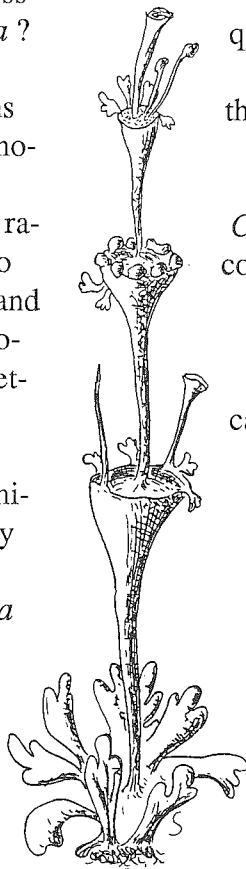


Sex and Taxonomy in *Cladonia*

SAMUEL HAMMER

Taxonomy in the large common lichen genus *Cladonia* is problematical. Such a claim fits many taxa, but the problems in this genus have resisted decades of assault and are especially challenging. What limits progress in solving systematic problems in *Cladonia*?

The study of *Cladonia* includes problems presented by a long-standing and intricate nomenclature and very broad, world-wide species concepts. Species concepts - those rationales for grouping individual variety into biologically meaningful and useful units - and their reflection in the names used by taxonomists have evolved as a method for interpreting an enormous range of morphological plasticity in *Cladonia*. Yet morphological plasticity and a poorly understood geographical distribution of *Cladonia* species are only the tip of the taxonomic iceberg. Basic questions regarding the biology of *Cladonia* are still not answered. Many of the questions demand an understanding of reproductive processes that is more complete than the present literature provides. A deeper understanding of the processes may ultimately confront how we define these fundamentally different organisms.



One of my greatest surprises has been to discover that the biology *Cladonia*, one of the most extensively studied lichen groups, is still largely a mystery to botany. For instance, a literature search surrounding the question of sexual reproduction in *Cladonia* has led me to conclude that virtually all of the work on the subject is conjecture. Many questions about the nature of the podetium (the unique, stem-like secondary thallus in *Cladonia*) are unanswered. Is the podetium comprised of sexually derived "generative" tissue as some authors have stated? Is it purely vegetative and haploid? Are there cells anywhere in the thallus to which we can attribute sexual function? Authors treat these questions variously and, as I stated earlier, speculatively. Various definitions of podetium have been offered, and depending upon authors' understanding of the sexual biology of *Cladonia* and the terms applied to it, these definitions have had widely differing applications.

One rewarding aspect of a literature search in this area is that I have sometimes succeeded in following authors' concepts back to their sources in attempting to pinpoint their usage of a term.

This has allowed me to grapple with the original context of a statement, clarifying for myself what later authors may have meant. Much of the lichenological work that has focused on explaining reproduction has its haustoria in the mycological literature. This is hardly surprising, as it is well understood that the non-algal partner in the lichen symbiosis is a fungus. However, until quite recently the lichenological community has strongly separated itself from the mycological mainstream, which has, in part, limited its ability to interpret the biology of lichens. Many of the concepts adopted, and sometimes ill-defined, by lichenologists have changed from their original usage in describing the non-lichenized fungi. It would be useful to bridge the conceptual gaps between lichenology and mycology in an attempt to clarify concepts as they actually reflect the biology of lichenized fungi. Working with Professor Pfister, with his profound understanding of the fungi, has enhanced my opportunities for progress in this area.



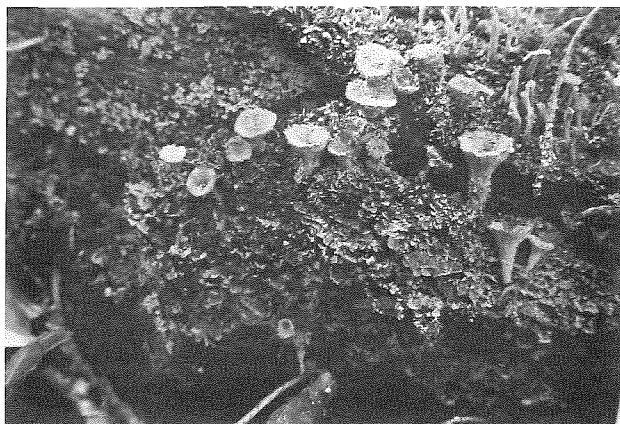
Another issue that I face in my encounter with the literature is later authors who, for whatever reason, have failed to acknowledge earlier sources. It is as though these concepts arose *ex nihilo* on the pages of more recent papers. When working at the Farlow Library, which is so rich in source material, one is shocked by the lack of an historical approach by many authors. An ignorance of historical precedents cannot help but make students poorer as they try to push into the future with their discoveries and analyses. As for discoveries, when I started my doctoral research at the Farlow two years ago I

fully expected to take the bull by the horns and tackle, among others, the problems of sexuality in *Cladonia*. Hundreds of thin sections later I have still not observed what I would stick my neck out to call an ascogonium!

