the coral reefs near Galle. He recognized the correlation of the occurrence of the algae with the timing of the monsoons.

At various times during his stay in Sri Lanka, Svedelius gathered specimens of *Martensia fragilis* Harv. from the coral reefs off

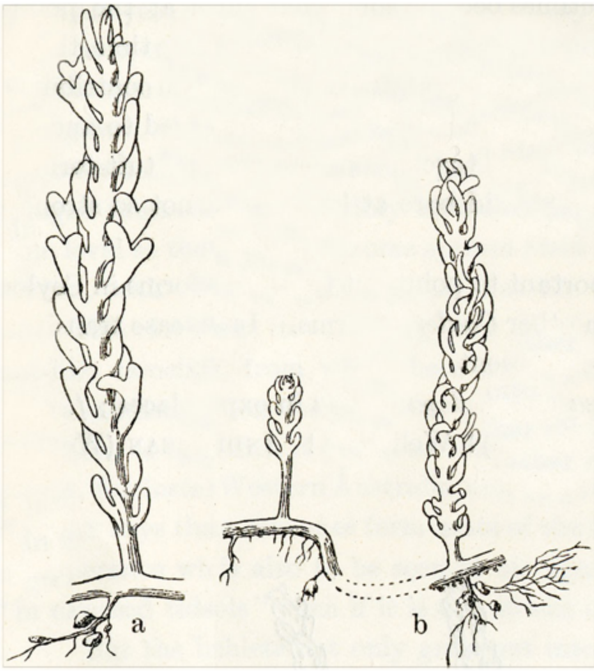


Fig. 1. *Caulerpa dichotoma* Sved. [Fig. 24 in Svedelius, 1906.]

Galle, allowing him to produce an elegant study of the structure and vegetative and reproductive development in this alga (Svedelius, 1908b). It was the most detailed monographic study of this handsome net-forming member of the Delesseriaceae produced up to that time.

A different net-forming genus that captured Svedelius' attention in Sri Lanka was *Dictyurus* of the Dasyaceae, "a beautiful red alga, characterised by its pretty reticulate thallus" (1947). The only location where he succeeded in finding *D. purpurascens* Bory was at Golcanda Rocks on the west coast, where there was a rocky intertidal with heavily shaded caverns and crevices covered by close mats of this red alga (Svedelius & Nygren, 1946). He showed how the male plants formed complicated compound branch systems, the sterile tips of the spermatangial branches fusing with other parts of the branch system. He proposed the term 'arrhenophore' for these compound male stands (Fig. 2).

Svedelius' attention was drawn more toward the phenomenon of the nature of the alternation of generations in the algae, and so he

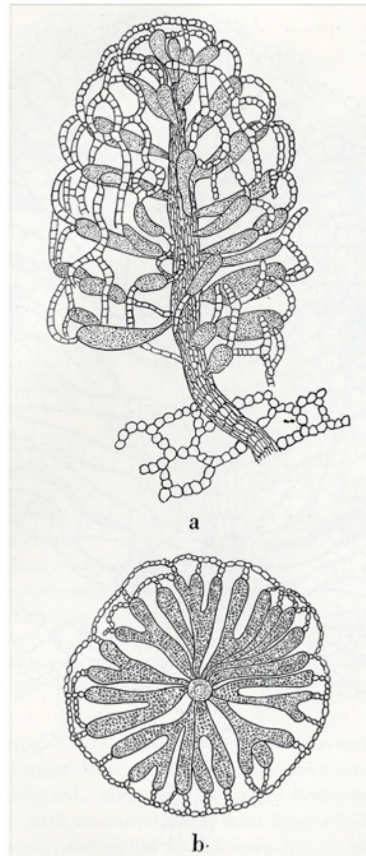


Fig. 2. Arrhenophore of *Dictyurus purpurascens*. a. in optical longitudinal section; b, in cross-section [Fig. 9 in Svedelius & Nygren, 1946.]

temporarily abandoned his pursuit of the classification of the marine algae of Sri Lanka. It was the papers by Yamanouchi on *Polysiphonia*, by Williams on *Dictyota*, and later by Sauvageau on the kelp *Saccorhiza* that stimulated much interest in the nature of algal life histories and the timing of meiosis. For those red algal taxa, such as *Scinaia furcellata* (1915), *Asparagopsis armata* (1933)(Fig. 3), and *Bonnemaisonia asparagoides* (1933), in which only gametophytes were known, Svedelius presented his observations that after fertilization (and before formation of the cystocarp) the zygote nucleus underwent meiosis, in the fertilized carpogonium (in *Bonnemaisonia*), in the hypogynous cell (in *Asparagopsis*), or in a fusion cell product with the fertilized carpogonium (in *Scinaia*). He (1937) introduced the term

