Newsletter of the FRIENDS OF THE FARLOW

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Ascomycota truffles: Cup fungi go underground

by

Karen Hansen

Fungi pursuing the truffle strategy by producing underground fruiting bodies have long been recognized as an artificial group with representatives in Zygomycota, Ascomycota and Basidiomycota. Those producing asci (a sac-like structure where the spores are produced) were at one time all placed in the order Tuberales (Ascomycota) (e.g. from Tulasne & Tulasne 1851 to Korf 1973). Similarities between tuberalean truffles and above ground fruiting bodies of cup-fungi (Pezizales) have been recognized for over a century and various hypotheses about the evolution from above ground fruiting bodies (apothecia) to below ground truffles were discussed. It was suggested that several distinct lineages of the Pezizales had given rise to members of Tuberales independently, but a formal fusion was not made until Trappe (1979) emended several families of Pezizales to include truffles and transferred selected families from the Tuberales to the Pezizales. Since then, the close relationship between truffles and cup-fungi have gradually been confirmed and expanded upon or in some cases corrected, using cytological and ultra-structural features of asci and spores, and most recently analyses of DNA sequences.

Fig. 1. *Humaria hemisphaerica,* fruiting bodies 2 cm. in diam., deeply cup-shaped, densely covered on

In my research on the Pezizales I have studied the evolution of truffles using LSU and SSU rDNA sequences. The most recent evidence from these genealogical analyses suggests that the truffle growth form has arisen independently at least 15 times from above ground fruiting ancestors within the Pezizales in six families

Clara Cummings Walk
Sunday, May 7. See page 11.

(Glaziellaceae, Discinaceae, Helvellaceae, Tuberaceae, Pezizaceae, and Pyronemataceae). The only family left with strictly underground fruiting is Tuberaceae. Thirty-eight truffle genera (or genera including truffles) are currently recognized within the Pezizales (Læssøe and Hansen, in review).

Fig. 2. Fruiting bodies of *Hydnotrya michaelis*, 3-4 cm in diam., hollow with an apical opening, two fruiting bodies cut open to show the single cavity lined with asci and paraphyses in a palisade. Photo: Jens H. Petersen.

Ascomycete truffles (the "true truffles") can be defined as producing fruiting bodies below or at ground level and having asci without a mechanism for forcible spore discharge. Above ground fruiting bodies of cup-fungi are typically open, disc- to cup-shaped (Fig. 1) and the spores are explosively ejected from the asci, through an apical, lid-like structure (the operculum) that opens. The spores are then dispersed by air. Operculate asci are cylindrical, usually with 8 spores in a row, and arranged in a palisade between tread-like sterile elements (paraphyses).

Fig. 3. *Peziza whitei*, fruiting body 2.5 cm, cut in half to show the folded inside, lined with a layer of asci and paraphyses. Photo: Michael Castellano.

Underground fruiting bodies are closed or nearly closed spherical structures. There is a continuous variation from truffles with a single cavity lined with asci and paraphyses in a palisade, often with a single opening (e.g. in *Genea* and *Hydnotrya*; Fig. 2), to truffles with intricate folding (e.g. in *Peziza whitei* and *Amylascus*; Fig. 3) or with pockets of asci in a firm, solid tissue (e.g. in *Tuber*; Fig. 4). The asci range from those that resemble asci of above ground species, being cylindrical with spores in a row, to those that are completely globose and often having a reduced number of very large spores. The paraphyses may extend above the asci, often branching and growing together toward the apices forming a tissue over the asci. In open apothecia such a tissue would impede ascus discharge. In the most derived species of truffles paraphyses have been lost.

Fig. 4. *Tuber rufum,* fruiting bodies, 1-3 cm., asci randomly imbedded in dense, firm tissue, with lighter colored sterile veins. Photo: Jan Vesterholt.

Species with intermediary characters can be found. *Sarcosphaera coronaria* is an example of a cup-fungus that has nearly become a truffle. It forms apothecia under ground and sometimes opens by a rather small aperture, but since the spores are still actively discharged we consider it a classic cup-fungus.

Fig. 5. *Geopora cooperi*, fruiting body 5 cm. diam., remains closed, cut surface showing inside of folded walls. Photo: Brian A. Perry.

The truffle genus *Hydnotryopsis*, which produces firm potato-like fruiting bodies, shares a most recent common ancestor with *Sarcosphaera*.

