

North American Fungi



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Howard Clinton Whisler—University of Washington

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Howard Whisler began his journey in Oakland, California in 1931. He spent his early years exploring nature in the natural areas and parks of the region. He attended Berkeley schools and then Palo Alto High School. Howard spent the next two years at Oregon State College (University) as an undergraduate having received a tuition scholarship. He then went to the University of California, Berkeley, where he completed a Bachelor of Science degree in plant pathology in 1954. From 1954 to 1956 Howard was in the United States Air Force, stationed at

Aviano, Italy. He returned to UC Berkeley in 1956 and completed his Doctoral Degree with Ralph Emerson in 1960. In 1959-1960 he held a NIH pre-doctoral fellowship, and after the completion of his work with Emerson was on a post doctoral NATO-NSF Fellowship in France, at the Université de Montpellier, 1960-1961. Howard was appointed assistant professor of Botany at McGill University in 1961 where he shared research interests with Charles M. Wilson, at that time a Professor and newly appointed chair of the Botany Department there.

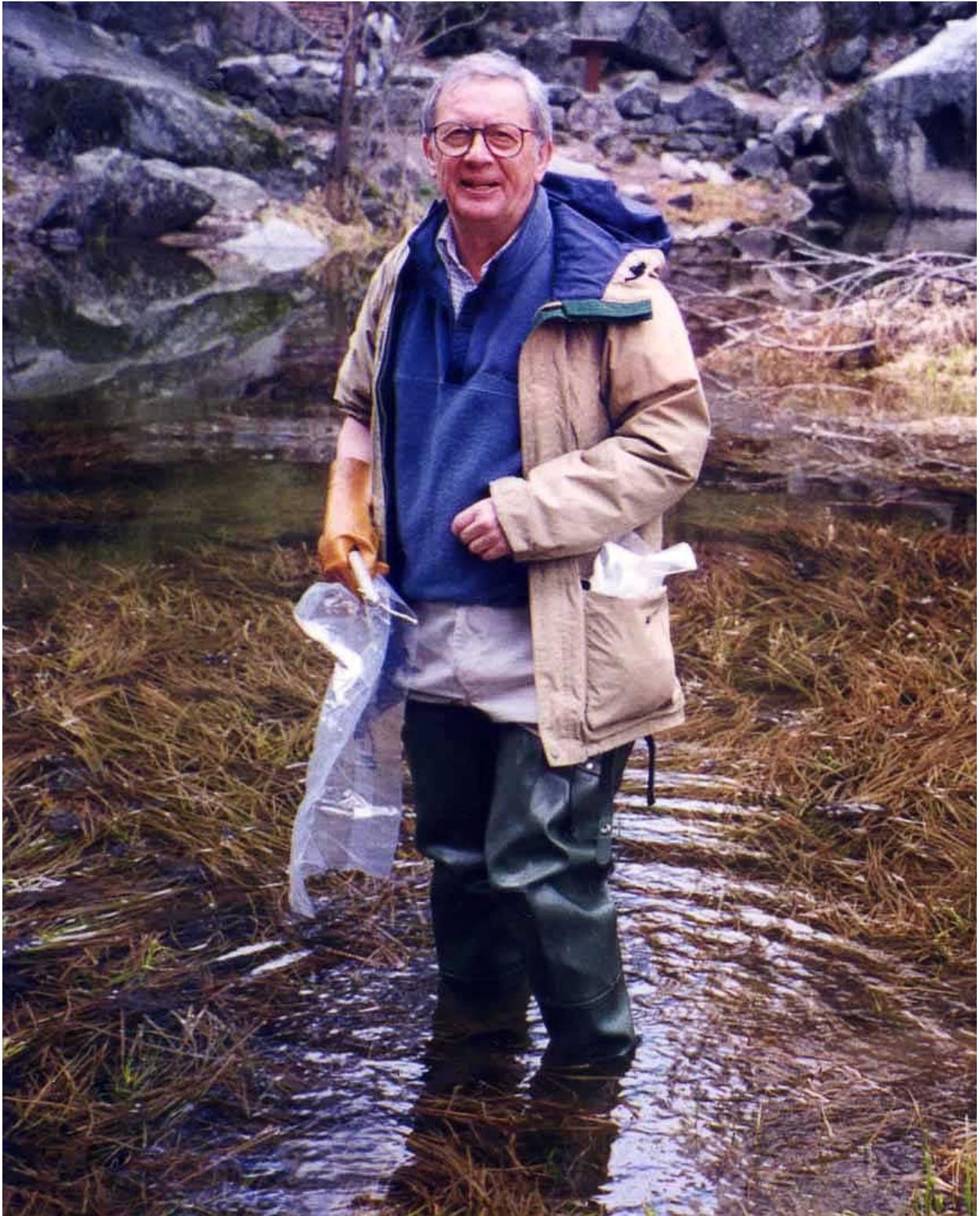


Fig. 1 Howard Whisler, Mirror Lake, Yosemite National Park, 1999.

How did Howard Whisler get to the Department of Botany, University of Washington? Ralph Emerson, University of California, Berkeley, in a letter solicited by and written to C. Leo Hitchcock, November 6, 1961, described Howard's scientific training and achievements in what was a successful attempt to convince Hitchcock of Howard's virtues as a biologist and potential faculty member at the University of Washington. Emerson explained how Howard had cultured and isolated the ecto-commensal, *Amoebidium parasiticum*, for his thesis, and had later gone to the Université de Montpellier, France as a post doc to work further with invertebrate zoologists on the "Trichomycetes". Emerson explained that Howard was well trained at Berkeley in "all classes of lower organisms", bryophytes, algae, protozoans and fungi. Emerson felt that Howard would complement Dan Stuntz, a specialist in "higher fungi" at the University of Washington. Most importantly he explained the importance and need for the study of marine fungi which could be done at Friday Harbor and Seattle, and