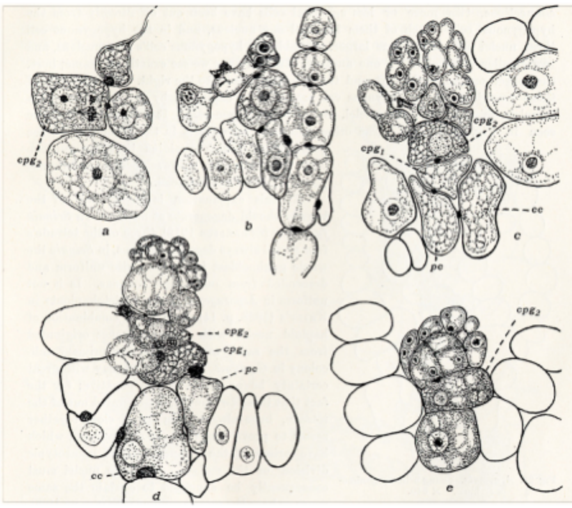


Fig. 3. *Aparagopsis armata* Harv. The earliest development of the cystocarp. [Fig. 28 in Svedelius, 1933.]

'haplobiontic' for that type of alternation with immediate meiosis, thus without tetraspore formation and with only sexual individuals (a single kind of 'biont'). He used the term 'diplobiontic' for the pattern with two kinds of individuals, sexual and tetrasporic (free-living individuals with tetrasporangia). Later culture studies of some of these genera, showing the existence of microscopic (heteromorphic) stages bearing tetrasporangia, have forced Svedelius' findings to be re-considered.

After Kjellman died, Svedelius inherited the job of completing a supplement on the red and the brown algae for Engler & Prantl's *Natürlichen Pflanzenfamilien* (1910, 1911a). Another research interest that seems to have been inherited from Kjellman was a life–long fascination with the tropical red algal genus *Galaxaura*. Kjellman (1900) had already produced a monograph of the genus, in which he recognized a total of 62 species. But for some of the species only tetrasporic plants were known, whereas in other species only sexual plants were known. Howe (1917, 1918) had published his findings of Caribbean species of *Galaxaura*, in which co-occurring tetrasporangiate and sexual plants on circumstantial evidence were interpreted to be one and the same species despite the fact that their cortical organizations were different and would be regarded as belonging to different sections of the genus based on the standard taxonomic scheme of the day. This caused a major re-thinking of the systematics of the genus. But Svedelius was also keen to understand the cytological events in the life history of the genus. His own material from Sri Lanka being fixed in formalin was not suitable for a study of chromosomes. So he requested that G. F. Papenfuss, who had spent some time in Svedelius' lab in Uppsala but who was then in South Africa, provide him with some suitably fixed material. Papenfuss was able to oblige, sending Svedelius fertile stages of several species. Over the following years, in fact, right through his entire productive period, Svedelius continued with a series of papers on *Galaxaura*, including investigations on its male stages (1939b), the development of its female plants and cystocarps (1942b) along with more general systematic papers (1944, 1945, 1953, 1956). His major paper on *Galaxaura* (1942a), dedicated to the memory of his mentor Kjellman, was a monumental treatment of the external morphology, internal anatomy, and reproductive stages (male, female, and tetrasporic) of several species in the genus.

Despite his notion (Svedelius, 1945) of a broadly circumscribed genus, more recent work has provided evidence for the recognition of segregate genera from *Galaxaura*. Huisman & Borowitzka (1999) established *Tricleocarpa* that differed from *Galaxaura sensu stricto* both on differences in development of the carposporophyte and in the life history (i.e., a microscopic filamentous tetrasporic stage is present in *Tricleocarpa*). More recently,in a study using gene-sequence data, Huisman et al. (2004) produced a phylogenetic tree in which the type species of *Galaxaura* (*G. rugosa*) was sister to *Actinotrichia*, while several other species of "*Galaxaura*" formed a clade sister to *Tricleocarpa*, *Galaxaura* s. s., and *Actinotrichia*. The solution to avoid this paraphyletic/ polyphyletic treatment of *Galaxaura* was to place those several species of "*Galaxaura*" into their own genus. For this purpose, the old generic name *Dichotomaria* of Lamarck was reinstated by Huisman et al. (2004). Conveniently, Huisman et al. (2004) were able to point out correlated anatomical differences: stalk cells laterally or terminally producing the tetrasporangia and a tetrasporophyte cortex with stalked epidermal cells in *Tricleocarpa* versus elongate filaments producing the tetrasporangia and a tetrasporophyte cortex with a filamentous organization in *Galaxaura* s. s.