Geopora cooperi (Fig. 5) has been said to be a "truffle-in-the-making." Biologically it behaves like an ordinary truffle, but has maintained its forcible spore discharge mechanism, even though the asci are enclosed within the fruiting body chambers. If a fruiting body breaks open by animal excavation, the spores could be discharged and dispersed by air. The other species of *Geopora* develop in the soil but open at the surface at maturity, splitting into vertical, irregular rays (Fig. 6) or completely expanding while still deeply immersed in the soil.

The species-rich truffle genus *Genea* produces fruiting bodies that still have an obvious apical opening, can be unfolded to strongly folded, and have cylindrical asci in a palisade, closely resembling a closed above ground cup-shaped fruiting body. Recently, the cup-fungus *Humaria hemisphaerica* (Fig. 1) was shown to be closely related to *Genea*. This is supported by the arrangement of the cells in the fruiting bodies and of the hairs on the outside. Once a fruiting body does not open fully, relaxation of selection for forcible spore discharge may permit loss of some or all of the accompanying morphological traits, such as the loss of the operculum and / or loss of the arrangement of the asci in a palisade. Highly derived truffles occur in Tuberaceae (for example *Tuber*) but also in the Pezizaceae with *Terfezia* and *Tirmania* being closely related to typical above ground species of *Peziza*. Species of *Tuber* are among the most highly prized edible fungi, with the Piedmont white truffle (*Tuber magnatum*) and the Périgord black truffle (*Tuber melanosporum*) as the best known. Inhabitants of North Africa and Middle Eastern deserts treasure fruiting bodies of *Terfezia* and *Tirmania*, and in the Kalahari Desert, *Kalaharituber* (Pezizaceae) is collected for consumption. In North America the Oregon white truffle *Tuber gibbosum* and other species are becoming popular edibles.

Fig. 6. *Geopora* sp., fruiting bodies 1-1.5 cm diam., at first globose, closed, underground or almost so, but opens at maturity, splitting into vertical rays, to actively disperse spores. Outside covered with brownish hairs. Photo: Karen Hansen.

In most truffles the operculum of the ascus is lost and the evidence is strong that the key dispersal vectors of truffles are animals.

Various small mammals, including Australian marsupials and North American voles and chipmunks, collect and often hoard fruiting bodies and by this activity play a dispersal role (e.g. Maser et al. 1978). Larger mammals such as boar and deer are also well known for their ability to locate and digest truffles and presumably act in a beneficial way to the truffles by their dispersal abilities. Truffles exude volatile compounds when ripe and in this way attract animals.

Selection for the truffle growth habit is probably driven and maintained by avoidance of desiccation, frost, and surface fires by fruiting in the soil. The high diversity of truffles in arid or seasonally dry areas favors this hypothesis. It is generally assumed that truffles form ectomycorrhiza (EM), a mutual interaction in which the fungus grows among the outer cells of plant rootlets, assisting plants in absorbing nutrients and water from the soil, while the plants provide the fungi with carbohydrates and vitamins. The direct proof has not been established in all cases, but circumstantial evidence clearly indicates the validity of this assumption. In collaboration with researchers in Estonia and Denmark, graduate student Brian Perry and I identified 33 species of Pezizales to be EM-forming, including 5 truffle genera (*Genea*, *Geopora*, *Hydnotrya*, *Pachyphloeus,* and *Tuber*) using morphology and DNA sequencing of EM root tips (Tedersoo et al. 2006).

We hypothesize that the EM lifestyle is a precondition for the switch from above to below ground fruiting. Our results indicate that the truffles are EM-forming and occur in lineages with above ground EM-forming cup-fungi. Spores of truffles probably persist for a longer time in the soil than those of air-dispersed relatives, which is likely of importance in respect to life in xeric environments. As EM-forming, it may also be an advantage that the spores are deposited in the rooting zone.

Generally, truffles seems to prefer warm, fairly dry climates and calcareous soils, but this may be slightly overstated due to the emphasis on the requirements for the edible *Tuber* species. Still, the overall species diversity appears to be highest in alkaline soils in warm temperate-subtropical climates. Also deserts around the world have a special truffle funga, which includes *Eremiomyces*, *Kalaharituber*, *Terfezia,* and *Tirmania* species (Pezizaceae). Although too little is yet known, it is clear that many endemics are to be found among pezizalean truffles.