ended by saying that Howard was ideally trained to work there on these remarkable fungi. C. Leo Hitchcock, Executive Officer (Chairman), Department of Botany, contacted Howard on December 6, 1961, asking him if he was interested in the position. Howard, consequently was very interested in coming to Seattle, and visited the University of Washington in March 1962 where he gave a research seminar. He was offered the position on March 19, 1962 by Richard B. Walker on behalf of Hitchcock; and accepted it on March 26, 1962. He was appointed to the faculty at the University of Washington on March 15, 1963 and shortly thereafter spent his first summer at Friday Harbor Laboratories. This was the beginning of his long career at the University of Washington that lasted well into the year 2007.

Howard Whisler came from a long lineage of very impressive North America mycologist. He had great admiration for Roland Thaxter and

Cap Weston, his mycological forbearers through Ralph Emerson. He also was a close colleague of Charles M. Wilson, an excellent microscopist, and another mycologist associated with the Harvard lineage. These workers, particularly Weston and Emerson, shared with Howard an enthusiasm and excitement for teaching and experimentation with fungi in cultivation. Their common interests also encompassed a broad diversity of zoosporic organisms, those of marine and fresh water habitats, including the water molds, and various symbiotic fungi, especially those associated with arthropods and copepods. Through his research and teaching Howard was able to expand the efforts of earlier workers and break new ground in the cultivation of protozoans, zoosporic fungi, members of the Oomycota, insect parasites in the Zygomycota and Ascomycota, and even delved for a bit into the Basidiomycota.

Howard's abiding preoccupation was with the "lower" fungi in a biological and traditional sense as opposed to the more recent phylogenetic definition. Throughout his career his hall mark was the ability to isolate and culture zoosporic fungi and biologically similar organisms. This allowed him to do a number of life history and developmental studies in the Emersonian tradition. Howard combined these talents with an intense interest for exploration of fungi in fields, lakes, ponds, estuaries, streams, piles of old tires, and elsewhere, in a series adventure that took him to numerous locations over more than five decades.

