



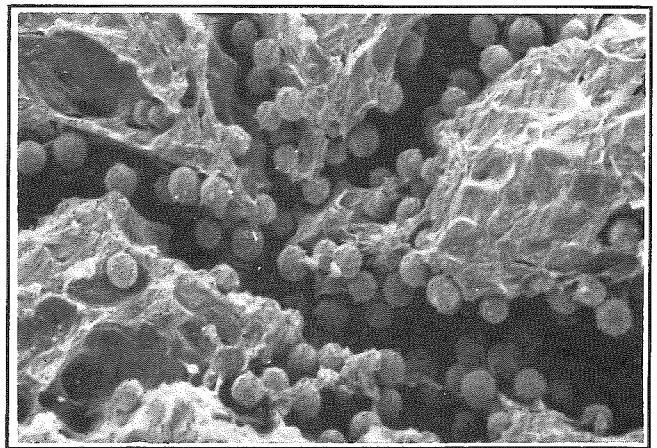
## PROCHLORON

Barry Wulff

For years we have recognized that blue-green algae, or cyanophytes, the most primitive type of algae, were distinguished from all other algae, and from land plants, principally by their lack of a defined nucleus and chloroplasts. The lack of a nucleus was the reason they were placed in the prokaryotes along with bacteria. The supposedly more advanced algae, higher plants and animals are all eukaryotic. The cyanophytes were also noteworthy for their lack of the photosynthetic accessory pigment chlorophyll b, instead possessing the phycobilin pigments, phycocyanin and phycoerythrin. Cyanophytes are found growing in just about every environment on earth; in fact, many are known for their broad ecological distribution. There are unicellular as well as filamentous forms of cyanophytes living today, and they are known from fossil deposits more than 3.5 billion years old.

Moreover, it had long been known to marine biologists that a variety of tropical sea squirts or tunicates, known as didemnid ascidians, harbored a green unicellular alga. Similar symbionts are found in anemones and other invertebrates. The didemnid-alga symbiosis, however, remained largely unanalyzed until very recently. In the early 1970's, Ralph Lewin of Scripps Institution of Oceanography examined some

algal material extracted from ascidians collected in the waters off Baja California. The spherical cells, ranging from 30-60 microns in diameter, of this symbiotic alga were prokaryotic and thus by recognized criteria would be placed in the Cyanophyta. However, he found that they possessed chloroplast structure and pigmentation similar to those found in the chloroplasts of the eukaryotic Chlorophyta. No phycobilins were present, either. Based on its unique combination of pigments and lack of a nucleus, the alga was assigned the name *Synechocystis didemni* (since changed to *Prochloron didemni*) and placed in a new division, the Prochlorophyta.

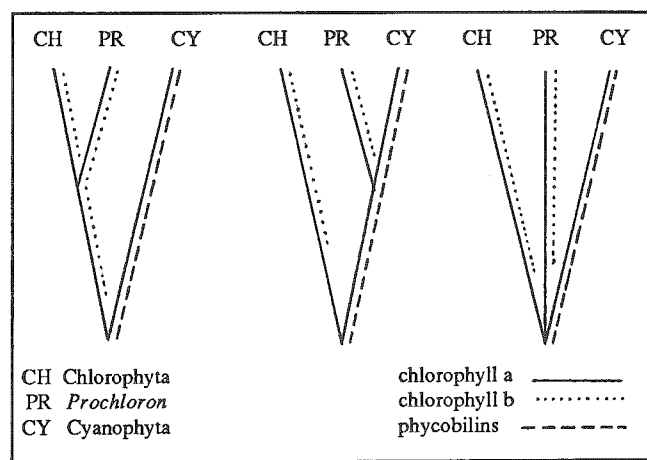


Scanning electron micrograph (x700)  
of *Prochloron* cells on ascidian  
From Lewin, Phycologia, v. 14 (1975)

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Intense study of numerous collections from didemnids from the South Pacific and elsewhere in the past decade has resulted in the conclusion that this prokaryotic alga indeed possesses chlorophylls a and b and lacks phycobilins. This finding has led to considerable speculation as to its evolutionary position *vis-à-vis* green algae and blue-green algae. If *Prochloron* were to be considered a chlorophyte, based on its pigmentation, the traditional means of algal classification at the division level, one would have to ignore the fact that it is prokaryotic. To place it among the Cyanophyta would mean to change the definition of that division to include algae with both chlorophylls a and b, but lacking phycobilins. Certainly, *Prochloron* posed a taxonomic enigma. *Prochloron* was indeed unique but a mosaic when compared with all other algae known at this time.