Much has been learned of truffle biology, taxonomy and genealogical relationships since the Tuberales were abandoned as an independent order, but all three fields are still very active research areas where many exciting results will be forthcoming in the near future.

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Note: Illustrations used in this issue are from the above cited reference of Tulasne and Tulasne.

Donald Pfister updates us with ….

News from the Farlow

Zhu-Liang Yang and his graduate student **Zaiwei Ge** from the Kunming Institute of Botany, Chinese Academy of Science, were here for two months. They were studying and identifying specimens of fungi collected in conjunction with the Biodiversity of the Hengduan Mountains Region, China, a project spearheaded by David Boufford of the Harvard University Herbaria. While here, they made use of the Farlow collections of lepiotiaceous fungi and in particular were able to annotate material in the N. Patouillard herbarium, which is very rich in Asian material.

On the lichen front, **Robert Lücking**, from the Field Museum of Natural History, and **Eimy Diaz Rivas Plata**, Universidad Peruana Cayetano Heredia, Lima, Peru spent one week examining material from Costa Rica collected by Carroll W. Dodge. Dodge made extensive collections in Costa Rica in 1929-1930. At that time Dodge was curator at the Farlow Herbarium.

Scott LaGreca has ventured back from the British Museum of Natural History for two short visits.

The extensive Farlow Library collections were used by **Lee Crane,** Illinois Natural History Survey, during a research visit in the fall. He sought some of the rare and elusive publications cited by Elias Fries in the Systema Mycologicum (1821-1832).

Meredith Blackwell, from Louisiana State University, made a short visit in the fall.

During two visits of several weeks duration **Michaela Schmull**, University of Göttingen, continued her study of apothecial development and structure in the select species of *Lecidea*. She made use of some of our lab equipment as well as the herbarium.

Karen Hansen, research associate in the Farlow and author of the lead article in this issue of the newsletter, participated in the Deep Hypha meeting held in Baton Rouge, Louisiana in late February. She presented a paper, co-authored with **Don Pfister**, on the current state of pezizalean classification.

In March **Don Pfister** was host on a Harvard Alumni Association trip to the north east coastal region of Brazil where the topics were botanical rather than mycological.

Kris Peterson and her husband Matias Cafaro are the proud parents of Massimo Joaquin Cafaro, born March 3, 2006. Congratulations to Kris and Matias.

Karin Ponader, a diatom ecologist interested in diversity of diatom assemblages and their relationship with environmental conditions, has been appointed Research Associate in the Farlow. She plans to pursue taxonomic research, which is a wonderful opportunity, given the Farlow Diatom Collection Library. She is currently working on a publication on the taxonomy, ecology, and distribution of *Achnanthidium* species in flowing waters of the Appalachian Mountains. This work will be presented at the annual meeting of the Northeast Algal Society (NEAS) held at Poughkeepsie, NY from April 21 - 23, 2006.

We in the building are very happy to say that construction of the Biological Laboratory underground facility is nearing completion. Landscaping has commenced and most of the internal damage to the Farlow building has been repaired.

Tulasne Brothers Exhibit

By Lisa DeCesare

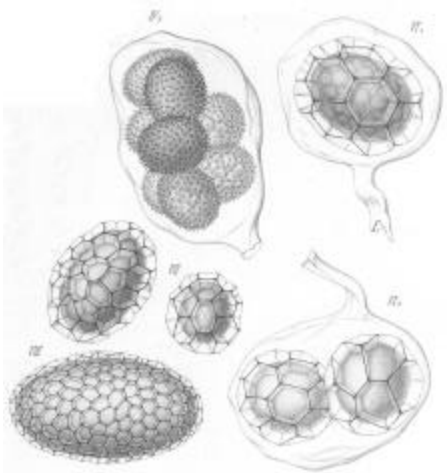
We invite you to come and enjoy a new exhibit in the Farlow about two extraordinary illustrators, Louis René Tulasne and his brother Charles Tulasne. Both of these men began their professional careers working in fields other than botany. Louis René studied to be a lawyer and worked as a notary in Poitiers, France and Charles practiced medicine in Paris. Fortunately, the brothers soon turned their considerable skills to the study of botany, focusing mainly on mycology, and proceeded to perform

groundbreaking research. To quote William Gilson Farlow (1844-1919), from his article "The Brothers Tulasne" in *The Botanical Gazette* (1886): "... it is in connection with their work on the structure and development of fungi that they are best known and, in this department of botany, their writings, we might also say, form the basis of modern views on the subject."