Howard was especially interested in light and electron microscopy and the photography of fungi, and frequently used both in teaching mycology and for research presentations. He delighted in sharing these efforts with his colleagues and impressed upon his students the importance of microscopy and photography in their studies. Howard was heavily involved in the development of the EM facility in Botany at the University of Washington and worked with



Fig. 2 Howard and Linda Travland, Johnson Hall Office, 1973.

John Luft, Biological Structure, University of Washington, to develop his EM skills in 1964-1965. He was also interested in the extended preservation of fungi through cultivation and cryopreservation, which he worked on for a number of years.

Howard published his first paper on *Amoebidium parasiticum* (Protozoan) on *Daphnia* in *Nature* in 1960. From that time until the late 1960's, while establishing his research program at the University of Washington, he published a number of articles on zoosporic "fungi"; further publications included those on the Trichomycetes, *Rubetella inopinata* and *Carouxella scalaris*, with J. F. Manier and L. Rioux; additional papers on *Amoebidium* with M. J. Torrter and others, including one with his long time friend and colleague M. S. Fuller; one on a new species of *Stigmatomyces* (Laboulbeniales) on flies; and a paper on *Oedogoniomyces* and *Harpochytrium* (Monoblepharidales) with Ralph Emerson. At the end of this period of his research Howard was appointed to Associate Professor.

Howard trained a number of graduate students and worked with others in Seattle at the main campus and at Friday Harbor Laboratories. It is important to note here (see publications) that

Howard followed Emerson's tradition of allowing his students to be sole authors on papers from his lab even though his direction and collaboration were often an important component of the research. In addition to students, Howard worked other talented researchers. Stephen L. Zebold, a very talented experimentalist, worked with Howard for many years and was a very important part of Howard's research lab; he authored a number of papers with Howard from 1974 to the present. George J. Mueller, another incredibly capable researcher, worked with Howard as a graduate student on *Coelomomyces* (see below) and then as a post doc on *Saprolegia* (see below), and edited and published in 1994 the treatment on Salmon Saprolegniasis.

The first student to complete a Ph.D. with Howard was David Porter in 1967. He studied the genus *Labyrinthula* (now classified as a Stramenopile), a species which causes the wasting disease of eelgrass; later publishing on its ultrastructure and biology. In 1969 David M. Gotelli completed studies on the morphology and nutrition of the marine Oomycete *Lagenidium callinectes*, with two papers in *Mycologia*. In 1971 he published on *Lagenisma coscinodisci* (Oomycetes) a parasite of the marine diatom *Coscinodiscus* occurring in Puget Sound. Further work on the Oomycota was done by Howard and his students in the 1990's (below).

It appears that Jolly Galt (Hibbits) in 1970 was the first University of Washington student to publish with Howard; she characterized the differentiation of flagellate spores of *Thalassomyces* a protozoan, as part of her study at Friday Harbor Laboratories of protists associated with marine arthropods. In 1978 she completed her dissertation on the marine Eccrinales (Trichomycetes) found in crustaceans of the San Juan Archipelago. James L. Kerwin completed a study of the potential for biological

control of Eurasian water milfoil, *Myriophyllum spicatum*, in 1979 and Jane Erickson completed work in 1979 but it is without known title.

Howard became interested in *Coelomomyces* in the early 1970's. A series of studies by his lab on *Coelomomyces* over a period of several years revealed that the fungus exhibits a complicated life cycle, with the haploid generation infecting copepods and the diploid generation occurring in mosquito larvae. These observations, in turn, made it possible for Howard and his co-workers to elucidate the sexual mechanism employed by *Coelomomyces* and permitted the systematic, *in vivo* culture of many species of this important pathogen of mosquitoes. Howard first published on this fungus with J. A. Shemanchuk, Lethbridge, Alberta, and Howard's graduate student L.B. Travland in 1972. He then published a paper in *Nature* in 1974 with Shemanchuk and S. L. Zebold on the "Alternate host for mosquito parasite *Coelomomyces*" and another on the life history of *Coelomomyces psorophorae* with these co-workers in 1975 in PNAS. He spent part of a sabbatical year in 1975 in France studying the genus *Cyclops* with Drs. Manier and Vago at Université de Montpellier. In 1979 he published papers on "Host penetration and specificity in *Coelomomyces*" with Travland and the above workers. A paper on meiosis in *Coelomomyces* with Wilson, Travland, L. Olson, B. Borkhardt, J. Alrich, C. D. Therrieu and Zebold attests to the extensive collaborations by Howard on this mosquito parasite. During the mid 1970's Howard took a sabbatical year on campus with the late D. Stadler to further develop his expertise in fungus genetics; something that interested him throughout much of his career. Howard continued to work and publish on a number of *Coelomomyces* species throughout his career, in part because of its potential use as a bio-control agent of mosquitoes. In 1982-1983 he was on sabbatical leave at the Department of Entomology, University of the Philippines, Los



