Hypocrea and *Trichoderma* studies marking the 90th birthday of Joan M. Dingley

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PREFACE

DEDICATION

We dedicate this work to Joan Marjorie Dingley on the occasion of her 90th birthday.

Joan Dingley was born in Auckland, New Zealand, on 14 May 1916. It is particularly fitting that we recognize the scientific contributions of Miss Dingley in this publication dedicated to the *Hypocreales*. Her works on the *Hypocreales* of New Zealand (Dingley 1951 a, b; 1952 a, b; 1953 a, b; 1956 a, b; 1957 a, b) established her as a mycologist of international standing while setting a very high standard of excellence for monographic study of the *Hypocreales*. Especially noteworthy is her early recognition of the necessity to document the entire life-history of pleomorphic ascomycetes.

Miss Dingley completed her M.Sc. in Botany in 1940 with a thesis on the ecology and morphology of the New Zealand tree-fern *Dicksonia squarrosa.* Soon afterward, she began her 35-year career with the Plant Diseases Division of the New Zealand Department of Scientific and Industrial Research (D.S.I.R.) at Mt. Albert in Auckland. During WW II, when men of military age were needed to fight in the war, Miss Dingley was one of the few women appointed to scientific agencies. She was the only one of these appointees whose work impacted directly on agriculture, horticulture and horticultural science, and she excelled despite battles in a generally unsupportive, male-dominated

environment. She can reasonably claim to be the first woman horticultural scientist in New Zealand, and she certainly paved the way for the many women involved as scientists in New Zealand's horticultural research today.

Miss Dingley played a critical role in envisioning and then establishing the Auckland Regional Botanic Gardens, which opened in 1982. She served for several years on the Garden's Technical Advisory Committee, and was Chairman of the Native Plant Evaluation Committee, as well as being a member of the Friends Committee and a member of the Board of Trustees.

Miss Dingley's first mycological research project involved searching for a way to rot-proof canvas. Canvas was quickly destroyed in the tropical conditions found in the Pacific war theatre. Having identified many hyphomycetes that were associated with rotting fabric, she tested agents that could prevent the destruction of canvas caused by fungi. After the war she was denied the opportunity to study for a doctorate that was offered to returning servicemen. Additionally, since mycology was not a subject taught during her graduate training, she had to learn her skills in fungal taxonomy and plant pathology on the job. Early in the 1950's she traveled to the Commonwealth Mycological Institute (CMI, then at Kew, U.K.), which at the time was the premier mycological institution of the world. Her strongest influence came from the taxonomist E.W. Mason. During that exhilarating time at CMI she joined her contemporary students of hyphomycetes, Colin Booth

and Stanley J. Hughes, in taxonomic discussions with Mason. It was Mason who encouraged them in their life-history studies. While at Kew, Miss Dingley developed an enduring friendship with the leading ascomycete systematist R.W.G. Dennis. By 1960 she was recognized as a world authority in taxonomy of the *Hypocreales*.

Miss Dingley was, for several years, the taxonomic mycologist in the Department for Scientific and Industrial Research and for much of New Zealand agriculture. She succeeded G.H. Cunningham as the mycologist at D.S.I.R.; as Cunningham's health deteriorated, she brought his bulletins on the *Thelephoraceae* and *Polyporaceae* of New Zealand to publication in 1963 and 1965, respectively. She was the "go to" person when questions arose about food health, fungal pathogens of plants, humans and animals, and microbial aspects of forensic enquiries. In 1959 she identified and characterized the cause of facial eczema in sheep as the hyphomycete *Sporidesmium bakeri* (now *Pithomyces chartarum*), and was part of the team that developed a management strategy for this serious disease affecting the mainstay of New Zealand's economy. In 1969 she published the first list of plant diseases found in New Zealand (Dingley 1969). She collected extensively – one might even say fearlessly – in remote forests of New Zealand at a time when roads were at best poorly developed. She often worked alongside foresters and stayed in truly rustic accommodations. She saw the number of collections in PDD rise from 4 000 to 35 000 before she retired in 1976.