Louis René Edmund Étienne Tulasne was born in Azay-le-Rideau, Indre-et-Loire, France on 12 September 1815. Although interested in natural history, Louis René acceded to his father's wish that he study law and attended the faculty of Poitiers. From all accounts he was not well suited to the practice of law because he was extremely shy and disliked speaking in public. Louis René went on, however, to serve as second clerk in an office in Poitiers until his father's death in 1839. Soon after this he left Poitiers to live with his brother Charles in Paris and it was here that he began his studies in botany.

A scant two years after moving to Paris, Louis René had begun working on a publication with Auguste Saint-Hilaire (1779-1853) on the flora of Brazil and had in July 1841, published his first monograph titled *Observations sur le genre Elaphomyces, et description de quelques espèces nouvelles*. A year later, in February 1842, Louis René was hired as a research associate, or aide-naturaliste, at the Muséum d'Histoire Naturelle, Paris.

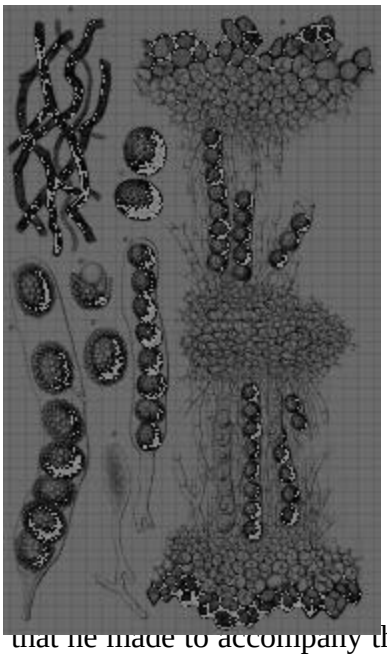
Louis René was described by colleagues as being an excellent writer and having an "unequalled exactitude and depth of observation." His work so impressed his colleagues that he was invited to join the Academy of Sciences on 9 January 1854, upon of the death of Adrien de Jussieu (1797-1853). In the 13 years that Louis René worked in the museum herbarium he published 57 papers. These included his work on the *Leguminosae*, the flora of Colombia,



the flora of Madagascar, the *Monimiaceae,* the *Podostemaceae,* as well as works on the *Gnetaceae, Quiina, Poraqueiba, Antidesma,* and the *Stiginella*.

In 1865, suffering from ill health, Louis René retired to Hyères, in the south of France, where he lived for 20 more years until his death on 22 December 1885. He left his herbarium of fungi to the Muséum d'Histoire Naturelle, Paris and his library to the Catholic University of Paris.

Much less is known about the younger of the brothers, Charles Tulasne. He was born 5 September 1816, at Langeais, Indre-et-Loire, France. He studied medicine in Paris, obtaining his degree in 1840. Charles practiced medicine in Paris until 1854 when his brother was nominated to the Academy of Sciences. At this point Charles left the practice of medicine and devoted all of his time to assisting his brother Louis René in his botanical endeavors.



Charles was an elegant and speedy draftsman. He was extraordinarily dexterous, and the illustrations that he made to accompany their publications are some of the finest and most detailed work ever created (examples are found throughout the newsletter). By all accounts Charles was an assiduous, eager, and indefatigable helper. He provided illustrations for 15 of their publications and it is believed that he assisted with many others. Although in better health that Louis René, Charles died first on 21 August 1884 in Hyères.

Among their considerable contributions to the study of mycology was their work on the structure of *Gasteromycetes*, according to Farlow "an order that was in chaotic condition at the time." They connected different means of multiplication that were related to the habit of the plant. They established that many parasitic fungi stay attached to their host and attain their complete development while others invade plant after plant and can produce some of their reproductive organs only on one or another of these host plants.

The Tulasnes also introduced the idea of pleomorphy in fungi. M.P. Duchartre, in a eulogy honoring Louis René Tulasne, wrote that "Following a great number of these plants, step-by-step, through the whole of their life-history, our regretted confrere proved that in them the reproductive organs, far from being of only a single kind as had been supposed, were on the contrary multifarious; that moreover those of each kind were produced in or on a special apparatus and that these forms of apparatus themselves developed successively in a definite order." Furthermore, and perhaps most significant for this exhibit, the Tulanes created some of the most detailed descriptions and clearest illustrations of the morphology and life history of the *Ascomycetes* ever produced.