Fig. 3 Howard and Ralph Emerson, Dominican Republic, 1977.

Baños where he worked on *C. indicus* an important pathogen of the medically significant anopheline mosquitoes. In 1968 Howard published with L. E. Padua, B.P. Gabriel and Zebold on the life cycle of *C. stegomyiae*, a fungus originally collected in the Philippines, in relation to the mosquito *Aedes aegypti*. J. Kerwin completed his dissertation on biological aspects of the interaction between two entomogenous fungi, *Coelomomyces psorophorae* and *Entomophthora culicis* (see more below), and their dipteran hosts in 1971. He published consecutive papers on biological aspects of the interaction between *Coelomomyces psorophorae* zygotes and the larvae of *Culiseta inornata*, on the environmental factors in 1982, and on the host-mediated factors in 1983. Observations on the Life Cycle of *Coelomomyces indicus* in anopheline mosquitoes from the Philippines and Thailand by Whisler, Gabriel, J. Chanpaisaeng, Zebold and Padua was published in 1999. George J. Mueller, Howard's last doctoral student worked on the histopathology of a harpacticoid copepod that is the alternate host of *Coelomomyces*; completing a detailed study of this work titled "*Phyllognathopus viguieri* Coelomomyciasis" in 1990. A paper in preparation in 2007 with D. M. Sabwa Karanja, Shemanchuk, Zebold, S. V. Romney, and L. T.

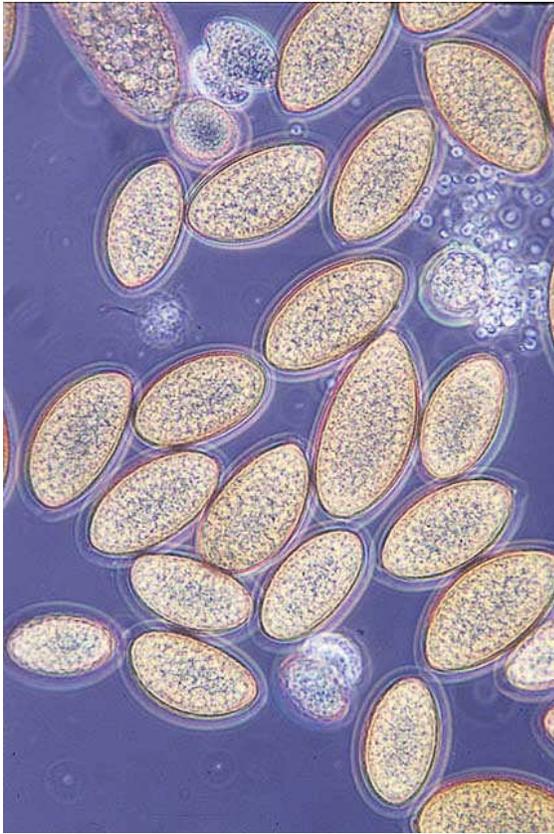


Fig. 4 *Coelomomyces stegomyiae*, thick-walled sporangia, zoospore release.

