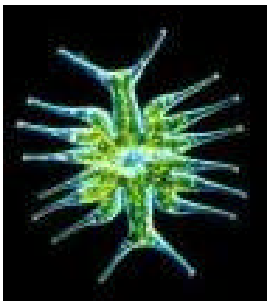

Newsletter of the FRIENDS OF THE FARLOW

Number 46 Fall 2005 K. Griffith, Editor

Helicosporidium parasiticum (Chlorophyta; Trebouxiophyceae), A Novel Entomopathogenic Alga with a Curious Life History

John Denton

The monophyletic Trebouxiophyceae is an eclectic freshwater algal clade comprised of four major orders: the Trebouxiales (ex. *Trebouxia*), the Microthamniales (ex. *Fusochloris*), the Prasiolales (ex. *Stichococcus*), and the Chlorellales (ex. *Prototheca*). Members of these lineages may be coccoid, filamentous, or have planar thalli, but all reproduce asexually by autospore or by zoospore[7]. Several Trebouxiophyceae have developed fascinating symbioses, including *Trebouxia* and *Stichococcus*, associated with lichens; certain *Chlorella*, associated with freshwater invertebrates; and certain *Coccomyxa*, endophytes of *Ginkgo biloba*. Still others such as *Prototheca zopfii* and *Helicosporidium parasiticum*, nested in an achlorophyllous clade within Chlorellales, have developed parasitic life histories. Whereas *Prototheca* spp., whose members cause protothecosis (cyst formation) in vertebrate hosts, is well-documented within agricultural and medical literature, *Helicosporidium parasiticum*, an entomopathogen with a more complex life cycle that includes an autapomorphic filamentous stage (which I study), has received less attention.

The life history of *H. parasiticum* is characterized by three cell phenotypes: a cyst, a filamentous cell, and 1-, 2-, 4-, and 8-cell autospores. The cyst stage, found in ditch water, moist soil, and tree sap, as well as within an insect host, is the most heterogenous phenotype and consists of an inert exterior pellicle composed of mannose and hexose enclosing a bilaminate, uninucleate filamentous cell wound 3-4 times around three ovoid cells[1,2,4,5,6,8,10,15]. *Helicosporidium parasiticum* cysts (Fig. 1) are ingested by mouth by foraging insects and passed through the digestive tract into the midgut where digestive fluids stimulate the cyst to swell and dehisce, releasing the filamentous cell.

In vivo, the filamentous phenotype, at times called the "harpoon cell," (Fig. 2) is transient but efficient, piercing the midgut peritrophic membrane by an as yet unknown

FoF Annual Meeting
Saturday, November 5. See page 10.

mechanism and gaining ingress into the hemocoel, where the cytoplasm undergoes a dramatic endomitotic transformation into four vegetative progeny which, upon release from the filament, autosporulate and invade

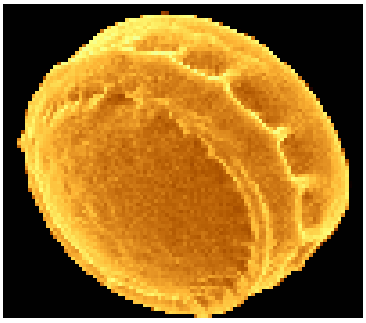

Fig. 1. A color-enhanced SEM micrograph of the cyst. The equatorial ridges indicate the filamentous cell, wound 3-4 times beneath the pellicle.

nearly all insect tissues. Cysts are regenerated from a portion of the autospores in the prepupal stage of the host and are released into the environment upon rupture of the host cuticle. The *Helicosporidium* life cycle is summarized in Figure 3.

Helicosporidium parasiticum was first identified by Keilin[4] from samples taken from a Ceratapogonid fly and was classified as a fungus for decades. Keilin classified *H. parasiticum* broadly within Cnidosporidia based upon the presence of multicellular spores with heterogenous elements, but was not able to resolve its taxonomic position further based on morphological characters.

Kudo[6] observed that spores of *H. parasiticum* were peculiar in shape but, like certain members of Cnidosporidia, possessed 1-4 "polar filaments," each coiled within a polar capsule, and were parasitic exclusively on invertebrates. Kudo assigned *Helicosporidium* to its own order within Cnidosporidia because the unique character states of the filamentous cell made it impossible to resolve within the three extant orders. Both Keilin and Kudo hypothesized that the three ovoid cells within the cyst were responsible for propagating vegetative autospores, and assigned no biological function to the unique filamentous cell.

