



Editorial to the topical collection dedicated to Prof. Dr. Franz Oberwinkler

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Professor Dr. Franz Oberwinkler passed away on 15 March 2018 after a short illness at the age of 78 years. For 34 years, he served as chair for Spezielle Botanik und Mykologie (Organismic Botany and Mycology) at the Eberhard Karls Universität Tübingen in southern Germany where he educated numerous mycologists and made important contributions to mycology. With his parting, we have lost an internationally outstanding mycologist, a leading pioneer in basidiomycete systematics, and a highly esteemed colleague, companion, and friend (Fig. 1).

Franz Oberwinkler was born on 22 May 1939 in Bad Reichenhall (Bavaria) in southern Germany, surrounded by beautiful nature of the Alps. After graduating from local schools, F. Oberwinkler started in 1958 with studies of Biology, Chemistry, and Geography at the Ludwig-Maximilians-Universität in Munich. There he received a Ph.D. in 1965 with a dissertation on “Lower Basidiomycetes” (“Heterobasidiomycetes”) as a student of Prof. Dr. Josef Poelt. He then worked for two years in Tübingen as a scientific assistant to Prof. Dr. Karl Mägdefrau at the Institute for Spezielle Botanik und Pharmakognosie (Organismic Botany and Pharmacognosy). From 1967 to 1974, he lived again in Munich and explored the systematics of Basidiomycota as a

scientific assistant at the Institute for Systematische Botanik (Systematic Botany) of the Ludwig-Maximilians-Universität. During this period, he worked as a scientific expert for the Food and Agriculture Organization of the United Nations (FAO) at the Instituto Forestal Latino-Americano in Mérida (Venezuela) from mid-1968 to mid-1969. After his habilitation in Systematic Botany in 1972, he was appointed to the Eberhard Karls University of Tübingen, where, in addition to being chair of Spezielle Botanik und Mykologie (Organismic Botany and Mycology), he was director of the New Botanical Garden from 1974 to 2008.

Research

During his first years as a mycologist, Franz Oberwinkler studied the morphology, taxonomy, and evolution of “Lower Basidiomycetes”, i.e., fungi which today are considered basal groups in the Agaricomycotina as well as the Ustilaginomycotina and Pucciniomycotina (Oberwinkler 1963, 1964, 1965). He formulated hypotheses about the evolution of Basidiomycota by using light microscopy to compare

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Fig. 1 Franz Oberwinkler in Taiwan, 2009. Photo by Chee-Jen Chen

cellular characteristics of specimens belonging to different systematic groups.

Traditionally, the classification of fungi was based primarily on the forms of fruiting bodies. Based on his detailed analyses of cellular structures (Baupläne), F. Oberwinkler recognized early that similar types of fruiting bodies evolved convergently in various systematic groups (Oberwinkler 1977, 1985). These discoveries were later confirmed by results obtained by electron microscopy, molecular phylogenies, and comparative genomics. Thus, F. Oberwinkler was the founder of modern systematics of Basidiomycota.

Over the years F. Oberwinkler acquired a tremendous knowledge on fungi through detailed and precise observation of fungal structures and fungal interactions with other organisms in natural ecosystems. These observations of morphological data and comparative anatomy of diverse fungal species were key to understanding their evolution and relationships. At the beginning of his mycological career, F. Oberwinkler recognized this principle when he investigated specimens of corticioid taxa. Macroscopically these fungi look similar, but,

based on microscopic features, fundamental differences were revealed (Oberwinkler 1965). This knowledge formed the basis for a similar interpretation of traits in other groups of fungi, later studied with modern methods. For some of these methods, the cultivation of fungi was indispensable, thus a strain collection was established and expanded over the years at the Spezielle Botanik und Mykologie.