Nielsen, titled "Observations on the life history of *Coelomomyces utahensis*" is currently being submitted for publication by Howard's co-authors, another extensive collaboration by Howard on this very interesting genus. To round out studies in the Blastocladales in Howard's lab, Sarah Gage in 1983 completed an evaluation of species in the genus, *Blastocladia*.

The Entomophthorales was the subject of several studies as Howard further developed his interest on fungi associated with insects. R. A. Humber first completed a taxonomic survey of the Entomophthorales with a special consideration of parasitism in that order. In 1975 he completed a dissertation titled, "Aspects of the biology of an insect-parasitic fungus, *Strongwellsea magna* (Zygomycetes: Entomophthorales)". Then in the early 1980's J.

Kerwin, an excellent biochemist, worked on the chemical control of the germination of asexual spores of *Entomophthora culicis*, a fungus parasitic on dipterans. In 1983 Kerwin also published on the Fatty acid regulation of *Erynia variabilis* conidia on adults and puparia of the lesser housefly, *Fannia canicularis*. In 1984 B. Tucker completed his dissertation on the biology and ultrastructure of the nematode destroying fungus *Macrobotophthora vermicola* (Zygomycota).

Howard's lab broke into the Basidiomycota in the late 1970's with the work by D. McCabe on the cultivation and developmental history of sporocarps of *Limnoperdon incarnatum*. This fungus, classified in the Cyphellaceae, was isolated from marshes and called a floating "gasteromycete" by G. A. Escobar, D. E. McCabe and C. W. Harpel.

Over the years Howard maintained an interest the Monoblepharidales, especially the factors regulating their reproduction and the application of this information to the general biology of eukaryotic micro-organisms. He cultured a number of these fungi while he was Université de Geneve, Switzerland working with Gilbert Turian, 1968-1969, and during a month-long summer study at the Douglas Lake Biological Station, known as the "Bug Camp". In 1976 he presented a film entitled *Sexuality of Monoblepharis* at the second International Mycological Congress, Exeter, United Kingdom. L. E. Marek studied reproduction in *Monoblepharis macrandra* and in 1984 published on how light affects *in vitro* development of gametangia and sporangia of this fungus. L. M. Johnson worked further on this group and in 1989 completed a study on the nuclear behavior during the sexual cycle and the induction of oospore germination in *Monoblepharella mexicana*. During his retirement years one of Howard's main interests was the completion of the life history of *Monoblepharis*, which he worked on



Fig. 5 *Monoblepharis macrandra*, zygotes inside oogonia.

continuously for several years. His culture collection of this genus features a number of isolates including cultures from North America, France, India, Thailand, China and the Philippines. Many of these cultures are presently being maintained and stored in the laboratory of Dr. Martha Powell at the University of Alabama.

In 1978 M. Fuller and A. Jaworski edited an excellent Lab Manual on Lower Fungi, in which Howard prepared sections on *Coelomomyces psorophorae*, *Monoblepharis polymorpha* and *Amoebidium parasiticum*; and in the same manual a treatment of *Zoophagus* (Zygomycetes), a parasite of loricated rotifers and nematodes, with R. J. Berman and W. O Pipes. L. R. Batra in 1979 edited a book on *Fungi Commensalate in Insects*, for which Howard contributed a chapter entitled "The fungi versus the arthropods". This paper was adapted from a

very animated keynote presentation that Howard gave at the Second International Mycological Congress in Tampa, Florida in 1977. In 1989 Howard published on a group of protozoans, the Ellobiopsida (at that time *Incertae sedis*) in the Handbook of Protoctista edited by L. Margulis, D. Chapman and J. Corliss, that apparently are related at least in part to the Apicomplexa.

In the early 1990's Howard worked with J. Kerwin, L. Johnson and A. Tuininga, on the infection and morphogenesis of *Pythium marinum* (Oomycota) in species of *Porphyra* and other red algae. Howard spent time on sabbatical leave, 1992-1993, working in John Taylor's lab at University of California, Berkeley, to learn molecular methods for phylogenetic and other studies of fungi. Howard later worked on *Saprolegnia* in salmon for the U.S. Department of Energy, Bonneville Power Administration, Environment, Fish and Wildlife Division, and published on the identification of *Saprolegnia* spp. pathogenic in Chinook salmon in 1996. While Howard worked on the systematics of this group George Mueller, did considerable basic research on Salmon Saprolegniasis.

