A tribute to Rolf Santesson (1916–2013)



Rolf Santesson passed away in September 2013, and thus we lost the nestor of Swedish lichenology and an internationally highly respected colleague.

Already as a teenager Rolf developed an interest in lichens and investigated the lichen flora of the plateau mountains of Halleberg and Hunneberg situated close to his home in the province of Västergötland. He subsequently commenced studying botany at Uppsala University and also worked at the Natural History Museum in Stockholm. He finished his master's degree in 1939, based on studies on aquatic lichens (*Verrucariaceae* e.g. 1) in Southern Sweden. This also triggered Rolf's interest in marine lichens, an area he later cherished (2, 24). During this period of time there was still a lingering interest among the public in 'exploration' of exotic areas, and travelogues were popular

reading and explorer/adventurers regularly lectured in the one widely available medium at the time, the radio. Possibly inspired by this, Rolf no doubt realized that great discoveries might indeed be made in botany, and certainly in his favourite area, the rather neglected lichens. That he became interested in South America and Tierra del Fuego is not strange, considering the many earlier successful Swedish scientific expeditions to southernmost South America and Antarctica, not least, probably, expeditions to Patagonia led by Erland and Otto Nordenskjöld, with botanists such as Per Dusén and Carl Skottsberg on the staff. Influenced by the interest in biogeography at the department of plant biology in Uppsala, then headed by G. E. DuRietz, Rolf was interested in the connection between the lichen flora of southernmost South America and that of Antarctica, both areas which around the turn of the century had been investigated during Swedish expeditions. Rolf recruited another young biologist, the zoologist Christian Olrog for an expedition and they set out in 1939. It turned out that they got caught in South America for two years while World War II roared on and made sea travel dangerous. Rolf made comprehensive and splendid collections in South America and on the boat during his way back he slept with his field note-books under the pillow, just in case... Olrog wrote an exhaustive and highly enjoyable book about their trip called 'Destination Eldslandet', tracking the adventures of the expedition. During this time Rolf started to collect material that was to become crucial in his perhaps most important contribution to lichenology, his work on foliicolous lichens found in such abundance in tropical and subtropical areas; the topic for his Ph.D. thesis (10). Other material was included in an extension of Malme's exsiccata 'Lichenes Austroamericani', now issued by Malme-Santesson. In Uppsala Rolf obtained a research position as 'docent' and together with John Axel Nannfeldt, the professor of the department of Systematic Botany, developed a view on the necessity of shaping a unified fungal and lichen systematics and taxonomy. Nannfeldt had already in his thesis very clearly formulated: "Das System

der Flechen ist desjenige ihrer Pilzkomponenten. An den Flechtenkonsortien nehmen sowohl ascoloculare Pilze als ascohymeniale teil." (Nannfeldt 1932). This view Rolf brought to lichenology and presented at the International Botanical Congress in Stockholm in 1950 (9) as "The new systematics of lichenized fungi", and however self-evident it might seem to us now - given its setting in the history of mycology – at that time it was by no means uncontroversial. This view Rolf championed in his thesis and also one of thorough and novel circumscriptions of genera, families, and generic and family relationships. Often in opposition to the remaining influence of Zahlbrucknerian emphasis on algal association and spore septation. Rolf's thesis (10) was a follow up of these views and at the same time a monumental world-wide presention of the foliicolous lichens, amounting to almost 600 pages and including a detailed treatment of 236 species, and more importantly, a critical appraisal of numerous genera and families bringing a new and rather revolutionary view to lichen taxonomy - the classical paradigm of Zahlbruckner finally crumbled. The taxonomic account of the thesis was organized by families and in accordance with Nannfeldt's classification in ascolocular and ascohymenial ascomycetes (Nannfeldt 1932). Families and genera are discussed and described in detail; the Arthoniaceae, Opegraphaceae and Graphidaceae may serve as examples of how Rolf discussed classical problems and from morphological evidence presented ideas on the taxonomic implications of, for example, ascoma ontogeny, photobiont association and de-lichenization. The nomenclature of these taxa was also dealt with in depth. Lopadium may serve as another example of Rolf's critical eye; when recognizing Sporopodium as distinct, and in Tapellaria he explicitly criticized Zahlbruckner's 'sporologic' generic concepts. The subsequent interest in the classification of lichens at generic and higher levels may safely be traced back to Rolf's thesis (e.g. Henssen & Jahns 1973, Poelt in Ahmadjian & Hale 1973). A recognition of its importance is also evident in a prophet of the next, or possibly 'nextnext'

paradigm in lichen classification: "Das schon klassischen Werk von Santesson (1952), ein beinahe unerschöpflicher Quell für taxonomische und nomenklatorische Fragen, kann nebenbei als erster konsequenter Versuch, ein natürliches System aufzustellen gelten, der über weite Strecken auch gelungen ist." (Hafellner 1984).

His work on epiphyllous lichens was continued in a series of papers (15, 17, 18, 19, 20, 23, 25, 26, 27).

The trip to South America also led to a harvest of taxonomic papers on various genera in South America: *Menegazzia* (3), *Cladina* (5), calicioids (6), and *Dolichocarpus* and *Xanthopeltis* (8), as well as floristic papers (4) and (7).