One of the first set of characteristics available to systematic mycology through improved methods was knowledge of natural products synthesized by fungi, which can be very informative for systematic relationships. Such research was established at the chair of F. Oberwinkler by T. Anke, who became professor at the University for Applied Sciences at Kaiserslautern and led the field for many years. The investigation of natural products of Basidiomycota later resulted in the discovery of antibiotics, strobilurins as well as other compounds useful in pharmacy and plant protection.

As a new professor at the University of Tübingen in 1974, F. Oberwinkler established a Transmission Electron Microscope (TEM). Thanks to the close collaboration with his longtime colleague Robert Bauer, Tübingen became a world-leading center of excellence for the analysis of ultrastructural traits of fungi. The ultrastructure of septal pores, spindle pole bodies, host-parasite interactions, and spore walls was explored in many fungi and used for phylogenetic interpretation. New exciting structures were discovered for several species, such as atractosomes, colacosomes, and symplechosomes, whose functions are largely unknown to this day (Oberwinkler and Bauer 2018 and references therein).

Since the beginning of molecular phylogenetic analyses, F. Oberwinkler recognized the value of DNA sequence data for systematics and developed corresponding expertise. Already in 1981, a molecular laboratory was set up by P. Blanz and A. Brennicke. Thus, F. Oberwinkler and colleagues with a few other groups worldwide played a pioneering role in developing the first molecular phylogenies for fungi. Later, his working group contributed data for an overwhelming diversity of fungal taxa.

These different methods were integrated into an evolutionary scenario of fungi by F. Oberwinkler and his team. Initially, fungi were discovered, observed, and collected in nature from domestic forests to tropical jungles worldwide. Subsequently, they were preserved, taxonomically processed, morphologically documented, illustrated by drawings, and cultivated when possible. Knowledge gained through these activities was combined with characteristics available through electron microscopy and molecular sequence analysis. This integrative approach led to well-founded phylogenetic hypotheses as well as exciting insights into the evolution of traits in the interplay of fungi with their environment. Due to the complexity of

these methods, such work requires networks of cooperating experts. These networks were established in Tübingen and included mycologists at research institutions all over the world. Thanks to the cooperation of taxonomic experts combined with those experienced in anatomy, ultrastructure, and molecular phylogeny, the systematics of Basidiomycota was substantially improved. Early on, F. Oberwinkler also recognized and used digitized materials and the internet for research and teaching.

In addition to the Basidiomycota, F. Oberwinkler and his collaborators worked on other groups of Fungi (Ascomycota and asexual fungi) as well as Oomycota, focusing on taxonomy and systematics. They studied ecological topics especially the interactions of fungi with roots of higher plants (mycorrhizae) and with liverworts (Oberwinkler 2012a). Fascinated with plant-fungus interactions, F. Oberwinkler supported many studies on plant parasites such as rust and smut fungi.

Franz Oberwinkler published more than 340 scientific articles alone or together with his students and collaborating partners. For these publications, he applied strict standards, not only in content, but also in language and quality of illustrations. He described numerous taxa (species, genera, families, orders) new to science; MycoBank contains 450 entries including his name! Two genera and six species were named after him by grateful colleagues and collaborators.

The Oberwinkler School of scientific drawing

Analysis by light microscopy is essential for the identification of fungal species. Therefore, when asked by a student “Which fungus is this?”, F. Oberwinkler answered by telling students to make a microscopic preparation and draw their observations. Inspired by the work of his teacher Josef Poelt, F. Oberwinkler emphasized the importance of scientific drawings of cellular structures of fungi evident by light microscopy during his entire academic life. In contrast to taking photographs, a mycologist must carefully look at microscopic structures and needs a complete understanding of the cellular organization before he or she is able to make a good drawing. The process of drawing leads to an internalization of the structures essential for identification, recognition of species and groups of species, ontogenetic studies, understanding of interactions with other organisms, and recognition of general structural patterns. This accumulated and internalized structural knowledge forms the basis for comparative morphological studies and an understanding of systematic relationships among fungi.