Weiser[14] elaborated the study of the filament by analyzing its granular content and found the material closely resembled that of the ascospores of *Monosporella unicuspidata*, in the subfamily Nematosporoidae, and furthermore that the pathogenesis of *H. parasiticum* within a hepalid lepidopteran suggested an association with the lower ascomycetes[15]. Later analysis moved *Helicosporidium* from the Microsporidia to the Protozoa. Lindegren & Hoffman[8] found through TEM that the vegetative autospores of *H. parasiticum* possessed well-defined Golgi bodies and strict mitotic nuclear division.

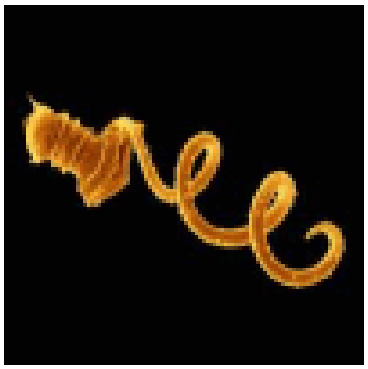

Fig. 2. A color-enhanced SEM of a dehisced filamentous cell unwinding from the three ovoid cells. The filamentous cell surrounds these cells within the cyst pellicle.

Recent molecular analysis of cyst 16S (*rrn16*), 18S, 28S and 5.8S rDNA, and of actin and ß-tubulin genes have contradicted the earlier identification based on morphological characters and identified *H. parasiticum* as a highly derived alga within the achlorophyllous Trebouxiophyte clade, which includes *Auxenochlorella protothecoides* and several *Prototheca*

spp.[11,12,13]. Recent EST analysis of 700 *H. parasiticum* gene clusters has shown that 47% are annotated proteins, 85 of which are involved in translation and biogenesis, and that 43% are unclassified at this time[3].

In the *Helicosporidium* life history, metabolism and synthesis are of paramount importance; this is not surprising. Two of the three shifts in cell type—filamentous transformation into vegetative progeny and cyst morphogenesis from autospore—require substantial metabolic input. These transformations have been my subject of study for the past year and a half.

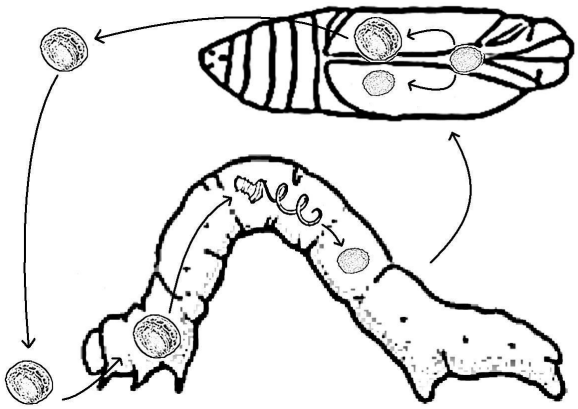

Fig. 3. The *Helicosporidium parasiticum* life cycle: A cyst is ingested by mouth and enters the midgut, where it dehisces to release the filament. The filamentous cell transforms into vegetative autospores that populate the tissues. Cysts are regenerated during host pupation and returned to the environment via rupture of the host cuticle.

Using solid media (modified Grace's media + 3% agarose) supplemented with FBS, I tracked individual filaments, artificially dehisced via incubation in lepidopteran gut fluid, to observe their growth with Difference Interference Contrast (DIC) microscopy. Viable filaments exhibit polarity, thickening at the "anterior end" to a diameter of 2µm over a 48 hour period. During the thickening process, the granular cytoplasm condenses and the nucleus and granular body undergoes two rounds of endomitosis to produce four autospores that are released into the hemocoel within 72 hours after dehiscing. Analysis using the fluorescent probe Alexa Fluor™ shows that the direction of cytoplasmic condensation within the filament appears to be influenced by the proliferation of F-actin, which itself begins at a node in one side of the filament. The relationship among the different filamentous cell polarities—barb direction, anterior/posterior orientation, and F-actin proliferation—warrants future study.

Helicosporidium parasiticum cyst morphogenesis from autospores *in vitro*, on the other hand, has presently proven much more difficult to investigate. First, vegetative autospores have a diameter of 3-5 µm and are surrounded by a pellicle, which presents a problem for most fluorescent probes. Using the Vybrant™ DiD lipophilic labeler and CFDA cell lineage tracer, I have managed to fluorescently label heterogenous suspensions of 1-, 2-, 4-, and 8-cell autospores. The dye is lost, however, during subsequent autosporulation and shedding of the pellicle. Second, the biochemical cascade leading to cyst morphogenesis seems closely correlated with the complex chemistry of host pupation; cysts form only within prepupae and pupae. Most curious of all is that the percentage of cyst formation from autospores within pupae mirrors the percentage of 4- and 8-cell autospores found in stationary-phase *in vitro* cultures, implying that cyst morphogenesis results from either an 8-cell reduction or from a 4-cell transformation.