Joan Dingley was the first New Zealand representative on the executive council of the International Mycological Association. Her international reputation as a mycologist brought New Zealand mycology to the world stage and she attracted such overseas mycologists as Egon Horak (*Agaricales*) from Switzerland, and the Canadians Stanley Hughes (metacapnodiaceous sooty moulds) and Bryce Kendrick (hyphomycetes) to collect and study the New Zealand species of their special groups of fungi.

In 1959 Robert Francis Ross McNabb joined the systematic mycology section as assistant taxonomist. Between 1961 and 1964 he studied for a Ph.D. degree in England; he returned to work on basidiomycete taxonomy at Mt Albert in 1964, and took up a position at Lincoln College in 1967. Ross McNabb died in 1972 (see biography in Thomson 1973). The present writer was on the staff of the systematic mycology section between 1973 and 1985. Today five mycologists are on the staff at the PDD herbarium: R.E. Beever, P.J. Buchanan, P.R. Johnston, E.H.C. McKenzie, and S.R. Pennycook. In 2004 the administration of Landcare Research/Manaaki Whenua, formerly D.S.I.R., officially named the mycology laboratory the J.M. Dingley Microbiology Laboratory in recognition of her many outstanding contributions and ongoing inspiration.

Miss Dingley has received many honours. In addition to her M.Sc., she received a D.Sc. (*honoris causa,* Massey University). She was named as an Officer of the Most Excellent Order of the British Empire (OBE). She is also an Associate of Honour of the Royal New Zealand Institute of Horticulture.

(This biography is derived in part from Joan Dingley's Honorary D. Sc. citation, many thanks to R.L. Bieleski for making this information available. The photo was provided by HortResearch, NZ, and A.R. Ferguson).

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INTRODUCTION

The 19th and early 20th centuries saw great expeditions of exploration to remote lands such as Australia, New Zealand, southern Africa, South America and Southeast Asia. Missionaries, traders, travelers, and naturalists sent biological specimens of all sorts to established scientific centres in Kew, Berlin and Paris. The Rev. M.J. Berkeley and M.C. Cooke, in the United Kingdom, E.M. Fries in Uppsala, Jean François C. Montagne and Narcisse T. Patouillard in Paris, Hans Sydow in Berlin, and others described the newly found diversity of hypocrealean fungi. Descriptions were published, most often without regard for – and possibly in ignorance of – species that had already been described. At least 400 species of *Hypocrea* were thus proposed. Early monographic efforts were made by G. Winter (1887) for European species and F.J. Seaver (1910) for North America. These were based on the morphology of the teleomorph or its substratum, and no regard was given to the whole life-cycle, to the anamorphs. By the mid to late 19th century, mycologists knew that ascomycetes could be pleomorphic, producing spores in addition to those found in the stroma. The Tulasne brothers' (1865) elegant illustrations conclusively demonstrated for the first time the link between *H. rufa* and *T. viride*. Ascomycetes were being grown in pure artificial culture late in the 19th century; this enabled mycologists such as von Tavel (1891) to elucidate life-cycles of hypocrealean fungi by germinating ascospores and observing the asexual forms that were produced in culture.

The first modern mycologist to have concertedly collected *Hypocrea* specimens and isolated their ascospores into pure culture, describing the anamorphs from pure culture, was Joan M. Dingley, in New Zealand. Miss Dingley described the *Trichoderma* anamorphs for ten species of New Zealand *Hypocrea* in her paper, Life-History Studies in *Hypocrea* (Dingley 1957b). This

work established a tradition that has been followed by most of the subsequent work with *Hypocrea* and the *Hypocreales*. Contemporaries of Joan Dingley, including Clark Rogerson, Colin Booth, and John Webster, were growing members of the *Hypocreales* in pure culture and documenting their anamorphs. Yoshimichi Doi, in Japan, fully integrated anamorphs into his monograph of *Hypocrea* for Japan (Doi 1972) and in a long series of publications describing *Hypocrea* species from the Pacific region and South America. Doi's elegant illustrations returned to the standard of documentation of anamorphs and teleomorphs that was established in the 19th century by the Tulasne brothers, von Tavel and others.