Svedelius was among the first to report chromosome counts in the algae, recording a haploid number of 10 in both *Scinaia furcellata* (1915) and *Asparagopsis armata* (1927d), a haploid number of 20 in both *Delesseria sanguinea* (1911b) and *Nitophyllum punctatum* (1914b), and a haploid number of about 20(18-[20]) in *Bonnemmaisonia asparagoides* (1933). His first paper in 1911 on the life history of *Delesseria sanguinea* was followed by papers on the formation of spermatangia (1912) and on the formation of cystocarps (1914a). He (1914b) showed how in *Nitophyllum punctatum* the tetrasporangial primordia are multinucleate and that all the nuclei but one degenerate. The sole persistent nucleus then undergoes meiosis, and four haploid tetraspores are produced. He showed that *Lomentaria clavellosa* underwent a typical life history with male and female plants (n = 10) and tetrasporic plants (2n = 20), in which meiosis occurred in the tetrasporangia. But in *L. orcadensis* [= *L. rosea*] only tetrasporic plants occurred in European waters, and tetraspore formation involved an apomeiotic process (Svedelius, 1937).

In his specimens of *Dermonema* brought back from Galle, Svedelius (1939a) observed the occurrence of only separate male and female thalli. He also saw that the carpogonial branches were lateral, or “accessory,” and that the cystocarps developed as a diffuse network of filaments bearing terminal carpospores. He later (1952) reported on his study of *Actinotrchia*, in which the calcified axes are terete but unlike *Galaxaura* s. s. there is no anatomical distinction between sexual and tetrasporic thalli.

His collections of the dasyclad genus *Neomeris* brought back from Sri Lanka allowed him to do a later study (1923), in which he detailed the vegetative and reproductive development. He also offered *Neomeris* as a useful example of a genus with a disjunct distribution (in the Caribbean Sea and in the Indo-Pacific Ocean). He concluded that *Neomeris annulata* and *N. dumetosa* had to be older than the Isthmus of Panama, that is, prior to the time when the continuity between the Caribbean and the Indo-Pacific was disrupted. His 1924 paper on the discontinuous nature of the distribution of some tropical and subtropical benthic algae showed his remarkable insight not only into the systematic relationships of these seaweeds but also into the historical factors that may have brought about the current patterns in their ranges. It remains a classic paper.

The seasonal occurrence of marine algal species was another topic of interest. Svedelius followed the occurrence of a species of *Ceramium* year-round, in the Baltic in the vicinity of Stockholm. Separate male and female plants were dominant in late summer, but only tetrasporic plants could be found in late autumn into winter. A luxuriant growth of this *Ceramium* on the shore and exposed to freezing was wiped out, but by forming holes in the ice in January of 1924 he found some tetrasporic plants surviving the winter (1927a). That publication came under attack by Sjöstedt (1928), forcing Svedelius (1929b) to defend his observations and causing him to show how Sjöstedt had taken some of Svedelius’ comments out of context.

The algae were not the sole taxonomic group that caught Svedelius’ attention. He published papers on such flowering plant families as the Gentianaceae and the Convolvulaceae as well as on such topics as pollination in the hydrophyte *Enhalus acoroides* and the seed morphology in members of the Dilleniaceae, He also asked questions about the nature of endemism and the theories on the origin of species.

From spring to mid-summer of 1913 Svedelius traveled to various marine stations. These included the one in Rovigno (now in

Croatia), the Plymouth lab in England, and Helgoland in the North Sea of Germany. Over the years he was a frequent participant in international meetings, such as botanical congresses, including the one in Cornell, NY, in 1926. During that summer he visited the marine lab in Bar Harbor, Maine, and the Marine Biological Laboratory in Woods Hole, where Dr. W. R. Taylor snapped his photo (Fig. 1). His numerous contributions were recognized by his being elected to membership in the Royal Swedish Academy of Science as well as to the Royal Science Society in Uppsala. Foreign societies, such as the Linnean Society of London and the British Royal Society, also elected him to honorary membership. In 1939, at the age of 65, Svedelius retired, but he continued to remain active in his research and in his productivity well into his retirement. He passed away on Aug. 6, 1960, shortly before his 87th birthday.

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