Yet, the existence of an alga with prochlorophytic characteristics had first been postulated in the nineteenth century. Such forms were believed to be the antecedents of chloroplasts, or the prokaryotic algae that evolved symbiotic associations with once achlorophyllous hosts. The idea was expressed early on by the Russian biologist Konstantin Mereshkovsky with his theory of "symbiogenesis." Today, Lynn Margulis of the University of Massachusetts has assembled considerable evidence to support the symbiotic origin of plastids and other organelles, thus invigorating Mereshkovsky's theory.



Alternative phylogenetic trees involving *Prochloron*  
Adapted from Lewin, Gior. Bot. Ital., v. 120 (1986)

There should be no doubt that *Prochloron* is related to blue-green algae. Many characteristics link *Prochloron* to the Cyanophyta, in addition to their common lack of a nucleus. They share such features as peptidoglycan walls, a paucity of unsaturated fatty acids, a low content of steroids, and complements of carotenoids and lipids. In addition, sucrose is not a product of photosynthesis as it is in the Chlorophyta and most other green plants. Finally, there is also a high similarity of the 5S and 16S ribosomal RNA nucleotide sequences.

The principal question to be asked is how is it that *Prochloron* makes chlorophyll b and the associated chlorophyll a + b protein complex, whereas cyanophytes do not? Lewin and others have suggested that perhaps chlorophyll b evolved more than once -- perhaps independently in chlorophytes and euglenoids, as well as prochlorophytes. It is significant to note that the make-up of the chlorophyll a + b protein complex in *Prochloron* differs from that found in the Chlorophyta and higher plants as would be expected given an independent origin. Chlorophyll b may be a more effective light harvesting system than the phycobilins, and where it has evolved, the adaptive value of phycocyanin or phycoerythrin may have diminished, resulting in their evolutionary loss.

Until recently, prochlorophytes were known almost exclusively in symbiotic association with didemnids. Peter Raven of the Missouri Botanical Garden had suggested in 1970 that free-living photobiotic prokaryotes with chlorophylls a and b but lacking phycobilins existed a billion years ago and that they could be the ancestors of green plant chloroplasts. Since the discovery of *Prochloron*, there has been a search for similar entities, perhaps free-living forms. In the past few years, however, two more and quite different algae with some features similar to *Prochloron* have been discovered. One is a free-living filamentous species now named *Prochlorothrix hollandica*. It was discovered in The Netherlands in 1986, growing in a shallow freshwater

lake system that originated from peat excavation. By independent investigation, recent studies, based on 16S rRNA sequences, indicate that *Prochlorothrix*, like *Prochloron*, is more similar to cyanophytes than to chloroplasts, while another study, based on amino-acid sequences in membranes of chloroplasts, places *Prochlorothrix* nearer to the chloroplast line. Neither sequencing study is considered definitive, however. Such apparently conflicting molecular sequence data may reflect differences in the rates at which nucleic acids and proteins evolve within these groups.

The other newly discovered alga, yet to be named, was discovered in 1987 growing in extreme abundance ( $10^5$  cells per milliliter) in the deep euphotic zone (100 m) of the oceans. These algae have avoided the attention of planktonologists for years because of their very small size. Labelled picoplankton, they easily slip through 0.8 micron filters but are retained on 0.6 micron filters. While they are definitely prokaryotic, they differ from *Prochloron* and *Prochlorothrix* by possessing alpha-carotene rather than beta-carotene and having a divinyl chlorophyll a-like pigment as the dominant chlorophyll.

As Stephen Gould has illustrated so well in his recent book, *Wonderful Life*, evolution produced an immense variety of organisms long ago, many of which have fallen by the wayside. Could the prochlorophytes be relics from a much larger group that existed in the past? Or are they much more recent arrivals, new twigs on a very old branch?

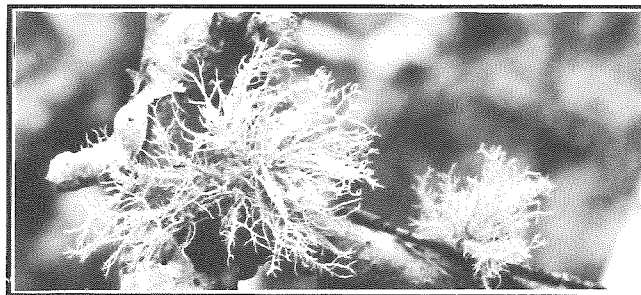
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- Chisholm, S. W. *et al.* 1988. A novel free-living prochlorophyte abundant in the oceanic euphotic zone. *Nature* 334: 340-343.
- Lewin, R. A. & N. W. Withers. 1975. Extraordinary pigment composition of a prokaryotic alga. *Nature* 256: 735-737.
- Lewin, R. A. & L. Cheng, eds. 1989. *Prochloron: A Microbial Enigma*. Chapman & Hall, New York.