The thesis also includes a theme that later was to become quite prominent in Rolf's scientific achievements; his interest in lichen parasymbionts and lichen parasites. In his thesis he comments on the host specificity of some 'Pyrenotrichum' species (i.e. anamorphic structures, at that time by Rolf considered to be lichenicolous fungi). Several species of 'Pyrenotrichum' were destined to be described in a part II of his thesis, that, however, was never published. Rolf published numerous further papers on lichenicolous fungi, sometimes in cooperation with other lichenologists (11, 15, 16, 17, 18, 19, 20, 23, 25, 26, 27), and not least his exsiccata of lichenicolous fungi being a very important reference in this connection (14); in all 16 fascicles containing 400 numbers.

In a collaboration with his son Johan (who contributed the chemistry of the lichens in Henssen & Jahns, 1973) Rolf also took part in the secondary chemistry paradigm in lichenology and the research projects undertaken by Johan were obviously often formed in discussions with Rolf (see e.g. J. Santesson 1970a, 1970b, and 1978).

Towards the end of his career Rolf spent much of his time and energy on producing a checklist of the lichens of Sweden and Norway (13). Later this list was extended also to include lichenicolous fungi (21) and Finland (28). His list, which we always quite simply refer to as 'Santesson's list' contains not just a list of species, but of species names that have been carefully scrutinized, brief information on the species' ecology and distribution and most importantly references to relevant literature. 'Santesson's list' has become a codex in lichenology and is also on the international scene very commonly referred to as a source of correct taxonomy and nomenclature. An updated version of the list is available at: http://www.evolutionsmuseet.uu.se/ databaser/santesson.html.

Rolf – the collector. Rolf was a prolific collector and visited many parts of the world after his expedition to South America. In 1954, as a participant in a field-trip organized in connection with the International Botanical Congress in Paris, Rolf had the opportunity to again collect foliicolous lichens in the Ivory Coast and French Guinea, where he among many other tropical lichens collected Racoleus trichophorus, which was to become the topic for his last published paper in 2011; Racoleus being a new genus (29). In addition to his South American expedition other major collecting efforts included: Switzerland (1946, 1987); Spain (1959); British Isles (1961, 1963); France (1946, 1954); U.S.A. (1966); Tenerife (1968); Iceland (1969); Ireland (1968); Kenya and Tanzania (1970, 1971); Madeira (1978); Peru (1981); Portugal (1991); China (1987); Far East of Russia (1991); Mexico (1995). Rolf's collecting always brought a rich material of exquisite specimens, now mostly kept at UPS, and many of them were utilized in his publications and exsiccata.

Rolf – the teacher and mentor. Rolf guided a group of younger lichenologists in Uppsala during the latter part of the 20th century. Not by offering formal courses at the university, but primarily by personal advice and by leading field-trips such as the one to the Varanger Peninsula in Norway in 1966 and Jämtland in Sweden in 1975. The pupils who were fortunate to obtain Rolf's mentorship were in Uppsala: Gunnar Gilenstam, Roland Moberg and Leif Tibell; in Stockholm Anders Tehler and Göran Thor; and for extended visits to Uppsala also Aino Henssen and Per-Magnus Jørgensen. Rolf also became a mentor of lichenology on a much grander scale. Very many manuscripts

of scientific papers and theses were sent informally to him from all parts of the (lichenological) world for a 'pre-review'. Sometimes he would moan over these or sometimes even an acrid comment escaped him, but nevertheless he engaged himself deeply in trying to meticulously correct/ improve every one of these manuscripts. In retrospect one would perhaps think that he should rather have allowed more time for his own publishing than helping others so extensively. However, by his zealousness the quality of many lichen papers was considerably enhanced and many an embarrassing mistake avoided publication. In this role Rolf's almost encyclopedic knowledge of the lichenological literature was crucial, as was the excellent lichenological library in Uppsala and his own.

Rolf's interest in nomenclature was demonstrated in a series of papers on various lichens (12, 22), and not least in his lists (13, 21, 28) and his keen interest in myxomycetes may come as a surprise for some, but not for those who joined him on fieldtrips.

Rolf's career. After finishing his thesis, Rolf obtained a research position as 'docent' at Uppsala university and then in 1958 as a director of the Botanical Museum (UPS) collections. In 1973 he was called to a professorship at the Swedish Natural History Museum in Stockholm (S), which he held until retiring in 1981. Being called to a professorship is a rare honour bestowed in the Swedish Academic system. Rolf was also awarded the 'Acharius medal' for 'outstanding contributions to lichenology' by the International Association of Lichenology in 1992. A 'Festschrift' that was slightly late for Rolf's 80th birthday was published (Tibell, L. & Hedberg, I. eds, 1997). Rolf was a member of the Royal Swedish 'Academy of Sciences and an Honorary Member of the British Lichen Society.

Although left at a loss and in sorrow after Rolf's definite retirement, lichenology in Uppsala and also internationally may profit for many a year ahead not only from his scientific ideas but also the vast collections left in prime condition mostly kept in Uppsala (UPS) and Stockholm (S).

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ROLF SANTESSON – SELECTED PUBLICATIONS

The following list includes a selection of some of the more notable papers and books from the 70 or more publications authored or coauthored by Rolf Santesson

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