Helicosporidium parasiticum is an organism with highly composite characters, and its phylogenetic resolution has reiterated the complexity of interplay between genetic and morphological data. The present techniques used to manipulate *H. parasiticum* cells require some sophisticated elaboration before the complete life cycle may be understood *in vitro*. *Helicosporidium parasiticum* remains a novel alga with a curious life history.

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Images - Reproduced with permission from the Helicosporidia Project Online, http://helicosporidia.ifas.ufl.edu/ .

Editor's note: The freshwater alga image on the first page, which is not *Helicosporidium parasiticum*, is from The Plant Information Network System of Botanic Gardens Trust, Sydney, Australia. http://plantnet.rbgsyd.nsw.gov.au/.

Stepping on Giant Diatoms

Elizabeth Kneiper

If you have flown into Boston's Logan Airport and seen the view of the Boston Harbor Islands and the Atlantic Ocean to the east from the air, you can appreciate Jane Goldman's wish to connect "Bean Town" to its coastline in her Logan Airport art installation *Atlantic Journey*. It took three years to create the pigmented terrazzo images embedded in 35,000-square feet of new walkways that connect terminals to terminals and terminals to parking lots at Logan Airport.

This man is standing on a *Lyrella* or a *Diploneis* according to Farlow diatom expert Robert Edgar.

Nearly ninety-four designs of marine creatures appear to float freely in the terrazzo floors. Forty-one custom colors developed by the artist and the DePaoli Terrazzo Company were used to create the designs of the creatures, outlined with brass, embedded in the floors. The placement of Ms. Goldman's creatures suggests oceanic themes - the abyss, the coastline, the open ocean - along different walkways.

This looks like a *Biddulphia* according to Robert Edgar.

This is an *Odontella* according to Robert Edgar.

What a surprise and delight to see diatoms, enlarged to 3—5 feet, creating abstractions that simultaneously highlight their details of structure and underscore the diatoms' importance to the oceans. The super sized phytoplankton and zooplankton are in the walkway leading to Terminal C at Logan Airport. Go walk on them and marvel.

For more information on Jane Goldman's *Atlantic Journey*, go to http://www.massport.com/logan/about_bio.html.

Here is a *Triceratum* or possibly a *Sheshukovia*, according to Robert Edgar of the Farlow.

For information on the Farlow Herbarium diatom collections and diatom links go to http://www.huh.harvard.edu/diatom.

A Study of the *Ramalina* and *Usnea* Collections in the R.H. Howe, Jr., Lichen Herbarium

Elizabeth Kneiper

Scott LaGreca working on lichens in the R.H. Howe Jr. Herbarium at the Farlow.

Scott LaGreca, now working at the Herbarium, Botany Department, of The Natural History Museum in London, and Philippe Clerc, of the Swiss Laboratoire de Botanique Systématique at the Conservatoire et Jardin Botaniques, Chambésy, Geneva, Switzerland, gave a very successful 2-day workshop on the lichen genera *Ramalina* and *Usnea* during their FoF sponsored visit to the Farlow Herbarium in September. Scott and Philippe spent two weeks studying the *Ramalina* and *Usnea* collection in the R. H. Howe, Jr., Lichen Herbarium, with a special emphasis on New England species.

Philippe Clerc (at the microscope) studying and discussing an *Usnea* collection belonging to Elisabeth Lay during the *Usnea* Workshop held in September at the Farlow Herbarium.

Philippe Clerc (center) showing Philip May (left) and Frances Anderson (right) characters used to identify species in the lichen genus *Usnea* .

Clara Cummings Walk 2005: Short and Wet

Elizabeth Kneiper

Thunder and cold, heavy rain shortened the April 30th Clara Cummings Walk on Pack Monadnock Mountain in Miller State Park, Peterborough, New Hampshire this year. Twelve of us chose to ignore the weatherman's prediction for rain for the day and gathered for what has become a spring FoF tradition. Although the weather on the summit was far from spring-like, the views of Mount Monadnock and surrounding New Hampshire, the lichen-encrusted trees and rock outcrops, and the drive up to the summit made the short day worthwhile.