Only few species of *Trichoderma* were ever described prior to 1969, despite the wide range of biochemical and biological activities attributed to *Trichoderma*, and the diverse ecological settings in which *Trichoderma* species were found. Change in this situation began in 1969 when Rifai recognized nine aggregate species in *Trichoderma*, an exponential increase over the approximately three species that Gilman (1945) had recognized in his *Manual of soil fungi*. John Bissett nearly quadrupled the number of *Trichoderma* species in several important publications (Bissett 1984, 1991a–c, 1992).

Prior to 1995, fungal taxonomy was based on intuitive analysis of morphology and biology. Although Hennigian cladistic analysis was being applied to other groups of organisms, most notably insects, mycologists did not adopt cladistic analysis. This is probably because the few phenotypic characters presented by fungi simply do not lend themselves to cladistic analysis. In about 1995, sequencing parts of the fungal DNA resulted in literally hundreds of characters in the form of nucleic acid base changes, and the combination of DNA sequencing and cladistic analysis was applied to fungal taxonomy. Notable early papers for *Trichoderma* include those of Kindermann *et al*. (1998) and Kuhls *et al*. (1997), the latter culminating in a monograph of the *Hypocrea schweinitzii* complex and its anamorph, *Trichoderma* sect. *Longibrachiatum* (Samuels *et al*. 1998). Since that time, several publications have documented the phylogenetic diversity in *Hypocrea* and *Trichoderma*.

Thanks to DNA sequence analysis, we now accept that morphological convergence has led us to false taxonomic conclusions. *Gliocladium virens* and *G. roseum*, two names that abound in the biocontrol literature, are now recognized to be quite distinct from the type species of *Gliocladium* (Rehner & Samuels 1994). *Gliocladium virens* is widely accepted as a species of *Trichoderma* while *G. roseum* is now *Conostachys rosea*, an anamorph in the *Bionectriaceae*. The hallmark morphological character of the genus *Hypocrea*, the disarticulation of the bicellular ascospores into two parts leading to the appearance of 16-spored asci, is now known to have occurred multiple times and the genera *Arachnocrea* and *Aphysiostroma* are accepted as being distinct from *Hypocrea*, while *H. pallida* requires its own genus in the *Hypocreaceae*. Through DNA sequence analysis we understand that sections of *Trichoderma* proposed by Bissett, with the exceptions of sect. *Longibrachiatum* and a modified *Hypocreanum*, do not hold up. The tendency today is to refer to "clades", but we also recognize that the sectional names carry morphological information and are convenient in an informal sense. Finally, DNA sequence analysis has led to an understanding that we must recognize that more morphological crypsis exists in the teleomorph and anamorph than we ever before imagined. Dozens of new species of *Hypocrea* and *Trichoderma* have been recognized following sequence analysis.

The four articles in this current issue of Studies in Mycology test morphological hypotheses of anamorph and teleomorph taxonomy. The species that Overton *et al*. studied are atypical in *Hypocrea* in having thin, semi-effused to effused stromata and anamorphs referable to *Trichoderma* sect. *Hypocreanum*. They have hyaline conidia held in drops of clear, colourless liquid on acremonium- or verticillium-like conidiophores. The core species making up this group include *H. citrina*, *H. pulvinata*, and *H. sulphurea*, species that are common and routinely collected. The name *H. citrina* has been inconsistently applied to terrestrial and polyporicolous forms. Although Rifai & Webster (1966) lectotypified *H. citrina*, correctly interpreting the original description as applying to a terrestrial species, misunderstanding of the species continued. Overton *et al*. stabilized the identity of *H. citrina* and establish its closest relatives. The species treated by Overton *et al*. in these two articles have been classified in *Hypocrea* mainly because their ascospores are typical of *Hypocrea*, being bicellular and disarticulating at the septum. However, given that this single character is no longer as predictive of membership in *Hypocrea* as it was once supposed, there was ample reason to hypothesize that these fungi could be excluded from *Hypocrea*. Sequences from three genomic regions – the internal transcribed spacer (ITS) regions of the nuclear ribosomal gene repeat, a partial sequence of RNA polymerase subunit II (rpb2), and partial sequences of the translation-elongation factor 1-α (*tef1*) – demonstrated conclusively that these fungi are derived from within *Hypocrea* and form a highly supported monophyletic lineage, but that the morphologically similar *H. citrina* and *H. sulphurea* are divergent from each other. In addition to redescribing *H. citrina* and clarifying its nomenclature, several common, and uncommon, species having thin, effused to semi-effused stromata and *Hypocreanum* anamorphs are redescribed or described as new.