In addition to their botanical works, the Tulasne brothers established a series of pious and charitable foundations including schools, almshouses, and churches. It was said of them that they did good, "nothing but good and always good" with their lives.

Harvard honors Professor Donald Pfister

by Judy Warnement

The Pfister family from left: Brigid, Meghan, Shea, Don, Cathy and Edith. Photo: Emily Wood.

Friends of the Farlow are well aware of Professor Donald Pfister's expertise, dedication, generosity and collegiality, but the Harvard community came out on November 16, 2005 to celebrate Don's contributions to the University. A reception was held at the Harvard University Herbaria and attended by Don's family, students, colleagues and friends.

Remarks were made by former dean Jeremy Knowles, who commended Don not only for his fifteen years of leading HUH, but for the many years he and his wife, Cathy, served as co-masters of Kirkland House. Dean Knowles noted that the Pfisters served as surrogate parents to more than 2,000 Harvard undergraduates. He also praised Don for his teaching and research endeavors.

Other speakers included Noel Michele (Missy) Holbrook, Professor of Biology and Charles Bullard Professor of Forestry; Bob Cook, Director of the Arnold Arboretum and the Harvard University Herbaria; Jay Taft, Director of Administration for the Department of Organismic and Evolutionary Biology, and herbaria staff members Emily Wood and Judy Warnement.

Emily Wood acknowledged Cathy Pfister's role as Don's ever-cheerful support system and presented her with a lovely bouquet. Judy thanked Don for his calm and steady leadership and support and presented him with a copper spiral water sprinkler for his garden. Jay Taft then presented Don with a custom-made coffee table with a cherry frame and with a surface made from a piece of salvaged glass from the old Farlow sky light. Jay saved the glass for many years and made the table himself.

Centerpiece created by Lisa DeCesare
Photo: Judy Warnement

Attendees enjoyed a spectacular centerpiece created by Lisa DeCesare with the invaluable assistance of Bill Neill. The team

Kathy LoBuglio, Emily LoBuglio, Karen Hansen

recreated a famous illustration of the Tulasne brothers that depicts a lavish display of brass microscopes surrounded by leather-bound books, beakers, and fresh specimens. Lisa borrowed microscopes from the Scientific Instrument Museum and the Collection of Historic Scientific Instruments at Harvard University and the New England Botanical Club, and Bill Neill collected an impressive array of fresh material.

Toasts, lively conversation, refreshments and good cheer were much in evidence and Don accepted all of the attention with his usual modesty and graciousness.

Eileen Macapinlac and Brian Perry.

From left: Lisa DeCesare, husband George, Bill Neill, Don Pfister. Photos: Eliz. Kneiper

FoF board welcomes new member

Bill Neill, former president of the Boston Mycological Club, has joined the Executive Committee of the Friends of the Farlow. Welcome Bill.

The Library staff has acknowledged its appreciation to the FoF Executive Committee for the allocation of $850 for the purchase a new facsimile of Stephani's "Species Hepaticarum" (1900-1925). Bishen Singh, an Indian publisher, will publish the reprint of all 6 volumes with a new introduction by Stephan Gradstein. The Farlow's original copy is very fragile, so the new copy will be much appreciated by Farlow researchers.

Jeremy Knowles offers a toast to Don while Bob Cook and Jay Taft look on.

Lichenologist visitors

Dr. Robert Lücking, The Field Museum, Chicago, and master's student Eimy Diaz Rivas Plata, Universidad Peruana Cayetano Heredia & Universidad Nacional de Ingeniería, Lima, Peru, visited the Farlow Herbarium at Harvard University from February 12th to 19th to study the lichen collections made by Carroll William Dodge in Costa Rica in the years 1925, 1929, 1930, 1936, and 1950.

Dr. Lücking is PI of the NSF funded TICOLICHEN project (https://www.fieldmuseum.org/research_collections/botany/botany_sites/ticolichen, the Costa Rican Lichen Biodiversity Inventory, which aims to produce a complete lichen flora for this Central American country, estimated to harbor some 3,000 species. Ms. Rivas Plata is receiving lichen taxonomic training within this project.

Besides more than 30,000 new collections made between 2002 and 2006, the project includes revision of previous gatherings, such as those published by the Swiss mycologist Müller Argoviensis in the late 19th century. Also, a large amount of specimens originated from the first international IAL excursion to Costa Rica in 1978 and 1979.