Book Sale

Thanks are due to **Judy Warnement, Ingrid McDonough** and **Elizabeth Kneiper** for their hard work in connection with this year's successful book sale. Twenty-one members participated, and once all the payments have been received, the total income raised will be nearly $1,300. Book donations for next year's sale are welcome at any time.

Usnea capensis
Georg Franz Hoffman (1761—1826)

When Lichens Inspire

Elizabeth Kneiper

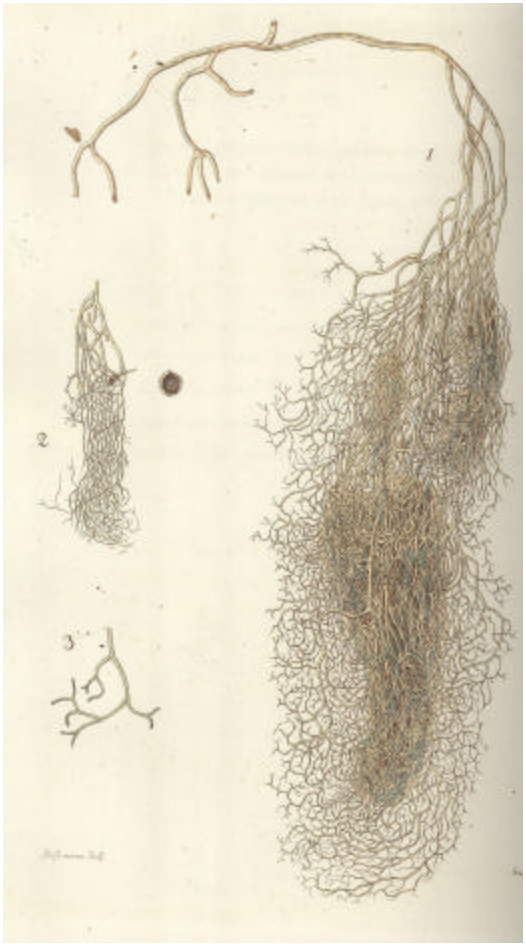
Three local artists, using lichens as the subject for their work, have mounted a multimedia exhibit at the Wellesley College Botanic Gardens' Visitor Center, Wellesley, MA. **Lichens: Three Perspectives** runs through November 10, 2005.

Ramalina menziesii,
illustrated by Issac Sprague for Asa Gray

Deborah Lievens, a photographer, Anita Sebastian, a botanic artist working with ink and watercolors, and Peggy Weber, a mixed media artist, will be at the **Meet the Artists** reception on Sunday, October 16th from 2:30 – 4 p.m.

Deborah Lievens will lead a **Lichen Hunt** through the Hunnewell Arboretum from 4 -5 p.m. following the reception.

For directions to the Wellesley College Botanic Gardens' Visitor Center call 781-283-3094 or go to www.wellesley.edu/FOH or email horticulture@wellesley.edu.



Usnea dichotoma
Georg Franz Hoffman (1761—1826)

Donald Pfister updates us with ….

News from the Farlow

The construction site around the Farlow has been somewhat cleared, although work continues in the courtyard of the Biological Laboratories. Inside the Farlow Building we are slowly beginning to get cleaned up and painted.

I have stepped down as Director of the combined Harvard Herbaria after many years of service. **Ingrid McDonough**, who has managed FoF affairs as assistant to the Director of the Harvard University Herbaria, has moved to the Farlow as my assistant.

Assistant Professor **Anne Pringle** has taken up residence in the Biological Laboratories. Dr. Pringle brings interest and expertise in fungal ecology, evolution and genetics. She will be our speaker at the FoF annual meeting (see page 10). **Lisa DeCesare**, our librarian/archivist, has prepared a special exhibit for the Farlow cabinets on *Amanita phalloides*, the topic of Anne's talk.

Pulmonaria herbacea
Georg Franz Hoffman (1761—1826)

Scott LaGreca, now of the Herbarium, Botany Department, The Natural History Mu

Cladonia coccifera
Dominic Francois Delise (died 1841)

seum, London, but formerly of the Farlow staff and **Philippe Clerc**, Conservatoire et Jardin Botaniques, Chambésy, Geneva, Switzerland, spent two weeks in September in the Herbarium studying the specimens in the herbarium of Reginald Heber Howe, Jr. Howe was an expert on lichens in the genera *Ramalina* and *Usnea* and also published on Boston area lichens. Scott and Philippe are re-examining his collections. We can look forward to reading about their findings in a future issue of the Newsletter.