A further problem related to lichen sexuality involves the question of dispersal, and in *Cladonia*, the problem starts at the point of spore production. Most species of *Cladonia* produce very few ascospores. Many an apothecial disc possessing numerous (promising!) incipient asci has been sacrificed in the search for a dozen or so spores. Whether numerous *Cladonia* ascospores are actually produced over a period of years in a perennial apothecium, or whether there really are an infinitesimally small number of them produced per disc is unknown. What is more tantalizing about the problem is that ascospores, when present, are borne rather mundanely in groups of eight: we can assume from this that something the textbooks teach us about discomycete reproduction is occurring here. The mycological literature holds promise for a more complete understanding. Further, and I shall stop here before I dive into too deep water, many *Cladonia* species are well endowed with soredia, the classic (and we presume effective) asexual propagule of the lichens. In my approach to taxa with asexual propagules I have considered problems of somatic mutation (hence speciation?), geographical isolation (hence speciation?), and locally unique populations (hence speciation?) of sorediate *Cladonias*. My considerations have led to more questions than answers for now. *Mea culpa*: I still can't find a species concept to call my own.

In *Cladonia* species we see numerous variations on a given morphological theme, often in very close proximity (within a contiguous population on a roadcut, for example) and not easily attributable to microenvironmental conditions. Halfway around the globe, in widely separated populations with whom gene flow is unlikely, we see what appear to be identical variations on the same theme. If we consider a non-sorediate

species to be worldwide in its distribution, with conspecific populations in Borneo, Norway, and southern California, we have a problem in attempting to name and apply taxonomic rank to its morphological variants.



If we accept the premise that lichen species are very old and that their rates of character evolution and speciation are very slow (none of which is supported by more than faith), we may see that a given species could have persisted for long periods of time and through vicariance or dispersal, (both slow processes), become distributed worldwide. On the other hand, we have numerous examples of taxa both sorediate and non-sorediate (readily dispersible and less so) that are clearly endemic. Through my studies of West Coast *Cladonia*s, and some critical comparisons with East Coast material, I have observed enough consistent variation between these *Cladonia* floras to make me think twice about speciation and rates thereof.

The problem of variation and plasticity might come clean were we to concern ourselves only with the *Cladonia* flora of California and the Pacific Northwest compared with that of the Eastern Seaboard. My intensive studies with Professor Teuvo Ahti, the world authority on *Cladonia*, have led me to observe specimens from all over the world and to admit that what I see as real morphological divergence *here* just happens to be repeated over *there*, with the consequence that there is no logical device with which to assign taxonomic meaning to any morphological variation. Does this signal taxo-

nomical chaos? I hope not. I suspect that we observe in these *Cladonia* a convergence of morphology. Morphology may well vary between populations simply in a way that we have not yet learned to define subtly enough, and *Cladonia*'s ability to change its morphology radically in disparate populations may well be limited, such that only a few variations on a morphological theme tend to be expressed in a given lineage. Further, in morphologically defined species, this paucity of morphology should not limit our assigning taxonomic status. Hardly a tenable position, to my dismay!

What then is scientifically meaningful here? How can we wrestle with the problems of repeated morphologies in widely separated localities? What viability can we assign to that rare *Cladonia* ascospore as a dispersal unit, when, in order to re-establish the lichen thallus, it must come into contact with an exploit an algal host, itself not free-living? How can we hope to interpret morphology in *Cladonia* when we still aren't sure what we can attribute to sporophytic tissue? What does seem to hold a promise of some meaning is a further consideration of the fundamental biology of *Cladonia* and other lichen-forming fungi; a deeper understanding of their sexuality, if, indeed, they are sexual, might lead us somewhere. For instance, it would give teeth to discussions of genetic isolation and gene flow, both of which have enormous implications for species questions. On the other hand, these questions may be intractable assuring that challenges to dogmas in the literature will remain an exciting but frustrating exercise. At present, I haven't much new to put in their place.