For a good drawing in the Oberwinkler School, the first step is careful observation of cellular structures typical of the species documented by individual drawings of details evident in several to numerous preparations. When the analysis of new

preparations no longer yields new findings, the individual drawings are assembled into a large drawing according to the newly gained knowledge. In the case of thin, corticioid fruiting bodies, F. Oberwinkler captured the cellular structures (Bauplan) of the entire organism by a single drawing. Such a drawing is the result of a thorough analysis of the organism and cannot be replaced by photographs (e.g., Fig. 2).

The members of the Oberwinkler chair regularly exchanged results of structural analyses and drawings with F. Oberwinkler in the context of morphological systematic exercises, called Zeichenkurs (Drawing Class). Everyone, including F. Oberwinkler, presented a description and drawings of one fungal species that formed part of current research activities during each meeting. Through repeated constructive criticism and diligence, the documentation of fungi reached a high scientific level over time and found its way into publications in international journals.

Franz Oberwinkler was not only a gifted observer and draftsman but at the same time artistically talented and active, which is why his drawings are not only scientifically valuable but also esthetically satisfying (cf. numerous drawings published by Oberwinkler 2012a and Fig. 2).

Academic teaching

Franz Oberwinkler offered high-quality, demanding courses in botany and mycology as lectures, seminars, internships, and excursions to train students in organismal biology. For advanced students, he taught about the systematics and phylogeny of fungi, ecology, mycorrhizae, and parasites. These lectures included the latest new findings in the expanded content in mycology, which is why even long-standing chair members visited them repeatedly. In his lectures, F. Oberwinkler used his own photographs and drawings developed into complex diagrams rich in content. Results of this process are evidenced in his overview of the evolution of Basidiomycota (Oberwinkler 2012b) and in his lectures of 2006 that are still available on the Internet (available at [http://timms2005.uni-tuebingen.de/List/List01.aspx?rpattern=UT_200\[56\]___00\[12\]_pilze_000_](http://timms2005.uni-tuebingen.de/List/List01.aspx?rpattern=UT_200[56]___00[12]_pilze_000_)).

Franz Oberwinkler was a fascinating and demanding teacher who liked to share his wealth of knowledge in order to learn something new himself. During his visits to Japan, he got the idea that disciples should climb on the shoulders of their teacher—he himself offered this possibility and several students used it.

F. Oberwinkler emphasized the importance of own observations of fungi interacting with other organisms in their natural environment. He was convinced that it is not possible to understand ecology without the knowledge of organisms. For the acquirement of this knowledge by mutual exchange of experience and by observations in nature, each year in autumn, the Oberwinkler group traveled to Oberjoch (Allgäu)

Fig. 2 Original drawing of *Helicobasidium hypochnooides* (cited as *Stypinella hypochnooides*, Helicobasidiales, Basidiomycota) growing in the hymenium of *Rhizoctonia fusispora* (cited as *Uthatabasidium fusisporum*, Ceratobasidiales, Basidiomycota), elaborated by F. Oberwinkler in 1988. According to notes written by F. Oberwinkler, this is the second record of *H. hypochnooides*. Specimen examined: Switzerland, Küssnachter Tobel (brook) below Allmend, on wood of *Fraxinus* sp., 480 m a.s.l., October 1988, leg. J. Schneller, det. F. Oberwinkler



at the border of the Alps for fieldwork on fungi and plants (Fig. 3). A guest house of the University of Tübingen, the Berghaus Iseler, was used by F. Oberwinkler from 1976 to 2011 for teaching activities each year. During the morning, fungi and plants were collected and, during the afternoon and evening, fresh specimens of fungi were analyzed by light microscopy, drawn, and discussed, often until late at night. Domestic and international beginners, advanced students, doctoral researchers, postdocs, and guest scientists enjoyed the exploration of these species-rich mountain ranges.