The myxomycete collections have seen considerable activity recently with the work of your newsletter editor, Kitty Griffith. The collection is being repacketed in anticipation of entering the collection and identification data into our local collection database. She has repacketed (and examined along the way) more than half of the collection.

The work on the myxomycetes brought us to an examination of some of our historic letters – particularly those between William G. Farlow and British father and daughter myxomycetologists, Arthur and Gulielma Lister. These, complete with detailed drawings, became the topic of a paper published in the Field Mycologist (vol. 6 (3): 94-97. 2005) written by our **Lisa DeCesare**.

Our curatorial assistants, **Eileen Wozek** and **Genevieve Lewis-Gentry** have been busy on many tasks. Eileen, who had organized and repacketed almost the entire moss herbarium and was entering information of type specimens in to the database, is now on maternity leave with newly born son, Max Batholomew Wozek. We wish her well. Genevieve has been entering data on myxomycetes types and has taken-up much of the general work on preparing and reinserting loan material.

The Farlow received by gift from **Vernon Ahmadjian**, of Clark University, his personal collection of lichens. This collection is worldwide in scope and numbers 2104 specimens. Ahmadjian was a student of Ivan M. Lamb, Director of the Farlow Herbarium from 1953 – 1971. His research was on lichen symbiosis and in particular he studied synthesis of lichen thalli in culture. He has been a life long Friend of the Farlow.

Hidetsugu Miwa, currently research associate at the Laboratory of Plant Taxonomy and Evolution, Kyoto University in Japan, will be joining the Farlow staff as a research associate in Bryology. He will be working on curatorial projects in the bryophyte collections and will do research on moss systematics and phylogeny. He will arrive in late October to take up this one year position.

The Annual Meeting of the Mycological Society of America was held in Hilo, Hawaii and was jointly organized with the Mycological Society of Japan. **Brian Perry** and I attended and Brian presented results of his work on the Pezizales family Pyronemataceae.

Graduate student **Kris Peterson** moved with her husband, Matias Cafaro, to the Biology Department at the University of Puerto Rico, Mayaguez. Matias is an assistant professor in the department and Kris has an adjunct position there and is teaching in the general biology program. Of historical interest is that this is the position I occupied prior to coming to Harvard in 1974.

David Hewitt, one of my graduate students, has won a graduate student research award from the New England Botanical Club. He will use the funds to study the distribution of *Neolecta vitellina* and *N. irregularis* in New England. David also attended the International Botanical Congress in Vienna, Austria in August.

FoF Sponsors Red Algae Interest

Elizabeth Kneiper

Susan Clayden, a doctoral candidate from New Brunswick, Canada, visited the Farlow Herbarium on an FoF Fellowship this September to study collections of red algae in the order Acrochaetiales and two related orders, the Colaconematales and Palmariales.

One of Susan's special interests is the algal epiphyte *Audouinella efflorescens* that grows on *Cystoclonium*. Susan's visit included a trip to Martha's Vineyard to collect fresh material for molecular work.

Susan Clayden discussing her work on red algae.

FoF Annual Meeting

The Annual Meeting will be held on Saturday, November 5 at 3:30 PM in the seminar room of the Herbaria and afterwards there will be a reception in the Farlow Reading Room. Professor **Anne Pringle** will be our speaker, and in Anne's words, this is what will be addressed:

"The biogeography of fungi is poorly understood and a species in a novel location may be an introduction, or an endemic newly identified within its native range. The death cap mushroom *Amanita phalloides* is a notorious fungus and a rich literature records its history in North America. The earliest publication on *A. phalloides* dates to 1834, and four different authors identified it as growing in California, Minnesota, Pennsylvania, North Carolina, and Maryland before 1910. In contrast, by mid-century field guides listed *A. phalloides* as rare on the West Coast and absent from the East Coast. In modern literature *A. phalloides* is described as a recently introduced and currently invasive species.

The contradictions raise two questions: first, is *A. phalloides* an exotic to North America, and second, how can literature be used to delineate the native distribution of any other less infamous fungus? The world is changing. As humans continue to facilitate species' migrations across continents, the biogeography of fungi must also be shifting, and yet the native ranges of most mushrooms are poorly known. It is literally our last chance to know the endemic habitats of a variety of species, even within Europe and North America. Basic research is needed, and in this talk I will argue that for a few especially charismatic fungi, including *A. phalloides*, a careful reading of the literature may in fact provide needed data."