## FARLOW VISITORS

Fall 1989-Spring 1990

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## SPRING BOOKSALE

The Library staff has amassed over 350 titles to be offered in this spring's sale. The sale will be particularly strong in works on lichens along with the usual bounty of mushroom tomes.

For the first time a collection of fine and rare titles will be set aside for silent auction. These include works by **Acharius, Badham, Harvey, Schimper, Sowerby, Vainio** and biographical accounts from the Oxford Press. Here is your opportunity to own an original!

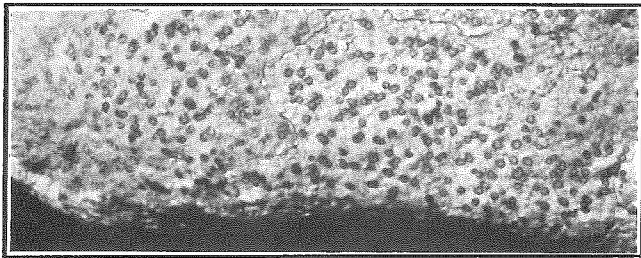
Hold your book donations until next year and anticipate the sale notice about the first of May.

## A TROVE OF SOUTHEASTERN ASIATIC MOSSES

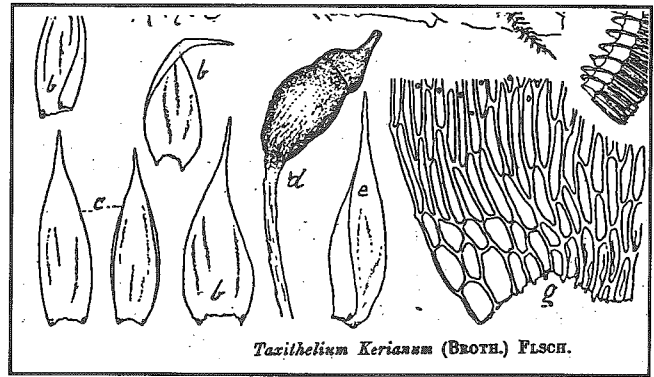
Few people outside the University Herbaria realize how important the moss collections at the Farlow Herbarium are to students of Southeastern Asiatic moss systematics. The presence of the personal herbaria of two eminent muscologists of this century, M. Fleischer and E. B. Bartram, makes the institution a potentially great center of research in Malesian muscology, rivaled only by the Rijksherbarium (Netherlands) and British Museum (England). During their time, Fleischer was the authority on Javan and Sri Lankan mosses, while Bartram excelled in his knowledge of Philippine, Bornean and New Guinean mosses. It is no wonder that the herbaria of these two men contain a trove of type specimens from the region as well as other important historical collections, even from areas outside their research interest.

As a student of Philippine and Bornean mosses for many years, I view my coming to work as a research associate at the Farlow as a God-given opportunity. In the next two years I plan to complete a modern systematic revision of the large tropical moss family, Sematophyllaceae, for western Malesia. This family has its primary center of diversification in the Paleotropics. I also plan to produce an illustrated field book for the identification of widespread and rare Philippine mosses. The effort aims to call public attention to the richness of a threatened moss flora. It further aims to rally support for the conservation of a flora under seige because of the accelerating disappearance of the rainforests in the Philippines.

BENITO C. TAN, FARLOW



*Porpidia* on a rock (x1)



From M. Fleischer, *Die Musci der Flora von Buitenzorg* (1915-1922)

## LICHENS & EVOLUTION

Little is known about the evolution and biology of lichens. The questions, however, are intriguing and are becoming approachable with the development of new techniques in systematics. One question I am facing while at the Farlow is: are our traditional species concepts based on the true biology and evolutionary relationships of lichens? (For a general outline of the species problem, see Brent Mishler's article in the October 1988 issue of the FOF Newsletter.)

With lichens, we usually place things that look different in different species. However, we also place things that look very similar in different species. For example, some would place two lichens which look alike but differ only in chemistry in different species. Species differing in reproductive mode (sexual versus asexual) are also usually placed in different species. On the other hand, some quite variable and widespread phenotypes are placed in a single species.

*Porpidia albocaerulescens* is a broadly ranging species, occurring in North America, Europe, Asia and Australia-New Zealand. I have found that distinct populations can be discerned within this one species. Using the Eastern North American specimens as a standard with which to compare others, I found that a distinct population exists from the British Isles south to Portugal. This population contains confluent acid rather than the Eastern North American stictic or norstictic acid; it also has larger

apothecia and a less continuous thallus. Another distinct population occurs in Southern Europe: Italy, France, Hungary, Germany and Austria. This population has more robust apothecial features and larger spores. So far, the Eastern North American and Eastern Asian populations appear similar.