Over the years, research for numerous master's, Staatsexamen, and doctoral theses was conducted at the chair of Spezielle Botanik und Mykologie. Guest scientists from all over the world were welcome for the exchange of expert knowledge and method development. Sixteen former students and postdoctoral scientists of the Oberwinkler group obtained professorships at universities worldwide (Agerer, Anke, Begerow, Blanz, Buscot, Chen, Deml, Hoffmeister, Hou, Kirschner, Kost, Langer, Mossebo, Pfenning, Piepenbring, Yang).



Fig. 3 Franz Oberwinkler in a forest close to Oberjoch in October 1997, together with a curious fruiting body of *Boletus edulis*. Photo by M. Piepenbring

Botany

In addition to fungi, Franz Oberwinkler emphasized knowledge of plants following the tradition of Anton de Bary, Karl von Goebel, Karl Suessenguth, and Josef Poelt (Oberwinkler 2018), and was an impressive example for his collaborators and students. He knew the scientific names of many plants as well as their classification in families, distinctive morphological characteristics, ecological context, and geographic origins. This knowledge is important for research on plant-associated fungi and for understanding the importance of fungi in ecosystems.

As director of the New Botanical Garden (1974–2008), F. Oberwinkler was interested not only in the esthetic value of plants but created scientifically sound garden areas including correct, informative labels. He initiated and cared for the collections, special exhibitions, guided tours, and activities of the garden for science and general public. He established the internet platform for the New Botanical Garden comprising instructive information on the garden and several thousands of his own pictures of plants (Oberwinkler 2016). He founded the group called Friends of the Botanical Garden and undertook numerous

excursions in Germany as well as in foreign countries under his guidance. From 1996 to 1998, as president of the Verband Botanischer Gärten (Association of Botanical Gardens, Germany), F. Oberwinkler promoted national and international networking and struggled against increasing bureaucracy and impediments to international biodiversity research caused by the Rio Convention (Oberwinkler 2016).

Franz Oberwinkler obtained his impressively broad knowledge of plants during expeditions to many countries. His collecting activities in Venezuela 1968 to 1969, a mycological expedition organized by the New York Botanical Garden to Colombia in 1978, and an expedition for teaching and research in Costa Rica in 1989 were particularly important for him in developing his fascination with tropical plants and fungi. Later, he visited other countries and constantly enlarged his botanical and mycological knowledge. At the same time, he was interested in cultures, people, and languages. In addition to English and German, he spoke fluently Spanish and Japanese and even presented lectures in these languages.

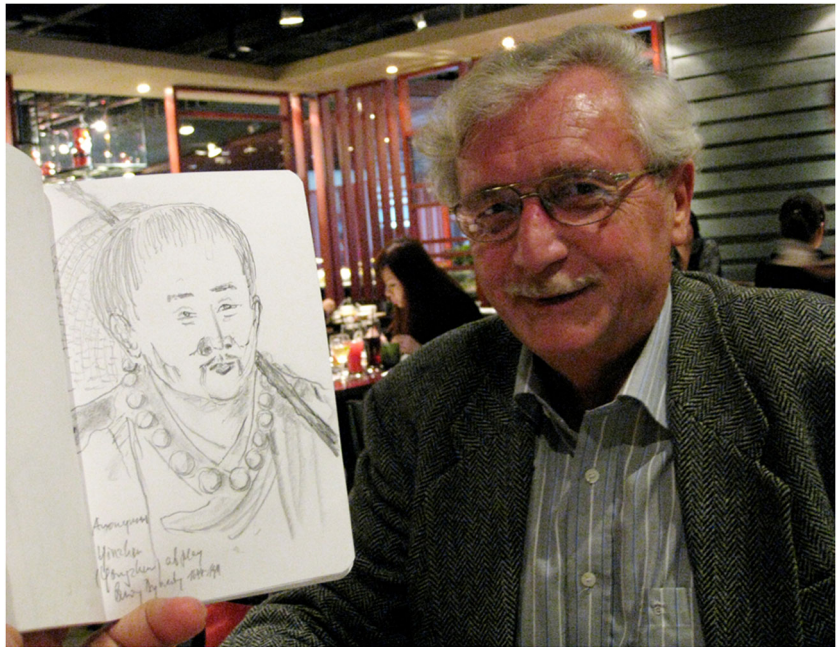
Perception of his work and service to mycology