Illustration by Harald Othmar Lenz
(1799-1870)

"Amanita phalloides" Exhibit

Lisa DeCesare, Farlow archivist

> "NO MUSHROOM is worthier of fear than the terribly poisonous Death Cap (*Amanita phalloides*). This single, widespread species of mushroom is solely responsible for the majority of fatal and otherwise serious mushroom poisoning cases, worldwide as well as in North America. Indeed, one might argue that the Death Cap's notorious, relatively frequent victimization of *Homo sapiens* is far and away the best explanation (or rationalization) for the widespread fear of edible wild mushrooms."
>
> - *Amanita phalloides:* The World's Most Dangerous Mushroom.
> by David. W. Fischer

There is a new exhibit featured in the Farlow Herbarium this fall. It is titled *Amanita phalloides*: The Death Cap Mushroom and features materials from the Farlow Library, Archives, and Herbarium of Cryptogamic Botany to illustrate the varied representations of *Amanita phalloides*, dating from 1727 through the present, in literature, illustration, specimen, and even in song!

Amanita phalloides, commonly

known as the death cap, is an ectomycorrhizal fungus, often found growing in association with the roots of oak trees. It forms a fungal mantle or sheath on the small root tips of the trees and derives its nutrition from the host tree or trees through this symbiotic relationship

Like other Amanitas, *A. phalloides* has a sack-like volva around its base and an annulus, or skirt-like ring, around the top of its stalk. The gills are white or cream and the spores are white. The cap is either slightly greenish yellow or white and is relatively clean, without the scattered patches that many of the other species of *Amanita* exhibit. As it ages *A. phalloides* also exhibits a foul almost sickly-sweet smell.

There are four sections to the exhibit. The Naming of *Amanita phalloides* is the first. Here we trace the development of the name from 1727-1823. Featured are the fungus' early incarnations as Fungus *phalloides*, *Agaricus phalloides*, *Amanita viridis* …

Next comes Images of *Amanita phalloides*. For such a deadly mushroom it is truly frightening how often it has been misidentified and misrepresented in mycological literature. We include images, both correct and incorrect, dating from 1783-1920.

The third section, *Amanita phalloides* Poisoning, delves into the poisonous aspect of this interesting fungus and discusses exactly what happens when a *A. phalloides* is ingested. Included are some stories of actual poisonings.

The last section, The Death Cap in Popular Culture, features some of the amusing, if not entirely accurate, appearances of *A. phalloides* in literature, poetry, and song.

This exhibit can be viewed in the lobby of the Farlow Herbarium through December 2005. It can also be visited online at http://www.huh.harvard.edu/libraries/Amanita_exhibit/intro.html.

Selected New Books at the Farlow

compiled by Judy Warnement

British Fungus Flora - Agarics and boleti. 9. Russulaceae: Lactarius. By R.W. Rayner. Edinburgh: Royal Botanic Garden, 2005.

The bryophyte flora of Israel and adjacent regions. By Clara Heyn and Ilana Herrnstadt, editors; drawings: Michael Boaz-Yuval and Esther Huber; colour plates: David Darom. Jerusalem: Israel Academy of Sciences and Humanities, 2004

Common mushrooms of the Talamanca Mountains Costa Rica. By Roy E. Halling, Gregory M. Mueller. Bronx, N.Y.: New York Botanical Garden Press, 2005.

Cortinarioid fungi of New Zealand: an iconography and key. By Karl Soop. 4th rev. ed. Mora, [Sweden] : Éditions Scientrix, 2005, c2004.

Lichen flora of the greater Sonoran Desert region, v. II: (most of the microlichens, balance of the macrolichens, and the lichenicolous fungi). Edited by Thomas H. Nash, III ... [et al.]. Tempe, AZ: Lichens Unlimited, Arizona State University, c2004.

Marchantiidae. By Hélène Bischler-Causse ... [et al.]. Bronx, New York: Published for Organization for Flora Neotropica by The New York Botanical Garden, 2005.

Moss flora of China, v. 8: Sematophyllaceae – Polytrichaceae. [English vers.] Beijing, New York: Science Press; St. Louis: Missouri Botanical Garden, 2005.

Sea lavender, rust and mildew: a perennial pathosystem in the Netherlands. By J.C. Zadoks. Wageningen : Wageningen Academic Publishers, 2005.

Join us!

Receive the FOF Newsletter, notification of the annual book sale, discount on Farlow publications and services, invitations to the annual meeting and other events, and a special welcome when visiting the Farlow.

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