FOF NEWS

Sr^a **Laura D. Toleda** of the Catedra des Plantas Celulares, Cirdoba, Argentina visited the Farlow in July for about three weeks as a recipient of a Friends of the Farlow Fellowship. She studied gastermycetous fungi, primarily *Arch-nion*, *Araenosa* and *Holocotylion*, in the Dodge, Patouillard, Curtis, von Hohnel and General Herbaria and made profitable explorations in the Farlow Library.

FOF Fellowships for graduate student work at the Farlow continue to be available. Interested students are encourage to apply.

The 1990 **FOF Book Sale** offered 331 books or sets of titles for sale this past spring. About 75% of the items were sold, including 4 of the 5 rare works offered in a silent auction. The sale, in which 36% of FOF's 135 members participated, netted FOF a profit of about \$5100, making it the most successful to date.

The book sale has annually been a major source of fundraising for FOF, and its success is largely a function of the generosity of FOF members. We continue to accept book donations for next spring's sale. Books should be sent to Jean Boise at the Farlow Library; an acknowledgement of your donation will follow.

Donald H. Pfister, Curator of the Farlow and the Harvard University Herbaria, was appointed in July to be the Asa Gray Professor of Systematic Botany at Harvard.

FAX communication to the Friends of the Farow, the Farlow Library & Herbarium, and the Harvard University Herbaria: 617-495-9484.

Cladonia photographs courtesy of
Sharon Gowan.

FARLOW VISITORS

April 1 - September 15, 1990

Excluding members of the
Harvard University community

V. Ahmadjian (Worcester), T. Ahti (Helsinki), C. A. Austria (Quezon City, Philippines), D. Batterby (Santa Cruz, CA), B. Berenfeld (Cambridge), M. Blackwell (Baton Rouge), A. L. Boyle (Durham, NH), C. Cahir (Auburn, CA), J. T. Chen (Boston), F. Chittinin (Belmont, MA), E. A. Christensen (Sarasota, FL), L. C. Colt (North Dartmouth, MA), A. Dichornay (Burlington, VT), M. S. Dobozi (Budapest), B. Drayton (Cambridge), A. du Pont (Klamath Falls, OR), D. W. Eisenberg (Jamaica Plain, MA), D. E. Eveleigh (New Brunswick, NJ), R. Farrell (Danvers, MA), H. Ferranti (Lexington, MA), S. Golubic (Boston), J. Hagman (Lexington, MA), D. Ryan (Brookline, MA), M. Landowne (Weston, MA), N. Lange (Providence), K. Martin (San Anselmo, CA), G. L. Penecilla (Iloilo City, Philippines), T. Riedlinger (Brookfield, IL), L. Rochefort (Cambridge), J. Seeler (Boston), H. M. Shamed (Kuala Lumpur), P. P. Soule (Belmont, MA), J. Strimatis (Boston), L. D. Toldeo (Cordoba, Argentina), R. Tryon (Tampa), R. E. Tulloss (Roosevelt, NJ), W. A. Unterreiner (Toronto), P. Wallace (Providence), W. C. Wong (Waltham, MA).

FOF FINANCIAL REPORT

BALANCE on hand 7/1/89	\$11 935.24
INCOME	
Members & donations	\$ 4 201.18
Book Sales	1 432.84
Other (mugs, etc.)	64.26
Total	\$ 5 698.28
EXPENSES	
Newsletter printing	\$ 550.00
Stationery, supplies, copy	209.62
Postage	301.91
Visitor travel	209.75
Annual meeting	524.37
Book purchases	190.15
Book repair	220.00
Staff	456.00
FOF Fellowship	323.31
Total	\$ 2 985.11
BALANCE on hand 6/30/90	\$ 16 648.41

HARVEY POFCHER

MASON HALE (1928-1990)

FRIENDS

On April 23, 1990, Mason Ellsworth Hale, Jr., a charter member of Friends of the Farlow and member of its advisory board, died of renal cancer at the age of 61. With his death lichenology has lost a most knowledgeable authority on and avid collector of lichens. Mason Hale's taxonomic skills were equal to his collecting skills, enabling him to describe many new species and to adapt new techniques (thin-layer chromatography and scanning electron microscopy) to the study of the foliose Parmelias and the Thelotre mataceae, a large tropical crustose family, and other lichen groups.