These preliminary results show that definable variation exists in traditional lichen species, suggesting that evolution is occurring on a regional scale. With our growing understanding of patterns of variation such as these, we can begin to face the questions haunting systematic botanists: what is the relationship between lichens of different reproductive mode within smaller regions? and how does variation among conspecific lichens compare with variation between traditional species?

As with *Prochloron*, there are many exciting ways to study lichens beyond their looks: culturing, chromatography of chemical products and even DNA analysis. With some of these techniques in hand, lichenologists are beginning to face fantasies of lichen evolution as intriguing but answerable questions.

SHARON P. GOWAN, FARLOW

## FARLOW NOTES

The Friends of the Farlow welcomes **Judith Warnement** as Head Librarian of the Botany Libraries at Harvard. The Farlow Reference Library of Cryptogamic Botany is one of five libraries in Judy's charge, all located at the end of Divinity Avenue and serving the Harvard University Herbaria staff and researchers. Judy, who is an Ohio native, joins the Farlow's Midwestern Caucus (*cf.* Don Pfister -- Ohio; Jean Boise and Carolyn Hesterberg -- Michigan; Sam Hammer -- Illinois).

**Teuvo Ahti** of the University of Helsinki will be visiting and working at the Farlow in April. He will be examining and annotating *Cladonia* specimens and will be participating in the qualifying examination of Samuel Hammer, a graduate student with D. H. Pfister.

## NORTH BENNET STREET SCHOOL

FOF recently decided on a modest program of conservation and restoration of some of the Library's more valuable and endangered volumes. The North Bennet Street School in Boston's historic North End was suggested as possibly being able to help us.

Chartered in 1885 and still located adjacent to the Old North Church, the School is a unique, historically independent, non-profit institution. For its first 30 years Mrs. Quincy Adams (Pauline Agassiz) Shaw, the daughter of Louis Agassiz, the founder of Harvard's Museum of Comparative Zoology, presided over the School.

Although the curriculum has changed over the years, it still adheres to its original charge of establishing and providing "for training in industrial occupations." Currently, it offers courses geared toward the preservation of traditional hand craftsmanship, such as bookbinding, preservation carpentry, and the construction and restoration of violins.

The bookbinding course was started in 1986, and with a total of 12 students in its two-year program is the only full-time bench course in bookbinding in this country. The instructor currently in charge is **Mark Esser**, who in 1972-1973 did curatorial work in the Farlow, where he met preservationists working in the Farlow Library. Mark subsequently pursued bookbinding as a career. After studying and working at the Newberry Library in Chicago and later in Iowa, he came back to Boston to start up the North Bennet Street School program.

A second-year student, **Molly Carlisle**, is currently working on Farlow books. After graduating from Wheelock, Molly studied the harp at the Longy School and worked part-time at the Harcourt Bindery. Her work - protective clamshell boxes and rebound volumes - will be on display at the annual meeting in November.

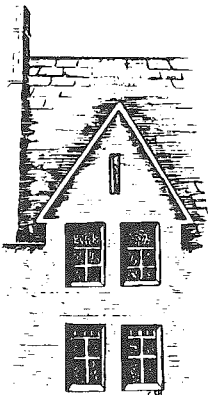
FOF plans to include further conservation and restoration with the School as part of its budget.

HARVEY POFCHER

FIRST CLASS

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## 1990 FOF ANNUAL MEETING

The 1990 FOF Annual Meeting will be held on Saturday, November 3<sup>rd</sup> at the Farlow. In addition to the usual business and social agenda, a lecture will be given by Andrew Knoll, Professor of Biology and Curator of the Paleobotanical Collections at Harvard. Dr. Knoll's interests focus on the (very) early evolution of life on earth, including the evolution of photosynthetic organisms. Details will follow in the fall.

## NEW MEMBERSHIP YEAR

Traditionally the FOF membership year has ended on June 30<sup>th</sup>, with renewal notices being mailed in early summer. We have decided to bring the membership year into phase with the calendar year, so that it will commence on January 1<sup>st</sup> and end on December 31<sup>st</sup>. Consequently, all current memberships will be extended through the end of 1990. Initial renewal notices for 1991 will be sent out in September.

Friends of the Farlow is an international group of amateur and professional botanists concerned with supporting the programs and resources of the Farlow Library and Herbarium of Cryptogamic Botany of Harvard University. Membership categories are: Associate member, \$5-15; Full member, \$25; Sponsor, \$50-1000; Benefactor, over \$1000. To join please make your check payable to the Friends of the Farlow and send to the address below. The membership year runs from January 1<sup>st</sup> to December 31<sup>st</sup>. Members receive a discount on Farlow publications and services, participate in book sales, annual meetings and other events, and receive a special welcome at the Farlow. This newsletter is published twice a year, in April and October. For more information, please contact the Farlow Reference Library, 20 Divinity Avenue, Cambridge, MA 02138, USA (tel. 617-495-2369).