The two additional papers that complete this issue, Samuels *et al*. and Jaklitsch *et al*., focus on the viride clade, known also as *Trichoderma* sect. *Trichoderma*. The taxonomy of these papers depends in large part upon sequences of the *tef1*, although Samuels *et al*. show that partial sequences of the actin and calmodulin genes support the tef-based taxonomy. In these papers a high degree of morphological convergence is reported in anamorphs and teleomorphs. Teleomorph phenotype is so highly conserved in the viride clade that it is virtually useless in taxonomy. While the anamorphs bring some diagnostic characters to the taxonomy, closely related species tend to differ only in combined details of growth rate and conidium characters. Species such as *T.*

viride/*H. rufa* and *T. koningii* that are generally thought to have a wide geographic distribution were found to have limited, mainly north-temperate distributions. Apart from refining the descriptions of *H. rufa*/*T. viride* and *T. koningii*, several new species are described and distinguished in keys.

The species in the viride clade differ so little in phenotype that the most reliable way to identify them is through their *tef1* sequences. The ITS region is not useful in species recognition in this group. Apart from what is described herein, several taxa – many based only on single collections – remain to be described. Whether this taxonomy, which is based on sequences of a single gene region and few indistinct, phenotypic characters, will be sustained in the future, remains to be decided. We can only say that species such as *T. stilbohypoxyli* have been supported by analysis of additional collections. This species, which is very similar to *T. koningii* and which was described from a few specimens of a *Hypocrea* collected during one day along a trail in Puerto Rico, has been reisolated as an endophyte in beech trees in the U.K., cacao in South America it was also found on the surface of wood in a forest in Ghana. The additional collections of *T. stilbohypoxyli* have confirmed it as a widespread species that is phylogenetically distinct from *T. koningii* and other species, despite having similar conidiophore and conidium morphology.

Fortunately, there exists a web site for interactive identification of *Trichoderma* and *Hypocrea* species (http://www.isth.info) where one can BLAST search ITS and *tef1* sequences against all described species of *Trichoderma* and many species of *Hypocrea*. Morphological comparison of most species can be made at http://www.isth.info/tools/morphkey.php (see also Druzhinina *et al*. 2006).

Trichoderma and *Hypocrea* are now among the taxonomically best-known anamorph/teleomorph pairs of ascomycetes. The present work, and a series of recent publications, have provided a taxonomy for all known species of *Trichoderma*. Several species of *Trichoderma* remain to be described in the viride clade, which we hope to accomplish before the end of 2007. The only large group that remains to be reevaluated is the *T. harzianum* complex. To be sure, many species remain to be discovered in new niches and newly explored geographic regions, but we believe that with the current publications, most of the common species are now known and can be identified easily if one has access to DNA sequencing.

We owe a debt of gratitude to Dr James C. Rodman, of the U.S. National Science Foundation, for envisioning and developing the PEET (Partnerships for Enhancing Expertise in Taxonomy) programme that has supported much of our work and enabled us to reach our current position of knowledge while providing for a next generation of taxonomic mycologists.

We have come a long way from Joan Dingley's (1957b) description of the anamorphs of ten *Hypocrea* species from New Zealand, but hers was a necessary first step on the long path upon which we have been treading.

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