However, the most important single contribution to the Costa Rican lichen flora was provided by Dr. Dodge who, together with his student W. Stephen Thomas and his North American and Costa Rican colleagues V. F. Goerger, Dr. Alberto M. Brenes, and Juvenal Valerio Rodriguez, among others, assembled and identified a collection of several thousand specimens. Unfortunately, little coherent taxonomic information on tropical lichens was available when Dr. Dodge made his identifications, and the genus and species concepts applied by him during the first half of the past century are naturally very different from those used today, with many novel tools and additional data available. Thus, a thorough revision of his identifications was necessary to make the collection data compatible within a modern-day context.

Robert Lucking and Eimy Diaz Rivas Plata at work

During their visit, Robert and Eimy checked about 900 collections, including those published by Dodge in his 1933 paper "The Foliose and Fruticose Lichens of Costa Rica I, " as well as all pyrenocarpous and graphidacean lichens and all available type material. Many collections were reidentified at the genus or species level and revealed quite a number of interesting findings, such as new records for Costa Rica or even some previously unrecognized taxa new to science. During their study, Robert and Eimy produced about 1,000 digital images of many specimens, which will be made available soon in The Field Museum's KE EMu online database (http://emuweb.fieldmuseum.org/botany/Query.php). All in all, the stay was very successful and also very pleasant, due, they said, to the warm welcome and support provided by Professor Don Pfister and his staff and students.

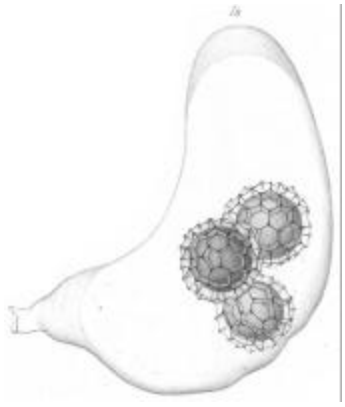
The Clara Cummings Walk

Bolton Lime Quarry and Kiln
Sunday, May 7, 2006 10:00 a.m.—3 p.m.

Started in the 1730s by John Whitcomb, the historic Bolton Lime Quarry and Kiln in Bolton, Massachusetts, are on 40 acres purchased for preservation by the Bolton Conservation Trust and the Bolton Conservation Commission in 1974. Join us for a walk along the trail to both the quarry site and the historic kiln site. Prepare to get your feet wet along the trail, bring a bag lunch, and carry rain gear, if necessary.

For checklists of the fungi and the ferns at the site go to:
http://www.bostonmycologicalclub.org/checklist1999/BMC_Checklist_1999.html
or go to
http://nefern.info/SiteList/sitestable.htm.

Directions: The dirt parking lot at the trailhead to the Bolton Lime Quarry and Kiln is on Route 117, in Bolton, MA, 1.5 miles east of Route 495 Exit # 27 -Bolton Stow. (If you pass the Bolton Spring Apple Farm you have gone too far!) Traveling west on Route 117 the parking lot is 0.8 miles from the "Welcome to the Town of Bolton" sign (immediately after the Bolton Spring Apple Farm).



Slime Mold Workshop Planned

The FoF Annual Meeting speaker for 2006 will be myxomycete (slime mold) expert **Steven Stephenson**. Dr. Stephenson, author of *Myxomycetes, A Handbook of Slime Molds*, has agreed to give a myxomycete workshop on Sunday, November 5, the day following the Annual Meeting.

This will be a day-long, hands-on, bring-your-own-lunch workshop in a lab at the Harvard Herbaria. Pre-registration will be required due to limited space. Registration will be offered to Friends of the Farlow first. If there are additional spaces, these will be advertised and offered to others. An announcement will be mailed out to members in the early fall. Anyone interested in participating might mark their calendars now.

Friends of the Farlow Book Sale

The 2006 book sale list is in the works and should be in the mail to members by early May. Judy Warnement reports that the offerings will be enticing and thanks go out to our generous donors.

This year we received another shipment of books from **Dr. Norihide Amano** of Osaka, Japan. **Ralph Pope** of Nelson, NH donated a copy of his *Lichens Above the Treeline*, and other books were sent to us by **Mary Cobb, Ingrid McDonough**, **Sam Hammer** and **Vernon Ahmadjian**. FoF President **Elizabeth Kneiper** traveled to Warwick, New York in early April to accept five boxes of mycological books from **Elmire Conklin**. We are very grateful to all of our donors.

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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