He authored some 190 publications; his The Biology of Lichens (1969, 1979) and How to Know the Lichens (1967, 1974, 1983) were especially widely read. Mason Hale was one of the first to document the impact of pollution on lichens with the work he started forty years ago on the growth rates and lead contents of lichens.

He was a founding member, President (1981-1987) and newsletter printer (1967-1974) of the International Association of Lichenology. A Yale man (1950), Mason's masters thesis (University of Wisconsin, 1951) was on Baffin Island lichens and his doctoral dissertation work (University of Wisconsin, 1953) was on the ecology of Wisconsin lichens. He taught at University of Wichita (1953-55) and West Virginia University (1955-57) before he joined the curatorial staff at the Smithsonian. Thanks to Mason Hale, the lichen collection at the Smithsonian is now the third largest in the world.

Death prevented this prodigious collector and meticulous worker from completing his projects on *Usnea* and the Graphidaceae. Certainly his life work will inspire someone to complete this task. The Friends of the Farlow wholeheartedly appreciate the lichenological legacy left by Mason Hale and sadly bid him farewell.

ELIZABETH KNEIPER

In the August 16th (1990) issue of the prestigious British journal Nature, three Australian botanists compared the space and curatorial costs of contemporary herbaria, derived from their immense inventories of dried specimens, against the perceived meagre returns of such an inert biomass and proposed that taxonomic botany ought now be put on a "rational economic basis."¹ Their proposal was that "pulping" most specimens in herbaria, except some nomenclaturally important, paleobotanical, and select others, would effect higher quality, more cost-effective institutions and science. I perceived the Farlow as being eyed by the grim-reaper armed with an M.B.A. and a shredder.

The friends of many herbaria found the proposal most unfriendly and erupted "In Defense of Taxonomy" in the September 20th issue of Nature. Their defense was one of herbaria, as critical resources for the study and preservation of plant variety, and as requisites for supporting taxonomy on a "rational scientific basis."² Taxonomy as not simply naming tasks and arrangements as arbitrary as the groupings of stars into constellations, but as intellectually honest, empirically rooted soundings of a complex world. Herbaria as arks and cornerstones, not simply as morgues. To Friends! Hear! Hear!

*Without taxonomy to give shape to
the bricks, and systematics to tell us
how to put them together, the house
of biological science would be
a meaningless jumble.³*

¹ Clifford, H.T. *et al.*, Nature 364:602 (1990)

² Stevens, P.F., Nature 347:222-223 (1990)

³ May, R. M., Nature 347:130 (1990)

R. EDGAR

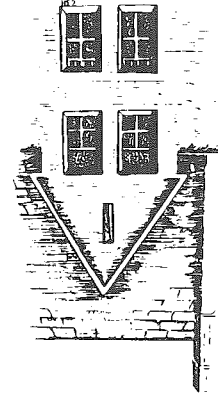
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OF CRYPTOGAMIC

FOF 1990 ANNUAL MEETING

The 1990 Annual Meeting of the Friends of the Farlow will be held on Saturday, November 3rd at the Farlow Herbarium. A business meeting will be convened at 3:30 pm and followed at 4:00 pm by the annual lecture.

Andrew Knoll, Professor Biology and Curator of the Paleobotanical Collections at Harvard, will lecture on "Photosynthetic Organisms in Precambrian Rocks." Professor Knoll is a graduate of Lehigh University (1973) and Harvard University (1974, 1977). From 1977 to 1982 he taught in the geology department of Oberlin College and returned to Harvard in 1982. His research has addressed questions relating to the early temporal and spatial distributions of fossil assemblages of both vascular plants and microbial photosynthetic organisms.

A reception in the Farlow Library for FOF members and their guests will follow Professor Knoll's lecture.

Friends of the Farlow is an international group of amateur and professional botanists concerned with supporting the programs and resources of the Farlow Reference Library and Herbarium of Cryptogamic Botany of Harvard University. Membership categories are: Associate member, \$5-25; Full member, \$25; Sponsor, \$50-100; Benefactor, \$1000 or more. 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 1st to December 31st. 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, contact the Farlow Reference Library, 20 Divinity Avenue, Cambridge, MA 02138 USA (Tel. 617-495-2369; FAX 617-495-9484).