Over his career F. Oberwinkler published an enormous number of papers, reviews and book chapters. He did not write a textbook on mycology, but his work found its way into many textbooks with his drawings and diagrams often used to illustrate morphology and anatomy of fungi.

From the beginning of his scientific life, he was a member of mycological societies and associations. He was a member of the Bavarian Botanical Society since 1960. He was active in the German mycological community and chair of the Deutsche Gesellschaft für Mykologie (German Society for Mycology, DGfM) from 1978 to 1983. He directed the annual meetings of the DGfM in Tübingen in 1977 and 2006. Since 2002, the DGfM has published the international journal *Mycological Progress*, which was led and shaped by F. Oberwinkler as editor-in-chief until 2016. In addition, he was a member of the editorial boards of several mycological journals and wrote numerous reviews for these journals and scientific institutions. From 1991 on, he was a spokesperson for the DFG-funded research training group Organismische Interaktionen in Waldökosystemen (Organismic Interactions in Forest Ecosystems). He was a member of the Fachkollegium Pflanzenwissenschaften (Review Board for Plant Sciences) of the German National Science Council (DFG) from 2008 to 2011.

F. Oberwinkler actively participated in all congresses of the International Mycological Association (IMA) since 1971 and made important contributions to promote mycology worldwide.

Fig. 4 Franz Oberwinkler with a sketch that he drew in Taiwan, 2009. Photo by Chee-Jen Chen



From 1994 to 1998, he was the president of the IMA who awarded him for his lifetime achievements with the Anton de Bary medal in 2010 in Edinburgh. He was one of the most influential mycologists of second half of the twentieth century.

Outside university

In addition to botany and mycology, F. Oberwinkler was a lover and connoisseur of classical music and art. He visited museums and concerts whenever possible during

his journeys and he always carried a sketchpad in order to spontaneously capture visual impressions of people, objects and landscapes (Fig. 4). These sketches drawn “mit Bleistift und Kreide” (in pencil and chalk) as well as paintings can be appreciated in internet on his private homepage (available at <http://dr.franz.oberwinkler.de/>).

Throughout the years, Dr. Barbara Oberwinkler was a reliable and loving partner to F. Oberwinkler (Fig. 5). She cared for the well-being of their large family and was an excellent traveling companion for F. Oberwinkler. As a trained botanist, she contributed to

Fig. 5 Barbara and Franz Oberwinkler in Frankfurt am Main in July 2013. Photo by M. Piepenbring



projects of the Botanical Garden, among other activities. Finally, she helped to write publications that were prepared by F. Oberwinkler just before the end of his life.

Concluding remarks

Prof. Dr. Franz Oberwinkler was a highly esteemed international scientist and teacher, who impressed many colleagues and students by his extraordinarily broad knowledge of the ecology, evolution, morphology, and systematics of fungi and plants. His scientific achievements were based on an exceptionally precise observational capacity and strong convictions which he consistently pursued as well as his visionary ability to identify promising new methods and scientific questions relevant in modern mycology. He adopted new research possibilities and made new methods available to his group and collaborators.

The students, staff, colleagues, and friends of Franz Oberwinkler appreciate his invaluable knowledge, scientific values, and great experiences in the field. Through his numerous publications and the extraordinary number of mycologists he educated, his valuable scientific contributions and approaches will survive. His publications and didactic material will continue to be used to gain organismal knowledge about fungi and plants as well as guidance and inspiration for the further exploration of the fascinating world of fungi.

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