In addition to continuing work during his retirement on *Monoblepharis* and *Coelomomyces*, Howard also worked on the cultivation of *Olpidium brassicae* and was developing a project with Professor Ben Hall and Dr. Yajuan Liu on the phylogenetic position of this interesting obligate plant symbiont. Always the cultivator, Howard had outlined a detailed approach for growing and maintaining this fungus in the roots of lettuce.

The Founders Lecture of Howard on John N. Couch: A Founder of Entomological Mycology, published in 1994, provides a good perspective on Howard's insights and understanding of the fungi associated with insects, and captures his long standing interest in these fungi and the people who worked on them.



Fig. 6 *Monoblepharis macrandra*, zygote emerged from oogonium.

Howard's enthusiasm for the zoosporic "fungi" struck me full force one day as I was sitting in our general mycology class listening to him expound on *Phytophthora infestans*, the Late Blight of Potato. As was his manner, he entered the classroom with a variety of loosely arranged lined, yellow legal-size pages, but on this particular day he also had a tattered and well worn copy of *The Advance of the Fungi* by E. C. Large. In full stride he began to read about The Potato Murrain, describing the "fatal malady" as if he himself were there in the fields and Covent Garden Market. As A. de Bary (1861) first observed the zoospores of this plant pathogen, "each of these naked spores was furnished with two propulsive hairs, and they jostled and dispersed when their mother-spore opened, much more like so many little unicellular animals let out of a bag, than anything one might expect to find belonging to the vegetable kingdom"; you could see the excitement in Howard's eyes and the thrill in his voice as he read and himself imaged seeing this phenomenon of the natural world for the first time.

Howard was considered an outstanding teacher at the University of Washington. He brought excitement, enthusiasm and a sense of discovery

to all of his teaching. He liked experimentation and used it extensively in his mycology courses, often drawing a close parallel between his own research on zoosporic aquatic and marine fungi and laboratory teaching. For Howard there was no separation of teaching from research, they all were closely entangled. He taught the "lower fungi" in the general mycology course for over three decades and also for many years a course in Phycomycetes. Until 1969 Howard was co-instructor of general mycology with D. E. Stuntz, and after that was a co-teacher with me or taught the entire mycology course on his own. In addition, Howard taught for many years in the general biology series as well as other courses, including the development of lower plants and marine mycology, the later at Friday Harbor Laboratories. Howard was a driving force in the establishment of the introductory biology courses at the University of Washington. A. R. Kruckeberg wrote the following about Howard concerning this matter in 1972 when Howard was being considered for promotion to Professor. "Whisler's activities in the current reorganization of Biology teaching, I would only remark here ... he has put very substantial amounts of time and energy into the development of the major's sequence, Biology 210-212, and the multi-sectioned Biology 100 series for non-science people. He has been a key faculty person in many phases of this important instructional program".

Howard Whisler spent much of his life in service to the University of Washington, especially as a teacher, if in fact the two can be separated one from the other. Richard B. Walker, Chairman of Botany, wrote to Howard on December 4, 1968, at that time Howard was on leave in Genève. The letter was mostly concerned with house-keeping details, but in it Walker introduced the letter with a few observations that I think characterize Howard as a faculty member - "Yes, things have been going smoother in the staff meetings in your absence. However, don't get the idea that we don't love you, because the only interesting

staff meetings we had last year where those in which you participated strongly". Howard was widely and extensively connected to research community, being involved in the study of zoosporic and other fungi at the "global" level before that term came into common usage. He was well known for his work on the "lower fungi", but as is always the case, other things got accomplished along the way.

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Patti Whisler provided the photo of Howard at Mirror Lake, Yosemite, and read a first draft of the manuscript. David Porter read and added to the substance of the manuscript, thank you!

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